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A dynamic model for a meniscus filled tunnel (*Ancorichnus* n. ichnogen.) from the Jurassic *Pecten* Sandstone of Milne Land, East Greenland

by
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Abstract

A new type of meniscus filled tunnel is described and designated *Ancorichnus ancorichnus* n. ichnogen., n. ichnosp. The trail is functionally analysed in terms of the anchor method used by soft bodied animals in penetrating soft substrates. The whole trace fossil assemblage, consisting of *Ancorichnus, Planolites, Muensteria,* small meniscus tunnels and *Gyrochorte,* is described. The structure and trophic groups of the different meniscus filled tunnels are compared.

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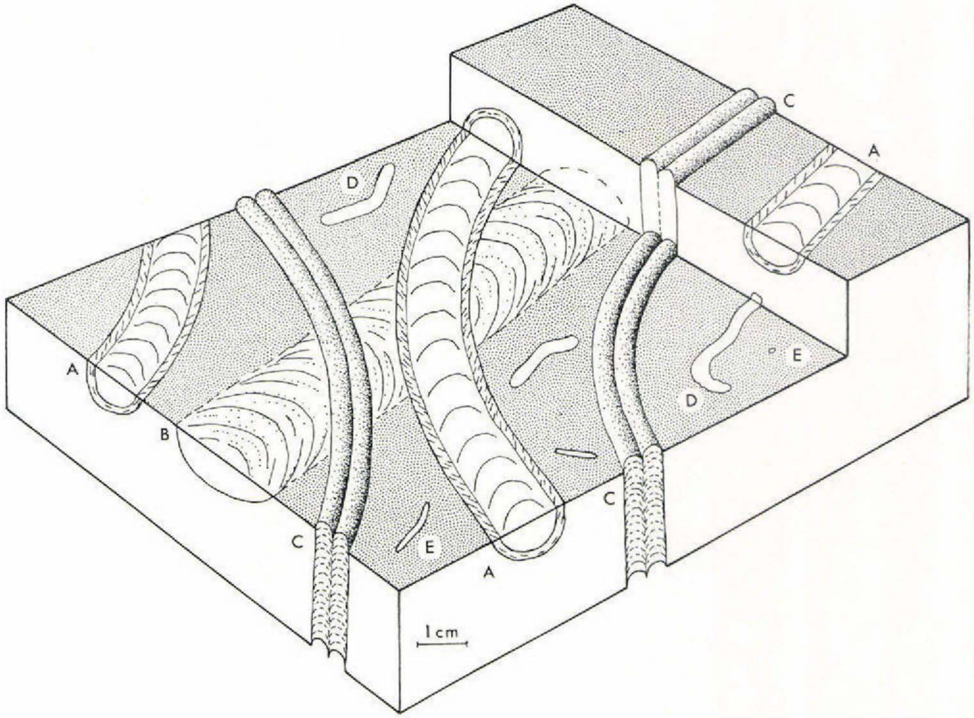

Fig. 1. Block diagram showing the trace fossil assemblage. **A.** *Ancorichnus.* **B.** *Muensteria.* **C.** *Gyrochorte.* **D.** *Planolites.* **E.** Small meniscus filled tunnels, parallel and perpendicular to bedding. Reconstruction based on specimens cited in the text.

INTRODUCTION

During geological mapping of the Mesozoic sediments on Milne Land in the Scoresby Sund district of East Greenland in the summer of 1970 an investigation into the trace fossils of the Upper Oxfordian *Pecten* Sandstone was carried out.

The *Pecten* Sandstone is a wedge-shaped near-shore sandstone unit within a series of shales, the so-called "shale and glauconite series" (Håkansson *et al.*, 1971). The wedge thins from a maximum thickness of c. 90 m in the west to zero in the east. The sandstone contains accumulations of pectinid bivalves and, in places, there is an abundance of lithified tree trunks. Trace fossils are abundant within the *Pecten* Sandstone and show regional variation of the different assemblages.

The meniscus filled tunnel–*Gyrochorte* community described in this paper is a rather unusual ichnocoenose within the Jurassic mica-rich sandstones of East Greenland. The most characteristic ichnocoenose of the thinly bedded sandstones in this area is the *Curvolithus* – *Gyrochorte* community which also occurs elsewhere within the *Pecten* Sandstone. While *Gyrochorte* occurs throughout the sandy facies, *Curvolithus* and meniscus filled tunnels are somewhat restricted in their distribution. Whenever present, however, these latter two trails occur in great numbers, normally dominating the rock, but they have never been found together. This mutually exclusive distribution pattern of *Curvolithus* and meniscus filled tunnels indicates ecological differentiation within these rather uniform sandstones, a differentiation which, however, has still to be fully explained.

MATERIAL AND SEDIMENT

This paper deals with an association (fig. 1) of trails from the central part of the sediment area, where the *Pecten* Sandstone is 5–10 m thick. Material was obtained from two localities on the slopes of 'top 530 m', the position of which is indicated on a map in Håkansson *et al.* (1971).

