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Morphologic adaptations of benthic invertebrates to soft substrata

by Charles W. Thayer

ABSTRACT

The static stress, \( \sigma \) (\( \text{gm/cm}^2 \)) which a benthic organism applies to the bottom is given by \( \sigma = (e-\rho_f) \left( \frac{S_2}{nS_1} \right) rg \) where \( g \) is gravitational acceleration, \( \rho_f \) the density of the fluid surrounding the organism, and the remaining terms are properties of the organism, \( e \) being bulk density (\( \text{gm/cc} \)), \( S_2 \) and \( S_1 \) shape factors, \( n \) the fraction (bearing area/surface area), and \( r \) the radius (size, cm). For certain shelled invertebrates (e.g., bivalves and brachiopods), \( \sigma \) often exceeds sediment strength. Organisms will sink in fluid sediments when their bulk density exceeds that of the sediment.

Adaptations to such soft bottoms involve:

1. Introduction

The low bulk density and physical instability of some fine-grained muds produce a hostile environment for many benthonic organisms. Clay and silt-sized particles are easily resuspended by currents and the burrowing activities of deposit-feeding organisms. Dense suspensions of these particles may clog feeding and respiratory structures of benthic organisms, especially suspension feeders. Also, the typically high water content of subtidal muds results in a structurally weak and fluid surface. \textit{A priori}, one might assume that these factors would prove to be limiting, especially for heavy shell-bearing organisms.

The oxidized zone of the sediment commonly extends only one to two centimeters below the surface of muddy deposits. Invertebrates unable to maintain a stable position at the sediment-water interface may sink below the oxidized zone. If these
organisms are unable to maintain connection with the aerated surface, they may die for lack of oxygen or be killed by the presence of hydrogen sulphide. The support problem is especially critical for suspension feeders as they risk losing contact with their food supply in the overlying water. The problems associated with living on soft subtidal muds are reviewed by Rhoads (1970, 1973) and Rhoads and Young (1970). Faas (1972) cited examples in which the distribution of organisms was related to water content and suggested that it would be difficult for animals to move or maintain burrows in week sediments. Quiet-water conditions favoring deposition of fine-grained clastic minerals also lead to the accumulation of organic detritus. This detrius in turn favors populations of deposit-feeders which rework the sediment in the course of their feeding activities, increasing sediment water content and decreasing bulk density (Rhoads 1970).

The only evidence that benthic organisms do, in fact, have difficulty remaining on the surface of the bottom was shown by Rhoads (1970). Preserved articulated specimens of epifaunal and shallow infaunal bivalves were placed on in situ subtidal mud. Timelapse photography showed that these clams were buried in place within a few hours.

It is the purpose of this study to investigate the relationship between the strength of soft muds, the static loading stress of selected shelled benthonic organisms, and morphologic adaptations for living on such soft substrata.

2. Analysis

a. Stress due to organisms and strength of the substratum. If an organism is to remain on the surface of the bottom, the stress \( \sigma \), which it applies must be less than the bearing capacity of the substratum. Bearing capacity is approximated by shear strength. The two are not identical because measurements of shear strength (e.g., rotating vane, axial compression of unconfined cylinder) are not directly comparable to punching into a flat plate (bearing capacity).

The static stress applied by the weight of three burrowing bivalves and four epifaunal brachiopods is shown in Table 1. In the case of bivalves, the area is measured in a horizontal plane relative to the animal in life position, i.e., anterior-posterior axis approximately vertical (Stanley, 1970). In gravel, *Astarte castanea* lives with its posterior oriented downwards and uses pore water for respiration, (Stanley, 1970). In finer-grained sediments, the need to draw water from the sediment surface would require a posterior-up orientation. Because the maximum bearing area is required, the section measured intersects the beak and the ventral extremely of the valves. Brachiopods attach to firm substrata. If dislodged, they would probably come to rest with the plane of commissure horizontal. Area is therefore measured in that plane. Because this is the maximum cross-sectional area, the result is a minimal estimate of \( \sigma \).

