

Design of a Small Cantilevered Sheet: The Sail of *Velevella velevella*¹

LISBETH FRANCIS²

ABSTRACT: The upright sail of the sailing hydrozoan *Velevella velevella* is supported by a very thin cantilevered sheet of colorless and transparent chitinous material. The skeletal material is a layered fibrous composite that is similar structurally to arthropod exoskeleton; but the appearance and mechanical properties (breaking stress, breaking strain, and stiffness or Young's modulus) are more similar to vertebrate hyaline cartilage. Since the homologous perisarc of some sessile hydroid species is both stiffer and stronger, the *Velevella* skeletal material probably has not been selected evolutionarily for extreme strength or stiffness.

Several specific design features make this thin cantilevered sheet of relatively floppy material a suitable support for *Velevella*'s permanent sail. The sail sheet is thicker than the rest of the skeleton, and is further reinforced by two overlapping patterns of raised ridges. The sheet is triangular-to-semicircular, and this tapering shape provides a larger cross section of material at the base to resist the greater bending moment there. A three-dimensional curve at the insertion line between sail and float provides more flexural stiffness, further reducing the tendency for the sheet to fold at the base. Consequently, the sail bends smoothly and progressively under an increasing load and quickly returns to the upright position when unloaded, rather than curling or kinking at the bottom. This, plus some tilting of the whole animal, may reduce stress on the sail in heavy gusting winds.

THE BY-THE-WIND SAILOR, *Velevella velevella* (Figure 1a), is a conspicuous surface-dwelling hydrozoan of the open ocean. Large flotillas are often reported by ships in both major oceans and from both hemispheres, from equatorial waters to latitudes as high as 55° (Bieri 1959, Savilov 1961). The animal is large: specimens 5 to 6 cm long are not uncommon among the large numbers blown ashore on the exposed beaches of central California in the late winter and spring (pers. obs.); and Savilov (1961) reports specimens up to 13 cm long. The flesh is bright blue, and the skeleton is complex, beautifully transparent, and colorless. Imprint fossils of obviously similar skeletons from the Precambrian show that animals of this kind were among the earliest of earth's

metazoans (Glaessner and Wade 1966, Chamberlain 1971, Yochelson, Sturmer, and Stanley 1983).

Since Totton (1954) reclassified these animals, creating the hydrozoan order Chondrophora, *Velevella velevella* and its near relative *Porpita porpita* are described as free-floating, solitary (Mackie 1959, Fields and Mackie 1971) hydroid polyps. The large central mouth is surrounded by budding medusae within a ring of tentacles (Figure 1b, from Agassiz 1833). Extending beyond the edge of the oral disc is a thin, skirtlike flap of tissue, the mantle, that adheres to the surface of the water and floats out around the animal like a blue halo. While the sessile hydroids typically have an aboral stalk supported by a tubular, external skeleton (the perisarc), the pelagic chondrophorans lack a stalk and secrete the aboral skeleton within an invaginated pocket of ectoderm (Leloup 1929).

¹ Manuscript accepted 27 September 1984.

² Bates College, Biology Department, Lewiston, Maine 04240.

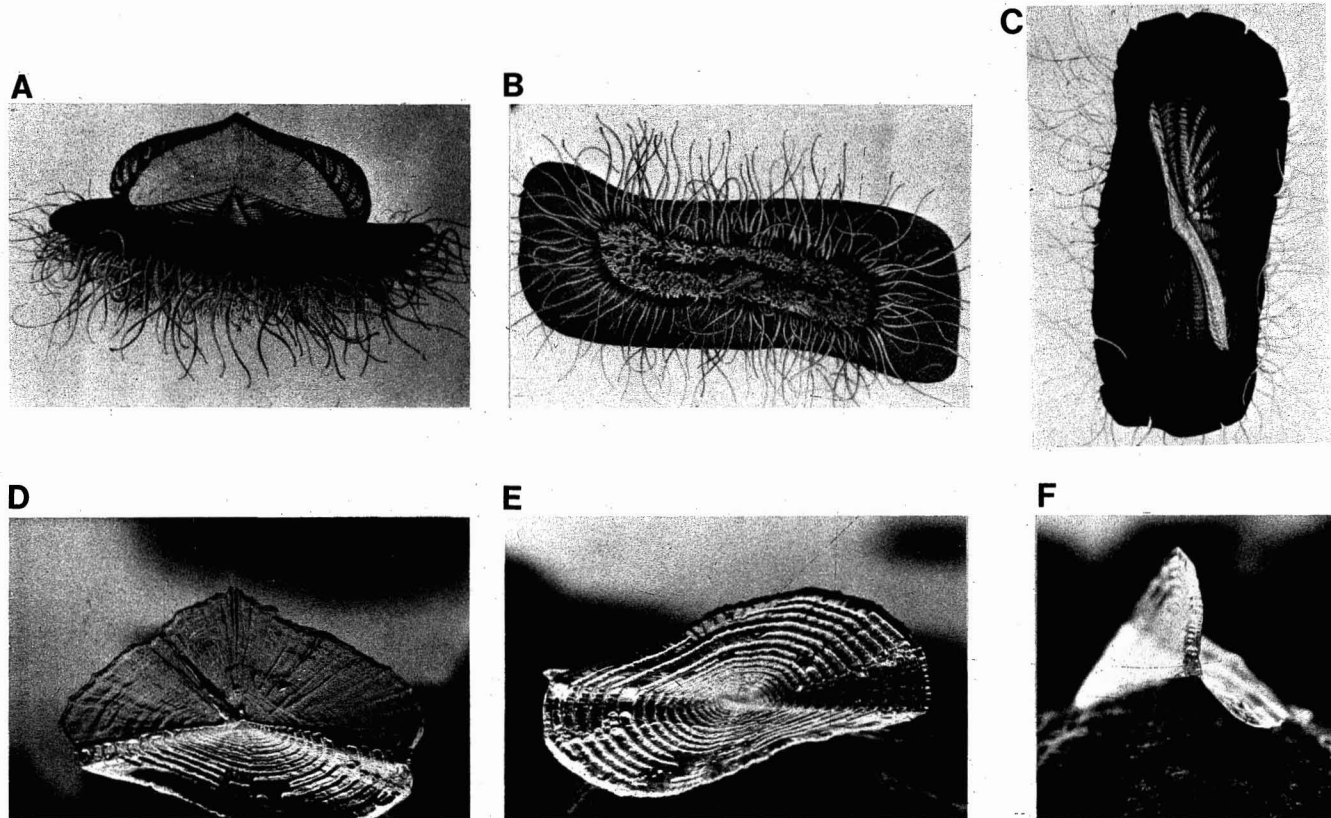


FIGURE 1. A whole specimen and a naked skeleton of *Velevella velevella* shown from several angles. Watercolor illustrations drawn by Agassiz (1833) show the whole animal (*a*) from a position broadside to the sail, (*b*) from underneath with the central mouth surrounded by budding medusae, a ring of tentacles, and the peripheral mantle, which clings to the water's surface when the animal is alive, and (*c*) from above, showing the shape of the float. Photographs of a 5.6 cm long skeleton from Winter Harbor, B. C., provide (*d*) a lateral view showing the conspicuous raised ridges on the sail, (*e*) the oral (underwater) surface, and (*f*) another lateral view oriented at 90° to *d*, which clearly shows the three-dimensional cupping of the hull/float and the curvature of the sail.

