THE FEEDING MECHANISM OF THE PERMIAN BRACHIOPOD *PRORICHTHOFENIA*

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ABSTRACT. The morphology of *Prorichthofenia uddeni* (Böse) and *P. permiana* (Shumard), from the Permian of Texas, U.S.A., is analysed and interpreted in functional terms. The methodology of such functional interpretations is discussed briefly. It is inferred that most of the anomalous characters of the genus (especially the unusually thin and recessed dorsal valve, the peculiar form of hinge and the internal spines) relate to an unusual feeding mechanism. On this interpretation rapid movements of the dorsal valve created powerful currents and eddies, from which food-particles were collected by the mantle surfaces. It is inferred that the spines projecting across the aperture of the shell, and those on the dorsal valve, served to supplement the particle-collecting capacity of the mantle surfaces, and to exclude harmfully large particles. Experiments with working models of the shells confirm that the morphology of both species would have been highly adapted to the efficient operation of this mechanism. The specific differences in morphology are taken to represent a minor functional differentiation.

INTRODUCTION

The detection of adaptation in fossils. Though adaptation stands at the centre of the modern debate on the mechanisms of evolutionary change, the problem of the recognition of adaptation in fossils, or the inference of function from structure has received surprisingly little attention. The problem is especially acute in the study of aberrant fossils such as the richthofeniids; for then neither homological nor analogical comparisons with living animals can yield reliable inferences about the functional significance of the morphology. Therefore a method must be used that does not depend upon specific similarities with living animals.

Many functions of the body demand, for their efficient operation, predictable modifications of the anatomy. For these, it is often possible to specify the nature of the 'ideal' structure that would be able to fulfil this function with perfect efficiency. But in actuality the materials (anatomical and environmental) involved in the function are never 'perfect' in their properties. For any given set of materials, the 'ideal' structure must, therefore, be modified into the *paradigm*. This is the structure that can fulfil the function with maximal efficiency under the limitations imposed by the nature of the materials. The degree of approximation between any paradigm and an observed fossil structure is a measure of the degree of efficiency with which the structure would have been physically *capable* of fulfilling the function; but it cannot establish the probability that the structure *did* fulfil it. But by analogy with adaptation in living animals, there are strong grounds for inferring that a fossil structure capable of fulfilling a certain function with great efficiency did fulfil that function, especially if it can also be shown that the structure would have been inefficient or inoperable as the agent of any other conceivable function. Thus, by transforming rival possible functions into their respective paradigms, rival structural predictions can be made; and these can be tested by direct comparison with the observed structure of the fossil.

The ease and confidence with which a function can be inferred by this method is

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directly proportional to the efficiency of the adaptation. A structure that was very efficient will approximate closely to the paradigm of its function, and thereby can be recognized as an adaptation with relative ease. A less efficient structure will be more ambiguous, because it will not be very similar to its paradigm, and is likely to show some points of fortuitous resemblance to the paradigms of other functions. A non-adaptive structure can never be recognized as such; for its apparent lack of correspondence to any paradigm might always be due to failure to consider the correct function and the correct paradigm. Thus there can be positive and cumulative evidence that a structure was an efficient adaptation; but it is methodologically impossible ever to demonstrate that a structure was non-adaptive.

This method involves an analysis of adaptation only as a static phenomenon. Theories of its causal origin (e.g. by natural selection) or of its temporal origin in a particular instance (by a particular evolutionary lineage) are irrelevant to the detection of an adaptation.

Material studied. The earlier descriptions of richthofeniids were based on rather poorly preserved material; and the morphology remained imperfectly understood until well-preserved silicified specimens were discovered in the Permian of Texas, U.S.A. More recently, such specimens have been recovered in great numbers from these rocks, by dissolving large masses of limestone in weak acid (Cooper 1950). The present work is based on a small collection of this material, from the Permian of the Glass Mountains, near Marathon, Brewster County, Texas. The specimens are deposited in the Sedgwick Museum, Cambridge (registration numbers E.15,577–95; E.15,706–35; E.15,740–91; E.17,124–39); some were donated by Professor A. Williams and some were received in exchange from the U.S. National Museum. The collection includes two of the species described by King (1930): *Prorichthofenia uddeni* (Böse) from the Leonard formation at Old Word Ranch, and *P. permiana* (Shumard) from the overlying Word formation in Hess Canyon.

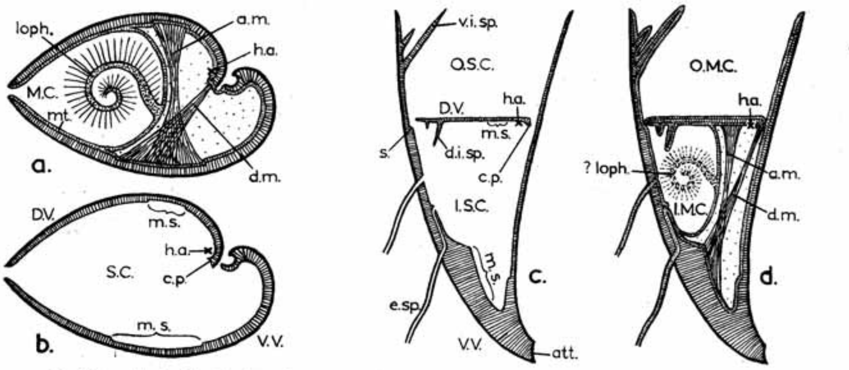
The basic morphology of Prorichthofenia. The normal form of a brachiopod shell is modified to an extreme degree in the richthofeniids. Nevertheless, the basic structure, of two shelly valves hinged together on the posterior side, is still recognizable. But the ventral valve is modified into an irregular cone; and the dorsal valve is reduced to a thin flat operculum, which closes the interior of the ventral valve some way below its rim (text-fig. 1*c*). The ventral valve is cemented to the substratum by its apex and by tubular external spines. Solid internal spines are usually developed on the internal surface of the ventral valve and on the lower surface of the dorsal valve.

For the purposes of this paper, the two species studied differ most significantly in the form of the internal spines on the upper part of the ventral valve. In *P. uddeni* they occur in a single row, they often branch and anastomose, and in some specimens they form a continuous mesh over the opening of the ventral valve (Pl. 73, fig. 2). In *P. permiana* they are relatively stouter, they occur not in a row but in an irregular 'thicket', and they rarely branch or anastomose (Pl. 73, figs. 7–9). The smaller specimens of both species have no internal spines.

The plane of the dorsal valve (when closed) will be taken as 'horizontal'; and the axis at right angles to this as 'dorso-ventral'. The space enclosed by the dorsal valve will be termed the *inner shell cavity* (text-fig. 1*c*, *I.S.C.*); the space above the dorsal valve, but below the rim of the ventral valve, will be termed the *outer shell cavity* (*O.S.C.*).

RECONSTRUCTION OF THE 'SOFT PARTS'

The mantle tissue. In living articulate brachiopods there is a uniform relationship between the valves and the mantle tissue that secretes them. There are normally two distinct shell layers: a thin outer 'lamellar' or *primary layer* and a thicker inner 'prismatic' or *secondary layer* (text-fig. 1*b*). The primary layer is deposited only by the extreme edge of the mantle lobe (text-fig. 1*a*, *mt.*), while the secondary layer is deposited, on the inner side of the primary layer, by the rest of the outer epithelium of the mantle lobe (Williams 1956). A precisely analogous mode of formation occurs in lamellibranchs (Beedham 1958). For any shell formed in this way the shell surfaces on which the secondary layer is exposed correspond to the areas originally covered by the mantle (text-fig. 1*b*, cf. 1*a*).



TEXT-FIG. 1. Homological relations between a 'normal' brachiopod (*a*, *b*) and a richthofeniid (*c*, *d*), shown in diagrammatic median longitudinal sections. *a*, Anatomy of a living 'normal' brachiopod; *b*, the same, after destruction of 'soft parts'; *c*, 'hard parts' of a richthofeniid; *d*, reconstruction of anatomy of richthofeniid. *a.m.*, adductor muscle; *att.*, attachment area; *c.p.*, cardinal process; *d.i.sp.*, dorsal internal spines; *d.m.*, divaricator muscles; *D.V.*, dorsal valve; *e.sp.*, external spines; *h.a.*, hinge axis; *I.M.C.*, inner mantle cavity; *I.S.C.*, inner shell cavity; *loph.*, lophophore; *M.C.*, mantle cavity; *m.s.*, muscle scars; *mt.*, mantle tissue; *O.M.C.*, outer mantle cavity; *O.S.C.*, outer shell cavity; *s.*, shelf; *S.C.*, shell cavity; *v.i.sp.*, ventral internal spines; *V.V.*, ventral valve; visceral cavity lightly stippled; mantle tissue and lophophore densely stippled; primary layer of shell, solid black; secondary layer of shell shaded.

In *Prorichthofenia* the two shell layers are readily recognizable even in silicified specimens, by their distinctive surface characters.

The shell structure is complicated by the development of vesicular texture in parts of the secondary layer, and by the existence of an apparently distinct internal 'third layer'. Waagen (1884–7, pp. 730–1), King (1930, p. 97) and others have identified this internal layer as the homologue of the external primary layer of other brachiopods, and the outer and vesicular layers as an external 'investment' without parallel in other brachiopods. This leaves unexplained the very close resemblance (e.g. in strong growth-lines and the bases of external spines) between the outer layer and the primary layer of other brachiopods; and the resemblance between the internal layer and the primary layer can be explained in terms of analogy. The internal layer bears vague growth-lines; but these merely represent the former position of the internal 'shelf' on which the dorsal valve rests (p. 455, Pl. 72, figs. 1–4). It also bears posteriorly a pair of flat 'sectors' separated by a rounded groove, resembling the cardinal area and arched deltidium (seen from within) of a 'strophic' brachiopod (Rudwick 1959). These represent the former positions of the 'fulcral ridges' (i.e. the functional hinge-line) and the median gap occupied by the cardinal process (p. 457), and are therefore analogous to a true cardinal area and deltidium; but there is no independent evidence that they are homologous. Thus the internal layer appears to be merely a modified part of the inner surface of the secondary layer; and the outer layer then represents the primary layer.

