

A *FAVREINA*-*THALASSINOIDES* ASSOCIATION FROM THE GREAT OOLITE OF OXFORDSHIRE

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ABSTRACT. The crustacean microcoprolite, *Favreina decemlunulatus* (Paréjas) is present in several beds of the Great Oolite Series at Kirtlington, Oxfordshire. It occurs in burrows of *Thalassinoides* type and was probably produced by a brachyuran crustacean. It is associated with a molluscan and annelid infauna in bioturbated sediments that have been interpreted as accumulating intertidally or just below low water mark (McKerrow *et al.* 1969).

THE ichnogenus *Favreina* Bronniman 1955 covers a variety of rod-like microfossils perforated by many fine calcite-filled longitudinal canals. Objects of this type have been described from many parts of the world, i.e. the Oligocene of Turkey (Altini, 1942), Jurassic of Switzerland (Joukowsky and Favre 1913), French Mesozoic (Cuvillier and Sacal 1956), Upper Jurassic and Lower Cretaceous of Cuba (Paréjas 1948, Bronniman 1955), and the Triassic to Miocene of the Middle East (Elliot 1962, 1963).

Recognition of the true nature of these objects, as crustacean faeces, was first made by Paréjas (1935, 1948) from the work of Moore (1932*b*) on recent forms.

We describe here the ichnogenus for the first time from Britain, on the basis of material from the Great Oolite Series (Jurassic, Bathonian) White Limestone and Forest Marble at Kirtlington Old Cement Works, Oxfordshire (National grid reference SP. 494199). This quarry has been described elsewhere (McKerrow *et al.* 1969).

The only previous records of faecal pellets of this type in Britain are from the Chalk (i.e. Type A faecal pellet of Wilcox 1953; see also Kennedy 1967*b*, p. 137, and Bromley 1967, p. 172), although unpublished observations suggest they occur at other localities in the Great Oolite and at other horizons in the Mesozoic.

SYSTEMATIC DESCRIPTION

Ichnogenus *FAVREINA* Bronniman 1955

Ichnospecies *Favreina decemlunulatus* (Paréjas) 1948

1948 *Coprolithus decemlunulatus* Paréjas, p. 519, figs. 46-8.

Emended diagnosis. *Favreina* with ten crescentic longitudinal canals. The pellet is ornamented externally by V-shaped transverse grooves.

Description of the Kirtlington specimens. The pellets are rod-shaped, up to 1 cm. long, 1 mm. in diameter, and circular in cross-section.

Externally (Pl. 99, fig. 2), there is a distinctive ornament of V-shaped transverse grooves.

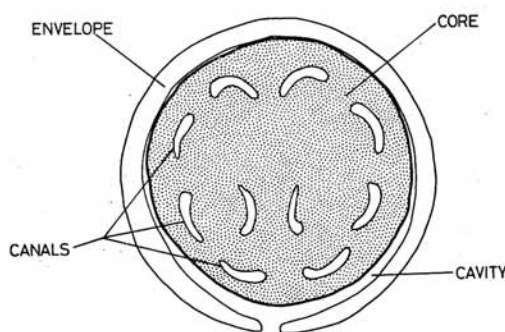
In section (Pl. 99, fig. 1, text-fig. 1), there is a distinct separation of the pellet into two zones, a central core and a surrounding envelope. The core consists of fine-grained carbonate sediment, the envelope of fine-grained calcite. They are distinguishable as a result of slight colour differences, the envelope being lighter than the core. The envelope may also be detached from the core around part of the pellet (Pl. 99, fig. 1).

There are ten crescentic calcite-filled canals in the core. They are arranged symmetrically into an outer ring of eight about a central pair (Pl. 99, fig. 1, text-fig. 1).

Discussion. *Favreina decemlunulatus* can be separated from all previously described *Favreina* and *Favreina*-like pellets by virtue of the form, number and arrangement of the canals (see Table 1 in Elliot 1962, also Elliot 1963, p. 299). It is also the only *Favreina* in which an external ornament has been noted.

Interpretation and occurrence. Faecal pellets of recent invertebrates have been described by a number of workers, i.e. Moore (1931*a, b*, 1932*a, b*) and Edge (1934).

It is clear from these works that only one group of animals, brachyuran crustaceans, could produce faecal pellets of *Favreina* type (Paréjas 1948, Bronniman and Norton



TEXT-FIG. 1. Diagrammatic cross-section of *Favreina decemlunulatus*. Actual diameter of pellet is 1.0 mm. approx.

