ENVIRONMENTAL FACTORS DETERMINING THE DISTRIBUTION OF BRACHIOPODS

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ABSTRACT. The distribution of depth-related Silurian brachiopod communities is shown to be correlated with a diminishing food supply towards deeper offshore water. On a palaeoslope, the distribution of brachiopod species is determined by their ability to collect adequate food; this in turn is related to the surface area of the lophophore and morphological adaptations which assist the feeding. It is argued that the Spiriferida and Pentameridina, which predominate in the deeper water, had the most complex lophophores: the Orthida, Strophomenida, and Rhynchonellida, which are common in shallower water, had less complex lophophores.

Morphological adaptations either increase the feeding capacity of the lophophore (e.g. development of plicae, large sulcus, and wings), or are a response to the physical environment (e.g. strong or weak pedicle, thick or thin shell, large resting area). These special adaptations enabled some brachiopod species to colonize niches not normally occupied by the other members of the same order. When forms with less complex lophophores inhabit deeper water there is a decrease in size of the individuals.

Complementary evidence from the Devonian, Jurassic, and Recent, as well as evidence from other lophophorate groups, shows that these principles are a basic pattern applicable throughout time, possibly to all suspension-feeders.

OVER the past ten years there has been a large increase in the amount of data published on fossil brachiopod communities, especially those in Palaeozoic rocks. Bretsky (1969, 1970) has described late Ordovician benthonic marine communities from the central Appalachians and north-central New York. Stevens (1966) and Sutton *et al.* (1966) have described communities in the Permian and Devonian respectively. However, the pioneer work was carried out by Ziegler (1965) on the Llandovery (Lower Silurian) of Wales and the Welsh Borderland. Knowledge of Llandovery marine brachiopod communities has been supplemented by several further studies (Cocks 1967; Ziegler *et al.* 1968a).

The purpose of this paper is to assess the factors responsible for the areal distribution of brachiopods. The evidence is drawn from studies on fossil and present-day brachiopod communities, but mainly from the Silurian. For the most part brachiopods will be treated at ordinal level; only where necessary will reference be made to individual species.

From both carbonate and clastic rocks of the Wenlock and Ludlow, about 40 000 fossils have been collected by Calef, Hancock, and Hurst. This represents over 200 collections, which have been grouped into several communities. The percentage occurrence of individual genera in the community spectrum has been calculated.

The Llandovery data have been obtained from Ziegler *et al.* (1968a) and from the unpublished theses of L. R. M. Cocks and A. M. Ziegler. This added another 17 000 fossils to the list of those already considered.

Statistical data from the Devonian (Winter 1971) and the Lower Jurassic (Tchoumatchenco 1972) were also considered.

SILURIAN BRACHIOPOD DISTRIBUTION

The Silurian brachiopod-dominated communities are related to water depth (Ziegler *et al.* 1968*a*; Calef and Hancock 1974). Evidence for this is derived from the distribution of the communities which successively border the land areas (Ziegler *et al.* 1968*b*). In the Llandovery, the full community spectrum from shallowest to deepest is represented by *Lingula, Eocoelia, Pentamerus, Costistricklandia,* and *Clorinda.* An equivalent succession has been found in the Wenlock and Ludlow clastic and carbonate rocks and is represented by *Lingula, Salopina, Homoeospira/Sphaerirhynchia, Isorthis, Dicoelosia,* and *Visbyella* communities, the latter exceeding the depth range of the Llandovery *Clorinda* community (Hancock *et al.* 1974). Calef and Bambach (1973) go a step further and suggest that this distribution is linked to a diminishing food supply in deeper water.

This food (mainly particulate organic matter) decreases in abundance up to fifty times from nearshore shallow water towards offshore deep water (Jørgensen 1966). Some Recent brachiopods have evolved to colonize regions of the sea where only small amounts of food are available, by increasing the surface area of their filter-feeding system, the lophophore.

In the Llandovery, a basic distribution pattern of brachiopods is present (Ziegler *et al.* 1968*a*, 1968*b*): the Spiriferida and Pentameridina preferred the deeper quieter water, whilst the Rhynchonellida were in the shallower more turbulent water. The Orthida and Strophomenida were scattered throughout the depth spectrum (text-fig. 1).

In the Wenlock clastic rocks there is a large increase in the number of Spiriferida, and a decrease in the common Llandovery Pentameridina. The Rhynchonellida still expressed a strong preference for the shallower water. However, the remaining orders do not conform with the distribution pattern observed in the Llandovery, Wenlock Limestone, and Ludlow (text-fig. 1).

An added factor which appears at the beginning of the Wenlock is a totally new community, deeper than the *Dicoelosia* one. This is the *Visbyella* community. It represents the establishment of a completely new ecological habitat (Hancock *et al.* 1974), and there is no direct Llandovery equivalent, other than the marginal *Clorinda* association (Cocks and Rickards 1969) which may be its approximate equivalent in depth, though not in content.

In the Wenlock carbonate rocks there appears to be a fairly rigid brachiopod distribution pattern (text-fig. 1). The majority of the Strophomenida and the Rhynchonellida are most abundant in the shallow water as inferred from sedimentary associations, and size, density, and biomass of brachiopods (Hancock *et al.* 1974). The Orthida occupy an intermediate position, and the Pentameridina and Spiriferida are more abundant in the deeper water.

In the Ludlow clastics the Spiriferida and Pentameridina are still far more abundant in the deeper water shelf facies, and the Rhynchonellida in the shallower water clastics. The Orthida and Strophomenida are again most abundant in the intermediate depths (text-fig. 1).

Hancock *et al.* (1974) give a full interpretation of the depths involved. They suggest that the Silurian communities inhabited depths from shallow sub-tidal, to possibly

	brachiopod	Llandovery					Wenlock Sh.					Wenlock L.				Ludlow Sh.				
		L	E	P	St	C	Sa	H	Is	D	V	Sp	Is	D	V	Sa	Sp	Is	D	V
ORTHIDA	Dalejina		■			▨	▨		■			■				▨	▨			
	Isorthis											▨					▨	▨		
	Resserella				■															
	Salopina						■	▨	▨								▨	▨		
	Visbyella								▨		■						■		▨	
	Skenidioides					■						■							▨	
	Dicoelosia																			
	Ptychopleurella											■								
STROPHOMENIDA	Amphistrophia						▨	▨						■			▨	▨		
	Leptostrophia		■				▨	▨								▨	▨			
	Protochonetes ludloviensis						▨	▨								▨	▨			
	Protochonetes minimus		■				▨	▨		▨	▨			▨	▨	▨	■		▨	
	Strophochonetes		■																	
	Shagamella											■					▨			■
	Aegiria											■								■
	Coolinia				▨		▨	■	▨			▨							▨	
	Leangella							▨	■				▨	■						
	Leptaena					■														
	Strophonella											■								
	Eoplectodonta					■														
	Pholidostrophia					▨														
RH.	"Camarotoechia" decemplicata	■	▨																	
	"Camarotoechia" nucula							▨	▨	▨		▨	▨	▨		▨	▨	▨	▨	
	Eocoelia		■	▨	▨	▨														
	Sphaerirhynchia						▨	▨		▨		▨	▨	▨		▨		▨	▨	
P.	Gypidula						▨	▨									▨	▨		
	Pentamerus			■																
	Stricklandia				■															
	Clorinda					▨														
SPIRIFERIDA	Glassia					■						▨							▨	■
	Cyrtia							▨	▨	■		■		▨		■				
	Atrypa				▨		▨		▨	▨		▨	■	▨		▨		▨		
	Eospirifer						▨		■			▨	▨			▨	▨			
	Protathyris							■												
	Homoeospira						▨	▨				■	▨			▨				
	Howellella						▨	▨		▨	▨	■	▨	■		▨				
	Nucleospira											▨	■							
	Athyris													■						
	Meristina																			
	Striispirifer						▨	▨		■		▨						■		
	Whitfieldella													■						
	Hyattidina							▨		■									▨	
	Lissatrypa																			