The primary layer is confined to the outer surface of the ventral valve, and is not present on any part of the dorsal valve (text-fig. 1*c*). Therefore, if the shell was formed by the 'normal' mode, the whole inner surface of the ventral valve, and both surfaces of the dorsal valve, must have been covered with mantle tissue (text-fig. 1*d*). If this tissue was permanently in this position, a large area of the mantle would have been permanently exposed to the external environment (cf. Williams's (1958) reconstruction of the mantle in oldhaminoids). The alternatives are to postulate (*a*) that the ventral mantle was frequently retracted off the walls of the outer shell cavity (in fact this would have been difficult, if not impossible, in specimens with spines in this position; cf. text-fig. 1*d*); or (*b*) that the process of shell formation was abnormal on the dorsal valve, and that its upper surface was not covered by mantle tissue at all (cf. Stehli's (1956) interpretation of oldhaminoids). The mantle must have been abnormal *either* in being permanently exposed, *or* in its mode of shell secretion. In other words, *Prorichthofenia* (and the oldhaminoids) differed from present-day brachiopods either functionally (analogically) or homologically. The manifest similarity in shell structure clearly favours the former. *Prorichthofenia* is therefore reconstructed with an outer shell cavity permanently lined with mantle tissue, forming an *outer mantle cavity* (text-fig 1*d*, *O.M.C.*).

The mantle tissue of *Prorichthofenia*, like that of living articulate brachiopods, was probably very thin, at least on the side of the outer shell cavity: for the edge of the dorsal valve often lies very close to the inner surfaces of the ventral valve. Its proximity to some of the spines which project across the outer shell cavity shows that the tissue sheathing the spines must have been equally thin.

The 'body'. In living articulate brachiopods the 'body' (i.e. the organs enclosed in the visceral cavity) is confined to a small median posterior portion of the shell cavity, and the body-wall lies closely against the muscles both anteriorly and laterally. In *Prorichthofenia* the muscle attachments are similar to those found in living articulate brachiopods. On the ventral valve both adductors and divaricators were attached either to the floor of the inner shell cavity or, more commonly, to the posterior face of the median ridge that runs up the anterior wall of the cavity (Pl. 72, fig. 10). On the dorsal valve there is a pair of adductor scars in front of the hinge axis (text-fig. 4*c*; Pl. 72, figs. 4, 6, 11: *a.m.*); and the cardinal process is situated in the median plane, on the posterior border of the valve (text-fig. 4*c*; Pl. 72, figs. 5, 6, 11, 12: *c.p.*). Thus the muscles would have been confined to the median posterior portion of the inner shell cavity (text-fig. 1*d*). Therefore, by homology, this was probably also the position of all the other organs of the 'body'; and the remainder of the inner shell cavity would have formed an *inner mantle cavity* (text-fig. 1*d*, *I.M.C.*).

The lophophore. The 'hard parts' of *Prorichthofenia* give no indications of the form, position, or even existence, of the lophophore. If it was present, and occupied a position homologous with its position in living brachiopods, it would have been attached to the anterior body wall below the hinge, and either suspended freely in the inner mantle cavity or perhaps attached to the lower surface of the dorsal valve (text-fig. 1*d*; here its size and form are purely diagrammatic).

FUNCTIONAL MORPHOLOGY OF THE DORSAL VALVE

The valve as a protective structure. It is generally accepted that one important function of the valves of a brachiopod is that of protecting the soft tissues and organs of the animal from the effects of harmful agents in the external environment. This function can only be fulfilled efficiently if the valves (*a*) are wholly external to the soft parts, and (*b*) have edges that are identical in form. Then, when the valves are closed, the edges will fit tightly together, and will seal all the soft parts from direct contact with the external environment. This 'paradigmatic' specification is fulfilled accurately in the shells of all living articulate brachiopods. But in *Prorichthofenia* the dorsal valve is more or less deeply recessed within the ventral valve. Even when it was closed, a considerable area of mantle tissue would still have been unprotected and therefore exposed to the action of predators and of harmful solutes and suspensions. It is true that the tight seal around the edge of the closed dorsal valve might have prevented them from penetrating to the 'body' of the animal; but the valve is so thin that even when closed it would have given little protection against larger predators. Thus it could not have provided efficient protection against any type of harmful external agent.

Richthofeniids have sometimes been compared with other operculate coralloid organisms, such as goniophyllid rugose corals (e.g. *Calceola*), other aberrant brachiopods (e.g. *Scaccinella*, *Gemmellaroia*), and the more highly modified rudist lamellibranchs (e.g. *Radiolites*, *Hippurites*). As Cloud (1948, p. 327) has suggested, the common coralloid form may be due to ecological convergence. But in the form of the 'operculum' the richthofeniids differ markedly from the other organisms. In the latter, the 'operculum' lies across the aperture of the 'coralloid cone' and is relatively thick and robust; and it could therefore have functioned efficiently as a protective structure.

EXPLANATION OF PLATE 72

Figs. 1–14. ***Prorichthofenia permiana.*** 1, Antero-lateral view of right lateral wall; dorsal valve preserved half-open, against arcuate zone (E. 17128, ×2). 2, Lateral view of left lateral wall; dorsal valve broken away except near hinge (E. 17129, ×2). 3, Antero-lateral view of right lateral wall; dorsal valve broken away except near hinge; note pustular surface of outer shell cavity (E. 15581, ×2). 4, Antero-ventral view of hinge; dorsal valve closed (E. 15589, ×3). 5, Anterior view of hinge; dorsal valve half-open (with small adherent brachiopod) (E. 17128, ×3). 6, Anterior view of hinge; dorsal valve fully open (E. 15787, ×3). 7, Dorsal view of hinge; dorsal valve closed (E. 15783, ×4). 8, 9, Oblique views of hinge structure of ventral valve (dorsal valve missing) (E. 15710, E. 15778, ×4). 10, Posterior view of ventral muscle scars (E. 15755, ×3). 11, Ventral view of dorsal valve (E. 15744, ×3). 12, Oblique postero-dorsal view of the same dorsal valve, showing spinules (E. 15744, ×4). 13, View of anterior edge of another dorsal valve, showing fluted spines projecting from ventral surface and spinules on dorsal surface (E. 15786, ×4). 14, Dorsal view (posterior side to left) of the same dorsal valve (hinge region broken off), to show spinules (E. 15786, ×3).

Dorsal and ventral views orientated with posterior side uppermost; anterior and posterior views with dorsal side uppermost, unless otherwise stated. *a.g.*, accommodation groove; *a.k.*, articulation knob; *a.m.*, adductor muscle scar; *a.z.*, arcuate zone; *c.p.*, cardinal process; *D.V.*, dorsal valve; *f.r.*, fulcral ridge; *h.*, hinge; *h.a.*, hinge-axis; *l.p.*, lateral plate; *s.*, shelf.

This comparison places the richthofeniids in an isolated and anomalous position. Though it might be inferred that they were merely less well adapted than the other organisms (invoking for a causal explanation such factors as 'low selection pressure' or 'phylogerontism'), this interpretation is methodologically inconclusive; for the dorsal valve, though relatively inefficient for protection, might have been highly efficient for some other function.

The range of movement of the valve. The total range of movement of the dorsal valve can be reconstructed from specimens in which it is preserved in different positions.

When fully closed it rests on a *shelf* (cf. King 1930, p. 97), which encircles the inner surface of the ventral valve (Pl. 72, figs. 1–3; Pl. 73, fig. 16: *s*). It makes an accurate contact with the shelf, so that during life the inner mantle cavity would have been tightly sealed from the outer mantle cavity and the external environment.

It is clear that the dorsal valve was able to move through a wide angle: parts of the walls of the cavity, and their derivatives (viz. the internal spines), lie extremely close to the inferable course of the edge of the dorsal valve, yet could not have obstructed its movement. (*a*) Parts of the lateral walls of the outer shell cavity are close to the edge of the valve. These parts are never pustular or spiny, but smooth or marked with faint arcuate striae. These arcuate zones (Pl. 72, figs. 1, 2: *a.z.*) represent parts of the surface of revolution described by the edge of the dorsal valve in rotating around the hinge axis. (*b*) In *P. uddeni* the mesh itself lay only just above the course of the edge of the dorsal valve (text-fig. 3*a*, *d*). Externally the mesh appears gently domed; internally it can be seen that this form is geometrically continuous with the arcuate zones. (*c*) Similarly in *P. permiana* the lowest of the anterior and lateral spines are inclined at such an angle that their lower sides were very close to the edge of the dorsal valve (text-fig. 2*b*, *d*). (*d*) In some specimens of *P. permiana*, however, the lowest spines lack the sharp point that normally terminates the smaller spines, and instead have a distinctive blunt termination (cf. Pl. 73, figs. 12, 13). This is not due to posthumous damage; almost certainly it is the result of resorption. The positions of these resorbed points are always very close to the course on which the edge of the dorsal valve would have moved; so that if these spines had not been shortened to that particular degree by resorption they would have obstructed the dorsal valve (text-fig. 2*a*, *c*). (At an earlier growth stage they were presumably sharp-pointed and uppermost in position; but with the upward migration of the dorsal valve during growth, they would have come to occupy a lower relative position, in which only terminal resorption could prevent them from obstructing the dorsal valve.)

The posterior wall of the outer shell cavity sets an upper limit to the possible range of movement of the dorsal valve. In most of the larger specimens the form of this wall suggests very strongly that the valve habitually moved into this extreme position, and in some specimens it is preserved there (text-fig. 3*a*, *c*). The wall is conspicuously flattened, and the outline of this *flattened area* (Pl. 73, fig. 1) corresponds exactly to the outline of the dorsal valve (if preserved) and to the outline of the shelf. In one specimen of *P. permiana* there is no flattened area, and the posterior wall bears solid spines; but all except the uppermost spines have resorbed points (Pl. 73, figs. 12, 13) which lie in a single plane (Pl. 73, fig. 7); clearly this plane was the limiting position into which the dorsal valve could move (text-fig. 2*c*).

