

THE MODE OF LIFE OF TWO JURASSIC SPECIES OF '*POSIDONIA*' (BIVALVIA)

by R. P. S. JEFFERIES and P. MINTON

ABSTRACT. On facies grounds *Bositra buchi* (Römer) was almost certainly not benthonic, but probably nekto-planktonic rather than pseudoplanktonic, since other possible pseudoplankton is rare in its typical facies, there is no sign of attachment at any stage of life, and there are morphological signs of swimming ability (anterior and posterior gapes, thin shell, and probable wide angle of opening in life). Experiment indicates that this mode of life is feasible. The hinge of *B. buchi* is described for the first time and the species is transferred from *Posidonia* to *Bositra* de Gregorio 1886.

'*Posidonia*' *radiata* Goldfuss was also almost certainly not benthonic on facies grounds. It was probably not pseudoplanktonic since it never occurs attached to wood like indubitable pseudoplankton in the same beds, and is much more abundant than such forms. Morphological evidence confirms that it was probably nekto-planktonic.

The method employed in the feasibility experiments should be widely applicable in studies of the functional morphology of small organisms.

THIS paper deals with the mode of life of *Bositra buchi* (Römer) (= *Posidonia alpina* and *P. ornati* of authors) and '*Posidonia*' *radiata* Goldfuss (= *Posidonia* (*Steinmannia*) *bronni magna* of authors). These bivalves are of interest because they belong to a group widely regarded as pseudoplanktonic.

The most important sources of evidence concerning the mode of life of fossil animals in general are facies, analogy with living relatives, and functional morphology. In the present case facies is the most important of these. Direct analogy with living relatives is unreliable but functional morphology is useful, particularly since many structures are analogous to those of living relatives.

B. buchi and '*P.*' *radiata* belong to a group of thin-shelled Pectinacea which characteristically occur in black shales, together with ammonites or goniatites, in rocks of Devonian to Jurassic age (Newell *et al.* 1953). The group includes *Bositra*, *Posidonia*, *Steinmannia*, *Daonella*, *Halobia*, *Monotis*, *Buchiola*, and *Dunbarella*, and three main views have been expressed about its ecology. A benthonic mode of life was assumed by Pompeckj (1901, p. 178), Haug (1907, p. 152), Vadász (1910, p. 41), Krumbeck (1921, p. 68; 1924, p. 128), Craig (1954, p. 108), and Zangerl and Richardson (1963, p. 135). A pseudoplanktonic mode of life, attached to floating seaweed, was suggested by Clarke (1904, pp. 199, 215), Pompeckj (1914, p. 458), Hundt (1939), Hudson and Cotton (1943, p. 149), Schwarzacher (1948, p. 38), Newell *et al.* (1953, p. 14), Newell (1955, pp. 13, 22), Nalivkin (1956, p. 188), Allan (1956, p. 369), Ichikawa (1958, p. 183), and Sadykov (1962, p. 86). Finally, the view that members of the group were pelagic and free-swimming was put forward by Molengraaf (1917, p. 255, not seen but see Krumbeck 1921, p. 68)—who compared *Halobia* and *Daonella* with pteropods—Guillaume (1928, p. 227), and Prokovlev (1959, p. 122). The views of Weigelt (1922, 1927) and Paul (1939) on the mode of life of *Posidonia becheri* and of Hauff (1921) on '*Posidonia*' *radiata* and *Steinmannia bronni* are discussed in more detail below. Recent works on Mediterranean microfacies refer to *B. buchi*, *S. bronni* and '*P.*' *radiata* as pelagic without discussing whether they were plankton or pseudoplankton (Peyre 1959, AGIP 1959).

Nearly all authors who have recently considered the matter in detail (e.g. Newell 1955, Ichikawa 1958, and Allan 1956) have strongly favoured a non-benthonic mode of life for this group of Pectinacea on facies grounds, regarding the animals as attached to seaweed. Schmidt (1935) was the first to give wide currency to this view. On the other hand, Craig (1954) believed that the Carboniferous *Posidonia corrugata* was benthonic, but this was based merely on comparison with living Pectinidae and is contradicted by his admirably detailed facies evidence.

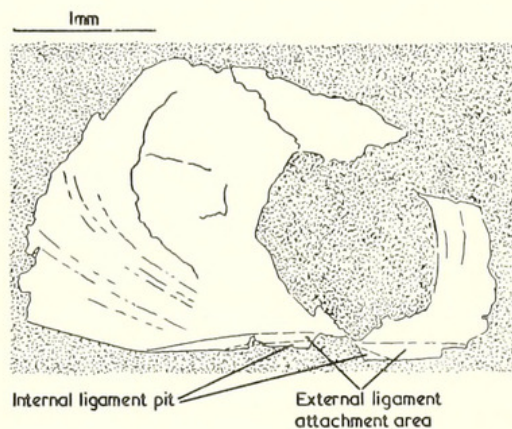
THE MODE OF LIFE OF *BOSITRA BUCHI* (RÖMER)

Bositra buchi (Römer) (*Posidonomya alpina* and *Posidonia ornati* of authors) is a pectinacean of Toarcian to Oxfordian age. The shell is very thin ($60\text{--}70\ \mu$ at a length of 1 cm.) with a prismatic, calcitic, outer layer, and a laminar, nacreous, inner layer; muscle scars are unknown; the outline is almost circular or elliptical, with a height/length ratio of 0.75 to 0.90, and is slightly oblique with prosogyrous, somewhat anterior umbones; rounded, concentric folds of variable spacing, which do not affect the shell thickness, are separated by angular furrows; weak, radial striae are sometimes present; wide anterior and posterior gapes are visible in uncrushed specimens; there is no pteriiform stage in the life history; the valve margins are often brownish.

The cardinal area (text-fig. 1, Pl. 19, fig. 9), which is somewhat thicker-shelled than the rest of the shell, has been seen in material collected by Mr. H. G. Owen from the Oxford Clay of Elstow, Beds. (data with Pl. 19, fig. 9). A shallow, triangular, median pit marked with strong growth lines occupies 45 per cent. of the hinge length; it is the site of the internal ligament, of which traces sometimes remain in the Elstow material. The anterior and posterior portions of the hinge, each representing about 27 per cent. of its length, are the site of the external ligament. Steinmann's description of the cardinal area (*in* Wanner 1907, p. 204) is incorrect.

Bositra buchi differs from the type species of *Posidonia* (*P. becheri* Bronn) in two important respects (cf. Weigelt 1922). The hinge is of pterioid rather than arcid type, since it has no chevrons for the attachment of external ligaments, and the life history is much simpler (see below, p. 170). These differences demand a separate genus and the name *Bositra* de Gregorio (1886, p. 11) is available. *Posidonia ornati* Quenstedt has been selected as type species of *Bositra* (Cox 1964, p. 47), and *P. ornati*, as explained below, is a subjective junior synonym of *Posidonia buchi* Römer.

The family relationships of *B. buchi* are somewhat obscure at present. The Pterinopactinidae, in which Newell (1937, p. 37) placed *Posidonia*, have an arcid ligament and cannot include *Bositra*. Nevertheless, *B. buchi* may be descended from *Posidonia becheri* or one of its relatives, since it has in common the very thin shell consisting of prismatic and laminar layers, similar outline and ornament, a long straight hinge line, and occurrence in the same very unusual black shale facies. The pterioid hinge of *Bositra* resembles



TEXT-FIG. 1. *Bositra buchi* (Römer) showing the cardinal area (LL17400). Data as Pl. 19, fig. 9.

that of an aviculopectinid, but may be an independent development by neoteny from an arcid hinge since Bernard (1896) has shown that modern Arcacea have a pteriid hinge when very young. The process is paralleled in the Arcacea by the evolution of *Limopsis* from *Glycimeris*.

With regard to the specific name, Guillaume (1928) ignored priority by favouring *Posidonomya alpina* Gras 1852 over its synonyms *Posidonia ornati* Quenstedt 1851 and *Posidonia buchii* Römer 1836. The form described by Römer (1835–6, p. 8, pl. 4, fig. 8) from the Lower Bathonian 'Walkererde' of North Germany is certainly identical to the other two, since the ornament and position of the umbo are the same, the specimen is in the characteristic valves-open position, and is described as having a straight hinge line and a very thin shell. The height/length ratio is lower in the type figure of *P. buchii* than in those of *P. alpina* and *P. ornati*, but this probably represents intraspecific variation since the tall form occurs in the Bathonian (e.g. LL17414 from the Fuller's Earth of Normandy).

Facies Relationships

Pelagic organisms are independent of the nature of the sea bottom and are widespread geographically. Their fossil remains are similarly widespread, and occur in a great variety of deposits. They are often abundant in deeper-water deposits, associated almost exclusively with plankton and nekton, even where the bottom waters seem to have been foul and uninhabitable. They may, however, also occur in shallow-water deposits with abundant benthos. The graptolites are the classic illustration of this. The conclusion that an extinct animal was pelagic is thus primarily based on facies, but must not be contradicted by its morphology.

The Typical Bositra buchii Facies. The typical facies in which *B. buchii* occurs is, as Haug (1907, p. 152) pointed out, very like the graptolitic facies. It consists mainly of shale, often bituminous, with subordinate limestone and radiolarian chert. Apart from *B. buchii*, which is often exceedingly abundant, almost the only macrofossils are ammonites, often including *Phylloceras* and *Lytoceras*, together with aptychi and cephalopod (? ammonite) beaks (*Rhynchoteuthis*), though tracks, including *Zoophycus*, may be present. This facies is widespread in Middle Jurassic rocks, and according to Arkell (1956) occupies large areas in south-east France, the eastern Alps, the Carpathians, Lombardy, Peninsular Italy, Greece and Albania, the Betic Cordillera, Morocco and Algeria, Anatolia, the Crimea, the Caucasus, Azerbaijan, Persia and Iraq, Kenya and Tanganyika, and the Southern Andes. Boehm (1912, p. 130) recorded it in the Sula Islands of Indonesia. Slight signs of posthumous drifting may be present in the typical *B. buchii* facies, but there is no possibility that such drifting explains the regular occurrence of the species, for the individual areas where the facies is developed are often hundreds of miles across.

Comparison of figures of geographically separate specimens of *B. buchii* from, for example, Peru (Steinmann 1881, pl. 10, figs. 3, 4), Indonesia (Boehm 1912, pl. 32, fig. 2), and the Crimea (Stremoukhov 1895, pl. 10, figs. 1–8), with those given here (Pl. 19) from France and Iraq shows a striking resemblance in form.

Few detailed studies of the typical *B. buchii* facies have been made. Haug (1892), in a classic work, recognized an area of deep-water sediments of Bajocian to Callovian age in the French Alps. In this 'faciès dauphinois' *B. buchii* and ammonites were by

far the commonest fossils. Indeed Haug (p. 59) said that 'Les céphalopodes [mainly ammonites] et les posidonomyes [*B. buchi*] sont, pour ainsi dire, les seuls fossiles que l'on rencontre dans le Bajocien et dans le Bathonien de nos chaînes subalpines.' It is true that this somewhat overstates the position since tracks, which Haug called *Cancellophycus* (*Zoophycus*), are sometimes abundant, though in places absent, and *Inoceramus* and belemnites occur at one horizon (Lower Bajocian, *op. cit.*, p. 62), but the broad impression conveyed is accurate. In the Bajocian the 'faciès dauphinois' extends continuously some 290 km. from north to south within France and 130 km. from east to west (*op. cit.*, fig. 14).

One of the authors (R.P.S.J.) has examined a small quarry in rocks of Bathonian or Callovian age in the 'faciès dauphinois' (0.6 km. north of the Church at St. Barthélemy-de-Vif, Isère). The rocks exposed were strongly folded, brown, bituminous shales with subordinate bituminous calcarenitic limestones. In order of decreasing abundance the fossils found during five days' collecting consisted of *B. buchi*, which thickly covered many of the bedding planes, tracks (not *Zoophycus*) mainly associated with the limestones, ammonite conchs (indeterminate pachydiscids and a phylloceratid), ammonite beaks (*Rhynchoteuthis*), aptychi, *Pinna* (one specimen only), and two spines of a diadematoïd sea urchin. A count of all the macrofossils encountered in 60 cm. of rock, of which 10 cm. was a band of limestone and the rest shale, revealed 119 single valves and numerous fragments of *B. buchi*, 2 complete ammonites and some fragments, and nothing else. All the fossils came from the shale except for one valve of *B. buchi* in the limestone. The comparative rarity of fossils in the limestones suggests that the latter were deposited quickly, possibly as turbidites.

