FUNCTIONAL STUDIES ON THE CRETACEOUS OYSTER *ARCTOSTREA*

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ABSTRACT. The three Cretaceous species-groups *Arctostrea colubrina* (Lamarck), *A. ungulata* (Schlotheim), and *A. diluviana* (Linnaeus) are described. Particular attention is paid to the detailed morphology of *A. colubrina*, from which its life history is reconstructed. It is inferred that the unusual characters of the genus (especially the arcuate shape, the zigzag commissure and the funnel spines) relate to the size and importance of the gills as primary food-collecting organs. The subspecies *A. colubrina ricordeana* (d'Orbigny) possesses, in addition to these special adaptations, a set of long spines secreted sub-parallel to the plane of the commissure on the lower valve; these are interpreted as a specific response to the hazards of inhabiting a substrate of soft ooze. Behavioural and structural adaptations used by Recent oysters for combating conditions of high turbidity are discussed, and it is suggested that similar methods were utilized by many extinct species. Funnel spines occur in other bivalves, including *Pinna* and *Etheria*; it is likely that they also are connected with inhalent current streams. Some taxonomic implications of the functional interpretation of *Arctostrea* are presented in an appendix.

MANY malacologists consider Recent *Ostrea* to represent the peak of bivalvian evolution (e.g. Atkins 1938), and few would dispute that its integrated gill/palp complex represents a feeding organ of outstanding power and efficiency. It is one of the very few Recent bivalve genera for which a large amount of published material is available, owing this distinction mainly to its economic importance. It appears that such spectacular success as oysters have achieved has at least partly been made possible by their adoption of a mode of life involving cementation to a hard substrate. Yet because of their irregular shell form consequent upon such cementation, oysters have understandably always been the *bête noire* of most systematists, palaeontologists included. It is the purpose of this paper to apply some of the available information on Recent *Ostrea* to a study of a distinctive group of extinct oysters in an attempt to better understand their morphology, and hence to clarify their taxonomy. It has become apparent to me during this study that however well known the biology of common European and American oysters may be, there is still a large amount of primary research needed on most of the more exotic tropical oysters before our knowledge of the family can be claimed to be reasonably complete.

The genus to be studied, *Arctostrea*, has its morphology exemplified by the species *A. colubrina* Lamarck, a common oyster in the Cenomanian rocks of Western Europe (Pl. 85, fig. 5). Particularly noteworthy are the superbly developed zigzag commissure (Pl. 86, fig. 1), and the highly characteristic arcuate shape in plan view (Pl. 85, fig. 5). Other groups of oysters have zigzag commissures, and virtually all lineages of oysters from the Jurassic onwards have at some time exhibited a tendency to arcuate shape, but only a relatively small group of species ranging through the Jurassic and Cretaceous was able to combine these two trends into a successfully adapted working complex.

To detail the biological and stratigraphical details of presently known populations of *Arctostrea* is far outside the scope of this paper. For the purposes of morphological description it will suffice to recognize three major infrageneric categories, conveniently termed species groups. They are the *Arctostrea colubrina* group (Pl. 85, fig. 5), the

A. ungulata group (Pl. 87, fig. 8), and the *A. diluviana* group (Pl. 85, fig. 1), and will be discussed in turn.

Terminology. In order to facilitate unambiguous discussion of detailed ontogenetic changes, the terms *proximal* and *distal* are preferred to the more normal dorsal and ventral (text-fig. 4); the shell margins are termed the *anterior* and *posterior arcs*. The term 'vertical zone' is useful in description of shells with steep (though not necessarily rigorously vertical) slopes around the valve edge. A vertical zone may occur virtually all round the commissure (as in *Arctostrea colubrina*), or may be limited to specific areas on the commissure (as in *Arctostrea diluviana*). It is the inevitable result of shell secretion along sectors of mantle edge where no mantle cell generation is taking place (see Carter 1967).

Note on captions and material studied. The following abbreviations are used consistently in all plate and text figure captions: *UMZC*, University Museum of Zoology, Cambridge University; SM, Sedgwick Museum, Cambridge University; BM, British Museum (Natural History), London. It should be emphasized that this study is based upon the examination of specimens in these museum collections; statements as to the type of substrate inhabited by different populations of *Arctostrea* are, in the main, inferences made from the matrix that still adheres to many specimens.

THE *ARCTOSTREA COLUBRINA* GROUP

This species group may be recognized by its regularly arcuate shape (Pl. 85, fig. 5), well-developed vertical zone, the numerous sharp zigzags around the commissure (Pl. 88, fig. 5), and the presence of small tubular spines situated at the crest of each commissural zigzag (Pl. 86, fig. 2); the growth track of these spines results in a characteristic divaricating ornament pattern on the flat shell top. The group was widely distributed, and common, in Lower Cretaceous times, and is known from the Middle East, North Africa, Austria, Germany, France, Portugal, and England.

A. colubrina ricordeana (*d'Orbigny*)

The availability of specimens of *ricordeana* preserving every detail of their life history in the form of well defined growth-lines enables an accurate ontogeny to be reconstructed. Though this reconstruction is based on populations of *colubrina ricordeana* inhabiting the Lower Chalk Sea of England, the greater part of it applies with only minor modifications to other populations of *colubrina* s.s., and also with slightly greater modifications to members of the *ungulata* and *diluviana* species groups.

The Chalk specimens of *ricordeana* are large, often very inflated, oysters with strong zigzag valve edges (Pl. 86, fig. 1). Adult specimens may possess a dimension greater than 110 mm. in the plane of the commissure, and have a maximum transverse dimension ('inflation') of up to 70 mm. During growth, mantle expansion is at a maximum distally on the commissure, in a narrow arc here named the *generative arc* of the mantle edge (text-fig. 1); elsewhere on the commissure, outside of the generative arc, the introduction of new mantle cells is minimal, though not altogether absent. Thus shell secretion during the life of the animal results in the building of a vertical zone around the greater part of the commissure; this vertical zone is crossed by steep plicae that represent the tracks of earlier growth stages of the zigzag commissure (Pl. 86, fig. 2).

The generative arc is not only the site of localized generation of new epithelial cells, it is also the site of introduction of *all* new plicae (Pl. 85, fig. 5). Any zigzag on the current

commissure can always be traced back up its own plica to the point of its inception as a gentle undulation in the generative arc of an earlier commissure (e.g. plica *a*, Pl. 86, fig. 1).
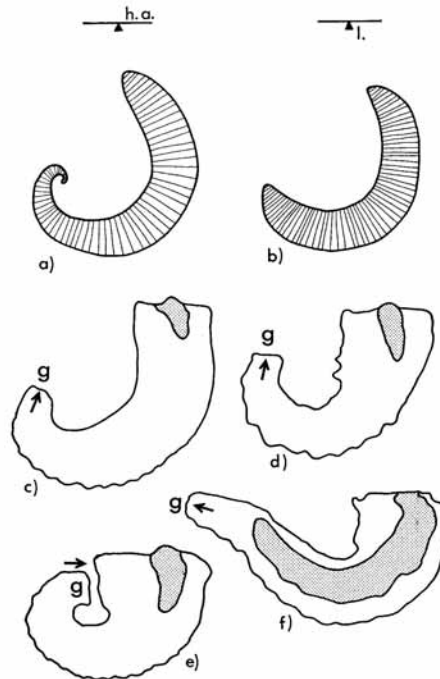
TEXT-FIG. 1. Comparison of the shape of the gill of (*a*) *Pecten* and (*b*) *Ostrea* with the adult shell outline of four specimens (*c–f* inclusive) of *Arctostrea colubrina* (Lamarck). All ×½.

All upper (right) valves viewed from above; stippled area represents the unornamented, pre-zigzag dissoconch, corresponding to the area of attachment on the left valve. *h.a.*, hinge axis; *l*, ligament pit; *g*, generative arc of the mantle edge, arrow indicating direction of mantle expansion.

Ontogeny. The significant stages in the life history of *ricordeana* are conveniently summarized in discrete steps:

1. Spatfall on to available hard attachment sites; commonly pieces of shell and echinoderm test. This was accompanied by immediate cementation by the surface of the left valve; by analogy with Recent oysters, it was followed in the next few days by metal morphosis from the veliger type organization to the adult anatomical form.

2. Continuing shell secretion eventually resulted in the size of the animal exceeding the size of the attachment object. At some stage after this the mantle edges changed

from being roughly planar to being sharply zigzag, passing through stages from gently flexed to more sharply folded (Pl. 86, fig. 4). This change in the morphology of the mantle edge may have been partly under muscular control, but it was probably also connected with localized epithelial generation. As shell secretion continued unabated, a clear record of these changes is shown by the successive growth-lines on the valve surface. In particular, there is always preserved an unornamented pre-zigzag dissoconch that is
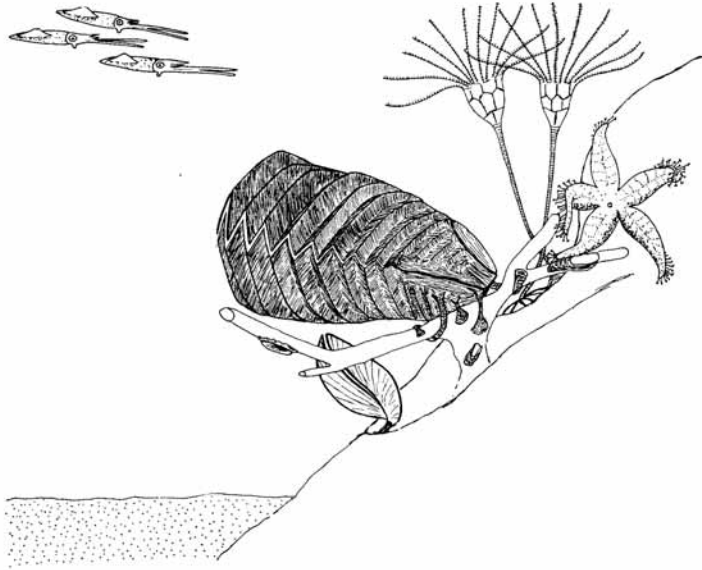
TEXT-FIG. 2. Reconstruction of life position of an early adult *Arctostrea* attached proximally by cementation and root spines.

sharply demarcated from the following growth stages and gives a clear indication of the size and shape of the attachment object (Pl. 88, fig. 3).

3. When the shell outgrew the area of cementation laterally, the mantle edges of the left (lower) valve on either side of the mantle isthmus secreted tubular spines which were attached in a root-like bundle either to the initial attachment object, or to closely adjacent objects (text-fig. 2). These root-spines were first secreted about the time of the inception of the zigzag commissure, and obviously served to attach the animal tightly to the substrate. They continued to be secreted so long as the animal was still attached to the substrate proximally. Some specimens do not progress beyond this ontogenetic stage.

4. At this stage in ontogeny, which occurred at very different shell sizes in different individuals, the shell either broke free from its proximal attachment or, if it was attached to a relatively small object, overbalanced, and hence came to lie free on the sea floor. Presumably stimulated by contact with the chalky ooze, the mantle edges of the left

valve secreted a set of long tubular spines at the crests of the zigzag of that valve (i.e. in the *troughs* of the commissure if the shell is viewed in the life position). These spines (Pl. 85, fig. 4; Pl. 87, figs. 6, 7; text-fig. 6) extended at right angles to the shell outline, were sub-parallel to the plane of the commissure, and sometimes half as long as the shell itself. They were only secreted along the anterior arc of the commissure. Occasional specimens (e.g. SM B6461) that did not progress beyond the attached phase of ontogeny (stage 3 above) were able to utilize their anterior arc spines as additional 'roots' or 'props' to further stabilize their attachment. In these cases, of course, the spines were not sub-parallel to the plane of the commissure, but became irregular, and were gener- ally directed downwards towards the surface of attachment.