Thus no 'hard part' could have prevented the dorsal valve from moving through the wide angle (between 60° and 90°: see text-figs. 2, 3) between the shelf and the flattened area; and the valve is preserved in all positions between and including these limits. The

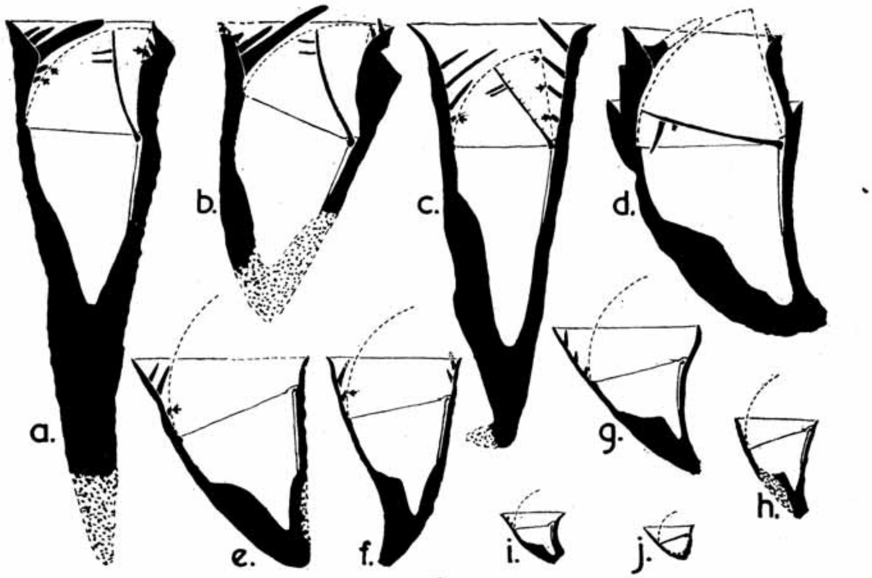


FIG. 2

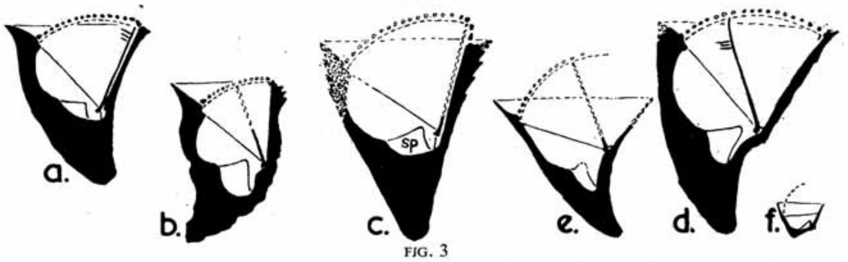


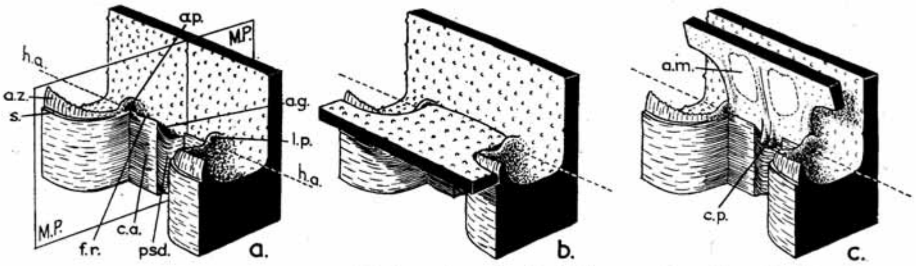
FIG. 3

TEXT-FIGS. 2, 3. Median longitudinal sections of representative specimens of *P. permiana* (text-fig. 2) and *P. uddeni* (text-fig. 3), based on camera-lucida drawings. All × 1·3. Reconstructed parts stippled or shown with dashed outline. Note inferred arcuate course of anterior edge of dorsal valve. Mesh of *P. uddeni* shown as row of solid dots; reconstructed parts, as open circles. All other spines shown as projections from shell, cut off at base by white line (the spines shown are those near, but not necessarily in, the median plane). Inferred 'resorbed points' of spines of *P. permiana* shown by short arrows. *sp.*, median septum of *P. uddeni*. (Text-fig. 2: *a*, E. 15787; *b*, E. 15785; *c*, E. 15786; *d*, E. 17136; *e*, E. 17135; *f*, E. 15583; *g*. E. 15778; *h*, E. 15756; *i*, E. 15746; *j*, E. 15591. Text-fig. 3: *a*, E. 17123; *b*, E. 15723; *c*, E. 15717; *d*, E. 17122; *e*, E. 15716; *f*, E. 17127.)

structural relations between the dorsal valve and the outer shell cavity remain inexplicable except on the assumption that the dorsal valve habitually moved through this wide angle when the animal was alive. (There is no direct evidence of the angle of movement in specimens in which the ventral valve does not extend far above the shelf (text-figs. 2*e–j*; 3*e, f*); but a wide angle of opening would have been physically possible.)

The relation of the valve to the lophophore. Among living brachiopods, only in *Lacazella* (Lacaze–Duthiers 1861) is the angle of opening comparable to that postulated for *Prorichthofenia*; but unfortunately the feeding mechanism of *Lacazella* is still undescribed.

In the diverse lophophores of all living brachiopods that have been investigated, steady one-directional water currents are set up by the lateral cilia on the filaments (e.g. Atkins 1956), and the brachia are virtually immobile and non-extensible. If the lophophore of *Prorichthofenia* was normal in this respect, it follows that, whatever the form of the lophophore, both incurrent and excurrent streams of water would have had to traverse the outer mantle cavity simultaneously. In whatever parts of the cavity currents flowed, contamination between them would have been inevitable, unless some 'soft part' diaphragm (analogous to the partition between the siphons of a lamellibranch) extended vertically across the cavity to separate them from one another; but it is difficult to conceive how a vertical diaphragm could have been related structurally to a dorsal valve that moved through such a wide angle. Therefore, if the lophophore functioned normally, the recessed position of the dorsal valve would have made its filtering system inefficient.



TEXT-FIG. 4. Hinge structure of *Prorichthofenia*, shown by block diagrams (cut edges of valves shown solid black). *a*, Dorsal valve removed; *b*, dorsal valve closed; *c*, dorsal valve open. *a.m.*, adductor muscle scar; *a.g.*, accommodation groove; *a.p.*, articulation pit; *a.z.*, arcuate zone (extreme posterior part); *c.a.*, false cardinal area, *c.p.*, cardinal process; *f.r.*, fulcral ridge; *h.a.*, hinge-axis; *l.p.*, lateral plate; *M.P.*, median plane; *psd.*, false 'pseudodeltidium'; *s.*, shelf.

The nature of the hinge. In most brachiopods a wide opening of the valves is prevented either by the proximity of the umbones behind the hinge axis, or by the tight enclosure of the teeth between the walls of the sockets.

The structure of the hinge of *Prorichthofenia* (text-fig. 4; Pl. 72, figs. 4–12) differs significantly from that of other brachiopods. When the dorsal valve is preserved resting on the shelf, the rectangular projection on its posterior side fits into the top of a vertical recess in the posterior wall of the ventral valve. Near the posterior corners of the projection, a pair of small *articulation knobs* (*a.k.*) fit into a pair of *articulation pits* (*a.p.*) on the inner sides of a pair of vertical *lateral plates* (*l.p.*), which project forwards from the posterior wall of the outer shell cavity. This clearly constitutes a spindle-like bearing. The hinge-axis thus lay slightly in front of the posterior border of the rectangular projection. Along the same line, the dorsal valve is supported ventrally by a pair of sharp-edged horizontal *fulcral ridges* (*f.r.*), one on either side of the median plane, running parallel to the posterior wall but separated from it by a deep *accommodation groove* (*a.g.*), into which the posterior border of the projection sank when the dorsal valve opened. This clearly constitutes a 'knife-edge' type of bearing.

This remarkable hinge structure would have had four significant mechanical properties. (*a*) Both elements of the dual articulation would have permitted the dorsal valve to rotate through a very wide angle. (*b*) The 'knob and pit' articulation would have prevented any lateral slewing or longitudinal shearing during rotation. (*c*) The fulcral ridge articulation would have enabled the hinge to withstand considerable stresses during rotation. (*d*) The frictional resistance to the rotation would have been extremely slight, because the minute articulation knobs and the sharp-edged fulcral ridges are the only bearing surfaces between the valves.

The musculature of the valve. The positions of the muscle attachments show that the system of muscular leverage was normal (text-fig. 1). It is clear that in every position of the dorsal valve the line of action of the adductors would have been anterior, and that of the divaricators posterior, to the hinge-axis. Therefore contractions of the adductors and divaricators, respectively, would have been capable of lowering and raising the valve through the wide angle already postulated. It is necessary, however, to consider the nature of the resistance that the muscles would have had to overcome. The possible sources of resistance would be the same for any brachiopod. (*a*) Resistance due to friction at the bearing surfaces of the hinge. (*b*) Resistance due to gravity. (*c*) Resistance due to the inertia of the dorsal valve. (*d*) Frictional and inertial resistance of the water displaced by the moving valve (this would depend, above all, on the angular velocity of the valve). In *Prorichthofenia* (*a*) would have been minimized by the structure of the

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EXPLANATION OF PLATE 73

Figs. 1–6. *Prorichthofenia uddeni.* 1. Anterior view of flattened area (outlined) and hinge region, with posterior attachment of mesh; cf. text-fig. 3*c* (E. 15717, ×2). 2, Dorsal view of mesh (broken in two places anteriorly) (E. 17123, ×2). 3, Enlargement of left lateral part of same mesh; anomalous zone visible at top of figure (E. 17123, ×4). 4, Dorsal view of aperture (mesh broken away except marginally), showing spines on lower surface of dorsal valve (E. 17122, ×2). 5, Enlargement of left postero-lateral part of mesh shown in fig. 2, to show anomalous zone; normal part of mesh visible at bottom of figure; cf. fig. 3 (E. 17123, ×4). 6. Enlargement of part of 'imperfect' mesh (broken posteriorly) on anterior side of aperture; (E. 15724, ×4).

