

A comparative analysis of the locomotory systems of medusoid Cnidaria

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KURZFASSUNG: Eine vergleichende Analyse der lokomotorischen Systeme von Cnidarier-Medusen. Auf der Grundlage einer funktionell-morphologischen Analyse des lokomotorischen Systems bei Hydro- und Scyphomedusen wurde der Versuch unternommen, den Mechanismus ihrer Schwimmbewegungen allgemein zu charakterisieren. An Vertretern von insgesamt 42 Gattungen wurden der Bau und die funktionelle Variabilität des Schirmes, der Mesogloea, der Fibrillen der Mesogloea, der kontraktilen Elemente der Muskulatur und des Velums bzw. des Velariums untersucht und verglichen sowie eine Klassifizierung der Medusen nach der Struktur der Mesogloea und der Art der Fortbewegung vorgenommen.

INTRODUCTION

The most complete discussion to date of the medusa as a functioning musculoskeletal system has been that of GLADFELTER (1972a) for the hydromedusan *Polyorchis montereyensis*. In another study the very different locomotory system of the scyphomedusan *Cyanea capillata* has been discussed (GLADFELTER 1972b). Other published works on the functional morphology of medusan locomotory systems have been fragmentary or have dealt with specialized aspects of the subject (KRASINSKA 1914, CHAPMAN 1953, 1959; MACKIE 1964, CHAPMAN 1968 and others), and works on general anatomy (CHUN 1897, CONANT 1898, THIEL 1938, HYMAN 1940a and others) though presenting some of the pertinent anatomy, have not discussed the locomotory system as a whole. A number of more specialized papers dealing with the physiology of medusan locomotion are also available but present only the essential rudiments of morphology (BULLOCK & HORRIDGE 1965, MACKIE 1971 and others). The purpose of the present study was to survey a broad taxonomic spectrum of hydro- and scyphomedusae examining the pattern of locomotory structures and function where possible, in order to draw generalizations about fundamental characteristics of medusan swimming mechanisms. Medusoid cnidarians representing nine orders, twenty-seven families and forty-two genera have been examined (Table 1). In a number of cases it has been possible to correlate structure with functional effectiveness, and it is hoped that future studies will enable us to make concrete statements about some of the general aspects of medusan locomotion which I have discussed at the end of this paper.

Table 1

Systematic survey of medusae examined. * Indicates those forms dealt with in text

Order	Family	Genus and species
Hydrozoa		
Anthomedusae	Corynidae	<i>Sarsia tubulosa</i> *
	Tubulariidae	<i>Euphyesa flammnea</i> *
		<i>Euphyssora</i> sp.
		<i>Hybocodon</i> sp.
	Cladonematidae	<i>Cladonema californicum</i>
	Rathkeidae	<i>Rathkea</i> sp.
	Bougainvilliidae	<i>Bougainvillia multitentaculata</i> *
	Pandeidae	<i>Endocrypta huntsmani</i>
		<i>Leuckartiara nobilis</i> *
		<i>L. octona</i>
		<i>Neoturris pileata</i> *
		<i>Pandeia</i> sp.
	Polyorchidae	<i>Stomotoca atra</i> *
		<i>Polyorchis montereyensis</i> *
		<i>P. penicillatus</i>
		<i>P. haplus</i>
		<i>Scrippsiapacifica</i> *
Leptomedusae	Melicertidae	<i>Melicertum octocostatum</i>
	Mitrocomidae	<i>Halistaurocellularia</i> *
		<i>Mitrocomella polydiademata</i>
		<i>Obelia</i> sp.
		<i>Phialidium hemisphaericum</i> *
		<i>P. gregarium</i>
		<i>Eutonina</i> sp.
		<i>Aequorea aequorea</i>
Limnomedusae	Eutimidae	<i>Gonionemus vertens</i> *
	Aequoreidae	<i>Vallentinia</i> sp.
	Olinidiadidae	
Trachymedusae	Proboscidactylidae	<i>Proboscidactyla flavicirrata</i>
	Geryoniidae	<i>Liriope tetraphylla</i> *
	Rhopalonematidae	<i>Aglantha digitale</i> *
		<i>Colobonema</i> sp.
		<i>Crossota brunnea</i>
		<i>Pantachogon haeckeli</i> *
Narcomedusae	Aeginidae	<i>Aegina citrea</i>
	Solmarisidae	<i>Solmaris</i> sp.
	Cuninidae	<i>Solmissus marshalli</i> *
Siphonophora	Monophyidae	<i>Muggiaeaa</i> sp.
	Diphyidae	<i>Diphyes dispar</i> *
Scyphozoa		
Cubomedusae	Charybdeidae	<i>Charybdea rastoni</i> *
Coronatae	Atollidae	<i>Atolla</i> sp.
	Periphyllidae	<i>Periphylla</i> sp.
Semaeostomae	Cyaneidae	<i>Cyanea capillata</i> *
	Pelagiidae	<i>Chrysaora melanaster</i> *
	Ulmaridae	<i>Pelagia noctiluca</i> *
		<i>Aurelia aurita</i>
		<i>Phacellophora camtschatica</i>

The present classification of swimming mechanisms has been established largely on the basis of gross features of the mesogleal skeleton (Table 2). All attempts have been made to objectively disregard taxonomic affinities and to consider the locomotory system alone in establishing the classification. There is obviously a subjective element

involved in distinguishing between minor and major similarities and differences, but I have at least tried to argue the case for each category.

The techniques used in the preparation of specimens for study have been the same as those used in the analysis of *Polyorchis montereyensis* (GLADFELTER 1972), as have been those methods of analyzing locomotion. The animals used were collected: by nightlighting from the floats at the University of Washington's Friday Harbor Laboratories (USA); by snorkelling in Monterey Bay during autumn periods of zooplankton abundance; by trawling over Monterey submarine canyon; and the cubomedusae were obtained by divers off Santa Barbara, California, USA.

HYDROMEDUSAE

Several outstanding features distinguish the hydromedusan locomotory system from that of scyphomedusae: (1) hydromedusae are generally of much smaller definitive size (see for example KRAMP, 1961 for a synopsis of sizes of various species of hydro- and scyphomedusae); (2) a velum is present around the inner margin of the bell (= umbrella); and (3) exumbrellar and subumbrellar mesoglea (see GLADFELTER 1972a) are united except at the radial canals. As will be seen, these are fundamental differences which are responsible for major differences in the operation of the musculoskeleton and swimming ability. Among the hydrozoans surveyed, two major categories could be recognized: those with mesogleal joints of the *Polyorchis* type, and those without.

Anthomedusae: forms with joint systems of the *Polyorchis* type

Of all the medusae examined, only among the Anthomedusae is there a system of joints present such as that found in *Polyorchis*, that is, a system of eight adradial triangular prisms of highly deformable joint mesoglea which lie between the subumbrellar epidermis and the gastrodermal lamella. Eleven of the fourteen anthomedusan genera studied (in six of the seven families examined) have such a system, these are: *Sarsia*, *Euphysa*, *Euphysora*, *Hybocodon*, *Rathkea*, *Bougainvillia*, *Leuckartiara*, *Neoturris*, *Pandea*, *Polyorchis*, and *Scrippspia* (Table 2). A twelfth, *Endocrypta*, has twelve such joints (inter- und adradial), and a thirteenth, *Cladonema* has nine (perradial). The only anthomedusan genus in which they are lacking is *Stomotoca*. As in the case of *Polyorchis* these adradial joints occupy a very minor proportion of the bell mesoglea (e.g., about 1–2 % of the cross-sectional area at midbell in *Polyorchis*) yet they play a very significant role in the mechanics of bell deformation during swimming (GLADFELTER 1972a). Because of the widespread occurrence of this system among the Anthomedusae and its restriction to that order, this type of bell will henceforth be referred to as the anthomedusan type. The fundamental structure of the tissues and their topographical relationships are virtually identical in all forms with the anthomedusan type of bell. It is primarily in proportions of the bell and velum, and in concentrations of