The sediment of the association is a mica-rich fine sandstone containing *c.* 80% fine sand (0.3 – 0.06 mm) and c. 15% silt (< 0.06 mm) with an average median $d_{50} = 0.104$ mm ($N = 2$). The sediment is well sorted: $S_0 = 1.3$. The rock is laminated (thickness of laminae ½–1½ cm), with each lamina covered by horizontally lying mica flakes, or small pieces of wood (½–1 mm in size). Within each lamina there is a random orientation of mica flakes indicating that the layer has been deposited as a unit with sand and mica mixed. Thus, each lamina is separated by a time gap when suspended mica was sedimented onto the surface to form the cover of horizontally orientated flakes which now controls the cleavage of the rock.

THE TRACE FOSSILS

Preservation

The trails are preserved in a three-dimensional manner within the rather homogeneous sandstone that forms the laminae. No alternation between sandy and clayey layers occurs. This 'sand in sand' preservation is characteristic for all the trails from the Jurassic sandstones in the Scoresby Sund area, due to the lack of alternating clayey layers (Heinberg, 1970, 1973).

According to Seilacher (1962) this type of preservation is rather rare. He states: "Of the sand-living animals only a few leave lasting galleries or other distinct traces in the sand itself, while all of them can leave sharp impressions when they touch, or crawl along, an underlying clay bed."

The 'sand in sand' traces are clearly visible on weathered surfaces, whereas they can only be recognised in fresh fracture surfaces by close examination of the orientation of individual mica flakes under a microscope. Weathering causes a slight difference in relief of the different parts of the trails and a difference in colour. Concentrations of mica produce a slightly positive relief and a darker colour.

The trails are classified as endichnia (Martinsson, 1965) since they occur within the sandstone. Except for *Gyrochorte,* they all occur as horizontal sections on weathered bedding planes. They show negligible relief so classification in terms of positive or negative demi-reliefs is not possible. The small differences in relief mentioned above are found within the trail, and since they are not larger than half a sediment grain they do not disturb the picture of a plane surface covered with 'hieroglyphs'. The new term 'plane relief' is therefore introduced for this situation between positive and negative relief. A trail may be said to occur in plane relief when it is visible on a surface from which it does not differ significantly in topography.

Ancorichnus n. ichnogen.

Type: *Ancorichnus ancorichnus* n. ichnosp.
Derivatio nominis: From Latin, *ancora:* anchor; and Greek, *Ikhnos:* trace.
Diagnosis: As for ichnospecies.

Ancorichnus ancorichnus n. ichnosp.

(figs. 1A, 2–4, 9A)

Holotype: MMH 13041 from GGU Sample 137846, several individuals in a slab of micaceous sandstone from a locality situated *c.* 2½ km south of 'top 530 m' (for map see Håkansson *et al.,* 1971) at 370 m above sea level, the only known locality where this type of trails was dominant. The sandstone is from the upper part of the *Pecten* Sandstone (Upper Oxfordian).

Paratypes: MMH 13042, 13043, 13044 and 13045 from GGU Sample 137846, same locality and horizon as holotype. MMH 13046 from GGU Sample 137882 from a locality 1.5 km west of 'top 530 m' (for map see Håkansson *et al.,* 1971).

Diagnosis: Cylindrical meniscus filled tunnel with a distinct mantle. The slightly undulating course runs subparallel to bedding (fig. 3).

Remarks: The trail differs from other meniscus trails, e. g. *Muensteria,* in having

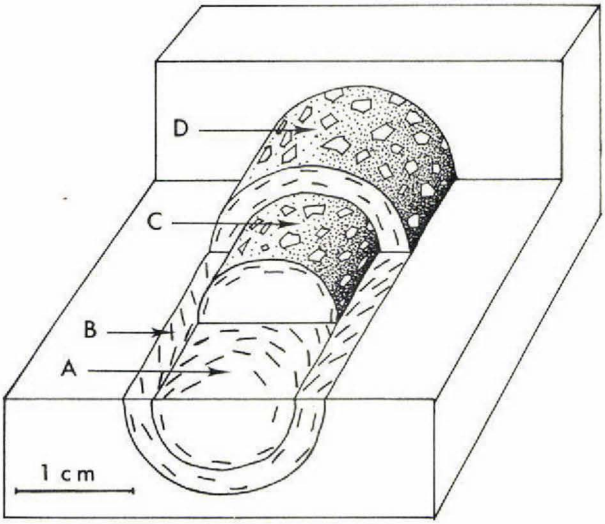

Fig. 2. Model of *Ancorichnus* showing internal mica orientation. **A.** Mica orientation of the fill in horizontal section. **B.** Mica orientation of the mantle in horizontal section. **C.** Mica covering the surface of the fill. Weathered examples might show annulation due to the meniscus structure (Heinberg, 1970, Fig. 3e). **D.** Mica covering the outer surface of the mantle.