Contemporary shallow-water rocks exist to the east and south of the Dauphiné facies (Briançon and Provence facies) and have abundant benthos, including many bivalves, brachiopods, echinoderms, &c., but *B. buchi* is not recorded.

There is no doubt, therefore, that in south-east France *B. buchi* had a different facies distribution to other bivalves. It is rare where benthonic fossils are abundant, and abundant where benthonic fossils (except for tracks) are rare. Its common associates, the ammonites, were most probably nektonic (cf. Diener 1912). It is true that benthos is not quite absent in the Dauphiné facies since, apart from the single *Pinna* and echinoid fragments noted above, tracks also occur. Tracks, however, particularly grazing tracks like *Zoophycus*, are necessarily much more abundant than the causative organism.

In Iraq a close analogue to the Dauphiné facies is provided by the thin-bedded, highly bituminous shales and limestones of the mainly Bajocian-Bathonian Sargelu Formation (Pl. 19, fig. 1) (Dunnington in van Bellen *et al.* 1960, p. 250). In its type section in Kurdistan this formation is 115 m. thick; the top 12 m. contains innumerable specimens of *Bositra buchi*, together with ammonites and fragments of wood; the middle 21 m. contains poor ammonite impressions; and the lowest 82 m. contains rhynchonellids, *Gryphaea* cf. *balli*, '*Posidonia* cf. *opalina*' and ammonites. The top of the Sargelu Formation therefore presents the *B. buchi* facies in very typical form. In thin section the formation is readily recognized by abundant specimens of '*Paleotrix*', which Peyre (1959) showed to be transverse sections of *B. buchi*. 'Ostracods' were also recorded, but these are probably juvenile specimens of *B. buchi*, which are very common in the rock and scarcely distinguishable from ostracods in thin section. Other fossils include radiolaria and 'minute frondiculariids and nodosariids' (Foraminifera). The Iraqi analogue

to the Provence or Briançon facies is the Bathonian Muhaiwir Formation, equivalent to the upper part of the Sargelu. This consists of well-bedded limestones and marly limestones, sandstones, and oolites, with abundant rhynchonellids, terebratulids, echinoids and gastropods together with bivalves including *Mactromya*, *Ceratomya*, *Homomya*, *Pholadomya*, *Mytilus*, and *Eligmus*; *B. buchi* is unknown, and therefore shows much the same facies relationships in Iraq as in Provence. Indeed Dunnington (loc. cit.) believed, presumably with particular reference to the upper part of the formation, that the Sargelu was euxinic, since benthos is rare and the rock highly bituminous; this being the case, *B. buchi* could not have been benthonic. The typical development of the Sargelu Formation is very extensive, being found from Kurdistan to Kuwait over a distance of 600 km. It is continuous with the *B. buchi* facies of Azerbaijan, the Caucasus, and Persia.

In the Bajocian of Argentina Gröber (1918) described a very similar contrast of facies. The area of typical *B. buchi* facies is here 300 km. from north to south and 200 km. from east to west.

In the Middle Jurassic of Greece and Albania the peculiar nature of the facies in which *B. buchi* occurs was emphasized by Renz (1927, p. 487). The rocks consist mainly of yellow, grey, or black shales and limestones with abundant examples of *B. buchi* (quoted as *P. alpina*), aptychi and beaks of ammonites, and, in one bed *Pseudomonotis* cf. *substriata* Ziethen. No other fossils were found. The presence of ammonite aptychi and beaks but not their conchs can be explained by differential solution; ammonite conchs, being aragonitic, are more soluble than the calcite of aptychi or the outer layers of *B. buchi*. This phenomenon seems to have led Arkell (1956, p. 585) to describe the *B. buchi* facies as 'inhospitable' for ammonites, although elsewhere in the same book he quoted long lists of ammonites from the facies. At St. Barthélemy the ammonites are preserved as shell-less moulds while aptychi and *B. buchi* retain their shells. Differential solution has operated here, therefore, and slightly different conditions might have destroyed the ammonites completely.

One of the most thorough thin-section studies of the *B. buchi* facies was made by Colom (1955, 1957) in the Betic Cordillera. The sections of *B. buchi* in his slides were rather confusingly referred to as '*Halobia*', though he said (1955, p. 112) that they were sections of *P. alpina* (*B. buchi*). The associated microfauna is probably entirely planktonic for it consists largely of globigerinids, while beds with abundant specimens of *B. buchi* tend to alternate with beds with abundant radiolaria. The macrofauna consists of *B. buchi* and ammonites.

Bositra buchi outside its Typical Facies. If *B. buchi* were found only in the typical *B. buchi* facies, scarcely ever had indisputable benthonic associates, and never occurred in shallow-water rocks, one might suspect that it was a deep-water form, insensitive to lack of oxygen. But such is not the case; *B. buchi* also occurs in rocks like those of its typical facies but with an abundant benthos of a few species, and in shallow-water deposits with abundant and varied benthos.

The Callovian rocks of la Voulte-s.-Rhône illustrate the first group. Hess (1960) described a sequence of calcareous marls and clays from this locality containing abundant examples of *B. buchi*, the ophiuroid *Ophiopinna elegans* (Heller), benthonic foraminifera, and a few specimens of a probably benthonic cumacean crab. Hess noted

(p. 377) that some beds contained *B. buchi* alone, often abundantly, but that beds with *O. elegans* and foraminifera always contained *B. buchi* as well. This suggests that the sea floor was sometimes uninhabitable and that *B. buchi* was independent of the bottom.

A rather similar case, but with a more varied benthos, occurs in the 40 feet of brown shale at the base of the Oxford Clay at Elstow. *B. buchi* is by far the commonest fossil here but is associated with *Meleagrinella*, *Nuculana*, *Procerithium*, an aporrhaid, and scolecodonts, as well as ammonites (*Kosmoceras jasoni*).

Cases where *B. buchi* occurs in shallow-water rocks, of very different lithology to its typical facies and containing an abundant and varied benthos, include:

1. Sandstone; 'grès à Murchisonae' of Alsace (Guillaume 1928, p. 227).
2. Shell fragment limestone; calcareous beds in Fuller's Earth Clay near Sherborne (thirteen more or less complete valves and many fragments, L84734-8); Inferior Oolite, *schloenbachii* Zone near Bradford Abbas (twelve more or less complete valves and some fragments, L84320-3).
3. Iron-shot oolite; 'oolite ferrugineuse de Bayeux' (Guillaume 1928, p. 227).

The numerous specimens in the British Museum collections just quoted show that *B. buchi* can be quite abundant when it occurs at all in shallow-water rocks. These occurrences are therefore not fortuitous, but need explanation. There is no difficulty in explaining them if *B. buchi* was pelagic. The sporadic nature of shallow-water occurrences is probably due to the thin shell (60-70 μ , see below, p. 164). In shallow-water rocks such a shell would usually break into unrecognizable fragments before burial; indeed it often fragmented before burial even in the Dauphiné facies of St. Barthélemy. It can be compared with a living pelagic mollusc: the thecosomatous pteropod *Spiratella* (= *Limacina*) is said to be the most numerous living mollusc but its fragile shell is a rarity in Recent, marine, shallow-water deposits.

The facies evidence for a pelagic mode of life for *B. buchi* may be summarized as follows: the species is extremely widespread geographically, is unlike contemporary bivalves or other indisputable benthos in its typical mode of occurrence, and resembles in its facies relationships the ammonites, radiolaria, and globigerinids, which were probably planktonic or nektonic. Its abundance in conditions that were probably euxinic and its sporadic occurrence, in considerable numbers, in rocks of shallow-water origin confirm that it was pelagic.

Nothing in the facies evidence is contradicted by the morphology of the shell. This was thin, as might be expected in a planktonic organism, the prodissoconch develops quite gradually into the adult shell without sign of settlement, and there are morphological signs of swimming ability (see below, p. 162).

Facies evidence bearing on the pseudoplanktonic hypothesis. If *B. buchi* was not benthonic it could have been either planktonic or pseudoplanktonic. Facies considerations do not decisively favour one of these possibilities over the other. However, if *B. buchi* was attached to flotsam it is surprising that other animals with a similar mode of life are so rare in the typical *B. buchi* facies. None were found at St. Barthélemy. It is true that *Pinna*, the only bivalve discovered other than *B. buchi*, was byssiferous, but like Recent members of the genus which it closely resembles, this form almost certainly lived umbones down in the sea floor, with the byssus spread out in the mud.

A comparison may be made with the fauna associated with gulfweed in the Sargasso Sea. Four species of epizoa which would be expected to occur fossil are found in every sample of this weed, viz. *Membranipora* sp., *Spirorbis* sp., *Lepas pectinata* and *Lepas* sp. (Timmermann 1932, p. 306), while others, such as crabs and gastropods, are found sporadically. It cannot be excluded that Jurassic gulfweed harboured only one common species, any others being exceedingly rare, but this would be surprising for there were many attached forms of life in the Jurassic. A hypothesis that does not demand abundant flotsam is therefore more acceptable, on facies grounds, than one that does.

Both at Elstow and St. Barthélemy the shells of *B. buchi* sometimes occur in clusters. These superficially resemble those described in *Posidonia becheri* by Paul (1939), who rightly used them as evidence of a partly pseudoplanktonic mode of life in that species. In *B. buchi*, however, some of the clusters (e.g. Pl. 19, fig. 4) consist almost entirely of single-valved specimens, as can be proved by dissection. Such clusters must have arisen by posthumous drifting together, and clusters containing mainly double valves could easily have arisen in the same way, since slight currents would separate double- from single-valved specimens. Zangerl and Richardson (1963, caption to pl. 24A, p. 131) have noted a similar case involving *Pteria* and *Dunbarella* in a Pennsylvanian black shale.

On facies grounds, therefore, *B. buchi* was more probably planktonic than pseudo-planktonic.

Functional Morphology

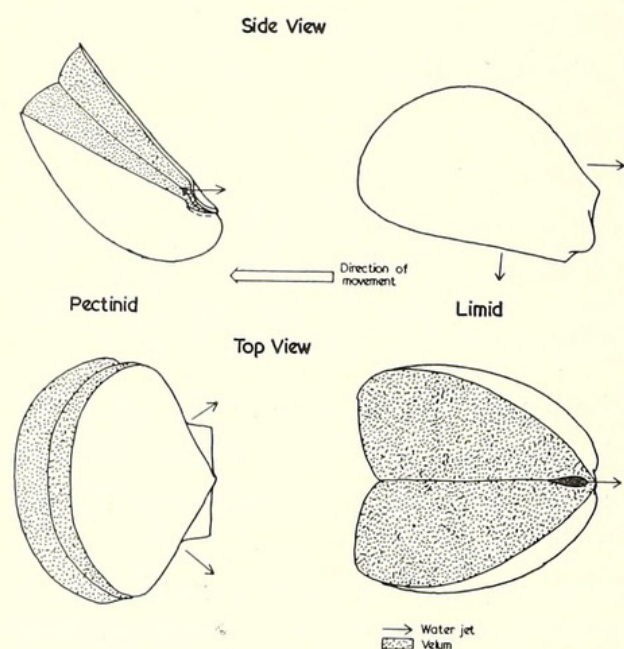
Swimming in relatives of Bositra and Posidonia. No living bivalves are nekto-planktonic but benthonic swimmers occur in two related superfamilies, the Pectinacea and Limacea.

The mode of swimming is very similar in both groups. The inner lobe of the mantle forms a pallial curtain or velum round the edge of each valve. In swimming the free edges of the vela are turned in and touch each other (text-fig. 2), except just anterior and posterior to the hinge, where the vela are exceptionally flabby.

Before swimming begins the valves are opened as wide as possible to increase the volume of water between them. When the adductor muscle contracts and the valves come together the vela form a 'valve' (in the engineer's sense) so that water can only escape at the flabby places near the hinge, which function like the nozzle of a bellows. Water easily enters between the vela when the adductor relaxes and the valves open. By opening and shutting its valves the animal thus pumps out water near the hinge and

moves through the water with the ventral margin foremost.

Though the mode of swimming is basically the same in both Limidae and Pectinidae there are differences in detail between the two groups. Thus the Limidae usually swim



TEXT-FIG. 2. Swimming position in a limid and a pectinid (diagrammatic).

with the commissure vertical except when tired (Studnitz 1931, p. 305) and swimming is assisted by the rowing action of the tentacles (Gilmour 1963, p. 85) round the edge of the mantle. Pectinidae, on the other hand, do not row with the tentacles and usually swim with the commissure roughly horizontal but raised at the ventral end; in addition to normal swimming, Pectinids can also propel themselves hinge first, in an 'escape reaction', away from a noxious stimulus. It is said (Haas 1941, p. 506) that equivalence Pectinidae are more likely to swim with the commissure vertical than inequivalence species.

