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Lund 1999
Examensarbete, 20 p
Geologiska Institutionen, Lunds Universitet
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Abstract: Non-marine trace fossils from the Permian of Antarctica are systematically described and possible depositional environments are discussed. The studied material derives from sedimentary sequences consisting mainly of sandstone and shale at Vestfjella and Kirwanveggen, western Dronning Maud Land. The ichnofauna is considered to represent the Scoyenina ichnofacies. Ichnotaxa present in the material are Aulichnites, Cochlichnus, Helminthopsis, Lockeia, Palaeophycus, Skolithos and a number of traces placed in open nomenclature. Depositional environments are represented by floodplain sediments at Vestfjella and glacial, post-glacial and fluvial sediments at Kirwanveggen.

Keywords: Trace fossils, Permian, Antarctica, non-marine, Scoyenina ichnofacies, Aulichnites, Cochlichnus, Helminthopsis, Lockeia, Palaeophycus, Skolithos.

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It is not until recent years that non-marine trace fossils have received the attention they deserve. For a long time non-marine trace fossils were put in the shadow of their marine counterparts. Today, however, that view has changed. It has been discovered that non-marine trace fossils are more abundant and varied than once believed (Buatois et al. 1997). Despite this only one non-marine ichnofacies has been recognized, the *Scyenia* ichnofacies, while there are eight formally defined ichnofacies in marine environments (Seilacher 1967; Frey and Seilacher 1980). Based on recent studies, Buatois and Mángano (1995) suggested a subdivision of the *Scyenia* ichnofacies into three different ichnofacies at the same hierarchical level: the *Termitichnus*, the *Scyenia* and the *Mermia* ichnofacies (Fig. 1).

The material studied for this paper was collected by Dr. Kent Larsson from the Department of Geology, Lund University, Sweden, during four field seasons in Antarc-

![Fig. 1. Subdivision of the nonmarine ichnofacies *Scyenia* into the *Termitichnus*, *Scyenia* and *Mermia* ichnofacies, according to Buatois and Mángano (1995).](image1)

![Fig. 2. Map of western Dronning Maud Land, Antarctica, showing the studied mountain ranges Kirwanveggen and Vestfjella.](image2)

tica in 1988/89, 1989/90, 1991/92 and 1997/98. These expeditions were part of the Swedish Antarctic Research Programme - SWEDARP - in their efforts for better understanding of the geological development of the north-
western part of Dronning Maud Land during the late Palaeozoic. In addition to the sampling of trace fossils, other palaeontological, sedimentological and mineralogical studies along with geophysical investigations were carried out. The trace fossils were collected for the purpose of better facial interpretation of the studied sequences (Larsson 1991). The sampled ichnofauna derive from fine-to coarse-grained sandstones and shales of Late Permian age at Vestfjella and from Early Permian strata at Kirwanveggen (Fig. 2).

The main purpose of this paper is to give a systematic description of the late Palaeozoic ichnofauna in this part of Dronning Maud Land. Facies analyses were also made which resulted in a new interpretation of the depositional environment in the Vestfjella area. The focus of the paper will be on Vestfjella since it is the most thoroughly studied area and the majority of the trace fossil material derive from there.

**Geological setting**

The area treated in this paper is situated in western Dronning Maud Land in the northwestern part of East Antarctica (Fig. 2). This part of Antarctica has scattered outcrops of Permian strata (Barrett 1991). The most common Permian sediments in Antarctica are cross-bedded fine- to medium-grained sandstones, shale and coal. Fine-grained overbank sediments often contain *Glossopteris* leaves and other fossilised plant remains (Barrett 1991).

Two different mountain ranges were studied: Vestfjella and Kirwanveggen (Fig. 2). The Vestfjella mountain range consists of scattered ridges and isolated nunataks bordering the Riiser-Larsen Ice Shelf at the margin of the East Antarctica craton (Lindström 1996). The only sedimentary rocks exposed occur at Fossilryggen, which is a low, narrow ridge about 2 km long (Fig. 3). The main lithologies are shales and sandstones, which have been intruded by Jurassic dolerite dykes, and the sequence is partly capped by a basaltic sill (Larsson 1990). A continuous sedimentary sequence of some 60 m is available for studies and sampling at the southern end of the ridge (Fig. 4). Sedimentary structures such as cross-bedding, ripples, and flaser bedding, together with rapid changes in grain sizes indicate various current regimes. The sequence is abundant in plant remains especially in the middle and upper part of the section (Larsson 1990).

Through palynological investigations of samples from the southern section at Fossilryggen made by Lindström (1996), the depositional sequence is considered to be of Late Permian age, i.e. Kazanian to Tatarian. Correlations are made with other palynofloras within Antarctica, for example the upper part of the Queen Maud Formation and the Mount Glossopteris Formation in the Ohio range, as well as with Australian palynofloras assigned to Upper stage 5, which is considered to be of Late Permian age (Fig. 5) (Lindström 1996).

Kirwanveggen forms a long mountain range situated about 300 km in on the continent. It divides two large ice sheets: Amundsenisen and Ritscherflyna. The sedimentary sequence belongs to the Amelang Plateau Formation and is most favourably studied in the southwestern part of Kirwanveggen, i.e. Lagfjell (Fig. 6) (Ahlberg et al. 1993). The best developed sequences are found at Frostbite Bluff, Mt. Alex du Toit, Concretion Point and Petrel Peak (Ahlberg et al. 1993).

The sediments at Kirwanveggen were deposited by glacial, post-glacial, and fluvial processes. The retreating ice left till and melt-out sediments in a wide valley, which was eventually completely filled with fluviatile deposits (Larsson, pers. comm. 1999). The sequence at Kirwanveggen can be divided into four different units (Ahlberg et al. 1993) (Fig. 7). The lowermost unit of the formation, "A", shows glacial development with tillites resting on a basement of gneiss or schist. The fabric of the tillites suggests a palaeocurrent direction towards the southwest of the ice. The following unit, "B", shows no sign of glacial influence. It indicates temperate conditions by the presence of abundant plant remains in well-stratified shales. Next in the stratigraphy is the Frostbite Bluff Member. This unit is entirely fluviatile in origin, which is indicated by different depositional structures such as cross-bedded sandstones suggesting a transport towards 225°, i.e. the same direction as for units "A" and "B". The Frostbite Bluff Member was deposited by a braided-river system with alternating deposition of sand, silt and rubble where the fluvial regime occasionally halted and clay was deposited during the more quiet conditions together with the growth of plants. The youngest member of the Amelang Plateau Formation is the Petrel Peak Member, which consists of sediments deposited after the valley was filled by the braided-river system. New flow conditions were formed and the flow direction changed towards the southeast, 135° (Ahlberg et al. 1993).