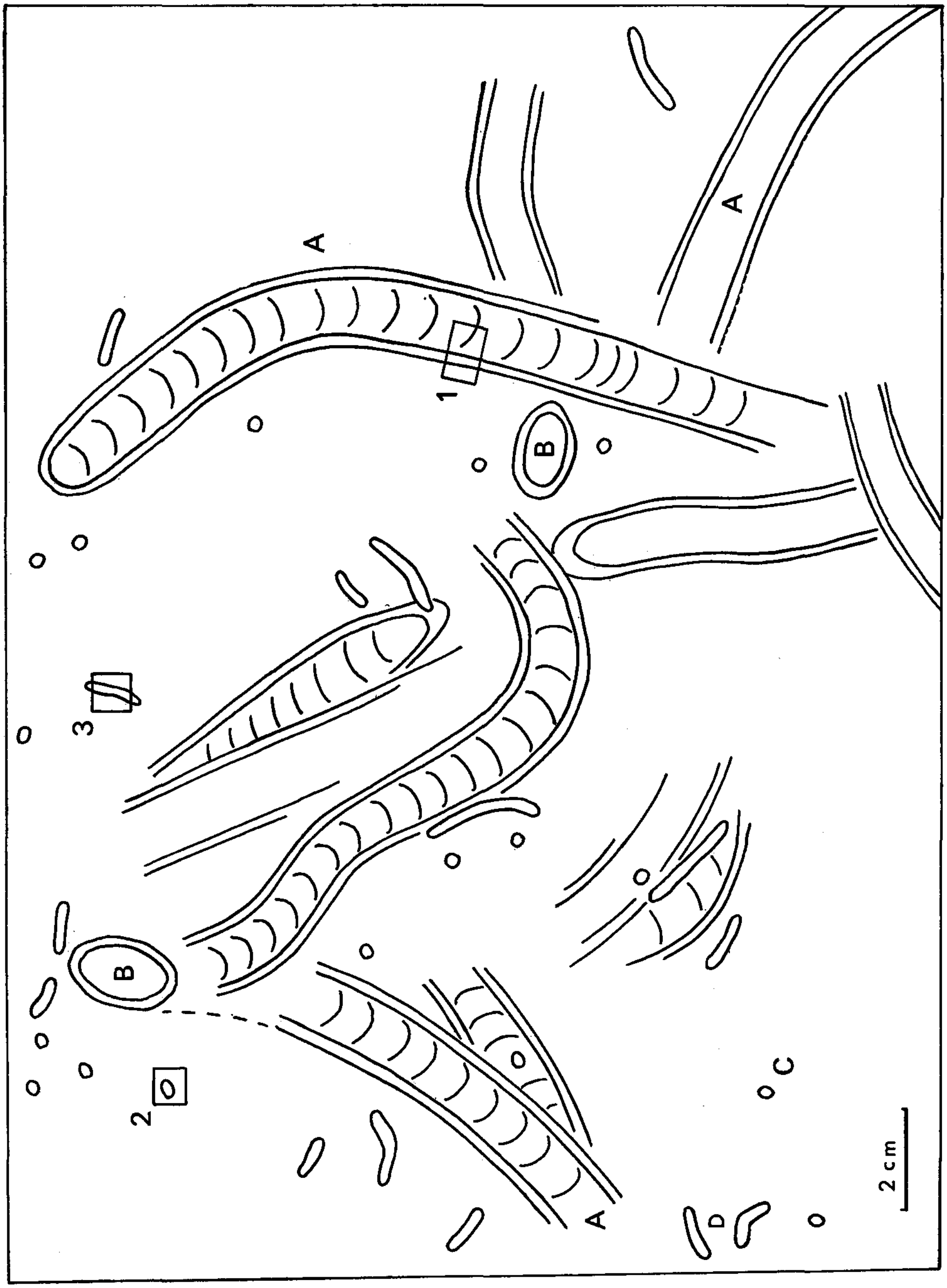

Fig. 3. Line drawing of holotype of *Ancorichnus,* MMH 13041 from GGU sample 137846. **A.** *Ancorichnus,* sectioned parallel to axes. **B.** *Ancorichnus,* oblique section of tunnels crossing the bedding plane. **C.** Small meniscus filled tunnel, perpendicular to bedding. **D.** Small meniscus filled tunnel, parallel to bedding. **1.** Area enlarged in fig. 4. **2.** Area enlarged in fig. 8. **3.** Area enlarged in fig. 7.

a mantle. The mantle is often weathered out as a groove at each side of the meniscus filled tunnel. High mica content shows a special internal structure described below.

Description: The trace has previously been described from the Scoresby Sund area under the heading 'meniscus tunnel fill' (Heinberg, 1970). A similar type has been described by Bromley & Asgaard (1972) but this trace differs clearly in its radial organisation around a central structure, and in details in the construction of the mantle.

The trace consists of a central cylindrical fill surrounded by a tube-shaped 'mantle' (fig. 2). The width of the trace varies from 12–16 mm with an average of 13.6 mm. The thickness of the mantle wall varies between 1.5 – 2 mm. The course is slightly undulating, subparallel to the bedding planes, following no distinct pattern (fig. 3). In most cases there is a distinct mica orientation in the central fill showing a clear meniscus structure, resembling a row of watch-glass-shaped elements, menisci. The concave side of the menisci is in the direction of movement. The mica grains in the mantle are orientated at an angle to the mica in the lateral part of the meniscus (fig. 4). There are sharp junctions between the mantle and the meniscus fill, and between the mantle and the surrounding undisturbed sediment. At these junctions the mica flakes are orientated tangentially to the trail covering the outer and inner surface of the mantle (fig. 2). Such sharp junctions in and around the trail indicate active digging as opposed to pushing aside of the sediment.