The fact that Recent Limacea and Pectinacea swim in basically the same way suggests that they may have inherited swimming ability from a common ancestor. The earliest known Limacea are Carboniferous in age (Cox 1943, p. 153), while the earliest Pectinacea are probably Devonian. Their common ancestor would therefore probably be Devonian or Silurian in age and would be a pterinopectinid (in Newell's sense (1937)) and therefore close to the ancestor of *B. buchi* and '*Posidonia*' *radiata*. These two forms could easily have inherited swimming ability from the same source.

Several additional facts are relevant here. Firstly, some Lower Carboniferous Pectinacea (e.g. *Pernopecten sowerbyi* (McCoy)) have smooth thin shells with an accurate plane of symmetry perpendicular to the commissure. Such forms could probably swim since they much resemble both the Recent *Cyclopecten groenlandicus*, which is a good swimmer (S. Jensen in A. S. Jensen 1905, p. 332), and *Amusium*, which Yonge (1938, p. 81) thought to be probably the best swimmer among bivalves as judged by the symmetry, thinness, and smoothness of its shell. Secondly, the musculature of Pennsylvanian Pectinacea, as judged by the muscle scars (Newell 1937, p. 23), was basically like that of Recent Pectinidae. Thirdly, Newell (1937, p. 20) thought that early Pectinacea were very active because they are seldom encrusted with epizoa. Fourthly, the Recent *Lima excavata* can swim (T. H. J. Gilmour, personal communication) and is identical in shell characters to *Plagiostoma*, which first occurs in the Trias.

It is therefore very probable that the common ancestor of the Limacea and Pectinacea in general, including that of *Bositra*, *Posidonia*, *Steinmannia*, *Dunbarella*, *Halobia*, *Daonella*, and *Monotis*, was able to swim.

Shell structure and thickness. The thickness of the shell of *B. buchi* has been determined in the following instances:

- (a) Bathonian; Fuller's Earth Clay. Cliff End, near West Bay, Dorset. LL17415; prismatic layer $47\ \mu$; laminar layer $10\ \mu$; total $57\ \mu$; length 1 cm. LL17416; prismatic layer $48\ \mu$; laminar layer $16\ \mu$; total $64\ \mu$; length 1 cm. Associated ammonites and nukulids were perfectly preserved, indicating that laminar aragonite like that of the inner layer of *B. buchi* was not dissolved. Associated heterodonts, consisting of crossed-lamellar aragonite, had partly lost the shell.
- (b) Lower Bajocian. Blue clay, Kidugallo borehole, Tanganyika. L88714; thickness of shell $73\ \mu$ at length 1 cm., $32\ \mu$ at length 1.2 mm. Laminar and prismatic layers not distinguishable.
- (c) Bajocian-Bathonian; Sargelu Formation. Sirwan Gorge, Kurdistan, Iraq. LL17402. Thickness of shell in several individuals $16\text{--}32\ \mu$ but difficult to measure because of recrystallization. Laminar layer brownish, about as thick as prismatic layer.

There are some relevant data in the literature. The sections of '*Posidonia alpina*' in Peyre (1959, pl. 1, fig. 4) show both layers of the shell and are about $50\ \mu$ thick. Rothpletz (1892, p. 93) described the shell of Triassic specimens of *Halobia* from Indonesia as consisting of laminar and prismatic layers and varying from 6 to $60\ \mu$ in thickness, and Krumbeck (1924, p. 126) quoted the shell thickness of *Halobia* as $15\text{--}25\ \mu$.

The thinness of the shells of *B. buchi* has led many authors to identify them as filamentous algae, as discussed by Peyre (op. cit.). The 'prodissococonchs of lamellibranchs' to which Peyre ascribed some of the sections he studied are probably juvenile stages of *B. buchi*; one of them (op. cit., pl. 1, fig. 2) is in the valves-open position (see below, p. 166).

The thickness of the shell of *B. buchi* therefore seems to have been about 60–70 μ at a length of about 1 cm. The thickness is very uniform all over the valve, since the concentric folds are corrugations affecting the whole shell and do not represent increased thickness. Only the cardinal area is appreciably thicker than the shell in general. This would strengthen the shell where specially needed without much increase of weight. The style of ornament closely resembles that of the Recent thecosomatous pteropod *Balantium*.

An interesting feature of the valves of *B. buchi* is that they are often brownish round the edges. This is seen for example at la Voulte-s.-Rhône (Pl. 19, fig. 7) on the top surface of Bed 9c and adjacent bedding planes (Hess 1960), where the margins are often the colour of haematite. Hess has shown that in ophiuroids from this locality pyritization is connected with original high organic content (op. cit., p. 343). The brown shell margins of *B. buchi* are probably due to oxidation of pyrite, and therefore also indicate a high organic content. They were noticed in valves of length (in mm.) 0.7, 1.0, 1.7, 2.8, 4.2, 4.3, 5.0, 7.8, 8.5, and 12.5. They are probably due, therefore, to new shell material not being completely calcified as soon as it was formed.

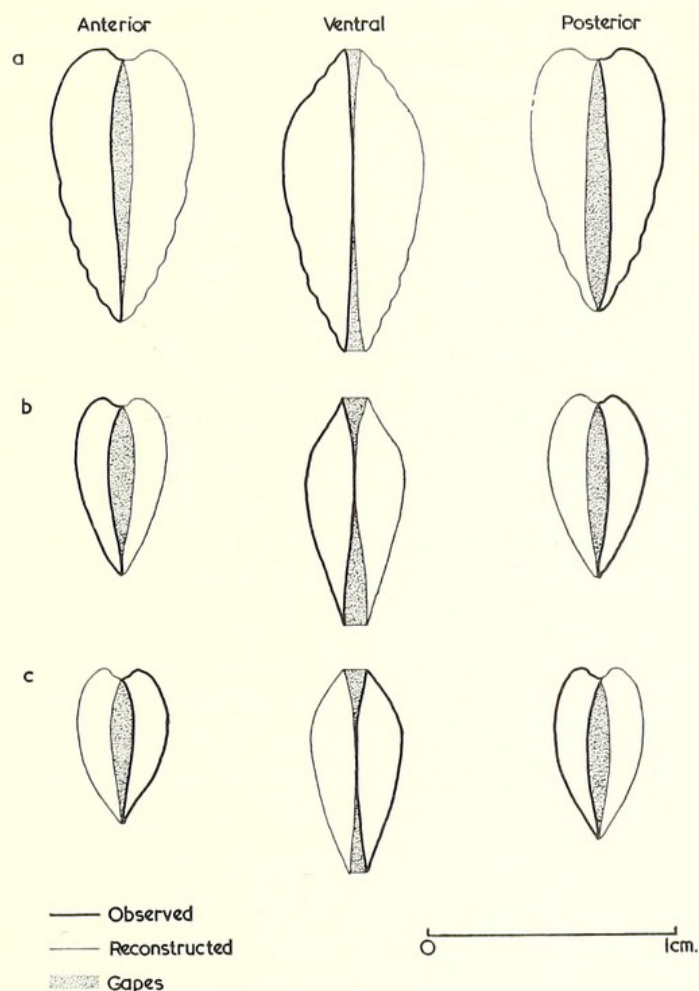
Shells as thin as that of *B. buchi* occur in both benthonic and planktonic living molluscs. This thinness, therefore, does not prove that *B. buchi* was planktonic—a conclusion which is based on facies. It is more relevant to whether *B. buchi* was planktonic or pseudoplanktonic, since a thin shell is a swimming adaptation in the Pectinacea (Yonge 1938, p. 81) and since the analogy of the pteropod *Cavolinia* (shell 40 μ thick at length 1 cm.) shows that a pelagic animal with a shell so thin would not require attachment. The analogy of *Cyclopecten groenlandicus* (right valve 80 μ thick, left valve 50 μ thick at length 2.3 cm.) is particularly suggestive, because this species, like *B. buchi*, is a Pectinacean and, though benthonic, is a considerable swimmer.

C. groenlandicus is also like *B. buchi* in having a high organic content round the edges of the valves. Indeed the whole shell is springy to the touch as if somewhat horny, and the shell margins sometimes flex outwards when the animal shuts its valves at death (Collin in A. S. Jensen 1905, p. 332). The shell of *B. buchi* probably had similar properties, for otherwise it would have been extremely brittle.

The presence of gapes. Examination of apparently uncrushed specimens of single valves of *B. buchi* from various localities suggested that the commissure was not plane. It is difficult to establish this feature, however, when the fossil is buried in the rock, and the shell is too thin to be excavated. Plaster casts were therefore made, using thick rubber moulds to avoid distortion, and trimmed away along a growth line. The model thus produced was mounted on a cover slip with the hinge line touching the cover slip throughout its length. Under these conditions, in the six cases tried, the only other places where the model touched the slip was a point on the ventral margin (Pl. 19, fig. 2). For growth stages much less than 1 cm. long the model was trimmed back to the relevant growth line and a plane cut parallel to the hinge and a point tangent to the ventral margin.

This produced a model of the growth stage on top of a short pillar of plaster-of-Paris, which was mounted on a cover slip. By this means it was shown that the commissure was not plane at a length of 3–3.5 mm. (Pl. 19, fig. 3).

The analogy of *Cyclopecten groenlandicus* suggests that the valves of *B. buchi* would probably have distorted very easily in life. Nevertheless, the curvature of the commissure



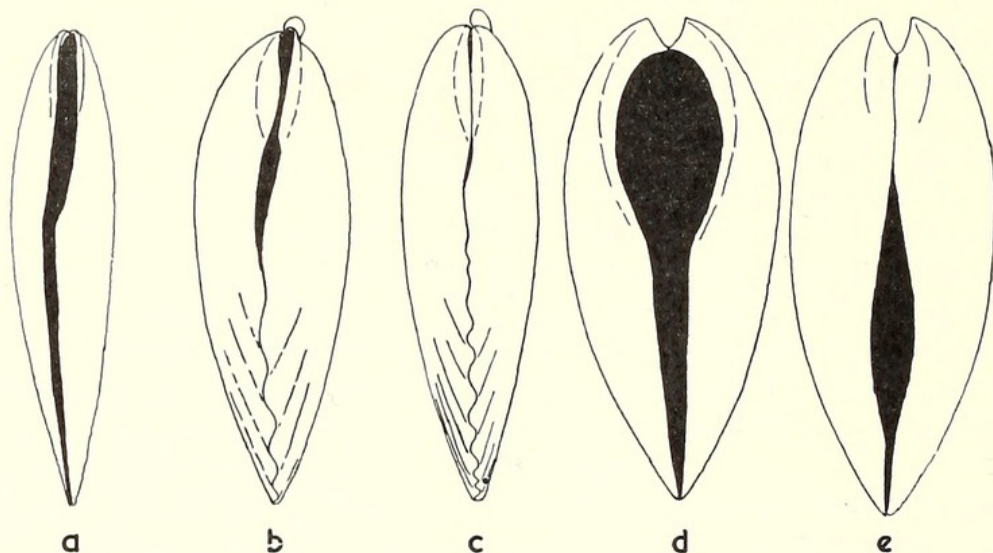
TEXT-FIG. 3. Gapes in *Bositra buchi*. Based on plaster models treated as explained in text. *a*, LL17402a (For data see Pl. 19, fig. 2); *b*, L84735 (Data as Pl. 19, fig. 3); *c*, L84734c (Data as *b*).

is so characteristic in shape, and occurs so often when the matrix is hard enough to prevent crushing, that it must correspond to the usual shape of the original shell. This indicates, since *B. buchi* was equivalve, that big gapes would normally be present at front and back as shown in text-fig. 3.

In Recent Pectinidae and Limidae anterior and posterior gapes serve to release the swimming jets (Jackson 1890, p. 339; Verrill 1897, p. 44) and their size is related to swimming ability (text-fig. 4). Thus *Chlamys opercularis* is a good swimmer and seldom byssally attached (Rees 1957, p. 27) and has large anterior and posterior gapes, whereas *C. varius*, which lives byssally attached to rocks (Dalmon 1935, p. 273) has very small gapes. *Lima hians* has large gapes and in speed and endurance is as good a swimmer as

C. opercularis (T. H. J. Gilmour, personal communication) although Studnitz (1931), perhaps through working with tired individuals, reported otherwise. Large gapes also occur in *Amusium*, e.g. *A. pleuronectes*, and *Cyclopecten groenlandicus*.