5. In large, and presumably old specimens of *ricordeana* there was a slowing of the rate of introduction of new epithelial material in the generative arc, whilst over-all shell secretion continued. As a result extremely high vertical zones were built up. When this was the case, there was often secretion of further sets of spines around the commissure; on any one plica there may have been up to four successive spines, each vertically above (with respect to life orientation) its immediate predecessor (Pl. 86, fig. 3).

Other populations of colubrina

The long spines sub-parallel to the plane of the commissure, diagnostic of *A. colubrina ricordeana*, appear to be restricted to very local populations from particular horizons in the Cenomanian Chalk Marl of England and Normandy. However, populations of the *colubrina* group agreeing with *ricordeana* in all other aspects are common from rocks of Cretaceous age.

1. The Haslingfield population. A rich fauna of *Arctostrea* is known from the locality of Haslingfield, a few miles south of Cambridge. Specimens from this population (Pl. 85, fig. 5) are virtually indistinguishable from the Folkestone *ricordeana*, apart from their lack of long spines along the anterior arc. Occasionally broken spine stumps suggest that some specimens did secrete spines in this position, but the majority of the population possess very strong clumps of root spines proximally, and were clearly attached throughout their ontogeny.

EXPLANATION TO PLATE 85

Fig. 1. *Arctostrea diluviana* (Linnaeus), Senonian, Essen, Germany. ×1. Internal view of a typical upper (right) valve of this species; note the well-developed gill-gutter anterior to the adductor scar, with pustulose shell texture along its bottom. BM L61234.

Fig. 2. *Arctostrea ungulata* (Schlotheim), Maastrichtian, Maastricht. ×2. Internal view of an upper (right) valve to show the flat floor; note that the marginal zigzag is of amplitude equal to the depth of the valve. BM LL8600.

Fig. 3. *Arctostrea ungulata* (Schlotheim), Upper Cretaceous, Buzi Valley, Portuguese East Africa. ×2. This specimen shows well the characteristic flat-topped shell, and open crested plicae, that are so typical of the species group. BM L56928.

Fig. 4. *Arctostrea colubrina ricordeana* (d'Orbigny), grey Chalk Marl, Folkestone, Kent. Approximately ×½. View of double valved specimen from below, looking up at the divaricating ornament and snowshoe spines of the under (left) valve. SM B.6451; specimen figured by Woods, text-fig. 122.

Fig. 5. *Arctostrea colubrina* (Lamarck), Lower Chalk Marl, Haslingfield, Cambridgeshire. ×1. A specimen showing the characteristic divaricating plicae and branchiform shape of the upper (right) valve when viewed from above. *g*, present position of the generative arc (growing edge) of the mantle margin; *g'*, a previous position of the generative arc. SM B.6559.

2. The Le Mans population. It was noted earlier that on the shell of an adult *Arctostrea* any given plica starts its history in the generative arc of the mantle edge as a small undulation in the growth-lines. In many populations of the *colubrina* group, for example, that from Cenomanian calcareous sandstones of Le Mans, this may develop next into a marked, short, tubular 'funnel spine' (Pl. 88, fig. 5), and only later grow into a sharp zigzag. The plica, of course, retains this funnel spine at its crest, and several more may be secreted in homologous positions as growth continues (Pl. 88, fig. 4). It is striking that these funnel spines are extremely well developed on the anterior margin, but are only rudimentary on the posterior (Pl. 86, fig. 2); they also tend to be rather better developed on the right (upper) valve.

THE *ARCTOSTREA UNGULATA* GROUP

Though the over-all shell morphology of *A. ungulata* is similar to *A. colubrina*, there are significant differences in detail.

New plicae are again introduced distally in the generative arc, but the commissural zigzag is of much greater wavelength and amplitude than in *colubrina*. There is thus an apparent tendency for new plicae to be introduced in pairs on the anterior and posterior sides of the distal growing edge (Pl. 85, fig. 3). The zigzag also has broad, rounded extremities in contrast to the sharp, pointed extremities of *colubrina*.

The initial mantle edge reflection at the start of a new plicae (Pl. 85, fig. 3; Pl. 86, fig. 6) is broad and strong, and it retains a similar aspect throughout ontogeny. This, linked with the angle at which the mantle edge is held, results in the characteristic 'open-crested' plicae that typify the species. A similar open-crested morphology may be seen in the *A. pusilla* group (Pl. 90, fig. 9). The growth lines on the shell of *ungulata* beautifully display the early stage of differential mantle expansion, during which an initially gently undulose commissure is transformed into the broad, strong mantle reflection at the head of each plica (Pl. 86, fig. 6). However, after this initial stage of differential mantle expansion, further shell secretion results in the building up of a vertical zone in the usual fashion (Pl. 85, fig. 3).

It is likely that the differences in morphology between *colubrina* and *ungulata* are at least partly related to a difference in habitat, *ungulata* being usually collected from medium-grained or coarser calcareous sandstones, whilst *colubrina* is often common in finer grained sediments. The attachment scar is generally small and not well marked, and whilst some specimens may have been attached proximally throughout life, the majority probably lay free on the sea floor.

The *A. ungulata* group is restricted to Upper Cretaceous rocks and has a wide distribution, ranging from Crimea, Bulgaria, and East Africa, as far north as Holland, Belgium, and Scandinavia. It seems to replace the *colubrina* group at this stratigraphic level. There is little doubt that *ungulata* developed from an attached species similar to *A. pusilla* (Nilsson) (see appendix).

THE *ARCTOSTREA DILUVIANA* GROUP

Members of this group have a larger and more solid shell than members of the previous two, this being a direct result of their being permanently cemented to the substrate throughout post-larval ontogeny.

It is characterized by its somewhat irregular, oval shape (Pl. 85, fig. 1) and its large size. Although there may be a zigzag all around the commissure, it is always best developed over the anterior margins, and it is only here that there is any vertical zone built up.

The *diluviana* group is in an Upper Cretaceous development, and seems to have a more limited distribution than *ungulata* or *colubrina*; specimens that I have examined all derive from northern Europe (Belgium, Holland, Germany, and Sweden).
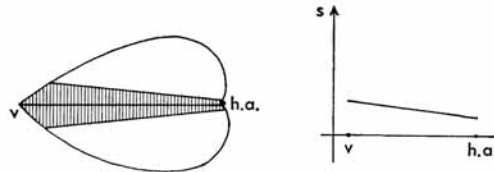
TEXT-FIG. 3. To illustrate the style of shell secretion in an equilateral bivalve; the growth increments (ruled area) on each valve are of wedge shape, tapering towards the hinge axis. *h.a.*, hinge axis; *v*, ventral margin; *s*, rate of secretion of shell material.

CONSIDERATIONS ON SHELL FORM

Fundamental tenets. Analysis of shell form in the Bivalvia becomes hopelessly confused unless a clear distinction is maintained between the basic phenomena of shell secretion *per se* on the one hand and generation of mantle cells (i.e. expansion of the area of mantle epithelium) on the other (Carter 1967). However, provided this distinction is maintained, it is possible to understand in detail the growth of even complex Bivalvia such as *Arctostrea*.

EXPLANATION OF PLATE 86

Fig. 1. *Arctostrea colubrina ricordeana* (d'Orbigny), grey Chalk Marl, Folkestone, Kent. ×2. Arrow marks the inception of plica 'a' in the generative arc; the shell is of a juvenile animal which had not secreted snowshoe spines at the time of its death. BM LL14751.

Fig. 2. *Arctostrea* cf. *colubrina* (Lamarck), Cenomanian, Trouville, Normandy. ×2. Note the development of funnel spines (more conspicuous on the anterior than on the posterior margins) in this view of the posterior vertical flank. BM 65748.

Fig. 3. *Arctostrea colubrina ricordeana* (d'Orbigny), Chalk Marl, Norman Cement Works, Cambridge. ×1½. View of part of the vertical zone developed on the anterior arc of the lower (left) valve, showing up to four broken snowshoe spine bases (one above the other) on individual plicae. SM B.6557.

Fig. 4. *Arctostrea colubrina ricordeana* (d'Orbigny), same specimen as 1. ×4. Note the suppression of the more dorsal plicae.

Fig. 5. *Pinna rugosa* J. de C. Sowerby, Recent, unlocated. ×1½. View of the ventral valve edge to show the funnel spines. Note how the earlier spines are sealed off by the secretion of a sheet of shell across their base. UMZC 2008 (Saul Collection).

Fig. 6. *Arctostrea ungulata* (Schlotheim), same specimen as Plate 85, fig. 2. ×4. View of the posterior arc, showing the characteristic open crested plicae and the high amplitude of the zigzag.

Fig. 7. *Arctostrea colubrina ricordeana* (d'Orbigny), grey Chalk Marl, Folkestone, Kent. ×4. Showing a plica whose growth lines display a zigzag that is starting to diminish in amplitude (3) after an initial increase from its inception in the generative arc (1) up to a point of maximal amplitude (2). Plica is situated on the posterior arc of the upper (right) valve. BM L.80734.

Practical implications. In a bivalve of simple equilateral form (e.g. *Glycymeris*), secretion of shell is at a maximum somewhere along the ventral margins, and decreases dorsally on either side of this around the lateral shell margins (text-fig. 3). By virtue of its most unusual pattern of mantle cell generation, *Arctostrea* (text-fig. 4) has its point of maximal shell secretion (Z) situated on the anterior arc of the shell, secretion diminishing at points around the commissure both distally and proximally to this; then there is a further
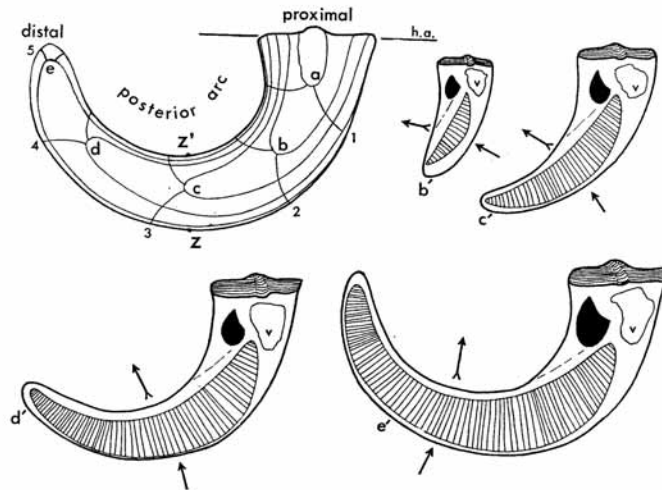
TEXT-FIG. 4. An idealized adult specimen of *Arctostrea* marking in selected growth-lines (*a* through to *e*) and plicae (1 through to 5). The growth stages corresponding to each growth-line are drawn separately as growth series *b′* to *e′*; adductor muscle, solid black; *h.a.*, hinge axis; *v*, visceral mass; gill, ruled lines; arrow marks functional centre of the inhalent current stream bathing the gill; feathered arrow centre of exhalent stream. Note how this point migrates relatively in a distal direction during growth. Z: point of maximal amplitude of zigzag on the anterior arc of the commissure, diminishing antero-proximally and antero-distally. Z′: point of maximal amplitude on the posterior arc of the commissure, diminishing postero-proximally and postero-distally. (It should be emphasized that growth-lines *a* to *e* and plicae 1 to 5 are only selected examples from the continuous series of growth-lines and plicae that occur on the shell surface; see also Pl. 85, fig. 5.)

maximum of secretion (Z′, but note that secretion here is itself absolutely less than at Z) on the posterior arc, secretion diminishing both distally and proximally from this point as well.