There are two exceptions from the mica orientation pattern mentioned above. There are a few examples in which the mica of the mantle is orientated opposite to the normal situation for part of the trail, without obscuring the sharp junction be-

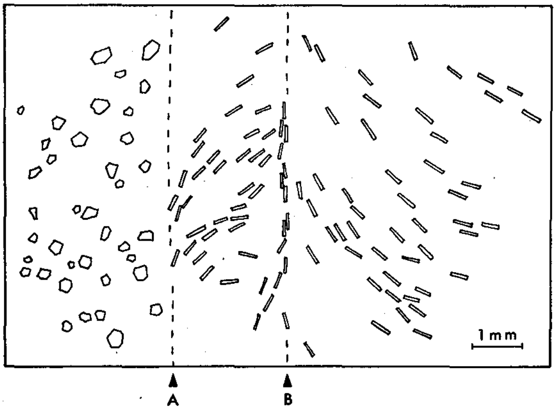

Fig. 4. Detail of *Ancorichnus*, enlarged from fig. 3, showing mica orientation. **A.** Junction between the mantle and the surrounding sediment. **B.** Junction between the mantle and the meniscus fill. Camera lucida drawing.

tween mantle and meniscus fill, and one case where the mantle is almost mica-free for some centimetres. The few remaining mica grains are here orientated in the abnormal way.

Interpretation of Ancorichnus ancorichnus

As previously pointed out (Heinberg, 1973) every trace can be defined as a repetition of a single unit, 'the modular unit'. In the case of *Ancorichnus* the modular unit is complex, constructed of a central watch-glass shaped body (a meniscus) surrounded by a flange. This flange can be interpreted as the periferal part of a meniscus orientated in the opposite direction to the central one, and thus, paradoxically, indicating an opposite direction of movement. However, it is possible to combine these two directions of movement in such a way as to allow the animal to move in only one direction. In order to do this, it is necessary to involve the fact that many soft-bodied animals move through sediment using two anchors (Clark, 1964). One anchor, the anterior or terminal anchor, is developed in order "to anchor the anterior end during the contraction of the longitudinal muscles" (Trueman, 1966), which results in a forward movement of the posterior part of the body. The other anchor, the posterior or penetration anchor, prevents the animal from being pushed backwards when the anterior end is pressed forward into the sediment.

In the case of *Ancorichnus,* the excavating animal has dug actively. Thus the following model may be offered as an explanation of the construction of the burrow.

When the anterior end of the animal was protruded by hydrostatic pressure into the sediment, it produced an excess of sediment which had to be relocated, since it has not been pressed into the sides of the trace (fig. 5, 2). This sediment was transported backwards along the sides of the animal, but could not pass beyond the anchor in order to get behind the animal.

The anchor simultaneously reduced in size in order to maintain the hydrostatic pressure which forced the anterior end forward. This decrease in anchor volume is equal to the volume of excess sediment produced anteriorly. The shrinking took place at the anterior end of the anchor providing a ring-shaped space where the sediment could be packed, forming the mantle (fig. 5, 2).

The shrinking of the anchor and the protrusion of the anterior end of the animal occurred simultaneously and continuously. Shrinkage of the anchor was caused by peristaltic contractions of the ring-muscles, from the anterior end backwards, and this continued until all the muscles were contracted and the animal was at its maximum length (fig. 5, 3, fig. 5, 4). The rearward movement of the peristaltic contraction of the anchor and the concomitant posterior emplacement of rings of sedi-

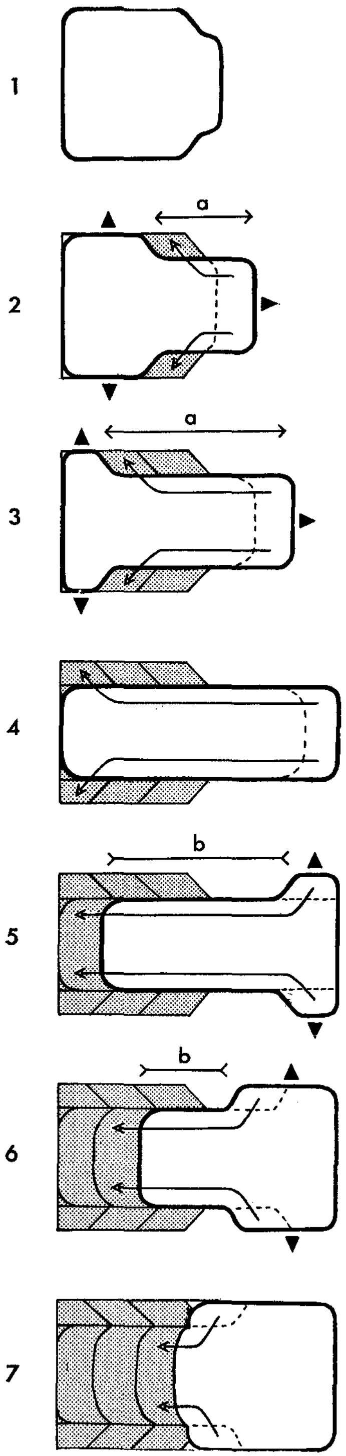

Fig. 5. Dynamic model of the construction of *Ancorichnus* and the movements of the causative organism.