TEXT-FIG. 1. Distribution of brachiopods in the Llandovery, Wenlock Shale, Wenlock Limestone, and Ludlow. Note the predominance of the Spiriferida and Pentameridina in the deeper water. The Rhynchonellida are found in the shallow water, whilst the Orthida and Strophomenida occupy intermediate depths. Key: black square = community in which the brachiopod species is most common; stippled square = community in which the brachiopod occurs. L. = *Lingula* community; E. = *Eocoelia* community; P. = *Pentamerus* community; St. = *Stricklandia* community; C. = *Clorinda* community; Sa. = *Salopina* community; H. = *Homoeospira* community; Is. = *Isorthis* community; D. = *Dicoelosia* community; V. = *Visbyella* community; Sp. = *Sphaerirhynchia* community.

Substrate - preference of spiriferide brachiopods
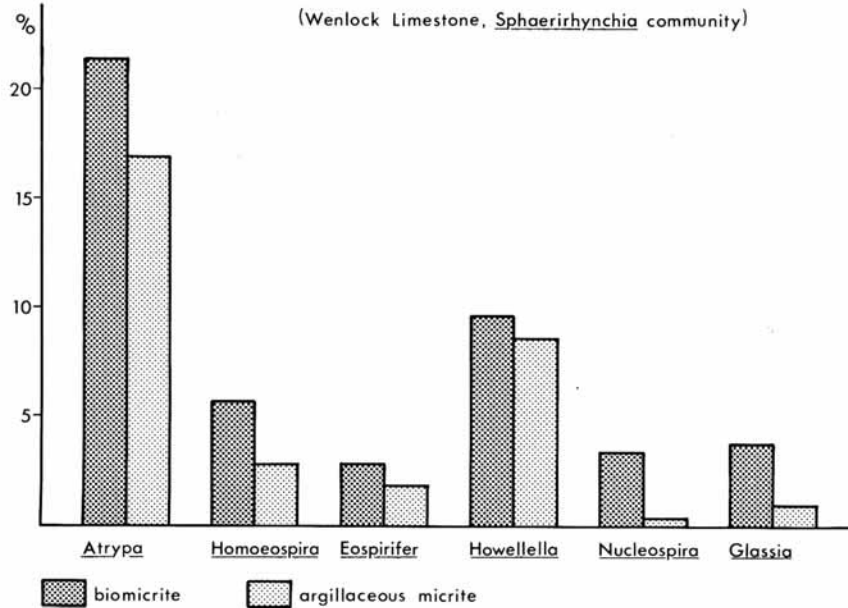
TEXT-FIG. 2. Note the predominance of spire bearers in the biomicrite as opposed to argillaceous micrite; perhaps a result of grain size influencing the distribution pattern of brachiopods. Vertical axis: average percentage of brachiopods in the opposing substrate-types of the *Sphaerirhynchia* community.

as great as 1500 metres. In the Wenlock of Wales the *Visbyella* community extends to the deepest parts of the basin, and there is no clear distinction between this community and the graptolitic shale facies.

However, the pattern is still not simple, as the sedimentary environment also influences the distribution pattern in the shallow-water *Sphaerirhynchia* community. Text-fig. 2 shows that in the Wenlock carbonate *Sphaerirhynchia* community every spiriferide is more common in biomicrite, than in argillaceous micrite. Similarly, text-fig. 3 suggests that strophomenide brachiopods in each Wenlock Limestone community may prefer argillaceous micrite to biomicrite.

There are no statistical data available on substrate preferences of brachiopods in any Silurian clastic rocks.

REASONS FOR BRACHIOPOD DISTRIBUTIONS

We believe that some of the factors responsible for the depth-related distributions of Silurian brachiopods are: 1, food supply; 2, the surface area of the lophophore relative to the whole brachiopod; 3, morphological adaptations which assist filter-feeding.

Substrate – preference of strophomenid brachiopods

(Wenlock Limestone)

substrate:
———— argillaceous micrite
– – biomicrite
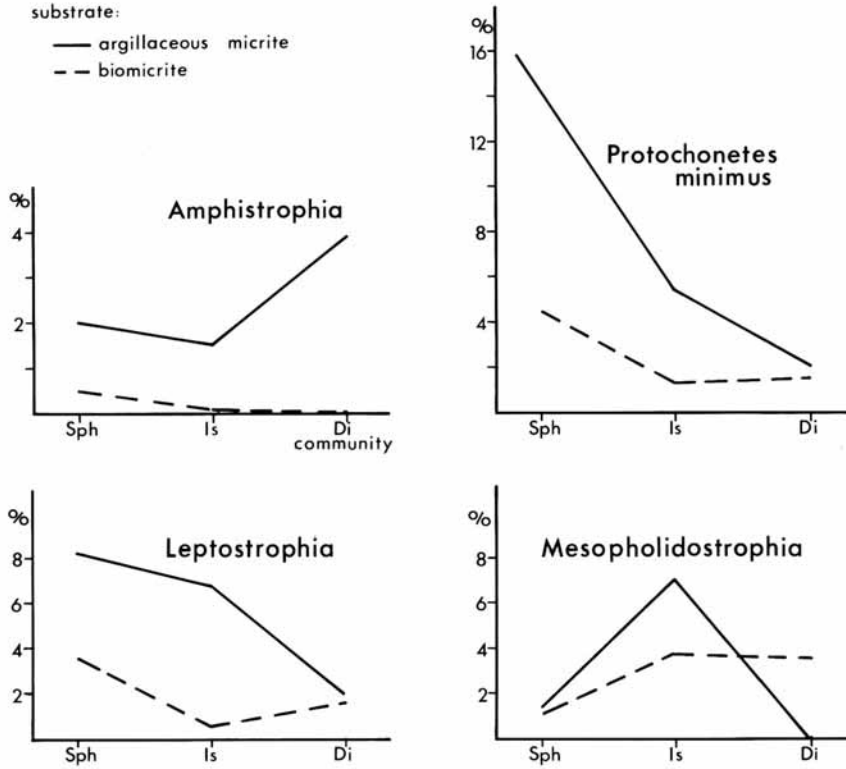
TEXT-FIG. 3. The Strophomenida show a preference for argillaceous micrite as opposed to biomicrite.
Vertical axis: average percentage of brachiopods in the opposing substrate-types of the Wenlock Limestone.