The first three units, "A", "B" and the Frostbite Bluff Member are supposedly of Early Permian age. This age is suggested by the close resemblance of the sequence to Early Permian strata at Heimefrontfjella, which has been

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**Fig. 3. Detailed map of the Vestfjella area showing the locality Fossilryggen.**
palynologically dated to the late Asselian to early Artinskian (Larsson et al. 1990; Lindström 1995). Unfortunately, no palynomorphs have been found at Kirwanveggen so far (Lindström, pers. comm. 1999). At the boundary between the Frostbite Bluff Member and the Petrel Peak Member there is a hiatus with signs of desiccation. Therefore, the age of the Petrel Peak Member is uncertain (Ahlberg et al. 1993). It lacks palynomorphs and the finds of plant-remanents and vertebrate bones are not enough for age determination. It might be Late Permian but it is also possible that it is early Triassic (Larsson, pers. comm. 1999).

Taphonomy and methods
When studying ichnologic material several aspects have to be taken into consideration. The effects of taphonomy due to weathering can make assignment to a specific ichnospecies difficult (MacNaughton and Pickerill 1995). Characteristic features such as burrow linings and wall structures are often absent. The reliability of ichnotaxo-
nomic diversity, community structures and paleoecology can therefore be seriously affected by taphonomy (MacNaughton and Pickerill 1995). The lithology of the casting medium can also cause problems if it shows insufficient variation in grain size or has a grain size too coarse to preserve important morphologic structures (MacNaughton and Pickerill 1995).

The collected material is very unusual from an ichnological point of view due to its preservation as epichnia in the majority of the slabs. The most common preservation for traces is otherwise on the sole of slabs, as hypichnia. The material is, when possible, classified at the ichnogenus and ichnospecies level but due to bad weathering and sometimes lack of enough material some of the material is left in open nomenclature.

The traces are described geometrically through parameters such as shape, diameter, curving, length, depth and orientation to the bedding plane. When necessary slabs were cut for cross-sections.

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**Fig. 5. Correlation of Fossilintogen and other localities within Antarctica and Australia based on palynostratigraphy (After Lindström 1996).**

**Fig. 6. Detailed map of the Kirwanveggen area where sampling was carried out in the southwestern part of Lagfjella, at Frostbite Bluff, Mt. Alex du Toit, Concretion Point and Petrel Peak.**
Ichnotaxa present in the material

The majority of the studied material derives from Fossilryggen. The ichnofauna found at Fossilryggen is therefore more diverse and larger in number of each ichnotaxon, compared to the ichnofauna at Kirwanveggen. The Fossilryggen material includes *Aulichnites*, *Cochlichnus*, *Helminthopsis*, *Lockeia*, *Palaeophycus*, *Skolithos*, feeding traces, Incerta No. 1, Incerta No. 2, Incerta No. 3 and Incerta No. 5 (Table 1). Only two ichnotaxa are defined at Kirwanveggen, *Cochlichnus* and *Palaeophycus*. Additional material from this area is described as Incerta No. 4 and Incerta No. 6 (Table 1).

Palaeoecology

Late Palaeozoic trace fossil assemblages are dominated by surface trails and extremely shallow burrows while Mesozoic associations show a dominance of burrows over trails (Maples and Archer 1989, Butoois and Mángano 1993b). Miller (1984) even suggests that aquatic burrowers did not colonize freshwater settings until the Permian. Pre-Permian non-marine ichnofaunas typically lack burrows with the exception of vertical burrows of suspension feeders and some other rare occurrences of burrowing activities (Buatois et al. 1998).

The ichnofauna from Vestfjella and Kirwanveggen consists mainly of horizontal shallow burrows and trails most probably produced by mobile predators and deposit feeders. The fauna includes burrows and trails produced as domicnia, pascichnia, fodiichnia, cubichnia and repichnia. Only a few specimens are vertical and penetrate further down into the sediment.

The studied sequence from Vestfjella is considered to be deposited in a floodplain environment with frequent crevasse splay (Fig. 8). Earlier interpretations of this sequence by Olaussen (1985) and later Larsson (1990), include a lithofacies development where the lower part of the sequence was deposited in coastal marine environments and the upper deposits formed in shallow marine to continental environments. The reason for not regarding the sediments to be of marine origin is the lack of any kind of marine indicators. The algae and echinoderms found in the assemblages from Fossilryggen are all of freshwater origin (Lindström, pers. comm. 1999). It is not possible to decide whether a depositional environment was marine or non-marine solely by using trace fossils (Maples and Archer 1989) but together with other indicators or with the lack of other fossil groups, more accurate conclusions can be made. This is in accordance with one of the most widely accepted ichnologic princi-
Table 1. Ichnotaxa present in the studied material from Fossilryggen and Kirwanveggen.

Ichnogenus *Aulichnites* Fenton and Fenton, 1937  
*Aulichnites* isp.

Ichnogenus *Cochlichnus* Hitchcock, 1858  
*Cochlichnus* isp.

Ichnogenus *Helminthopsis* Heer, 1877  
*Helminthopsis* isp.

*Ichnogenus Lockeia* James, 1879  
*Lockeia* isp.

Ichnogenus *Palaeophycus* Hall, 1847  
*Palaeophycus tubulans* Hall, 1847  
*Palaeophycus striatus* Hall, 1852  
*Palaeophycus* isp.  
Small *Palaeophycus*  
Teichichnial *Palaeophycus*  
*Ichnogenus Skolithos* Haldemanni, 1840  
*Skolithos* isp.

Feeding traces

Ichnogenus *Icnerata* No. 1

Ichnogenus *Icnerata* No. 2

Ichnogenus *Icnerata* No. 3

Ichnogenus *Icnerata* No. 4

Ichnogenus *Icnerata* No. 5

Ichnogenus *Icnerata* No. 6

Turbation, especially across facies boundaries in the non-marine realm, while abiotic and biotic factors may control how the traces are preserved and their character. The second most important parameter, next to water availability, is the presence of organic material in the sediment (Gierlowski-Kordesch 1991). An organism living on or within the substrate takes no interest in exploiting sediment totally devoid of potential food. The more organic content in the sediment the more biogenic activity will take place.

