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LOPHOPHORE OF THE EOCENE BRACHIOPOD TEREBRATULINA WARDENENSIS ELLIOTT

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ABSTRACT

Some specimens of *Terebratulina wardenensis* from the London Clay of Kent, England, have a coherent spicular lophophore support preserved. The structure is compared with that of two Recent species of the genus in which the support conforms closely to the outline of the lophophore. It is concluded that within the genus, the form, relative size and filament density of the organ have undergone little change since the Cretaceous, the only notable difference being that the ablabial filament bases of *T. wardenensis* are more heavily spiculated than those of the two Recent species examined.

INTRODUCTION

Our understanding of the anatomy of the soft parts of fossil brachiopods is primarily based on the form and distribution of skeletal elements of the animals. Information derived from a detailed study of shell morphology is commonly interpreted with the aid of modern representatives of the phylum in which both skeleton and tissue are available for investigation. Living brachiopods reveal the interrelations between these two elements, and the assumption is made that similar relationships existed between homologous skeletal structures of extinct species and their associated organs. This approach may also be supplemented by a consideration of functional aspects; Rudwick's *(14)* discussion on the lophophore of spire-bearing forms is one of the earliest of such studies on the Brachiopoda.

Although these approaches have been fruitful they have certain basic limitations. Several organs of modern brachiopods are devoid of skeletal support and as they are also not in close contact with the outer epithelium responsible for secretion of the shell, they fail to produce any scar or impression on the inner surface of the valves. We have no direct knowledge, for example, of the location or form of the alimentary canal or metanephridia of any fossil species and their nature and disposition can only be inferred from their ubiquitous occurrence in all living species. There seems no *a priori* reason why the larger and more robust organs should not occasionally be preserved by being either cast or molded in fine sediment. Such freak occurrences as the preservation of the intestines are known in other phyla, although they may be associated with feeding habits or digestive processes that are unknown among brachiopods. The Early Jurassic bivalve, *Nuculana (Dacryomya) gaveyi,* whose gut has recently been redescribed by Cox *(6),* is thought to have been a deposit-feeder like present-day species of the genus. To some slight extent, the presence of a sediment-filled intestine predisposes this organ to fossilization. In contrast, the brachiopods are suspension-feeders and sedi-

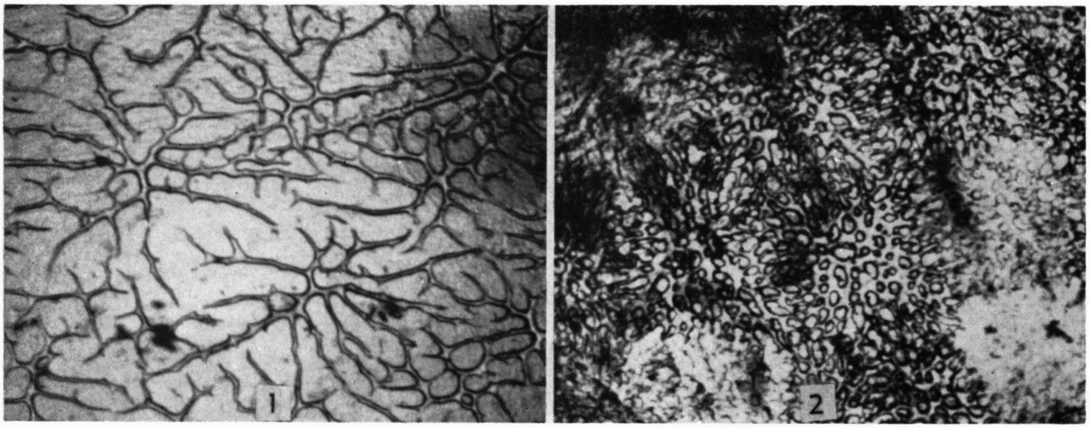


Fig. 1. Spicules from near central part of ventral mantle (transmitted light), X50.——*1. Terebratulina unguicula,* Recent, from off San Juan Island, Washington, USA (BB41744).——*2. T. retusa,* Recent, from Crinan Bay, Argyll, Scotland (BB41741). [All specimens are deposited in the British Museum (Natural History).]

ment in appreciable quantities typically stimulates rejection mechanisms *(1, 4).* However, the gut of suspension-feeders can on rare occasions be fossilized, as shown by Casey's *(3)* find of a specimen of the Cretaceous trochid gastropod *Margarites (Atira) mirabilis* which retains a cast of the intestines. Comparable material has not as yet been found among brachiopods, even though some of them (e.g., *Lingula, 5)* compact the intestinal contents to form rigid fecal pellets in an analogous manner to the trochids.