Brachiopod feeding and source of food. Brachiopods are ciliary suspension-feeders, whose lophophores act as a combined pump and filter (Rudwick 1965). In most suspension-feeders, feeding does not seem to be regulated by the need for food; when the valves are open, feeding is carried on more or less regardless of particle concentration in the water and therefore regardless of the amount of the material collected (Jørgensen 1966). Similarly, the rate of water transport inside the shell is independent of concentration and quality of the suspended particles. According to Jørgensen (1966, p. 138). It 'must to a great extent depend upon the structure and size of the feeding organs, and thus be more or less genetically fixed' (see also Nicol 1960).

Observations on living brachiopods are still rare, but those available show that these general characteristics of suspension-feeders are also true for brachiopods (Rudwick 1965; Savage 1972). However, Atkins (1959, p. 130) observed on specimens of *Platidia davidsoni* (Études-Deslongchamps) that 'at times animals gape without detectable currents entering or leaving the shell'. This observation has been confirmed by McCammon (1971) who also noted that the velocity of the flow created by the ciliary activity is not constant in any individual.

The food. According to Rudwick (1962a) brachiopods feed mainly on diatoms and dinoflagellates. This observation has lately been questioned by McCammon (1969) who argued that the food of brachiopods consists preferably of dissolved organic matter. As both observations seem to be valid (although McCammon could not exclude the presence of micro-organisms during her tank experiments) it is possible that both food sources can be used by brachiopods under natural conditions (see also Cowen 1971). Phytoplankton is probably used as food whenever available (Friedrich 1965) but when scarce, the brachiopods may be able to rely on the intake of dissolved organic nutrients. In both cases, however, brachiopods depend upon the phyto-plankton, as even dissolved organic matter ultimately comes from primary plant production.

Distribution of organic matter in present-day oceans. Potential food sources for filter-feeders are (*a*) phytoplankton; (*b*) suspended particulate dead organic matter (organic detritus); (*c*) dissolved or colloidal organic matter; (*d*) heterotrophic organisms (bacteria, fungi, microzoa) (Jørgensen 1966). As all these sources may be used by brachiopods, their distribution necessarily strongly influences the distribution pattern of brachiopods.

Summarizing the present-day distribution of organic matter in the sea from an extensive review in Jørgensen (1966) it becomes clear that there is a higher con-centration of particulate organic matter (phytoplankton and organic detritus) in coastal and inshore waters (see also Emery 1960) than in the open ocean or, even more, the deep sea. Within the shelf region, large variations occur which depend on the special geographic situation, climate, and current pattern. Dissolved organic matter seems to constitute the main part of the organic matter present in deeper water.

The distribution of organic matter in Palaeozoic oceans. Applying the principle of actualism, the distribution of organic matter outlined above was probably more or less the same during the Palaeozoic, although there were some minor differences. For example, the actual composition of the Lower Palaeozoic plankton was very different from that of modern-day plankton (Bulman 1964). Diatoms, the chief producer of organic matter in present-day oceans, did not exist. The phytoplankton consisted of relatively few forms, i.e. blue-green algae, acritarchs, dinoflagellates, and hystrichosphaerids. However, no estimations of the biomass can be inferred as the place of the diatoms might have been occupied by some other group of algae less likely to be preserved (Pitrat 1970).

Upwelling and currents from deeper water may have played a lesser role than they do in the present (Tappan 1970) but it is impossible to assess their actual relevance.

In conclusion, one can say that the distribution pattern of organic matter in ancient oceans was much the same as in present ones: a relative enrichment in organic matter of shelf waters compared with deeper offshore water.

THE BRACHIOPOD LOPHOPHORE

Lophophore development and history. In articulate brachiopods the morphology of the lophophore varies to a large extent in different groups. When reconstructing the lophophore types of extinct brachiopods, two points have been borne in mind:

(*a*) Shell-shape: it may be argued that the lophophore determines the shell-shape. Grant (1972, p. 233) states 'The major principle in the relationship of shell form to lophophore is that, regardless of its form, the lophophore tends to fill whatever space within the shell is not occupied by viscera and muscle. In most brachiopods this amounts to the greater part of the shell chamber, perhaps the anterior two thirds.' Consequently, valuable insight into the basic form of the lophophore may be gained from a study of the shell-shape.

(*b*) Further information about the size and shape of the lophophore may be gleaned from a study of the supporting structures, which are of two types: 1, a hydrostatic skeleton; this is a fluid-filled tube, with thin muscular walls, which runs along the base of the brachia (Rudwick 1962*a*). Muscle fibres in the tube wall counteract the pressurized fluid enclosed, thus maintaining an equilibrium position for the canal (Rudwick 1970). 2, a calcareous skeleton, termed the brachidium. This rarely, if ever, provides total support for the lophophore. It usually acts as a supplementary means of support alongside the hydrostatic skeleton.

Unfortunately, the hydrostatic component of the lophophore's supporting skeleton is never preserved in fossil forms, but some information may be gained from the brachidial apparatus. However, as a word of caution Rudwick (1970, p. 127) states, 'There is no simple nor necessary relation between the form of the brachidium and that of the lophophore, and the reconstruction of the lophophore from the brachidium of a fossil brachiopod is therefore never a straightforward task'.

Thus, when inferences are made about the size and shape of the lophophores of extinct brachiopods, evidence from shell-shape and brachidial apparatus must be used cautiously, and supplemented with comparative information from living forms.

Lophophore reconstructions

Orthida. Very little is known about the size or extent of orthide lophophores. They lacked calcareous supports (Williams and Wright 1965) although it has been suggested that the brachiophores provided support for the base. Presumably, the lophophore was supported mainly by a hydrostatic skeleton which has left no trace in the fossil state. Williams and Wright (1965) infer that the lophophore varied from a schizolophe to a spirolophe. We believe that the orthides had a lophophore which never became more complex than a simple spirolophe, as the relatively small shell chamber would prohibit this.

Strophomenida. These constitute the largest order within the Brachiopoda, and consequently developed a variety of lophophore types, from the schizolophe to the spirolophe and attached plectolophe (Muir-Wood and Williams 1965).

Inferences on the lophophore types of this group are very problematical. Once again the lophophore is rarely supported by any skeletal means, but the general shell-shape of this group does throw light on the possible lophophoral extent. Occasionally, some fossil strophomenides show impressions on the inner surfaces of the valves, apparently corresponding to the soft support for the lophophore (Rudwick 1970). However, this is the exception and not the rule.

In the superfamily Plectambonitacea, the brachial valve platform and septa are presumed to have given support to a ptycholophous lophophore (Muir-Wood and Williams 1965). The Strophomenacea are thought to have had a schizolophous, ptycholophous, or spirolophous lophorphore, and the Davidsoniacea a spirolophous lophophore (Muir-Wood and Williams 1965).

Problems arise with the Chonetidina and Productidina. Muir-Wood and Cooper (1960) and Muir-Wood and Williams (1965) deduced that the productidine lopho-phore was spirolophous, from the shape of the brachial ridges. However, recent work by Grant (1972) suggests that the Productidina and Chonetidina had a ptycholophous lophophore.