Crevasse splays are created through breaks in the banks of the channel during different flooding events, such as storms or flash-floods. Floodwater and sediment is spilled out over the floodplain. The deposition of coarse material, transported as bedload, is rapid since the flow velocities quickly decrease (Smith et al. 1989). When the flooding episode is over, the splay channels are left with standing water. These quiet conditions allow suspended material to settle creating a thin layer of fine-grained material (Smith 1993). Trace fossils found in crevasse splay deposits are the result of post-depositional activities when animals recolonize the floored surface. The animals using the substrate have caused an imprint through the thin mudlayer resulting in epirelief preservation in the sandstone beneath (Smith 1993). Organisms such as nematodes exploited the sand/mud contact leaving the sinuousoidal trail *Cochlichnus* behind. *Cochlichnus* indicates shallow water environment, maybe just a thin film of water, and is restricted to preservation in medium- to fine-grained sandstone.

One specimen of large *Cochlichnus*, from Fossilryggen, is well preserved which indicates a softground substrate with a water-content not too high, preventing the trails from being deformed. A part from *Cochlichnus*, crevasse splay-surfaces also contains *Palaeophycus* and *Aulichnites*. *Cochlichnus* preserved as hypichnia at the sole of sandstone slabs are imprints of activities that took place at the surface of an underlying mudlayer.

![Fig. 8. Suggested depositional environment for the Vestfjella area. A floodplain environment with vegetation, ponds, and a meandering channel with frequent crevasse splay.](image-url)
*Palaeophycus* is not restricted to medium or fine-grained facies but also occurs in coarse-grained sediment at several levels in the section. The coarse grain size together with cross-bedding indicate temporary high water energy conditions. *Palaeophycus* preserved in coarse-grained sandstone shows deformation of the original shape in several of the specimen. The specimens were probably formed in a transitional soupy to soft substrate characterised by high water content resulting in deformation. Some slabs with preservation of *Palaeophycus* in medium-grained sandstone show cylindrical to sub-cylindrical burrows very well preserved, indicating a firm er substrate, i.e. less water content than the coarse-grained sandstone, probably softground.

The majority of the *Palaeophycus* specimens show signs of clay lining. This suggests that the animals have been feeding at the interface between the sand, in which it later has been preserved, and a thin overlying organic-rich layer. In coarse grained sediments the animal has to create this kind of wall-supporting mechanism to keep the burrow from collapsing. The secretion of mucus together with clay or mud from above controls the grains as the animal passes its body through and it also reduces the energy needed for locomotion (Bromley 1996).

The feeding traces were created by animals searching the fine-grained floodplain sediment for food. Preservation of these traces was possible through deposition of coarser clastic material on the floodplain; which caused infilling of the open feeding burrows. The traces are found as convex hypichnia in sandstone slabs representing the lower surfaces of crevasse splays. The feeding traces occur together with possible *Lockeia*, which are interpreted as resting traces of bivalves. The substrate must have been moist and rich in organic material.

Only one sign of activity of a larger animal is found in the material. The resting traces of a toad or another amphibian were produced in wet sediment where the animal could keep moist. Preservation in sandstone as convex hypichnia is evidence of an overbank deposit with clastic channel sediments infilling the trace.

*Helminthopsis* is very abundant in the Fossiliferous material. The preservation as a carbon film is due to the severe heating the sediments have been exposed to at a later stage. Both *Helminthopsis* and the similar trace described as Incerta No. 3 were collected from a part of the section representing more quiet sedimentary conditions.

The few vertical traces present in the material are placed under the ichnogenus *Skolithos*. This ichnogenus occurs in a wide variety of environments so nothing will be said about the specific depositional environment of these traces.

It can be concluded that high energy settings with coarse sediments are the host of burrows of larger size. The preservation of smaller biogenic structures such as *Helminthopsis*, *Lockeia*, and feeding burrows on the other hand are clearly related to deposition of fine-grained sediments in low energy settings. The occurrence of *Cochlichnus* on top of crevasse splays also represents low-energy settings.

Additional material described in the section about systematic ichnology but not discussed further here, is either too weathered or there is not enough material to make any conclusions from it. This is particularly the case with the material from Kirwanveggen, which is very limited.

Only one ichnofacies has previously been recognized in non-marine settings, the *Scyenia* ichnofacies (Seilacher 1967). After reworking the status of non-marine assemblages Buatois and Mángano (1995) suggested a subdivision of the *Scyenia* ichnofacies into three different ichnofacies at the same hierarchical level. These three are the *Termitchnus*, *Scyenia* and *Mermia* Ichnofacies (Fig. 1). The *Termitchnus* assemblage represents terrestrial sediments while the *Scyenia* assemblage is characteristic of transitional terrestrial/non-marine aquatic environments and the *Mermia* assemblage indicates fully aquatic, non-marine environments (Buatois and Mángano 1995).

The *Scyenia* ichnofacies represents low energy, moist or wet non-marine substrates, which occasionally are exposed to air or inundated. Commonly it is represented by fluvialite floodplains and more rarely lacustrine environments (Frey et al. 1984).

The *Scyenia* ichnofacies typically, but not necessarily, contains backfilled feeding burrows (meniscate burrows), bilobate traces, arthropod trackways, simple horizontal burrows, simple vertical burrows, sinuous crawling traces, spreiten burrows and various vertebrate tracks (Buatois and Mángano 1998). An assemblage can be considered as *Scyenia* ichnofacies even if there are no meniscate burrows present (Buatois and Mángano 1998).

The ichnofauna present in the collected material is concluded to represent the *Scyenia* ichnofacies based on its agreement with the information given above.

**Conclusions**

Trace fossils found at Vestfjella and Kirwanveggen in western Dronning Maud Land, Antarctica, are interpreted as representing the non-marine ichnofacies, *Scyenia*. The trace fossil material was in some cases limited and badly weathered but in several cases it was possible to place specimens within a specific ichnogenus. Ichnotaxa found in the material are: *Aulichnites*, *Cochlichnus*, *Helminthopsis*, *Lockeia*, *Palaeophycus*, *Skolithos* and several others placed in open nomenclature. *Palaeophycus* is by far the most common ichnotaxon in the material. The depositional environments represented are glacial, post-glacial, fluvial, and floodplain facies. This is a preliminary description of the ichnofauna in the area and there is potential for more detailed analyses if further ichnological studies, especially in the field, were done.