The chondrophoran skeleton is a gas-filled float which provides shape and buoyancy for the soft, fleshy parts of the animal. Thin sheets of a chitin-containing, composite material (Rudall 1955, Rudall cited in Fields and Mackie 1971) form the walls of the float, which is subdivided into a series of concentric tubes (Figure 1e). The *Porpita* skeleton is relatively flat and circular, while that of *Veleva* is cupped and rhomboidal, with a flat keellike projection that extends above the water's surface, where it acts as a sail (Figures 1d, f). Fossil skeletons of several kinds have been described, including some that are radially symmetrical and some that are bilateral, some that may have a sail sheet and some that do not (Caster 1942, Glaessner and Wade 1966, Chamberlain 1971, Glaessner 1971, Wade 1971, Yochelson, Sturmer, and Stanley 1983).

Observers report that *Veleva veleva* orients its sail nearly broadside to the wind, and that it sails at angles of up to 45° off the downwind direction (Mackie 1962).

Since *Veleva*'s skeletal sail sheet cannot be folded or furled during rough weather, I wondered how that apparently vulnerable structure survives the rigors of the open ocean. Is the skeletal material especially stiff and strong, or does the design avoid stress concentrations that could cause kinking? To address these questions, I investigated the mechanics of the skeletal material and the structure and design of the cantilevered sheet that supports the *Veleva* sail.

MATERIALS AND METHODS

Collection and Handling of Specimens

During April, May, and June of 1981, I collected and froze live specimens of *Veleva veleva* from among a large number that came ashore near Santa Cruz, California. Several hundred were kept sealed in plastic bags and held frozen as a large mass in a household freezer. Six additional specimens were collected alive in July of 1983 near Winter Harbor, British Columbia, and kept refrigerated in seawater until they were used.

Preparing the skeletons for microscopic

examination and tensile testing was quite easy; the flesh was gently torn, allowing the skeleton to slide free. Before cutting samples, I traced the outline of the skeletons as a record of the size of each individual. Pieces cut from the flat, sheetlike sail support were kept refrigerated in seawater or in various other solutions until they could be examined or tested. To prevent desiccation during mechanical tests, wet specimens were dampened with a few drops of seawater or other aqueous holding solution.

Near Friday Harbor, Washington, specimens of the sessile hydroid *Tubularia marina* were collected from docks and pilings and by diving. These animals were kept in tanks supplied with running seawater, and sections of the tubular perisarc were examined microscopically and used in tensile tests.

Determining Dry Weight and Density

Four specimens of *Veleva* that had been held frozen for 6 months were thawed and the skeletons freed of flesh. Large pieces of skeletal material were cut from the sail support sheets, weighed, dried in a sealed container with a chemical desiccant for 15 hours, and then reweighed to determine wet weight, dry weight, and water content of the material.

To estimate the density of the *Veleva* skeletal material, small sections of sail skeletal material from thawed specimens were placed in dextrose solutions whose density ranged from 1.09 to 1.28. When the specimen and solutions were free of bubbles, the density of the skeletal material could be estimated by noting the solutions in which the specimens just began to sink or float.

Microscopic Examination

Whole specimens, hand-cut sections, and sections cut with a freezing microtome were examined using compound and dissecting microscopes equipped with crossed polaroid filters and a first order red interference compensator (Red I). The presence or absence of birefringence and the sign of that birefringence were used as indications of macromolecular orientation in the material (Wood 1964, Frey-Wyssling 1953).

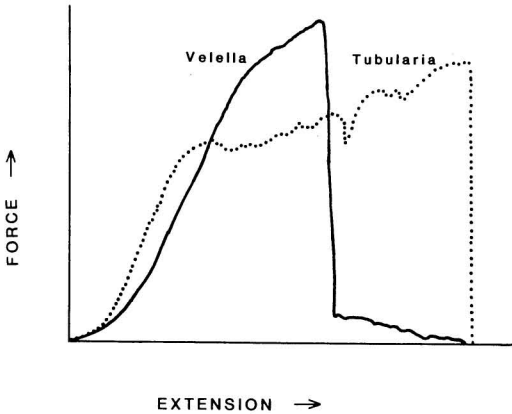


FIGURE 2. Sample force/extension curves for *Velella* skeletal material (solid line) and for a distal segment of perisarc from a specimen of the hydroid *Tubularia marina* (dotted line). As force was increased, the specimens stretched until they tore. Some specimens of each species broke suddenly, as this *Velella* specimen did, producing a sudden drop in the curve with little or no evidence of terminal yielding. The tailing off at the end of that curve was caused by some raggedness in the tear. Others, like the *T. marina* specimen shown here, yielded first, producing some unevenness in the final section of the curve before final failure.

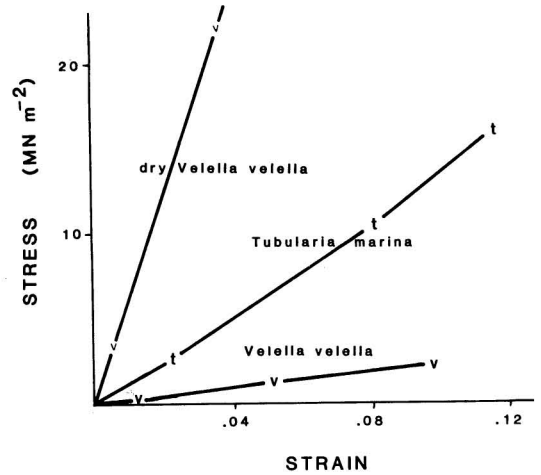


FIGURE 3. Sample stress/strain curves for fresh and dry specimens of *Velella* skeletal material and for a fresh sample of perisarc from *Tubularia marina*, showing stretching of the samples before they began to tear. (The shape of these curves is different from that of the force/extension curves shown in Figure 2 because data from the terminal, descending portions of those curves was not included here.) Differences in the slopes of these three curves reflect large differences in material stiffness.