First demicycle

1. Initial situation.
2. Formation of the posterior anchor, and protrusion of the anterior end of the animal by hydrostatic pressure (black solid triangle). The pressure is produced by peristaltic contraction of ring muscles along the length *a*. Sediment (shaded) is transported from the front of the animal along its surface to the space vacated by the shrinking anchor.
3. The same situation at a later stage. As the anchor 'moves' backwards leaving space at its anterior end sediment is transported backwards and packed as the mantle fill. Circular muscles are contracted along the length *a*.
4. Relaxed situation. Posterior anchor has disappeared and the construction of the mantle fill is completed.

Second demicycle

5. Relaxing of anterior ring muscles and contraction of longitudinal muscles resulting in the construction of the anterior anchor by hydrostatic pressure. Sediment from the volume occupied by the anterior anchor is transported behind the animal, forming the meniscus fill. Circular muscles contracted along the length *b*.
6. The same situation at a later stage. As the anchor 'moves' backwards, the posterior end of the animal 'moves' forwards leaving a meniscus fill behind.
7. Final situation leading to the start of the next cycle.

ment explain the mica orientation of the mantle, which indicates a direction of movement opposite to that of the progress of the animal. If the shrinking for some reason took place posteriorly, causing a posterior protrusion of the animal, it would produce the reversed mica orientation seen locally in the mantle. After attaining maximum length, construction of the anterior or terminal anchor takes place (fig. 5, 5). This anchor was formed by simultaneous relaxation of the anteriormost ring-muscles, and contraction of the longitudinal muscles. Contraction of the longitudinal muscles caused an increase in hydrostatic pressure which led to dilation anteriorly where the ring-muscles relaxed. This dilation produced an excess of sediment which was transported backwards and packed behind the animal to form the central fill of the burrow (fig. 5, 6). This process continued with further relaxation of the ring-muscles and contraction of the longitudinal muscles until the situation of minimum length was attained (fig. 5, 7), and a new digging cycle could begin.

The proportions of this model may be varied in such a way that three basically different trails can be produced.

In the first case, we may assume that the posterior anchor is reduced at a faster rate than the anterior end of the 'animal' advances. As usual the posterior anchor will produce one length of mantle equal in length to the anchor but, in the next digging cycle, owing to overlap of activity of successive anchors, the reformation of the anterior anchor will destroy the anterior part of this piece of mantle. As this second cycle anchor disappears it produces a new length of mantle as a continuation of what is left of the preceding one (fig. 6, 5). However, it is unlikely that the discontinuities between succesive mantle lengths would be identifiable in the trace fossil.

In the second case the posterior anchor is reduced at the same speed as the anterior end progresses. The successive cycles of mantle lie accurately in contact with each other.

In the third case the posterior anchor is reduced at a slower speed than the anterior end progresses. This situation will result in a trail with a normal fill, but with a discontinuous mantle.

The three situations would be expected to occur when the area of cross section of the mantle is respectively smaller, equal to, and larger than the area of cross section of the fill. On grounds of efficiency, it seems reasonable to suggest that the animal would not dig through the same sediment several times. If this is so (and if the model is correct), we should expect the two areas to be equal, or rather the mantle area to be a little smaller than the area of the fill, since no trace of contact between the successive cycles of the mantle is visible.

To test this paradigm measurements were taken of the trails. The calculated areas of cross section of the mantle and the fill differed by 7% – 15%, the mantle invariable being the smaller. It can thus be concluded that of the two areas, that of the mantle is the smaller by a slight degree. According to the model these