**Systematic ichnology**

For easier reference the common ichnological practice of listing trace fossils alphabetically is adopted in this paper. Those trace fossils that are left in open nomenclature are listed after the formally named ichnotaxa. Preservational terminology is used according to that of Mar-
Ichnogenus *Aulichnites* Fenton and Fenton, 1937
*Aulichnites* isp.

Fig. 11 A

**Material and occurrence.** - Four slabs (ANT 89-24, ANT 90-11) from Fossilryggen deriving from thin medium-grained sandstone at 26 m above the base of the section (Fig. 4).

**Description.** - Horizontal surface trails preserved on a rippled surface. Traces occur as epichinal grooves with a V-shaped cross section. Some of the traces have lobes of sediment along one, or more commonly, both sides (Fig. 12). The trace can then be described as a bilobate trace with a median furrow. Trails are oriented randomly on slabs and sometimes cross each other in an asymmetric pattern. No true branching occurs. Width of trails varies from 4.0-7.0 mm between specimens. Width is constant along each separate trace. Depth is about 1.0-1.5 mm. None of the specimens are complete so the length of the traces cannot be measured. No ornamentation is present.

**Associated ichnotaxa.** - *Cochlichnus* isp.

**Remarks.** - Assignment of the specimens to the ichnogenus *Aulichnites* is based on the presence of the lobes in the majority of the specimens. The absence of the same in some specimen may be due to bad preservation. Hântzchel (1975) describes *Aulichnites* as a trail commonly strongly curved and consisting of two convex ridges, which are separated by a median groove. This ichnogenus is generally considered as a repichnia (Hântzchel 1975). Gastropods are considered to be the trace maker (Hântzchel 1975; Ekdale, pers. comm. 1999). The type ichnospecies is *Aulichnites parkerensis* Fenton and Fenton 1937 (Fillion and Pickerill 1990). According to Hakes (1977) *Aulichnites* is generally characteristic of marine shallow-water settings but it can also occur in deeper marine (Hill 1981) or brackish water (Pollard 1988).

Bradshaw (1981) described similar traces, from the Devonian of Antarctica. Bradshaw placed the trails in the ichnogenus *Agrichnium* but pointed out that this ich-
nogenus, first described by Pfeiffer 1968, was in need of a redescription. Initially the traces in this sample were considered as Agrichnium but since Agrichnium is considered to be a name no longer used the traces were instead placed under Aulichnites (Ekdale, pers. comm. 1999).

Ichnogenus Cochlichnus Hitchcock, 1858

*Cochlichnus* isp.

Fig. 11 B-D

**Material and occurrence.** - Ten slabs, two from Fossilryggen (ANT 90-11) and eight from Kirwanveggen (ANT 91-1, 98-15). The samples from Fossilryggen derive from thin, medium-grained, sandstone beds in an otherwise shaly part, at a level of about 26 m above the base of the section (Fig. 4). Specimens from Kirwanveggen are preserved in yellowish medium-grained sandstone from Frostbite Bluff (Fig. 7).

**Description.** - Sinusoidal, unbranched, unlined burrows. Traces are horizontal to bedding plane. Two different sizes
are present. One single large specimen occurs as negative epirelief on a rippled surface on one slab. Small sized Cochlichinus as well as larger specimens occur as positive epirelief on the other slabs. Several of the specimens are incomplete. Small Cochlichinus have a diameter that ranges from 1.5-2.0 mm; wavelength varies from 5.5-6.5 mm; amplitude varies from 4.0-5.0 mm and the maximum length is 27 mm. Larger Cochlichinus have a diameter of 3.0-5.0 mm; wavelength varies from 10 - 25 mm; amplitude of the trace varies from 7.0-10 mm and the maximum length in a complete specimen observed is 77 mm. Overcrossing occurs frequently among specimens on one of the slabs.

Associated ichnotaxa. - At Kirwanveugen, Cochlichinus occurs together with small Palaeophycus isp. 1. At Fossilryggen Aulichnites occurs at the same level.

Remarks. - Cochlichinus is a very distinctive ichnogenus due to its sinusoidal form (Butoais et al. 1997). Cochlichinus is also known to be represented by true burrows (Webby 1970). There has recently been a discussion concerning the separation of sinusoidal trails and sinusoidal burrows into two different ichnogenera. Rindsberg (1994) would like to include sinusoidal burrows in the new ichnogenus Cymatalus. Pickering and Narbonne (1995), on the other hand, were of the opinion that it is often hard to distinguish between sinusoidal burrows and trails so it is better to include them both in the ichnogenus Cochlichinus.

Three different ichnospecies of Cochlichinus are valid. These are Cochlichinus anguineus Hitchcock 1858, Cochlichinus antarcticus Tasch 1968 and Cochlichinus annulatus Orlowski 1989 (Butoais et al. 1997). Assignment to a specific ichnospecies in this case has to be either to Cochlichinus anguineus or C. antarcticus since C. annulatus is characterised by its annulated outer walls (Orlowski 1989), a feature not present in this material.

There have been discussions about the ethological interpretation of Cochlichinus. According to Butoais et al. (1997) the ethologic significance of Cochlichinus should be assigned to it for each occurrence. Butoais and Mângano (1993a) interpreted it as a pascichnia while Elliot (1985) assigned it as a repichnia and Edgar et al. (1985) interpreted it as a fodichnia. Studies of similar traces in modern floodplain and lake-margin environments have shown that sinusoidal trails, today, are made by nematodes (Moussu 1970; Chamberlin 1975) or ceratopogonid larvae (biting midge). Formation of sinusoidal traces by a biting midge was observed by Metz (1987) along the periphery of a small pond. Metz (1987) observed the larvae moving over a thin film of water-covered mud. There is a fossil record of diptera extending back to the Late Permian (Ross and Jarzembowski 1993) but ichnofossil evidence is rare (Mângano et al. 1996). The traces here are considered as repichnia made by nematodes.

Cochlichinus dates back to the Precambrian (Hântzschel 1975; Metz 1998) and is a facies-crossing form (Mccann and Pickering 1988) which has been found in several different marine, marginal-marine, and non-marine environments (Butoais et al. 1997). Cochlichinus is with almost total certainty formed subaquously (Butoais et al. 1997).

An ichnogenus similar to Cochlichinus is Belorhapa. Distinction between the two is made by the shape of the turns. Cochlichinus has rounded turns while Belorhapa has angular turns (Butoais et al. 1997). If there is frequent overcrossing, Cochlichinus can give a false appearance of a Paleodictyon network (Buatois et al. 1997).