Mechanical Testing

To measure the tensile properties of the materials, I stretched whole sections of the *Tubularia* perisarc, and 5 mm-wide, rectangular strips of the *Velella* sail support in a racklike device called a minitensometer. Before testing, I measured the thickness of all samples and the width of the perisarc samples using a microscope equipped with an ocular micrometer. These data allowed calculation of cross-sectional areas for the samples. Then the sample was mounted in the grips of the tensometer. For wet sail material, the grips were padded with damp strips of paper toweling to prevent slippage. Dry pieces of sail were attached to each grip with a piece of tape before being clamped, and a drop of cyanoacrylate glue was used to help secure the tubular perisarc. After a sample was firmly mounted, I measured the length of the section exposed between the grips with vernier calipers.

By turning a hand crank, I stretched the specimen at a rate of approximately 0.05 mm per second. A force transducer attached to the

fixed grip of the tensometer measured increasing force, and a linearly variable differential transformer attached to the movable grip measured extension. Connected to an x/y recorder, the electronic output from these two instruments produced a continuous force/extension curve (Figure 2). Machine compliance (deformation of the machine itself under stress) was measured by recording force and displacement with the grips attached directly to each other. This was subtracted from total experimental deformation to give the deformation of the specimen.

Increasing stress (force/cross-sectional area) and natural strain (\ln [instantaneous length/initial length]) were calculated from the force/extension curves (Figure 3). In doing those calculations, I made the following assumptions: (1) that the sheet of material was of uniform thickness, (2) that there was no change in sample volume during testing, (3) that the specimen was deformed uniformly along its length, and consequently (4) that the changing cross section of the sample could be calculated by dividing the initial (calculated) volume by the instantaneous length (the initial

length plus the measured displacement, minus displacement due to machine compliance). Since the specimens actually varied somewhat in thickness along their lengths, the calculated cross-sectional areas are only estimates. As a further consequence of this, the assumption that the sample is distorted uniformly during testing must also be false. This means that the calculated figures for Young's modulus (hereafter referred to simply as "stiffness" or "material stiffness"), breaking stress (hereafter called "strength"), and breaking strain (called "extensibility" here) are only order-of-magnitude estimates, and that it will be possible to detect only relatively large differences in the material properties of samples receiving different experimental treatments.

To explore the nature of the *Velella* material, and to determine whether handling procedures might effect the mechanical properties, I cut and tested multiple samples from each sail sheet. To determine the effects of sample orientation, vertical and horizontal samples from the same five specimens were tested and compared. To determine the effects of freezing on the tensile properties of the material, two strips were cut from each of six specimens. One from each specimen was tested immediately. The others were frozen in a standard household freezer, then thawed and refrozen a total of five times before testing. To further test the effects of handling, several additional strips were cut from four of the previous six specimens. One from each was sealed in a plastic bag, and aged in the freezer for several months before it was tested. One was held in distilled water for an hour. One was held in an isotonic solution of magnesium sulphate for an hour. One was dried flat between two paper towels weighted with a book, and tested after four to six hours, when it was fairly dry. These data were then compared to determine whether the treatments had substantially affected the tensile properties of the material.

Swelling and Shrinking of the Velella Skeletal Material in Hypotonic and Hypertonic Solution

Hydrostatically stiffened materials like vertebrate hyaline cartilage and anemone

mesoglea swell in distilled water and shrink in concentrated saline solutions, becoming stiffer or less stiff, respectively, as they do so (Wainwright et al. 1976; Gosline 1971). In addition to measuring the stiffness of samples held under different osmotic conditions, I examined handcut cross sections of the material under a dissecting microscope before and after changing the osmotic concentration of the medium. Using an ocular micrometer, I measured the thickness of the sections, first in seawater (29 ppt), and then at regular intervals for several hours after placing them into distilled water, or a hypertonic solution of sodium chloride (150 ppt or 300 ppt).

Bending of the Sail under Load

The float of a freshly thawed *Velella* skeleton was pinned to a mound of modeling clay on a small sheet of lead. The skeleton, thus secured and with the sail exposed and upright, was placed in the bottom of a flow tank filled with flowing seawater (Vogel and LaBarbera 1978). As the water velocity in the tank was slowly increased, it was possible to observe the bending of the sail under an increasing load.

Modeling the Effects of Sail Shape on Bending

To explore the effects of sail shape and the importance of the three-dimensional curve at the base of the *Velella* sail, I worked with paper models. Sheets of different shapes and sizes were cut from ordinary notebook paper and taped to a flexible plastic ruler. The ruler provided support at the base of the sheet, making it possible to change the shape of the "insertion line" simply by bending the ruler. By blowing air against these models I could mimic loading of the sail in gusting winds and compare the bending and righting behaviors of various models.

RESULTS

General Observations

The skeletal material of *Velella* looks quite different from that of *Tubularia* species. The

perisarc of *Tubularia marina* varies from whitish or transparent at the distal tip to light tan and somewhat opaque at the base, while the skeleton of *Velevella* is colorless and quite transparent throughout. The sail sheet of *Velevella* is much thicker than the perisarc wall of *Tubularia* species (commonly 0.2 mm for the sail support sheet of *Velevella*, as compared with 0.05 mm for the distal perisarc wall of *Tubularia marina*). Nonetheless, the *Velevella* material feels softer and more flexible when it is handled.

Although nonliving, both the skeleton of *Velevella* and the perisarc of *Tubularia* are in contact with the living tissues of the animals, which may thicken and extend the skeletons by adding layers of material. Cross sections of the *Tubularia* perisarc are obviously layered; and since large sails are thicker than small sails (data used to calculate specimen cross sections), the *Velevella* skeleton is probably also thickened by accretion.

Dry Weight and Density of the Velevella Skeletal Material

The average water content of the *Velevella* skeletal material (estimated by drying the specimens, and calculated using the arcsine transformation) was 87 percent (s.d. = 0.3 percent). The density of the *Velevella* skeletal material, estimated using the gravimetric method, was 1.28.

Birefringence

Mounted in seawater and viewed with crossed polaroid filters through the broad flat surface, the sail support sheet of *Velevella* shows little or no birefringence, indicating that there is no net preferred macromolecular orientation in the plane of the sheet. Any cross section of the sheet mounted in seawater is strongly birefringent, indicating that there is preferred orientation of the macromolecules through the thickness of the sheet. Birefringence decreases progressively as cross sections are dehydrated by transfer from seawater to increasingly more concentrated alcohol solutions, then into toluene and finally to

cedarwood oil. This large, variable component is form birefringence (caused by oriented discontinuities between two materials with different refractive indices—presumably matrix and chitin fibers in this case) rather than birefringence intrinsic to the macromolecules themselves.