We believe that in general the Strophomenida had lophophores varying between a schizolophe, plectolophe, and a simple spirolophe.

Pentameridina. Very little is known about this group. There is no calcareous support for the lophophore other than the crura at the base (Amsden and Biernat 1965). Presumably the main part of the lophophore was again supported by a hydrostatic skeleton. As most adult pentamerids are large and bulbous it is reasonable to assume that they housed a fairly complex spirolophe.

Rhynchonellida. Present-day rhynchonellids have a simple spirolophous lophophore supported at its base by crura, and along its length by a hydrostatic skeleton (Thomson 1927; Rudwick 1962a). It is unlikely that early rhynchonellids had a more advanced lophophore than present-day forms: the early forms were probably similar to those living now.

Spiriferida. This group of brachiopods developed a complete skeletal support for the lophophore in the form of a pair of spiral lamellae. The spires are directed in various ways, from dorsally in *Atrypa* to laterally in true spirifers (Rudwick 1960). However, the exact reconstruction of the lophophore is still in doubt. Rudwick (1960, 1970) suggests that the brachial axis of the lophophore ran parallel to the course of the lamellae, forming a complex spirolophe. Counter to this Williams and Wright (1961) proposed the idea of a double loop of the brachial axis, supported on the lamellae, forming a deuterolophe.

Whether the spiriferides had a spirolophe or a deuterolophe is still problematical. What can be stated with certainty is that the spiriferides had the largest, most advanced lophophore of any brachiopod order.

Terebratulida. In present-day terebratulides there is a short or long loop to support in part the lophophore which may be a schizolophe in early growth stages and plectolophe in later stages (Rudwick 1962a). Probably fossil terebratulides had analogous lophophores, as the support structures are very similar to present-day forms.

Filtering capacity

Rudwick (1962*a*) suggests that the filtering capacity of the lophophore is directly proportional to the area of filter that it contains. Consequently, the longer the brachial axis is, the greater the volume of water which can be filtered (Hancock 1858). Also, a stronger current should be set up in the mantle cavity due to the beating of the cilia. Thus spire bearers, which have longer brachial axes should have an inherent advantage in filtering over non-spire bearers of a given size.

In brachiopods of a given size, those with a spirolophe supported by a hydrostatic skeleton will not have as many filtering whorls of the lophophore as those with a calcareous brachidium, and therefore they will filter less water per unit time. The whorls in living articulate brachiopods which have a hydrostatic skeleton are not as closely spaced as those in the calcareous spiriferid brachidium. In the Spiriferida the development of the brachidia may have been accompanied by the reduction or atrophy of the hydrostatic skeleton, and hence the support for the lophophore is slender when compared to that of the hydrostatic skeleton.

The following statements about the lophophore capacity in the various brachiopod orders is based on comparison of individuals of the same size.

The Orthida and the majority of the Strophomenida probably had the lowest capacity filters. Their lophophores were probably supported by a hydrostatic skeleton, and as most forms of these two groups had small mantle cavities, the lophophores would have been of very limited size and length.

The more bulbous Rhynchonellida probably support a larger lophophore than the previous two groups, but they would not have had as much space in the mantle cavity for lophophore development as the still more bulbous Pentameridina. Both the rhynchonellids and the pentamerids probably had a lophophore supported by a hydrostatic skeleton, but that of the Pentameridina is thought to have been larger and probably of a higher filtering capacity than that of the Rhynchonellida. The latter probably had a slightly higher capacity than the orthide or strophomenide lophophore.

The Terebratulida have a fairly large lophophore, probably with a similar capacity to that of the Pentameridina.

Undoubtedly the Spiriferida had the most powerful filtering system of any group. With the reduction of the hydrostatic skeleton and formation of a spiral brachidium came the most highly developed and largest lophophore. If Williams and Wright's (1961) view that the spirifer lophophore is in fact a deuterolophe is correct, then this adds substantially to the filtering capacity of this group.

MORPHOLOGICAL ADAPTATIONS

We distinguish two marine benthonic environments which have specially adapted brachiopod morphotypes (text-fig. 6). These are: turbulent water and, often linked with it, a hard bottom; quiet water and, often linked with it, soft substrate.

Turbulent environments. Adaptations which have evolved in turbulent water include large pedicle openings and thick shells. The former indicates a stout pedicle which attached the brachiopod firmly to the substrate; this environment was not suitable for brachiopods which in the adult stage were characterized by an atrophied pedicle

unless they possessed heavy shells, as in *Pentamerus*, which would also stabilize brachiopods under these conditions.

It is to the brachiopod's advantage to keep as much sediment out of the valves as possible. Rhynchonellids and some other forms developed strong angular plicae which help to restrict the amount of coarse sediment which can enter the mantle cavity (Schmidt 1937; Rudwick 1964).

The mantle edges of living brachiopods are extended outwards by a series of projecting chitinous bristles, the setae. The mantle edge and setae are extremely sensitive (Rudwick 1964) and if some drifting sand grain should touch this area, the shell will snap shut (Rudwick 1962b). Consequently, setae appear to be a fairly adequate means of restricting the entrance of unwanted material into the mantle cavity. Rudwick (1970) suggests, judging from the abundance of radial costellae which are present in many Orthida and most Strophomenida, that setae may have been a common feature in these groups. Both groups are most abundant in water of shallow to intermediate depth where setae may have functioned in the way described above.

Quiet-water environments. In the Silurian, the vast majority of the brachiopods which occur in quiet water are characterized by one or more of the following features:

(1) A fairly large median sulcus
(2) Development of alae (wings)
(3) Thin, smooth shells
(4) Reduction of pedicle foramen.

In extremely quiet water there is a need to give maximum separation for the inhalant and exhalant currents set up by the lophophore, so that there is no recirculation. In turbulent water, the need is not as great, as the movement of water surrounding the brachiopod will quickly disperse the exhaled water. In quiet water, this separation of the inhalant and exhalant current will be facilitated by the development of a sulcus and alae (Schmidt 1937). Most brachiopods in deep quiet water are thin-shelled and smooth, as there is no need for plicae. This is well illustrated by the rhynchonellid *Plagiorhynchia*, which is the only smooth form of this order in the Silurian, and the only rhynchonellid to occur abundantly in association with other brachiopods interpreted as deep-water forms.

Many Silurian species in deep water have a reduced or atrophied pedicle, as there is no need for a stout pedicle if there is no turbulence.

Soft muddy substrate. This environment may occur at any depth, though is most common in quiet water. Brachiopods adapted to this environment develop a large resting area, either in the form of a large flattened valve, or a large interarea.

Those brachiopods which rest on their interarea, keep the commissure as far away from the substrate as possible, thus reducing the possibility of substrate-sediment entering the mantle cavity. Brachiopods lying on one valve either develop an exaggerated median sulcus or a 'skirt' (an anterior deflection in the valves, very common in the Strophomenida, and at right-angles to the substrate) which have the same function. The plectambonitids do not have a true 'skirt' but are extremely concavo-convex, which is an analogous adaptation.