A further point of interest may be mentioned here: the hinge axis in *Arctostrea* is situated at the proximal end of the shell, and hinging takes place by rotation about this axis (text-fig. 4). However, the extension of the axis itself has a limiting effect upon the adult shell form of the animal for, if efficient hinging is to be maintained, it is impossible for the distal growing edge of the shell to transgress over the extension of the hinge axis. Individual specimens of *Arctostrea* show many modifications in late adult life to cope with this restriction, two of the commonest of which can be seen on text-fig. 1. Fig. 1*e* shows an individual that has solved the problem by increasing the curvature of its

growing edge so as to grow directly back towards the umbones—extreme specimens may actually fuse their shell into a complete 'circle'. Fig. 1*f* shows the other alternative, where the growing edge is directed away from the umbones.

Consequences of cementation. Populations of *Arctostrea* convincingly demonstrate the close relation that exists between shell cementation and irregularity of form; the greatest regularity of adult shape is always found in those members of the *colubrina* and *ungulata* groups that were unattached during the major part of their adult life (Pl. 85, fig. 4). However, all extremes of variation can be found throughout the Jurassic and Cretaceous, from specimens that are cemented throughout life, and hence have a morphology mimicking the '*diluviana* group style' (even though they may actually be *ungulata* or *colubrina* group), to specimens that are briefly cemented but break free early in adult life; these may be said to have a '*colubrina* group style'. It is possible to find specimens approaching these two morphological end members from a single population at almost any locality possessing *Arctostrea* in abundance. It is small wonder, in the light of this, that the systematics of the group is burdened by a plethora of unnecessary names; nor is there any hope of substantial improvement until the adaptive significance of these morphological trends is understood.

In oysters that remain attached throughout ontogeny by a considerable portion of their left valve, the shape of the left valve is mainly dependant upon the form of the surface to which the oyster is attached; in turn, the shape of the right valve is influenced by the fact that its edge everywhere has to meet that of the left. Consequently the form of the whole animal is strongly influenced by the shape of the substrate to which it is cemented. This is clearly demonstrated in the specimens of *A. pusilla* figured on Pl. 90, figs. 3–4, 6–10.

All adult *Arctostrea* have a sharply zigzag valve edge. Assuming that the shell is cemented to a reasonably flat surface, it is, of course, only possible for the animals to

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EXPLANATION OF PLATE 87

Figs. 1, 2, and 3. *Arctostrea alaeformis* (S. Woodward), Upper Chalk, Norwich. ×1. Internal, ventral and external views of the lectotype. NCM F.C.2100; specimen of Woodward 1833, plate 6, fig. 3.

Fig. 4. *Arctostrea colubrina ricordeana* (d'Orbigny), grey Chalk Marl, Folkestone, Kent. ×2. Internal view of the upper (right) valve. Note especially the lack of room for a promyal passage dorsal to the adductor (arrow); and the characteristic pustulose nature of the shell on the floor of the valve. SM B.6462.

Fig. 5. *Arctostrea pusilla* (Nilsson), Upper Chalk, Norwich. ×2. A specimen with the more usual open textured plicae along the lateral margins, but with large open folds of the '*larva*' type along the distal margins. View looking into the generative arc. NCM. F.C.2129a; specimen figured by Woods, plate 58, fig. 2.

Fig. 6. *Arctostrea colubrina ricordeana* (d'Orbigny), grey Chalk Marl, Folkestone, Kent. ×4. Specimen showing a funnel spine located at the top of a plica (arrow). In the adult growth stage, the same plica is the site of secretion of a snowshoe spine, subparallel to the plane of the commissure. SM B.6459.

Fig. 7. *Arctostrea colubrina ricordeana* (d'Orbigny), grey Chalk Marl, Folkestone, Kent. ×2. Typical development of short snowshoe spines in a specimen of only moderate overall size. SM B.6451; specimen figured by Woods, text-fig. 122.

Fig. 8. *Arctostrea ungulata* (Schlotheim), same specimen as Plate 85, fig. 3. ×1. View from antero-dorsal aspect.

Fig. 9. *Chlamys asperrimus* (Lamarck), Recent, Tasmania. ×2. Note the presence of a true zigzag commissure (and not merely an interlocking valve edge) of low amplitude; this is one of the very few examples of this feature in the Bivalvia outside of the Ostreacea. SM D.20869.

produce a regularly zigzagged valve edge if shell secretion has been such that after a particular stage in ontogeny the growing edge of the shell is *not in contact with the substrate*. This may be accomplished in one of two ways: either the rate of mantle expansion is such that the shell soon comes to grow outside the edge of the object to which it is attached, which hence must be relatively small; or, if the attachment object is large, there must be a cessation of mantle cell generation during continued shell secretion, resulting in the formation of a marginal 'vertical zone'. The former is the dominant solution utilized by members of the *colubrina* and *ungulata* species groups; the latter by the *diluviana* species group. In either case, adult animals possess a regular and very sharply zigzagged commissure, the form of which is entirely independent of the form of the animal's attachment surface.
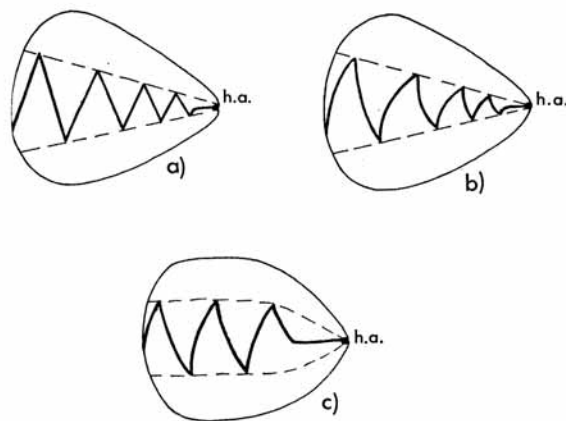
TEXT-FIG. 5. Theoretical types of zigzag commissure. (*a*) zigzag with diminution of amplitude dorsally, but with straight flanks; efficient hinging of the shell is impossible; (*b*) a geometrically graded zigzag, with both diminution of amplitude dorsally, and curved flanks to enable unimpeded opening and closing of the shell; (*c*) zigzag without diminution of amplitude dorsally; note that such a zigzag cannot reasonably cover any length of the lateral shell margins, and that it involves a non-linear secretion gradient across the shell.

The problem of grading. Interesting questions are raised by the interaction of the secretion pattern of *Arctostrea* with its possession of a zigzag commissure.

In a closely reasoned analysis of zigzag commissures in the Brachiopoda, Rudwick (1964) has introduced the concept of a *graded zigzag slit*, which is defined as a slit 'of uniform width all round the commissure, from one suppression point [the point where the zigzag dies away to nothing on the lateral shell margins] to the other'.

It is useful to isolate the morphological components that go to make up a graded zigzag slit:

1. Diminution. For a zigzag slit that occupies any appreciable length of the whole commissure there is a gradual diminution of amplitude of the zigzag as the hinge axis is approached (text-fig. 5*a*). This is inevitable if a linear secretion pattern is to be

maintained across the shell, though it is, of course, possible to imagine a shell form in which the zigzag does not diminish in amplitude dorsally and hence does not possess a linear secretion pattern (text-fig. 5c).

2. Curvature of the flanks. As Rudwick has already clearly pointed out (1964), by virtue of the hinging motion of any bivalved shell, it is impossible for a zigzag situated on the lateral margins to have straight flanks. Such a shell (text-fig. 5a) would be unable to open because of the occlusion of the shell edges in the crests and troughs of the zigzag. It is therefore necessary that the flanks of the zigzag be curved, concave dorsally, in order to overcome this occlusion (text-fig. 5b). An inevitable *result* of such flank curvature is that there is a tendency to equalization of width of the slit.

Rudwick is of the opinion that the actual flank curvature is due 'partly to the . . . (requirements) . . . of a slit of uniform width, and partly to the fact that the valve edges move apart by rotation'. In other words, he suggests that there was a positive selective value in favour of a slit of uniform width during the evolution of zigzag slits, and that their flank curvature cannot be explained on a basis of shell secretion tenets alone.

Whilst this may be the case in the Brachiopoda, within the limits of accuracy of the measurements it is possible to make, it appears that the curvature of the flanks of the zigzag in species of *Arctostrea* is no more than is necessary to ensure the adequate hinging of the shell. An inevitable result of this is a slit of roughly equal width all round the commissure, but economy of hypothesis precludes treating this equality of width as of prime selective significance. As the term 'grading' is of considerable usefulness in morphological description, it is necessary to distinguish 'adaptive grading' where the equalizing of the width of the slit is thought to have adaptive significance over and above that concerned with shell hinging (i.e. grading *sensu* Rudwick), from 'geometric grading', where all elements of the grading, including both diminution of amplitude and curvature of the zigzag flanks, are thought to be explicable in terms of basic tenets of shell secretion.

EXPLANATION OF PLATE 88

Fig. 1. *Etheria elliptica* Lamarck, Recent, Africa. ×1. Well developed funnel spines at spaced intervals around the edge of the commissure. These spines must be secreted by reflected lobes of mantle tissue, and are sealed off as soon as they are no longer right at the growing edge of the shell. UMZC 2000 (McAndrew Collection).

Fig. 2. *Crassostrea echinata* (Quoy and Gaimard), Recent, Australia. ×6. A juvenile shell (umbo arrowed) showing the extreme development of flaring, funnel spines on the ventral side of the shell. The long, thin funnel spines of a slightly later growth stage can be seen out of focus in the background. UMZC 2007.

Fig. 3. *Arctostrea colubrina* (Lamarck), Lower Chalk, Cherry Hinton, Cambridgeshire. ×1. Note the presence of two folds (arrowed) on the posterior ear; these probably reflect the presence of persistent pseudo-siphons in the mantle edge. SM B.358; figured by Woods, text-fig. 135, and Rudwick (1964), plate 29, fig. 5.

Fig. 4. *Arctostrea* cf. *colubrina* (Lamarck), Cenomanian, Le Mans, Normandy. ×7. A specimen exhibiting the successive secretion of several funnel spines on individual plicae; note the very low amplitude of the zigzag. BM LL26833.

Fig. 5. *Arctostrea* cf. *colubrina* (Lamarck), Cenomanian, Le Mans. ×7. View of the generative arc (distal end) of the right valve of a young individual. Note the sharp commissural zigzag with funnel spines developed at the crests. BM LL26832.

The uniqueness of individual specimens. The shell of any specimen of *A. colubrina* has a unique morphological construction, yet its secretion was none the less governed by certain basic conditions:

1. The vast majority of new epithelial cells were introduced in a narrow generative arc of the mantle edge.

2. The absolute secretion of shell material was a function of distance from the hinge axis, being maximal at the point on the commissure furthest from the hinge axis.

3. After a certain growth stage had been passed, the shell possesssed a zigzag commissure; at all further growth stages this was geometrically graded in such a way as to ensure the free hinging of the shell and the tight approximation of the valve edges when shut.

The consequence of these conditions is that *every single plica* on the shell of a typical *Arctostrea* has a morphologically unique ontogeny.

Considering (for convenience only) the hinge axis as a fixed direction, it is apparent that the generative arc of the mantle edge occupies a geometrically unique position for every successive commissure throughout the life of the animal (text-fig. 4, positions *a* through to *e*). Since the generative arc is the site of inception of all new plicae, each plica starts its ontogeny in a geometrically unique position, and its detailed structure is a reflection of its exact positions on either the anterior or posterior margins.

These detailed structural changes are mirrored on the valve surface in the form of growth-lines (Pl. 86, figs. 1, 7). A study of these reveals that the earlier formed plicae (e.g. plica 1 of text-fig. 4) pass through a series of growth stages which may be idealized for conceptual convenience. This series generally follows the pattern illustrated by the plica of Pl. 86, fig. 7.