The brachiopods and *Mya* were weighed intact and full of seawater. The brachio-
pods were dredged from subtidal localities in the San Juan Islands, Washington, and were weighed alive. *Mya* were collected alive from subtidal mud in New Haven Harbor, Connecticut, but were dead when weighed; gases trapped within them may have reduced their weights. The weights of the other bivalves were estimated from articulated valves. The volume of shell material was determined by immersion with the valves open. The valves were then filled with plasticene and closed tightly to measure the total enclosed volume. The difference between these two measurements provided the internal volume. A minimum estimate of the weight of the soft parts and sea water was made by assuming a density of 1.0 gm/cc. The volumes of *Astarte* and the brachiopods were determined by weighing in air and water. All other volumes were measured directly by displacing water in a graduated cylinder.

Many sediments are unable to support *Astarte* and *Mercenaria* ($\sigma = 1.58 - 1.85$ gm/cm$^2$). Because these bivalves are burrowers, they apply dynamic stresses in addition to the static stress calculated here. Keller and Bennett (1970) report shear strengths as low as 1 gm/cm$^2$. Most of their measurements were made on silts and clays. Cohesion values were published, but such fine-grained, water-saturated sediments have little or no internal friction. Consequently, shear strength equals cohesion (e.g., Faas, 1974). Morelock (1969) found cohesion values to be within 15% of shear strength.

Shear strength generally increases with depth beneath the bottom (e.g., Harrison et al., 1964; Rhoads, 1970) due to compaction by the overlying sediment. (Hereafter “depth”, “z”, will refer exclusively to the vertical distance beneath the sediment-water interface.) The weak surface layer is of greatest ecologic significance, but conventional measurement techniques average its properties with those of the stronger sediments below. Keller and Bennett (1970) used a single average value for each core; the shortest core was 30 cm long. The development of a high-resolution *in situ* penetrometer represents an important advance (Gordon, 1972). Using this device in Long Island Sound an unconsolidated surficial layer 2.0 cm thick was detected in which strength was too small to measure. With continued application of such refined techniques, many more areas are likely to be recognized in which the surficial bottom sediments are so weak that their strength may be a significant limiting factor for certain benthic invertebrates.

b. **Bulk density of organisms and substrata.** Sediment containing more than 75% water (weight H$_2$O/weight wet sediment) is permanently fluid. In addition, clay-rich muds with 50–75% water are thixotropic and become fluid when mechanically disturbed (Boswell, 1961). The surface of most surficial submarine sediments contains more than 50% water, and many silts and clays contain more than 75% (Keller and Bennett, 1970; Moore, 1931; Faas, 1972). In such fluid or thixotropic sediments, the bulk density (gm/cc) of the individual organism becomes the limiting factor for successful colonization. If the organism is more dense than the sediment, it will sink. In many cases this will result in death.
Table 1. Bulk density of eight benthic genera and the stress which they apply to the substrate. 