Figs. 7–16. *P. permiana.* 7, Dorsal view of aperture (cf. text-fig. 2*c*), to show distribution of spines (broken on left antero-lateral sector), spinules and pustules; note 'resorbed points' of posterior spines lying in a single plane (E. 15786, ×1·5). 8, The same, of another specimen (cf. text-fig. 2*b*) (E. 15785, ×1·5). 9, The same, of another specimen (cf. text-fig. 2*a*); note 'resorbed points' of right posterior spines, in same plane as flattened area (E. 17130, ×1·5). 10, 11, Enlargements of anterior spines shown in fig. 7; note sharp points on unbroken spines (E. 15786, ×4). 12, 13, Enlargements of posterior spines of same specimen; note characteristic blunt ('resorbed') points (E. 15786, ×4). 14, Enlargement of antero-lateral spines of specimen shown in fig. 8 (E. 15785, ×4). 15, Postero-ventral view of dorsal valve (posterior part broken away), to show spines along anterior edge (above) and 'resorbed' stumps behind; cf. Pl. 72, fig. 11 (E. 15743, ×3). 16, Oblique postero-ventral view of inner shell cavity of specimen cut in median plane; dorsal valve nearly closed; cf. text-fig. 2*d* (E. 17136, ×2).

Dorsal views orientated with posterior side uppermost; anterior and posterior views, with dorsal side uppermost. *an.*, anterior limit of anomalous zone; *h.*, hinge; *s.*, shelf; *sp.*, median septum.

hinge; and (*b*) and (*c*) by the unusually thin and light dorsal valve. Therefore the muscles would have encountered much less resistance on contraction than their counterparts in 'normal' brachiopods—excepting only the unknown factor of the resistance of the water. The sizes of the muscle scars (Pl. 72, figs. 4–6, 10, 11) show that the muscles were certainly not reduced in size relative to those of comparable 'normal' brachiopods. If their strength corresponded to the demands made upon them, the dorsal valve must habitually have moved with great rapidity.

This does not imply that the *intrinsic* speed of the muscles was necessarily high. The lines of action of both sets of muscles, and especially that of the divaricators, pass close to the hinge-axis (text-fig. 4*c*; Pl. 72, figs. 4–6, 11). Hence even a relatively slow contraction of either set of muscles would have served to rotate the valve rapidly. It is possible that the valve would have opened and closed with equal rapidity: observations on living brachiopods suggest that adductors have a higher intrinsic speed than divaricators (the valves are usually 'snapped' shut but opened slowly, yet the adductors are farther from the hinge-axis than the divaricators). More significantly, the cardinal process is so unusually close to the hinge-axis that the contraction of the divaricators would have occurred under almost isometric conditions. (For instance, in *P. permiana*, specimen E. 17128, the length of the muscle would have shortened by only about 5% of its total length during a full opening of the dorsal valve.) This would have given maximal efficiency in a rapid contraction, by reducing to a minimum the 'viscous' effects in the muscle.

To postulate that the dorsal valve moved rapidly up and down thus gives a consistent functional explanation of the thin opercular form of the valve, of the peculiar structure of the hinge, and of the apparently powerful musculature. Powerful muscles were required to overcome the resistance of the water displaced by the valve; other sources of resistance were minimized by the lightness of the valve and by the friction-free hinge; yet the stress at the hinge could be borne by the robust fulcral ridges.

THE BASIC FEEDING MECHANISM

An experimental study of a moving dorsal valve. A working model of *Prorichthofenia* has been constructed, and the physical effects of a rapidly moving valve have been studied experimentally. The model (Pl. 74, figs. 5, 6), constructed at natural size to avoid the need for dimensional corrections, represents a large specimen of *Prorichthofenia*. The interior is exposed to view by the removal of the left lateral wall; the cut surface (a plane parallel to, but well distant from, the median plane) is cemented against the front wall of a perspex tank. Fine nylon threads are attached to the dorsal valve at the positions corresponding to the adductor scars and the cardinal process; they run across the inner shell cavity, and pass through fine holes in the wall of the ventral valve at the points corresponding to the ventral muscle scars. Thus the degrees of leverage and the lines of action of both sets of muscles are accurately reproduced. Outside the model the threads pass over very small pulleys to a device that simulates the contractions of the muscles. The contracting forces are provided by a pair of elastic rubber threads, which, during contractions at varying velocities and under varying loads, simulate closely the physical behaviour of actual muscles. Either rubber thread can be made to contract, and so to move the dorsal valve of the model, by extending it and then releasing a trigger. The power of the contraction can be controlled by varying the degree of extension of the thread or by use of stouter or finer threads.

The tank is filled with water. The movements of the water, when the dorsal valve is opened or closed, are made visible by the use of a suspension of very small oil droplets with the same density as the water (a mixture of olive oil and nitrobenzene, adjusted to this density, is used). These droplets become visible when brightly illuminated. Light from a photoflood lamp above the tank is passed through a condenser and through a narrow slit, and so illuminates only those droplets that lie in a thin vertical sheet of water. For most of the experiments the zone of illumination was arranged to coincide with the median plane of the model. Since the dorsal valve is carved from Perspex, the flow within the inner shell cavity is visible even when the dorsal valve is closed. The movements of the water, as revealed by the oil droplets, were studied visually and with ciné photography. The length of exposure of the films reproduced here (Pl. 74) was such that the droplets moved far enough to appear as streaks on the film; in this way the velocity and the direction of the water movements can be determined with ease.

Two varieties of the model were used in the experiments. One simulates the more typical specimens of *P. uddeni* (cf. text-fig. 3*a–d*). The other simulates specimens of *P. permiana* such as those figured in text-fig. 2*a–d*.

The use of models representing the 'hard parts' is justified by the evidence that much of the mantle tissue was very thin and that the 'body' occupied only a small part of the inner shell cavity; thus the results of the experiments would scarcely be modified by the reconstruction of the 'soft parts'. The impossibility of inferring the actual strength and rates of contraction of the muscles may seem to be more serious. But in fact the basic features of the flow patterns are constant over a wide range of angular velocities of the dorsal valve (the experiments have covered velocities from about 100° to about 1,000° per second).

Flow patterns in models of Prorichthofenia. Owing to the development of arcuate zone (p. 455) on the lateral walls of the outer shell cavity, the currents caused by the dorsal valve are mainly confined to the median region; it is therefore sufficient to describe and figure the currents as they are seen in the median plane in the models.

When the dorsal valve moves upwards (Pl. 74, figs. 1, 3, 5) the space below it expands in volume and the space above and behind it contracts. Therefore there is a *downflow* into the former and an *upflow* out of the latter (text-fig. 5*a*: *d.*, *u.*). Some of the downflow

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EXPLANATION OF PLATE 74

Sequences of ciné film to show water currents induced in models of *Prorichthofenia* by rapid movements of the dorsal valve. The first frame of each sequence is at the top, and is the first frame exposed after the dorsal valve had begun to move. Photographed at 24 frames per second (exposure $\frac{1}{48}$ second per frame); except fig. 2, which was taken at 16 frames per second (exposure $\frac{1}{32}$ second per frame). *s.* marks position of shelf in each model.

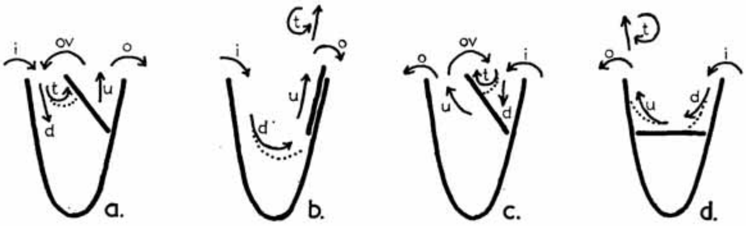
Figs. 1, 2, Model of *P. uddeni* (× 1); enlargement of region near dorsal valve; angular velocities 400° and 360° per second, respectively.

Figs. 3, 4, Model of *P. permiana* (× 1); enlargement as figs. 1, 2; angular velocities 340° and 530° per second, respectively.

Figs. 5, 6. Model of *P. permiana* (× 0·5), showing almost whole model; angular velocities 360° and 540° per second, respectively. (The threads representing the muscles can be seen crossing the inner shell cavity, and the divaricator thread is also visible outside the model.)

is derived from the upflow by an *overflow* current (*ov.*) which passes over the anterior edge of the dorsal valve. The remainder of the downflow is derived from an *inflow* (*i.*) over the anterior lip of the ventral valve; and the remainder of the upflow passes into an *outflow* (*o.*) over the posterior lip. Even at low angular velocities, a *trailing eddy* (*t.*) develops against the lower surface of the dorsal valve. After the valve has come to rest the downflow continues, though with diminishing velocity, to flush out the shell cavity, emerging posteriorly as an upflow (text-fig. 5*b*, Pl. 74, figs. 1*e*, *f*; 3*f*). At the same time (unless the dorsal valve has moved very slowly) the trailing eddy moves upwards with the upflow, away from the shell.

When the dorsal valve moves downwards (Pl. 74, figs. 2, 4, 6) the currents are simply reversed (text-fig. 5*c*). After the valve has come to rest on the shelf, the downflow continues to flush out the outer shell cavity (text-fig. 5*d*; Pl. 74, figs. 2*d*–*f*; 4*e*, *f*), though with diminishing velocity; and the trailing eddy moves away from the shell (Pl. 74, figs. 6*d*–*f*). It is important to note that during this movement the water below the level of the shelf is never disturbed.



TEXT-FIG. 5. Water currents in model of *Prorichthofenia*, shown by diagrammatic longitudinal sections of shell, with dorsal valve opening (*a*), fully open (*b*), closing (*c*), and fully closed (*d*); cf. Pl. 74. This diagram also shows (by dotted lines) the inferred courses of suspended particles heavier than water. *d.*, downflow; *i.*, inflow; *o.*, outflow; *ov.*, overflow; *t.*, trailing eddy; *u.*, upflow; minor eddies omitted.

When the valve moves with relatively high angular velocity (more than about 500° per sec.) turbulence develops in the currents that flush out the shell cavity after the valve has come to rest.