By analogy with living relatives, therefore, the gapes of *B. buchi* suggest swimming ability. They are not to be confused with the gapes of burrowers such as *Mya* through which the foot protrudes anteriorly and the siphons posteriorly. Such burrowers are not related to *B. buchi*, for which a benthonic mode of life is most unlikely on facies grounds, and siphons could hardly have been present in *B. buchi*, since they were absent in



TEXT-FIG. 4. Gapes in living relatives of *B. buchi*. a, *Amusium pleuronectes*, posterior. b, *Chlamys opercularis*, posterior. c, *Chlamys varius*, posterior. d, *Lima hians*, posterior. e, the same, anterior. The anterior gapes of a-c are like the posterior gapes.

Palaeozoic Pectinacea (cf. Newell 1937) and are lacking in all living representatives of the order Pteronchida (Cox 1960) in which the Pectinacea and Limacea are included.

If the valves were elastic, *B. buchi* may have been able to eliminate the gapes by pulling the valves tightly shut, just as *Cyclopecten groenlandicus* can. It is the *normal* presence of gapes which suggests swimming ability, however, as the analogy of *C. groenlandicus* shows. The disposition of the gapes on either side of the hinge in *B. buchi* suggests that water was forced out at these points and that swimming resembled that of living Limacea and Pectinacea. This supports the suggestion that the common ancestor of these superfamilies could probably swim.

The valves-open position. When *Bositra buchi* is found with both valves together they are nearly always open and spread out on the bedding plane. This is well shown, for instance, in Plate 19, figs. 1 and 7, and was emphasized by Guillaume (1928, p. 225) and Boehm (1912, p. 131). Wanner (1907, p. 204) described the same feature in *Daonella indica* and examination of the literature shows that it is usual in Triassic and Jurassic examples of *Halobia*, *Daonella*, '*Posidonia*', *Bositra*, and *Steinmannia*.

In *B. buchi* the valves-open position seems to be more often concave-up than concave-down. Thus in a specimen from the Oxford Clay at Elstow twelve specimens were concave-up and one concave-down. In specimens from the Sargelu Formation of

Northern Iraq in which the weathered side was assumed uppermost, the corresponding numbers were 21:6, 30:2, 2:10, 5:3, 8:2, 0:4, and 11:2, or 77:29 in total. This is probably because the concave-down position is unstable in bivalves with rounded ventral margins that are wafted about by slight currents after death with the ligament intact (Schäfer 1962, p. 187). The valves-open position is not fortuitous in *B. buchi*; it is very characteristic of this species and other Triassic and Jurassic bivalves whose facies suggests they were pelagic, and is not present as a regular feature in other Pectinacea or Limacea.

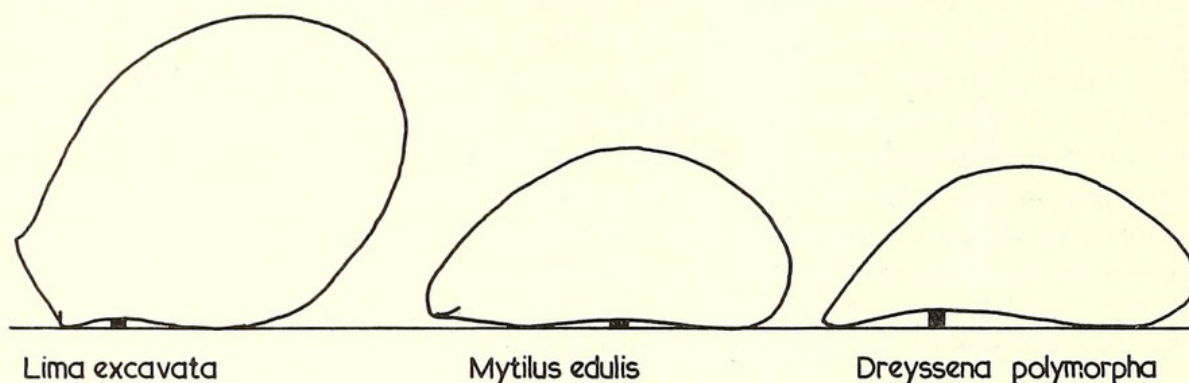
Wanner (loc. cit.) held that the regular occurrence of the valves-open position indicated swimming ability. This proposition is probably true for a pectinacean and can be re-argued as follows: for the valves regularly to have fallen open, whether concave-up or concave-down, suggests that before burial they opened to a very wide angle. The angle in question would be determined by the ligament after the soft parts had rotted. In Pectinacea (though not in many other bivalves) this angle is equal to the maximum angle of opening during life, which is that used in swimming. A wide angle of opening is advantageous to a swimmer and, therefore, the regular occurrence of the valves-open position in a pectinacean suggests swimming ability.

The stages in this argument can be elaborated. Firstly, experiments using an aluminium model of *B. buchi* with valves of the right convexity and a ligament of glue, showed that when the ligament rotted in water with the valves concave-up on hard bottom, the valves fell open when the initial angle of opening exceeded about 60°. This would probably be roughly correct for the sort of bottom over which *B. buchi* could be wafted by currents. The conclusion that the angle of opening was very wide, however, is based primarily on the rarity of the valves-open position in normal Pectinacea and Limacea. Secondly, in Pectinacea the maximum angle of opening in life is very precise and is determined by the ligament alone. It therefore equals the angle of opening when the soft parts are removed. In two newly dead individuals of *Chlamys opercularis* and *Pecten maximus* the means of this angle were respectively 31° and 34°; this is about equal to the maximum angle of opening in life observed during swimming. Many bivalves differ from Pectinacea in this respect, including some that often occur in the valves-open position on beaches. In these the angle of opening when the soft parts are removed is rather imprecise and greatly exceeds the maximum angle in life, which is determined by ventral muscular connexions between the valves. The tellinaceans *Arcopagia crassa* and *Donax vittatus*, and *Cardium edule*, are examples of this condition. *B. buchi* was a pectinacean and therefore almost certainly lacked ventral muscular connexions, for these are absent in all modern related forms included in the Pectinacea, Anomiacea, Limacea, Pteriacea, and Ostreacea. Further, as already mentioned, Upper Palaeozoic Pectinacea had musculature much like that of living ones. In addition, the ligament of *B. buchi* resembled that of modern Limidae and Pectinidae. It therefore probably controlled the maximum angle of opening in life, which may have been about 60°, as compared with 30° for modern Pectinidae. Lastly, a wide angle of opening is advantageous to a swimmer because it increases the volume of water expelled at each contraction of the adductor.

In summary, therefore, Tellinacea and other bivalves are often found in the valves-open position on beaches, but this has no biological significance. The regular occurrence of the valves-open position in *B. buchi*, on the other hand, suggests swimming ability.

The valves-closed position. Specimens of *B. buchi* with the valves closed are uncommon.

Apart from examples where the valves were not properly articulated, two cases were encountered in the present work. The first was in a hard limestone from the Sargelu Formation (LL17402). In this, the microcoprolite *Aggregatella pseudohieroglyphicus* Elliott (1962, p. 40) is abundant in the matrix but absent within the closed valves. The specimens had evidently closed their valves before they died and did not open again before burial. Their gapes must have been small enough to prevent the coprolites from entering, perhaps because the valves were slightly elastic, and pulled hard together by the adductor; four single valves from the same block showed the characteristic curvature of the commissure (e.g. Pl. 19, fig. 2). The second instance was described by Hess (1960) from the upper surface of Bed 9c in the Callovian of la Voulte-s.-Rhône, where specimens of *B. buchi* up to 1.2 mm. long are sometimes preserved with the valves closed and



TEXT-FIG. 5. Three living bivalves with the byssus (black) protruding from a concavity in the lateral outline (diagrammatic).

filled with pyrite (Pl. 19, fig. 8). The commissures are roughly perpendicular to the bedding, with the anterior or posterior end (one cannot say which), or the umbones, pointing stratigraphically downwards (my observation, cf. Hess, p. 377). These specimens probably fell into the superficial, almost liquid layer of bottom mud, closed their valves and died.

B. buchi could, therefore, close its valves in life. This fact is important in estimating its hydrostatic properties (see p. 174).

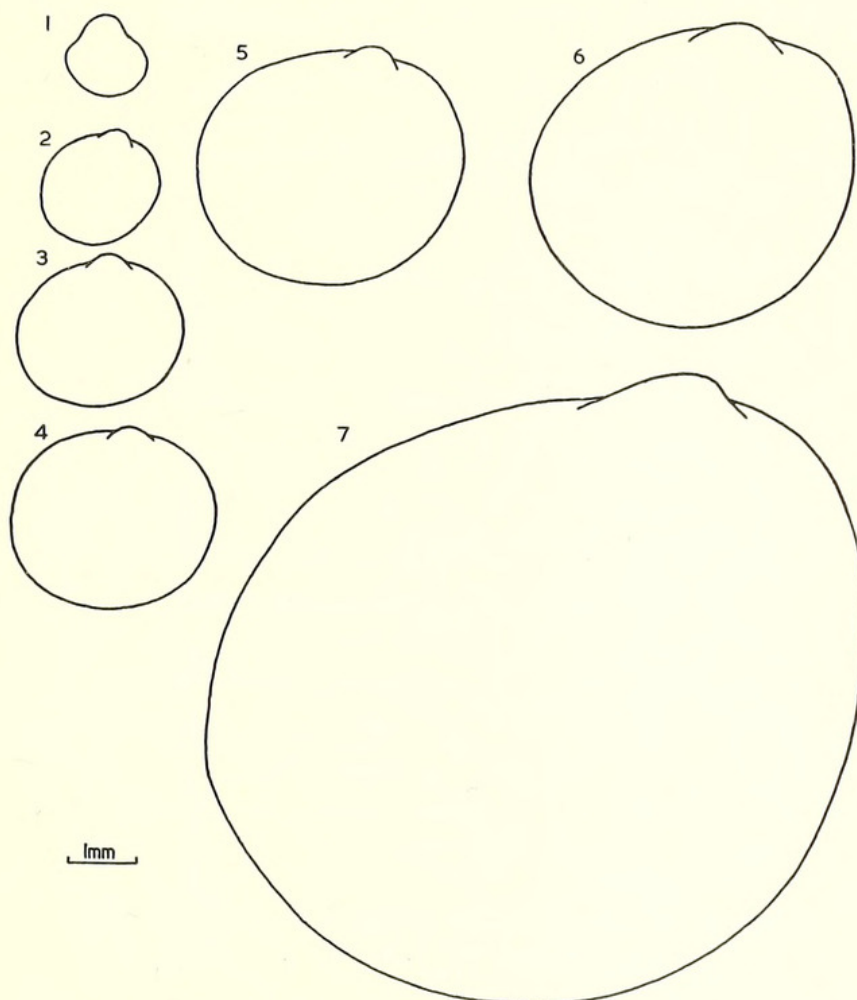
Adult outline and convexity. The adult outline of *Bositra buchi* is at every point convex outwards; there is no byssal notch, no ears, and the shell is exactly equivalve.

If *B. buchi* lived attached to a floating support it could either have rested on one valve, or held the commissure perpendicular to the substratum. In the first case, which is typical in Pectinacea, one would expect the valves to be unequal in convexity, probably with the right less convex than the left as in young individuals of *Anomia* (Odhner 1914) or young *Posidonia becheri*, and with a byssal notch. It is most unlikely, therefore, that *B. buchi* rested on one valve.

If the commissure were perpendicular to the substratum the antero-ventral margin would probably be flat or concave where it touched the substratum and the byssus emerged, as in *Mytilus edulis*, *Lima excavata* and the independently evolved *Dreysena polymorpha* (text-fig. 5). This gives a firmer grip on the substratum. It is true that some byssally attached shells are almost circular in outline, e.g. *Kellia suborbicularis*. This

species, however, like other Erycinacea, lives in very sheltered positions under shells or holdfasts (Step 1951, p. 101), which is not comparable to a life fixed to floating seaweed.

The adult outline and convexity of *B. buchi*, therefore, suggests that the adult was almost certainly not attached, so that it lay habitually on one valve, with the commissure perpendicular to the substratum. The adult outline and convexity, in fact, provide no evidence whatever of attachment.



