A NEW JURASSIC SCAPHOPOD FROM THE OXFORD CLAY OF BUCKINGHAMSHIRE

by CHARLES PHILIP PALMER

ABSTRACT. A new fossil scaphopod *Prodentalium calvertensis* from the middle Callovian, *Coronatum* Zone, of Calvert, Buckinghamshire, is described and assigned to the genus *Prodentalium*. It is suggested that this essentially Palaeozoic genus ranged into the Mesozoic and was there replaced by *Fissidentalium*, and that the two genera formed an evolutionary sequence.

The association, with *P. calvertensis*, of the foraminiferan *Epistomina* is taken to indicate that these probably formed part of the diet of the scaphopods. Arguments, based on comparative shell morphology of *Prodentalium* and *Fissidentalium*, suggest that *P. calvertensis* lived at a depth in excess of 200 m in the Oxford Clay sea.

STRATIGRAPHY AND LOCATION

The material forming the subject of this report was collected by Mr. Keith Duff (Department of Geology, University of Leicester) from Bed 6 (Callomon 1968, p. 286) in the Lower Oxford Clay at Calvert Pit in Buckinghamshire (G.R. SP 6723).

The bed consists of a light fawny-grey shale lying between two pyritic 'Nucula' beds and includes ellipsoidal septarian nodules at the top. Callomon (1968) placed this bed in the Obductum Subzone of the Coronatum Zone, Callovian Stage, and records from it the ammonites Kosmoceras obductum, K. castor, and K. gulielmi. Other fossils occurring in the bed with the scaphopods are: the nuculoid Mesosacella morrisi (Deshayes), Inoceramus sp., fragments of Bositra buchi (Roemer), a small axially ribbed rissoid gastropod, and fish scales. Scattered throughout the bed, and sometimes concentrated into dense patches, are abundant tests of the foraminiferan Epistomina.

GENERIC ASSIGNMENT

The small (<15 mm) scaphopods are longitudinally sculptured with numerous unequal, and unsymmetrically placed, riblets. This character relates them to the *Prodentalium-Fissidentalium* group, and distinguishes them from the *Dentalium-Paradentalium-Tesseracme* group which have a symmetrical arrangement of primary ribs, and secondary riblets. None were seen to have an apical notch or fissure, the absence of which indicates a closer affinity with the palaeozoic genus *Prodentalium* with its simple apex, than with the essentially Cainozoic genus *Fissidentalium*, the apex of which is fissured.

These scaphopods are, however, considerably smaller than the average Palaeozoic *Prodentalium*, barely reaching a length of 15 mm; Emerson (1961, p. 467) records some species of *Prodentalium* which reach a length of 200 mm. Nevertheless, in all other respects, these small scaphopods are related by their shell characters to *Prodentalium* rather than to *Dentalium*.

SYSTEMATIC DESCRIPTION

Genus Prodentalium Young, 1942

Type species. Prodentalium reynardi Young, 1942.

Prodentalium calvertensis n. sp.

Plate 52, figs. 1-11

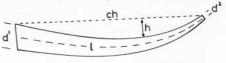
Diagnosis. Small, <15 mm, dentaliid with numerous unequal and unsymmetrically placed riblets, and a simple apex. Differing from palaeozoic species of *Prodentalium* in its smaller size and sharper ribs, and from the Lower Jurassic *Prodentalium*? *liassicum* (Moore) in having about forty-four riblets at the aperture (compared with 'twenty-four longitudinal ridges at rather irregular distances' (Moore 1867, p. 202)).

Material. Eleven moderately well-preserved, but crushed, shells from the Lower Oxford Clay (Callovian) of Calvert, Buckinghamshire.

Holotype. B.M. (N.H.) GG 13330 (Pl. 52, fig. 11). Paratypes. B.M. (N.H.) GG 13331-13339 (Pl. 52, figs. 1-10).

Description. The shells, being more or less crushed at the aperture, required that the original diameter be reconstructed from $2W/\pi$ where W= width of crushed shell. It is probable that some of the shells were crushed in a dorso-ventral position so that figures indicating arcuation (text-fig. 1) under column h below are probably more diverse than they would be in an uncrushed sample.

It should be noted that arcuation, as used in this report, is only a rough measure of 'curvature' and not the Curvature of mathematicians; and also the statistics on text-fig. 1 are not identical to those of Henderson (1920) or Fantinet (1959).