The larger specimens of the two species differ in the total angular range of the dorsal valve and in the form of the outer shell cavity. This causes some differences in the flow patterns. In *P. permiana* the shelf is well below the anterior lip of the outer shell cavity, whereas in *P. uddeni* it is very near the lip (text-figs. 2, 3). Therefore in the lower part of its total range of movement the gap between the edge of the dorsal valve and the anterior wall of the outer shell cavity is much narrower in *P. permiana* than in *P. uddeni*, and is differently orientated. Hence, as the dorsal valve of the model rises, the downflow is more prolonged in *P. permiana* than in *P. uddeni*; and it sweeps down to the floor of the inner shell-cavity in *P. permiana*, but along the plane of the shelf in *P. uddeni* (Pl. 74).

The functional significance of the flow patterns. The experiments show that a rapidly moving dorsal valve would have created in the water some distinctive patterns of powerful currents. If food particles of any kind were suspended in the water, these flow patterns could have been the basis of a mechanism of food collection.

A. In its simplest form, such a mechanism would depend on the fact that when the dorsal valve of the model of *P. permiana* opens, the inner shell cavity is flushed out by the downflow, whereas the closure of the valve does not disturb this region at all. Therefore, if the dorsal valve of the living *P. permiana* was opened rapidly and then closed again, some particles would have been swept down into the inner mantle cavity as the dorsal valve rose, and then trapped there when it returned to the shelf (this could not have occurred in adult *P. uddeni*). The downflow, as the dorsal valve rose, would have been much more powerful than the inhalant currents of living brachiopods, and would have been capable of sucking relatively large particles into the inner mantle cavity.

This mechanism would be closely analogous to that of the living Septibranchs (Yonge 1928), a group of lamellibranchs which have lost the filter-feeding mechanism of food collection. A muscular septum, which can be raised or lowered, divides the septibranch mantle cavity into a dorsal and a ventral chamber. The feeding cycle begins when the septum is lowered slowly, the water in the ventral chamber being transferred to the dorsal through the pores in the septum. The pores are then closed and the septum is raised suddenly. This causes a powerful inflow of water through the inhalant siphon into the ventral chamber, and simultaneously a powerful ejection of water from the dorsal chamber through the exhalant siphon. The force and rapidity of the flow are such that comparatively large fragments of detritus and small animals are sucked into the ventral chamber. In this process the muscular septum and ventral and dorsal chambers are, respectively, the analogues of the dorsal valve and the inner and outer mantle cavities of *Prorichthofenia*.

Once the particles were trapped in the inner mantle cavity there are two possible mechanisms of collection. (*a*) If a special food-collecting organ (e.g. the lophophore) existed in the cavity, it might have been able to strain the particles out of the water and transport them to the mouth (as, in the Septibranchs, they are transported by the palps). If the filaments on the lophophore, like those of living brachiopods, bore cilia and mucus cells on their frontal surfaces, and were swept through the inner mantle cavity, they might have captured and transported small particles in the normal way. Or if they were flexible and muscular, like those of living brachiopods, they might have been adapted to seize and hold larger particles. But despite these possibilities, the circumstantial evidence presented in the remainder of this paper strongly suggests that the lophophore was either lost completely (cf. text-figs. 7, 8) or at least reduced to a subordinate function. (*b*) If there was no collecting organ (i.e. if the lophophore was lost) the particles could only have been transported by the mantle tissue lining the cavity.

But first they would have had to settle on the surface of the tissue. The microscopic particles utilized by normal filter-feeding animals are so small or so light that they remain in suspension almost indefinitely. But larger fragments of detritus, having been kept in suspension externally by current or wave action, would have settled on to the floor of the inner mantle cavity soon after the dorsal valve had closed. Small free-swimming animals, which might also have been trapped in the cavity, would have settled out only if they were first narcotized or poisoned, for which process the tightly sealed inner mantle cavity would have been highly effective. In living brachiopods the mantle surfaces are ciliated and secrete mucus. But the cilia invariably function as a rejection mechanism, and transport particles towards the edge of the mantle (Orton 1914; Richards 1952; Chuang 1956, &c.). Nevertheless, it is possible that on parts, at least, of the mantle surfaces of *Prorichthofenia* the cilia might have been orientated in the opposite direction and have been able to transport particles to the mouth. Such 'acceptance tracts' of cilia occur, for example, on the mantle of *Lucina*, which has adopted a somewhat comparable means of particle capture (Allen 1958). Alternatively, it is possible that the mantle cilia were capable of reversal, and thereby were able to transport particles either towards the mouth or towards the mantle edges according to circumstances: though reversal is not known in the mantle cilia of living brachiopods, it occurs in the frontal cilia of many species (Atkins 1958, p. 576).

B. If the mantle surfaces functioned as areas for the collection and transport of particles, the simplest form (A) of the mechanism could have been modified significantly. For many particles would have been thrown centrifugally on to the mantle from the strongly curved parts of the currents, as shown by the dotted lines in text-fig. 5. The rate at which this would have occurred would have depended (*a*) on the rotational velocity of the currents, and (*b*) on the size, form, and density of the particles present. The greater the angular velocity of the dorsal valve, the more efficient the method would have been; and, as in (A), it would have been most effective with relatively large and heavy particles of detritus or free-swimming animals, rather than with planktonic micro-organisms. But particles striking the mantle surface would have had to be retained there. This would have been possible if the mantle tissue secreted mucus, but would have been aided (especially if the flow was turbulent) by a rugose or papillose mantle surface. It is probable that the surfaces of the outer mantle cavity, at least, had this character; for except on the arcuate zones the surfaces of the outer shell cavity are conspicuously covered with small pustules (Pl. 72, fig. 3; Pl. 73, figs. 7–13) or even spinules (Pl. 72, figs. 12–14).

This reconstruction emphasizes the importance of the outer mantle cavity as a food-collecting area; and provides a functional explanation of the recessed dorsal valve, the permanently exposed mantle tissue, and the pustular surfaces of the shell.

Both (A) and (B) imply that *Prorichthofenia* had evolved a feeding mechanism which was fundamentally different from that of all living brachiopods, both in the mode of creation of water currents and in the type of food particle utilized.

THE FUNCTIONS OF THE INTERNAL SPINES

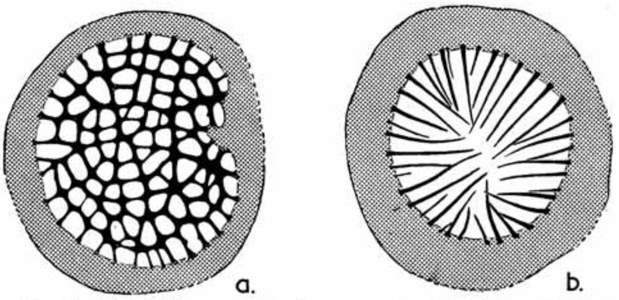
Spines on the ventral valve. A. *P. uddeni*. On most of the larger specimens of *P. uddeni* (text-fig. 3*a–d*) the ventral spines are so fully branched and anastomosed that they form a continuous mesh across the outer shell cavity. The simplest interpretation of this mesh is that its function was protective (cf. Stehli 1954, p. 286). Whatever the feeding mechanism within the shell, a mesh could have prevented the entry of large and possibly harmful 'particles' (e.g. either inert particles of debris or actively moving animals). This interpretation can be tested by comparing the actual form of the mesh with the paradigm.

A paradigmatic mesh would have the following characters. (*a*) The bars must be stout enough to withstand the stresses to which the mesh is subjected, yet slender enough to minimize the reduction in the effective area of the aperture and the frictional resistance to the flow. These conflicting demands are most effectively reconciled if the bars are elongated in cross-section in the direction of flow. (*b*) The spaces between the bars must be uniform in effective size (i.e. in the size of the largest particles that could pass through them). (*c*) The mesh must cover the whole aperture, leaving no part unprotected.

This specification does not set a standard far beyond attainment in 'natural' meshes.

For example, the osculum of the Recent sponge *Euplectella* is covered by a 'sieve-plate' (Ijima 1901), in which the bars are fairly uniformly slender, and usually elongated in cross-section; the spaces between them though irregularly polygonal in form, are subequal in effective size; and the mesh gives a uniform degree of protection to all parts of the osculum (text-fig. 6*a*).

The same specification can be compared with the mesh of *P. uddeni* (Pl. 73, figs. 2, 3). (*a*) The bars are fairly uniformly slender, and usually elongated in cross-section. (*b*) The spaces between the bars appear to be rather unequal in size. But this is a direct corollary of the mode of growth of the mesh. It was evidently not formed once and for all at a final stage of growth, but developed gradually during ontogeny. It must have migrated upwards, as the ventral valve grew in height, by continuous accretion on the upper surface of each bar and simultaneous resorption on its lower surface. Unless the size of the largest particles tolerated increased at precisely the same rate as the size of the whole aperture, the mesh would have had to increase in relative complexity during ontogeny. Clearly this was in fact occurring: for many of the larger spaces in the mesh are partially subdivided by projections (Pl. 73, fig. 3). Thus exact uniformity in the sizes of the spaces was unattainable. Nevertheless, they were moderately uniform: in the mesh figured in Pl. 73, figs. 2, 3, they are quite closely grouped about a norm corresponding to a spherical particle of diameter 0·7 mm.; the minimum is 0·4 mm. and the maximumis 0·9 mm. (*c*) The mesh normally covers the whole of the aperture of the outer shell cavity. But near the posterior border there is an 'anomalous zone': here most of the bars are much stouter than in the rest of the mesh; they are often angular in cross-section; and the spaces between them are much more irregular in size (Pl. 73, figs. 2, 5). (This part of the mesh was not included in the measurements summarized above; the spaces there range up to 1·3 mm. in effective width.) However, on comparing the position of the anomalous zone with the water-currents in the model, it is clear that no large particle could have penetrated through it to the inner mantle cavity. As the dorsal valve rose, no *inward*-flowing current would have traversed it at any phase (in the final phase it is traversed by the recoil of the trailing eddy (text-fig. 7*c*, *d*)). As the dorsal valve was lowered, it was traversed by an inward-flowing current (text-fig. 7*f*–*j*; Pl. 74, fig. 2). But any large particles that entered the outer mantle cavity during this phase (text-fig. 7*i*, *j*) could



TEXT-FIG. 6. Oscula of euplectellid sponges, to show approximations to paradigmatic mesh (*a*) and grille (*b*). *a*, *Euplectella* sp., × 1·5 (from specimen in Sedgwick Museum); *b*, *Regadrella komeyamai*, × 1 (after Ijima 1901, pl. 9, fig. 3).

never have penetrated to the inner mantle cavity. For, as the valve rose again, the close proximity of the mesh to the edge of the valve would have prevented them from passing over the edge in the overflow; and at the end of the movement they would have been expelled through the anomalous zone (cf. text-fig. 7*a–d*). Thus in conjunction with the postulated feeding mechanism the deficient degree of protection in the anomalous zone would have been immaterial. Its chief function may have been to strengthen the mesh by anchoring it posteriorly to the wall of the outer shell cavity. In some specimens of *P. uddeni* the mesh apparently did not extend into the area corresponding to the anomalous zone, for the posterior wall of the outer shell cavity extends only a little above the hinge, and the mesh was not attached to it; but in terms of protection such specimens would have been no less efficient than the more typical specimens with a complete mesh.