<table>
<thead>
<tr>
<th>Valve Type</th>
<th>Length (cm)</th>
<th>Density $\rho$ (gm/cm$^3$)</th>
<th>$N(\rho)$</th>
<th>Stress $\sigma$ (gm/cm$^2$)</th>
<th>$N(\sigma)$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>BIVALVES</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Astarte castanea</td>
<td>2.7–3.1</td>
<td>2.01–2.07</td>
<td>3</td>
<td>1.58–1.75</td>
<td>3</td>
</tr>
<tr>
<td>Mercenaria mercenaria</td>
<td>6.6–7.2</td>
<td>1.56–1.60</td>
<td>3</td>
<td>1.85</td>
<td>1</td>
</tr>
<tr>
<td>Mya arenaria</td>
<td>1.3–2.4</td>
<td>1.02–1.43*</td>
<td>24</td>
<td>0.64</td>
<td>1</td>
</tr>
<tr>
<td>Dutch oysters†</td>
<td></td>
<td>1.71–2.00</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>BRACHIPODS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Terebratalia transversa</td>
<td>2.9–3.2</td>
<td>1.27–1.37</td>
<td>7</td>
<td>0.28–0.48</td>
<td>7</td>
</tr>
<tr>
<td>Terebratulina unguicula</td>
<td>1.5–2.1</td>
<td>1.24–1.34</td>
<td>5</td>
<td>0.12–0.16</td>
<td>5</td>
</tr>
<tr>
<td>Laqueus californianus</td>
<td>2.5–2.9</td>
<td>1.13–1.24</td>
<td>6</td>
<td>0.20–0.38</td>
<td>6</td>
</tr>
<tr>
<td>Hemithiris psittacea</td>
<td>1.5–1.9</td>
<td>1.20–1.44</td>
<td>8</td>
<td>0.11–0.26</td>
<td>8</td>
</tr>
</tbody>
</table>

* Mean = 1.17, standard deviation = 0.07.
† $\rho$ calculated from data given by Havinga (1928) for 1 to 3+ year-old individuals. Genus and species not specified.

The bulk densities of a few benthic animals have been determined from the weight and volume data used to calculate $\sigma$ (Table I). Consequently, the values based on shells alone are minimal estimates.

Moore (1962) reported a minimum density of 1.14 gm/cc (average for upper 5 cm) in North Pacific sediments. Such low densities indicate high water contents and fluid behavior. All of the organisms in Table I would sink to a depth of 5 cm or more at this station. Other minimum densities in the literature include 1.15 in St. Andrews Bay, Florida ($z = 2.5$ cm, Keller, 1965), 1.19 in the Clyde Sea ($z = 0.5$ cm, calculated from data in Moore, 1931, Sta. 11), 1.23 in the York River ($z = 0–15$ cm, Faas, 1972), and 1.25 from the North Atlantic (Keller and Bennett, 1970). Of the benthos in Table I, only Mya and Laqueus are potentially able to “float” in these low-density muds.

The water content of marine muds usually decreases with depth (e.g., Moore, 1931; Rhoads, 1970; Harrison, et al., 1964). As a result, the bulk density of the sediment increases downwards. An organism too dense to remain on the surface will sink to a depth where its density is equal to that of the surrounding sediment. In many water-rich muds, this equilibrium depth will be too deep to permit respiration or feeding at the surface of the sediment. For example, the Clyde Sea muds (Sta. 11: Moore, 1931) at $z = 27.5–30.0$ cm have a density of only 1.3 gm/cc. Astarte, Mercenaria, and Terebratalia would sink even deeper than this depth range.

c. Adaptations to soft bottoms. To examine systematically the adaptations for physical support on soft bottoms, it is necessary to develop a quantitative expression of the stress applied by an organism. For any solid body, the surface area, $A_s$, can be expressed as
\[ A_s = S_1 r^2 \]  
(1)

in which \( S_1 \) is a shape factor and \( r \) the radius (or any other linear dimension). The bearing area, \( A_b \), will be some fraction \( n \) of the total surface area. Thus

\[ A_b = nS_1 r^2. \]  
(2)

From Newton's second law

\[ \sigma = \frac{mg}{nS_1 r^2} \]  
(3)

where \( m \) is the mass of the object and \( g \) is gravitational acceleration. The mass, however, is given by

\[ m = \varrho V \]  
(4)

where \( \varrho \) and \( V \) are the density and volume, respectively, of the body. Volume in turn, is

\[ V = S_2 r^3 \]  
(5)

in which \( S_2 \) is another shape factor.

Substituting Eq. (5) in (4), and (4) in (3),

\[ \sigma = \frac{\varrho S_2 r^3 g}{nS_1 r^2} \]  
(6)

or

\[ \sigma = \frac{\varrho S_2}{nS_1} rg. \]  
(7)

For a body in fluid, this becomes

\[ \sigma = (\varrho - \varrho_f) \frac{S_2}{nS_1} rg \]  
(8)

where \( \varrho_f \) is the density of the fluid.