Initially the amplitude of the zigzag is small, corresponding to its inception on the generative arc of the commissure (position 1 of Pl. 86, fig. 7), but this rapidly increases towards a maximum. Meanwhile, further mantle expansion has been taking place distally (in the generative arc), causing the relative migration of the zigzag around the commissure in a proximal direction. The amplitude of the zigzag reaches a maximum (position 2 of Pl. 86, fig. 7), and then starts to come under the influence of the diminution of amplitude along the antero-proximal part of the commissure; it hence decreases in amplitude (position 3 of Pl. 86, fig. 7). On the very earliest formed plicae (e.g. plica 1 of text-fig. 4; Pl. 86, fig. 4) this decrease in amplitude may be carried as far as total suppression of the zigzag.

THE FUNCTIONAL INTERPRETATION OF *ARCTOSTREA*

Plicae. Viewed from above, the shape of an adult *Arctostrea* is crescentic (text-fig. 1; Pl. 85, fig. 5); it is immediately obvious that the inner arc of the crescent (i.e. the posterior margin) is shorter than the outer arc of the crescent (the anterior margin). It follows that for a zigzag of given wavelength, on any given commissure there are fewer zigzags (and therefore plicae) on the posterior margin than on the anterior. The more sharply crescentic is the over-all shell shape, then the fewer plicae there are posteriorly compared with anteriorly. For example, on a fairly sharply recurved specimen (SM B.6557) there are 13 posterior plicae, and 19 anterior plicae. There is no need to seek

a functional interpretation of this fact; it is an inevitable consequence of the mode of growth.

Spines. There are three different types of spine on *A. colubrina ricordeana*, and it is possible to attribute to each a discrete functional role:

(*a*) Attachment spines. It is self-evident that the complex of spines secreted at the proximal end of the shell around the attachment area served to strengthen the attachment of the shell to the substrate. Their restriction to this part of the shell, their irregular
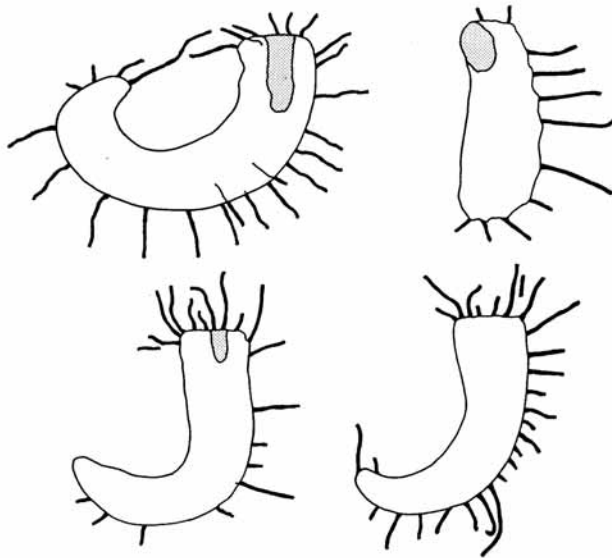
TEXT-FIG. 6. Shell outlines of *Arctostrea colubrina ricordeana* to show the disposition of spines on the left valve with respect to the over-all shape of the shell; specimens viewed from above. Note especially their concentration around the umbonal end of the shell (attachment spines), and their disposition at right angles to the shell margins (snowshoe spines). Stippling as for text-fig. 1; specimen without stippling is a left valve only. ×½. All specimens from the grey Chalk Marl, Folkestone, Kent. BM L4855.

and intertwined shape, and the fact that they are occasionally preserved attached to hard objects such as other oysters, all support such an interpretation.

(*b*) Snowshoe spines. Similarly, it was self-evident to Woods over fifty years ago that 'the long regular outgrowths from the margin of the valves occur [only] in specimens from the Chalk Marl, and were no doubt adopted for the purpose of fixation in the soft sediment of the sea floor', but it is worth noting how closely the observed morphology of the spines approaches the paradigm for a 'snowshoe' function. By virtue of its arcuate shell shape, the distal and proximal ends of the shell in an adult *colubrina*

morphologically define one 'side' of the shell, whilst the curved anterior margin defines the other (text-fig. 6). Most of the weight of the shell is concentrated on the anterior margins, and it is clearly there that the animal was in most danger of sinking into the substrate. Hence it is there that the spines are developed, one at the trough of every zigzag. Their length, their sub-parallelism to the plane of the commissure, their disposition at right angles to the shell outline, and the successive secretion of more than one spine on individual plicae in large adults with high vertical zones (Pl. 86, fig. 3), all add up to unequivocal evidence that the spines prevented the animal from being smothered by sinking into the soft ooze.

(*c*) Funnel spines. The function of the small funnel-like spines, developed at the crest of the zigzags on the right (upper) valve, will be discussed in a later section on the function of the zigzag itself.

The arcuate shape. From the very early stages of ontogeny of *Arctostrea*, the localized generation of epithelial material in the generative arc of the mantle edge exercised a controlling influence on the shell form; it is directly responsible for the characteristic arcuate shape in plan view. This arcuate shape approaches a logarithmic spiral, since the shell always tends to grow in such a way as to preserve over-all similarity of shape.

However, the tendency of oyster shells to arcuate shape is by no means confined to *Arctostrea*, and Lang (1923) has coined the term lunate to describe it. Functional explanations are not common; most writers seem content to follow the suggestion of Douvillé (1910) that this shape of shell is ideally suited to resist water currents. At its best this postulate is difficult to understand; and the fact that a lunate trend can be recognized so frequently in groups of oysters at such different points in time and space (e.g. *Liostrea anabarensis* Bodyl from the Valanginian of Russia (text-fig. 7); *Crassostrea ameghinoi rocana* von Ihering from the Danian of Argentina (text-fig. 8); and the Recent *Crassostrea angulata* (Lamarck)) leads one to be dissatisfied with Douvillé's explanation and to suspect that some basic adaptation is involved.

The soft-part anatomy of *Ostrea edulis* (text-fig. 9) is fairly characteristic of the Ostreacea as a whole, and most members of the Pectinacea have a grossly similar anatomy. This anatomical similarity is undoubtedly a result of their mode of life *on* the substrate with the commissure horizontal, possessing the ability to take in water (and hence food) over a large part of their commissure. Many bivalves that live with their commissure at right angles to the substrate (e.g. *Arca*) have gills which hang vertically in the mantle cavity, and which are not fused laterally to the general mantle surface. Generally speaking, however, the assumption of a horizontal mode of life necessitates the lateral fusion of the gills (particularly the upper) with the mantle surface; otherwise gravity would cause them to fold together in a most inefficient way. It is thus perhaps significant that the advanced pseudo lamellibranch gill condition is characteristic of the Ostreidae, Pectinidae, and Pteriacea—all groups which live with the commissure sub-parallel to the substrate.

The presence of an inhalent current along a considerable part of the commissure requires the development of larger and more complex organs to catch, sort, and process the available food supply. The Pectinacea and Ostreacea have dealt with this requirement by enlarging the gill and expanding it into a characteristic crescentiform organ fitting snugly between the major adductor muscle and the free valve margins. A

comparison of the shape of the gill of a typical pectinid and ostreiid with the shell shape of 'lunate' oyster species (text-fig. 1) can leave no doubt that this lunate shape is a direct reflection of the size and importance of the gill in fossil species such as *A. colubrina*. This organ was of such paramount importance to these fossil species that it assumed a dominance over all other soft parts.
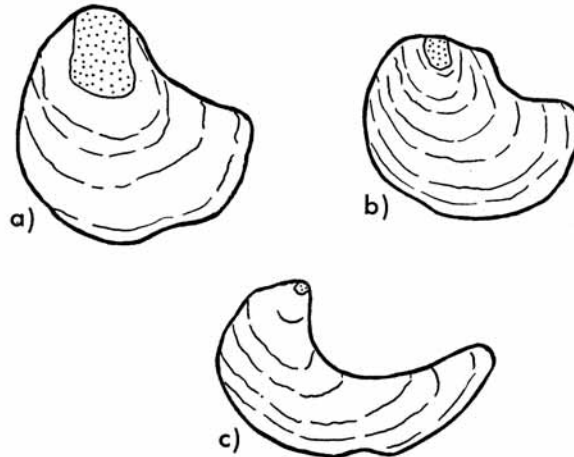
TEXT-FIG. 7. A lineage of oysters from the Upper Jurassic and Lower Cretaceous of Siberia that exhibits a continuous trend towards branchiform shape; notice the concurrent reduction in size of the attachment scar (stippled). (a) *Liostrea* ex. gr. *delta* (Smith), Kimmeridgian; (b) *Liostrea praeanabarensis* Zakharov, Volgian; (c) *Liostrea anabarensis* Bodyl, Valanginian. All ×⅓ (after Zakharov 1965, fig. 1a, e, and i).

The gill of Recent bivalves, including oysters, grows by the addition of filaments to its distal end (Yonge 1960). This corresponds exactly with the position of the 'generative arc' in fossil *Arctostrea*; as the gill grows by distal addition of new filaments, so must the shell have been expanded in a similar direction in order to provide protection for the growing gill. Examination of Recent oysters (e.g. *Pycnodonte hyotis* (Linnaeus)) in which the *over-all* shell shape is not arcuate, reveals the presence on the floor of the valves, particularly the left, of a marked arcuate gutter in which the gill is situated. There is a similar 'gill gutter' in many fossil species (e.g. *Arctostrea diluviana* (Linnaeus), Pl. 85, fig. 1). In both fossil and Recent species the floor of this gutter is often lined with shell of a peculiar pustulose character; in specimens of *Arctostrea* similar pustulose structure can be observed along the length of the shell (Pl. 87, fig. 4).

In view of the close functional relationship between the gill and shell shape, the term *branchiform* will be used to describe species that reflect this relationship in their external shell form.

Sanitation. Sanitation is a general problem that arises amongst animals that have adopted a horizontal mode of life on the sea floor. In the Bivalvia it is usually effected
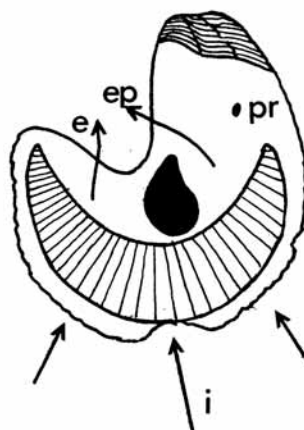
by the accumulation of pseudofaeces around the edge of the mantle cavity, and their periodic ejection by sharp contractions of the adductor, but such a mechanism may be insufficient in turbid waters. It appears to be accepted amongst writers on Recent oysters (e.g. Menzel 1955) that the presence of a promyal chamber in Recent *Crassostrea* is a specific adaptation to allow a greater flow of water through the shell, and hence to aid with sanitation and to prevent the exhalent chamber from being invaded by sediment. (The promyal chamber (present in the right valve only) is an additional passage for the exhalent current situated *dorsal* to the adductor muscle; it is formed by the local separation of the mantle from the underlying body-tissues.)

Certain extinct oysters certainly possessed promyal chambers. For instance, the Danian *Crassostrea ameghinoi rocana* has an adductor scar situated distant from the dorsal margin (text-fig. 8), a sure sign of the promyal chamber in Recent species. In addition there is a conspicuous pedal retractor scar in this species, suggesting that the foot was an active aid to mantle cavity cleansing.