SIZE PATTERNS IN SILURIAN BRACHIOPODS

From the data which have already been presented (text-fig. 1) it can be seen that each brachiopod is most abundant in one particular community, but that it is very rarely limited to that one community. Several genera occur throughout the whole community spectrum. However, apart from the Spiriferida and Pentameridina every brachiopod species decreases in size from the shallow- to the deep-water communities (text-figs. 4, 5).

Several different species of Orthida, Strophomenida, and Rhynchonellida have been measured in the Llandovery, Wenlock, and Ludlow to show this variation in size. The data are not biased by water sorting of the shell material, as all collections contain large and small shells belonging to different genera. In the Llandovery (text-fig. 4) the size of *Eocoelia* (Rhynchonellida, L. R. M. Cocks, pers. comm.) was found to decrease quite substantially from the shallow-water *Eocoelia* community to the deep-water *Clorinda* community. Similarly in the Wenlock Limestone, *Sphaerirhynchia wilsoni* (Rhynchonellida) and *Protochonetes minimus* (Strophomenida) were found to decrease in size from the *Sphaerirhynchia* community to the *Dicoelosia* and *Visbyella* communities (text-fig. 4). In the Ludlow, both *Sphaerirhynchia wilsoni* (Rhynchonellida) and *Isorthis* (Orthida) showed the same trend with a decrease in size from the shallow *Salopina* community to the deeper *Isorthis* and *Dicoelosia* communities (text-fig. 4).

However, most spiriferides and pentamerides show a slight size trend in the opposite direction. In the Wenlock Limestone, examples of this include *Eospirifer radiatus*, *Cyrtia exporrecta*, *Striispirifer plicatellus*, *Atrypa reticularis*, and *Gypidula galeata* (text-fig. 5). No species belonging to these two orders showed a decrease in size from the shallow *Sphaerirhynchia* community into the deeper *Dicoelosia* community.

The size decrease in Orthida, Strophomenida, and Rhynchonellida into deeper water is a general feature of these groups and is not confined to the genera presented above. Similarly, the reverse is true for most of the Spiriferida and Pentameridina. Consequently, apart from the Spiriferida and Pentameridina, the *Dicoelosia* community is always represented by small shells.

DISCUSSION

Text-fig. 6

Brachiopods living in the deeper water may be at a disadvantage in collecting food as there is less available. However, certain brachiopod groups can adapt to the situation: the Spiriferida and Pentameridina for example, probably developed an advanced form of spirolophe which enabled them to flourish under these adverse conditions. The complexity of the lophophore meant that the spirifers and pentamerids were able to create a stronger current into the mantle cavity and therefore increase the amount of food collected. Orthides, strophomenides, and rhynchonellides, which had smaller lophophores, collected less food in deep water and were thus correspondingly smaller in size. Very few members of these groups had morphological adaptations to assist

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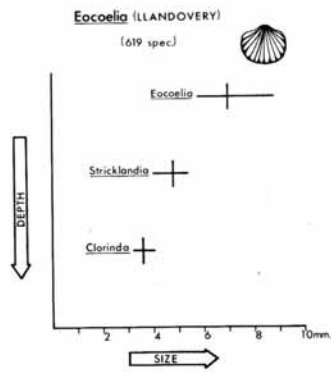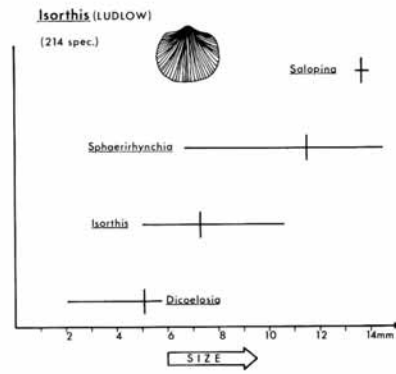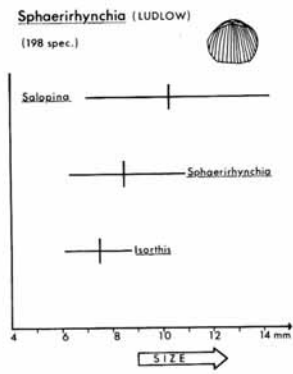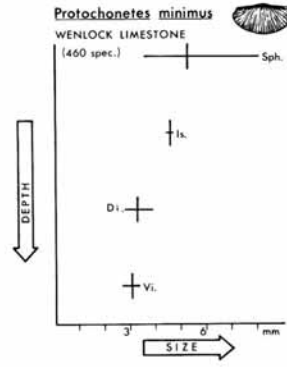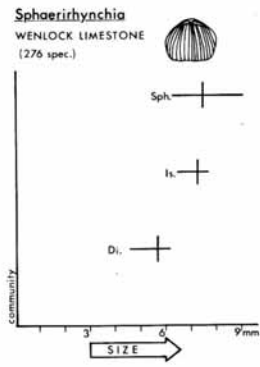
TEXT-FIG. 4. Size decrease of Silurian rhynchonellids, strophomenides, and dalmanellids from the shallow into the deep water; the result of a relatively inefficient lophophore. Key: vertical line = average size of specimens in that community; horizontal line = observed size range of specimens in that community.
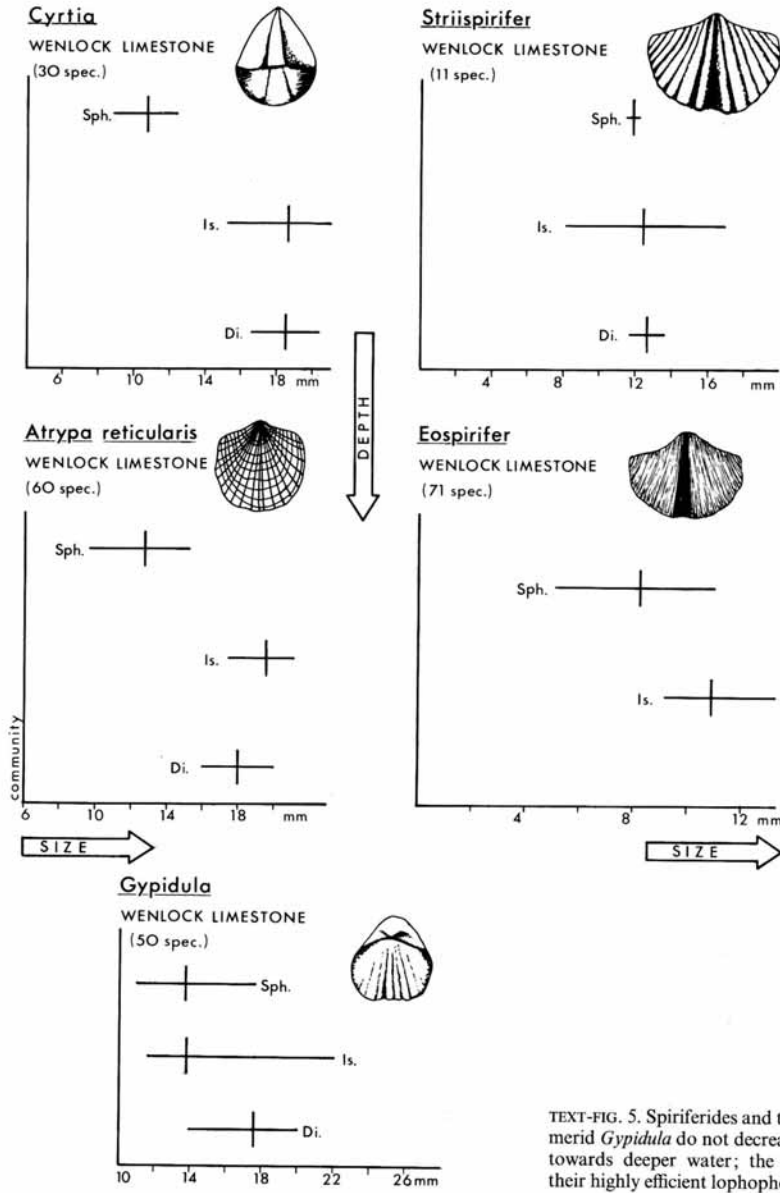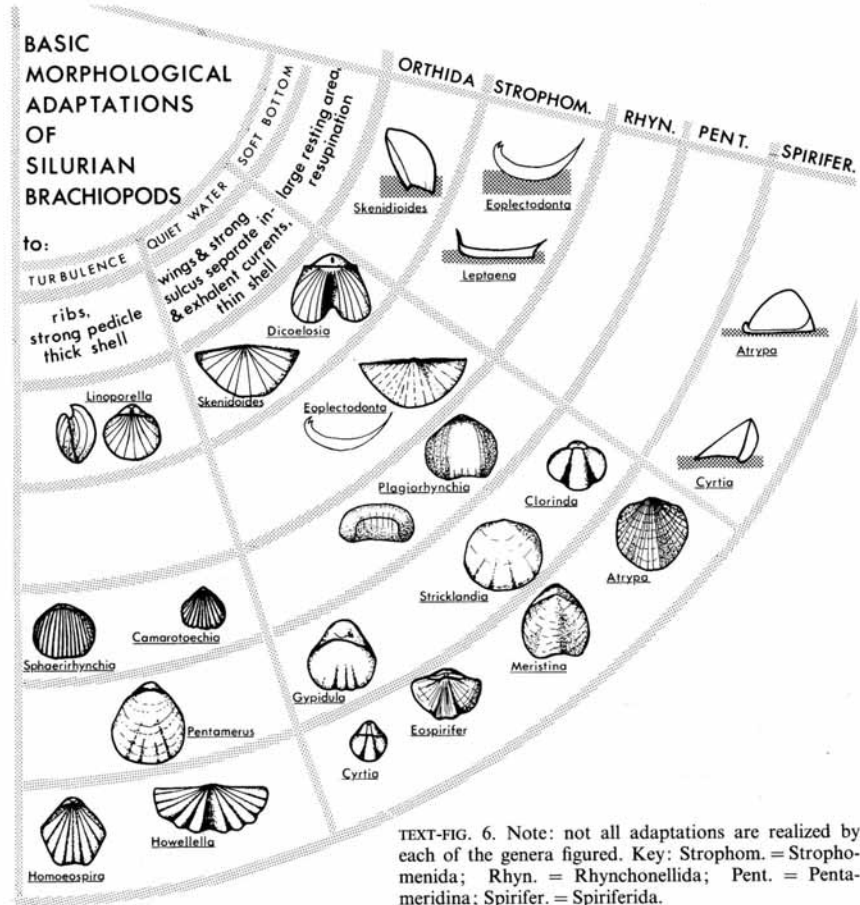
TEXT-FIG. 5. Spiriferides and the penta-merid *Gypidula* do not decrease in size towards deeper water; the result of their highly efficient lophophore.