Cochlichinus isp. is known from other localities in Antarctica as a specific Permian trace fossil (Cooper and Shergold 1991). For example there are records of Cochlichinus antarcticus from the Mount Glossopterus Formation in the Ohio Range (Cooper and Shergold 1991) which is correlated with Fossilryggen through palynomorph assemblages. Correlations were carried out by Lindström (1996). Cochlichinus isp. also occur in the Polar Star Formation at Mt. Weems, Sentinel Range, Ellsworth Mountains (Cooper and Shergold 1991).

Ichnogenus Helminthopsis Heer, 1877

Helminthopsis isp.

Fig. 11 E & F

Material and occurrence. - 14 slabs (ANT 90-22) from Fossilryggen. Numerous specimens preserved in dark fine-grained shale at 38 m above the base of the section (Fig. 4).

Description. - Horizontal traces that exhibit overcrossing which gives a false impression of branching. Abundant occurrence on slabs. Traces are straight to slightly bent where the bends are sometimes fairly sharp. Two different sizes are present - large and small Helminthopsis. The diameter of small Helminthopsis varies from 0.5 -8.0 mm. Two specimens are assigned as large Helminthopsis. The largest one of these has a diameter of 16 mm. Occasionally there is a slight variation in diameter within the same specimen. The difference is not more than 2.0 mm. Length of traces is highly variable and the majority of the specimens are incomplete. Some specimens occur as hypichnial grooves while the majority of them have been exposed to compaction and are therefore preserved as a flat print, both as epichnia and hypichnia. The flattened traces predominantly occur as a carbon film.

Remarks. - The preservation as a carbon film is probably a result of the original material of the burrow wall consisting of mucus which is very degradable and therefore leaves a carbon film behind (Bromley, pers. comm. 1999). The sediments have been severely heated and are therefore quite burnt. The traces therefore do not appear as they originally were preserved. Helminthopsis usually resembles other simple grazing traces such as Gordia and Helminthoidichnites (Butoais et al. 1997) but it is hard to see any similarities in this case because of the post-depositional heating of the sediment.
The ichnotaxonomy of *Helminthopsis* has recently been reviewed by Wetzel and Bromley (1996) who re-evaluated the ichnogenus through looking at the type material collected by Heer 1877. The three ichnospacies originally assigned to *Helminthopsis* actually belong to three different ichnogenea. This has, of course, caused several problems since they cover a wide range of morphologies and since 1904 the ichnogenus has been used for curved, irregularly meandering trace fossils (Wetzel and Bromley 1996).

Wetzel and Bromley (1996) suggested that *Helminthopsis hieroglyphica* should be the new type ichnospecies of *Helminthopsis*. *Helminthopsis hieroglyphica* was never validly introduced by Heer as the name for this ichnospacies, but the holotype was collected at the same locality as the other specimens of *Helminthopsis* described by Heer in 1877 (Wetzel and Bromley 1996).

As a result of the re-evaluation three ichnospaces are considered to be valid: *Helminthopsis abeli* Książkiewicz 1977, *Helminthopsis hieroglyphica* Wetzel and Bromley 1996, and *Helminthopsis tenius* Książkiewicz 1968. These three clearly differ in their geometrical pattern and the definition of the different ichnospacies is therefore based on this. *Helminthopsis abeli* has irregular open meanders and horseshoe-like turns, *H. Hieroglyphica* shows irregular low-amplitude windings, partly straight and *H. tenius* has irregular, high-amplitude windings, but only with U-turns, horseshoe-like turns are not present (Wetzel and Bromley 1996).

Small *Helminthopsis* can probably be assigned to *H. Hieroglyphica* considering the presence of straight segments and the sharp bends, but the larger specimens are better assigned to any of the other two ichnospacies.

Wetzel and Bromley (1996) interpret *Helminthopsis* as a fodinicchia, which is normally produced at shallow depth within the sediment and which also has to be rich in food for the animal. Bradshaw (1981) also considered *Helminthopsis* as a fodinicchia. *Helminthopsis* does not show any distinct lining which can be used to separate it from similar traces (Wetzel and Bromley 1996). In modern pond environments, irregularly meandering trails are produced by soldier fly larvae (Diptera: Stratiomyidae) (Mángano et al. 1996). Even though stratiomyids were not present in the Palaeozoic, the traces could have been made by similar, more primitive, fly larvae, in that case considered as grazing traces (Mángano et al. 1996).

**Associated ichnotaxa.** - Occurs together with feeding burrows.

**Remarks.** - The very few specimens present may be an indication of that these are not actually *Lockeia* isp., but just feeding burrows that incidentally have a shape that resembles *Lockeia*. In most cases *Lockeia* occurs in clusters where the individual traces commonly belong to the same ichnospacies (Kim 1994). Anyway, the possibility of the traces being *Lockeia* has to be taken in consideration and discussed. The occurrence of only a few specimens should not rule out the possibility of the traces being *Lockeia* since the material available for study is limited. More *Lockeia* might have been present at an initial stage, but due to the active bioturbation at the surface they have been destroyed. The slabs are of small size, which could lead to misinterpretations about the activities on the palaeosurface. *Lockeia* is now considered to be resting traces of burrowing bivalves (plecty pods) (Hántszschel 1975) but its original interpretation by James 1879 was as an alga (Kim 1994). *Lockeia* is the senior synonym of *Pelecypodichnus* Seilacher 1953.

*Lockeia* has been reported from shallow marine (Pickett 1977), deep marine (Crimes et al. 1981) and non-marine (Bromley and Asgaard 1979; Archer and Maples 1984) environments and ranges from the Precambrian to the Cretaceous in age in North America, Europe and Asia (Kim 1994).

**Ichnogenus Palaeophycus** Hall, 1847

Since *Palaeophycus* is very abundant in the material, several separate descriptions of this ichnogenus are needed, starting with a general description.

**Fig. 13 A-F, 14 A & B**

**Material and occurrence.** - 15 slabs (ANT 89-11, 90-1, 90-2, 90-8, 90-15, 90-27, 90-30) from Fossilryogen containing three specimens. Preserved in medium-grained sandstone at 26 m above the base of the section (Fig 4).

