THE ANCHORAGE OF ARTICULATE BRACHIOPODS ON SOFT SUBSTRATA

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FOSSIL articulate brachiopods are often abundant in rocks that appear to have accumulated as soft sediments. In some species there is evidence (e.g. a diminutive or plugged foramen) that the pedicle atrophied during ontogeny and that the adult shells were free-living. But in many other species a large foramen is found in all sizes of shell, and it is evident that the pedicle was functional throughout life; yet there may be no evidence of any firm material-except other shells-to which the pedicle could have been attached. Elliott (1956) has commented on the ease with which brachiopod shells can be transported after death, without damage, even by gentle currents. It is therefore possible that in some cases these fossil occurrences may be the result of shells having drifted, e.g. from a rocky environment near a shoreline into an offshore area in which soft sediment was accumulating. But it is also possible that such brachiopods may have lived on the soft sediment in which their shells are now preserved. Most articulate brachiopods living at the present day seem to require some hard and firm substratum (e.g. rock or shell) for attachment. But exceptions to this rule show that it is possible for the pedicle to obtain satisfactory anchorage in soft materials; and this type of attachment may have been much more common in the past. (The ability of inarticulates (e.g. Lingula) to anchor in soft substrata is well known; but their pedicles are not homologous to those of articulates, and differ completely in their structure.) Some records of the attachment of articulates to soft materials are given below.

The abyssal brachiopod *Chlidonophora chuni* Blochmann was dredged from *Globigerina* ooze, and was found to have an exceptionally long pedicle, dividing distally into fine rootlets attached to *Globigerina* shells. Blochmann (1906) inferred from this that the shell had been rooted in the soft ooze by this unusual pedicle. The pedicle of *Terebratulina* also shows a tendency to split distally into short rootlets (Ekman 1896), which may be attached to small shell-fragments in a fine shell gravel.

Gray (1872) noted that in *Kraussina rubra* (Pallas) from South Africa the pedicle is usually attached to the stem of a large alga or to an ascidian. A similar habit has been observed occasionally in other species. Attachment to algae was noted by Forbes in *Megathiris*, and by Jeffreys in *Terebratulina* (see Gray 1872). I have found specimens of *Terebratella (Waltonia) inconspicua* (Sowerby) attached to ascidians on rocky shores in New Zealand, and Ekman (1896) noted the same habit in *Terebratulina*. In an assemblage of *Terebratella (Magasella) sanguinea* (Leach), dredged from a muddy bottom at about 54 fathoms (100 m.) off Oamaru in New Zealand, all the shells were attached by their pedicles to the tangled 'horny' tubes of the chaetopterid worm *Phyllochaetopterus socialis* Claparède. Neither algae nor ascidians nor 'horny' worm-tubes would be

fossilized under normal circumstances. Therefore all these occurrences, if they were fossilized, would yield no trace of the substratum used for anchorage.

These examples suggest that the pedicles of many fossil brachiopods may have been able likewise to anchor the shells either (a) into bottoms composed of soft unconsolidated sediment, or (b) on to organic materials that would normally escape fossilization. Therefore it may not be necessary to invoke drifting as an explanation of the occurrence of pediculate fossil brachiopods in rocks that accumulated as soft sediments. Such brachiopods may often be undrifted life-assemblages, fossilized in the environment in which the living population existed.

The fact that living brachiopods can be attached to organic materials may also help to explain the 'nests' of fossil brachiopods so common in certain rocks (e.g. Hallam 1955, 1960). It is possible that each 'nest' may represent a colony of brachiopods that was attached to a small patch of organic material, e.g. to the stem of a single large alga. The shells as fossilized might represent either (a) an assemblage of shells which fell off the supporting material into the sediment after death, and gradually accumulated there; or (b) a living population suddenly annihilated by the collapse of the supporting material into the sediment. In this connexion it is noteworthy that in the Red Crag brachiopods have been found in similar clusters, in each of which the original material of attachment -a large stone-is still preserved in position (Bell 1872, pp. 191-2).

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