THE PRESERVATION OF MOULDS OF THE INTESTINE IN FOSSIL *NUCULANA* (LAMELLIBRANCHIA) FROM THE LIAS OF ENGLAND

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ABSTRACT. The paper describes specimens of *Nuculana* from the Lower Lias in which clear moulds of the coiled intestine are preserved. The Nuculacea are deposit feeders in which the stomach and intestine become filled with compacted sediment from which nutriment is derived. In the present instance the shells remained closed and unfilled by sediment after death, while impregnation of the intestinal moulds with ferruginous matter and their hardening seems to have taken place very rapidly. The rather complicated coiling of the intestines resembles that now characteristic of *Nucula* rather than of *Nuculana*, and seems to be a primitive feature. Longitudinal grooves on the moulds, corresponding to ridges on the interior of the actual intestine, are clearly preserved, and resemble those seen on the faecal pellets of modern *Nucula*. The species to which the specimens belong is described as *Nuculana (Dacryomya) gaveyi* sp. nov.

INTRODUCTION

MORE than a century ago G. E. Gavey (1853, p. 34), when listing the fossils he had collected from the railway tunnel (marked Campden Tunnel on modern maps) and cuttings between Chipping Campden and Mickleton, Gloucestershire, recorded the discovery of a series of specimens which he described as '*Nucula*; with cast of the intestinal canal present in most of the specimens'. The specimens came from shales belonging to the Zone of *Prodactylioceras davoei*, that is, from the top of the Lower Lias, as understood by British stratigraphers. Gavey acknowledged help from P. B. Brodie, H. E. Strickland, and T. Wright in the identification of his fossils, but it is uncertain if they saw these particular specimens. Remarkable as it was, the discovery attracted no attention, possibly because the recognition of casts of the intestinal canal was assumed to be an amateur's mistake. Even in so comprehensive a work as that of Abel (1935), which brings together much information on the evidence of the fossil record on the life processes of extinct animals, there is no reference to any comparable occurrence.

In 1956 the Rev. J. Crompton, O.B.E., then of Winterbourne Zelston, near Blandford, Dorset, presented to the British Museum (Natural History) a series of fossils from the Gavey Collection which had come into the possession of Mrs. Crompton, a granddaughter of their collector. It was while looking through this material that Messrs. C. P. Palmer and D. L. F. Sealy, of the Palaeontological Department of the Museum, discovered and called my attention to a series of small shells, recorded as coming from Mickleton Tunnel, which had been broken to disclose the presence of worm-like coils inside them. The presence of longitudinal grooves on the coils showed that these were not worm casts and at once recalled Moore's (1931) illustrations of faecal pellets of *Nucula* and other genera. Further investigation has confirmed the fact that Gavey, long before any detailed work on the feeding and digestive processes and organs of the Nuculacea had been carried out, or faecal pellets described, had interpreted the nature of the coils

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quite correctly. The specimens containing the fossil intestines belong to a species of *Nuculana* which, although quite well known, has had no valid name, so that it is here described as *Nuculana* (*Dacryomya*) *gaveyi* sp. nov. Specimens of this species from the same bed, with the shell complete, were acquired from Gavey long ago by the British Museum (Natural History) and the Geological Survey, and with them, in the collection of each Museum, was found a single broken specimen in which the intestine is just visible. Evidently, however, Gavey had not parted with the best specimens illustrating his remarkable find.