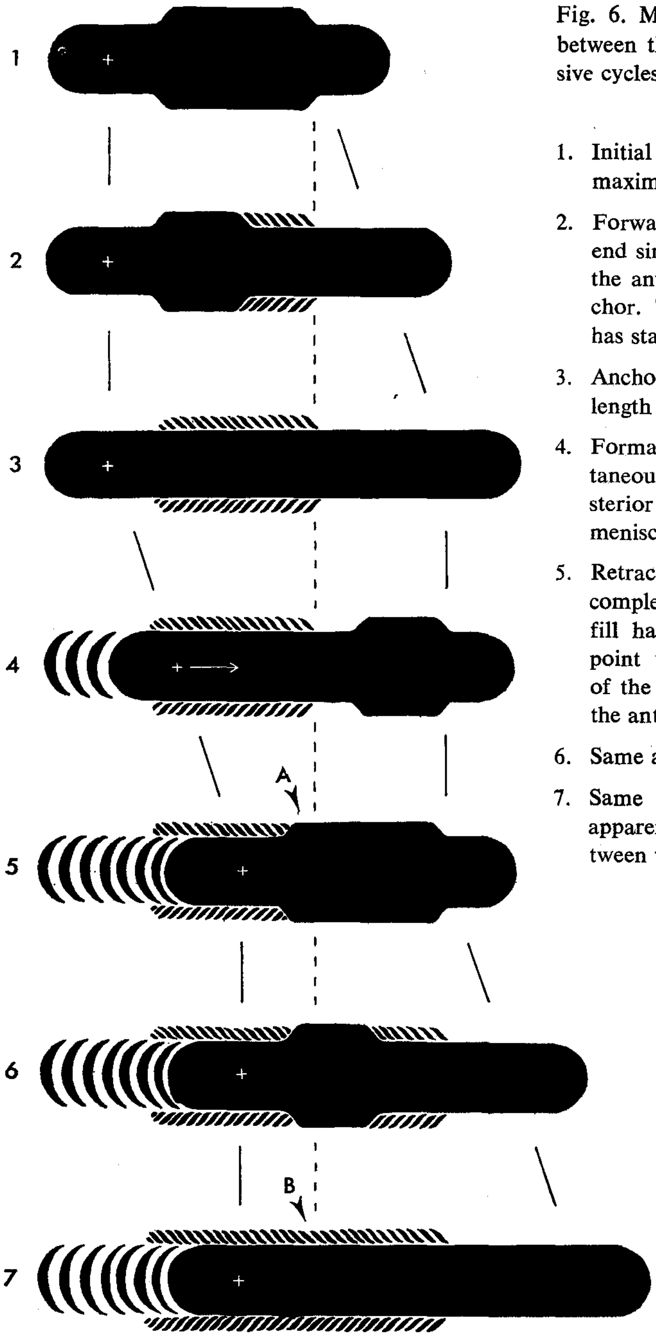

Fig. 6. Model showing the relationship between the mantle, the fill and successive cycles of anchors.

1. Initial situation with anchor at its maximum length.
2. Forward protrution of the anterior end simultaneously with shrinking of the anterior part of the posterior anchor. The formation of the mantle has started.
3. Anchor retraction is completed. One length of mantle has been formed.
4. Formation of anterior anchor simultaneously with retraction of the posterior end. The formation of the meniscus fill has started.
5. Retraction of the posterior end is completed. One length of meniscus fill has been formed. **A** shows the point where the backward advance of the anterior anchor has destroyed the anterior part of the mantle.
6. Same as situation 2.
7. Same as situation 3. **B** shows the apparently continuous contact between the two mantle cycles.

proportions will produce a continuous mantle due to a slight overlapping of successive cycles of the posterior anchor.

The model is purely mechanical and illustrates neither the shape nor the size of the animal which made the structure. It must be emphasized that transportation of sediment from the anterior end to the mantle, and from the side of the animal to the meniscus fill, is a continuous process causing a sequence of thin lamellae (fig. 4). Fig. 5 is merely a schematic representation.

It should also be noted that the formation of anchors possibly takes place only in a restricted part of the animal, as in *Arenicola,* instead of involving the whole body.

The model can be modified in many ways in order to reflect the great taxonomic and morphologic variety of organisms which use the 'anchor' method in burrowing. Among polychaetes, *Arenicola maritima* has already been mentioned as an example. Trueman's (1966) description of the locomotion of this animal gives a detailed explanation of the anchor principle in burrowing. *Arenicola* is a 'soft' animal, and its anchors are produced by hydrostatic pressure. While *Arenicola* represents a worm with a stationary mode of life, sipunculids and priapulids represent 'worms' with an active burrowing habit. Many are sediment feeders and burrow freely around in the sediment.

A sipunculid can be divided into two sections, an anterior proboscis-like structure, the introvert, and the cylindrical trunk. The introvert can be retracted into the trunk by muscular force and extruded from it by hydrostatic pressure, the trunk acting as a penetration anchor. The mouth is situated at the tip of the introvert, and around it there is a fringe of tentacles which functions as an anterior anchor during retraction of the introvert (Schäfer, 1962).

Priapulus burrows in much the same way as sipunculids. Hammond (1970) states, that "when the proboscis has become everted it acts as a terminal anchor while the trunk shortens and is drawn toward it." The shortening takes place in the trunk only, and not in the proboscis as is the case in *Sipunculus.* The formation of the penetration anchor takes place at the posterior part of the trunk. Figure 3 in Hammond (1970) provides a detailed analysis of the locomotion of *Priapulus.* Situations H & I of this figure are parallel to situations 1, 2 & 3 in the model given in this paper (fig. 5) while J, K & L parallel situations 5, 6 & 7. Hammond points out that the animal can improve the effect of the penetration anchor by curving the trunk. Such a curvation would produce an undulating trail as found in *Ancorichnus* and many other fossil burrows.

Burrowing bivalves differ from 'worms' in having a hard structure, the shell. In open position the valves function as a penetration anchor, securing the animal in the sediment while the foot is protruded by hydrostatic force. The foot then produces an anterior anchor and the half closed shell is drawn towards it, within the sediment, by contraction of the pedal retractor muscles (Trueman, 1967, 1968). By opening and closing the shell the bivalve can control the shape and function of its 'hard' part. This is not the case in gastropods, and consequently most snails use other methods in burrowing. However, there are exceptions, for example, *Terebra*. This gastropod has a narrow unspecialised foot which forms an anchor by a terminal distension. The animal is drawn into the sediment by contraction of the column (Morton, 1964). Scaphopods are in much the same situation as *Terebra*, having a shell of constant shape. They have an efficient anchor consisting of the epipodial membrane. When the foot has been pressed into the sediment the membrane is expanded forming the terminal anchor (Morton, 1964).

