for the body and investigating by methods of trial and error how deep the body may be to give the observed amplitude of anomaly and the observed marginal gradients. While this method is not rigorous, it is likely to be reasonably reliable. Comparison of the observed Weardale profile with two-dimensional computed profiles (using the Durham University electronic computer) suggests that for a density contrast as great as $0 \cdot 20$ g./cm.^{3}, the observed marginal gradients of $7 \cdot 5$ mgals/mile could only occur if the top is about 3,500 feet or less below the surface.

In extending these deductions to Weardale and Rookhope, both of which are north of the critical profile, it is assumed that the top surface of the granite does not become appreciably deeper towards the centre of the mass. Detailed studies on the gravity anomaly suggest that this assumption is broadly correct. Nevertheless local fluctuations could occur without noticeably affecting the anomalies.

It is concluded that the top surface of the postulated Weardale granite is shallower than about 4,000 feet beneath the Stanhope-Cotherstone road, about $4\frac{1}{2}$ miles south of Stanhope. Taking into account the variation in topographic height, the top of the granite should be less than 3,500 feet beneath Weardale and less than 4,000 feet beneath Rookhope provided the stated assumptions are correct. It is not possible from the gravity anomalies to place a minimum limit on the depth although absence of metamorphic effects at the surface suggests it is at least 1,500 or 2,000 feet deep. Thus it is expected that the granite will be reached in the Rookhope borehole between depths of 1,500 and 4,000 feet and most likely between 2,000 and 3,000 feet.

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M. H. P. BOTT.

DEPARTMENT OF GEOLOGY,
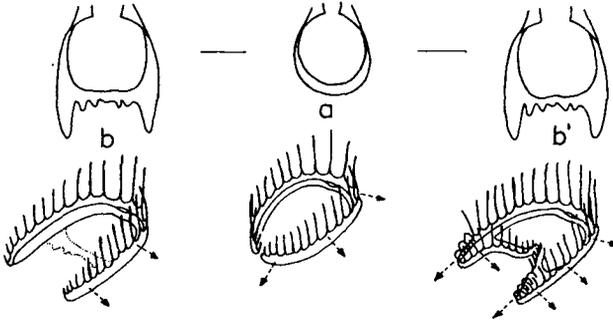 SOUTH ROAD,
    DURHAM.

10th October, 1960.

FEEDING MECHANISMS OF SPIRE-BEARING BRACHIOPODS

SIR,—The recent article by Dr. M. J. S. Rudwick on " The feeding mechanisms of spire-bearing fossil brachiopods " is a splendid example of the bold and imaginative use of living material to infer the habits of extinct groups and will certainly be appreciated by all those who decry the rarity of this event in palaeontological practice. But a sincere welcome for the approach is not necessarily an unqualified approbation of the conclusions which, as outlined below, appear to involve some inadequately considered assumptions.

Having demonstrated in 1956 that the internal skeleton of the brachiopod is secreted by outer epithelium in the same way as the secondary shell layer, I can only concur with Rudwick's reiteration that the growth of the lophophore and its calcareous support are independent functions. This, however, does not preclude the intimate connection of one with the other. It is significant, for example, as Mr. A. D. Wright and I have recently said in an article on the origin of the loop (now in press—*Palaeontology*) that even in the

terebratuloids the growth of the loop seems to have exercised sufficient physical constraint to retain the generative tips of the lophophore medianly. In respect of the loop, which is, after all, the fundamental structure of all spire-bearing brachiopods, Rudwick is wrong to speak of the antero-median tip of the *Zygospira* loop *splitting* so that the generative ends of the lophophore " might have diverged, remaining on the tips of the prongs " (p. 371). No split developed: the loop was simply enlarged by resorption along its inner edge and secretion along the outer one, a process which included the accelerated deposition of a pair of antero-lateral extensions. This mode of development is especially well seen in *Protozyga*, newly formed loops of which were rounded or truncated anteriorly (Text-fig. 1a) and the growth of the antero-
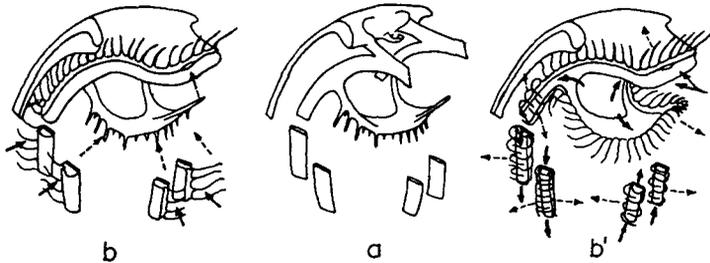