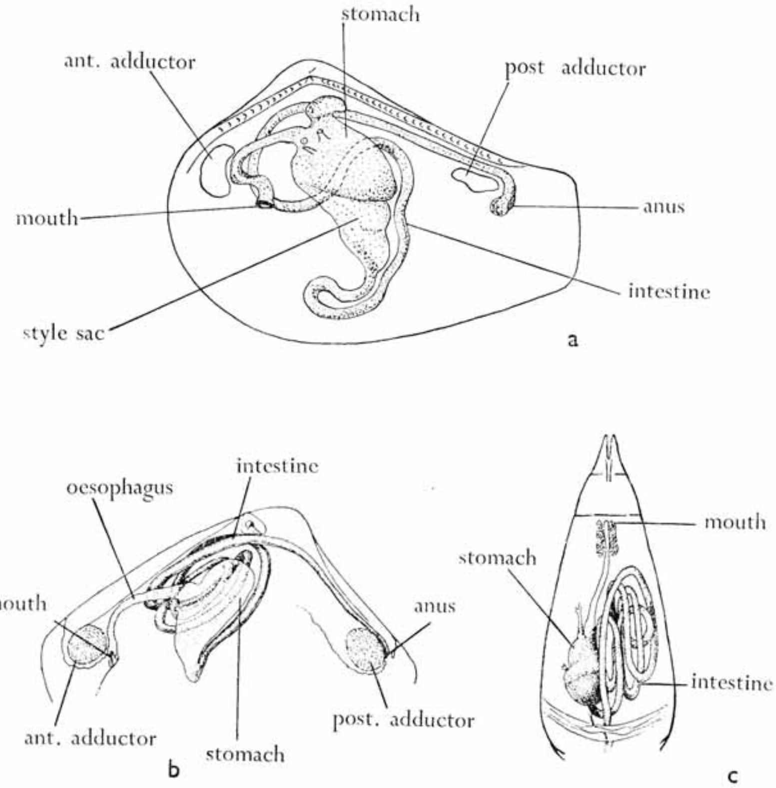
FEEDING HABITS AND DIGESTIVE SYSTEM OF THE NUCULACEA

The most important papers on the general anatomy of the Nuculacea are those of Pelseneer (1891), Drew (1897), Stempell (1898), and Heath (1937). Yonge (1939) has given a valuable account of the mode of life and the mechanisms of respiration, feeding, and excretion in several genera belonging to the superfamily. Caspers (1940) has described experiments on the feeding habits of *Nucula*, but his observations have been considered of little value by Owen (1956) in an interesting paper on the stomach and digestive processes in the Nuculidae.

The Nuculacea live on a sea bottom of mud or muddy sand, burrowing into it until the shell is just or almost covered by the sediment, and feeding while so buried. According to Yonge's observations, *Nucula* buries itself with its antero-dorsal margin nearly horizontal and its short posterior end pointing obliquely downwards, its exhalant current (the animal has no siphons) reaching the surface of the substratum by a small pit formed by expulsion of water from the shell. Forms such as *Nuculana* and *Yoldia*, in which the shell is elongated posteriorly and often rostrate, and in which the animal has inhalant and exhalant siphons, usually burrow with their long axis vertical or steeply inclined, the tips of their siphons, and sometimes also the posterior end of the shell, just protruding above the surface of the substratum.

The mouth is situated near the anterior adductor muscle, on its posterior or postero-ventral side. Extending backwards from it on each side are large, paired, flap-like structures, the labial palps, here developed as palp-lamellae, and, attached to the postero-dorsal corner of each outer lamella, is a feeler-like process, known as a palp proboscis, which is capable of extending far beyond the shell margins, and has at its proximal end a small receptacle known as the palp pouch. The Nuculacea are essentially deposit feeders, material suspended in the inhalant current contributing very little to their food. During feeding the palp proboscides are extended between the opened shell valves and grope about (within the sediment in the case of *Nucula* and over its surface in the case of *Nuculana*) for food. The material collected at the tip of each proboscis passes along a ciliated groove in the latter to its proximal end, and thence by way of the palp pouch to the palp lamellae. It is then conveyed between these, still by ciliary action, to the mouth, a certain amount being sorted out in the process and carried to the edges of the lamellae, where it is rejected. The material that finds its way from the mouth through the rather short oesophagus to the stomach includes sand grains and more finely divided mineral matter, together with living organisms and organic detritus. In freshly caught animals the stomach is invariably distended.

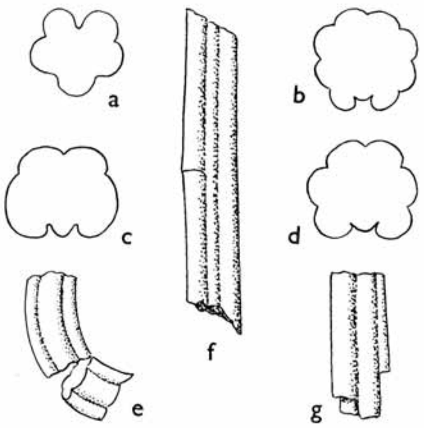
The stomach consists of a globular dorsal region and, below, of a large, tapering, funnel-shaped ventral region, termed the style sac, although a crystalline style is absent. The intestine emerges from the ventral end of the style sac. Digestion takes place by means of secreted enzymes, which are thoroughly mixed with the food-bearing matter by the rotating action of cilia of the style sac. The soluble products of digestion are absorbed by the epithelium of the stomach and intestine. The compacted faecal mass is