the filter-feeding (e.g. wings, deep sulcus) and, therefore, one would expect these groups to have predominated in shallower water where there was more food.

However, the brachiopods with the simplest lophophores, i.e. Orthida and Strophomenida are not most abundant in the shallow water, but at intermediate depths. This is explained in the following ways:

(a) Most of the Orthida in the Silurian probably had a weak pedicle not suitable for life in a very turbulent environment; in most Strophomenida the pedicle had atrophied (Muir-Wood and Williams 1965).

(b) Most Silurian Orthida and Strophomenida had a small mantle cavity. To feed, they probably had to open their valves wide so as to give maximum display to the

TEXT-FIG. 6. Note: not all adaptations are realized by each of the genera figured. Key: Strophom. = Strophomenida; Rhyn. = Rhynchonellida; Pent. = Pentameridina; Spirifer. = Spiriferida.

lophophore (Rudwick 1962a). Thus they were in danger of allowing unwanted sediment to enter the mantle cavity; this would have been more likely in a shallow, turbulent environment.

As we have seen, one adaptation which inhibits sediment from entering the mantle cavity, is the development of setae. This feature is widespread amongst brachiopods, and the setae appear to have been common in the Orthida and Strophomenida (Rudwick 1970), but the absence of these groups in shallow turbulent deposits suggests that the setae still did not provide adequate protection for life in this environment.

These problems did not affect the Rhynchonellida. They probably had a fairly advanced lophophore compared to the Orthida (although not as advanced as the Spiriferida). Thus they did not need to open the valves far, and furthermore, they developed strong plicae which allowed the necessary intake of water through as small an aperture as possible and may have strengthened the shell. This prevented unwanted material entering the shell (Schmidt 1937; Rudwick 1964). In the deep water this danger was considerably reduced and the only Silurian deep-water rhynchonellid, *Plagiorhynchia*, is therefore smooth. The Rhynchonellida also had strong pedicles, a necessary adaptation to shallow turbulent water.

The advantage of a strong pedicle (indicated by a large pedicle foramen) is shown by *Linoporella*, the only orthide to occur in the most turbulent environment (the rocky bottom community) of Ziegler et al. (1968a).

The spirifers which occur in shallow water show the same adaptations, i.e. plicae for shell strengthening, and inhibiting sediment from entering the mantle cavity, e.g. *Homoeospira* and *Howellella*. They also have strong pedicles.

Pentamerus does not show obvious adaptations to a shallow-water turbulent environment, in which it is most abundant (Ziegler, pers. comm.). Examination of the shell, however, reveals posterior thickening of the valves (Ziegler *et al.* 1966), another method of stabilizing the animal on the substrate.

Similarly, there are a number of specific adaptations to life in deep water to assist the filter-feeding. We have already suggested that the main problem confronting a brachiopod in deep quiet water is the separation of the inhalant and exhalant currents, so that there is no recirculation of exhaled material. This can be attained in several ways:

(a) Certain brachiopods developed wings to give maximum possible separation of the currents in a horizontal plane, e.g. *Cyrtia* and *Striispirifer* amongst the Spiriferida, the orthide *Skenidioides*, and to a lesser extent the pentamerid *Stricklandia*.

(b) The development of a strong sulcus thus separating the currents in a vertical plane, e.g. *Atrypa* and *Meristina* in the Spiriferida, *Clorinda* and *Gypidula* in the Pentameridina, and *Plagiorhynchia* in the Rhynchonellida.