Regardless of how the section is cut (horizontally, vertically, radially, or otherwise), cross sections of the *Velevella* sail support sheet always show retardation by the Red I compensator when the long axis of the section is oriented parallel to the slow direction of the filter. This indicates preferred orientation parallel to the plane of the section. Random orientation of chitin in thin layers parallel to the surface of the sheet would give this result, and is therefore the choice of parsimony.

Cross sections of the *Tubularia* perisarc are also much more birefringent than are flattened pieces of the whole tube. Again, this suggests preferred orientation of fibers through the thickness of the walls of the perisarc tube, but little or no preferred orientation parallel to the surface of the tube. The polarity of this birefringence is the same as for the *Velevella* skeleton, indicating again that the chitin fibers could be randomly arranged within thin layers that are parallel to the surface of the tube.

Mechanical Properties: Response in Tension

Typical force/extension curves for *Velevella* skeleton and for *Tubularia marina* perisarc are shown in Figure 2. The initial steepening of the force/extension curve is characteristic of fiber/matrix composites, and may indicate any of several things: (1) the sample might simply be pulling taut and straightening between the grips; (2) there may be some stretching of the amorphous matrix before tension is transmitted fully to embedded chitin fibers; and (3) fibers may be realigning as the material is pulled. The middle section of the curve is quite linear. Sometimes the material breaks sharply (curve for the *Velevella* specimen, Figure 2) and sometimes it yields first, producing a flattened and uneven section in the curve (*Tubularia* specimen, Figure 2). Most specimens tore raggedly, producing a jaggedly de-

TABLE 1

TENSILE PROPERTIES OF *Veleva* SKELETON AND *Tubularia* PERISARC: EFFECTS OF SAMPLE ORIENTATION, HYDRATION, IONIC AND OSMOTIC STATES, FREEZE/THAW, AND SAMPLE AGE

MATERIAL SOURCE AND TREATMENT	E STIFFNESS (MN m ⁻²)	σ_t STRENGTH (MN m ⁻²)	ϵ_t EXTENSIBILITY (%)	N SAMPLE SIZE
I. <i>Veleva veleva</i>, sail support sheet				
Santa Cruz, CA freeze/thaw, horizontal strip	*25 ± 10	0.4 ± 0.2	2.5 ± 0.05	5
SC, f/t vertical strip	15 ± 8	0.6 ± 0.2	4.0 ± 0.04	5
Winter Harbor, BC fresh sample	15 ± 6	3 ± 2	19.5 ± 1.9	6
WH, f/t, fresh	17 ± 5	3 ± 2	18.9 ± 1.6	6
WH, f/t, aged	27 ± 11	4 ± 2	9.9 ± 3.0	4
WH, f/t, distilled water	30 ± 14	7 ± 3	9.8 ± 9.5	4
WH, f/t, 0.58M MgSO	24 ± 11	3 ± 1	11.1 ± 0.4	4
WH, f/t, dry	400 ± 157	5 ± 3	9.3 ± 3.4	4
II. <i>Tubularia marina</i>, untanned perisarc				
Friday Harbor, WA fresh	140 ± 19	20 ± 4	14.6 ± 0.1	5

* Values given are means, plus or minus their standard deviations. The arcsine transformation was used for extensibility calculations.

NOTE: Abbreviations used are as follows: SC = Santa Cruz, California; WH = Winter Harbor, British Columbia; f/t = freeze/thaw; MN m⁻² = meganewtons per square meter; σ_t = maximum tensile stress at breaking = force/cross-sectional area; E = stiffness = σ/E ; ϵ_t = extensibility = $\{\ln(\text{final length}/\text{initial length})\} \times 100$.

scending terminal portion (*Veleva* specimen, Figure 2).

The material responds similarly when the sheet is stretched in any direction. There are no large differences in the tensile properties of strips cut straight across the sail (at right angles to the water line), as compared with strips cut vertically (Table 1); nor are samples from the middle obviously different from peripheral samples. This again indicates a lack of preferred orientation parallel to the plane of the sheet.

Not all specimens showed the same tensile properties (Figure 4). Within both popula-

tions, some were consistently stiffer than the rest. Eight of the eleven specimens tested had an average elastic modulus of 1.2×10^7 N m⁻² (s.d. = 0.22). The other three specimens were consistently about twice as stiff (E [stiffness] = 2.4×10^7 N m⁻²; s.d. = 0.61×10^7).

In addition to individual differences in stiffness, there were also populational differences in strength (Table 1, Figure 4). Those collected at Winter Harbor in 1983 were consistently stronger than those collected at Santa Cruz in 1981 (i.e., they broke at higher stress and strain levels).

The 1983 Winter Harbor specimens also

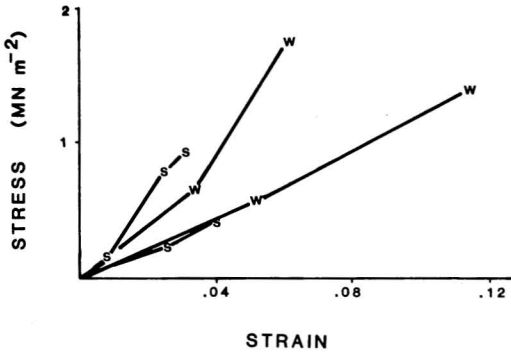


FIGURE 4. Sample stress/strain curves for skeletal material from four specimens of *Velella*, showing stretching of the samples until they began to tear, and demonstrating differences in tensile properties within and between populations. Samples from the 1983 population collected at Winter Harbor, B. C. (w) broke at higher strain levels than did samples from the 1981 population collected at Santa Cruz, Calif. (s). A few of the specimens from each population were about twice as stiff as the rest (e.g., the two steeper curves).

had more conspicuous radial and concentric ridge patterns than did the 1981 specimens from Santa Cruz; many of the 1983 sail support sheets had jagged margins (Figure 1d), while the 1981 specimens had smooth margins. However, the differences in strength and extensibility were probably not due simply to sculpturing differences. Samples from relatively flat sections of highly sculptured sails showed the same properties as samples from more sculptured areas of the same sails.

None of these differences within and between populations were associated with individual size. Some larger and some smaller specimens were examined from both populations: of the three stiffer specimens, one was among the largest, one was among the smallest, and one was in the middle of the size range of those tested (ranges for maximum sail lengths: Santa Cruz specimens, 3.0 to 5.7 cm; Winter Harbor specimens, 3.9 to 5.7 cm; less stiff specimens from both populations, 3.9 to 5.7 cm; stiffer specimens, 3.0 to 5.7 cm).