TEXT-FIG. 1. Alimentary canal in modern Nuculacea. *a*, *Nuculana sulculata* (Gould), ×10 (after Stempell, slightly modified). *b*, *Acila fultoni* (Smith), ×1·8 (after Heath). *c*, *Nucula taeniolata* Dall, ×6 (after Heath).

allowed to enter the latter periodically by relaxation of a sphincter muscle. In the Nuculidae the intestine, illustrations of which are here reproduced (text-fig. 1*b*, *c*), is long and rather complicated. After leaving the style sac it bends in a dorsal direction past the posterior side of the stomach, and then takes an anterior course; it next describes a series of coils before merging into the relatively straight rectum, which leads to the anus on the posterior side of the posterior adductor. About mid-way along the intestine in most species, and in two or more places in some, there is a sharp backward bend so that the direction of coiling is reversed. The coils lie more to the right-hand side of the sagittal plane of the animal, while the stomach lies more to the left-hand side (text-fig. 1*c*). In *Nucula nucleus* (Linné) there are about four coils, but in *N. cancellata* Jeffreys, as figured by Heath (1937, pl. 1, fig. 2), there are about nine, with three sharp reversals of the direction of coiling. Heath found that in *Nucula* the coiling is most complicated in species living at the greatest depths, and thought that this might be because the amount of nutritive material in the sediment decreases with depth, so that a greater length of intestine is necessary for its absorption.

In living Nuculanidae and Malletiidae the intestine is less complicated and varied than in the Nuculidae. In *Nuculana sulculata* (Gould) (text-fig. 1*a*), from the coast of Chile,



TEXT-FIG. 2. Faecal pellets of *Nucula* seen in cross-section or in side view. *a*, *N. tenuis* (Montagu), × 100. *b*, *N. sulcata* Bronn, × 100. *c*, *N. nitida* G. B. Sowerby, × 100. *d*, *N. nucleus* (Linné), × 100, *e*, *f*, *g*, *N. nucleus* (Linné), × 40. (After H. B. Moore.)

it bends back and up, remaining close to the posterior side of the stomach, and then bends forward, passing the stomach on the right-hand side, until it almost reaches the anterior adductor, and finally bends round again, occupying a dorsal position until it terminates, behind the posterior adductor, at the anus. In *Nuculana minuta* (Müller), from Norway, as figured by Yonge (1939, p. 96, fig. 14) its general course is almost exactly the same.

The intestine in the Nuculacea has thickened longitudinal ridges bearing long cilia. The faeces are voided as rods of compact mud which break up into faecal pellets up to about 1 mm. in length and bear longitudinal grooves which are impressions of the intestinal ridges. Moore (1931), some of whose illustrations are reproduced as text-fig. 2, has recorded that in British species of *Nucula* the number of ridges ranges from five to nine. Galliher (1931) has figured faecal pellets of *Acila castrensis* (Hinds). So far as I know, the faecal pellets of *Nuculana* have not yet been illustrated. Moore states that the diameter of the faecal pellets of a *Nucula* with a shell 1 cm. long is 0·15 mm. Schenck

(1936, p. 12) records that the diameter of faecal pellets from shells of *Acila castrensis* (Hinds) 14·5 mm. long may be as much as 0·8 mm. In Heath's (1937) figures of *Acila* the diameter of the intestine is represented as being 0·7–0·8 mm. in shells about 30 mm. long. Its diameter in a specimen of *Nuculana sulculata* (Gould) figured by Stempell (1898, pl. 24, fig. 24), whose illustration is here reproduced (Text-fig. 1*a*) appears to have been about 0·2 mm. for a shell only 6 mm. long, and in a specimen of *Yoldia thraciaeformis* (Storer) 37 mm. long the corresponding diameter, according to Heath's illustration (1937, pl. 9, fig. 78), was as much as 1·0 mm. Moore states that faecal pellets of *Nucula* are still well enough preserved for specific identification after fifty years on the sea-floor, but Galliher and Schenck found them to be much less permanent.

From these facts it may be seen that there is a remote possibility of the preservation fossil of the compacted mass of mainly argillaceous material that occupies the intestine and much of the stomach in the Nuculacea, when the actual organic tissues have decayed away, although usually it would become obscured by or mixed with the very similar sediment which would fill the shell after the death of the animal. The possibility of the occasional preservation of faecal pellets in sedimentary formations would appear to be much less remote. Dr. R. Casey has called my attention to a paper by Stoyanow (1949) in which (p. 63, pl. 8, figs. 5, 7, 8) three supposed faecal pellets, found near a specimen of that author's species *Acila* (*Truncacila*) *schencki*, are described from the Lower Cretaceous of Arizona. The objects in question, however, are about 2 mm. in diameter and the shell only 14 mm. long, so that considerable doubt remains as to their identity, as comparison with the measurements cited above will show. I know of no other published record of fossil faecal pellets.