1961, Elliot 1962, 1963). Here, material is passed down the stomach, and canals are produced by a system of fleshy processes which project inwards from the stomach wall. These processes are at first flanges, but traced posteriorly, they become detached from the stomach wall, projecting as fleshy cylinders.

As matter passes down the gut it is compacted around these cylinders, and faeces are voided with minute canals inside. When fossilized, these canals become filled with calcite, thus preserving traces of the passage of the soft parts of the animal concerned.

In the recent crustaceans, there is variation in the type of pellet produced, in particular in the number and distribution of canals. This is a reflection of specific and generic differences in stomach structure. In particular the Galatheidae produce a pellet which has a well-differentiated ventral cap. We had thought to interpret the separation of the Kirtlington pellets into core and envelope as a comparable phenomenon, presumably the result of a comparable sorting mechanism in the Jurassic animal, but Dr. A. Kendall (Reading University) has told us that petrographic studies on the White Limestone of the Cotswolds show that such envelopes occur on non-skeletal grains. He suggests that

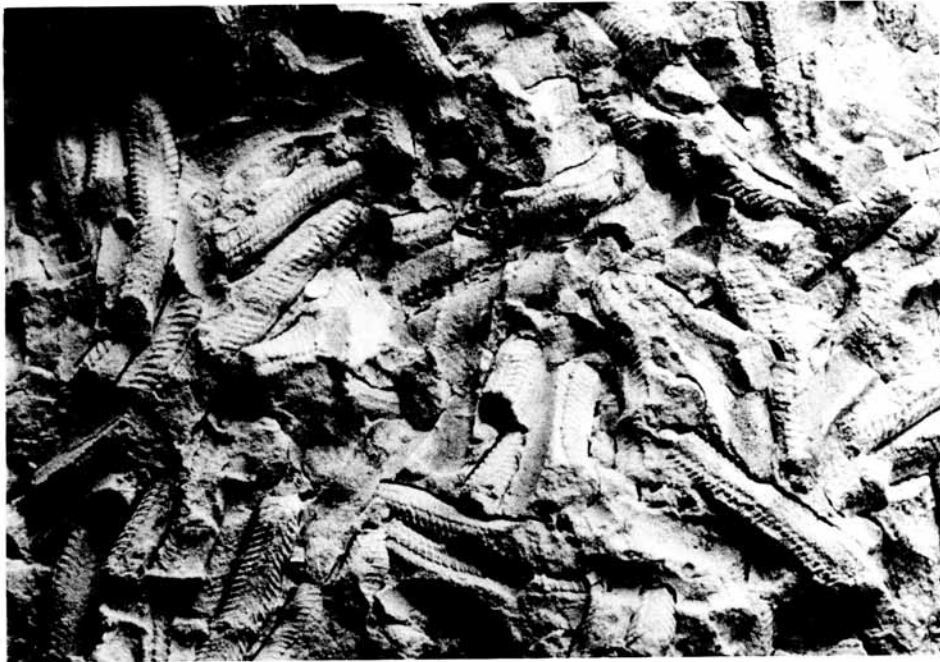
EXPLANATION OF PLATE 99

Fig. 1. Thin section of part of a *Favreina* packed burrow, $\times 6$.

Fig. 2. Fractured surface of a *Favreina* packed burrow showing external ornament of pellets, $\times 6$.



1



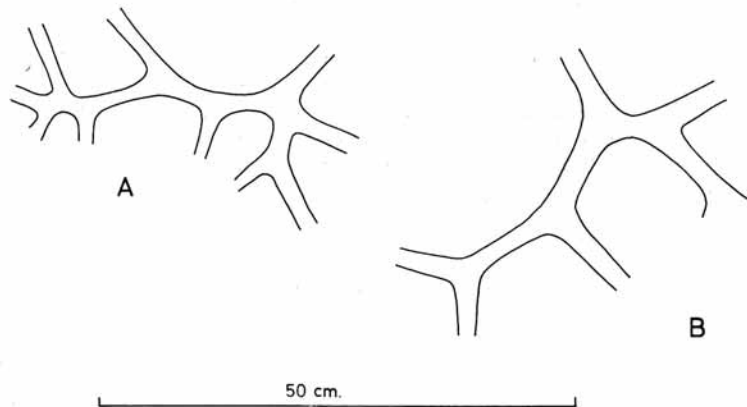
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KENNEDY, JAKOBSON and JOHNSON, *Favreina*

these envelopes are a diagenetic replacement of organic sheaths. In the case of *Favreina*, the sheath was probably a mucilaginous coat, present at the time of extrusion, but now replaced by calcite.