E, expansion rate of shell = $\frac{d^{1}-d^{2}x100}{l}$ % A, arcuation of shell = $\frac{h \times 100}{l}$ %

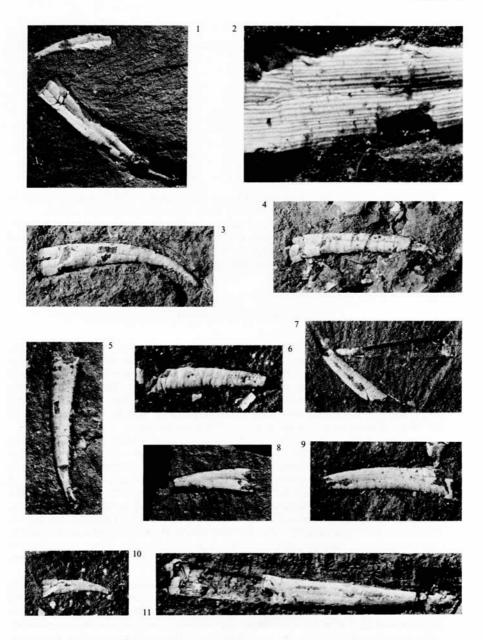
TEXT-FIG. 1. Explanation of the terms Expansion (E), and Arcuation (A), as used in this report.

E is the difference between the apertural diameter d^1 and the apical diameter d^2 , expressed as a percentage of the length of the tube (l).

A represents the maximum distance from the dorsal surface of the shell to the chord connecting d¹ and d², expressed as a percentage of the length of the chord.

EXPLANATION OF PLATE 52

Figs. 1–11. *Prodentalium calvertensis* sp. nov., from Bed 6, Lower Oxford Clay, Calvert Pit, Buckinghamshire. G.R. SP 6723. 1–10, paratypes, B.M. (N.H.) GG 13331–13339; 11, holotype, B.M. (N.H.) GG 13330. Magnifications: 1, 3, 6, c. ×5·3; 4, 5, 7–10, c. ×6·6; 2, enlarged section of specimen in 1, c. ×31.



PALMER, Prodentalium calvertensis

The following table of dimensions in millimetres represents the best readings possible. Key to notation in text-fig. 1.

ch	h	1	d^1	d^2	ribs, increasing to		
7.0	0.7	7.5	0.7	0.4	18	,,	44
6.5.	0.5	7.0	0.7	0.4	18	,,	44
8.0	1.0	9.0	0.83	0.4	20	,,	48
7.5	0.4	8.0	0.76	0.3	20	,,	40
7.5	0.3	8.0	0.76	0.3	20	,,	40
8.5	0.8	9.0	0.96	0.4	24	.,	40
5-8	0.3	6.1	0.76	0.4	16	**	38
14.8	0.3	15-1	0.96	0.3	18	**	56
7.6	0.5	8.0	0.7	0.3	16	**	44

Calculations of arcuation yielded a mean figure of A = 7.9%, and the mean of expansion rates was E = 5.1%. The apices were, in all observed cases, simple.

The very fine riblets increase by intercalation so that the density of ribbing remains more or less constant along the length of the tube. The riblets are crossed by lines of growth, about twelve to the millimetre at about 0.7 mm diameter, which run obliquely backward dorso-ventrally. In some specimens these growth lines give the shells a slightly cancellated appearance.

PALAEOECOLOGY

Diet

The scaphopods are randomly distributed, sometimes two to three close together, but usually lying 2-7 cm apart. Associated with them are tests of the foraminiferan *Epistomina* sp. (cf. Barnard 1953, p. 193, fig. A, 7a-c) which are more or less evenly distributed except for scattered patches of concentrated tests. These concentrations are often associated with the shells of *P. calvertensis* (Pl. 52, figs. 1, 4, 6, 10) but not always so. The suggestion that these foraminiferans formed the major part of the

diet of P. calvertensis is supported by the following records.

More than a century ago Clark (1849, p. 323) recorded six forms of foraminiferan from the 'stomach' of *Antalis vulgare* (da Costa) together with the small bivalve *Kellia suborbicularis* (Montagu) and juvenile *Goodalia triangularis* (Montagu). Jeffreys (1882, p. 658) stated that the 'stomach' of *Antalis vulgare* was a 'repertory of littoral Foraminifera' but did not specify which species they were. Pilsbry (*in* Pilsbry and Sharp 1897, p. vi) described the captaculae as '-prehensile, catching foraminifera, etc., upon which the Scaphopod feeds'. Morton (1959, p. 232) recorded four genera of Foraminifera from the proboscis of *Antalis entalis* (Linné), these being *Elphidium*, *Quinqueloculina*, 'Discorbis, and the empty test of *Globigerina*. These records alone confirm that scaphopods are basically carnivorous and will take Foraminifera when they are available.