Difficulties of interpretation may arise even in those organs whose presence is reflected in some manner by the shell. If the relationship between shell and organ is not intimate, it may be possible to hold divergent views of the disposition and form of the organ in question. Among older species of fossil brachiopods, the absence of a closely comparable modern form whose morphology could act as a control for speculation inevitably adds to the problem. These difficulties are rarely serious when trying to reconstruct the musculature, pedicle, or mantle canals of extinct articulates, but are frequently encountered when the lophophore is considered. There is no unanimity of opinion on form of the lophophore in fossil spire-bearers, and closely associated with this problem, there is a lack of agreement on the function of their jugum. Rudwick *(14)* defends the more conventional view, that in species with but a pair of spiral calcareous ribbons, each spire supported a single brachial axis with its growing tip near the apex of the spiral. Williams *(19)* and Williams & Wright *(20),* however, maintain that in these forms, the spiralium was associated with a double loop of the brachial axis and that the spirally disposed segments of the organ were homologous with the side arms of a plectolophe. Concomitantly, they are of the opinion that the growing tips of the brachia were typically carried by the jugum. The known differences in attitude between the lophophore and its supporting loop in Recent Terebratulida must necessarily introduce a degree of caution in interpreting the form of the organ in some fossil members of the order and as Stehli (*16,* p. 737) has noted, diverse opinions of its nature exist.

Several authors have discussed the interrelations of the lophophore and its support among Recent Terebratulida *(9, 15, 19, 20).* They have concentrated attention on relations between the lophophore and the loop, the calcareous support secreted by infolds of outer epithelium. The other form of lophophore support, calcareous spicules embedded in the organ, has commonly been mentioned but not discussed in any detail by paleontologists. This bias is understandable, for although the loop is frequently preserved in fossil specimens of the order, until recently no fossil terebratuloid spicules had been described or figured, although they were mentioned by Muir-Wood *(12),* as occurring inside the valves of some specimens. Indeed, after the idea that the loop might be formed by amalgamation of calcareous spicules had finally been abandoned

(*19,* p. 266), it was generally considered that internal structures formed of these elements were either unknown or probably unpreservable (*16,* p. 737). Steinich's (*17, 18*) recent descriptions and elegant preparations of Cretaceous cancellothyridids which retain the spicular network essentially in place, show that under exceptional conditions such skeletal support may be preserved. In terms of information about the disposition of the lophophore, this form of skeletal support is superior to loops, whether of the long or short variety. In all modern brachiopods that possess them, the spicules are actually in the walls of the organ. The arrangement of the spicules in the few known fossil forms is completely consistent with a comparable relationship, and not only can one see the gross form of the lophophore, but even the distribution of the filaments may be recorded (*17,* fig. 4).

The purpose of the present paper is to record the preservation of a spicular support in an Eocene *Terebratulina* and to compare both this structure and its associated lophophore with those developed in two living species of the genus.

SPICULES IN RECENT TEREBRATULINA

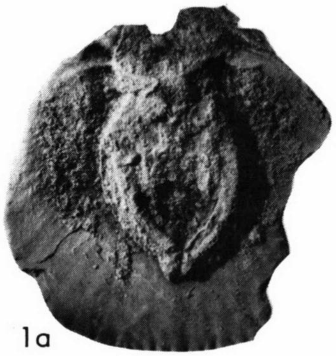
The existence of spicules in the mantle, body wall, and lophophore of *Terebratulina* has been known for more than a century. Their general form and distribution was described by Hancock (*10*), although they had been noted some five years earlier. Speaking of the lophophore spicules of *Terebratulina caputserpentis* (probably *T. retusa*), Hancock observed ". . . Were this species fossilised, it is quite possible that their arms might be so preserved as to give the appearance of their having been sustained by some apophysary apparatus, and in that case the roots of the cirri would be found projecting much in the same way as the salient spines or processes on the calcareous spirals of *Spiriferina rostrata*" (*10,* p. 830).