Table 2
Classification of locomotory types in medusae

Hydromedusae:	
	(1) Exumbrellar and subumbrellar mesoglea united except at radial canals, (2) velum, (3) small size
(A) Anthomedusae:	
	(1) Relaxed bell with sides more or less parallel, (2) joints of soft mesoglea between subumbrellar epidermis and bell mesoglea
(1)	8 adradial joints
	(a) No exumbrellar creases <i>Polyorchis, Scrippia, Leuckartiara, Neoturris, Hybocodon, Rathkea</i>
	(b) With exumbrellar creases <i>Sarsia, Euphypha, Bougainvillia, Pandea</i>
	(c) With extremely thick soft bell <i>Euphysoora</i>
(2)	9 perradial joints (1) <i>Cladonema</i>
(3)	12 inter- and adradial joints (1) <i>Endocrypta</i>
(B)	Broad hydromedusae with marginal creases only
(1)	Strong swimming muscle
	(a) Small or no peduncle or apical mass <i>Gonionemus, Vallentinia</i>
	(b) Large peduncle and/or apical mass <i>Stomotoca, Proboscidactyla, Liriope</i>
(2)	Weak swimming muscle (Leptomedusae)
	(a) Small or no peduncle or apical mass <i>Melicertum, Halistaura, Mitrocomella, Obelia, Phialidium</i>
	(b) Large peduncle and/or apical mass <i>Eutonina, Aequorea</i>
(C)	Forms with rigid mesoglea and permanent exumbrellar creases
(1)	Radial symmetry (Rhopalonematidae) <i>Pantachogon, Crossota, Colobonema, Aglantha</i>
(2)	Radiobilateral symmetry <i>Diphyes, Muggiae</i>
(D)	Narcomedusae: rigid central disc and thin marginal skirt <i>Aegina, Solmaris, Somissus</i>
<hr/>	
Cubomedusae:	
	(1) Exumbrellar and subumbrellar mesoglea united only at interradii, (2) velarium, (3) bell tall with more or less parallel sides, (4) moderate size <i>Charybdea</i>
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Scyphomedusae (other than Cubomedusae):	
	(1) Subumbrella and exumbrella united only along certain radii, (2) no velum nor velarium, (3) large, broad umbrella
(A)	System of coronal and radial joints
(1)	Coronal muscle only
	(a) External coronal joint <i>Atolla</i>
	(b) Internal coronal joint <i>Pelagia, Chrysaora</i>
(2)	Coronal and radial swimming muscles
	(a) External coronal joint <i>Periphylla</i>
	(b) Internal coronal joint <i>Cyanea</i>
(B)	No joints except marginal creases <i>Aurelia, Phacellophora</i>

muscles and mesogleal fibers, that the locomotory systems of the various genera differ. The basic structure of the locomotory system which is common to all these forms is summarized below.

Four radial canals are present usually and these establish the perradial axes. The gastrodermal lamella is anchored to the radial canals perradially and to the subumbrellar epidermis interradially. Between the per- and interradii and the subumbrellar epidermis and gastrodermal lamella there are relatively thin areas of fiberless joint mesoglea, not distinguishable in its properties from that found in *Polyorchis*. The bell mesoglea, which lies peripheral to the gastrodermal lamella, is traversed by numerous radial fibers very similar in appearance to those of *Polyorchis* but varying considerably in thickness and number per unit area. These fibers are very sparse or absent in the apical region of the bell; they are concentrated along the joints as was seen in *Polyorchis* (GLADFELTER 1972a). The consistency of the bell mesoglea varies but is usually of moderate firmness. The swimming muscle consists of cellular processes of subumbrellar epidermal cells, arrayed circularly to form a sheet such as seen in *Polyorchis*. The morphology of these epitheliomuscular cells varies among different genera (see HERTWIG & HERTWIG 1878, KRASINSKA 1914) but the arrangement of fibers to form a sheet is virtually identical; the striated, circular epitheliomuscular processes lie side by side in staggered fashion to form a subumbrellar sheet continuous between radial canals and from the subumbrellar summit to the ring canal. This was determined by direct staining of the tissue with 0.5 % hematoxylin solution (GALIGHER & KOZLOFF 1964). A second stratum of radially oriented smooth muscle fibers is present in a few forms such as *Neoturris* (KRASINSKA 1914). Anchorage of the swimming muscle sheet to the bell mesoglea at the perradii and interradii occurs in all other genera in the same manner as in *Polyorchis*. While the basic morphology of the anthomedusan type of bell is constant through the group, there are a variety of interesting variations on this fundamental plan. A few are considered below.

Scrippssia pacifica TORREY 1909

From the point of view of locomotory function, *Scrippssia* is essentially a large *Polyorchis* and has, in fact, been treated as a subgenus of *Polyorchis* by SKOGSBERG (1948). Large individuals approach 100 mm in height. One feature present in the locomotory system of *Scrippssia* which was not seen in *Polyorchis* and which is most likely directly related to its greater size, is a series of thin horizontal folds of the subumbrellar epidermis. A small amount of mesoglea extends into the fold and the spacing between muscle processes is the same as in the remainder of the subumbrella. There are more than a dozen of these folds in each of the eight sectors of the bell; they are most closely spaced near the subumbrellar summit and become gradually farther apart to a point about one-fourth of the way up from the margin, where the terminate. The average height of each of these folds is about 0.5 mm. The surface area of the swimming muscle is thus usually increased by about 4 %. Since the swimming muscle is essentially a two-dimensional structure, as the bell increases in size the ratio of muscle area to mass of the bell decreases. Any means of increasing the muscle area

would clearly be of selective advantage. The relatively great force exerted by these folds as compared to other portions of the muscle can be seen from the scalloped outline imparted to the mesoglea on contraction; that is, these regions represent concentrations of muscle processes, and the umbrella is pulled inward at these points more than in other regions.

Neoturris pileata (FORSKAL 1775)

The bell of *Neoturris* (and *Leuckartiara* and some other anthomedusan genera as well) is beset by a peculiar apical projection, the function of which is unknown. This apical projection is set off from the lateral wall of the bell by a distinct exumbrellar furrow in each quadrant. Along each perradius, however, the apical mass sends a mesogleal buttress onto the upper part of the bell wall; the buttresses apparently serve to support the flimsy apical projection during swimming. Visible mesogleal fibers are absent from the apical projection.

The primary difference between the swimming system of *Neoturris* and that of *Polyorchis* lies in the thickness of the lateral wall of the bell, which is merely 2–3 % of the resting diameter at midbell in *Neoturris* compared to 12–15 % in *Polyorchis*. This extreme thinness of the bell wall is responsible for a very different deformation than occurs in *Polyorchis*. In a cross section through the midbell of a resting *Neoturris* the joints are barely visible as very thin lens-shaped areas. The subumbrellar swimming muscle (see KRASINKA 1914, for details) is anchored to the bell mesoglea per- and interradially and when the contracting swimming muscle pulls these points together it causes the bell mesoglea (which is more rigid than the joint mesoglea) to fold around the apex of each joint. Measurements made on axial photographs of the relaxed and contracted animal reveal that a 29 % reduction in the length of the swimming muscle (i.e., the circumference of the subumbrella at midbell) causes only a 2 % reduction in the perimeter of the medial surface of the bell mesoglea (or gastrodermal lamella) and a 6 % decrease in the exumbrellar perimeter due to folding. This means that virtually all the deformation in the bell mesoglea is in the form of folding (in *Polyorchis* folding and thickening were both important components of deformation about the polar axis). It appears likely that this deformation by folding alone occurs as a result of the unusual thinness of the bell wall relative to the bell diameter.

Euphypha flammea (LINKO 1905)

The bell of *Euphypha* is 1.5–2.0 times as high as its greatest diameter (which is located between midbell and the margin, but always above the latter). In lateral view, opposite walls are nearly parallel, so the bell appears nearly tubular. The manubrium, which bears the gonad, is quite large and when ripe occupies roughly 10–15 % of the volume of the relaxed subumbrellar cavity. Thickness of the bell wall tapers slightly from subumbrellar summit to the margin (where it is 60–70 % as thick as the subum-

brellar summit). At midbell the thickness of the wall is about 15 % of the diameter of the whole bell, as is the case of the bell of *Polyorchis montereyensis*. In polar view the exumbrellar wall is seen to be marked by a series of longitudinal grooves in the ad- and interradii (Fig. 2a, b). These grooves extend from the bell margin to the level of the subumbrellar summit. The circular apical joint and the eight adradial joints of the subumbrella can be seen respectively in Figures 1b and 2a, b.