**Description.** - Horizontal, cylindrical to subcylindrical, sometimes tubular burrows. Highly variable forms are present. Predominantly preserved as epichnial ridges but preservation as endichnia and hypichnia also occur. It occurs in medium to coarse-grained sandstones. No true branching is visible but crossovers and interpenetrations are very common in most of the material. Lining is rarely preserved in larger *Palaeophycus* except for small mud-minerals along the edges of some traces as well as fur-
Fig. 13. A. *Palaeophycus tubularis*, Fossilrygen. B. *Palaeophycus striatus*, Fossilrygen. C. *Palaeophycus tubularis* with draught canal, Fossilrygen. D. *Palaeophycus tubularis* and *Palaeophycus striatus*, Fossilrygen. E. *Palaeophycus* isp. 1, Fossilrygen. F. *Palaeophycus* isp. 1, Fossilrygen. Scale bar 1 cm.
rows alongside the traces, which have been reinforced by weathering. In several samples of smaller *Palaeophycus* the lining is distinctive. Burrow fill is massive and of same lithology as the host rock. Burrow sculpture can, in some cases, be distinguished. There is a broad variation in the diameter of the traces both between the different traces as well as within the same trace. Most of the material is severely weathered.

**Associated ichnotaxa.** - At Kirwanvæggen, *Palaeophycus* occurs together with *Cochlichnus*. Hypichnial *Palaeophycus* occurs with feeding traces and *Lockeia* at Fossilyrangen.

**Remarks.** - *Palaeophycus* is distinguished from *Planolites* by the presence of lining and the nature of the burrow fill (Pemberton and Frey 1982). *Planolites* lacks the characteristic lining of *Palaeophycus*. The burrow fill of *Planolites* differs from the host sediment.


*Palaeophycus heberti* and *P. tubularis* are described as distinctly lined, smooth-walled, unornamented burrows where *P. heberti* is a thick-walled burrow and *P. tubularis* is a thin-walled burrow. *Palaeophycus striatus*, *P. sulcatus* and *P. alternatus* are described as very thinly lined, longitudinally striated burrows where *P. striatus* is characterised by continuous parallel striae, *P. sulcatus* by irregularly anastomosing striae and *P. alternatus* by alternately striate and annulate (Pemberton and Frey 1982).

*Palaeophycus* is a domicinia, which represents the passive infill of an open dwelling burrow of a predaceous or suspension-feeding animal (Pemberton and Frey 1982). *Palaeophycus* has been reported from a wide variety of environmental settings (Buatois et al. 1997) and it is a common component of non-marine ichnofacies (Buatois and Mángano 1993a). *Palaeophycus* occurring in non-marine settings were probably produced by insects or other arthropods (Buatois and Mángano 1993a).

**Palaeophycus tubularis** Hall, 1847

Fig. 13 A, C & D

**Material and occurrence.** - Two slabs (ANT 90-8, 90-15) from Fossilyrangen containing numerous specimens. Preserved in coarse-grained sandstone at 29.7 m above the base of the section (Fig. 4).

**Description.** - Dominantly horizontal, cylindrical to sub-cylindrical traces preserved as convex epichnia in medium-grained sandstone, but some just occurs as vertical "knobs". Traces are straight to slightly curved. There is no branching but traces frequently show overcrossing. Burrows are unornamented and have an even shape. Diameter of traces is constant within each specimen. Maximum length of one specimen is 155 mm but it is not complete. The diameter of a trace is about 9.0 mm in all specimens. It is possible to see lining along several of the traces both viewed in cross-section and from top of the slab. The lining material consists of mud. Remains of thin lining are present along some parts of the traces. Several burrows show a bilobed character in parts of the trace. Remains of clay minerals are present on top of slab.

**Remarks.** - *Palaeophycus tubularis* is the type species of *Palaeophycus* (see Pemberton and Frey 1982). *Palaeophycus tubularis* lacks any kind of striae and is therefore easily distinguished from the other species. Separation from the similar species *P. heberti* is made by the presence of a thicker lining in the latter (Pemberton and Frey 1982).

The animal that produced these traces was feeding on detritus on the seafloor. This detritus was probably available in a thin layer of mud covering the sand in which the traces are preserved (Bromley, pers. comm. 1999). This mud-layer was also the source of the material of the lining of the traces. The animal worked at the interface of the two layers. The clay minerals on top of the slabs are evidence of an overlying mud-layer.

The bilobed appearance that some of the burrows show at the end of the trace are interpreted as draught canals (Fig. 11 C) (Bromley, pers. comm. 1999). These are produced during the filling of a burrow with sediment. As the sediment fills the burrow it replaces water and as the water leaves the burrow it creates the draught canal (Bromley, pers. comm. 1999). The presence of draught canals indicates that the traces represent domicinia that were filled passively. Another explanation is that this feature is the result of diagenetic effects. The vertical "knobs" represent the spot where the animal has come up or gone down.

**Palaeophycus striatus** Hall, 1852

Fig. 13 B & D

**Material and occurrence.** - Two slabs (ANT 90-8, 90-15) from Fossilyrangen. Preserved in medium-grained muddy sandstone (ANT 90-8) at 25.2 m and coarse-grained sandstone (ANT 90-15) at 29.7 m above the base of the section (Fig. 4).

**Description.** - Preserved as convex epichnia in ANT 90-15 while ANT 90-8 has endichnial preservation. Traces are straight to slightly curved and are sub-cylindrical to tubular in shape. There is no branching. Diameter of traces varies from 10-12 mm. Lining is present and the lining material is mud. The burrows have few coarse longitudinal striations, which are only vaguely visible. Burrow-fill is massive and same as the host rock.
Remarks. - *Palaeophycus striatus* has ornamented walls with striae, which separates it from *Palaeophycus tubularis*, which has smooth walls. It is distinguished from other striated species of *Palaeophycus* by the continuous, parallel striae (Pemberton and Frey 1982).

*Palaeophycus* isp. 1

Fig. 13 E & F

Material and occurrence. - Nine slabs (ANT 89-11, 90-1) from Fossilryggen containing numerous specimens. Occurs in coarse-grained sandstone at 12.9 m (ANT 89-11) and 22.9 m (ANT 90-1) above the base of the section (Fig. 4). Two slabs (ANT 98-15) from Kirwanveggen (Frostbite Bluff) deriving from a medium-grained sandstone containing numerous specimens (Fig. 7). The material has been exposed to weathering.

Description. - Traces are preserved as convex epichnia on a rippled surface in the Fossilryggen material. Specimens from Kirwanveggen are preserved as epichnial ridges on a flat surface. The material from Fossilryggen contains large burrows while the burrows from Kirwanveggen are small. Traces are horizontal or appear as oblique shafts. The filling of the traces is the same as the host sediment. The slabs have been exposed to severe weathering. Traces are straight to slightly curved with irregular shape and size. There is no true branching but several cases of overcrossing. All specimens do not have the same diameter and there is also a variation of the diameter within each separate trace. In the majority of the samples lining is not visible at all but in a few cases it is actually represented by sharp furrows along the sides of the burrows, created by weathering effects. Some slabs have a thin layer of mud covering the surface.