The mesh of *P. uddeni* thus approximates closely to the paradigm of a protective mesh; and may therefore be interpreted with confidence as a protective device that served to exclude from the inner mantle cavity all particles larger than a certain critical size. It would have been 'self-cleansing'; for a particle caught by it out of the downflow as the dorsal valve rose would have been propelled away from it by the upflow as the dorsal valve closed again (text-fig. 7).

B. *P. permiana*. Ideally, any aperture can be protected with equal efficiency against the entry of large particles (assuming they are spherical) either by a mesh or by a grille. The ventral spines of *P. permiana* cover the aperture in rather the same manner as those of *P. uddeni*, and this suggests that they might have fulfilled the same function by actualizing the alternative basic 'design'.

A paradigmatic protective grille would have the following characters. (*a*) The bars must be strong yet slender (as in a mesh). (*b*) They must all lie in a single row (i.e. a 'thicket' of bars would increase the resistance but not the degree of protection). (*c*) The spaces between them must be uniform in effective width. (*d*) They must cover the whole aperture. For a circular aperture with radially arranged bars, the most efficient arrangement would be one of intercalated 'cycles' of bars of differentiated lengths (rather like the septa of a Hexacoral); the aperture would then be given complete protection with a minimum total length of bars and therefore minimal resistance to flow.

As before, this specification is not far beyond attainment in 'natural' grilles. The osculum of *Regadrella komeyamai*, a Recent sponge closely related to *Euplectella*, is covered by a grille (the 'corona': Ijima 1901, pp. 259–60) that approximates closely to the paradigm: the bars are slender, and are arranged in a single row, and collectively cover the whole aperture; and the spaces between them are subequal in width (text-fig. 6*b*). (Since they project upwards, differentiated 'cycles' are not strongly developed.)

The same specification can be compared with the spines of *P. permiana* (Pl. 73, figs. 7–14). (*a*) Many of the spines are very stout, relative to the size of the whole aperture and to the width of the spaces between the spines. Moreover, they are generally circular in cross-section, and they are 'roughened' with sharp longitudinal ridges. (*b*) They are placed in an irregular 'thicket'. (*c*) The spaces between them are fairly uniform in width. They are arranged roughly in intercalated 'cycles': the longest spines converge towards the centre of the aperture, and the relatively broad spaces between their bases are filled by intercalated shorter spines. (*d*) They cover the whole aperture, except for a posterior space (not due to imperfect preservation) corresponding in position to the anomalous zone in the mesh of *P. uddeni* and explicable in the same manner (Pl. 73, figs. 8, 9; text-fig. 2*a*–*d*).

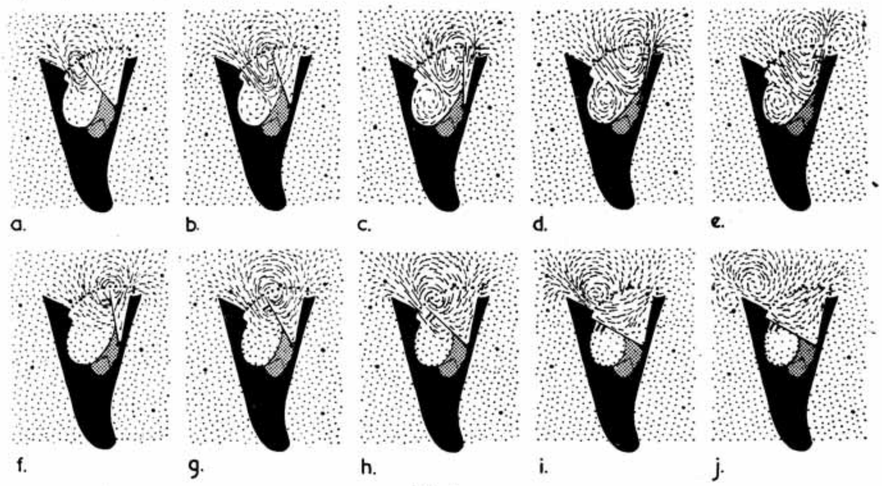


FIG. 7

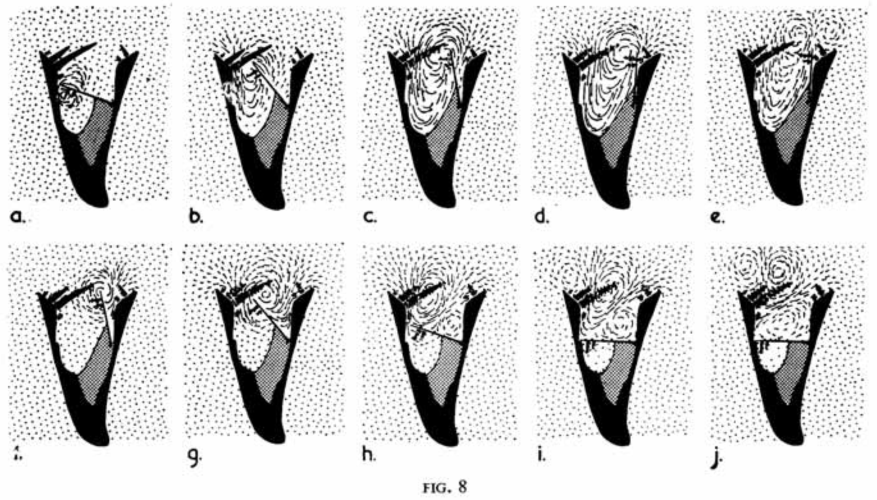
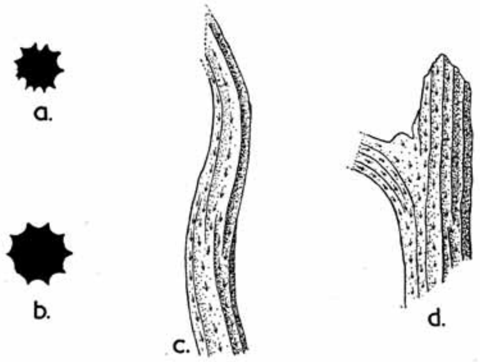


FIG. 8

TEXT-FIGS. 7, 8. Reconstructions of feeding mechanisms of *P. uddeni* (text-fig. 7) and *P. permiana* (text-fig. 8); shown by five successive phases (*a*-*e*) of upward movement of dorsal valve and five phases (*f*–*j*) of downward movement. Suspended particles shown by irregular stippling; direction and relative velocity of particles shown by 'tails' behind dots. Visceral cavity shown by close regular stippling. A few 'large' particles (above critical size of mesh) are shown in text-fig. 7.

Points (*c*) and (*d*) indicate that the spines would have been fairly efficient in preventing the entry of large particles. But points (*a*) and (*b*) indicate that they would have given great resistance to the flow of the currents (especially if the currents were rapid) and would have greatly reduced the effective area of the aperture. Any grille must represent a compromise between protection and obstruction, but these spines are not an effective compromise; yet a comparison with those of *P. uddeni* shows that the inefficiency is not due to any limitation inherent in the material utilized. Therefore the grille should not be judged merely 'less efficient' than the mesh, for its obstructive character might have been related to another function, coexisting with the function of protection.



TEXT-FIG. 9. Morphology of grooved spines of *P. permiana*. *a*. Cross-section of a spine, × 10 (from a photograph of the end of a broken spine on E. 15786). *b*, Cross-section of grooved cylinder used in hydrodynamical experiments. *c*, Spine with anastomosing grooves, × 10. *d*, Branched spine, × 10; arrows in grooves of these spines indicate inferred course of captured particles towards base of spine (these spines are figured in Pl. 73, figs. 11, 13 respectively).

If some of the suspended particles collided with the spines while traversing the grille, the grille might have acted as a supplementary food-collecting device. This would be an extension of the mechanism of collection by the mantle-surfaces, as postulated above: for the spines must have been sheathed with outgrowths of the mantle tissue (text-fig. 1*d*). When a non-turbulent fluid flows past a cylindrical obstacle, the rate at which suspended particles collide with the cylinder is always less than if they were undeflected by the laminar flow of the fluid around it. The ratio between these rates of collision is the 'collision efficiency' (see East and Marshall 1954, pp. 31–32). For a given fluid, this is a complex function of the diameter of the cylinder, the size and density of the particles, and the velocity of flow. The rate of collision is highest when (*a*) the particles are relatively large and dense; (*b*) the velocity of flow is high; and (*c*) the diameter of the cylinder is relatively great. Hence the paradigm for a food-collecting grille would have the following characters: (*a*) the spines would be relatively stout; (*b*) they would be closely spaced and abundant; and (*c*) they would be sited where the currents would be most rapid and most prolonged. The grille of *P. permiana* approximates closely to this paradigm. The stoutness, close spacing, and thicket-like arrangement of the spines have been noted already. In addition, they are most abundant along the anterior side of the aperture, which in the model is traversed by long-continued rapid currents; they are less abundant towards the centre, where in the model the currents are weaker; and they are moderately abundant along the posterior side, where in the model there are fairly powerful currents (Pl. 73, figs. 7–9; Pl. 74, figs. 3–4). If the dorsal valve moved sufficiently rapidly for the currents to become turbulent, the efficiency of this particle-capturing mechanism would have been enhanced still further.