However, the morphology of *Arctostrea* is such that we can be equally certain that it lacked a promyal chamber. The adductor scar is generally very close to the dorsal margin, and there is no room at all for an efficient flow of water dorsal to it (Pl. 87, fig. 4). Yet the most branchiform specimens of *Arctostrea* in the Jurassic and Cretaceous are found in fine-grained muddy sediments such as the Oxford and Kimmeridge Clay, and the Chalk. It is in just that type of environment that efficient water circulatory and cleansing

TEXT-FIG. 8. *Crassostrea ameghinoi rocana* von Ihering, Danian, Argentine. ×1. Reconstruction of the gill and feeding currents. *I*, inhalent current; *E*, exhalent through current; *EP*, exhalent current from promyal chamber; *PR*, pedal retractor muscle; adductor in solid black; gill, ruled lines. BM LL26838.

mechanisms are of paramount importance; in the absence of a promyal chamber it must be assumed that the large size of the gill itself was adaptive in this respect, since it would ensure a very powerful current of water through the branchiform shell.

The zigzag commissure. Rudwick (1964) concluded that in the Brachiopoda zigzag commissures serve two purposes, both fundamentally protective: firstly, for any given gape a zigzag prevents the entry of particles above a certain size, whilst conferring a relative increase in the area of slit actually functioning as intake; secondly, since the mantle tissue lining a zigzag slit is sensitive, there is also a relatively larger amount of sensitive warning tissue available to the animal in proximity to its shell edge.

One would expect it to be significant that the only Bivalvia that possess plicate commissures homoeomorphic with the brachiopods are those that have adopted the brachiopod mode of life and ecologic niche. Whatever the significance of zigzag commissures might be, one would *a priori* expect it to be similar in the two groups. Yet it does not seem to me that Rudwick's explanation is applicable to *Arctostrea*.

I i

The first of the above postulates is unsatisfactory on two counts. Firstly, *Arctostrea* lives dominantly in finer-grained sediments, generally of or below sand grade; I know of only one locality where it is collected associated with small pebbles. Secondly, and more seriously, bivalves do not remain feeding whilst being pelted with a miniature hailstorm of sediment, no matter how paradigmatically rigorous their zigzag commissures may be. In conditions of high turbidity, the average bivalve firmly closes its shell. It is fair to conclude that *Arctostrea*, when inhabiting its usual facies, would have had its valves gaping more widely than the average size of particles present in the substrate and therefore that the zigzag commissure would have offered virtually no protection at all against ingestion of such material.

The second of the postulated functions has the same structural paradigm as the first (one of the problems of mechanistic analyses is that differing functional interpretations can have very similar structural paradigms), and there is little that can be added to Rudwick's original discussion. Undoubtedly, given that the mantle edges are sensitive to clouds of (say) silt, and will cause the shell to close on contact with such a cloud, then a zigzag commissure is relatively more efficient than a similarly long planar commissure. But whether this gain in efficiency is sufficient to explain the evolution of a zigzag slit is open to some doubt, particularly as this interpretation fails to account for one of the more striking features of the morphology of *Arctostrea*—that the zigzag is conspicuously just as well developed over the *exhalent* posterior borders as it is over the inhalent anterior borders (Pl. 86, figs. 2, 6, 7). (This was not as marked a feature of the earlier Jurassic members of the group, where the zigzag is noticeably not as well developed over the exhalent as over the inhalent currents.)

Assuming that the zigzag is a significant feature of the morphology, how then is it to be interpreted? It would not seem likely that the zigzag was for the purpose of preventing anything from leaving the shell. We are left with two alternatives:

1. The zigzag was physically preventive against the entry of harmful agents. We have already concluded that it is unsatisfactory to believe that the zigzag slit served to keep out large 'ball-bearing' type particles, particularly since it is equally developed all round the shell. The implication is that, if the zigzag was to prevent the entry into the shell of some harmful agent or other, then this agent must have been capable of penetrating against the powerful exhalent stream of the oyster. This immediately precludes sediment and suggests a motile, and hence organic, agent. Thus it might be considered that the zigzag served to prevent the penetration of small irritants such as crustacea and fish into the mantle cavity (M. J. S. Rudwick, personal communication). Whilst this is a function which a zigzag commissure must inevitably fulfil by nature of its morphology, it is open to some doubt whether or not this is an explanation that can explain the evolution of the zigzag.

2. The zigzag had a beneficial hydrodynamic effect on feeding currents. A zigzag slit has an inevitable hydrodynamic effect on the water flowing through it. First, and most important, due to the geometry of the zigzags there is an effective vertical spatial spread of the inhalent and exhalent currents; this is so whether the current was an external one or was merely the feeding current intrinsically generated by the oyster itself. Accompanying this, there would probably be a tendency for jet streams to form at the crests and troughs of the zigzags; any such tendency would be of considerable value, particularly on the exhalent margin where it would assist in carrying ejected sediment away from the

edge of the shell (cf. the exhalent gill streams of the Lamprey). It must also be remembered that it is not only the topology of the shell edges that affects the inhalent current stream of a feeding oyster. In all Recent oysters the muscular flexibility of the actual mantle edges is an important factor influencing the direction and strength of feeding currents. By approximating its mantle edges along the flanks of the zigzag, but leaving them parted at the crests and troughs, *Arctostrea* could have greatly enhanced any natural tendency for jets to form at these points.
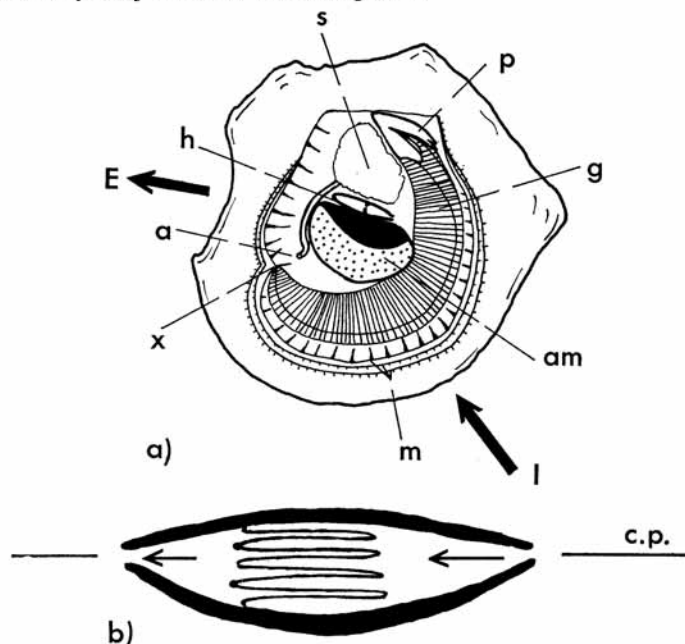
TEXT-FIG. 9. (*a*) Soft part anatomy of *Ostrea edulis* Linnaeus (after Yonge 1960). *p*, palps; *g*, gill; *am*, adductor muscle; *m*, mantle edge; *x*, distal point of junction of the gill and mantle lobes; *a*, anus; *h*, heart; *s*, visceral mass. *I*, inhalent current stream; *E*, exhalent current stream. (*b*) Diagrammatic cross-section through the mantle cavity and gills of *Ostrea edulis*, with feeding currents indicated by arrows. *c.p.*, plane of the commissure.

The pseudolamellibranch gill of an oyster is roughly W-shaped in cross-section, each V corresponding to a demibranch (text-fig. 9*b*). There are two such gills, which are attached to the mantle surface marginally and distally, and thus effectively partition the mantle cavity into two chambers and act as a 'sieve-strainer' to the inhalent current stream. In a typical oyster the gills are fairly close together and form thin high Ws (text-fig. 9*b*). Since the lateral cilia on each filament draw the water through the gill at right angles to the gill lamellae, the general inhalent current stream is impinging on the gill lamellae at a very oblique angle and filtering is somewhat inefficient. Obviously more efficient feeding, and in particular a higher rate of water filtration, will be possible if the gill-W becomes wider, for this would ensure that the current stream impinges on

the individual gill lamellae at a high angle (text-fig. 10). Of course, in order for this adaptation to be possible, the animal first has to have evolved a deeper body cavity. However, given such a deeper body cavity, feeding would obviously still be relatively inefficient if the commissure were to remain planar, for the inhalent current would not spread laterally far enough to meet directly the majority of the gill surface. But should the valve edge become plicate, then these problems are solved at a single stroke: the
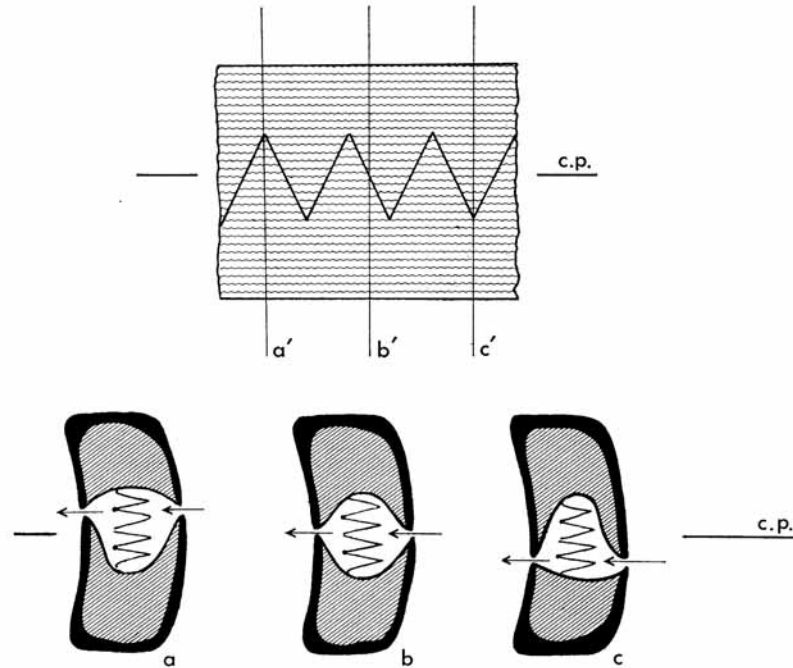
TEXT-FIG. 10. Reconstructed cross-sections through the gill and mantle cavity of *Arctostrea*. (*a–a'*) an inhalent current entering the shell at the crest of a zigzag is best situated to bathe the upper gill; (*b–b'*) an inhalent current entering medially on the flank of a zigzag is best situated to bathe the inner demibranchs of both gills; (*c–c'*) an inhalent current entering at the trough of a zigzag is best situated to bathe the lower gill. *c.p.*, theoretical plane of the commissure.

gill-W can become relatively wider and still be bathed directly in strong inhalent current streams. The effect of a zigzag slit such as that of Pl. 86, fig. 6, *must* be to effectively separate the inhalent current into a set of streams (at the crests of the zigzags) for the upper gill, and a set of streams (at the troughs of the zigzags) for the lower gill. And since it is equally important that there be efficient exhalent current streams the zigzag is developed over the exhalent length of the commissure as well. Phylogenetically one would expect the inhalent zigzag to be the first to be selected for, which is just what is observed in primitive populations of *Arctostrea*.

Further comments on diminution. It was earlier noted (p. 468) that it is theoretically

possible to construct a shell in which the zigzag does not diminish in amplitude along the lateral flanks, but only by assuming that the secretion pattern across such a shell be non-linear (text-fig. 5c). In view of the almost axiomatic presence of linear secretion patterns in the Bivalvia (this contrasts with their common absence in the Brachiopoda), it is possible to argue that no specific functional (or adaptive) significance be attributed to diminution of amplitude of a zigzag on the lateral shell margins, for such diminution is an inevitable result of a linear secretion rate. By terming the zigzag commissure of *Arctostrea* a 'geometrically graded' zigzag, I have aligned myself with this view. However, should it be felt that a more strictly adaptive explanation is necessary in order to satisfactorily account for the diminution of zigzag amplitude, the interpretation given above for the over-all shell shape and initial presence of the zigzag (that they are linked with the size and importance of the gills) may also be applied here.