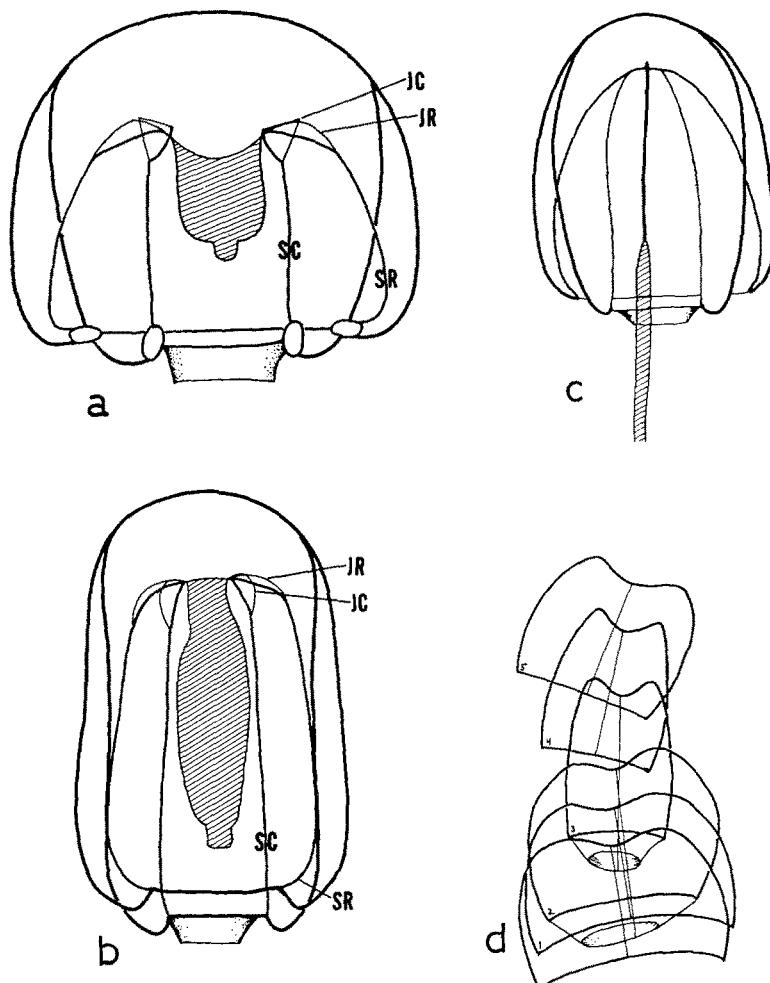


Fig. 1: *a* Lateral view of *Bougainvillia multitentaculata*, relaxed and contracted conditions superimposed; traced from cine sequences. JC = apical joint, contracted, JR = same, relaxed, SC = subumbrella, contracted, SR = same, relaxed. *b* Lateral view of *Euphysa flammnea*, relaxed and contracted conditions superimposed; traced from cine sequences; *c* Lateral view of *Sarsia*, relaxed and contracted conditions superimposed; traced from cine sequences. *d* Lateral views of subumbrellar outline of *Bougainvillia multitentaculata* during turning, showing actual change in position; traced from cine sequences. Time interval equals 1/8 sec. Notice initial asymmetry of both subumbrella and velum

On contraction the swimming muscle shortens (i.e., decreases the subumbrellar circumference) by about 50 % on the average. In polar view it is seen that the adradial joints function in the same way as the joints in *Polyorchis montereyensis*. Quite a different mechanism operates in the exumbrella however. The exumbrellar grooves act as fulcra for the folding of the bell wall on contraction. Thus in *Polyorchis* it was seen that the eight adradial joints provided a system whereby a 44 % decrease in the subumbrellar circumference produced only a 14 % decrease in the perimeter of the inner surface of the bell mesoglea. There was a 19 % decrease of the exumbrellar circumference, only slightly less than would be expected in the hypothetical jointless system discussed. In *Euphysa*, however, because of the folding of the exumbrellar wall around the exumbrellar grooves, the exumbrellar surface shortens by only 3–5 %, whereas the expected decrease in the absence of such grooves would be 20 %.

The action of the circular apical joint can be seen in Figure 1b. In going from a fully relaxed to a fully contracted condition, the distance along the subumbrellar wall underlying the joint decreases by about 30 %. This decrease, accompanied by the 50 % reduction in subumbrellar circumference which contraction brings about, causes an increase of more than 100 % in the thickness of the joint mesoglea between the contracting muscle sheet and the bell mesoglea of the subumbrellar summit (JR to JC). The thickness of the bell mesoglea opposite the apex of this joint increases by only a few percent during contraction. In other words, as the contracting muscle pulls the bell wall inward this apical joint is acting as a furcal point for the bending of the lateral bell wall around the apical mass. Below the level of the apical joint the subumbrellar wall remains the same length between relaxed and maximally contracted conditions, that is, the subumbrellar wall in this region simply straightens out as seen in lateral view.

On the average, contraction of the swimming muscle reduces the circumference of the subumbrellar cavity by slightly less than 50 %. Due to the large proportion of the subumbrellar cavity occupied by the manubrium and gonad, however, the volume of water in the subumbrellar cavity is reduced by about 80 % at maximum contraction. The contraction lasts about 1/4 sec and the recovery about 1/3 sec.

During a single contraction the bell of *Euphysa* increases its velocity by about 2.5 cm/sec (Table 3) by the time it is 75 % of the way through the contraction phase of the swimming cycle. *Euphysa*, however, swims with moderately long intervals between successive contractions (up to a second or more from the beginning of one contraction to the start of the next, during normal swimming). During recovery the velocity of the bell decreases so that the average velocity over a series of successive beats is only about 1 cm/sec.

The mechanism of turning in the long tubular bell of *Euphysa* is similar to that seen in *Polyorchis*. To demonstrate visually the action of the velum in directing a jet of water asymmetrically from the bell, milk was injected into the subumbrellar cavity of healthy individuals of *Euphysa* which were being filmed. The results, seen in Figure 3, show that the jet of water exits at an angle from the axis of the bell, creating a net force on the bell wall on the side which is to lie on the outside of the turn.

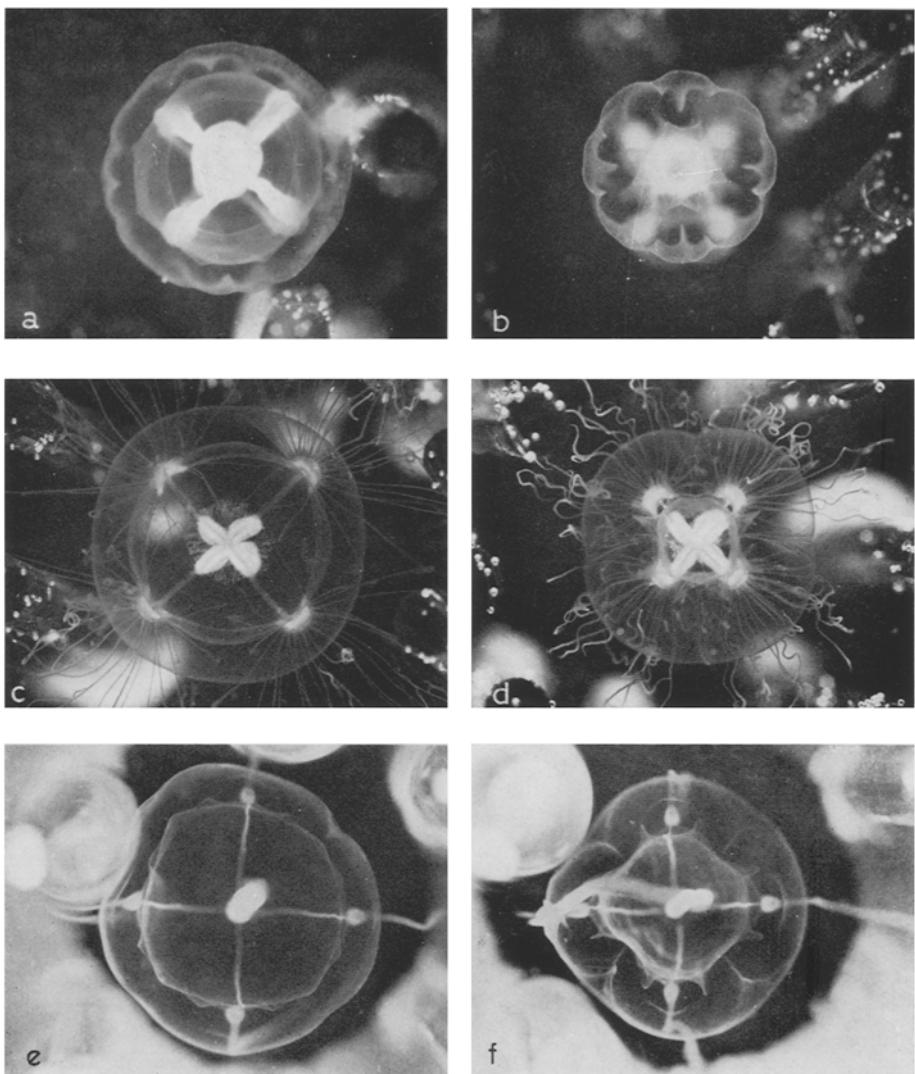


Fig. 2: Axial view of *Euphysa flammnea* in relaxed (a) and contracted (b) conditions, showing action of the adradial joints and exumbrellar creases. Axial view of *Bougainvillia multitentaculata* (c, d) and *Sarsia tubulosa* (e, f) in relaxed and contracted (d, f) conditions, showing action of the joints