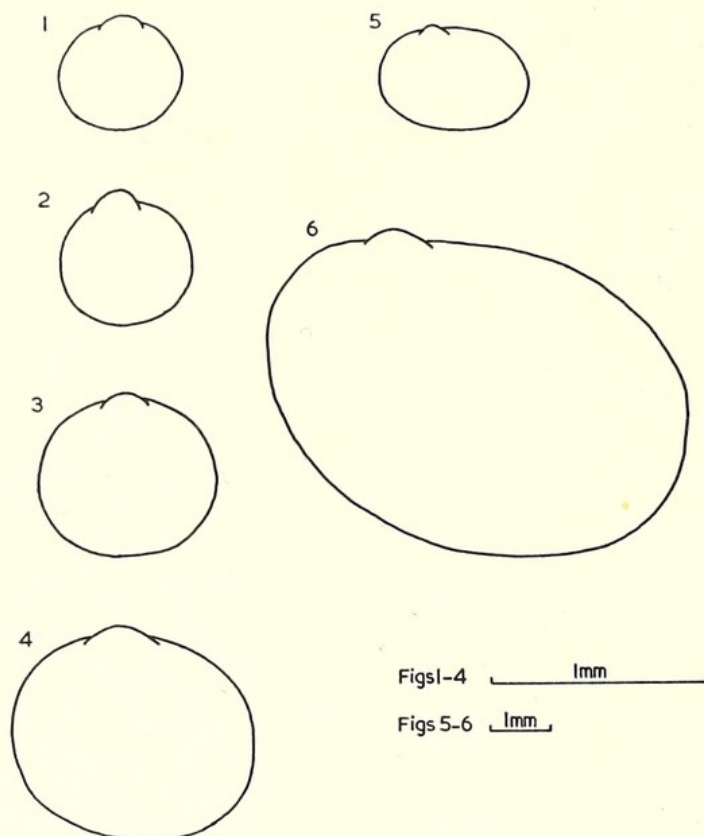
TEXT-FIG. 6. Ontogeny of the outline of *B. buchi*, LL17402a. For data see Pl. 19, fig. 2.

Ontogeny. The ontogeny of the outline of *Bositra buchi* has been worked out by drawing with a camera lucida the troughs between successive concentric ribs (text-figs. 6, 7). Only uncrushed specimens with perfect umbones can be used for this work. The ontogeny of the outline is remarkably simple. A form with roughly median umbones at a length of 0.5 mm. changes gradually into a form with somewhat anterior umbones at a length of about 1 cm. The outline may become somewhat more elongate.

Double-valved specimens never have the valves unequal in outline or convexity at any stage of growth. This is shown by specimens from la Voulte with the valves closed up to a height of 1.1 mm. (Pl. 19, fig. 8, estimated length 1.2 mm.) and by specimens with the valves open, which are somewhat more difficult to interpret in this respect, from la Voulte (Hess Collection B. 52, length 1.2 mm.; B. 56, length 2.5 mm.), St. Barthélemy

(LL17406, length 2.6 mm. and others of similar size) and the Kidugallo borehole (L88713, length 1.6 mm). Double-valved specimens of greater size are also exactly equi-valve (e.g. Pl. 19, figs. 1, 7). The valves-open position occurs at a length of 0.6 mm. (at la Voulte) and at all larger sizes.

Plots of length against frequency for single bedding planes (text-fig. 8) very often show a peak at a nominal length of 1 mm. This peak is not due to some form of post-humous drifting, since it occurs in nine out of twelve randomly selected bedding planes



TEXT-FIG. 7. Ontogeny of the outline of *B. buchi*, L84734c.
For data see Pl. 19, fig. 3.

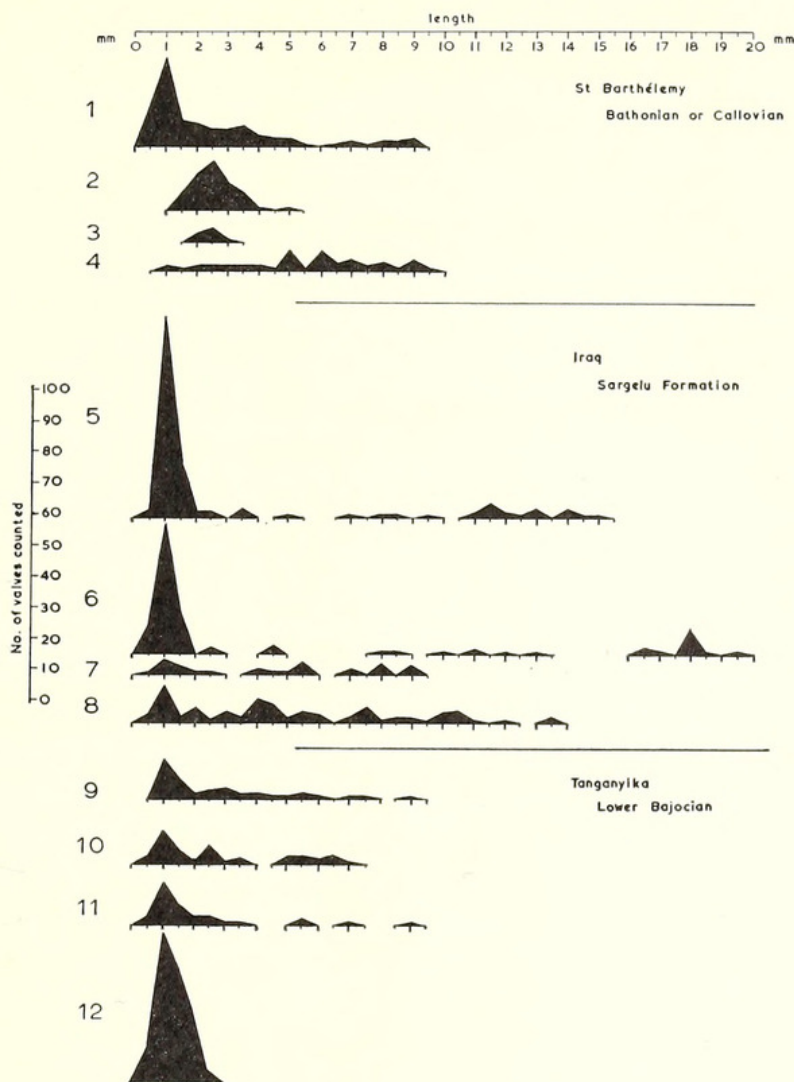
from France, Tanganyika, and Iraq. It must represent high natural mortality (i.e. that not due to predation) at this length.

The thickness of the shell, on the basis of material from Kidugallo, increases from about $30\ \mu$ at a length of 1.2 mm., to about $70\ \mu$ at 1 cm.

The ontogeny of *B. buchi* is much simpler than that of *Posidonia becheri* as described by Weigelt (1922, cf. text-fig. 9). At a length of 0.5 mm. this species is equilateral and equi-valve; at a slightly greater size the umbones become somewhat anterior, the right valve becomes flatter than the left, and a byssal sulcus develops in its antero-ventral margin; later the shell becomes still more pteriiform, remaining so to a length of about 1 cm., when the adult form begins to be attained.

Weigelt (1922, p. 74; 1927) thought that the earliest stage was the prodissoconch of the veliger larva, that subsequent changes were due to settlement (right valve downwards as usual in Pectinacea) on flotsam, and that the change in outline at a length of about 1 cm. was due to attachment on the sea floor with the commissure vertical. The changes

at a length of about 0.5 mm. must indeed be due to settlement, since the sequence is almost exactly as in *Pecten irradians* (Jackson 1890, p. 342) and *Anomia* spp. (Odhner 1914; Miyazaki 1935) except that settlement took place in *P. becheri* at a larger size. It is also



TEXT-FIG. 8. Plot of number of valves against length of *B. buchi* for various bedding planes. 1-4, Bathonian or Callovian of St. Barthélemy, respectively LL17405, 4, 6, 3. 5-6, Bajocian, Sargelu Formation; Ruwanduz, Northern Iraq (LL17407). 7, Bathonian, Sargelu Formation; Ser Amadia, Northern Iraq (LL17409). 8, Bathonian, Sargelu Formation; Barsarin, Ruwanduz, Northern Iraq, LL17408. 9-11, ? Bajocian, Kidugallo borehole, Tanganyika, LL88715. 12, ditto, LL88713.

probable that settlement usually took place on flotsam, since Hind (1893, p. 541) recorded small specimens of *Posidonia* attached to *Calamites* fragments and Paul (1939) recorded medium-sized and large examples of *P. becheri* attached to wood and to each other. Weigelt (1927, p. 75) suggested that the forms attached to wood figured by Hind (1896-1901, p. 94, pl. 6, fig. 24) as *Posidoniella laevis* were intermediate stages of *P. becheri*.

Weigelt's suggestion that at a length of about 1 cm. *P. becheri* settled on the sea floor is unlikely, however, in view of the facies in which the species usually occurs. Schmidt (1935, pp. 138, 142) thought that the adults were attached to flotsam like the intermediate stages, and Paul's evidence shows that the adult could attach itself. Nevertheless, some change in habit between the two stages seems necessary to explain the change in shape, and it may be that the adult was a habitual swimmer that attached itself occasionally.

In any case, the absence in *B. buchi* of any abrupt change in shape at a length of 0.5 to 1.5 mm., and the fact that the valves are never unequal or a byssal notch present, together with the gradualness with which the adult form is acquired with only a small increase in shell thickness and little change in outline, suggests that this species (unlike its relatives *Posidonia becheri*, *Pecten irradians*, and *Anomia*) was never attached, and indeed never settled on a substratum, and that the adult, in accordance with facies considerations, was pelagic like the larva.

This implies that swimming by clapping the valves developed in ontogeny as soon as swimming by cilia was abandoned. This is not improbable since gapes already existed at a length of 3 mm. The 1 mm. mortality peak may indicate the change from ciliary to muscular swimming. It need not be ascribed to unsuccessful settlement, of which there is no other sign in the ontogeny. Thorson (1946, p. 467) noted that benthonic opisthobranch gastropods sometimes metamorphose in mid-water, without touching a substratum. In *B. buchi*, as in thecosomatous pteropods which are descended from benthonic opisthobranchs, this had probably become a regular part of the life cycle. The ontogeny of *B. buchi* is therefore analogous to that of the pteropod *Spiratella* (Lemche 1948, p. 24), in which the shell of the pelagic larva enlarges gradually into that of the pelagic adult.

EXPLANATION OF PLATE 19

Figs. 1-4, 6-9, *Bositra buchi* (Römer). Fig. 5, '*Posidonia*' *radiata* Goldfuss.

Fig. 1. Rock specimen (bituminous limestone) of the typical facies. Note the valves-open position of many individuals. Bathonian, Sargelu Formation; Ser Amadia, Northern Iraq. LL17409, $\times 0.66$.

Fig. 2. Plaster cast of LL17402a. Bathonian, Sargelu Formation; Sulemanya, Sirwan Gorge, Northern Iraq. Right valve. Model trimmed along growth line and mounted on a flat surface to show gapes. *a*, Anterior oblique; *b*, posterior oblique; *c*, ventral oblique; *d*, lateral aspects. $\times 3.5$.

Fig. 3. Plaster cast of L84734c. Left valve. Bathonian, Lower Fuller's Earth Clay; Silverslake Farm, near Sherborne, Dorset. Model trimmed to length of 3.5 mm. *a*, lateral; *b*, ventral aspect. Note curvature of commissure in ventral aspect. $\times 10$.

Fig. 4. Posthumous cluster of single valves. LL17411. Bathonian or Callovian; St. Barthélemy-de-Vif, Isère. $\times 2.6$.

Fig. 5. L93741. Upper Lias, base of *acutum* Zone; Bracebridge Brick Pit, 2 miles south of Lincoln. $\times 0.66$.

Fig. 6. Aluminium model with tentacles used in feasibility experiments. $\times 0.66$.

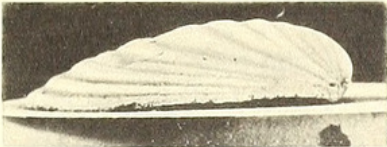
Fig. 7. Two specimens showing brown shell margins. Hess Collection, Basel University, B.50. Bed 9c, Callovian; la Voulte-s.-Rhône, Ardèche. $\times 3.3$.

Fig. 8. Individual 1.1 mm. in height with valves closed and embedded with hinge line perpendicular to bedding. Hess Collection, Basel University, B.55. Top surface of Bed 9c. Callovian, la Voulte-s.-Rhône, Ardèche. $\times 10$.

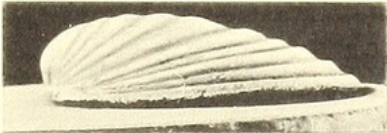
Fig. 9. Specimen showing internal ligament tissue, outlined in black. LL17412. *Kosmoceras jasoni* Zone, Callovian, base of Oxford Clay, 20 in. above oyster bed at base of quarry; Elstow, Bedfordshire (Nat. Grid Ref. TL043456). $\times 33$.