Of the treatments tested, only drying had a detectable effect on the mechanical properties of the material. Samples that were deliberately dried before testing were much stiffer than wet specimens (Table 1). Samples kept in a freezer for 3 months apparently suffered "freezer

burn" (freeze drying), because they also were significantly stiffer than fresh samples from the same skeletons (Table 1). The tensile properties were not affected by the osmotic characteristics of the holding solution or by the charge of ions in solution. The material responded similarly in tension when freshly removed from the animal, when held in cold seawater for up to a week, and when held in distilled water or in an isotonic solution of magnesium sulphate either for a few minutes or for several hours.

The distal tip of the perisarc of *Tubularia marina* is stiffer and stronger than the wet skeletal material of *Velella*, and both materials break at about the same strain levels (Table 1 and Figure 3).

Swelling and Shrinking of Velella Skeletal Material in Response to Desiccation and Osmotic Variation

The *Velella* skeletal material shrinks dramatically when it is dried; however, in contrast to vertebrate hyaline cartilage, the *Velella* material neither swells nor shrinks in solutions with osmotic concentrations that vary considerably from those of natural seawater.

Bending of the Sail: Behavior of the Specimen in a Flow Tank

When the sail was loaded in drag underwater at low water velocities, only the tip of the sail bent. As the velocity was increased, the whole sheet inclined at an increasingly steep angle.

After several hours in the tank at one velocity, the sail did not stretch or bend greatly beyond the initial response. When the force was removed by turning off the flow, the specimen quickly returned to the original position. Apparently the skeletal material does not creep appreciably under a small, steady load.

Effect of Sheet Shape on Bending: Behavior of Models

A rectangular sheet of paper that is supported along the straight, bottom edge will tend to collapse by curling over near the base

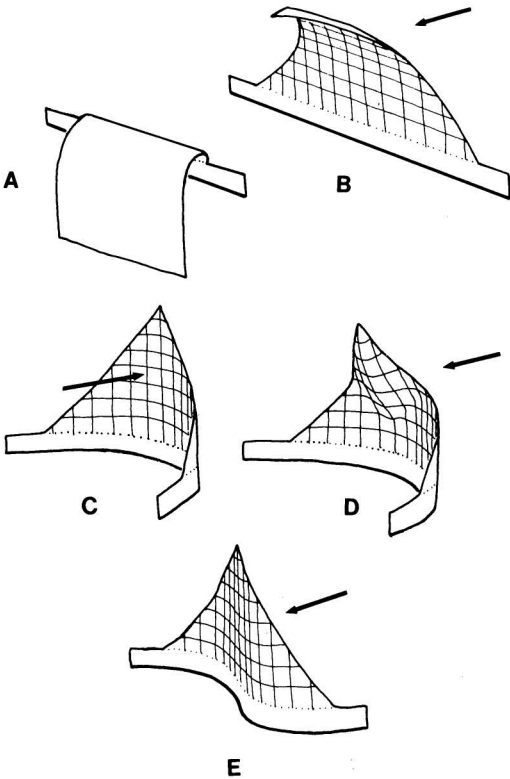


FIGURE 5. Bending of paper models in a wind. Sheets of notebook paper were taped to a flexible plastic ruler and their behavior was observed as puffs of air (indicated by arrows) were blown at right angles to the center of one surface. A flat rectangular sheet (a) tends to kink at the base even without wind. A flat triangular sheet (b) bends more gradually along its length. A triangular sheet with a simply curved base remains upright at relatively high velocities if the wind blows from inside the curve (c); but above some critical velocity, wind from the opposite direction causes kinking (d). An S-shaped curve at the base of the sheet (e) supports it equally well no matter how the wind blows.

of the sheet (Figure 5a). In contrast, a flat triangular sheet that is held upright, supported only at the bottom edge, tends to remain upright. Blow gently against one face of the triangular sheet and it bends slightly (Figure 5b), inclining more steeply in a more vigorous wind and recoiling when the force is removed.

When the wind blows against the concave side of a simply curved sheet, the sheet remains upright under much heavier loads than will a flat sheet of the same dimensions; but

the curved sheet kinks readily when the same force is applied from the opposite direction, against the convex face (Figures 5b–d). A slight S-shaped curve at the base increases the flexural stiffness equally for loading from either direction (Figure 5e).

DISCUSSION

Although the skeletal material of *Veleva veleva* has been identified as a chitinous composite (Rudall 1955; Rudall cited in Fields and Mackie 1971), the mechanical properties of the material, including macromolecular orientation and the functional morphology of the skeleton itself, apparently have not been investigated. In the discussion below, I compare the properties of the *Veleva* material with homologous and analogous materials, discuss the probable microstructure of the material, and present an analysis of miniature sail design.

I am presently studying the sailing dynamics of *Veleva* and the behavior of living animals. Effects of body design and behavior on orientation and movement will be discussed at a later date.

Material Properties and Submicroscopic Structure

In the realm of animal skeletal materials, there is nothing very remarkable about the tensile properties of the *Veleva* skeletal material. It is neither particularly strong nor unusually extensible. This is probably not surprising, considering its function. A force strong enough to stretch or tear the skeleton would probably capsize the animal or tear the flesh free instead.

What does seem surprising is that the material is also not very stiff. It is about as stiff as vertebrate hyaline cartilage, but less stiff than insect cuticle by more than two orders of magnitude (Table 2). In fact, as the name “chondrophoran” would suggest, the *Veleva* skeleton looks and acts remarkable like vertebrate hyaline cartilage. The two materials have about the same tensile stiffness, strength, and extensibility (Table 2); however, changes in

TABLE 2
COMPARATIVE DATA: THE TENSILE PROPERTIES OF SOME PLIABLE MATERIALS

MATERIAL	DENSITY (Kg m ⁻³)	EXTENSIBILITY (% increase)	STRENGTH (N m ⁻²)	STIFFNESS (N m ⁻²)	DATA SOURCE*
Organic rubbers	1.3 × 10 ³	> 200	3 × 10 ⁵	.6–4 × 10 ⁵	†
Anemone mesoglea		> 200	3–4	3 × 10 ⁴	*
Vertebrate hyaline cartilage	1.1 × 10 ³	9–31	2–5 × 10 ⁵	1.3 × 10 ⁷	‡, †
Wet <i>Veleva</i> skeleton	1.3 × 10 ³	2–20	4–30 × 10 ⁵	2 × 10 ⁷	§
Dried <i>Veleva</i> skeleton		9	5 × 10 ⁶	4 × 10 ⁸	§
<i>Tubularia</i> perisarc		14	2 × 10 ⁷	1.4 × 10 ⁸	§
Locust cuticle	1.2 × 10 ³		9.6 × 10 ⁷	2 × 10 ⁹	†

* Sources of data: (*) Alexander 1968; (†) Currey 1970; (‡) Yamada 1973; (§) new data reported here. A blank space indicates lack of information.

the osmotic concentration or the ionic composition of the medium do not measurably affect either the dimensions or the stiffness of the *Veleva* skeletal material. This suggests that the material is not stiffened hydrostatically, as is hyaline cartilage.