Dinamani (1954) observed the feeding habits of *Dentalium conspicuum* Melville, and described how the animals used their captaculae to carry organic matter to the proboscis. Although he reported no foraminiferans from the stomach and intestines of the animals he studied he did observe 'large diatoms, single algal cells, and unidentifiable particles of detritus'. He described in detail how the captaculae transport,

along ciliated tracts, deposit-particles which accumulate just inside the mantle fringe in a longitudinal furrow on the dorsal side of the foot. Some selection takes place here, probably by the frilly lips of the proboscis, and acceptable food particles pass into the proboscis and thence into the stomach. Dinamani's final observation may also explain the patches of concentrated foraminiferan tests associated with *P. calvertensis* in the Oxford Clay. 'Periodically the foot is withdrawn completely, the mantle fringe is drawn across the aperture and a small mass of rejected matter is found to accumulate near the anterior pallial pore, which is pushed out by the foot during its next emergence' (Dinamani 1954, pp. 3–4).

In collecting Foraminifera it seems probable that the 'conveyor-belt' system described by Dinamani is not very selective and that some empty tests must accumulate on the foot of the scaphopod, together with live material. Selection then results in transference of live specimens, or acceptable material, into the proboscis; but as Morton recorded an empty test of *Globigerina* in the proboscis of one of his animals it is clear that the selection is not infallible. However, Dinamani's observations seem sufficient to support the suggestion that the concentrated accumulations of foraminiferans associated with *P. calvertensis* are simply those empty tests of *Epistomina*

collected by the captaculae and finally ejected by the foot.

Depth

A hint as to the depth at which these scaphopods lived in the Oxford Clay sea is offered by comparative shell morphology. The argument is tenuous and the con-

clusion no more than a low probability.

Modern ribbed dentaliid scaphopods (excluding Antalis and Graptacme) may be divided into two categories; Dentalium (s.s.), Tesseracme, and Paradentalium which have a symmetrical arrangement of primary and secondary ribs and riblets; in contrast Fissidentalium, Compressidentalium, and Compressidens have an unsymmetrical arrangement of many unequal riblets. The first group is usually found at depths which, in round figures, range between 20 m and 2000 m (Pilsbry and Sharp 1897, pp. 1–30). The second group, with which the fossil Prodentalium must be associated, is generally found between 200 m and 2000 m (Ludbrook 1954, pp. 99–102). These figures suggest that P. calvertensis may have lived in the Oxford Clay sea at depths of at least 200 m.

EVOLUTION

According to Emerson (1961, p. 466, and fig. 2) the genus *Prodentalium* ranges from the Devonian to the Permian, while *Fissidentalium* ranges from the Cretaceous to Recent; today some forty-four species of the latter are found in relatively deep waters in the Atlantic and Indo-Pacific provinces. Both genera are characterized by having numerous unsymmetrically placed riblets; *Fissidentalium* is distinguished by the development of a long apical fissure. Study of these two genera strongly suggests that they are more closely related to each other than to, say, *Dentalium* (s.s.), *Tesseracme*, or *Paradentalium*; and that *Prodentalium* was probably ancestral to *Fissidentalium*.

Adoption of this view is frustrated by a gap during the Triassic and Jurassic periods. Of the sixteen described species of Triassic scaphopod known to me none have the characteristic ribbing of the *Prodentalium-Fissidentalium* group. However, in the

Jurassic two forms have it and these are 'Dentalium' liassicum Moore and Prodentalium calvertensis; the former is from the lower and the latter from the upper Jurassic. These two examples indicate that a Prodentalium-Fissidentalium sequence is possible and might be given equal consideration with Emerson's Prodentalium-

Dentalium sequence which is outlined below.