Bougainvillia multitentaculata FOERSTER 1923

The relaxed bell of *Bougainvillia* is wider than it is high (the average height/width ratio is about 0.85) with the greatest width occurring anywhere between midbell and margin. The sides of the bell are roughly parallel as in most other Anthomedusae. The bell wall is thickest aborally near the apical joint and tapers to 20–30 % of this

toward the margin. At midbell the bell wall thickness is 12–15 % of the bell diameter at that level. A low peduncle bearing a broad manubrium projects into the subumbrellar cavity. The subumbrellar cavity is broader than it is high (height/width ratio 0.6–0.8), the widest point occurring anywhere between midbell and the margin.

The apical joint (Fig. 1a) resembles that of *Euphysa* very closely in both structure and function. The adradial joints differ somewhat in that in the polar view of the relaxed animal (Fig. 2c) they occupy low lens-shaped areas with no marked apices of the sort seen in the relaxed joints of *Polyorchis* and *Euphysa*. However, in the contracted state (Fig. 2d) they behave in an entirely typical manner. Exumbrellar creases are lacking in the relaxed bell, but four longitudinal interradial grooves develop on contraction; these act in the same way as those of *Euphysa*.

When *Bougainvillia* contracts, there is a 60 % decrease in the subumbrellar circumference at midbell (Fig. 2c, d). This large decrease is accompanied by a tremendous thickening of the bell wall at maximum contraction (85 % perradially, 103 % interradially and 105 % adradially). At the apices of the adradial joints this involves a 31 % increase in the thickness of the bell mesoglea and a 700 % increase in the thickness of the joint mesoglea. The real effectiveness of the adradial joints, however, is seen when one considers the circular component of deformation; a 57 % decrease in length (circumference) of the swimming muscle at midbell produces only a 10 % decrease in the perimeter of the inner surface of the bell mesoglea, as the bell mesoglea is bent around the apex of the joint by the swimming muscle anchored to it at the per- and interradii. Swimming statistics for *Bougainvillia* are tabulated in Table 3.

Turning is accomplished by means partly different than those in *Polyorchis*. In *Bougainvillia* contraction begins strongly in the marginal half of one side of the bell (right side, Fig. 1d) while no contraction occurs on the opposite side (left). After this strong initial contraction by the right side, the left begins contracting, and by the middle of the contraction phase it is contracting at a greater rate than the right. At about this point the bell begins to turn clockwise (toward the right). The circular muscle of the velum contracts at the same times as the subumbrellar muscle contracts. During the initial phase, when the swimming muscle of the right side is contracting more strongly, the circular muscle of the velum on the same side also contracts more strongly causing the velum on this side to widen and also to stiffen, so it is not pushed outward so much during expulsion of water. The two actions effect turning thus: (1) the initial asymmetry of the velum causes it to act as a nozzle directing water to the right of the axis of the bell, creating a force tilting the bell apex toward the right; (2) during the later part of the contraction phase the swimming muscle of the left side contracts more strongly, and the force created by the exiting water on that side further turns the bell clockwise. During recovery the bell continues to turn. Unilateral or asymmetrical contraction of the swimming muscle was not very pronounced in *Polyorchis* (GLADFELTER 1972a); it evidently provides a more effective means of turning in a broad flat medusa, and the other method is encountered repeatedly in medusae of this sort (see other Hydromedusae and Scyphomedusae).

Sarsia tubulosa (SARS 1835)

The swimming system of *Sarsia* operates in essentially the same way as that of *Bougainvillia*, with one exception (Fig. 1c): there is no circular apical joint. This is probably correlated with the absence of a broad peduncle or a flat area at the top of the subumbrellar cavity such as seen in *Polyorchis*, *Euphysa*, etc. The adradial and exumbrellar joints act in the same way as those of *Bougainvillia* (Fig. 2e, f).

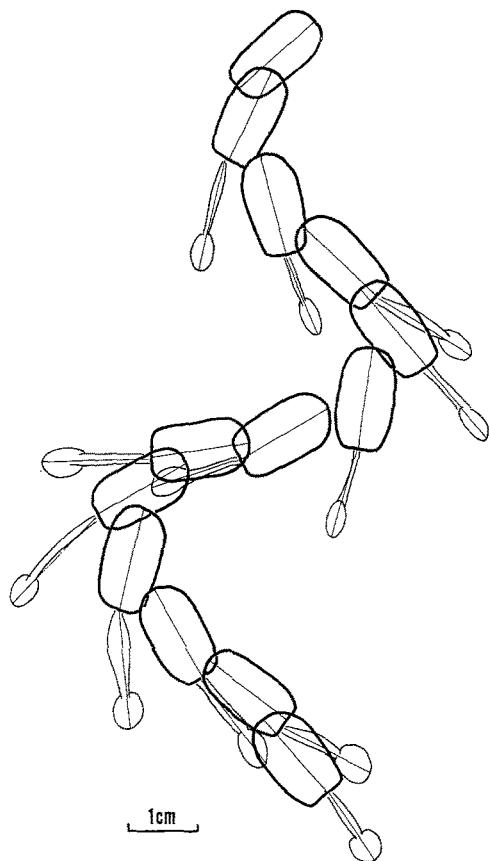


Fig. 3: Lateral view of *Euphysa flammea* during turning, after milk has been injected into the subumbrellar cavity to show the direction of expulsion of subumbrellar water during the early part of the contraction. Each outline shows the subumbrella shortly after the beginning of a contraction. The jet of milky water in each case is directed at an angle to the axis of the bell such that a net force is exerted on the wall on the outside of the turn. Traced from cine sequences

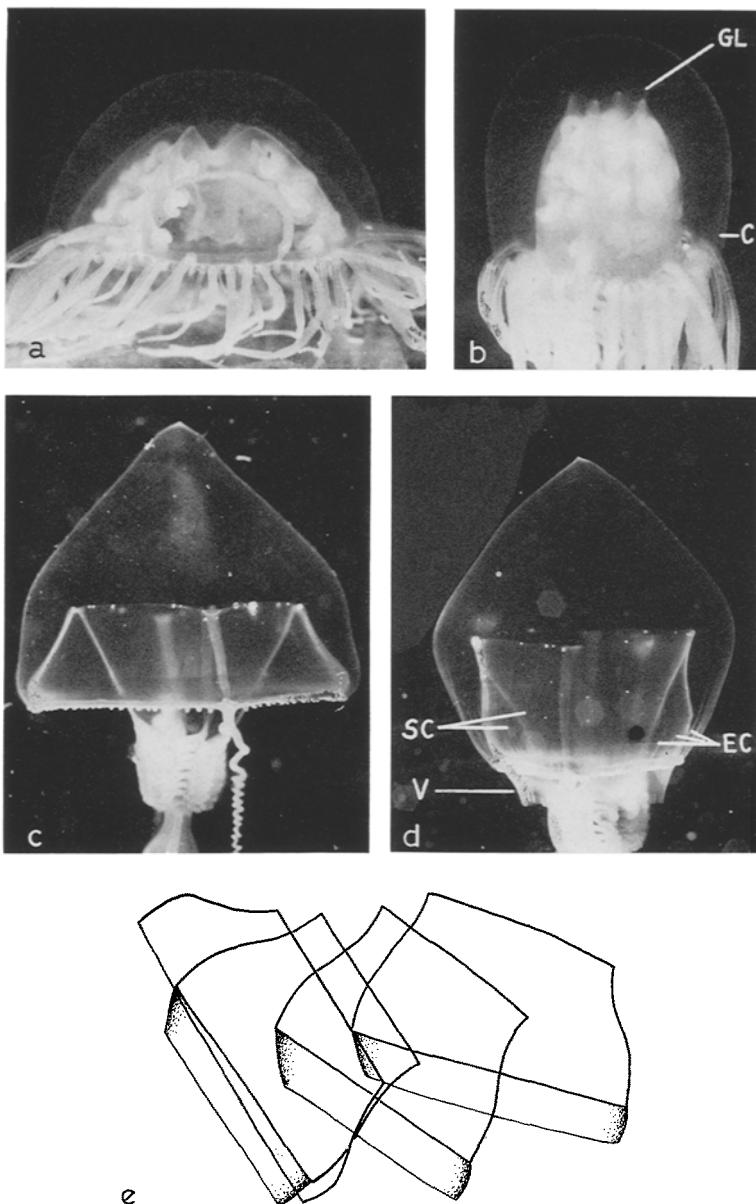


Fig. 4: a, b Lateral view of *Gonionemus vertens* in relaxed (a) and contracted (b) conditions, showing the exumbrellar marginal creases that develop on contraction. C = marginal crease, GL = gastrodermal lamella at subumbrellar summit. c, d Lateral view of *Stomotoca atra* in relaxed and contracted (d) conditions, showing exumbrellar and subumbrellar creases that develop on contraction. EC = exumbrellar creases, SC = subumbrellar creases, V = velum. e Lateral view of subumbrellar outlines of *Stomotoca atra* during turning; traced from cine sequences. Time interval equals 1/2 sec except for first interval, which equals 1/8 sec