DESCRIPTION OF THE FOSSIL SPECIMENS FROM MICKLETON TUNNEL

The material consists of about twelve shells broken open by Gavey to show the coiled intestine inside and seven more completely dissected coils. In addition there are a number of complete bivalve specimens from the same locality and horizon, together with part of a small ironstone nodule containing a cluster of specimens, one broken to show the coiled intestine inside. In this nodule (Pl. 40, fig. 3), presumably one of several from which Gavey obtained his specimens, the shells lie in all directions. There is no question of their being preserved in the original position of growth. They are hollow except for a varying amount of ferruginous matter which has been deposited inside them and serves to cement the fossil intestines in the positions which they occupy. Presumably, as the result of some disturbance, the molluscs, while still living, were swept together on the sea-floor with their valves closed for protection, and very soon afterwards were

EXPLANATION OF PLATE 40

Figs. 1–6. *Nuculana* (*Dacryomya*) *gaveyi* sp. nov., from the uppermost Lower Lias of Mickleton Tunnel, Glos. 1, Interior of a right valve (Brit. Mus., LL. 8232), with coils of intestine partly embedded in ferruginous matter; ×9. 2, Interior of a right valve (LL. 8231), showing coils of intestine. The chondrophore is visible, but the hinge-teeth are hidden by a piece of shell broken away from the other valve: ×10. 3, Fragment of ironstone nodule containing several specimens, one broken to show coiled intestine inside (L. 6556); ×4. 4*a*, *b*, Holotype (LL. 8226), ×3. 5, Interior of a left valve (LL. 8233), with hinge-line broken away. The intestine ends near the top left-hand corner of the figure, very close to the position of the anus in modern *Nuculana*; ×9. 6, Interior of fragment of a left valve (LL. 8238), showing coils of intestine; ×14.

subjected to the action of iron-bearing waters; concretions were formed with clusters of the shells as nuclei, and at the same time the intestinal moulds became impregnated with ferruginous matter and hardened. Within most of the shells the coils, some of which are now cemented to the right valve and some to the left, have been displaced to some extent from the positions which they occupied during life, but in one specimen (Pl. 40, fig. 5) the last, straight part of the intestine can be clearly seen to run just below the postero-dorsal margin and terminate near what must have been the position of the posterior adductor muscle. This same feature is visible, although less clearly, in at least two other specimens. In one or two cases the intestine originates in a globular or pyriform mass which appears to be the internal mould of the stomach or part of it.

A most interesting fact is that these intestines, with their somewhat complicated series of coils, more closely resemble those of modern species of *Nucula* than of *Nuculana*. The number of coils is about three, and a crossing over and reversal of direction of the intestine is seen near the middle of its length (Pl. 40, fig. 6), as in Recent *Nucula*. Of great interest is the presence of a series of longitudinal grooves exactly like those on the faecal pellets of modern *Nucula*. The number of grooves appears to be seven; the deepest and broadest lies on the concave side of the coil, and the remainder are almost equal in depth and spacing. The diameter of the intestinal moulds ranges from about 0·2 mm. to 0·45 mm. This measurement agrees quite well with the intestinal diameter in Recent species of *Nucula* and *Nuculana* of comparable size.

DESCRIPTION OF THE SPECIES IN WHICH THE FOSSIL INTESTINES ARE PRESERVED

Family NUCULANIDAE
Genus NUCULANA Link 1807
Subgenus DACRYOMYA Agassiz 1840
Nuculana (*Dacryomya*) *gaveyi* sp. nov.

Plate 40

1833 *Nucula inflata* Sow.; Zieten, *Versteinerungen Württembergs*, p. 77, pl. 57, figs. 4*a–c* (*non* J. de C. Sowerby 1827).

1837 *Nucula acuminata* v. Buch; Goldfuss, *Petrefacta Germaniae*, 2, p. 155, pl. 125, figs. 7*a–c* (*non* Zieten *ex* v. Buch MS. 1833).

1853 ?*Nucula inflata* Zieten; Oppel, *Württemb. naturwiss. Jahreshefte*, 10, p. 122, pl. 4, fig. 24.

1855 *Arca* (*Nucula*) *minor* Simpson, *Fossils of Yorkshire Lias*, p. 115 (*non Arca minor* v. Hagenow 1842).