Emerson (1961, p. 463) expressed the view that 'the available data indicates the development of two major lines of descent, namely *Plagioglypta-Fustiaria* and *Prodentalium-Dentalium* sequences'; he also suggests that the latter sequence may be linked by the genus *Antalis*. No quarrel is offered against a *Plagioglypta-Fustiaria* sequence except that the present writer has expressed the view (1974) that Emerson's taxon '*Fustiaria* sensu lato' is better regarded as of the family Laevidentaliidae. On the other hand, the sequence *Prodentalium-Dentalium* presents many difficulties since the type species of *Prodentalium* has about 80 irregular and unsymmetrically placed riblets, while the type species of *Dentalium* has about 10 symmetrically placed ribs with concave interspaces. These differences, not only in the number of ribs but also in their character, are considerable and consequently a *Prodentalium-Fissidentalium* sequence is here suggested as an alternative. The type species of *Fissidentalium* has about 26 riblets at the apex increasing to about 75 irregular riblets at the aperture. It seems to differ from *Prodentalium* only in the presence of an apical fissure and appears a more likely direct descendant than *Dentalium*.

If this view is correct then it is relatively easy to derive the symmetrically ribbed scaphopods, centered on *Dentalium*, from the *Prodentalium-Fissidentalium* sequence somewhere in the late Cretaceous or early Palaeogene without the embarrassment of *Antalis* acting as an intermediate between *Prodentalium* and *Dentalium* during the Mesozoic. The type species of *Antalis* is *Dentalium entalis* Linné (Emerson 1961, p. 470), a Recent, virtually smooth, species with an apical notch and living in northern British waters. It is not easy to apply the genus *Antalis* to fossil scaphopods earlier than the Cainozoic. Below the Palaeocene partly or faintly ribbed scaphopods resemble *Antalis* only very remotely and reference of these to that genus is probably

incorrect.

CONCLUSIONS

The genus *Prodentalium* ranges beyond the Palaeozoic and at least into the Jurassic. The probability that a *Prodentalium-Fissidentalium* sequence gave rise to *Dentalium* and allied forms in the late Cretaceous is here offered as an alternative to Emerson's postulated *Prodentalium-Dentalium* sequence.

Prodentalium calvertensis probably had the foraminiferan-eating habit of many living scaphopods and it is suggested that it may have lived at a depth in excess of

200 m in the Oxford Clay sea.

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REFERENCES

BARNARD, T. 1953. Foraminifera from the Upper Oxford Clay (Jurassic) of Redcliff Point, near Weymouth England. *Proc. Geol. Ass.* **64** (3), 183–197.

CALLOMON, J. H. 1968. The Kellaway Beds and the Oxford Clay. *In* SYLVESTER-BRADLEY, P. C. and FORD, T. D.

(eds.). The Geology of the East Midlands. Leicester, pp. 264-290.

CLARK, W. 1849. On the animal of Dentalium Tarentimum [sic.], Ann. Mag. nat. Hist. (ser. 2), 4, 321-330. DINAMANI, P. 1954. Feeding in Dentalium conspicuum. Proc. malac. Soc. Lond. 36 (1), 1-5.

EMERSON, W. K. 1961. A classification of the scaphopod mollusks. J. Paleont. 36, 461-482, 5 plates.

FANTINET, D. 1959. Contribution à l'étude des Scaphopodes fossiles de l'Afrique du Nord. Publs. Serv. Carte géol. Alger., (n.s.) Paléontologie, Mem. 1, 1-112, 12 plates.

HENDERSON, J. B. 1920. A monograph of the East American scaphopod mollusks. Bull. U.S. natn. Mus. 111, 1-177, 20 plates.

JEFFREYS, J. C. 1882. On the Mollusca procured during the 'Lightning' and 'Porcupine' Expeditions, 1868–70 (Part v). *Proc. zool. Soc. Lond.* (for 1882), 656–687, 2 plates. LUDBROOK, N. H. 1954. Scaphopoda. John Murray Expedition Scientific Reports, 10 (2), 91-120, 1 plate.

MOORE, C. 1867. On the Middle and Upper Lias of South-west England. Proc. Somerset archaeological nat. Hist. Soc. 13, 119-230, 4 plates.

MORTON, J. F. 1959. The habits and feeding of Dentalium entalis. J. mar. biol. Ass. U.K. 38, 225-238, 5 text-figs.

PALMER, C. P. 1974. A supraspecific classification of the scaphopod Mollusca. Veliger, 17, 115-123, 4 figs. PILSBRY, H. A. and SHARP, B. 1897-1898. Scaphopoda. In TRYON, G. W. (ed.). Manual of Conchology, 17, xxxii-1-348, 39 plates.

YOUNG, J. A. 1942. Pennsylvanian Scaphopoda and Cephalopoda from New Mexico. J. Paleont. 16, 120-125, 2 figs., pl. 20.

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