(c) The development of a strong median deflection, as in the orthide *Dicoelosia*. This is similar to the Upper Jurassic *Pygope* (Vogel 1966), in facilitating the separation of the inhalant and exhalant currents of the mantle cavity.

Several brachiopods are adapted to a life on soft bottom muddy sediments, which are not necessarily linked to depth, but rather to quiet water. The primary adaptation is the development of a large resting area which enables the brachiopod to sit on the

substrate in a stable position, usually without a pedicle. This resting area was provided by one of the valves in *Leptaena, Amphistrophia, Protochonetes, Leptostrophia, Mesopholidostrophia*, and the plectambonitids (Cocks 1970), and by a very large interarea in *Cyrtia* and *Skenidioides*. A further adaptation is the resupination of the valves which elevates the commissure well above the sediment. This is seen in *Leptaena*.

The strophomenides show a distinctive preference for argillaceous micrites as opposed to biomicrites (text-fig. 3). The reason for this preference is not clear.

Quiet water conditions favour the development of thin shells, as in the case of *Eoplectodonta* and *Leangella* (Cocks 1970).

For less obvious reasons, spirifers in the shallow-water *Sphaerirhynchia* community preferred the less muddy sediment (text-fig. 2). It is possible that particles held in suspension in the biomicrite were too large to enter the mantle cavity, whereas the clay particles of the argillaceous micrite were small enough to enter the mantle cavity, causing cessation of feeding.

Another feature of the Spiriferida and the Pentameridina is that they show a slight decrease in size in the shallower water. These two groups predominate in the deeper water where environmental conditions are far more stable. When they move into the shallower water, where environmental stress is greatest (i.e. changes in temperature, salinity, and turbulence), these unstable conditions may prevent them from thriving.

FURTHER EVIDENCE FROM THE DEVONIAN, JURASSIC, AND RECENT

Devonian. In a quantitative study of a Devonian brachiopod fauna from the Lower Ahrdorf Beds (Eifelian) of the Eifel region, Germany, Winter (1971) investigated the relationship between brachiopod morphology and biotope.

In the Devonian there were two main facies types, the Rhenish and Hercynian, but intermediate developments are also present. The nearshore Rhenish was characterized by shallower turbulent water, mainly clastic deposits, with a predominance of strongly ribbed brachiopods; in contrast, the offshore Hercynian was represented by a deeper water marl and clay facies with limestones on swells and smooth brachiopods (Schmidt 1926; Erben 1962).

Winter's investigations concentrated on the intermediate facies, which does not cover the shallowest and deepest ends of the bathymetric scale. However, he still deals with brachiopod biotopes scattered over a considerable palaeoslope. He grouped the brachiopods into several morphotypes. Close examination of these groups reveals that they usually represent brachiopods of the same order and therefore of a similar lophophore type, which are thus of a similar feeding efficiency.

Text-fig. 7 shows a striking similarity between the distribution of the major lophophore groups in the Devonian and those in the Silurian. The Orthida are again found predominantly in an intermediate position, between the deepest and the shallowest water. The shallowest facies dealt with here is in fact the upper limit of the intermediate zone: the most nearshore, most turbulent Rhenish is dominated by winged, ribbed brachiopods (Schmidt 1926).

On the whole, the Spiriferida show a numerical increase in abundance into the deeper water. This basic distribution pattern is modified by morphotypes. Large,

Distribution of Middle Devonian (Eifelian) brachiopods from the rheinisch-herzynischen Mischfazies of the Eifel region, Germany
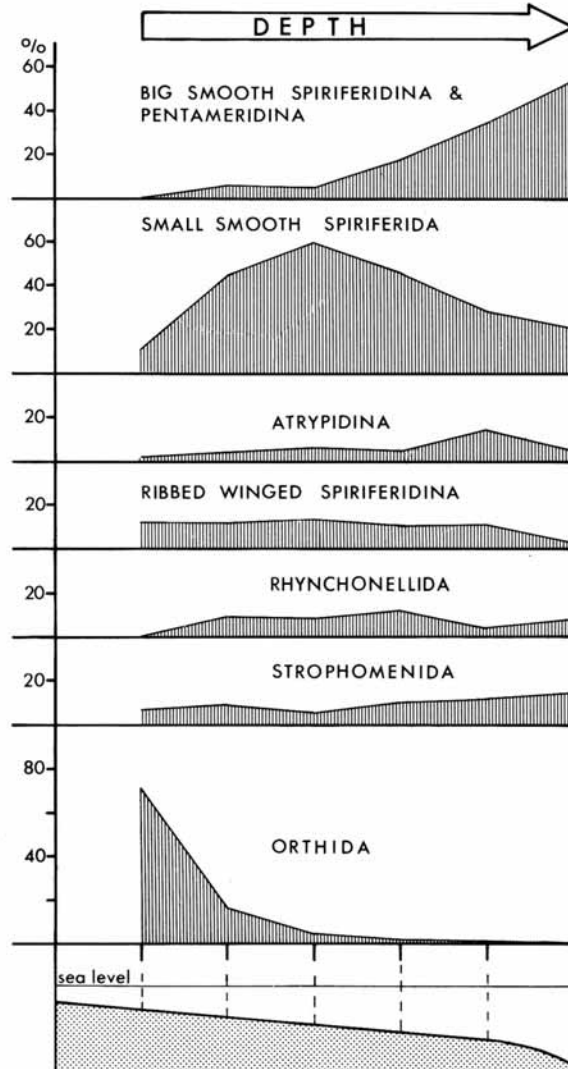
TEXT-FIG. 7. The distribution of the various brachiopod groups along a depth gradient, reflecting their feeding efficiency. Adaptations to the physical environment are responsible for modifications of this basic pattern (e.g. in the Spiriferida) (modified from Winter 1971).

smooth spire bearers overwhelmingly predominate in the deepest water. The winged, ribbed spire bearers decrease into deeper water, and are most abundant in the shallowest Rhenish which Winter does not consider.

As in the Silurian smooth spirifers appear to be smaller in shallower water, where they prefer limestones to silts. They may act as opportunistic species (Winter 1971). Mass occurrences of the smooth spirifer *Martinia inflata* (Schnur) are found in very shallow water in the Middle Devonian of the Gladbach-Paffrather Mulde (Germany). As in the case of the Silurian *Eospirifer*, they occur not in the high-energy environment but in quiet-water lagoons behind massive stromatoporoid reefs (Jux and Strauch 1965). This environment requires (especially when densely populated) morphological adaptations usually found in deeper water (efficient lophophore, big sulcus).

In his large, smooth spirifer group, which is most common in the deeper water, Winter included *Gypidula*. This preference for deeper water is identical to the behaviour of the Silurian form.

The Rhynchonellida and Strophomenida do not show a distinctive distribution pattern. This we would expect, as we are dealing with an intermediate facies. Winter attributed the distribution of the brachiopods purely to the morphotypes. However, he did not differentiate between the morphological adaptations which assist the filter-feeding and those which are a response to the physical features of the environment. The former, together with the complexity of the lophophore, governs the feeding efficiency of a brachiopod and are, therefore, the prime factor for its distribution on a palaeoslope.