The spicules are embedded in the connective tissue below the ectoderm and each consists of a single crystal of calcite (*13*). As Blochmann (*2*) has emphasized, the form of the spicules varies even within a single individual and is dependent both on their position in the animal and its age. He believed that providing spicules from the same region of the body of an adult were compared, they were of use in discriminating between different species. Helmcke (*11*) has cast doubts on this assertion as far as species of *Terebratulina* are concerned, finding that there is seemingly wide regional variation in forms that he refers to *T. abyssicola.* It is possible that this variability is limited to some species of the genus and is not ubiquitous in occurrence. Only a few specimens of *T. retusa* from Crinan, Argyll, Scotland, and *T. unguicula* from Friday Harbor, Washington, USA, were available for study, but the mantle spicules differed widely between the two species, and the intraspecific variation was slight. In both the Scottish and American forms the spicules are well developed in the mantles and not confined to tissue overlying the mantle canals. In both, the spicules are flattened, but whereas the individual elements are stellate and commonly connected only by their tips in *T. unguicula,* they are more platelike in *T. retusa,* the plates being perforated by numerous apertures. Only at the extreme mantle margins are the spicules of the two species at all comparable, but calcification proceeds more rapidly in the Scottish forms (Fig. 1, *1, 2*).

The lophophore of adults of both species is plectolophous. When relaxed, the filaments extend from the lophophore and are relatively long and straight (Fig. 2, *3a*). Unless narcotized before being fixed, however, they are typically strongly contracted (Fig. 2, *2a*).

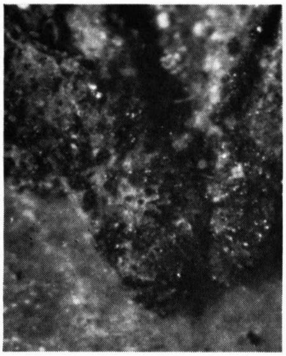
The lophophore spicules are visible through the walls of the organ, particularly if the specimen has been dehydrated and cleared before examination, but the gross form of the support is revealed more clearly if the tissue is removed. The specimens used in the present study were so prepared by immersing them for a few minutes in a 25-percent aqueous solution of Chloros (a liquid bleaching agent).

The spicular lophophore support of both species is closely comparable. The individual spicules in the lophophore walls are fused with one another to form a delicate but coherent structure. The outer surface of the structure, particularly that part which in life covered the great brachial canal, is relatively smooth. In this region the spicules are in close union, rather platelike and


1a


1b


1c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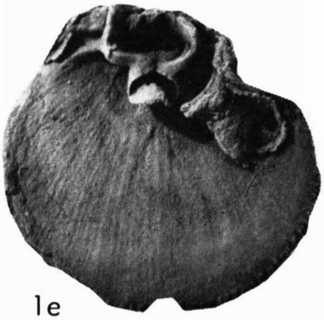
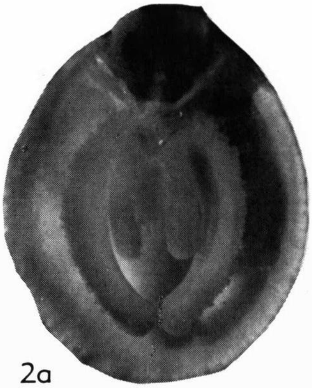
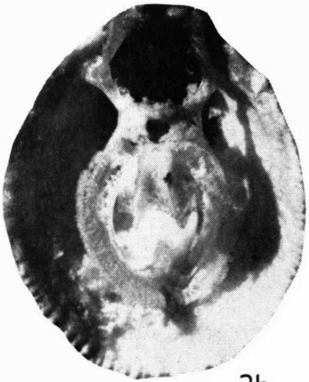