Medusae with broad bells and marginal creases

Medusae with broad bells and no joint system other than marginal creases occur in a number of orders: Anthomedusae, Leptomedusae, Limnomedusae and Trachymedusae. *Gonionemus* will serve as a prototype of this group. In all other forms studied, the locomotory system operates in essentially the same way as in *Gonionemus*, differing mainly in such matters as proportions, rates of contraction, magnitude of contraction, velar effectiveness, velocity, etc. The Leptomedusae differ from the other forms in this group in the nature of their swimming muscle and the relative flatness of their bells, and will be considered last.

Gonionemus vertens AGASSIZ 1862

The bell of *Gonionemus* is dome-shaped, its greatest diameter being 1.5–2.0 times its height. The bell is thickest at the apex and tapers gradually toward the margin where it is about half as thick as at the subumbrellar summit. The sides are not roughly parallel as in the case of the Anthomedusae just studied, but slant markedly outward from apex to margin; the bell is always widest at the margin when the animal is in a relaxed condition (Figs 4a, b, 7a). The greatest width of the subumbrellar cavity averages slightly more than twice its height.

The histological structure and relationships of the various tissues are fundamentally the same as in *Polyorchis* with the following exceptions:

(1) There is no detectable region of soft joint mesoglea between the gastrodermal lamella and the subumbrellar epidermis (with the possible exception of the region of the subumbrellar summit; see later discussion). Thus the system of joints characteristic of Anthomedusae is lacking.

(2) The bell mesoglea has a consistency similar to that of *Polyorchis*. The radial mesogleal fibers, however, are distributed uniformly around the bell circumference, and are not concentrated along certain radii. They are densest near the margin and decrease in concentration toward the apex, where they are very sparsely distributed (Fig. 7a).

(3) The swimming muscle forms four sheets of circularly oriented muscle between the four radial canals, extending from the base of the peduncle to the ring canal as in *Polyorchis*. The epitheliomuscular sheet, however, is anchored to the bell mesoglea around the entire circumference of the umbrella, not just per- and interradially as in *Polyorchis*. The actual contractile elements are bandlike as in *Polyorchis* and the epitheliomuscular cells of the swimming muscle of the two species are very similar (see FRASER 1962).

(4) The velum is slightly stiffer than that of *Polyorchis* and is relatively less wide (about 25% of the radius of the relaxed bell aperture in *Gonionemus*). In other respects the velum is the same in the two forms; i.e., there is a system of radial and circular mesogleal ridges and the velar skeleton is constricted at its base.

On contraction, the lateral wall of the bell is drawn inward uniformly around the circumference. The greatest displacement is at the margin, with an average de-

crease in subumbrellar circumference of slightly over 50 % (Table 3); the least displacement is at the subumbrellar summit, with a corresponding decrease in circumference of 30 %. In lateral view, the subumbrellar wall undergoes no oral-aboral

Table 3

Swimming statistics of various medusan species. Abbreviations: A = Bell height (cm); B = % Reduction in average subumbrellar circumference; C = % Reduction in subumbrellar volume; D = Duration of contraction phase (sec); E = Duration of recovery phase (sec); F = Ratio of velar aperture area to area at base of velum, at maximum contraction; G = Initial velocity (cm/sec); H = Maximum velocity (cm/sec); I = Increase in velocity (cm/sec); J = Average velocity during complete contraction cycle (cm/sec); K = Acceleration during contraction (cm/sec²)

A	B	C	D	E	F	G	H	I	J
<i>Gonianemus vertens</i>									
*									
2.5	51	52	0.18	—	—	1.6	10.5	8.9	4.9
2.5	52	52	0.16	—	—	1.9	9.5	7.6	4.5
2.5	51	53	0.15	—	0.67	0.0	6.1	6.1	2.4
2.5	47	58	0.17	—	0.22	4.9	11.0	6.1	6.0
2.7	52	62	0.27	—	0.46	0.9	6.4	5.5	3.4
2.7	53	59	0.26	—	0.70	1.8	8.9	7.1	4.4
2.7	49	54	0.24	—	0.50	1.3	8.9	7.6	5.0
2.0	52	57	0.16	—	—	0.0	7.1	7.1	3.4
2.0	53	66	0.19	—	—	2.7	11.8	9.1	5.9
2.0	51	61	0.17	—	—	1.5	8.4	6.9	5.4
2.0	54	61	0.19	—	0.45	3.0	10.7	7.7	5.1
∅	51	58	0.19	—	0.50	1.8	9.0	7.5	4.5
<i>Stomotoca atra</i>									
1.3	31	55	0.25	0.27	0.55	0.5	2.7	2.2	1.3
1.3	37	53	0.21	0.29	0.56	0.9	2.0	1.1	1.3
1.3	46	60	0.23	0.29	0.52	1.3	3.0	2.7	—
1.3	44	58	0.17	0.30	0.78	1.7	4.0	2.3	2.1
1.1	37	50	0.25	0.33	0.54	1.1	2.5	1.4	1.4
1.1	43	52	0.25	—	0.60	1.8	3.8	2.0	—
∅	40	55	0.23	0.30	0.59	1.2	3.0	1.8	1.5
<i>Liriope</i>									
1.5	32	56	0.13	0.18	0.46	1.9	4.8	2.9	3.6
1.5	27	42	0.14	0.13	0.38	3.0	5.0	2.0	3.8
1.5	28	46	0.14	0.16	0.37	2.1	6.5	4.4	3.2
1.5	26	42	0.14	0.16	0.39	2.2	4.7	2.5	3.3
1.5	30	46	0.13	0.13	0.36	2.4	6.6	4.2	5.0
1.5	30	58	0.15	0.13	0.45	1.7	4.1	2.4	3.5
1.5	25	40	0.14	0.15	0.42	1.3	3.6	2.3	2.6
∅	28	47	0.14	0.15	0.40	2.1	5.0	2.9	3.6
<i>Phialidium hemisphericum</i>									
1.8	22	31	0.25	0.31	0.52	1.2	3.0	1.8	2.0
2.0	28	36	0.27	0.35	0.76	0.7	3.3	2.6	1.9
2.0	26	32	0.29	0.35	0.70	0.6	2.6	2.0	1.7
2.0	26	34	0.25	0.33	0.61	1.0	2.9	1.9	1.9
1.8	23	32	0.28	0.34	0.68	0.4	1.6	1.2	1.2
∅	25	33	0.27	0.33	0.66	0.8	2.7	1.9	1.7

A - Diameter of bell at margin when relaxed

B through J - These headings are the same as those in Table VI

* These values for *Gonianemus* represent decrease at the bell margin

Table 3 (continued)