Organisms may adapt to life on or near the surface of a weak substrate by adjusting all the variables in this expression (\( g \) is a constant).

1. **Reduce density \( \varrho \).**

2. **Increase \( nS_1 \) more rapidly than \( S_2 \), i.e., increase the bearing area relative to the total volume (or mass). This is best described as a "snowshow effect". \( S_1 \) increases relative to \( S_2 \) when an equidimensional body becomes flatter. \( n \) increases as most bodies (e.g., spheres) sink into the sediment.

3. **Reduce linear dimension \( r \), i.e., become (or remain) small.**

4. **Increase \( \varrho_f \).** Buoyancy increases as the animal sinks from the base of the water column into the denser mud. Thus \( \sigma \) may be reduced until it is less than the strength of the underlying "solid" sediment. Under these conditions, limited sinking can maintain critical portions of the animal above the interface; this may be termed
an "iceberg" adaptation. Bearing area usually increases simultaneously (by increasing \( n \)).

Density adaptations and allometry. Although others have commented on the value of low bulk density to animals inhabiting soft bottoms (Stanley, 1970; Rhoads, 1970; Levinton and Bambach, 1970), the present paper is apparently the first to document the importance of density with actual determinations on benthic organisms.

Ager (1965) noted that coarsely-ribbed brachiopods were localized in high-energy environments. The adaptive value of ribbing (costation) in such settings has been discussed by Lamont (1934), Rudwick (1964), and Stanley (1970). Because a smooth shell will contain less skeletal material than a ribbed one of equal thickness, elimination of ribbing in quiet, soft-bottom environments (where it is not needed to strengthen the shell) reduces the bulk density of the organism.

The role of density per se is relatively clear-cut. However, it must be considered in concert with the other factors which determine \( \sigma \). If a sediment is just strong enough to support a juvenile organism, continued growth (increasing \( r \)) will cause the organism to sink into the bottom unless there is a compensating reduction of another factor, such as density.

In the absence of included gas, the bulk density of a marine organism is controlled primarily by the volume of skeleton (e.g., calcite, \( \varrho = 2.72 \)). Changes in the relative proportions of sea water (\( \varrho = 1.021-1.028 \)) and soft parts (\( \varrho \) of cytoplasm = 1.03–1.10; Jacobs, 1935) will have little effect on bulk density. If the fractional volume of the organism occupied by skeleton remains constant throughout ontogeny (isometric growth), its bulk density will not change and the mass of the skeleton will be proportional to the cube of the organism's length. Thus

\[
\text{Weight} = k (L)^3
\]

where \( k \) is a constant and \( L \) is shell length.

Changes of density during growth can result only from allometry. If density increases with size, weight must increase faster per unit increase of length, so the exponent \( m \) will be greater than 3. Conversely, a decrease in density with increasing size will require an exponent less than 3. These generalizations apply if the weight measured is that of the whole organism, both valves, or a single valve. \( m \) is readily determined from the slope of the line obtained by plotting weight vs. length on log-log paper.

Successful inhabitants of soft bottoms should generally yield values of \( m \) less than 3, reflecting an allometric reduction of bulk density to counter the increasing stress produced by growth. Density is not likely to be a limiting factor on firm substrata, and \( m \) may exceed 3 in such environments. However, bottom properties are not the only limiting factors which favor reduced density. Stanley (1970) pointed out that most rapid-burrowing bivalves have thin shells (and therefore low bulk density) so that metabolic energy is not wasted by moving unnecessary mass. The
Table 2. Values of $m$ for twelve benthic bivalves. $m$ is defined by weight = $K$ (length)$^m$ in which $k$ is a constant. If $m$ for the shell (or the whole organism) is less than 3.0, bulk density (gm/cc) decreases during ontogeny. If greater than 3.0, bulk density increases.