1e

Terebratulina wardenensis


2a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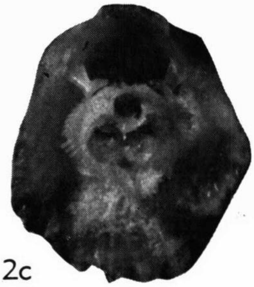
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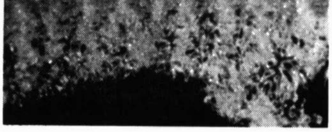
Terebratulina retusa


3a

Terebratulina unguicula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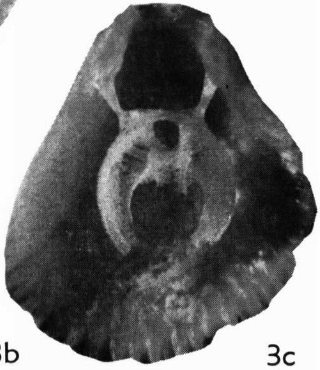
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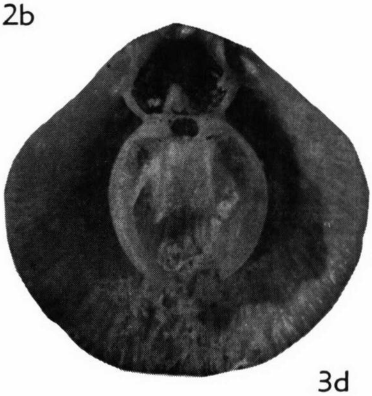

3d

For explanation, see facing page.

perforated by numerous lacunae; inwardly directed projections anastomose (Fig. 2, *3b*).

The support closely conforms to the disposition of the lophophore arms, for the spicules were originally embedded in the relatively thin layer of tissue between the brachial canals and the surface of the organ. The posterior part of the spicular support is attached to the anterior and ventral surfaces of the fused crural processes that are characteristic of *Terebratulina*. Anteriorly the spicular mesh is free of the loop and extends forward as two laterally convex projections, this section of the skeleton supporting the side arms of the lophophore. The medially coiled, distal part of the adult plectolophe is strengthened by a spicular mesh that ventroposteriorly is attached to the support of the side arms and dorsally is connected, together with the side arm supports, to the transverse band of the loop (Fig. 2, *3d*).

The spicules are not uniformly distributed through the lophophore (*19*, fig. 4). They are well developed and form a complete mesh along the ventral, dorsal, and lateral facing surfaces of the side arms, but along the median facing surfaces of the latter, the spicules are relatively sparse and unconnected. Consequently, after preparation of the material, there is a gap in the spicular mesh along the length of each side arm support which forms a conspicuous plane of weakness. Indeed, in the present preparations only a few of the side arm supports remained intact (Fig. 2, *2b*), the remainder fractured so that the ventral part either collapsed (Fig. 2, *3d*), or floated away as the specimen was removed from the bleaching solution.

Although the gross form of the spicular support is comparable in both *Terebratulina retusa* and *T. unguicula* there are differences in the spiculation of the filament bases. In the American specimens, both adlabial and ablabial filaments possess long, relatively narrow, disconnected spicules along much of their length, but the bases of the filaments, where they pass into the filamentar ridge, are virtually devoid of spicules. After the death and decay of the tissue of these individuals, the distribution of the lophophoral filaments is inevitably not recorded in the remaining spicular support. In contrast, the bases of the ablabial filaments of the Scottish specimens have a high spicule density, the individual elements are fused with one another and form projections from the remainder of the spicular lophophore mesh. Consequently the position of the ablabial filaments is commonly reflected by the skeleton (Fig. 2, *2c*).

TEREBRATULINA WARDENENSIS

The specimens of *Terebratulina wardenensis* were collected from pyritic concentrates formed by wave action on the foreshore near Warden Point, Sheppey, Kent. The concentrates are derived from the slipped, sparsely fossiliferous, blue gray clay exposed in the lower part of the cliffs. The beds at this locality are thought (*21*) to be the equivalent of division 5 of the London Clay of the London Basin.