TEXT-FIG. 1.—The loop of *Protozyga* with its inferred lophophore below, and interpretations of the subsequent development according to Rudwick (b) and Williams (b¹). Broken arrows show the passage of filtered water.

lateral prongs, which were the beginnings of the spiral ribbons, and of fine spines along the anterior margin was patently independent of any " migration " from the median line. Consequently I am still convinced that the lophophore must have surrounded such prongs in such a way as to form a doubled brachial axis like that making up the side arms of *Terebratulina* and that the tips of the lophophore remained adjacent to each other on the jugum (Text-fig. 1b′). I am therefore also of the opinion that " the question of the relation and function of the jugum " is not as open as Rudwick believes it to be (p. 371) and there is some ancillary evidence to support this view. Rudwick (p. 374) has used the disposition of fine spines developed on the spiralia of fossil brachiopods to orientate the lophophore thereon. Such spines are equally common along the anterior edge of the jugum and in some stocks like *Hustedia* (Text-fig. 2a) they also occur in the medio-ventral line of the jugal stem and are disposed in such a way as to fit in very neatly with a postulated pair of incoiled ends to the lophophore situated on the dorso-posterior side of the jugal apparatus (Text-fig. 2b′). Certainly if the spines can be guides to the attitude of the lophophore on the calcareous spires they can be used with equal impunity for its inferred position on the jugum.

In 1956 when attempting to reconstruct the spiriferoid lophophore, I homologized it with the terebratuloid plectolophe and in this light it is less than fair for Rudwick to say " it is difficult to see how the lophophore of spiriferoids as reconstructed by Williams could, for all their wealth of filaments have produced any workable current system " (p. 377). If a system of filter feeding can be demonstrated for terebratuloids then clearly it can also be adapted for the spiriferoids, but before doing so it is pertinent to examine the systems proposed by Rudwick.

One segment of the lophophore which deserves some attention is that containing the mouth. In this ventrally facing median arc the filaments must

always occur on the outer edge so that any current induced by the transverse beating of cilia must move outwards from the centre towards the postero-lateral regions of the mantle cavity. In atrypaceids, with the bases of their spires more or less in the same plane as the median arc, a complete current system could have worked in the manner described by Rudwick and observed by him in *Tegulorhynchia* and by Orton in *Crania*. But in the spiriferoids the entire brachial axis beyond this segment must have rotated through 90° relative to its attitude along the median arc ; and if each calcareous ribbon supported, as Rudwick contends, a single brachial axis the only feasible current system is that described by him as " exhalant ". The system is, as he admits, unknown in any living inarticulate or articulate

b   a   b'

TEXT-FIG. 2.—The jugal apparatus of *Hustedia sp.* (a) from the Word. of Texas and the disposition of the lophophore thereon according to Rudwick (b) and Williams (b'). Unbroken arrows show the passage of unfiltered water, broken ones the passage of filtered water.

brachiopod and although this in itself is not important it may reflect a fundamental disadvantage because in such an exhalant current system the mouth region can only receive filtered water for further filtering.