Several writers (e.g. Yonge 1926) have noted that in Recent *Ostrea* the inhalent current is strongest in the middle of the gill, and falls off considerably to either side of the mid-point (cf. text-fig. 9). The diminution of amplitude of zigzag in *Arctostrea* is such that it occurs towards the two ends of the gills, thus automatically ensuring that the inhalent current be relatively weaker here than in the centre of the gills. Obviously, though a shell such as text-fig. 5c is theoretically possible, such a zigzag would furnish undesirably strong inhalent currents right at the ends of the gills. It may also be noted here that the complete suppression of the more dorsal zigzags on the commissure of *Arctostrea* (cf. Pl. 86, fig. 4) only takes place after the zigzags in question have migrated relatively dorsal of the functional end of the gill (Plica 1, text-fig. 4).

Zigzag commissures in other bivalve genera. The presence of a true zigzag commissure is rare in the Bivalvia; the only other occurrence known to me is in the Australian pectinid *Chlamys asperrimus* (Lamarck) where a sharp zigzag of low amplitude and relatively constant wavelength can be seen (Pl. 87, fig. 9). It seems probable that zigzags are related to the demands made by inhalent currents spread round most of the commissure, and hence are restricted to bivalves that live lying on the substrate with their commissures horizontal.

Funnel spines

1. *Arctostrea*. Granted that the zigzag valve edge has the functional significance attributed to it above, we have an important clue as to the function of the small 'funnel spines' of *Arctostrea*. It will be remembered that these spines are invariably developed at the crests of plicae on the anterior valve margins but are usually poorly developed over the posterior valve margins (cf. Pl. 86, fig. 2; Pl. 88, fig. 5). Thus they are concentrated over the inhalent arc of the commissure and are only developed during that part of the ontogeny of a plica before the true zigzag of the plica has fully developed. It would, therefore, seem likely that they serve the same function as the zigzag itself does later; in other words they enable all parts of the gills to be irrigated with currents of water impinging as far laterally as possible. It is worthy of further note that those few populations that habitually secrete several of these funnel spines on a single plica, one beneath the other (Pl. 88, fig. 4), are just those populations that have a zigzag of conspicuously small amplitude.

It should be stressed at this point that though the above discussion has attributed a function to the shell spines themselves, it is, of course, flaring funnels of epithelium

along the mantle edge that have the primary functional significance as far as inhalent current streams are concerned; the actual funnel spines on the shell are doubtless secreted partly as support, and partly as protection for such epithelial funnels. It is possible, particularly in fossil species, that flaring funnels of epithial material could have reached well away from the shell edge; similar funnel spines are known in fossil productoids (Muir-Wood and Cooper 1960, pl. 21).

2. Other Bivalvia. Discussions of inhalent and exhalent currents in the Bivalvia usually tacitly assume that the ideal inhalent current is one of constant velocity and magnitude, covering as great a length of commissure as is consistent with other structural demands. There is considerable circumstantial evidence that this view is erroneous: The vast majority of infaunal bivalves receive their inhalent current either down a closely confined siphonal passage or else through a narrow restricted part of the mantle edge. It is likely that gill morphology and function has evolved in step with this, and is in many cases better suited to deal with strong localized inhalent currents than with weak, widely spread ones.

There are other bivalves apart from *Arctostrea* that have conspicuous tubular spines. *Pinna rugosa* Sowerby (Pl. 86, fig. 5) and *Etheria elliptica* Lamarck (Pl. 88, fig. 1) are two of the more striking examples, and it is reasonable to interpret their spines too as reflecting the presence of epithelial funnels that provide the gills with a series of laterally spread, spaced inhalent streams. It is noteworthy that in both these species the spines are only open to the exterior when they are situated right at the very edge of the shell; as soon as they have been displaced even slightly dorsally by further mantle expansion and shell secretion they are sealed off with a thin layer of shell. There is a definite need for observational and experimental evidence to test this theory; but even should it ultimately prove to be untenable it is certainly the most reasonable explanation for these tubular spines in our present state of knowledge. None of the paradigms for other favourite functions attributed to spines (sensory, camouflage, protective, etc.) is closely approached by the morphology of the spines of *rugosa* and *elliptica*. In particular, none of these functions will fit in with the known ecology of *Etheria*—cemented to rocks in the rapids of fast flowing, turbid freshwater rivers. Yet the funnel hypothesis might well be particularly applicable here; for *Etheria* has a conspicuously elongated shell in a dorso/ventral direction. If this should be oriented parallel to the flow of the river, with

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EXPLANATION OF PLATE 89

Figs. 1, 2. *Lopha folium* Linnaeus, phenotype *folium*, Recent, Farsan Islands, Red Sea. ×1. External and lateral view of a left valve, attached to a thin twig by the secretion of clasping spines. Note the dorsal diminution of amplitude of the zigzag commissure. SM D.20866.

Figs. 3, 4. *Lopha folium* Linnaeus, phenotype *cristagalli*, Recent, unlocated. ×1. External and lateral view of a double valved specimen. Note the large amplitude of the zigzag commissure and the secretion of spines as 'props' for assisting in stability of fixation. UMZC 2002 (Saul Collection).

Figs. 5, 6. *Lopha folium* Linnaeus, phenotype *bresia*. Recent, unlocated. ×1. External and lateral view of a double valved specimen. Attachment is in this case by cementation of a large area of the left valve (reflected in the large unornamented area on the right); the zigzag commissure is of a moderate amplitude. UMZC 2003 (Saul Collection).

Fig. 7. *Pycnodonte hyotis* (Linnaeus), Recent, unlocated. ×2. An extreme example of development of funnel spines at the crests and troughs of a strong marginal zigzag. UMZC 2001 (McAndrew Collection).

the dorsal end upstream, then an advantageous eddy effect could well be created around the spines on the ventral periphery.

Many other species of oyster possess funnel spines of greater or lesser significance. *Pycnodonte hyotis* (Linnaeus) is one species that has beautifully moulded funnel spines placed in the crests and troughs of its marginal zigzag (Pl. 89, fig. 7). Even more striking is the juvenile stage of *Crassostrea echinata* (Quoy and Gaimard) (Pl. 88, fig. 2). At a very early stage after spatfall this species has secreted a most complex set of funnel spines. In the light of its favoured habitat of mangrove swamps, it would seem certain that the epithelium lining these spines directly aids the circulation of uncontaminated water and indirectly helps to provide an adequate oxygen supply to the animal. At a slightly later growth stage, the spines become less obviously funnel-shaped, but project as long tubular structures reaching well away from the shell edge. The animal is presumably at this stage even more concerned with gathering an inhalent current stream from as far away from its mangrove attachment site as possible (the roots to which these animals are attached are generally covered with an evil-smelling slime). There are no spines at all in the adult growth stage, perhaps because the left valve of the shell is by then large enough to ensure that the mantle edge is removed from immediate proximity to the substrate.

RECENT OYSTERS: TURBID WATER ADAPTATIONS

Students of Recent oysters currently recognize two major groupings into the genera *Ostrea* and *Crassostrea*. These genera are distinguishable on several counts, but the major structural difference is the presence in *Crassostrea* of an exhalent passage dorsal to the posterior adductor in the right valve; this passage is termed the *promyal chamber*, and ever since its discovery by Nelson (1938) it has been envisaged as an adaptation enabling *Crassostrea* to inhabit turbid waters. This hypothesis agrees well with the known preference of *Ostrea* for offshore clear water, whilst *Crassostrea* favours a muddy estuarine habitat. Such an ecological distribution might also be suggested to be linked to the other major difference between the two genera: *Crassostrea* is oviparous, and *Ostrea* is larviparous.

In a lucid comparison of local American species of *Ostrea* and *Crassostrea*, Menzel (1955) listed several adaptations, additional to the presence of a promyal chamber, that he considered to increase the efficiency of life in turbid waters; most of these adaptations were connected with the development of better cleansing mechanisms.

It is especially noteworthy that *Crassostrea* has more frequent snapping of the valves to eject pseudo-faeces, regardless of the turbidity of the water that it is placed in, and this is linked to a tendency to form and expel much larger quantities of mucus and pseudo-faeces than does *Ostrea*. Two further adaptations come into play in really turbid water: first, the tentacles of the mantle edge are intermeshed, and thus form a partial guard against excessive amounts of sediment entering the mantle cavity; and second, there is the formation of what Nelson (1938) has termed 'pseudo-siphons' in the presence of very heavy suspensions. These pseudo-siphons are formed by contraction of the mantle edges of the right valve to form a groove along which entering particles are then funnelled. In *Crassostrea* there is one inhalent pseudo-siphon, and two exhalent, the second corresponding to the presence of the promyal chamber.

It should further be noted that of all the adaptations serving for greater efficiency in turbid waters, only the promyal chamber involves a structural adaptation; all the other mechanisms, whose efficacy can scarcely be doubted, involve only behavioural adaptation. There is, therefore, no reason to suppose such adaptations to be limited to *Crassostrea*, and, indeed, Menzel makes it clear that Recent *Ostrea* also possesses most of these behavioural adaptations, but to a very much lesser degree than does *Crassostrea*.

Because it involves a structural adaptation, the presence of a promyal chamber can be inferred in fossil species, and, as pointed out earlier, there can be no doubt that *Arctostrea* did not possess a promyal chamber. However, it is virtually certain that the environment favoured by *Arctostrea colubrina ricordeana* was one that could become locally extremely turbid should something disturb the bottom sediment. It would therefore seem inherently highly likely that *ricordeana* (and probably many other species of *Arctostrea*) possessed behavioural adaptations similar to those outlined above for Recent oysters. These would include tentaculate mantle edges, the frequent ejection of pseudo-faeces, and the formation of pseudo-siphons. It is likely that in spite of the large flow of water through the whole shell, brought about by the large gill and branchiform shape, there was a concentrated exhalent flow just posterior to the adductor muscle where the anus debouches its load. The presence of a double plica in the shell edge of occasional specimens of *Arctostrea* (e.g. Pl. 88, fig. 3) at this point is strong evidence for the presence of persistent pseudo-siphons here.

One further facet of the habits of Recent oysters is relevant to discussion of *Arctostrea*. Oysters are in constant danger of being buried under their own pseudo-faeces, together with encroaching sediment. Nelson (1938) observed that 'through . . . movements of the valves, together with adaptive adjustments of the mantle borders, the oyster on soft bottom clears an open zone about itself, and wards off encroaching mud'; and Lund (1957) has shown that even at relatively low turbidities (70–95 per cent. light transmission), oysters on the bottom of an aquarium which has no through currents will completely bury themselves in 36 days.

EXPLANATION OF PLATE 90

Fig. 1. '*Lopha*' *semiplana* (J. de C. Sowerby), Upper Chalk, Hartford Bridge, Norwich. ×1½. Left valve of a double valved specimen that was attached in life to a straight cylindrical object. Note the few, spaced, strong ribs. SM B.6803.

Fig. 2. '*Lopha*' *semiplana* (J. de C. Sowerby), same locality as 1. ×1½. Internal view of a right valve displaying well the gill attachment scar ventral to the adductor; note also that the dorsal margin of the adductor scar is convex dorsally. SM B.6796.

Figs. 3 and 4. *Arctostrea pusilla* (Nilsson), Upper Chalk, Norwich. ×1½. Right and left valves of a well-preserved specimen probably attached in life to a belemnite. SM B.1122; figured by Woods, plate 47, fig. 11.