Indirect evidence from polarizing microscopy suggests that the chitin fibers in the *Veleva* skeleton may be randomly arranged within thin layers, with relatively few fibers running through the thickness of the sheet. However, this is a weak deduction which should be confirmed or denied by fixing, staining, and sectioning the material and examining it using transmission electron microscopy.

Most, if not all, natural fiber/matrix sheets are birefringent in cross section, because the fibers tend to be oriented parallel to the sheet's surface. Developmentally, this may be because these structures are secreted as thin layers; relatively long fibers within a thin sheet are almost certain to show preferred orientation parallel to the surface of the sheet. For example, noodles poured onto a flat surface show this alignment, and Wainwright (1963) argues that the mechanical interactions of fibers and crystals during the formation of ceramic composites should produce a similar

alignment. Structurally, fibers arranged parallel to the surface of a sheet can also provide much greater reinforcement, both in tension and in shear, than fibers arranged at right angles to the plane of the sheet (Wainwright et al. 1976). Arthropod exoskeleton, nematode cuticle, and fish skin are also fiber/matrix sheets that are birefringent in cross section (Wainwright et al. 1976).

Evolution of the Veleva Skeleton

Cnidarians may have anticipated the arthropods in developing a layered chitinous exoskeleton.

Members of all three cnidarian classes are known to secrete cuticular chitinous structures (Rudall 1955, Neville 1975, Muzzarelli 1977). Examples include the perisarc of the hydrozoans, *Tubularia* and *Veleva* (Rudall 1955), the calcareous skeleton of the (anthozoan) coral *Pocillopora damicornis* (Wainwright 1962), and the cuticle of polypoid generation of the scyphozoan jellyfish *Aurelia aurita* (Chapman, 1968).

Electron micrographs of the *Aurelia* polyp cuticle (Chapman 1968), show a parabolic pattern that is typical of the helicoidal ar-

rangement of fibers found in the arthropod cuticle (Richards 1951, Neville 1975). Since we do not yet know the details of fiber arrangement in the layered skeletons of *Tubularia*, *Veleva*, or the fossil chondrophorans, it is possible that there, too, the arrangement is helicoidal.

Like the arthropods, modern sessile hydroids produce long, thin support structures by enclosing parts of the body in an external, tubular sheath; and like the arthropods, some hydroids construct flexible joints that allow them to bend the stiff cuticular tube (Murdock 1976). However, these animals also retain the typical cnidarian commitment to feeding with nematocysts, which requires exposing the soft tentacles to contact rather than completely encasing the body in armor as the arthropods do.

While soft flesh completely enfolds the elaborate chondrophoran skeleton, the derivation of that complex endoskeleton from the tubular perisarc of sessile hydroids is not difficult to imagine (Figure 6). Since it is secreted inside a fleshy pocket instead of on the outside of the stalk, the chondrophoran skeleton must be inside-out relative to the perisarc tube (Fields and Mackie 1971). If one end of a tube were flattened, it would form a double-layered sheet, like the sail support. (In fact, when the sail sheet of *Veleva* is cut into very thin strips, it delaminates readily into two equal layers, indicating that it probably is formed as two adjoining sheets.) By abruptly belling out below the sail, the tube could form the upper surface of the float, and by rapidly pinching in again, it could form the lower surface of that float. As the animal grows, the sail support sheet is easily enlarged by the addition of material at the edges. Enlarging the float requires adding gas-filled tubes at the periphery. Since the *Veleva* skeleton is secreted and molded by the ectoderm, it would presumably take the shape of the enfolding flesh, so drastic distortions of the kind proposed here might be quite simply accomplished.

Design of Cantilevered Sheets: The Veleva Sail Sheet

Since the dried skeleton of *Veleva* and the wet perisarc of *Tubularia* are both stiffer than

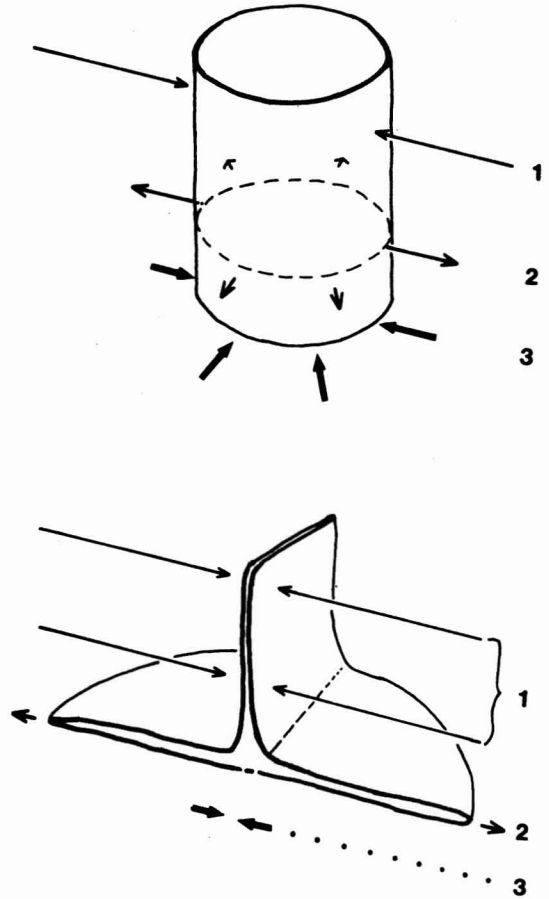


FIGURE 6. Suggested derivation of the *Veleva* skeleton from an inverted, tubular perisarc. To form the sail, the tube is flattened at the top (arrows at 1) and the oppressed faces are joined. An abrupt bulge in the middle (2) is immediately constricted again at the base (3), producing a flattened balloon, which is the first, central chamber of the gas-filled float.

the wet *Veleva* skeleton by an order of magnitude (Table 1), we must conclude that natural selection has not favored maximal stiffness for this material.