Associated ichnotaxa. - At Kirwanveggen *Palaeophycus* occurs in association with *Cochtichnus*.

Remarks. - These traces were produced a few centimeters below the seafloor. The animals were active at the interface between the top layer, consisting of mud, and the sand below. Evidence for the presence a mud layer is the thin film of mud on top of several of the slabs. There can not have been much food available in the coarse-grained or medium-grained sandstone in which the traces are preserved. The animals were feeding on organic material in the mud and the traces are just preserved in the sandstone.
Palaeophycus isp. 2

Fig. 14 A

Material and occurrence. - Two (ANT 90-2) slabs from Fossillygen containing only a few specimens. Preserved in fine-grained sandstone at 25.5 m above the base of the section (Fig. 4). The material has not been exposed to weathering.

Description. - Horizontal, straight to slightly curved burrows preserved as endichnia. Burrows show overlapping but no true branching. Burrow fill is identical to the surrounding sediment. Varied diameter creates a division of the burrows into small (3.0 mm), medium (6.0-9.0 mm) and large (17-18 mm) Palaeophycus. One trace shows a collapsed structure. This collapsed Palaeophycus has a length of 110 mm. Other burrows are incomplete. The traces are preserved on a fresh surface, which has not been exposed to weathering. There is a thin coating of clay on top of the slab.

Remarks. - The thin film of clay is evidence of the presence of a mud layer on top of the sand. The collapsed trace is assigned to Palaeophycus because of the lack of any signs of back-fill structures. It is probably a Palaeophycus tubularis.

Small Palaeophycus

Fig. 14 B

Material and occurrence. - Six slabs (ANT 90-27, 90-30) from Fossillygen. Preserved in fine-grained muddy sandstone at 48 m (ANT 90-27) and at 52 m (ANT 90-30) above the base of the section (Fig. 4).

Description. - Small, horizontal, needle-shaped traces with lining. Preserved as endichnia. Traces are straight to slightly curved. No sharp bends. Filling of traces is similar to the host sediment. The lining material is different. Diameter of traces is 1-2 mm. No specimen is complete so the length of the traces cannot be measured.

Remarks. - The slabs have not been exposed to weathering. The assignment of the material to the ichnogenus Palaeophycus is based on the presence of the distinct lining and the structureless burrow fill which is the same as the host sediment.

Teichichnial Palaeophycus

Fig. 15

Material and occurrence. - One (ANT 90-8) slab from Fossillygen containing one single specimen. Preserved in medium-grained muddy sandstone at 25.2 m above the base of the section (Fig. 4).

Description. - One trace preserved as endichnia. It shows a tendency to spreite, which makes it resemble Teich-

ichnus isp. The burrow shows some striations. Lining of mud is present. The diameter is 10.5 mm and the thickness of the trace including spreite is 18 mm. Trace occurs as an oblique tube.

Remarks. - The name teichichnial Palaeophycus is applied to this specimen because of the resemblance to Teichichnus isp. by the presence of spreite. Other traces occurring in the same slab are referred to as Palaeophycus isp. 2 and Palaeophycus striatus.

?Ichnogenus Skolithos Haldemann, 1840

?Skolithos isp.

Fig. 16 A & B

Material and occurrence. - Four slabs (ANT 90-20) from Fossillygen. Preserved in fine-grained sandstone at 37.4 m above the base of the section (Fig. 4).

Description. - Slightly curving, vertical to near-vertical shafts with a dark, thick clay lining. Several surface openings are present on top of slabs. Burrow fill is massive and similar to host sediment. Diameter of traces is between 1-3 mm. Penetration depth is different between specimens. The longest trace measures 60 mm but it is not complete. Since most traces are incomplete the shape of the lower termination of the traces is unknown.

Associated ichnotaxa. - Slabs also contains numerous specimens of the horizontal association discussed as Incerta No. 5.

Remarks. - The traces are regarded as domicinia. The animal has been pulling material down into the burrow as there was probably a mud layer present on top of the sand layer before the bioturbation started, resulting in the burrow lining. Therefore, the traces are regarded as post-depositional. Since the longest trace is incomplete there is a possibility that traces may extend even further down into the sediment. Due to the fact that most traces are incomplete and the material is insufficient, assignment to the ichnogenus Skolithos is uncertain. Even though it is most likely that the traces belong to the ichnogenus Skolithos, which has I-shaped burrows, there is also a possibility that the traces belong to the ichnogenus Arenicolites, which has simple U-burrows. According to Häntszschel (1975)Arenicolites only occasionally has lining. If regarding this feature as distinctive, assignment to Skolithos is the most appropriate in this case.
Feeding traces

Fig. 14 D

Material and occurrence. - Five slabs (ANT 90-11, 90-30) from Fossilryogen preserved in medium-grained sandstone at 26 m (ANT 90-11) and muddy fine-grained sandstone at 52 m (ANT 90-30) above the base of the section (Fig. 4).

Description. - Preserved as hypichnial ridges and other irregular shapes. Small "bloppy" traces. The size and shape of the traces are very variable.

Associated ichnotaxa. - Occurs together with Lockeia isp.

Remarks. - The deposit-feeding animal exploited a muddy surface randomly in search for food. This classifies the traces as fodiichnia. The feeding burrows have been preserved by infilling of clastic material.

Ichnogenus Incerta No. 1

Fig. 16 C

Material and occurrence. - One slab (ANT 90-21) containing three specimens from Fossilryogen. Preserved in medium-grained sandstone with an influx of larger clasts at 37.9 m above the base of the section (Fig. 4).

Description. - Large, horizontal, straight to slightly curved traces preserved as convex hypichnia. Burrows are uneven in shape. The diameter of the traces varies between the specimens as well as within the same trace. The largest one measures 52 mm across at the widest part. Diameter of a smaller one is 37 mm at the widest part and 18 mm at the narrowest part. Burrow fill is massive and same as the host sediment. The burrows show no over-crossing but the traces merge into each other.