Fig. 5. *Arctostrea pusilla* (Nilsson), Upper Chalk, Fareham, Hants. ×1½. Internal view of a right valve. Note the lack of any gill attachment scar, and the fact that the adductor scar has a dorsal border concave dorsally. SM B.66558.

Fig. 6. *Arctostrea pusilla* (Nilsson), same specimen as figs. 3, 4. ×2½. Lateral view. Note the open crested plicae, and the dorsal diminution of amplitude of the zigzag.

Figs. 7 and 8. *Arctostrea pusilla* (Nilsson), Cambridge Greensand. ×2. Specimen attached to an ammonite shell, and hence reflecting the shape of an ammonite in its own shell form. BM LL26835.

Fig. 9. *Arctostrea pusilla* (Nilsson), grey Chalk Marl, Folkestone, Kent. ×2½. BM LL26830.

Fig. 10. *Arctostrea pusilla* (Nilsson), Cambridge Greensand. ×2½. Specimen attached to an ammonite shell. BM LL26837.

It is obvious that the narrow, high shell of *Arctostrea* is ideally shaped to avoid problems of this sort. Though one would hesitate to assign any primary functional significance to this aspect of over-all shell shape, it must certainly have been a beneficial side-effect of the over-all morphology.

THE ITERATIVE EVOLUTION OF ZIGZAG VALVE EDGES

It is easy to understand how 'pre-adapted' the ostreiiform mode of life is for the iterative evolution of zigzag valve structures. As oysters usually settle on flattish sur-faces, and as initial shell form is entirely dictated by the shape of the attachment surface, the gills of a juvenile oyster of any kind must of necessity be a thin, high W. But should there be at any subsequent stage a tendency for shell secretion to continue whilst mantle expansion is inhibited, i.e. any tendency for the formation of a vertical zone, then the gill *of necessity* (because it is attached to the valve interior laterally) becomes pheno-typically a broader, less acutely angled W. Now the attachment surface, of course, is rarely quite flat and may in fact be possessed of considerable relief; this relief, again *inevitably*, is reproduced in the growing edge of the vertical zone, and we thus have a ready-made undulose commissure.

These two phenomena, lateral widening of the gill-W and the inception of an undulose commissure, may both be predicted to occur phenotypically in a proportion of any population of oysters; the first is an inevitable result of building a vertical zone, and the second an additional result of this plus the irregularity of most attachment surfaces. On selection, there will be a tendency for muta-tions in a similar direction to accrue in the gene pool of a population in which it was advantageous to possess a zigzag valve edge and a widened gill. Thus an initially phenotypic undulose commissure might be rapidly trans-formed into a genetically stable and functionally more efficient zigzag commissure.

TEXT-FIG. 11. *Arctostrea colubrina* (Lamarck), Chalk Marl, near Cambridge. × ⅔. A cross-section through the closed shell some distance distal to the adductor; view looking distally. Note the deep body cavity (infilled with sediment, stippled) and the pre-sence of a series of calcareous plates, or 'septa' (all calcareous shell material in solid black), separated by cavities. SM B.6594.

There is obviously a limit to the amount of lateral widening that the gill can accept without detrimental effects on its basic physiology. It would seem that *Arctostrea* has exploited this structural plasticity almost to that limit; internally the genus secretes a series of calcareous plates (or septa, text-fig. 11) which serve to keep the floor of the valve (and therefore the lateral edges of the gills) progressively in line with the crests and troughs of the zigzag (Pl. 85, fig. 2). In other words, the depth of the body cavity is adjusted so as to coincide with the amplitude of the peripheral zigzags, thus ensuring that the most lateral parts of the gills are kept in a zone of continued strong inhalent currents.

CONCLUSION

The interpretation of the morphology of *Arctostrea* as dominantly due to increased efficiency of feeding and cleansing habits has the major advantage that it enables the morphology to be understood as an integrated whole. The animal can be viewed as 'all adaptation', and not merely as a bundle of discrete adaptations. The shape and detailed morphology of *Arctostrea* are the result of selection for an ever larger and more efficient set of gills. The subsidiary, but important, adaptation found in *A. colubrina ricordeana* was initially a phenotypic response to a specific and difficult environmental regime; though it is not possible to demonstrate rigorously, it would seem likely that the spines characteristic of this subspecies became incorporated in the genotype before its early extinction.

APPENDIX: TAXONOMIC NOTES ON *ARCTOSTREA*

It is customary in England to use the generic name *Lopha* for oysters throughout the Jurassic and Cretaceous that possess a plicated valve edge of any type. This usage obscures the fact that there are, in fact, several morphologically discrete groups of oysters which happen to possess in common the character of a more or less plicate valve edge. Indeed, if anything is commoner in the Ostreiidae than the iterative evolution of gryphaeate shape, it must be the repeated evolution of plicate valve edges.

The type species of *Lopha* Bolten 1798 (and also of *Alectryonia* Fischer 1807) is *Ostrea cristagalli* (Linnaeus), a Recent species from the Indo-Pacific with very coarsely plicated commissure, and a generally rounded valve outline. Thomson (1954) has placed this species in synonymy with *Ostrea folium* Linnaeus, which species is thought to contain three phenotypic variants formerly considered as discrete species—*cristagalli* Linnaeus (Pl. 89, figs. 3, 4), *folium* Linnaeus (Pl. 89, figs. 1, 2), and *bresia* Iredale (Pl. 89, figs. 5, 6). Even allowing for the notoriety that oysters have achieved as variable animals, there is still sufficient morphological range here to tempt even the most conservative to establish two genera for its accommodation. Yet Thomson, after a close study of the animals as well as shells, is quite specific that it 'is inescapable that this is one species which responds variably according to the substrate and to degree of immersion' (p. 148).

Oysters with plicated valve edges are common in the Chalk, and fall into three quite distinct morphological groups. Only one of these groups—that of *Lopha semiplana* (J. de C. Sowerby) (Pl. 90, figs. 1, 2)— is at all reasonably placed in *Lopha* s.s.; the other two groups are best placed in the genus *Arctostrea* Pervinquière 1910. They are *Arctostrea colubrina ricordeana* d'Orbigny and *A. pusilla* (Nilsson).

'*Lopha*' *semiplana* (J. de C. Sowerby)

In his detailed monograph on Cretaceous Bivalvia, Woods (1899–1913) carefully discussed the forms of *Lopha* known in the Upper Chalk horizons and concluded that there was only one valid common species, that of *L. semiplana*. That this species was very variable was both explicitly noted and implied by the vast synonymy that was quoted. Examination of large numbers of Chalk oysters has convinced me that there are two quite distinct forms presently included in *L. semiplana* (Sowerby) *sensu* Woods, and this is confirmed by an examination of type material held in the Norwich Museum and British Museum (Natural History). Whether these two forms represent genetically different species, or whether they are merely phenotypic variants of a single species, is a moot point. In the light of Thomson's

work on the Recent *L. folium* it is virtually impossible to state categorically that any two oysters collected from the same horizon are not conspecific, no matter how different their morphology. However, amongst several hundreds of specimens I have not seen a single one that is not obviously one form or the other, and this points to their being true genetically isolated species; it is, however, conceivable that they represent phenotypes responding to two quite different environmental niches, and that the lack of intermediates is due to the lack of intermediate environmental niches.

The two forms are illustrated on Plates 87 and 90. The true *L. semiplana* has a large irregularly rounded shell (Pl. 90, figs. 1, 2) and is usually attached either to a large flattish surface, or to other specimens of its own kind, or to thin branching objects. It possesses a few (commonly less than 12) broad undulations around the free margins of the commissure which give rise to rounded spaced ribs on the shell surface during shell growth. There is conspicuous crenulation of the margins on either side of the ligamental area, often spreading some distance distally around the commissure; often a well-marked and characteristic gill attachment scar is visible just antero-ventral to the adductor muscle (Pl. 90, fig. 2). The adductor muscle scar itself is large, and has a dorsal margin that is usually *convex* dorsally (Pl. 90, fig. 2); in rare specimens it may be straight.

Of the two specimens originally figured by Sowerby (1812–46, pl. 489) only one, the larger and left hand of the two specimens, is still known. It is here designated lectotype, and is in the collections of the British Museum (Natural History).

The other form has a small lozenge-shaped shell generally reflecting, as Woods pointed out, the preferential attachment to a *Belemnitella*, crinoid stem or similar object. When the attachment surface allows, this species develops the branchiform shape so characteristic of *Arctostrea* (Pl. 90, figs. 3, 4). It possessses a plicated commissure, but the plicae are sharp, numerous (rarely if ever less than 17; commonly over 40), and of the type described as open-textured earlier in this paper (cf. Pl. 86, fig. 6; Pl. 90, figs. 6, 9). The ligament area is small, and without the very marked central pit of *semiplana* s.s., and though crenulations on either side of the ligament area may be developed, they are generally somewhat inconspicuous. The adductor scar is of moderate size and has a dorsal border that is markedly *concave* dorsally (Pl. 90, fig. 5).

The earliest British name available for this form is *Ostrea alaeformis* S. Woodward 1833. Of the three specimens originally figured by Woodward, only one, that of his Plate 90, fig. 3, is still extant. It is here re-figured (Pl. 87, figs. 1–3) and designated lectotype. However, there is an earlier named species of this type from the Upper Cretaceous of Scandinavia—*Ostrea pusilla* Nilsson 1827. Unfortunately the type of *pusilla* is missing from the collection of Nilsson's types at the University Geology Museum, Lund, but there are many specimens of a small *Arctostrea* conspecific with *alaeformis* in Swedish Upper Cretaceous ('mammillatuskrita') faunas. Following Woods's monograph, these specimens are usually labelled as *semiplana* Sowerby, but occasionally an early label reveals that this is the form called *pusilla* Nilsson by Scandinavian workers of the pre-Woods era. On balance, it seems best to adopt the name *pusilla* for this species and to place *alaeformis* in synonomy accordingly.

Though *pusilla* is common in Britain only in the Middle and Upper Chalk, rare specimens from the Cambridge Greensand (Pl. 90, figs. 7, 8, 10) and the Lower Chalk (Pl. 90, fig. 9) demonstrate that it was present in British seas as early as the Cenomanian. These early occurrences are interesting for they serve to show that the species was sympatric with its relative *Arctostrea colubrina*. These early specimens seem to show a strong preference for attachment to ammonite shells (Pl. 90, fig. 10), though this may be due to the small number of specimens available for study.

The introduction of Arctostrea. This name was first introduced as a subgenus of *Alectryonia* by Pervinquière 1910*a*. The subgenus—based on *Ostrea carinata* Lamarck from the Cenomanian of Le Mans —received the immediate approval of Douvillé.

Alectryonia, as noted earlier, is an absolute synonym of *Lopha*, the two genera being based on the same type species; but, anyway, modern European practice is to use *Lopha* and *Arctostrea* as discrete genera, which course is followed in this paper.

Ostrea carinata Lamarck 1806 (Pl. 86, fig. 2; Pl. 88, figs. 4, 5) possesses well the characters that Pervinquière and Douvillé used to distinguish the group they called *Arctostrea*. Particularly diagnostic is the branchiform shape, the sharply zigzagged commissure, and the presence of low, rounded, divaricating ribs on the flattened shell top (Pl. 86, fig. 2). Unfortunately, the name *carinata* is preoccupied by *Ostrea carinata* O. C. Schroeter 1802. However, Pervinquière (1910*b*) has already provided

reasons for treating *carinata* Lamarck 1806 and *colubrina* Lamarck 1819 as merely varieties of a single species, and his excellent plates enable one to agree with this conclusion. Thus, though the genus *Arctostrea* must continue to be based on the holotype of *O. carinata* Lamarck, it is permissible to use the name *colubrina* for this group of Cenomanian forms. It may well transpire that a new subspecific name is necessary for the Le Mans *carinata* population, but this must await a thorough revision of the whole genus.