Ichnogenus *Planolites* Nicholson 1873

(figs. 1D, 9B)

Material: MMH 13047, 13048, 13049, 13050 from GGU sample 137846, same locality as holotype of *Ancorichnus ancorichnus*, above.
Description: This trail is a simple tunnel with circular cross section, having a diameter of c. 3.5 mm. In several cases there is a zone 0.5 – 1 mm wide around the fill with a concentration of tangentially orientated mica grains. There is a sharp junction between this mica zone and the fill, whereas the junction between the zone and the surrounding sediment is not sharp. It is a characteristic feature that the burrow has a distinct light colour due to a total lack of mica within the fill. This difference in lithology between the fill and the sediment is taken as an indication of a coprolitic origin of the fill. Consequently the animal must have been a sediment feeder.

The mica zone shows that mica has been excluded before ingestion of the sediment while the vague outer junction indicates pressing of mica into the wall of the burrow. This contrasts with a mica orientation caused by transportation of sediment along the sides of the animal which would have resulted in a sharp outer junction. Exclusion of mica took place at the anterior end of the animal, at the same time as the tube was filled by coprolitic sand at the posterior end. The sharp junction between the fill and the mica zone thus represents a depositional time gap between the two.

The course of the trail is irregular, curving from side to side and up and down, so it cannot be followed for more than a few centimetres on a single bedding plane.

This type of *Planolites* was found in the *Pecten* Sandstone at several localities and is easily recognizable by its light colour, and rather small diameter.

Small meniscus filled tunnels

(figs. 1E, 3, 7, 8)

Material: MMH 13050 from GGU Sample 137846, associated with the holotype of *Ancorichnus ancorichnus*, above.
Description: The trail consists of a central fill with a diameter of c. 1 mm, sur-

rounded by a mica mantle with a thickness of *c.* 0.5 mm. The central fill is in most cases characterized by a total lack of mica, which gives it a light colour. When mica occurs it is arranged in such a way as to show a distinct backfill structure (fig. 7).

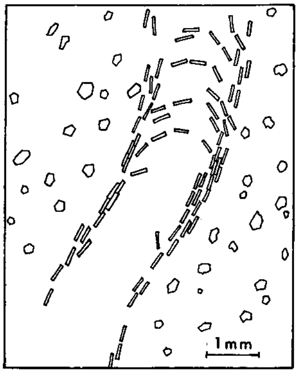

Fig. 7. Small meniscus filled tunnel, enlarged from fig. 3, sectioned parallel to axes. Mica orientation shows the meniscus structure. Camera lucida drawing.

The mantle consists of tangentially orientated mica flakes, and varies considerably in its degree of development. The course of the trail is irregular, only following the same bedding plane for 5 – 10 mm. In many cases it crosses the bedding planes at right angles forming a ring of concentric, vertically orientated, mica flakes around the central mica free fill (fig. 8).

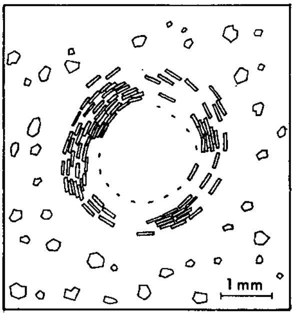

Fig. 8. Cross section of small meniscus filled tunnel, enlarged from fig. 3, showing mica orientation. The dotted line shows the limits of the light coloured fill. Camera lucida drawing.

The whole structure indicates a sediment feeder which has avoided mica. The animal has been an active digger, pressing mica into the side of the tube and leaving behind a regular backfill structure as it progressed through the sediment. This backfill generally consists of mica free faecal sediment which has passed through the animal. In places, however, the fill contains mica which reveals a meniscus structure. It can be assumed that this mica has been transported laterally (i. e. externally as opposed to internally) along the sides of the animal during periods of locomotion only, probably when the animal was searching for a nutrient-rich layer where it would resume eating and the production of a mica free, coprolitic fill.

Ichnogenus *Muensteria* Sternberg 1833

(figs. 1B, 9C)

Material: MMH 13050 from GGU Sample 137846 associated with *Planolites,* from same locality as *Ancorichnus ancorichnus,* above.
Description: In the two specimens which were found, the width is *c.* 2.5 cm and length is *c.* 15 cm. The cross section is probably subcircular, the upper half being unknown. The structure, which is rather vague and a little darker than the surrounding sediment, shows darker, curving, backfill menisci. Mica orientation is rather obscure except for certain places where the flakes can be seen to lie along the menisci. In the lateral part of the trail the mica flakes are orientated tangentially in a zone 2–3 mm wide.

The assumption that direction of sediment transport is parallel to the mica flakes (Heinberg, 1973) allows the interpretation that the lateral zone is the location of sediment transport along the sides of the animal as its body progressed forward.

There are no signs of an ‘anchor’-activity so the sediment transport is assumed to have been continuous, indicating a ‘hard’-bodied animal. This suggests that an echinoid may be a likely originator (cf. Reineck, 1968).