The majority of the specimens were found with their valves in apposition and the chance discovery of three individuals that retained some indication of their spicular lophophore support occurred while opening valves, searching for shells that had the loop preserved. These three specimens give the impression that the lophophore has

FIG. 2. Eocene and Recent specimens of *Terebratulina* showing morphological features of lophophore.

1. T. wardenensis ELLIOTT, London Clay, Eocene, from Sheppey, Kent; *1a*, brachial valve interior showing side arm supports, X4.5 (BB41733); *1b*, complete shell with supports for side arms and spirals seen through opening in pedicle valve, X6.2 (BB41735); *1c*, brachial valve interior showing disturbed side arm supports, X4.5 (BB41734); *1d*, detail of anterior end of side arm supports of specimen shown in *1a* with outer surface of spicules visible, X27; *1e*, brachial valve interior with complete loop, X6.5 (BB41736).

2. T. retusa, Recent, from Crinan Bay, Argyll, Scotland; *2a*, brachial valve interior showing plectolophe with filaments contracted (photographed under water), X4.5 (BB41740); *2b*, similar view of same specimen after removal of tissue revealing support of plectolophe, X4.5; *2c*, brachial valve interior of young individual which had zygolophous lophophore, X9 (BB41737).

3. T. unguicula, Recent, from off San Juan Island, Washington, USA; *3a*, brachial valve interior showing plectolophe with filaments relaxed (photographed under water), X3.6 (BB41742); *3b*, fragment of ventral surface of spicular side arm support, X22.5 (BB41743); *3c*, brachial valve interior showing lophophore support, X6.2 (BB41738); *3d*, brachial valve interior with well-developed plectolophe support, X3.1 (BB41739).

[All specimens are deposited in the British Museum (Natural History).]

been cast (Fig. 2, *1a-c*). In all of them, the internal structure is pyritized to a considerable extent, although the major part of the valve has escaped this diagenetic effect. Only one (Fig. 2, *1a, d*) reveals anything of the form of the individual lophophore spicules. These are preserved sporadically on the ventral surface of the side arm supports, particularly the left one; seemingly they still have their original calcitic composition. Only the outer surface of the spicules is exposed and in its perforated, platelike form (Fig. 2, *1d*) is broadly comparable with the external surface of spicules from the corresponding region of the two Recent species that were examined.

Pyritization has been more extensive in the other two specimens, but although the individual spicules are not preserved, their distribution has influenced the deposition of pyrite. The major outlines of the spicular lophophore support are retained and even relative details are reflected, like the sparsity of spicules along the median facing surfaces of the side arms.

Two of the shells display only these side arm supports, but the third is more perfect and, clearly shows the support for the distal, spirally coiled segments of the lophophore (Fig. 2, *1b*). The connection of the spicular support to the loop is not visible in any of the specimens, the loop being concealed by irregular deposits of pyrite. The location and form of the spicular support, however, suggests that it was attached to the loop in a manner closely comparable to that described for the Recent species. Another specimen from the same locality retained the loop (Fig. 2, *1e*), which agrees closely with ELLIOTT's *(8)* description. The structure is more massively built than is typical of Recent representatives of the genus.

Because of the intimate relation between the lophophore and its spicular support the nature and disposition of the former can be inferred with a high degree of confidence in the Eocene material. The adult lophophore was undoubtedly plectolophous. The relative proportions of the supports for the side arms and median spirals (Table 1) are comparable with those of *Terebratulina retusa* and *T. unguicula,* and the lophophore itself was presumably very similar in its proportion to those of these two Recent species. This similarity seemingly extends to the filament density, although this is only known from one specimen of *T. wardenensis*. The plectolophous lophophores of all three species had between eight and nine ablabial filaments per millimeter along the anterior ventral surface of the side arms. The total filament density in the side arms of the Recent species approximates twice this value, since the filaments of the adlabial row alternate in position with those of the ablabial series. It is highly probable that the same situation prevailed in the Eocene species, but this cannot be proven since the ablabial filament bases effectively block any view of the adlabial row. If the single individual of *T. wardenensis* is typical, the most notable difference between its lophophore and that of the two modern species studied lies in the development of spicules in the filament bases. These unite to form a coherent skeleton in *T. retusa,* but are seemingly developed more extensively in *T. wardenensis* and rigidly support a greater length of the ablabial filaments.