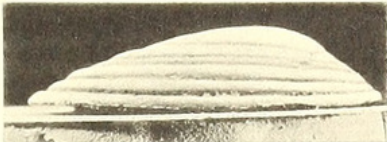
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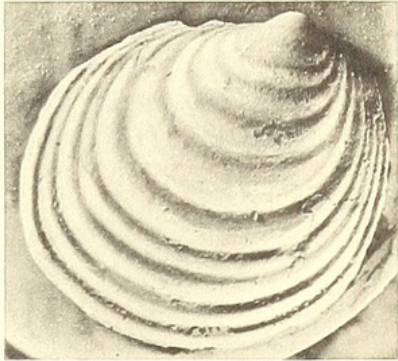
2a



2b



2c



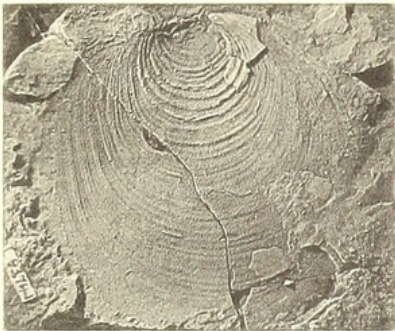
2d



3a



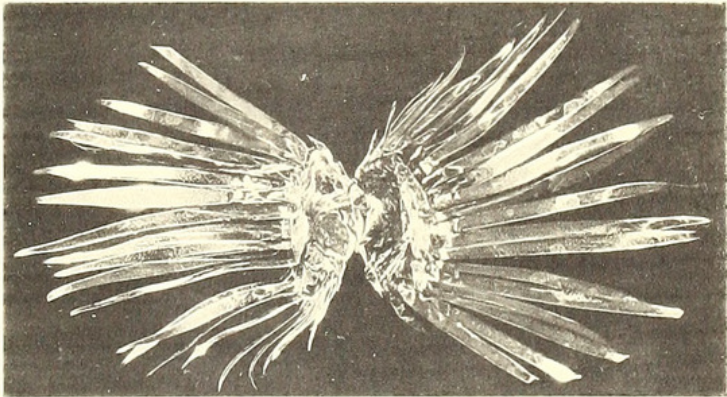
3b



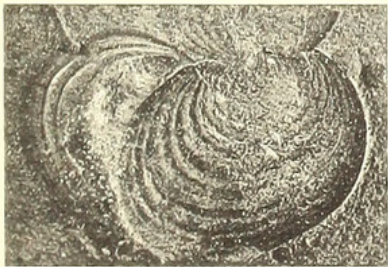
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4



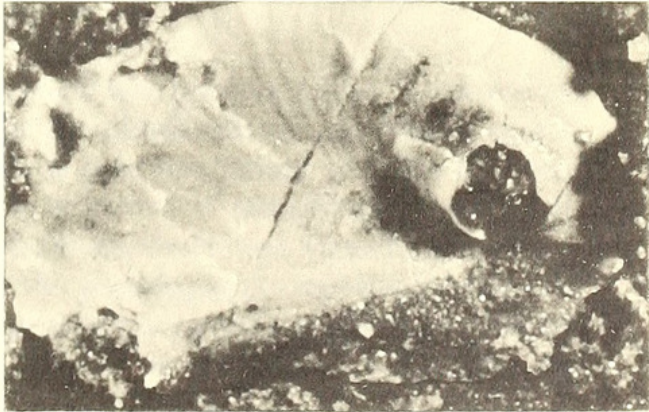
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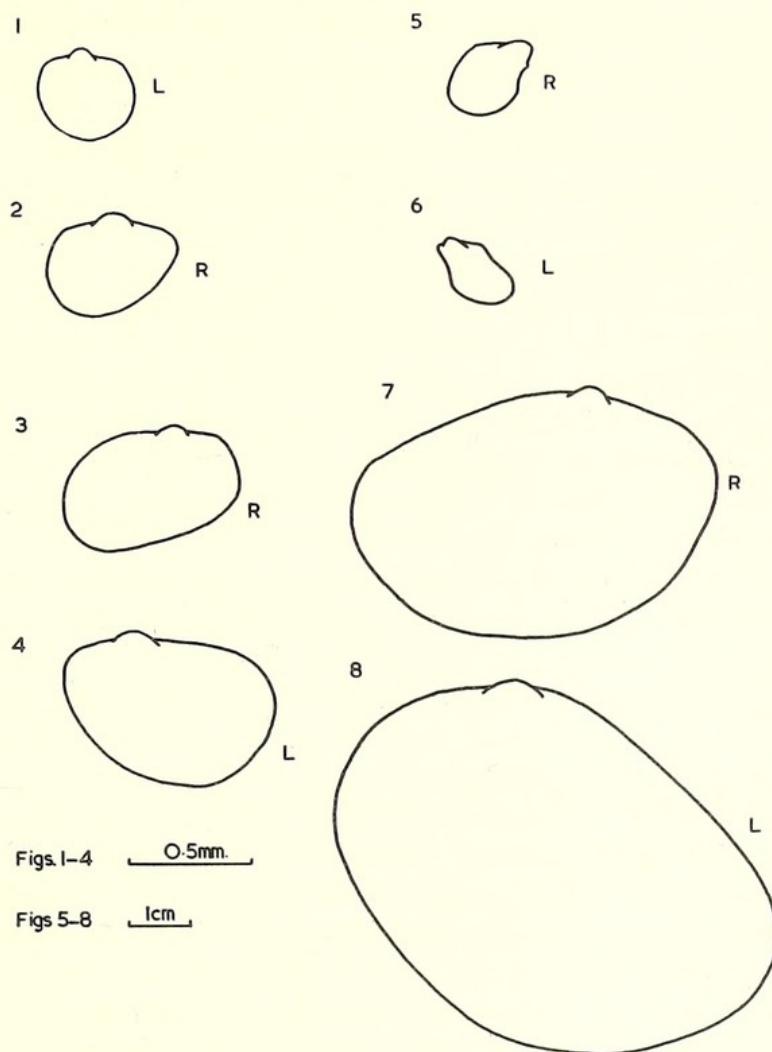


8



9

It is true that *Lima*, which is perhaps as closely related to *B. buchi* as the *Pecten irradians* studied by Jackson, has no inequivalve stage in development, though it settles in the usual manner and the adult is benthonic (Odhner 1914; Lebour 1937). This is because on settlement the post-larva, like an adult *Lima*, crawls with the commissure vertical instead of lying on one valve. As already mentioned, however, if this was the



TEXT-FIG. 9. Ontogeny of *Posidonia becheri* Bronn.

mode of life of *B. buchi* one would expect to see a straight anterior margin, and this does not exist.

Conclusions. Assuming, on facies evidence, that *B. buchi* was not benthonic, it was either attached to flotsam or a planktonic swimmer. The pseudoplanktonic hypothesis meets with three main difficulties. Firstly, where *B. buchi* is abundant other possible pseudoplankton is usually very rare. Secondly, there is no evidence of attachment in the shell outline. Thirdly, by contrast with living and fossil relatives, there is no sign of an attached stage in the life history. Arguments in favour of the pseudoplanktonic hypothesis are weak; thus the occurrence of clusters of *B. buchi* is probably due to posthumous drifting and does not indicate attachment; and a mortality peak at a length of 1 mm. can be explained by metamorphosis rather than unsuccessful attachment.

Directly in favour of the nektoplanktonic hypothesis are the presence of gapes, the thinness of the shell, and the regular occurrence of the valves-open position. All these indicate swimming ability by analogy with living relatives. A nektoplanktonic mode of life is therefore much more likely than a pseudoplanktonic one.

The feasibility of a planktonic mode of life in Bositra buchi

So far it has been shown that a planktonic mode of life for *B. buchi* is most likely. Experimental evidence that the animal could reasonably have stayed up in the sea by using structures present in Recent Limidae and Pectinidae, i.e. by swimming, without the aid of a pneumatophore, is now examined.

Swimming plankton may remain at a roughly constant level by moving horizontally, like the pteropod *Cavolinia* (Schiemenz 1905, p. 6) or by swimming up and sinking down like the pteropods *Spiratella* (= *Limacina*) (Morton 1954, p. 298) or *Creseis* (Kornicker 1959), or even by swimming up and swimming down as the copepod *Calanus finmarchicus* sometimes does (Hardy and Bainbridge 1954, p. 425). Only passive sinking can be investigated in the present instance so we have assumed that *B. buchi* remained at one level by swimming up and sinking down. This would probably be less efficient than horizontal swimming, which would be aided by hydrodynamic lift, so that if 'hopping and sinking' is feasible, horizontal swimming is also feasible.

We have assumed that *B. buchi* sank umbones downwards in the observed position of stability for models when tentacles are present or when the valves are open to more than 45°. This is reasonable since in 'hopping and sinking' the animal sinks in the position of passive stability (e.g. *Spiratella*, *Creseis* and *Calanus*). It is consistent with the equi-valve character of *Bositra*, since bilaterally symmetrical swimmers like *Lima*, *Chlamys*, *Pecten*, plaice, herring (and submarines) swim with the median plane of symmetry vertical.

We have also considered the effect of a fringe of tentacles from the median lobe of the mantle margin, which exists in many Recent relatives of *B. buchi*, including *Spondylus gaderopus*, *Anomia ephippium*, *Ostrea edulis*, and *Pteria hirundo*, and is very well developed in the Pectinidae (e.g. *Chlamys opercularis* and *Pecten maximus*) and Limidae (e.g. *Lima hians*). *L. hians* rows with the tentacles when swimming (Gilmour 1963, p. 85), which shows that they are stiff enough to be hydrodynamically effective.

The object of the feasibility studies, therefore, was to determine settling velocity for *B. buchi* of different lengths, corresponding to different phases of the life history, different specific gravities of protoplasm, and with and without tentacles.

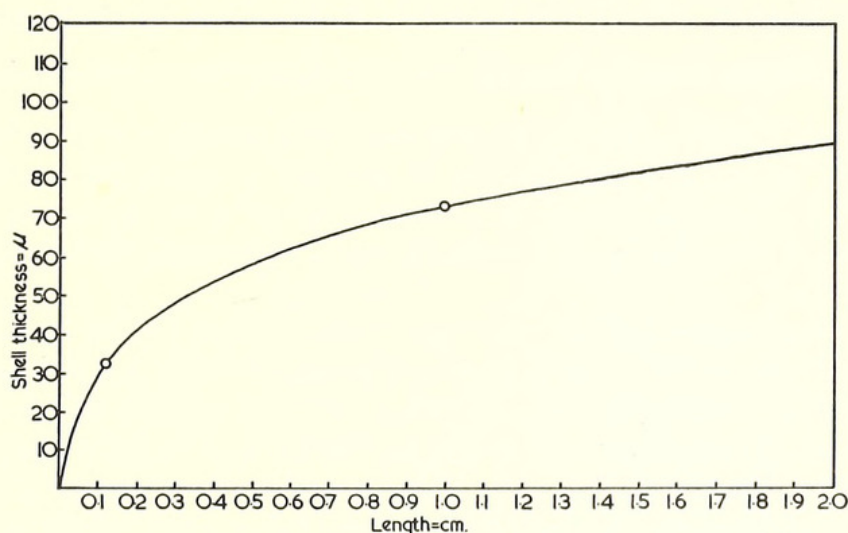
The hydrostatic properties of *B. buchi* of different lengths were estimated by comparison with a model 2 cm. long, having a shell of aluminium of specific gravity 2.7, shell thickness 49.4 μ and weight 96 mg. in air, and with an internal volume when closed of 1.4 cm.³ The internal volume at different lengths was calculated assuming geometrical similarity, and the weight of the shell by assuming geometric similarity for the surface area, a specific gravity of 2.7 (calcite), and a thickness deduced from text-fig. 10. The volume of protoplasm was assumed to equal the internal volume of the shell, which might be true when all the soft parts were retracted inside, as seems to have been possible (see p. 168). This gives a maximum value for the buoyancy for a given specific gravity of protoplasm.

It was also assumed that the specific gravity of the soft parts was not less than 0.9,

when the whole internal volume would be filled with fat. The possibility of a gas-filled float was neglected, as already explained. If the soft parts were extended by being inflated with sea water, their buoyancy would be unaffected. The tentacle array (Pl. 19, fig. 5) was assumed to be roughly like that of *Lima hians*. The valves were assumed to be open at 45° .

The ambient sea-water was assumed to be at 20°C . and 35‰ salinity with a specific gravity of 1.025 (Harvey 1955, p. 128) and viscosity 1.07 centipoises (Miyake and Koi-zumi 1948, p. 65).

At this point it is necessary to consider the hydrodynamics of a passively sinking



TEXT-FIG. 10. Plot of shell thickness against length in *B. buchi* as used in feasibility study. Circles indicate values obtained from thin section of LL88714, ? Bajocian, borehole 5 miles N. of Central Railway, Kidugallo, Tanganyika.