<table>
<thead>
<tr>
<th>INTERTIDAL</th>
<th>$m$</th>
<th>Weight used</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mya arenaria</td>
<td>3.13-3.48</td>
<td>shell</td>
<td>Newcombe &amp; Kessler, 1936</td>
</tr>
<tr>
<td>Mya arenaria</td>
<td>2.57-3.30</td>
<td>shell</td>
<td>Op. cit. recalculated by Swan, 1952</td>
</tr>
<tr>
<td>Mya arenaria</td>
<td>3.81-3.93</td>
<td>shell</td>
<td>Swan, 1952</td>
</tr>
<tr>
<td>Mya arenaria</td>
<td>3.03</td>
<td>whole, drained</td>
<td>Feder &amp; Paul, 1974</td>
</tr>
<tr>
<td>Tapes philippinarum</td>
<td>3.11</td>
<td>shell</td>
<td>Nomura, 1928</td>
</tr>
<tr>
<td>Mactra sulcataria</td>
<td>3.22-4.5</td>
<td>whole</td>
<td>Hanoaka &amp; Shimadzu, 1949</td>
</tr>
<tr>
<td>Meretrix meretrix</td>
<td>3.00</td>
<td>shell</td>
<td>Nomura, 1928</td>
</tr>
<tr>
<td>Donax cuneatus</td>
<td>2.81</td>
<td>whole, including</td>
<td>Nayar, 1955</td>
</tr>
<tr>
<td></td>
<td></td>
<td>preservative</td>
<td></td>
</tr>
<tr>
<td>Donax faba</td>
<td>3.17</td>
<td>whole</td>
<td>Algarswami, 1966</td>
</tr>
<tr>
<td>Pinctada sp.</td>
<td>3.22</td>
<td>both valves</td>
<td>Galtsoff, 1931</td>
</tr>
<tr>
<td>Tivela stultorum</td>
<td>3.16</td>
<td>whole</td>
<td>Weymouth, 1923</td>
</tr>
</tbody>
</table>

| FRESH WATER                 |         |                   |                                       |
| Sphaerium heterodon         | 3.22    | shell? (or whole) | Nomura, 1927                          |

| "SUBTIDAL"                  |         |                   |                                       |
| Nucula proxima              | 2.75    | one valve         | This paper                            |
| Mulinia lateralis           | 2.57    | one valve         | This paper                            |
| Meretrix casta*             | 2.81-2.99| whole            | Durve & Raja, 1965                    |

* From fish ponds and a shallow estuary. No indication of intertidal vs subtidal is given, but the substrata (fine to medium "grade" muds) are like those of many subtidal environments.

The strength of a muscle is proportional to its cross-sectional area, so muscular strength increases as $r^2$. Because mass increases with $r^3$, burrowing becomes increasingly sluggish during growth. However, burrowing ability can be prolonged by ontogenetic reduction of density.

These predictions are tested with bivalves (Table 2). Several determinations of $m$ have been published. In some cases (e.g. Hamai, 1934), the material weighed (body vs. shell) was not specified and the results cannot be interpreted in terms of density. Most of the earlier work sought only to show that bivalve growth could be described by an equation, and the environments sampled were described inadequately or not at all. More recently, variation of the constants in growth equations has been investigated as a function of environmental variables (Newcombe and Kessler, 1936; Swan, 1952), but no one has interpreted this variation in terms of density. Previous work shows a pronounced sampling bias: it appears that none of the bivalves studied were from subtidal environments. Current washing usually removes the fine-grained fraction of shallow-water sediments, leaving a relatively firm, coarse-grained bottom. The strength of fine-grained bottoms in quiet intertidal environments is probably enhanced by periodic exposure and drying. Consistent with the inferred nature of the bottom, values of $m > 3$ have been reported in all but one of the non-subtidal
Figure 1. Log-log plot of weight vs. length for single valves of *Mulinia* (*N* = 50) and *Nucula* (*N* = 39). Straight line fitted by least squares regression. The slope of the line (*m*) is 2.57 (standard deviation of slope, S.D. = 0.052) and 2.75 (S.D. = 0.082) respectively, indicating that bulk density decreased during ontogeny in both genera.