Apparently it is possible, and perhaps even advantageous, to construct a thin, free-standing sheet of relatively floppy material. The question, then, is how such a structure can be stiff enough to stand upright. A flat sheet of very floppy material would simply crumple under its own weight, while a flat sheet of slightly stiffer stuff would tend to

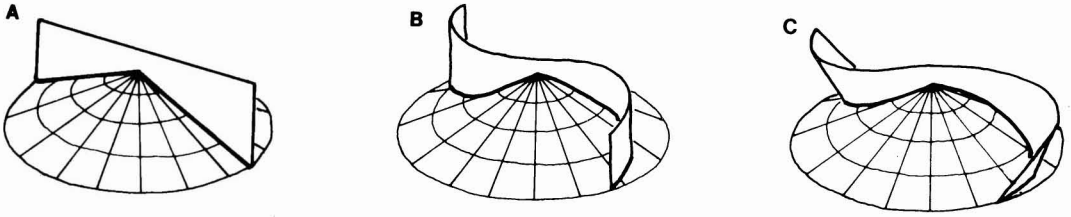


FIGURE 7. Three successively more realistic models showing the shape of the joint between the sail and the low, cone-shaped float of *Verella*. (a) A flat sail intersects the upper surface of a cone, producing an inverted, V-shaped insertion. (b) The base of the sail is often S-shaped rather than straight, so the arms of the inverted "v" are curved in opposite directions along the surface of the cone. (c) The sail surface is not vertical, but slopes oppositely at the two ends. Both the steepness of the cone and the curvature of the sail are exaggerated here.

collapse by bending near the bottom (Salvadori and Heller 1963, Figure 5a).

In engineering shorthand, the sail is a cantilevered, sheetlike beam that is loaded in bending (Wainwright et al. 1976). The bending resistance (flexural stiffness) of a beam is the product of the material stiffness (E) and the second moment of area (I), which is a complex morphological term describing the distribution of material in the beam's cross section (Wainwright et al. 1976). Given that the *Verella* skeletal material is not very stiff, the resistance of the sail to bending must be largely due to the shape of the beam's cross section, described by the second moment of area.

An obvious way to stiffen a beam by increasing the second moment of area is to make that beam stouter. A thick sheet is stiffer in bending than a thin sheet of the same material. However, doubling the thickness of a flat sheet more than doubles its flexural stiffness, because material contributes to the I component of flexural stiffness in proportion to the square of its distance from the axis of bending of the beam. The axis of bending, in this case, is the plane at the center of the sheet. Not only is there more material to bend in a thicker sheet than there is in a thinner one, but the additional material is all farther from the axis of bending than that in the thinner sheet. The sail support of *Verella* is about twice as thick as the walls of the float, and four times as thick as the perisarc of *Tubularia marina*.

But a thicker sheet is heavier and more expensive to make than a thin sheet. For a relatively smaller increase in weight, the sail support of *Verella* is stiffened further by

the addition of superficial thickened ridges. The degree of sculpturing varies considerably among specimens, but the pattern is quite consistent, and strikingly reminiscent of leaf venation patterns, (Figure 1d). A set of radial ridges that fans out from the middle of the bottom edge could be described as palmate venation. Another set runs parallel to the free edge of the sail and looks like concentric growth lines. The concentric set plus the central vertical rib of the radial set form an oppositely branching, pinnate venation pattern. For the same net increase in weight, this build-up of material as a pattern of thickened ridges places material farther from the axis of bending than would uniform thickening of the whole sheet. In addition, this specific arrangement of the ridges provides disproportionate reinforcement vertically, at the midline. The palmate set converges in the middle at the bottom of the sail, and the pinnate set produces a series of V-shaped reinforcements along the central rib, where the shape of the pointed sail tip is repeated as a series of thickened growth lines (Figure 1d).

The second moment of area may also be increased by changing the shape of a beam *without* adding material. Many specimens of *Verella* have a slight, S-shaped curve at the bottom of the sheet (Figures 1c, 5e, 7b, 7c), which increases the flexural stiffness equally for loading from either direction.

Under some circumstances, a somewhat flexible sheet may be more advantageous than a maximally stiff one. If it is brittle or deforms plastically, a stiff sheet may crack or kink permanently when bent. A flexible structure that is tough and springy may bend smoothly

when loaded, and recoil when the force is removed. Many biological structures respond to transitory forces in this accommodating, stress-reducing fashion. Leaves, branches, and whole trees sway in the wind (Vogel 1984). Skins and arteries stretch and recoil as they are repeatedly loaded and unloaded (Wainwright et al. 1976). By bending in high winds, the sail of *Veleva* presents a lower profile, thereby reducing the drag forces acting on it. To be advantageous, this bending must be smooth and reversible rather than sharp and catastrophic.

Because the sail projects upward and at right angles to the surface of the float, it could be quite vulnerable to failure by kinking at the base. Two design features reduce that risk: (1) the shape of the sail itself and (2) the design of the joint between the sail and float.

The pattern of bending under an increasing load depends not only on the characteristics of the material and the thickness of the sheet, but also on the shape of the cantilevered sheet and the way that it is supported at the base. Under uniform loading, a square or rectangular sheet tends to bend suddenly near the base when the load reaches a critical level (Figure 5a), because the moment arm is longest at the base, providing the greatest bending moment there. This may explain the advantage to *Veleva* of having a triangular to semicircular sail rather than a rectangular one. The tapered shape provides an increasingly larger cross section of material toward the bottom of the sail, where it resists the increasing bending moment.

The insertion line between sail and float is a three-dimensional curve (Figures 1, 7c) which provides an additional increase in the second moment of area and better resistance to bending at the base of the sail. From the side, the insertion line is an inverted "V", where the sail attaches to the low, cone-shaped, upper surface of the float (Figures 1d, 7a). It is therefore impossible for the sail simply to fold over at the base by bending straight along the insertion line. Many specimens also show a slight S-shaped curve at the base of the sail (Figure 7b). This again increases the second moment of area, providing greater bending resistance, especially at the base of the sail. Furthermore, the joint between the float and the sail support

is not a sharp right angle, but a smoothly sloping curve (Figure 1c). The impression this gives is that the sail is twisted oppositely at either end where the concave face of the sheet becomes the upper surface of the float (Figure 7c). When loaded in drag by wind blowing against one face, the sail angles backward, and tension along that face can be transferred to the upper surface at one end of the float. The opposite, leeward face may then act as a leaf spring, absorbing and storing energy as the sail is bent backward. Bubbles of gas that extend into the base of the sail (Figure 1d) may also be compressed, reversibly storing energy and providing an outward pressure that would counteract any tendency for kinking when the sail is bent. Bending of the sail and tilting of the whole animal provides a purely passive mechanism for reducing stress and moderating sailing speed in the face of unpredictably variable wind velocities.