B. buchi. The slow settling of bodies through a stationary fluid has been the subject of many investigations, from the classical work of Stokes to, for instance, White (1946). When a body settles through a uniform fluid at a steady velocity, i.e. with no acceleration, and therefore with no resultant vertical force acting upon it, the weight acting downwards equals the sum of the buoyancy force and drag force acting upwards.

The weight (W) of *B. buchi* can be estimated from the information given above and depends on the specific gravity of the protoplasm S_p and the weight of the shell. The buoyancy force (B), due to the weight of liquid displaced, depends on the volume (V) and the density (ρ_w) of the surrounding water, while the drag (D) depends, among other variables, on the velocity of fall.

Now, as already stated,
$$W = B + D \quad (1)$$

or
$$V_s \rho_s g + V_p \rho_p g = (V_s + V_p) \rho_w g + D,$$

where V_s = volume of shell, ρ_s = density of the shell, V_p = volume of the protoplasm, ρ_p = density of the protoplasm, and g = acceleration due to gravity.

If W_s = immersed weight of shell

$$= V_s \rho_s g - V_s \rho_w g$$

and

ρ = density of fresh water, then

$$\begin{aligned} W_s &= gV_p(\rho_w - \rho_p) + D \\ &= \rho gV_p(1.025 - S_p) + D \end{aligned}$$

assuming ambient sea water of specific gravity 1.025.

The drag (D) may be estimated from experiments with models. The drag of *B. buchi* can be expressed as

$$D = \alpha \mu v l,$$

where μ = viscosity of fluid, v the settling velocity, l the length and α a dimensionless coefficient of resistance. The value of α depends on the shape of the falling body and the pattern of flow round it. Geometrically similar bodies have geometrically similar flow patterns, and equal values of α , if they fall such that their Reynolds' numbers ($R = \frac{\rho_w v l}{\mu}$) are the same. Consequently α can be determined experimentally with models of *B. buchi* of any length (l), by varying viscosity (μ) to give the required Reynolds' numbers. In studying the effect of change in size it is more convenient to use one model in liquids of varying viscosity, than models of different sizes, sometimes microscopic, in a liquid of constant viscosity.

The experiments were carried out in a cylindrical glass jar 19 cm. in internal diameter and 36 cm. deep, at about 20° C. Four bands of paper about 8 cm. apart were fixed round the jar. Preliminary experiments with tap water, in which models were timed with a stop clock, falling from first to third and from second to fourth bands, gave very similar velocities for both distances. The time taken to sink from second to fourth bands, 16.3 cm. apart, was therefore assumed to give terminal velocity. These experiments also showed that the presence or absence of concentric ribs on models carefully shaped to the convexity of *B. buchi* did not affect settling velocity, at least at length 1–2 cm. Models open at 60° and without tentacles fell at roughly 75 per cent. of the velocity of models open at 45°. Models open to 45° or more always fell umbones downwards. At a smaller angle they tended to fall one valve underneath. With tentacles of specific gravity equal to water the models always fell umbones downwards.

The final experiments were carried out in a mixture of glycerine and water, the mixture being varied to give viscosities from about 8 poises to 1 centipoise. Viscosities were measured with a series of U-tube viscometers. Temperature was constant at 20° ± 0.5° C. and the specific gravity, measured with a hydrometer, varied from 1.257 to 1.000.

Two models of length 2 cm. were constructed of aluminium foil of thickness 100 μ shaped to resemble *Bositra buchi* in outline and convexity, with the valves open to 45°. One of the models was provided with a fringe of flat tentacles of aluminium foil (Pl. 19, fig. 5) and weighed 950 mg., while the other was without tentacles and weighed 190 mg.

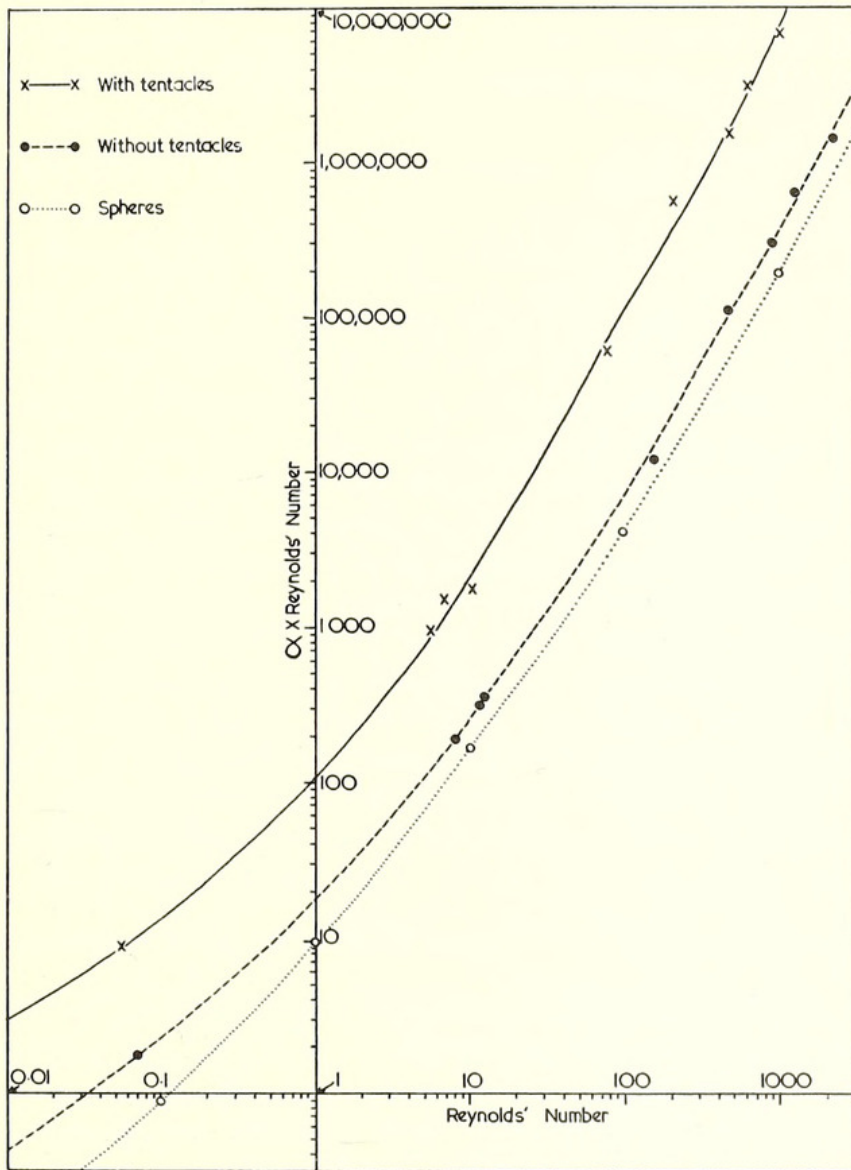
From the experimental results the drag (D) of the models was tabulated for various settling velocities (v) in solutions of viscosity (μ) and density (ρ).

$$\begin{aligned} \text{Now } D &= \alpha \mu v l = \alpha \mu \times \frac{\rho v l}{\mu} \times \frac{\mu}{\rho} = \alpha R \frac{\mu^2}{\rho}, \\ \therefore \alpha R &= \frac{D \rho}{\mu^2}, \end{aligned} \quad (2)$$

where αR is a function only of R , the Reynolds' number. The experimental results were reduced to this form and plotted logarithmically (text-fig. 11) over a range of Reynolds'

numbers from 10^{-2} to 10^3 (Note: *B. buchi* of $l = 1$ mm. and settling velocity 1 mm./sec has a value of $R = 1$). Values of αR for spheres from Goldstein (1938, p. 16) were plotted for comparison on the same axes and produce a very similar curve.

To present these results in a biologically useful form it was decided to compute a graph

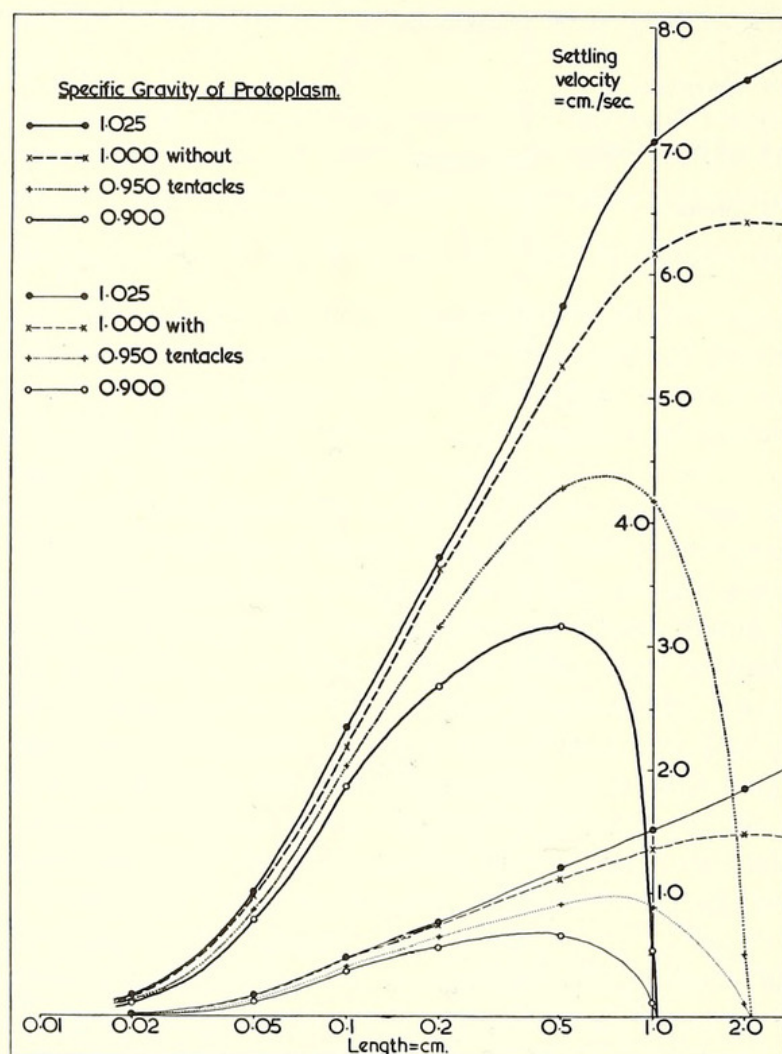


TEXT-FIG. 11. Coefficient of resistance (α) \times Reynolds' number against Reynolds' number for *B. buchi* with and without tentacles, and for spheres.

of settling velocity against length (text-fig. 12). Values of specific gravity of protoplasm (S_p) were chosen, the buoyancy (B) and weight (W) calculated for various lengths (l) and the drag (D) found from equation (1). R was calculated from equation (2) assuming sea water of the characteristics already mentioned. Reference to the appropriate line on text-fig. 12 led to the Reynolds' number from which the settling velocity was calculated.

In considering the biological significance of these results an analogy can be drawn between *B. buchi*, living as here postulated, and the Recent thecosomatous pteropods such as *Spiratella* and *Creseis* which likewise are shelled, microphagous planktonic

mollusca that stay up by 'hop and sink', are roughly the same size as *B. buchi*, and are able to withdraw into the shell. There is little information concerning passive settling velocities in this group, but in *Spiratella trochiformis* the mean of three descents was 1.3 cm./sec. varying from 1.2 to 1.5 cm./sec. (J. A. McGowan, personal communication),



TEXT-FIG. 12. Calculated passive settling velocities of *B. buchi* with and without tentacles, for various sizes and specific gravities of tissue.

and in *Creseis acicula* the mean of 24 descents was 1.15 cm./sec. ranging from 0.72 to 1.80 cm./sec. (Kornicker 1959, p. 334).

The graph suggests that *B. buchi* provided with tentacles could have sunk passively at a comparable velocity of less than 2 cm./sec., if the specific gravity was about equal to sea water or less. Without tentacles even extremely buoyant tissues (specific gravity = 0.9) would not have kept the settling velocity below 3 cm./sec. at one stage in the life history. It therefore seems that a planktonic mode of life for *B. buchi* is feasible if it was provided with a long fringe of tentacles. It should be noted that cylindrical tentacles would probably be somewhat, but not much, less effective than the flat ones in the model.

During the preliminary experiments it was noted that an empty shell of the Recent

pteropod *Cavolinia globosa* of length 0.8 cm. sank at 6.3 cm./sec. in tap water. This is the same as the settling velocity of a model of the shell of *B. buchi* of length 1 cm., angle of opening 60° and shell thickness 50 μ . This experiment, in itself, establishes the feasibility of a nekto planktonic mode of life for *B. buchi*.

The method of sinking large models in viscous solutions to give low Reynolds' numbers should be widely applicable in studies of the functional morphology of small biological objects such as microplankton and pollen grains.