genera of Table 2. *Donax*, the single exception, is a rapid burrower (Stanley, 1970) and its density reduction is probably an adaptation for that habit. Abraham (1953)
reported shell weight as a percentage of total weight for *Meretrix casta* from intertidal mud-clay (Panikkar and Aiyar, 1937). Initially 50\%₀, shell weight remained 66\%₀ or more during subsequent growth. Large shells of *Mya* are proportionately heavier than small ones (Swan, 1952). These results indicate an increase of bulk density in *Meretrix* and *Mya*.

*Pinctada* attaches to hard surfaces, so its ontogenetic increase in density is not likely to be limiting. Galtsoff (1931) inferred that *Pinctada* continued to deposit shell material on the inside of the valves when growth in length was greatly reduced or stopped. Such allometry is precisely that required to increase density. In *Mytilus*, another inhabitant of hard surfaces, deposition of internal nacre continues throughout life, and the shell weight of older specimens increases with little or no increase in length (Seed, 1968, p. 571 & 567). The *Tivela* studied by Weymouth (1923) lived in a beach of pure sand. He attributed the large value of \( m (> 3) \) to allometric thickening of the individual valves.

For comparison, *Mulinia lateralis* and *Nucula proxima* were dredged from a soft, sub-tidal mud (harbor of New Haven, Connecticut); in this sediment \( m \) equalled 2.57 and 2.75, respectively (Fig. 1). Levinton and Bambach (1970) found it “curious” that *Mulinia lateralis*, a shallow-burrowing suspension feeder, seems to prefer muddy habitats. They suggested that a low bulk density enabled it to remain near the surface of the mud. The very low value of \( m \) probably represents a specific adaptation to this environment. In growing from a length of 0.5 to 1.0 cm, these *Mulinia* added 20\%₀ less weight than if they had followed a strictly cubic growth equation.

**Snowshoe adaptation.** The potential value of a broad, flat form to distribute the weight of an organism has long been recognized. In 1909, Hornell (p. 92) suggested that the windowpane oyster, *Placuna placenta*, was able to live on soft mud by employing “the same principle as is embodied in the use of showshoes”. Herrington (1962) found that the valves of the fresh-water bivalve *Pisidium* were more inflated in soft than in firm sediments, “perhaps to keep them from sinking into the bottom”. Rhoads (1970) has reviewed some of the “snowshoe” adaptations of bivalve mollusces and fossil articulate brachiopods. Other weight-distributing mechanisms of brachiopods are discussed by Rudwick (1970). Durham (1966, p. U259) interpreted the large-tipped oral spines of certain echinoids as snowshoes.

Fossil crinoids (Lane, 1963) and trilobites (Cisne, 1973, p. 8–9) both inhabited soft bottoms. The extended cirral root systems of the crinoids (up to 15 cm diameter; Lane, 1963) and the flat shape of trilobites would have been highly adapted to such conditions. The horizontal flanges and spines often seen in trilobites would have reduced further the stress on the substrate.

A small discoidal coral (*Pleurodictyum*) occurs in shale in the Devonian Hamilton Group at East Bethany, New York. Specimens (YPM) bear the impression of the object, usually a gastropod, on which the original polyp settled. The flattened form probably helped to prevent the colony from sinking into the mud.
Flattening does not always imply a snowshoe function. The resultant high ratio of surface to volume (or mass) also increases respiratory and food-gathering capacities relative to the mass of the organism.