The spines are marked with conspicuous, sharp, longitudinal ridges separated by rounded grooves (Pl. 73, figs. 10–14; text-fig. 9). If they were sheathed with uniformly thin mantle tissue, the surface of the tissue would have been marked by similar ridges and grooves. Experiments with a fluted cylinder (text-fig. 9*b*) show that the effect of such ridges is to increase the eddying in the wake of the cylinder at moderate Reynolds Numbers, and to lower the critical velocity at which the wake becomes turbulent. Possibly the collecting efficiency of the spines might have been increased thereby; but this is unlikely to represent the true function of the ridges, because (*a*) the scale involved is such that even with rapid currents the Reynolds Numbers would have been low, and (*b*) the ridges are no coarser on the stout than on the slender spines (Pl. 73, figs. 10–13). This uniformity in the width of the grooves suggests a different function. Even after entanglement in mucus, particles that had been captured by a spine would have been liable to become detached again by the force of the strong currents flowing past. But if the ciliary tracts which transported them to the base of the spine were sheltered within the longitudinal grooves, this risk would have been lessened. This reconstruction is supported by the fact that the grooves, but not the ridges, are invariably continuous to the base of the spine (text-fig. 9*c*, *d*). It implies that the spines served to collect *relatively* small particles, for the grooves average only 0·15 mm. in breadth.

Thus every character that would have made the spines inefficient merely as a protective device would have made them highly efficient as a device combining the function of protection with that of collecting particles.

Spines on the dorsal valve. The dorsal spines project from the lower surface of the dorsal valve, and lie near its anterior edge (text-figs. 2*a*–*d*; 3*a*, *d*). Those of *P. uddeni* are very slender, fairly regularly spaced, and arranged somewhat in a 'thicket' (Pl. 73, fig. 4); those of *P. permiana* are stouter, grooved, and arranged less regularly (Pl. 72, fig. 13, Pl. 73, fig. 15). They cannot have had a protective function, for they are enclosed within the mesh or grille and could have encountered particles smaller than the critical size transmitted by the protective structure (on no specimens do they strictly 'interlock' with the ventral spines; cf. King 1930, p. 97; Stehli 1954, p. 286). At every phase of the movement of the dorsal valve, they would have stood in the path of the strong outward-flowing currents (text-figs. 7, 8; Pl. 74). If suspended particles collided with them, they could have acted as another supplementary food-collecting device. They are in a paradigmatic position for this function. If they had been nearer the edge of the dorsal valve they would have interfered with the shelf (text-fig. 2*a*–*d*; 3*a*, *d*); if they had been any farther from the edge they would have failed to intercept the main force of the currents. But since the dorsal valve grew by accretion, the optimal position of one growth stage would have become an inefficient position (i.e. too far from the edge) at a later stage. The distribution of the spines was apparently kept optimal during ontogeny by the resorption of the more posterior spines and by the formation of new spines nearer the edge; for there is a series of smooth knobs, which appear to be the stumps of resorbed spines, behind the actual spines (Pl. 72, fig. 11; Pl. 73, fig. 15).

The specific differences in the form and arrangement of the spines possibly relate to a difference in the size of particles collected. Those of *P. permiana*, being similar to the ventral spines, would probably have collected relatively small particles in their grooves. The more slender and uniformly spaced spines of *P. uddeni* suggest the collection of larger particles, in the size-range comparable to the width of the spaces between the spines (on the specimen figured in Pl. 73, fig. 4, the spines are about 0·4 mm. apart, whereas the mesh would have admitted particles up to a spherical size of 1·0 mm.).

THE DEVELOPMENT OF THE FEEDING MECHANISM

Development during ontogeny. The smallest specimens in the collection have a thin recessed dorsal valve hinged in the same manner as larger specimens. Therefore rapid movements of the valve were probably habitual from an early stage in ontogeny, and food particles could have been captured either by being trapped below the dorsal valve or by impinging directly on the mantle surfaces. Then the gradual development of spines later in ontogeny must represent the acquisition of (*a*) a means of protection that was altogether lacking in earlier stages, and (*b*) a supplementary means of collecting particles.

(*a*) When the dorsal valve opened, 'harmfully large particles' would have been sucked downwards only if the power of the downflow overcame their inertia or their ability to escape (if they were actively swimming animals). The water currents induced by the movement of a small dorsal valve would have been much less powerful than those induced by a larger, even if the angular velocity was the same. Therefore during the growth of an individual increasingly large particles would have become liable to be sucked into the inner mantle cavity; and the risk from harmfully large particles would have increased progressively. Hence a protective device across the aperture might have been unnecessary in the early stages of growth but increasingly advantageous in later stages. Moreover, since the downflow in the models is most rapid near the anterior side, the need for protection would have occurred in that region first, and would have spread over the rest of the aperture only in later stages. This corresponds to the mode of formation of the mesh and the grille, for in both species the spines developed first from the anterior wall of the outer shell cavity, and only gradually spread across the remainder of the aperture. At the same time the quality of the protection improved (Pl. 73, cf. fig. 6 with fig. 3).

(*b*) The rapidity of the currents near the anterior side would also have made that area the most suitable for spines that served to capture food particles; and, as noted above, this is the area in which the first spines appear. In *P. permiana*, particle capture on the ventral spines (supplemented by the dorsal spines) probably became far more important in adult specimens than the original means of capture. In *P. uddeni* these original means probably became altogether inoperable, owing to the gradual changes in the orientation of the shelf and in the form of the outer shell cavity; and therefore, since the ventral spines became modified into a primarily protective structure, the dorsal spines must have become the major food-collecting device in adult specimens of this species.

The morphogenesis of the two species thus seems to reflect a gradual divergence into two varieties of the feeding mechanism. The first-formed spines functioned, perhaps, both for protection and for food collection (it may be noted that the paradigms have some features in common). But in *P. uddeni* the ventral spines became modified into a primarily (if not exclusively) protective device, and the dorsal spines developed into the major food-collecting device; whereas in *P. permiana* both sets of spines developed into food-collecting devices, though the ventral spines continued to confer some degree of protection. It is also possible that there was a divergence in the size-range of food-particles utilized. This suggested functional differentiation between the two species may perhaps be confirmed when preliminary accounts of the palaeoecology of *Prorichthofenia* (Newell *et al.* 1953) have been supplemented by more detailed studies.

Development during phylogeny. The origin of the richthofeniids is obscure, even in purely morphological terms. Until the morphology of other, less aberrant, productoids has been fully analysed in functional terms, it will be impossible to determine whether the feeding mechanism of *Prorichthofenia* represents an evolutionary novelty or merely a development of a mechanism already utilized by some of its forerunners.

The mesh of an unnamed species of *Prorichthofenia* (Newell *et al.* 1953, pl. 21, fig. 33; Stehli 1954, p. 286) approximates even more closely to the protective paradigm than that of *P. uddeni*. This species occurs at a higher stratigraphical level than *P. uddeni*, and may possibly indicate some evolutionary progression in the development of the feeding mechanism.

The inferred efficiency of this feeding mechanism cannot properly be used as evidence for any theory of the origin of adaptation. But any causal explanation that interprets the bizarre morphology of richthofeniids as non-functional or detrimental, as 'phylogerontic' explanations have commonly done, is definitely unacceptable. Similarly there is no warrant for 'phylogerontic' explanations of the rather sudden extinction of the family towards the end of the Permian.

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REFERENCES

ALLEN, J. A. 1958. On the basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia). *Phil. Trans. Roy. Soc.* (B), **241**, 421–84, pl. 18.

ATKINS, D. 1956. Ciliary feeding mechanisms of brachiopods. *Nature*, **177**, 706–7.

—— 1958. A new species and genus of Kraussinidae (Brachiopoda) with a note on feeding. *Proc. Zool. Soc. Lond.* **131**, 559–81.

BEEDHAM, G. E. 1958. Observations on the mantle of the Lamellibranchia. *Quart. J. micr. Sci.* **99**, 181–97.

CHUANG, S. H. 1956. The ciliary feeding mechanisms of *Lingula unguis* (L.) (Brachiopoda). *Proc. Zool. Soc. Lond.* **127**, 167–89.

CLOUD, P. E. 1948. Some problems and patterns of evolution exemplified by fossil invertebrates. *Evolution*, **2**, 322–50.

COOPER, G. A. 1950. Permian faunas of the Glass Mountains, Texas, and their environment. *Trans. N.Y. Acad. Sci.* **12,** 80–81.

EAST, T. W. R. and MARSHALL, J. S. 1954. Turbulence in clouds as a factor in precipitation. *Quart. J. R. met. Soc.* **80,** 26–47.

IJIMA, I. 1901. Studies on the Hexactinellida. Contribution I. (Euplectellidae). *J. Coll. Sci. Tokyo,* **15,** 1–300, pl. 1–14.

KING, R. E. 1930. The geology of the Glass Mountains, Texas. Part II. *Univ. Texas Bull.,* No. 3042.

LACAZE-DUTHIERS, H. DE. 1861. Histoire naturelle des Brachiopodes vivants de la Méditerranée. *Ann. Sci. nat.* **15,** (4), 259–330, pl. 1–5.

NEWELL, N. D., RIGBY, J. K., FISCHER, A. G., WHITEMAN, A. J., HICKOX, J. E., and BRADLEY, J. S. 1953. *The Permian Reef Complex of the Guadalupe Mountains Region, Texas and New Mexico.* San Francisco.

ORTON, J. H. 1914. On ciliary mechanisms in Brachiopods and some Polychaetes, with a comparison of the ciliary mechanisms on the gills of Molluscs, Protochordata, Brachiopods, and Cryptocephalous Polychaetes, and an Account of the Endostyle of Crepidula and its Allies. *J. Mar. biol. Ass. U.K.,* N.S. **10,** 283–311.