A	B	C	D	E	F	G	H	I	J	K
<i>Euphypha flammnea</i>										
1.2	51	84	0.28	0.36	0.36	1.8	2.6	0.8	1.3	4.0
1.2	36	77	0.24	0.31	0.35	0.0	3.8	3.8	—	21.0
1.0	45	73	0.26	0.30	0.29	0.8	3.4	2.6	2.0	12.0
1.0	44	75	0.26	0.30	0.40	0.6	3.0	2.4	1.5	12.0
1.2	49	81	0.28	0.34	0.41	0.6	3.5	2.9	1.9	14.0
Ø	45	78	0.26	0.32	0.36	0.8	3.3	2.5	1.3	13.0
<i>Bougainvillia multotentaculata</i>										
0.7	45	78	0.24	0.34	0.58	0.6	2.4	1.8	1.1	9.0
0.8	49	74	0.25	0.34	—	1.0	2.7	1.7	1.6	9.0
0.7	51	78	0.28	—	—	1.0	2.4	1.4	—	6.0
0.7	42	65	0.25	0.36	0.47	0.2	1.3	1.1	0.5	5.0
0.8	45	74	0.25	—	0.42	—	—	—	—	—
0.8	36	67	0.23	0.38	0.45	1.1	3.3	2.2	1.9	11.0
0.8	47	70	0.26	0.36	0.48	0.8	2.7	1.9	1.5	9.0
Ø	45	72	0.25	0.36	0.48	0.8	2.5	1.7	1.3	8.0
<i>Charybdea rastoni</i>										
3.5	17	26	0.2	—	0.42	4.6	8.5	3.9	5.7	—
3.5	33	52	0.2	—	0.20	4.1	8.6	4.5	7.5	—
3.5	23	35	0.2	—	0.36	3.8	8.6	4.8	6.0	—
3.5	31	50	0.2	—	0.26	4.6	9.3	4.7	5.5	—
Ø	26	41	0.2	—	0.31	4.3	8.7	4.4	6.2	—

shortening as the sides are pulled inward. At maximum contraction the sides of the bell become parallel (Fig. 4a, b), and the diameter at the margin is usually slightly less than that of the region just above it. Most of the deformation consists of circular compression and radial thickening of the bell mesoglea. On careful inspection of Figures 4a, b and 7a, however, it is seen that a series of definite grooves develops in the exumbrellar side of the marginal third of the lateral bell wall. These grooves are regularly spaced, alternating with the tentacles, and provide an auxiliary means of deformation of the marginal region where the proportional decrease in circumference is greatest; that is, these grooves ease the burden imposed on the contracting muscle by the elastic forces generated in the compressed mesoglea by allowing the mesoglea in this region to fold. The second auxiliary means of deformation is also seen in Figures 4a, b and 7a in the region of the subumbrellar summit: radial mesogleal fibers here anchor the gastrodermal lamella to the exumbrella so that this region can act as a fulcrum for the flexing of the lateral bell wall inward. The thickness of the mesoglea between the exumbrella and the gastrodermal lamella remains constant during contraction, but the subumbrellar muscle pulls away from the gastrodermal lamella as the lateral wall is bent inward. It is most likely that a small amount of joint mesoglea occupies this small space at the subumbrellar summit, and that the circular apical joint here is homologous to that of *Polyorchis*. It will be noticed in this case, as was seen in *Polyorchis* (and in fact all other Hydromedusae examined), that the location of radial mesogleal fibers corresponds to the region of deformation of the bell; they are virtually absent in the undeformed apical region (Figs 7a-d).

In *Gonianemus* contraction normally begins at the margin of the bell and proceeds toward the subumbrellar summit. The velum contracts along with the subumbrellar swimming muscle, reducing the area of the bell aperture by an average of about 50 %. The contraction proceeds roughly as in *Polyorchis*, beginning slowly, passing through a period of maximum rate of contraction and slowing toward the end of the contraction. Generally 50–60 % of the water in the subumbrellar cavity is expelled during a contraction which lasts an average of slightly less than 0.2 sec in individuals 2.0 till 2.5 cm in diameter at the margin (Table 3). During the powerful contraction the bell undergoes an immense acceleration of about 45–50 cm/sec², increasing its velocity by 6–7 cm/sec three-quarters of the way through (Table 3). After maximum velocity is reached the bell decelerates for the remainder of the contraction and during the recovery period.

Although the velum only reduces the area of the bell aperture by an average of 50 % at maximum contraction, it plays a disproportionately large role in the swimming of *Gonianemus*. When the velum here was removed (as was done in *Polyorchis*) and the animal was allowed to recover so that deformation of the bell on contraction was normal, the maximum velocity achieved was never more than 3 cm/sec and was often less than 1 cm/sec. Since removal of the velum only doubles the area of the contracted aperture and leaves other parameters of the contraction essentially unchanged, the greater than fourfold decrease in maximum velocity in the dekulimized animal indicates that the velum plays some role beyond simply reducing the area of the aperture by 50 % (which would only double the velocity at 100 % efficiency). It is possible that the elongation and slight tapering of the subumbrellar cavity brought about by the extended velum makes the flow of water from the subumbrellar cavity much less turbulent, thus increasing its effectiveness as a propulsive agent.

Turning is accomplished in *Gonianemus* in the same way as in *Bougainvillia*. At first, contraction begins strongly on one side of the bell while no contraction occurs on the other side (Fig. 5c). After several hundredths of a second contraction begins on the opposite side but is of slight magnitude. Then contraction on the lagging side becomes stronger than that on the side which began the contraction, and the bell begins to turn with the now more strongly contracting side on the outside of the turn. The action of the velum during turning is presumably similar to that of *Bougainvillia*, but it was not observed or recorded in *Gonianemus* because of the tentacles. This mode of turning is considerably more effective than the method relying strictly on velar action which occurs in *Polyorchis*, for the turning radius in *Gonianemus* (and *Bougainvillia*, etc.) is much smaller.

Stomotoca atra AGASSIZ 1862 and *Liriope tetraphylla* (CHAMISSO & EYSENHARDT 1821)

While *Stomotoca* and *Liriope* swim in the same way as *Gonianemus*, they differ from *Gonianemus* in possessing a large peduncle depending from the top of the subumbrellar cavity (Figs 4e, 7b, d), around which the lateral wall of the bell flexes on contraction. As in *Gonianemus*, the radial mesogleal fibers converge on the subumbrellar summit and are located only in the region of the bell deformed during swim-

ming. The exumbrellar marginal creases are clearly seen in *Stomotoca* in Figures 4e and 7b, and in *Liriope* in Figure 7d. These creases are not evident in the relaxed medusa but always appear in the same position in the contracted bell, alternating with the cirri along the margin. In *Stomotoca* a series of fine longitudinal wrinkles develops in the gastrodermal lamella in the contracted bell (Fig. 4d), evidently serving the same function as the adradial joints in *Polyorchis*; that is, when the swimming muscle shortens on contraction, this fine folding of the gastrodermal lamella along the inside of the bell mesoglea provides a means whereby the mesoglea need not be circularly compressed to such a great degree, some of the deformation being in the form of folding. (Though this was not seen in *Gonianemus* its presence there cannot be excluded.)

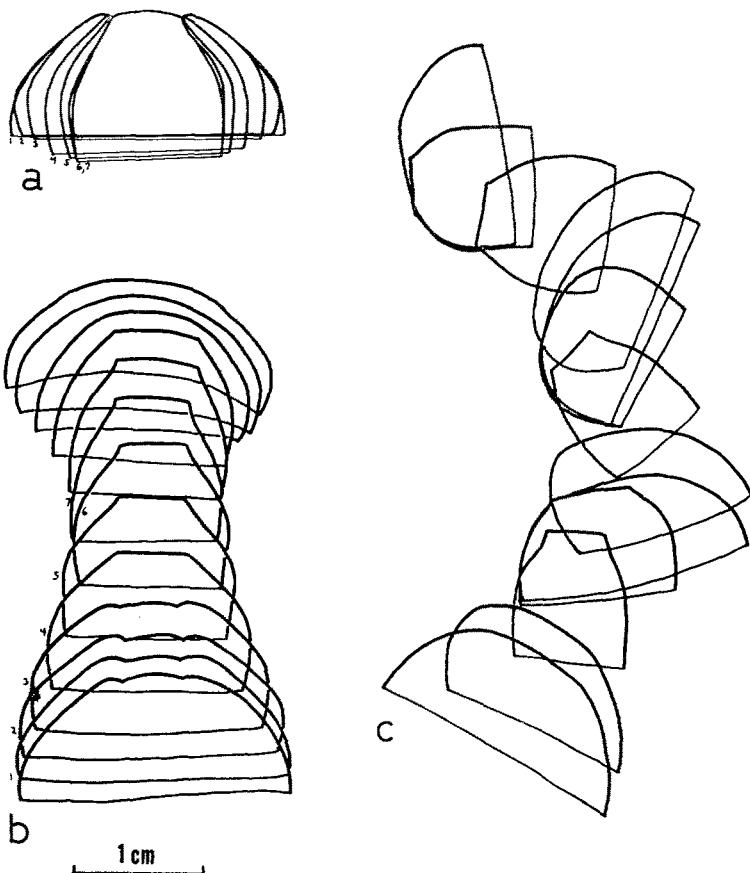


Fig. 5: Lateral views of contraction and recovery of the subumbrella of *Gonianemus vertens*; traced from cine sequences. Time interval equals 0.4 sec. a Outlines of contracting subumbrella superimposed to show relative amount of contraction during each interval. b Outlines of contracting and expanding subumbrella showing actual change in position during swimming; outlines of contraction phase are the same as those in a. c Lateral views of subumbrellar outline of *Gonianemus vertens* during turning; traced from cine sequences. Time interval equals 1/8 sec