**Small size.** In muddy environments, populations of bivalves and fossil brachiopods are dominated by small individuals. This has been interpreted as an adaptation reducing the force per unit area applied by the animal (Stanley, 1970; Levinton and Bambach, 1970; Rhoads, 1970). However, other factors may be involved. Water over fine mud have low concentrations of dissolved oxygen. Because of their higher surface to volume ratio, small animals will be favored where oxygen is limiting (e.g., Raff and Raff, 1970; Rhoads and Morse, 1971), regardless of the substratum.

Self-limiting conditions may produce dwarfed suspension feeders capable of remaining on the surface of soft substrates. The abundance of suspended detritus associated with resuspension of a soft bottom leads to clogging and reduced efficiency in suspension feeding mechanisms. Levinton and Bambach (1970) cited reports of this effect in bivalves and of stunted growth which is the apparent result. Individuals could also sink into the substrate and die when they exceed a critical size. This may explain the uniformly small size of the coral *Pleurodictyum* (YPM) mentioned above. However, the dominance of small species on Recent soft bottoms (e.g., Okhotsk Sea; Savilov, 1957) indicates that adaptation has in fact occurred. Snyder and Bretsky (1971) interpreted the diminutive fauna of an Ordovician soft bottom as the result of paedomorphic1 adaptation.

**Buoyancy adaptations and limited sinking: The iceberg strategy.** I have previously interpreted two Devonian fossils, the bivalve *Grammysia* and the brachiopod *Warrenella*, as benthic icebergs (Thayer, 1974). Other fossil brachiopods are likely to have functioned in this manner. Examples include the nearly infaunal productids (Grant, 1966), and brachiopods that lived with their unusually long beaks buried in soft sediment (Ager, 1965, p. 165–6).

The extraordinary morphology of the Permian proboscidellids is also consistent with an iceberg function. These brachiopods developed a long tube on the anterior of the pedicle valve. The tube was perpendicular to the plane of commissure, giving the shell a boot-like configuration. Muir-Wood and Cooper (1960) believed that these animals were attached to crinoid stems, although none were found in such a position. The small size of the attachment cicatrix suggests that this was only a juvenile adaptation. The growing brachiopods probably broke loose and fell onto the soft bottom. Even after sinking to an equilibrium position in the substrate, they could have fed and respired by using the tube just as a eulamellibranch uses its siphon. This hypothesis is consistent with the fact that the tube was a post-juvenile development. Alternatively, these brachiopods could have been epifaunal, using the tube as an exhalant chimney to produce passive ventilation from the velocity gradient.

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1. Paedomorphic = resulting from retention of juvenile characteristics (e.g., small size) in the adult.
above the bottom (see Vogel and Bretz, 1972). However, it is likely that a much shorter chimney would have been sufficient for this purpose.

Scyphocrinites is a large crinoid with a bulbous, chambered “anchor” which Moore et al. (1952) believed to be a float. Measurements of a Scyphocrinites “float” (YPM) indicate a mean density (filled with air at 1 atm) of 0.8 gm/cc. Assuming solid columnals 1 cm in diameter, a stem 80 cm long would add 60 cc of calcite and cause the mean density of the entire crinoid to exceed 1.0 gm/cc. A planktonic habit was thus impossible, but the “float” could have buoyed up the crinoid in soft sediments even if it were filled with water ($\rho = 1.5$ gm/cc).

Crinoid “holdfasts” found in place at Crawfordsville, Indiana, were described by Lane (1963). They were swollen cylinders oriented normal to the bedding. Such structures would provide very insecure anchorage, and the fine-grained matrix indicates a low-energy environment in which there would have been little need for firm attachment. These “holdfasts” may have provided support in soft mud, rather than attachment. Although their calculated density is greater than the probable density of the substrate, buoyancy due to displaced sediment would have reduced the stress on the underlying solid substrate. This function would have been enanced by the bulbous expansion.

A diminutive conical solitary coral, Streptelasma, is found in the Devonian Hamilton Shale of East Bethany, New York. Specimens (YPM) lack an epifauna, suggesting that they lived with only the polyp exposed above the substrate. The corallite might then have acted as an iceberg.

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