Cox (1962) has adopted the name *colubrina* Lamarck for the English Cenomanian populations of *Arctostrea*. However, there are definite differences between the fossils from Le Mans and the typical English specimens. Conspicuously the English specimens (Pl. 86, fig. 1) have a more open commissural zigzag of greater wavelength, besides possessing the long 'snowshoe' spines described elsewhere in this paper; for their part, the Le Mans specimens have a zigzag of small wavelength, and the presence of conspicuous funnel spines (Pl. 88, fig. 4) results in the strong development of divaricating ribs on the flat top of the valve (Pl. 86, fig. 2). Accepting, on the authority of Coquand (1869), that the name *Ostrea ricordeana* d'Orbigny 1850 refers to a Cenomanian *Arctostrea* possessing long 'snowshoe' spines, it is convenient to distinguish the English forms as *Arctostrea colubrina ricordeana* (d'Orbigny).

It remains to give brief mention to other English members of *Arctostrea*. The common Jurassic species '*Lopha*' *gregarea* (J. de C. Sowerby) is certainly an *Arctostrea*, and ranges from the Bathonian up to the Kimmeridgian. The genus is not found again in any numbers until the Aptian, where it is a common constituent of the faunas of the Lower Greensand on the Isle of Wight, at Farringdon, and Upware. Woods (1899–1913) considered that these forms were conspecific with the chalk populations, but there are significant differences that warrant the resurrection of the name *macroptera* J. de C. Sowerby. The chalk populations themselves are concentrated at two localities—those of Haslingfield and Folkestone. Specimens of *Arctostrea* are known from other scattered quarries in the Lower Chalk (e.g. Norman Cement Works, Cambridge; Cherry Hinton quarry, Cambridge), but are very rare.

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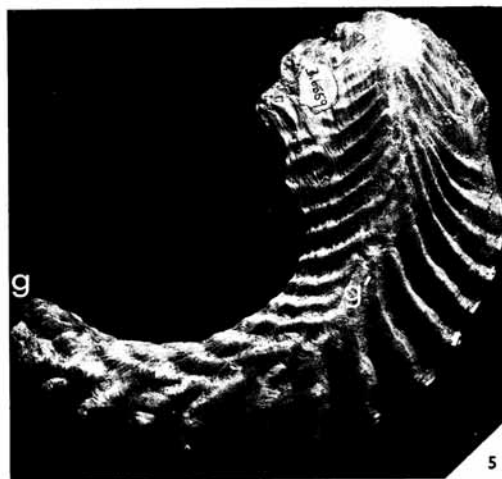
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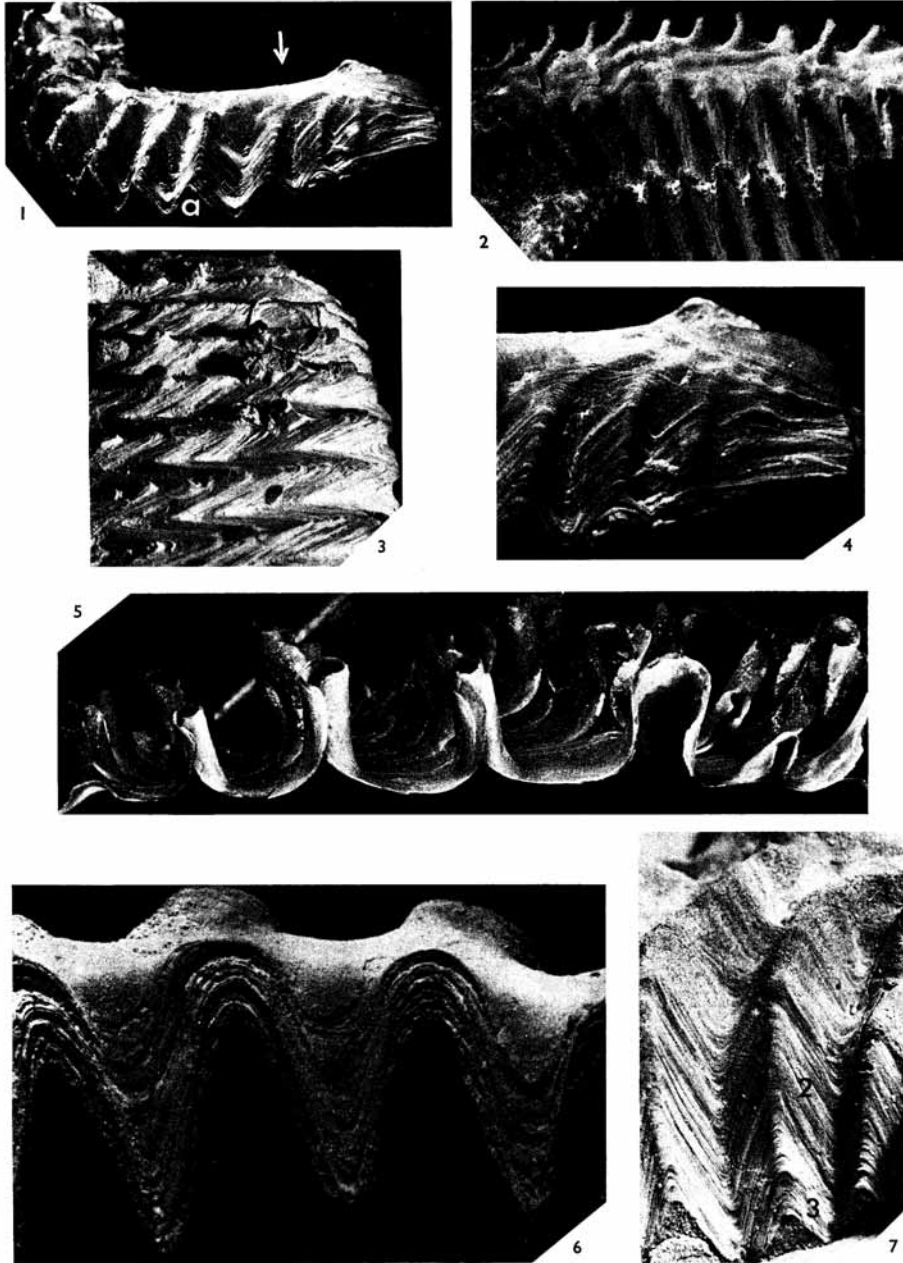Cambridge
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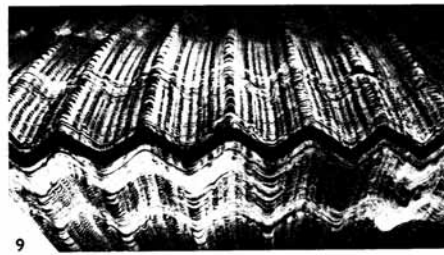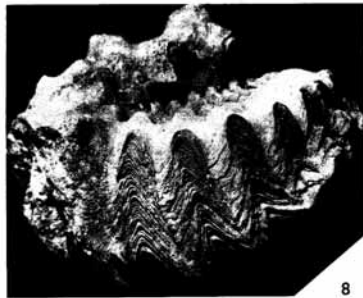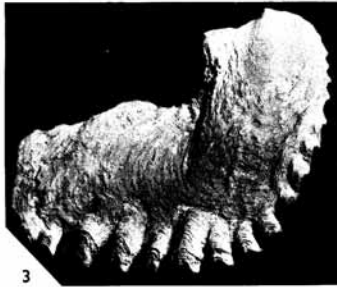University of Otaga
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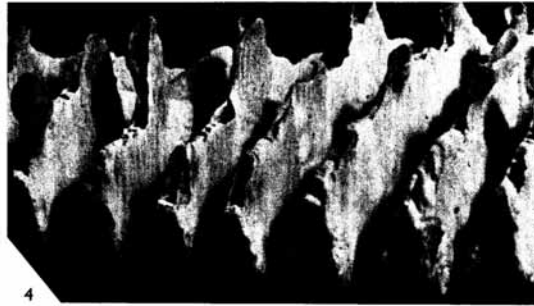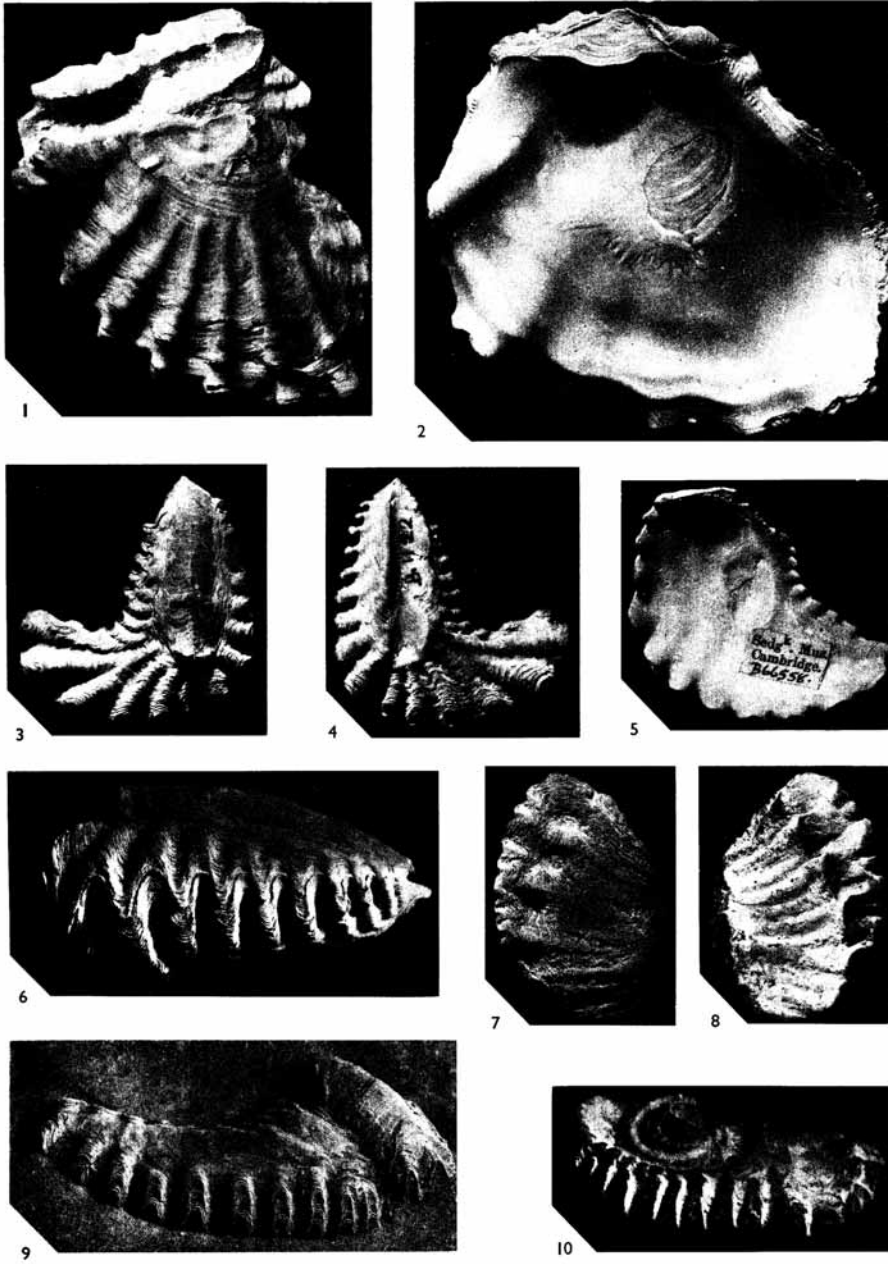Typescript received from author 19 October 1967

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