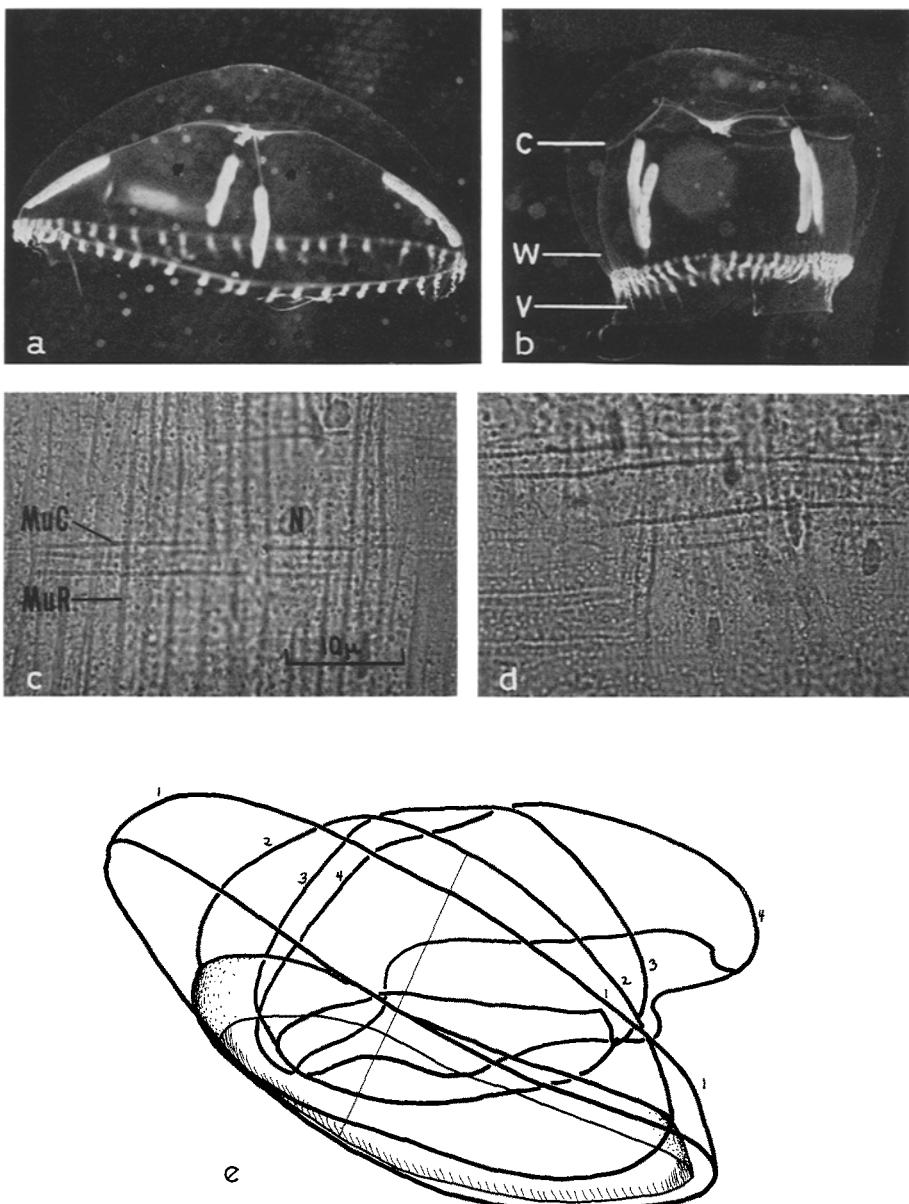


Fig. 6: Lateral views of *Phialidium hemisphaericum* in relaxed (a) and contracted (b) conditions, showing marginal creases and irregular creases of gastrodermal lemella in contracted condition. C = crease of gastrodermal lamella, V = velum, W = marginal wrinkles. c, d Swimming muscle of *Phialidium hemisphaericum*, showing sparse distribution of circular striated fibers and radial fibers. c Near the subumbrellar summit. d Near the margin. MuC = circular muscle fiber (note striations), MuR = radial muscle fiber, N = nucleus of epithelial cell. e Oblique views of the subumbrella of *Halistura cellularia* from somewhat below the level of the opening of the subumbrellar cavity during turning; traced from cine sequence. Successive outlines are numbered. Time interval equals 5/18 sec

Swimming statistics of *Stomotoca* and *Liriope* are given in Table 3. During swimming the presence of the peduncle (and gonad in *Stomotoca*) greatly decreases the area through which water exits from the subumbrellar cavity. In Figure 4d, for example, the cross-sectional area of the gonad at the level of the velar aperture is almost 50% of the total area through which water exits. This does not seem to increase the relative effectiveness of *Stomotoca* as a swimmer, however, as can be seen in Table 3. The relatively large mass of inert bell mesoglea and gonad compared to the small locomotory portion of the bell is probably partly responsible for this.

Turning is achieved in the same way as in *Gonianemus* and *Bougainvillia* (Fig. 4e).

Leptomedusae: weak swimmers with weakly developed swimming muscle

Phialidium hemisphericum (L.) and the Leptomedusae in general differ in several important respects from the forms just examined. In the first place the bell is relatively thinner and flatter than the bells of *Gonianemus*, *Stomotoca*, and *Liriope*. The velum is very thin and flimsy. Most important are differences in the swimming muscle. In *Polyorchis*, the other Anthomedusae, *Gonianemus*, *Liriope*, etc., the strongly developed striated muscle processes are all circularly arranged and lie side by side to form a strong continuous sheet. In contrast, the circular muscle processes in *Phialidium* are widely spaced and weakly developed and form a loose mesh with equally loosely arranged radial muscle fibers (Fig. 6c, d). No striations were detected in the radial fibers of formalin fixed *Phialidium*, though the radial fibers of the leptomedusan *Obelia* are striated (CHAPMAN 1968). The radial fibers in *Phialidium* are more densely arranged toward the apex of the bell. Detailed observations of muscle action in *Phialidium* are lacking, but in such a relatively flat medusa, contraction of the radial fibers would increase the inward curvature of the bell and thus increase the effectiveness of the contracting circular muscle (the more parallel the sides of the bell, the more efficient is the contracting circular muscle; see GLADFELTER 1972b). At maximum contraction, in addition to the series of exumbrellar creases in the mesoglea near the margin (Figs 6a, b, 7c), the gastrodermal lamella becomes irregularly creased near the summit of the bell, and in fact there is a very sharp bending about midawy between the manubrium and the proximal end of the gonad.

Leptomedusae in general are slower swimmers than most of the other medusae examined; those recorded in Table 3 were exceptionally vigorous specimens. On the other hand, if the radius of curvature of the path of turning is taken as an index of effectiveness of turning in medusae, then the Leptomedusae are indeed effective turners, virtually rotating around a point (Fig. 6e).

Leptomedusae often tend to swim persistently either up or down. If a leptomedusan in the process of swimming in one direction or the other is turned 180° by an observer and then released, it usually executes an immediate turn, and continues swimming in its original direction. This very characteristic leptomedusan behavior pattern was not observed in any other hydrozoans.

The recovery phase in most Leptomedusae is characterized by the irregular conformation assumed by the bell. That is, in polar view the outline of the bell does not

remain circular during recovery but becomes irregularly folded and scalloped. This is certainly a result of the broad, thin shape and relatively soft consistency of the bell, which is more subject to deformation by unevenly distributed forces in the water than are the firmer, thicker medusae.

Forms with rigid bells and permanent exumbrellar creases

The forms included in this section exhibit the highest development of swimming found in medusae. This category includes the siphonophore *Diphyes* and two members of the trachymedusan family Rhopalonematidae, *Pantachogon* and *Aglantha*. These are extremely powerful swimmers with very stiff mesoglea which is necessary to provide support for the action of their highly developed swimming muscle. The exumbrellar is marked by a series of radial or longitudinal grooves which act during contraction.