An alternative scheme applicable to the atrypaceids and spiriferoids alike is one involving the existence of a doubled brachial axis on the calcareous ribbons beyond the jugum. It is shown in Text-figs. 1b' and 2b'. Unfiltered water arrived postero-medianly and passed antero-laterally into a pair of filter tubes fashioned from interlocking filaments which arched over paired brachial lips. According to this interpretation the filter tubes of *Protozyga* were nothing more than slightly arcuate prolongations of the central lophophorous organ but in later stocks they were spirally coiled. The system may be a cumbersome one, but at least it has the advantage of being a modified in-halant one and is moreover not unique because the filter tube, coiled in a planar spire, is characteristic of living terebratuloids. I concede that in view of Rudwick's studies the coextensive spires of spiriferoids like *Diplospirella* more likely gave additional support to a doubled brachial axis on the primary ribbons. This emendation, none the less, has in no way affected my opinion that the generative tips of the lophophore remained in the median plane of all spire-bearing brachiopods where they were almost invariably supported by the jugal apparatus.

DEPARTMENT OF GEOLOGY,   ALWYN WILLIAMS.
    QUEEN'S UNIVERSITY, BELFAST.
October, 1960.

SIR,—I am grateful to Professor Williams for enlarging on his interpreta-tion and for giving me an opportunity to clarify my own.

In describing the tip of the loop of *Zygospira* as " splitting " into two prongs, I was aware that this would probably have occurred by differential secretion on the outer edge of the loop and simultaneous resorption on the inner edge—

the growth lines which give evidence for this mode of growth can be clearly seen on the loop of any Recent species. Williams' figures of the loop of *Protozyga* show that the term " splitting " is not appropriate in this genus. But this question of nomenclature does not affect my argument. Once it is agreed that the lophophore is a structure essentially distinct from its supports, the mode of growth of the prongs is irrelevant to the problem of locating the tips of the lophophore. I await with interest Professor Williams' and Mr. Wright's paper on the origin of the loop. Doubtless this will clarify their conception of the " constraint " exercised by the loop on the tips of the lophophore. At present I do not follow this; for in terebratuloids the tips are adjacent to the loop only until the zugolophous stage, and they grow independently throughout the plectolophous stage. I have still to be convinced that the tips ever lay close together on the future jugum; or, if they did, that they could not have migrated on to the prongs as the prongs developed. Such a development of a ring-shaped into a horseshoe-shaped lophophore occurs in *Tegulorhynchia*, and I can still see no reason for drawing a fundamental distinction at this point between rhynchonelloids and spiriferoids.

The crux of my interpretation of current directions depends only on the basically possible orientations of the filaments. The evidence of the fine spines on the spiralia is adduced merely to suggest a more precise reconstruction of the attitude of the filaments. Since writing this paper I have been able, through the courtesy of Dr. G. A. Cooper, to examine some of the specimens of *Hustedia* from Texas, to which Williams refers; and I agree that the spines on the jugum are indeed similar to those on the spiralia. But it does not follow necessarily that the brachial axis extended on to the jugum. Strictly speaking, the spines on the loops of Recent species merely show that surfaces with spines are those not immediately adjacent to other tissues (i.e. the lophophore invariably occurs on the opposite surface). This may be as far as the homology should be taken, Then the spines on the jugum of *Hustedia* may only indicate the presence of *some* organ adjacent to the other side. This would involve modifying my use of the spines as definitive indicators of the presence of the brachial axis; but I am prepared to concede this point, since the main evidence for my interpretations lies elsewhere.

It is not true that on my interpretation of *Spirifer* the filaments near the mouth would have received filtered water, and that an " exhalant " spirolophe would thereby be inherently inefficient. In living species with "inhalant " spirolophes (e.g. *Tegulorhynchia*) these filaments touch some ventral part of the mantle surface, isolating a small exhalant space (leading laterally into the main exhalant spaces) between them and the body wall. Without changing the basic orientation, it is perfectly possible that in *Spirifer* the tips of the same filaments touched some *dorsal* part of the mantle surface, isolating a small *inhalant* space (leading laterally into the main inhalant spaces) between them and the body wall. Thus there is no reason to deny the inherent possibility that *Spirifer* could have had a current system with inhalant and exhalant chambers completely isolated—that is, a system just as efficient as that of *Tegulorhynchia* or *Atrypa*. Regrettably this point, though simple topologically, is difficult to demonstrate clearly without three-dimensional models.