Jurassic. Tchoumatchenco (1972) studied brachiopod biotopes related to bathymetry, energy, and bottom type in the Lower Jurassic of central and western Bulgaria. The data for this study were obtained from his *Zeilleria cornuta* brachiopod zone (Pliensbachian). Similar data are available for his other brachiopod zones, but that of *Z. cornuta* provides the most comprehensive information.

Like Winter, Tchoumatchenco also relates the brachiopod distribution to morphological adaptations. Text-fig. 8 again shows the basic distribution pattern previously seen in the Silurian and Devonian. The Spiriferida, with the most efficient lophophores predominate in the deeper quieter water, whilst the less efficient Rhynchonellida and Terebratulida mainly occur in the shallower more turbulent water.

Morphological adaptations (i.e. large sulcus, wings) alongside the lophophore complexity are primarily responsible for the distribution. In the Rhynchonellida and Terebratulida, the deeper-water forms are strongly sulcate as well as being smooth, thin-shelled, and fairly small; these features are typical of deep-water forms in the Devonian and Silurian. In the shallower more turbulent environment the Rhynchonellida and Terebratulida predominate. Typical secondary morphological adaptations of these groups are thick shells and a large pedicle foramen, presumably through which a large pedicle protruded, which helped to stabilize the brachiopods in this environment.

Recent. Except for the aberrant Thecideaceans, all Recent articulate brachiopods are members of the Terebratulida and Rhynchonellida; therefore, the distributional patterns described above are not so distinctive today as in the past. The brachiopods

Distribution of brachiopod assemblages from the Lower Jurassic of Bulgaria
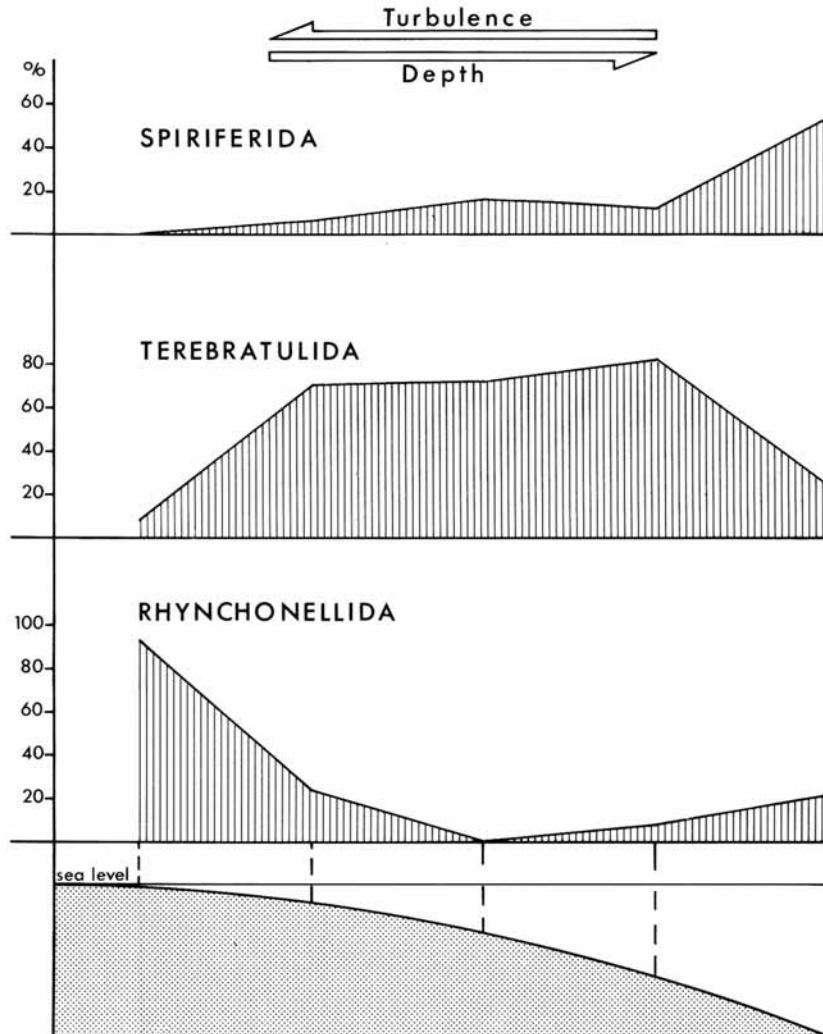
TEXT-FIG. 8. The distribution of the three brachiopod groups is primarily governed by their feeding efficiency. Adaptations to the physical environment are responsible for changes in the basic distribution-pattern (modified from Tchoumatchenco 1972).

with the most efficient lophophores (Pentameridina and Spiriferida) and the least-efficient lophophores (Orthida and most Strophomenida) are extinct. Nevertheless, the small amount of data available confirms the general principles of morphological adaptations. Cooper (1972) describes terebratulides and rhynchonellids (e.g. *Neorhynchia profunda* Cooper and *Abyssothyris elongata* Cooper) from the abyssal depths of the Baja plane off California. As we would expect, they are thin-shelled, smooth, and sulcate and are therefore well adapted to life in deep water.

On the other hand, Rudwick (1962*b*) described several Terebratulida and Rhynchonellida from intertidal and subtidal coastal areas of New Zealand. The forms found in the intertidal zones have large pedicle openings and are usually ribbed (even some of the normally smooth terebratulides show signs of ribbing).

These two examples from the Recent are consistent with the brachiopod distributions which we have described from the stratigraphical column. The ecological distribution of brachiopods throughout the stratigraphical column is primarily governed by the efficiency of their filter-feeding. This is accomplished by (*a*) the size and complexity of the lophophore, and (*b*) morphological adaptations which assist the filter-feeding. Furthermore, this distribution is modified by secondary morphological adaptations which are a response to the physical environment.

These fundamental principles governing brachiopod distributions may be generally applicable to other groups of filter-feeders. For instance, the bryozoans, another group of lophophorate suspension-feeders, behave in a similar manner. In the Gymnolaemata, Ryland (1970, p. 64) reports that species found at abyssal depths have longer lophophores than comparable shelf species. This is undoubtedly an adaptation to cope with less food in deep water.

The Phoronida, the third lophophorate phylum, are also sessile epibenthonic ciliary suspension-feeders. Their lophophore is horseshoe-shaped (corresponding to the primitive schizolophe of brachiopods), and consequently of limited capacity. Therefore it is not surprising to learn that they are limited to the upper 50 m of the sea (Hyman 1959, p. 263). This is further evidence that the size and complexity of the feeding organ may control the distribution of all lophophorate groups.

Applying these concepts to non-lophophorate suspension-feeders, it becomes apparent that several factors make a straight comparison impossible. Barnacles, for instance, are predominantly passive suspension-feeders and therefore dependent on turbulence, but may switch to active suspension-feeding when in quiet water (Jørgensen 1966).

A large number of bivalves are suspension-feeders and may act in a similar way to the lophophorate group. However, no work has been attempted in this line. There is an efficiency range in the gill-types of the various bivalve groups, but the picture is not as clear as with the lophophorate groups as the bivalves have developed a far greater range of morphological adaptations and inhabit a far wider range of ecological niches. Nevertheless, there is scope for a study of this type in bivalves.

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