SUMMARY

The skeletal material of *Veleva* is a layered chitinous composite that is neither especially stiff nor particularly strong. Various design features increase the flexural stiffness of the cantilevered sheet that supports the thin, flat sail of the animal: the sheet is thicker than the rest of the skeleton and decorated with a pattern of raised ridges. However, a somewhat flexible sail is probably better design, in this case, than a maximally stiff one. The sail shape and sculpturing, and the shape of the insertion line between sail and float, all help to prevent kinking as the sail bends and recoils, absorbing and reducing the drag forces acting on it under what must commonly be very capricious wind conditions.

Unlike many other natural cantilevered sheets, the skeletal sail sheet is relatively simple, both structurally and functionally: (1) it is a solid structure, made entirely of a single kind of composite material, without conductive elements, and without included living tissue of any kind, and (2) its only known function is support. This makes it a good subject for the analysis of design in natural cantilevered sheets.

ACKNOWLEDGMENTS

I thank S. Vogel and M. LaBarbera for guidance and encouragement; K. P. Irons, S. Smiley, R. L. Miller, and S. F. Norton for collecting specimens of *Verella* and *Tubularia*; and the visitors, staff, and faculty of the Friday Harbor Laboratories, and the Duke University Zoology Department for valuable ideas, information, and advice. The work was largely done at the University of Washington's Friday Harbor labs with electronic equipment generously supplied by M. LaBarbera. S. A. Wainwright and B. A. Best kindly read and commented on the manuscript, and Lisa J. Croner drew Figures 5 and 7.

LITERATURE CITED

- AGASSIZ, A. 1833. Exploration of the surface fauna of the Gulf Stream III, Part I. The *Porpitidae* and *Velellidae*. Mem. Mus. Comp. Zool. Harvard 8(2): 1-16.
- ALEXANDER, R. McN. 1968. Animal mechanics. Univ. of Wash. Press, Seattle. 346 pp.
- BIERI, R. 1959. Dimorphism and size distribution in *Verella* and *Physalia*. Nature 184: 1333.
- CASTER, K. E. 1942. Two siphonophores from the Paleozoic. Palaeontographica Amer. 3(14). 34 pp. New York and Ithaca.
- CHAMBERLAIN, C. K. 1971. A "by-the-wind-sailor" (Velellidae) from the Pennsylvanian Flysch of Oklahoma. J. Paleont. 45: 724-728.
- CHAPMAN, D. M. 1968. Structure, histochemistry and formation of the podocyst and cuticle of *Aurelia aurita*. J. Mar. Biol. Ass. U. K. 48: 187-208.
- CURREY, J. D. 1970. Animal skeletons. Studies in biology, no. 22. Edward Arnold, London. 52 pp.
- FIELDS, W. G., and G. O. MACKIE. 1971. Evolution of the Chondrophora: Evidence from behavioral studies on *Verella*. J. Fish. Res. Bd. Canada 28: 1595-1602.
- FREY-WYSSLING, A. 1953. Submicroscopic morphology of protoplasm. Elsevier Pub. Co., New York. 411 pp.
- GLAESSNER M. F. 1971. The genus *Conomedusites* Glaessner and Wade and the diversification of the Cnidaria. Paleont. Zeits. 45: 7-17.
- GLAESSNER, M. F., and M. WADE. 1966. The Late Precambrian fossils from Ediacara, South Australia. Paleontology 9: 599-628.
- GOSLINE, J. M. 1971. Connective tissue mechanics of *Metridium senile*: II. visco-elastic properties and macromolecular model. J. Exp. Biol. 55: 775-795.
- LELOUP, E. 1929. Recherches sur l'anatomie et le développement de *Verella spirans* Forsk. Arch. Biol. Paris 39: 397-478.
- MACKIE, G. O. 1959. The evolution of the *Chondrophora* (*Siphonophora-Disconanthae*): New evidence from behavioral studies. Trans. Roy. Soc. Canada: 53, ser. 3, sect. 5: 7-20.
- . 1962. Factors affecting the distribution of *Vellela vellela* (*Chondrophora*). Internationale Revue der Gesamten Hydrobiologie 47: 26-32.
- MURDOCK, G. R. 1976. Hydroid skeletons and fluid flow. In G. O. Mackie, ed. Coelenterate ecology and behavior. Plenum, New York.
- MUZZARELLI, R. A. A. 1977. Chitin. Pergamon Press, New York. 309 pp.
- NEVILLE, A. C. 1975. Biology of Arthropod cuticle. In D. S. Farner, ed. Zoophysiology and ecology, Volume 4/5. Springer-Verlag, New York. 448 pp.
- RICHARDS, G. 1951. The integument of Arthropods. Univ. of Minnesota Press, St. Paul. 411 pp.
- RUDALL, K. M. 1955. The distribution of collagen and chitin. Symp. Soc. Exp. Biol. 9: 49-70.
- SALVADORI, M., and R. HELLER. 1963. Structure in architecture. Prentice-Hall International Series in Architecture, M. Salvadori, ed. Prentice-Hall, Englewood Cliffs, New Jersey. 370 pp.
- SAVILOV, A. I. 1961. The distribution of the ecological forms of the by-the-wind sailor, *Verella lata* Ch. and Eys., and the Portuguese man-of-war, *Physalia utriculus* (La Martiniere) Esch., in the North Pacific. Trudy Inst. Okeanol. Akad. Nauk SSSR 45: 223-239.

- TOTTON, A. K. 1954. Siphonophores of the Indian Ocean. *Discovery Rep.* 27:1-162.
- VOGEL, S. 1984. Drag and flexibility in sessile organisms. *Amer. Zool.* 24:37-44.
- VOGEL, S., and M. LABARBERA. 1978. Simple flow tanks for research and teaching. *Bio-science* 28:638-643.
- WADE, M. 1971. Bilateral Precambrian chondrophores from the Ediacara fauna, South Australia. *Proc. R. Soc. Vic.* 84:183-188.
- WAINWRIGHT, S. A. 1962. An anthozoan chitin. *Experientia* 18:1-3.
- . 1963. Skeletal organization in the coral, *Pocillopora damicornis*. *Quart. J. Micr. Sci.* 104:169-183.
- WAINWRIGHT, S. A., W. D. BIGGS, J. D. Currey, and J. M. GOSLINE. 1976. *Mechanical design in organisms*. Edward Arnold, London. 423 pp.
- WOOD, E. A. 1964. *Crystals and light, an introduction to optical crystallography*, 2nd rev. ed. Dover, New York.
- YAMADA, H. 1973. *Strength of biological materials*. Krieger, New York. 297 pp.
- YOCHELSON, E. L., W. STURMER, and G. D. STANLEY. 1983. *Plectodiscus discoideus* (Rauff): A redescription of a chondrophoran from the Early Devonian Hunsrück slate, West Germany. *Palaont. Z.* 57:39-68.