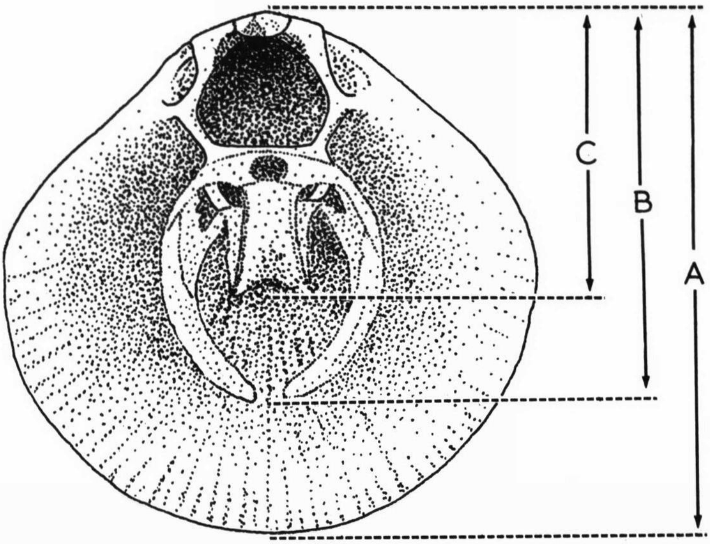
ENVIRONMENT

DAVIS & ELLIOTT *(7)* in their account of the paleogeography of the London Clay considered that in general the formation accumulated in a shallow, muddy sea. ELLIOTT had previously commented on the presence of *Terebratulina wardenensis* and believed that "The Sheppey occurrence apparently represents fossilised *Terebratulina* grounds *in situ*." (*8*, p. 131). The present material adds weight to his view. The spicular lophophore support of Recent species is extremely delicate and is readily broken even by gentle movement. That this structure is essentially intact in the Eocene material can only imply that during the interval between decay of the tissue and subsequent burial, the shells were not displaced. It would seem that the brachiopods must either have been rapidly buried after death, or alternatively, that they lived at depths greater than those affected by wave action. In either event, unlike the associated flora, they were buried essentially where they had lived.

CONCLUSIONS

A coherent spicular support for the lophophore is seemingly a characteristic feature of *Terebratulina*. It is known to occur in many Recent species, has been observed by STEINICH *(17)* in the Cretaceous *T. gracilis* and *T. faujasii* and is here recorded from the Eocene *T. wardenensis*.

TABLE 1



Species	A	B	C	D	Ratio B/A	Ratio C/A
T. wardenensis	7·5	6·2	3·1	8	0·83	0·41
	10·0	8·0	—	—	0·80	—
T. unguicula	7·8	5·5	4·1	9	0·70	0·53
	14·8	10·0	7·5	9	0·68	0·51
	15·0	11·5	7·7	9	0·77	0·51
T. retusa	4·0	3·0	—	12	0·75	—
	11·5	9·4	6·5	8	0·82	0·57

A – length of brachial valve B – length of brachial valve to anterior end of spicular support for sidearms C – length of brachial valve to front of spicular support for spiral D – density of ablabial filaments per mm. along ventral anterior surface of sidearm.
All dimensions in mms.

Adults of these three fossil species possessed plectolophous lophophores as do Recent representatives and the form, relative size, and filament density of the organ appear to have undergone remarkably little change since the Cretaceous.

Comparable spicular supports are presently known in fossil brachiopods only from related Cretaceous cancellothyridid genera *(18)*. However, until a few years ago, they were unknown other than in Recent species and the possibility that they occur in older stocks cannot readily be eliminated. Because of the close relationship between support and lophophore, the finding of such structures in extinct loop- and spire-bearers would resolve some of the current uncertainties concerning the form of the lophophore in these animals.

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