The remarkable ornament present on the 'solid' Jurassic specimens of *F. decemlumulatus* (the original account is based on sections of Oligocene material) is the first record of such structure in *Favreina*.

Pellets of recent brachyurans appear to be smooth; the ornament of our material may have been produced in the gut of the animal, but it seems more likely that it is the result



TEXT-FIG. 2. Sketch of *Thalassinoides* burrow systems on bottom surfaces of limestones from the basal Forest Marble, Kirtlington, Oxfordshire.

of a rhythmic contraction of the anus during defecation. Miller (1910) records such contractions in related crustacea.

F. decemlumulatus ranges throughout the whole of the White Limestone at Kirtlington although it is absent in some beds. It also occurs at the base of the Forest Marble (beds 3k, 4d, 6e, McKerrow *et al.* 1969).

Two modes of occurrence can be recognized, as loose pellets in sediment, and as closely packed masses which are clearly filled burrows (Pl. 99, figs. 1-2). In section, these burrows are elliptical, compressed parallel to the bedding, and have a breadth of from 2 to 5 cm. On bottom surfaces the burrows weather out, and have a striking polygonal branching form (text-figs. 2a, b).

The burrows lie horizontally, and branch at 5-15 cm. intervals, widening at the point of branching. Several levels of burrowing can be recognized, but burrows rarely cut each other; the sediment is not intensively disturbed.

These burrows can be referred to *Thalassinoides*. This ichnogenus was erected by Ehrenberg (1944), for ramifying burrow systems with Y-shaped branching points and local swellings, described by him from Miocene sands. These burrows were intimately associated with remains of *Callianassa*.

Subsequently, these burrows have been recorded from many horizons and lithologies; in the British Mesozoic they have been recorded by Hallam (1961), Farrow (1966), Kennedy (1967 *a, b*), and Bromley (1967). There is no doubt that these are crustacean burrows. In the Chalk they have been described associated with 'anomuran' faecal pellets (Kennedy 1967*b*, Bromley 1967), and inferred to be the products of sediment eating crustaceans.

This is also our interpretation of the *Favreina*-*Thalassinoides* association described here, although the dense packing of the burrows is unusual.

The only comparable examples of this type of which we are aware are *Ophiomorpha* ('*Halymenites*') burrows described by Brown (1939). These too are callianassid burrows (Häntzschel 1952), and the pellets appear to be of *Favreina* type.

That these pellets belong to some organism other than the excavator of the burrows is possible, but we see no evidence for this, i.e. traces of re-working within burrow fills.

The explanation of the filling is far from clear. The nature of the packing is such as to preclude a passive filling by pellets washing into burrows by current action. It seems that the animals stuffed their burrows with pellets, rather than moving them some distance to eject them at the surface.

CONCLUSIONS

Favreina and *Thalassinoides* occur associated in the Great Oolite Series at Kirtlington, Oxfordshire. This is in keeping with previous suggestions that both trace fossils are produced by anomuran crustaceans.

As with most other occurrences of these trace fossils (Kennedy 1967*b*) actual crustacean skeleta are rare in associated sediments. Three brachyurans are described from the Great Oolite Limestone of the Midlands by Woods (1925-31). These are the palinurids *Mecochirus clypeatus* (Carter) and *Glyphea regleyana* (Desmerest), and the astacurid *Eryma bedelta* (Quenstedt). Phillips (1871) also records *Glyphea rostrata* Phillips from Kirtlington.

Of these, *M. clypeatus* is of a suitable shape and size to have occupied our *Thalassinoides* burrows, and seems the most likely of the known crustacean fauna to have produced both burrows and faecal pellets. Some poorly calcified form, not preserved at all could equally have been responsible.

The beds in which the trace-fossils occur consist of shelly, oolitic, and marly limestones, often bioturbated, with a rich and variable fauna. Some beds, yielding brachiopods (*Epithyris*) and mytilid bivalves (*Modiolus*) are interpreted as subtidal channel fills; other beds, with infaunal bivalves and annelids represent tidal flat deposits (McKerrow *et al.* 1969).

The *Favreina* crustacean thus lived at, or close to low water mark; even if the animals colonized tidal flat environments, their burrows probably reached waterlogged sediments.

The extension of the recorded range of *Favreina decemlumulatus* into the Jurassic is not particularly remarkable. It does not automatically imply the altogether improbable occurrence of the same crustacean during 120 million years, rather it should be compared with the great time-range of other trace-fossils (Häntzschel 1962).

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