The absence of a central canal such as is found in burrows of *Echinocardium cordatum* and other spatangoids is considered to be due to the fact that these particular Jurassic burrowing echinoids were probably all shallow burrowers belonging to the order Cassiduloida (Kier, 1966).

Ichnogenus *Gyrochorte* Heer 1865

(fig. 1C)

Material: MMH 13051 from GGU Sample 137883, 1.5 km west of ‘top 530 m’, associated with *Ancorichnus ancorichnus* (for map see Håkansson *et al.,* 1971).
Description: The *Gyrochorte* trail is a penetrative structure producing positive epireliefs and negative hyporeliefs on successive bedding planes. The positive epirelief is a double ridge, and the corresponding negative hyporelief is a double furrow.

Width of the trail varies from 3–5 mm. *Gyrochorte* reaches its greatest known vertical extent, 16 cm, in specimens from the *Pecten* Sandstone elsewhere in Milne Land (Heinberg, 1973). The trail is curved sinuosly. The *Gyrochorte* trail, which was produced by an obliquely orientated organism moving horizontally through the sediment, is described in detail in Weiss (1940, 1941), Seilacher (1955) and Heinberg (1973). In the present study it has served as a useful indicator for 'way-up' of specimens not collected *in situ.*

DISCUSSION AND CONCLUSIONS

Comparison of the tunnels

The four tunnels comprising this ichnocoenose have in common a structure consisting of a central cylindrical fill, and a surrounding mantle or mica zone. However, they differ markedly with respect to (1) the origin of the central fill, (2) the origin of the mantle and (3) the nature of the junction between the mantle and the surrounding sediment, and between the mantle and the fill (fig. 9).

1. The fill. In *Ancorichnus* and *Muensteria* the central fill is a backfill made of sediment transported backwards along the sides of the animal. In *Ancorichnus* the progress of the animal is divided into two cycles because of the anchoring technique. On the other hand, progress in *Muensteria* was continuous, the sediment pas-

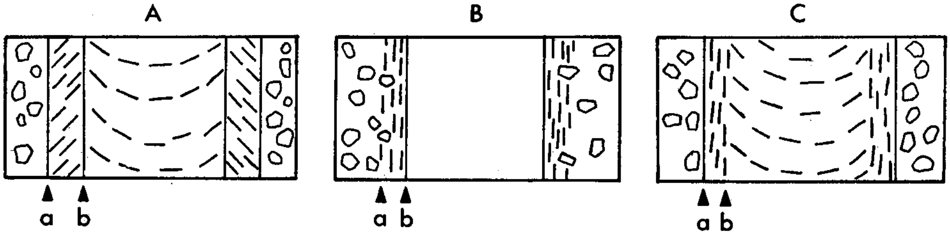

Fig. 9. Comparison of the structure of three tunnels. (Individual tunnels not to scale. Based on samples cited in text).

A. *Ancorichnus.* **a:** Distinct junction between the mantle and the surrounding sediment. **b:** Distinct junction between the mantle and the fill. The small arrows point in the direction of movement of the animal.

B. *Planolites.* **a:** Gradual junction between the mantle and the surrounding sediment. **b:** Distinct junction between the mantle and the fill. The direction of movement cannot be judged.

C. *Muensteria.* **a:** Distinct junction between the mantle and the surrounding sediment. **b:** Gradual junction between the mantle and the fill. The small arrows point in the direction of movement of the animal.

sing from front to rear without interruption. In *Planolites* the fill is coprolitic, i. e. the sediment has passed through the animal before packing behind.

2. The mantle. In *Ancorichnus* the mantle is produced by the *packing* of sediment against the anterior edge of a 'moving' anchor. In *Planolites* the mantle is formed by the *pressing* of mica into the wall of the tube at the anterior end of the animal prior to digestion of the sediment. The mica has not been transported along the animal. In *Muensteria* the mantle is produced by *gliding.* As the sediment was transported along the animal, mica flakes were orientated tangentially parallel to direction of movement.

3. The junction. Where the mantle is formed by packing *(Ancorichnus)* or gliding *(Muensteria),* there is a sharp junction between the trail and the surrounding sediment. The two types are distinguished by the orientation of the mica flakes, and the junction between the mantle and the fill. This junction is sharp in *Ancorichnus,* indicating a difference in time and mode of packing of the sediment on the two sides of that junction. In *Muensteria* the junction is indistinct owing to the transport of sediment from the mica zone into the meniscus. In *Planolites* the junction between the mantle and the surrounding sediment is vague because the mica flakes are pressed into the sediment. On the other hand, the junction between the fill and the mantle is sharp because of the lack of mica in the fill. The junction represents a time plane since mica flakes have been pressed into the wall at the anterior end of the animal at the same time as coprolitic fill was deposited in the tube at the posterior end.

The four tunnels in this assemblage therefore represent at least three basically different kinds of behaviour, reflecting three different ways of exploitation of the sediment for food. This may reflect a reduction of competition, allowing animals belonging to the same trophic group and with three *superficially* similar behavior patterns, to co-exist in the same environment.

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