1856 *Nucula acuminata* Quenstedt, *Der Jura*, p. 187, pl. 23, fig. 14.

1869 *Leda acuminata* (v. Buch); Dumortier, *Études paléontologiques. Lias-moyen*, p. 259, pl. 30, fig. 3.

1871 *Leda zieteni* Brauns, *Der untere Jura im nordwestlichen Deutschland*, p. 373 (*non Leda zietenii* d'Orbigny 1850).

1876 *Leda minor* (Simpson); Tate, *in* Tate and Blake, *Yorkshire Lias*, p. 383, pl. 11, fig. 9.

1876 *Leda zieteni* Brauns; Tate, op. cit., p. 383.

1883 *Nucula inflata* Zieten; Langenhan, *Versteinerungen des Lias am Grossen Seeberge bei Gotha*, pl. 3, figs. 33*a*, *b*.

1918 *Leda minor* (Simpson); Richardson, *Trans. Woolhope Nat. Fld. Cl.* (for 1916), p. 150, pl. 155, fig. 1.

1935 *Leda zieteni* Brauns; Kuhn, *Neues Jb. Miner.*, Beil.-Bd. 73, p. 475, pl. 18, figs. 8*a*, *b*.

Holotype. Brit. Mus. (Palaeont. Dept.) no. LL. 8226, from the uppermost Lower Lias (*Prodactylioceras davoei* Zone) of Mickleton Tunnel, near Chipping Campden, Gloucestershire.

Description. Of medium size for the genus, longitudinally pyriform, not greatly elongated, gibbose, with submedian, moderately prominent, incurved, opisthogyrous umbones; posterior extremity narrow, subrostrate. Antero-dorsal outline convex, merging in an even curve with the strongly convex anterior margin, which is continued by the evenly and rather strongly convex ventral margin. Escutcheon cordiform, unimpressed, not limited by distinct umbonal ridges; postero-dorsal margin visible in side-view of shell except where the umbonal region projects to a moderate extent above it. Hinge with about ten teeth on each side of a projecting, spoon-like chondrophore. Pallial line without sinus. Shell with nacreous inner layer.

Measurements of holotype. Length 8·3 mm., height 6·0 mm., inflation 4·6 mm.

Remarks. I have described *Nuculana gaveyi* as a new species instead of publishing the name as a *nomen novum* for either of the homonyms (*minor* Simpson and *zieteni* Brauns) cited in the synonymy, as no type specimen would have been available if the latter course had been adopted. It is probable that several specimens in the Whitby Museum identified as *Leda minor* are Simpson's unfigured syntypes, but they are not so labelled. The holotype of *N. gaveyi* and a number of topotypes in the collections of the British Museum (Natural History) and the Geological Survey had been identified as *Nuculana minor*, and, after comparing them with specimens of Simpson's species from Yorkshire I agree that they are conspecific with them. Moreover, comparison of the Gloucestershire specimens of *N. gaveyi* with the above-cited illustrations of Zieten, Goldfuss, Quenstedt, and Kuhn of the species from Germany to which Brauns assigned the name *Leda zieteni* has revealed no differences of specific importance. Tate recorded both *Leda minor* and *L. zieteni* from the Yorkshire Lias, supposing the former to occur in slightly higher zones than the latter, but he hinted that they might prove to be the same species.

I have commented previously (Cox 1940, pp. 27, 28) on the presence of nacre in Jurassic Nuculanidae (in modern species of the family the shell is porcellanous), and also on the frequent absence of a pallial sinus (one is present in the modern representatives). Brauns also mentioned the entire pallial line when describing *L. zieteni*. The feature is clearly seen in specimens of *Nuculana gaveyi* from Mickleton Tunnel in the British Museum (Natural History) (reg. no. L. 17905).

Occurrence. Lower and Middle Lias (*oxynotum-margaritatus* Zones) of Yorkshire, Lincolnshire, Northamptonshire, Oxfordshire, Warwickshire, Gloucestershire, Somerset, and Raasay (Inner Hebrides). It is probable that records of '*Leda minor*' from the Upper Lias of Gloucestershire refer to *Nuculana rostralis* (Lamarck) or to *N. claviformis* (J. de C. Sowerby). Specimens in the Geological Survey Museum said to come from the *semicostatum* Zone of Scunthorpe, Lincs., are from a much lower zone than any others seen. Brauns records that in north-west Germany the species occurs in the *davoei* and *margaritatus* zones.

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