Remarks. - The traces are regarded as domicinia, which were passively infilled with sediment. Due to the large size and shape, some kind of vertebrate could be a possible trace maker. Most likely some kind of amphibian. Today toads produce this kind of trace, but they usually produce a back-fill structure, which is not present in these samples (Bromley, pers. comm. 1999). Another possibility is some kind of cray-fish, since they were fully developed in the Permian (Bromley, pers. comm. 1999).

Bromley and Asgaard (1979) described similar traces from the Triassic of Greenland. They described them as large burrows made by an unknown trace maker, but speculated about small amphibians, reptiles, large insects.

Fig. 16. A. Vertical cross-section of ?Skolithos isp., Fossilryogen. B. Top view of ?Skolithos isp., Fossilryogen. C. Possible vertebrate resting trace, Incerta No. 1, Fossilryogen. D. Incerta No. 2, Fossilryogen. Scale bar 1 cm.
or primitive crustaceans as possible producers (Bromley and Asgaard 1979).

Ichnogenus Incerta No. 2

Fig. 16 D

Material and occurrence. - Two small slabs (ANT 90-6) from Fossilryggen. Preserved in medium-grained sandstone at 22 m above the base of the section (Fig. 4). Slabs are badly weathered.

Description. - Open shafts on a rippled surface. Diameter of openings is about 2.0-3.0 mm. No filling of the burrows.

Remarks. - Nothing can be said about where the traces belong taxonomically. They are just referred to as openings on a bioturbated surface. The shape and angle of the traces indicate that the trace maker was probably just passing through this level in the sediment. There was probably a change in grain size and material at the interface between this layer and the overlying layer (Bromley, pers. comm. 1999). The burrows were probably clay-filled but there are no clay minerals left to prove this. The ethological affinity is uncertain.

Ichnogenus Incerta No. 3

Fig. 17 A & B

Material and occurrence. - One slab (ANT 90-19) from Fossilryggen containing several specimens on top of slab. Preserved in dark, fine-grained shale containing larger clasts of quartz at 37.3 m above the base of the section (Fig. 4).

Description. - Horizontal, straight to slightly curved traces that show true branching (Fig. 17 B). The traces have a flat structure almost without any relief at all. With all certainty this is due to compaction. Most traces are incomplete. The diameter of the traces is 1.0-3.0 mm. Diameter is constant within the same specimen. The length of one incomplete trace is 72 mm. The traces have a thick lining.

Remarks. - The traces are interpreted as fodiichnia. It was probably an open burrow where the animal could move around freely to different parts of the burrow. The lining indicates that the burrow had an organic or clay wall (Bromley, pers. comm. 1999). To produce this kind of open system the animal would have had to be there for quite some time so it must have been produced in an environment with slow sedimentation and overall quiet conditions. The true branching distinguishes this trace from Helminthopsis.

Ichnogenus Incerta No. 4

Fig. 17 C & D

Material and occurrence. - Four slabs (ANT 91-28, 98-11) from the section at Mt. Alex du Toit, Kirwanveggen. Traces are preserved in pink fine-grained sandstone, approximately 13 m below the basalt (Fig. 7).

Description. - The burrow fill is coarser than the host sediment. Two size populations are present - large and small. The large burrow is about 10 mm wide and has sharp branching. The shape is irregular. Small burrows are cylindrical in shape. Small burrows are preserved as endichnia and have no preferred orientation in the sediment. All specimens are incomplete.

Remarks. - Regarded as a fodiichnia. The material of the smaller burrows seems to be a mixture of the casting medium and the larger burrow. Smaller burrows were probably produced later, maybe using material from the larger burrow. The large and small burrows probably represent two different ichnogenera. The studied material is not good enough for making any assignment to a specific ichnogenus.

Ichnogenus Incerta No. 5

Fig. 17 E

Material and occurrence. - 11 slabs (ANT 89-30, 89-38, 90-14, 90-20) from Fossilryggen preserved in a grey fine-grained sandstone at 29 m (ANT 89-30), 34.8 m (ANT 89-38), 29.5 m (ANT 90-14) and 37.4 m (ANT 90-20) above the base of the section (Fig. 4).

Description. - Small, needle shaped, straight to slightly curved traces. In cross section traces are flat. No sharp bends. Preserved as endichnia. Filling material is dark and is different from the host sediment. Traces are very abundant in slabs. Diameter of the traces is 1.1-1.5 mm. The edges of the traces are rounded. Length is varied. The longest trace measures 43 mm.

Remarks. - The traces are very abundant in the slabs. Slabs have not been exposed to weathering. The traces could be Planolites, which is characterised by having unlined walls and a burrow fill that differs from the surrounding sediment (Pemberton and Frey 1982). Planolites represents a back-fill structure created as the animal was deposit-feeding and moving forward (Pemberton and Frey 1982).

According to Bromley (pers. comm. 1999) Palaeophycus is another option. If the traces are considered as Paleophycus, the dark fill of the traces represents collapsed lining.

Ichnogenus Incerta No. 6

Fig. 17 F

Material and occurrence. - Three slabs (ANT 98-23) from Mt. Alex du Toit, Kirwanveggen. Preserved in yellow
fine-grained sandstone with siltstone, approximately 34 m below the basalt (Fig. 7).

Description. - Irregular burrows with uncertain preservation. Very abundant. Irregular burrowing pattern.

Remarks. - The material does not reveal very much. All that can be said is that it represents a bioturbated surface. Approximately 80% bioturbation of the surface.

Acknowledgements
I would like to extend my deepest gratitude to my supervisor Dr. Kent Larsson, Lund, for introducing me to this project and for all the help with literature, figures and comments, during the making of this paper. Further I would like to thank Dr. Richard Bromley, Copenhagen, for the hospitality during my visit on Bornholm and for giving me guidance through the world of trace fossils. I
thank Hanna Calner, Lund, for inspirational discussions about trace fossils, comments on early manuscripts, creative ideas and good support. Mikael Calner, Lund, gave me guidance concerning the sedimentology at an early stage, which was a big help to get started. I am also grateful to Dr. A. A. Ekdale, Utah, USA, for taking time to meet me for a couple of hours in Copenhagen during his very busy stay there. It gave me inspiration. A special thank you goes to Anne Sluhan-Reich, Copenhagen, who proof-read this paper and made it through the whole thing without knowing anything about palaeontology. I would also like to thank Mattias Jacobson, Lund, for help with the computer, Dr. Sven Stridsberg, Lund, for help with layout and comments on my manuscript, Mikael Siverson and Sofie Lindström, Lund, for critical reading and useful comments, and everybody else at the Department of Geology in Lund who helped me in some way.

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