In the light of the criteria of an efficient filter-feeding system (p. 376) I still cannot see how the filaments of *Spirifer*, on Williams' interpretation, could have operated with any efficiency. I made this remark originally with his interpretation of *Diplospirella* chiefly in mind; but even with his retraction of that interpretation the criticism still applies, and I cannot agree that it is unfair. His Text-fig. 2b′ fails to show how the stream of inhalant water (from a median inhalant aperture ?) could have been kept separate from the exhalant water emerging from the nearby spiral " filter tubes "; and thus it ignores the basic prerequisite of functional efficiency. Moreover the whorls of spiriferoid spiralia are placed so close together, and are often so numerous, that Williams' interpretation would demand very long and very narrow " filter tubes "; and on the scale involved these would be very inefficient for

hydrodynamical reasons. (The median spiral of a plectolophe is not a true parallel here, for it is a relatively short and rapidly tapering tube—a shape perfectly adapted to its function.) Finally, his interpretation leaves unexplained the characteristic form of spiralia—the closely-spaced whorls surrounding a wide central space—and their characteristic " moulding " to the shell; and it also leaves as an anomaly the close similarity (in these features) between spiriferoids and atrypoids.

As in most other branches of geology, here too the validity of our interpretations must be judged by the range of unexplained phenomena which they render intelligible. In the present state of knowledge of brachiopod morphology, I prefer to leave open the question of the jugum, since the only apparent alternative is to deprive a much wider variety of structures of any meaningful significance.

SEDGWICK MUSEUM,   M. J. S. RUDWICK.
   CAMBRIDGE.
3rd November, 1960.

ON *GRYPHAEA*

SIR,—In a recent paper in this magazine (1959a) I sought to demonstrate that the evidence does not support Trueman's classic hypothesis on the gradual evolution of *Gryphaea* from *Liostrea* in the basal zones of the Lias. That part of my work based upon a statistical study of *Gryphaea*, which has a critical bearing on the hypothesis, has been questioned by Dr. K. A. Joysey (1959) on two grounds, involving technique and results respectively.

My choice of measurement of the periphery to assess the amount of coiling of the left valve is criticized because it is based upon the erroneous assumption that the left valve conforms to a perfect logarithmic spiral. No such assumption is necessary for the matter in question and I persist in my contention that length of the periphery provides an effective measure of coiling accurate enough to test Trueman's hypothesis. I shall try to demonstrate this. In fig. 1 of his 1922 paper Trueman gave drawings of four specimens from different horizons to illustrate his *Liostrea-Gryphaea* lineage, which one may reasonably presume he regarded as more or less modal, since otherwise the figure loses its point. I have made determinations of the ratio of the periphery (P) to length of right valve (R) of the Glamorgan gryphaeas from the *angulata* Subzone (fig. 1b) and a much higher horizon, queried *gmuendense* Subzone (fig. 1d). (The fact that the specimen of fig. 1b is named as *G. dumortieri* does not affect the issue, since the whole figure purports to illustrate a gradual transition and is misleading in giving no hint that highly incurved gryphaeas occur commonly in the *angulata* Subzone (see below).) I have also determined the mean P: R ratio for my own collections from Glamorgan. The results are given below:

	P:R
Trueman's fig. 1b (R = 3·00 cm.)	1·40
„ fig. 1d (R not determinable since diagram of shell " slightly reduced ".)	3·00
Personal collection:	
angulata Subzone (mean of total)	2·55
„ „ (R = 2·9 — 3·1 cm.) . . .	2·67
gmuendense Subzone (mean)	2·67

The ratio for the specimen of fig. 1b is markedly at variance with my data; in fact highly incurved forms such as that illustrated in fig. 1d are the dominant element in all my *angulata* Subzone material from England and Wales, as anyone who cares to examine my collections may confirm.

Admittedly this simple method of comparison leaves something to be desired, but it is the best I can do in the absence of an original collection to refer to. It serves adequately, however, to illustrate the point I wish to make, namely that Trueman claimed striking changes in the adult organism which should be clearly revealed even using the periphery only as an approximate