THE MODE OF LIFE OF 'POSIDONIA' RADIATA GOLDFUSS

Synonymy.

Posidonia radiata Goldfuss 1836, p. 119, pl. 114, fig. 4. Vadász 1910, p. 41, fig. 8.

Posidonia bronni Zieten var. *magna* Quenstedt 1858, p. 260, pl. 37, fig. 8. (N.B. *Posidonia bronni* Voltz 1830 = *Posidonia bronni parva* Quenstedt 1858.)

Posidonomya (? *Daonella*) *radiata* (Goldfuss); Guillaume 1928, p. 219, pl. 10, fig. 1.

The two forms of 'Posidonia' of the German Posidonienschiefer are commonly called *Posidonomya bronni* Voltz var. *magna* Quenstedt and *Posidonomya bronni* Voltz var. *parva* Quenstedt (e.g. Hauff 1921, p. 19). They are probably distinct species since *magna* reaches a length of about 5 cm. and *parva* only about 1 cm., and the detailed stratigraphical distributions are different. *Magna* is of rock-forming abundance in the lowest beds of the Posidonienschiefer, but scarcely occurs higher, where 'parva' is very abundant.

Posidonomya bronni magna is identical with *Posidonia radiata* Goldfuss as judged by Goldfuss's figure. Goldfuss's material came from the Lias of Boll, a famous locality for Posidonienschiefer 7 km. east of Holzmaden. The 'faint, scarcely visible, radiating lines' which gave it its name can be seen on material that can certainly be identified as *P. bronni magna* from Holzmaden. The generic allocation of *Posidonia radiata* is uncertain since the hinge is unknown. It is expedient to leave it in the genus *Posidonia* Bronn 1828 (= *Posidonomya* Bronn 1837).

'*Posidonia*' *radiata* is larger and taller ($\frac{h}{l} = 0.95$) than *B. buchi*, with more median umbones. It is mainly Toarcian in age. It is figured in Pl. 19, fig. 5.

Facies. '*Posidonia*' *radiata* occurs in much the same facies as *Bositra buchi*. Thus Renz (1927, p. 487) notes its abundance as *Posidonia bronni* var. *magna* in the black, Upper Liassic 'Posidonienschiefer' of Albania and Western Greece—which otherwise contains only '*P. bronni parva*', aptychi, and in some beds a bivalve compared with *Pseudomonotis substriata*.

The best investigated occurrence, however, is in the Upper Lias of Holzmaden in Swabia (Hauff 1921, p. 20). Hauff examined the quarries there for many years and presented his results in semi-quantitative form (op. cit., pl. 7–13).

The beds in which Hauff records '*P.*' *radiata* in extreme abundance are the somewhat bituminous Koblenzer II₁ (mainly at the top), Hainzen II₂ and Fleins II₃, representing 40 cm. of rock. Associated fossils recorded by Hauff include: '*Pentacrinus*' *briareus* (rare), '*P.*' *briaroides* (rare), '*P.*' *subangularis* (rare), '*P.*' *hiemeri* (rare), '*P.*' *colligatus* (rare), *Ostrea* sp. (common), *Inoceramus dubius* (common); four species of ammonite (one very common, one common and two rare), and aptychi; three species of belemnites (one common and two rare); four species of squid (all rare); two species of eryonid crab

(both rare); ten species of fish (all rare); two species of ichthyosaur (both rare); and coprolites. The abundances are deduced from Hauff's distribution charts.

At first sight, as Hauff remarked (op. cit., p. 38) of the Posidonienschiefer in general, there seem to be many benthonic species. However, the '*Pentacrinus*' spp. occur attached to fossil wood and must be regarded as having floated in; the oysters (*Ostrea* sp.) are found attached to wood or ammonite shells, or in little nests where the ammonite shell to which they were attached has apparently disappeared. *Inoceramus dubius* is also commonly attached to wood. The only remaining possible benthos (leaving aside '*P.*' *radiata*) are the crabs; no conclusions can be based on these, however, for they are exceedingly rare; moreover, modern eryonids may have a certain degree of swimming ability, for almost adult juveniles have been taken in mid-water (Dr. I. Gordon, personal communication).

Among forms which die out at the base of the Koblenzer, where '*P.*' *radiata* becomes common, are the burrow *Fucoides granulatus*, *Rhynchonella amalthei* and *Plicatula spinosa*, which must have been benthonic. Belemnites become much rarer than lower in the sequence. Thus *B. paxillosus*, which occurs abundantly ('Massenvorkommen') beneath the Koblenzer, is merely constantly present ('durchgehendes Vorkommen') in the Koblenzer, Hainzen, and Fleins. The heavy skeleton of the belemnites suggests that they were habitually benthonic, but, being swimmers, they might be expected occasionally where the bottom was uninhabitable.

Thus there was probably no benthos in the beds with abundant '*P.*' *radiata*. The apparent cases can be explained as pseudoplankton, or need not always have been strictly benthonic, or are too rare to be used in evidence. In view of this, and the bitumen in the rock, these 40 cm. of beds were probably deposited under stagnant conditions with poisonous anaerobic bottom water. Hauff (op. cit., p. 42), following Pompeckj (1901), compared the Posidonienschiefer with the bottom deposits of the Black Sea.

The view that the Posidonienschiefer are euxinic deposits is generally accepted in Germany (discussion in Hauff, Jr. 1960, p. 36). Objections were raised by Beurlen (1925), who held that the bivalves and crabs must have been benthonic. His views were reiterated by Kuhn (1952, 1953, 1955) as regards Franconia, where crabs are commoner than at Holzmaden and a conglomerate is present. Faber (1931) pointed out that in Luxembourg the bivalves were often single valves only, indicating water movement. Finally, Einsele and Mosebach (1955, p. 340) favoured gyttja rather than sapropel conditions for the Holzmaden area, because of the presence of burrows at the base and at one level within the Posidonienschiefer, the ubiquitous abundance of the tiny gastropod *Coelodiscus minutus*, which had not been observed by Hauff, and the presence of eryonid crabs.

These objections, however, are lacking in force. In the first place, at Holzmaden crabs are exceedingly rare, and not common even in Franconia. Limited swimming ability is enough to explain their occurrence. The conglomerate suggests that conditions in Franconia were not exactly as in Swabia. Secondly, the water movement required to shift valves of *Steinmannia bronni*, '*Posidonia*' *radiata*, or *Inoceramus dubius* would be extremely slight, since these are very thin-shelled. Indeed an oscillation rather than a current would be sufficient. Since deposition was probably slow such movements need only be infrequent, and disarticulation of the valves is therefore compatible with euxinic conditions. Thirdly, burrows are a sensitive indicator of benthos, in the sense that a few benthonic animals can cause a great number of tracks. The absence of burrows,

except at the base of the Posidonienschiefer and one horizon within them, is therefore a strong argument for euxinic conditions in most of the formation. Burrows are absent in the beds where '*P.*' *radiata* is abundant. Fourthly, the tiny thin-shelled *Coelodiscus minutus*, which is also abundant in the equivalent Jet Rock of Yorkshire, was probably pelagic. It much resembles the Recent and Tertiary pelagic gastropod *Spiratella*. Hauff's conclusion that the Posidonienschiefer in general, and the Koblenzer, Hainzen and Fleins in particular, were deposited in anaerobic bottom water therefore remains extremely probable.

Pieces of wood are common in the Holzmaden Posidonienschiefer, including the Fleins. '*Pentacrinus*', *Inoceramus dubius* and *Ostrea* sp. are often attached to them, and, assuming euxinic conditions, must have settled and grown on the wood when it was floating. However, neither '*P.*' *radiata* nor *S. bronni* has ever been found attached to wood. A particularly striking specimen is preserved in the Hauff Museum (Hauff 1960, pl. 63). This is a slab of Fleins, 112×68 cm. in size, with a piece of driftwood near one edge to which are attached *Inoceramus dubius* and '*Pentacrinus*' *subangularis*. Distributed over the rest of the surface of the block are innumerable valves of '*P.*' *radiata* and there must be several thousand more of these buried in the block. Those on the surface have been smoothed off during preparation, so that on Hauff's photograph they merely appear as a pepper-and-salt effect. They can readily be seen, however, on the block itself. A very similar specimen (E25388) from Boll is displayed in the British Museum (Natural History). This shows a mass of '*Pentacrinus*' *subangularis* embedded in Fleins with numerous specimens of '*P.*' *radiata* scattered over the rock. *I. dubius* and pieces of wood do not occur in this specimen but it was probably formed in much the same way as the specimen in the Hauff Museum.

These specimens show that '*P.*' *radiata* had a different mode of life from, for instance, *Inoceramus dubius*. Since conditions were euxinic, it must have been pelagic. It is improbable that it was pseudoplanktonic, since other pseudoplankton was dependent on lumps of wood or ammonites to remain afloat. A nektoplanktonic mode of life is strongly indicated.

Functional morphology. At Holzmaden '*P.*' *radiata* is always so compressed that studies of functional morphology are very difficult. The anterior margin, however, appears to be circular with no sign of an anterior ear or any concave portion that might suggest attachment. It can be contrasted with *Inoceramus dubius*, which is mytiliform.

Specimens in the Fleins sometimes occur with the valves open like *B. buchi*. In a quarry on the south side of the road from Zell to Ohmden near Holzmaden, 33 such specimens were concave-up and 5 concave-down. The same conclusions apply as with *B. buchi*. Guillaume (1928, p. 10, fig. 1) figured specimens of '*P.*' *radiata*, including one in the valves-open position, which seem less crushed than usual. The figures confirm that the anterior margin was circular while the posterior dorsal part of each valve was convex outwards in a way that strongly suggests a posterior gape. As in *B. buchi* this would indicate swimming ability. Guillaume's figured specimens were not available to the present authors.

Because of the lack of well-preserved specimens, the shell thickness of *B. buchi* cannot be accurately estimated but it was much thinner-shelled than *Inoceramus dubius* in the same bed.

Feasibility of a planktonic mode of life. Experiments show that, with the same shell thickness, 5 cm. models sink slower than 2 cm. models. For example, with a shell thickness of 50 μ , angle of opening 60° and no tentacles, settling velocity was respectively 5.3 cm./sec. and 6.7 cm./sec. This decrease in velocity with size may be due to the hydrodynamic effect of the sides of the jar in which the experiment was carried out, but there is no reason to doubt that, in an infinite medium, the settling velocities would be similar to each other. In addition, the available tissue buoyancy at 5 cm. could be greater than at smaller sizes. A nektoplanktonic mode of life is therefore feasible for '*P.*' *radiata* as for *B. buchi*.

Conclusions. The evidence concerning '*P.*' *radiata* may be summarized as follows: firstly, on facies grounds as with *B. buchi*, the species was almost certainly not benthonic, and its failure to occur attached to wood, like obvious pseudoplankton in the same beds, indicates that it was not pseudoplanktonic. Secondly, the circular anterior margin confirms that it was not attached. Thirdly, the thin shell, the probable presence of a posterior gape, and the occurrence of the valves-open position suggest swimming ability. '*P.*' *radiata* was therefore probably nektoplanktonic.

The same conclusions may apply, at least in the adult, to the relatives of *B. buchi* and '*P.*' *radiata* occurring in the same characteristic facies, including *Steinmannia*, *Halobia*, *Daonella*, *Dunbarella*, *Monotis*, *Buchiola* and Palaeozoic and Triassic occurrences of *Posidonia*. Each species needs to be examined ecologically from this point of view using the twin approaches of facies and functional morphology.

Acknowledgements. The authors wish to thank numerous colleagues with whom they have discussed the subject of this paper, and in particular Dr. L. R. Cox for help with systematics, Prof. C. M. White for discussion of the hydrodynamics, and also Mr. G. F. Elliott, Dr. C. G. Adams, Dr. W. T. Dean, Dr. A. Smith, and Prof. R. G. S. Hudson. Dr. T. H. J. Gilmour kindly supplied information on the habits of Recent Limidae, and Dr. K. W. Ockelmann drew attention to *Cyclopecten groenlandicus*.

For help in the field, response to inquiries, or permission to work at the institutes under their charge they wish to thank Dr. B. Hauff, Jr. (Hauff Museum, Holzmaden), Dr. F. S. Russell (Plymouth Marine Biology Laboratory), and Dr. J. P. Thieuloy (Department of Geology, University of Grenoble). Dr. H. Hess kindly supplied specimens from la Voulte-s.-Rhône. Mr. A. E. Rixon made many helpful technical suggestions. Mr. H. G. Owen helped with the experiments, took some of the photographs and discovered the material of *B. buchi* showing the hinge.

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