RICHARDS, J. R. 1952. The ciliary feeding mechanism of *Neothyris lenticularis* (Deshayes). *J. Morph.* **90,** 65–91.

RUDWICK, M. J. S. 1959. The growth and form of brachiopod shells. *Geol. Mag.* **96,** 1–24.

STEHLI, F. G. 1954. Lower Leonardian Brachiopoda of the Sierra Diablo. *Bull. Amer. Mus. nat. Hist.* **105,** 257–358, pl. 17–27.

—— 1956. Notes on Oldhaminid Brachiopods. *J. Paleont.* **30,** 305–13, pl. 41–42.

WAAGEN, W. 1884–7. Salt Range Fossils: Productus Limestone Fossils. *Palaeont. Indica* (13), **1.**

WILLIAMS, A. 1953. The morphology and classification of the Oldhaminid Brachiopods. *J. Wash. Acad. Sci.* **43,** 279–87.

—— 1956. The calcareous shell of the Brachiopoda and its importance to their classification. *Biol. Rev.* **31,** 243–87.

YONGE, C. M. 1928. The structure and function of the organs of feeding and digestion in the Septibranchs *Cuspidaria* and *Poromya*. *Phil. Trans. Roy. Soc.* (B), **216,** 221–63, pl. 12–14.

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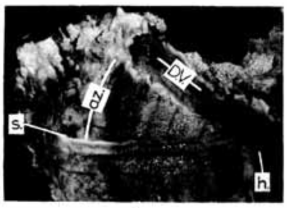

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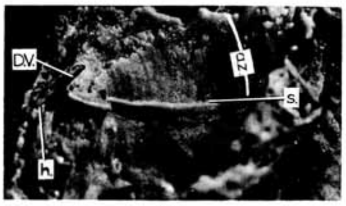

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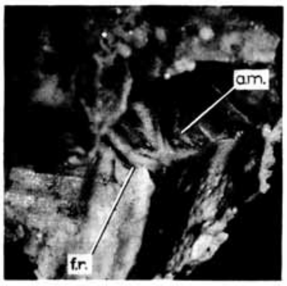

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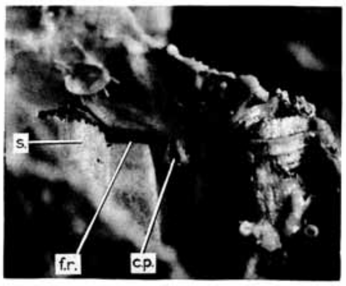

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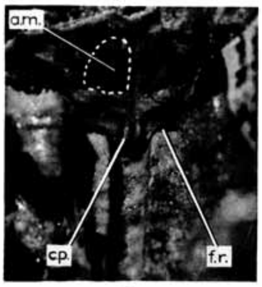

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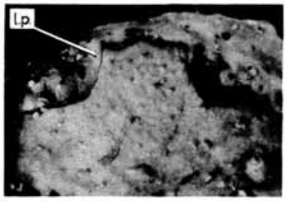

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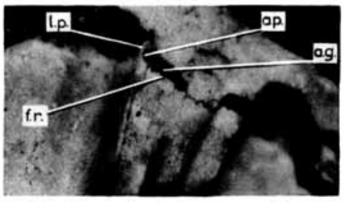

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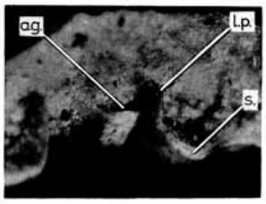

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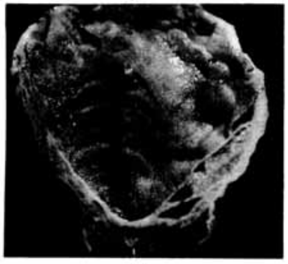

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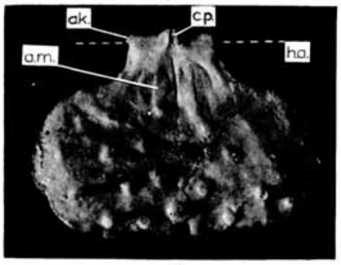

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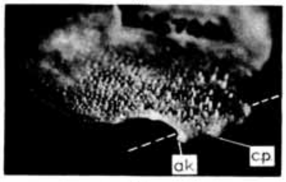

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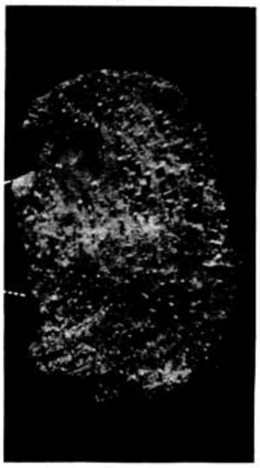

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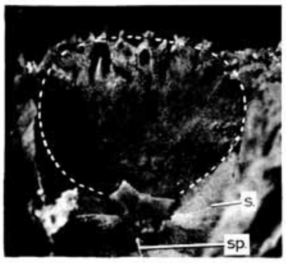
RUDWICK, *Prorichthofenia*



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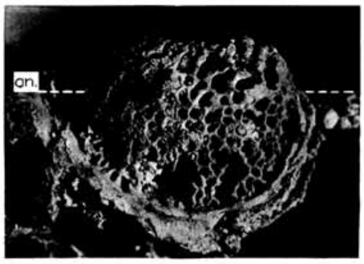

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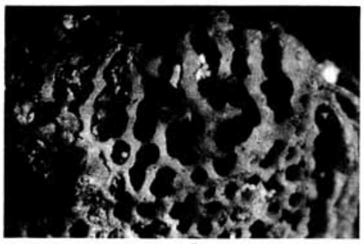

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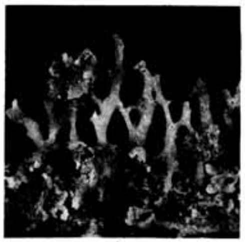

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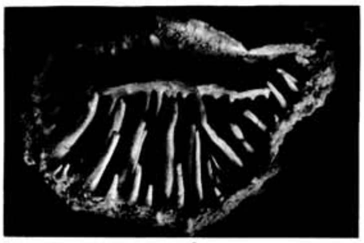

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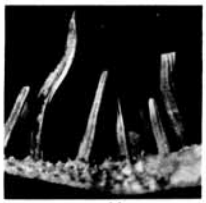

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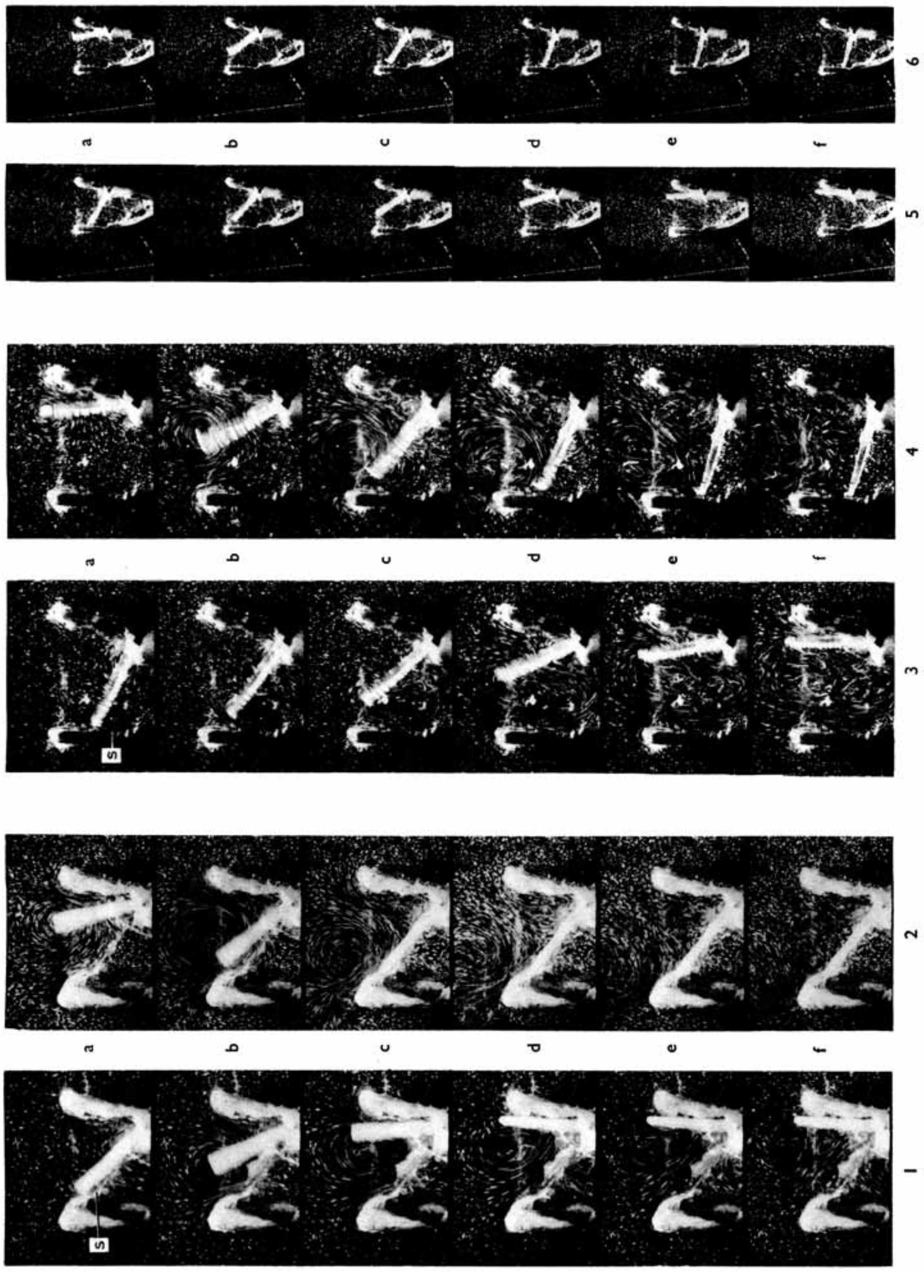

RUDWICK, Water currents induced in models of *Prorichthofenia*