Diphyes dispar CHAMISSO & EYSENHARDT 1821

Siphonophores are aggregations of medusoid and polypoid members (or "persons") of several types, each of which is specialized for one or more particular functions. In two of the three suborders of siphonophores (Physonectae and Calycophora), one to many medusoid persons (nectophores) are specialized for the sole function of locomotion. They are prominent members of the colony and are placed at or near its functional anterior end. The region bearing the nectophores is the nectosome; the remainder of the colony (the siphonosome) consists of a highly contractile tube along which serially repeated groups of polypoid and medusoid persons are spaced.

The nectosome of *Diphyes* consists of two nectophores slightly different in form but fundamentally alike. The medusoid derivation of these nectophores is quite evident. In contrast to the hydromedusan bells hitherto considered, however, each nectophore has a pronounced radiobilateral symmetry. A sagittal plane divides each bell into equal halves (left and right), and dorsal and ventral surfaces can be established arbitrarily for ease of orientation (Fig. 8). The subumbrellar cavity lies in the dorsal part of each nectophore. A third cavity, the hydroecium, occupies the ventral portions of the nectophores. The portion of the hydroecium in the anterior nectophore is completely enclosed by the wall of the nectophore except at its posterior end. That part of the hydroecium formed by the posterior nectophore is open at the anterior and posterior ends as well as along the entire ventral surface (Fig. 8). The entire siphonosome can be withdrawn into this capacious cavity.

Both bells bear one low dorsal ridge, two lateral ridges, and two ventral ridges. Between the dorsal and lateral ridges, and the lateral and ventral ridges are exumbrellar creases. In the anterior nectophore the crests of the ridges begin at the very apex of the bell and terminate in processes which extend posteriorly beyond the velar aperture; on the posterior nectophore these crests are limited to the portion not en-

closed by the hydroecium of the anterior bell. The creases between ridges extend forward from the rear margin of each bell to a level slightly behind the summit of the subumbrellar cavity. The bell wall between the subumbrellar cavity and the hydroecium is quite thin (Fig. 8, 9c, d).

The mesoglea of *Diphyes* is extremely rigid. As in other medusae it is traversed by conspicuous radially oriented fibers, very densely arrayed. These fibers are uni-

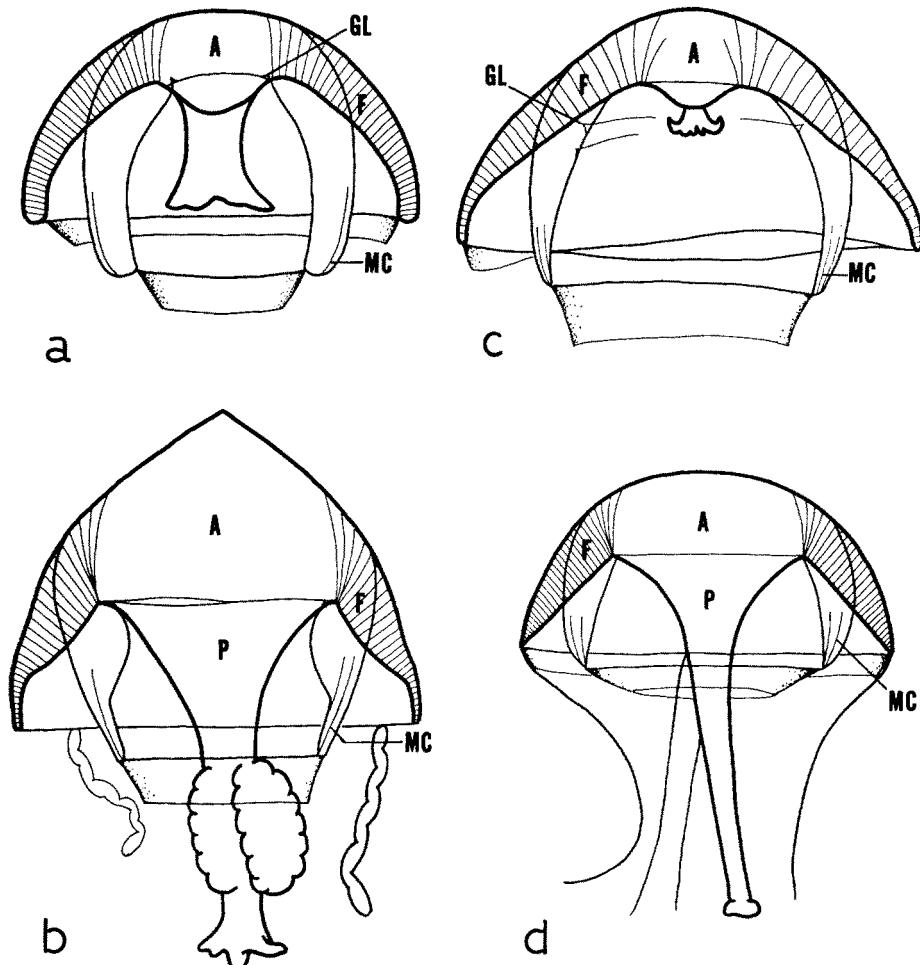


Fig. 7: *a* Lateral view of *Gonionemus vertens*, relaxed and contracted conditions superimposed, showing distribution of radial mesogleal fibers; traced from cine sequence. A = apical region devoid of radial mesogleal fibers, F = radial mesogleal fiber, GL = gastrodermal lamella, MC = marginal crease. *b* Lateral view of *Stomotoca atra*, relaxed and contracted conditions superimposed; traced from cine sequence. P = peduncle. *c* Lateral view of *Phialidium hemisphaericum*, relaxed and contracted conditions superimposed; traced from cine sequences. *d* Lateral view of *Liriope tetraphylla*, relaxed and contracted conditions superimposed; traced from cine sequence

formly distributed around nearly the whole circumference of the subumbrella, with greater density only in the thin region between the subumbrellar cavity and the hydroecium. In both bells between the subumbrella and the exumbrella there are two regions: an inner region of radial fibers and an outer region where the fibers are not

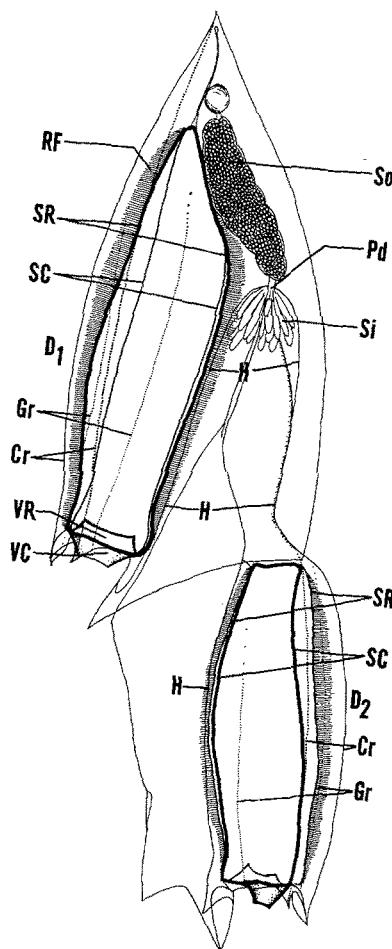


Fig. 8: Anatomy of swimming structures of *Diphyes dispar* in lateral view; traced from cine sequence. Cr = exumbrellar crest, D₁ = dorsal surface of anterior nectophore, D₂ = dorsal surface of posterior nectophore, Gr = exumbrellar grooves, H = hydroecium, Pd = peduncle by which posterior nectophore is attached to anterior, RF = radial mesogleal fibers, Si = base of siphonosome, So = somatocyst, SC = subumbrellar wall, contracted, SR = subumbrellar wall, relaxed, VC = velum, contracted, VR = velum, relaxed

easily discernible by dissecting or a compound microscope. There is no morphological boundary evident between the two regions, but the line is quite distinct. The fibers reach the exumbrella only in the regions of the four creases; they extend about $\frac{2}{3}$ of the distance from the subumbrella to the exumbrella opposite the crest of the dorsal

and lateral ridges. In the ventrolateral regions the fibers are about as long as they are beneath the dorsal and lateral crests. Those ventrolateral fibers nearer to the exumbrellar wall curve slightly towards this; those fibers nearer to the wall of the hydroecium curve toward that. In the thin region between subumbrella und hydroecium the fibers occur in denser concentration than elsewhere. Fibers are absent in the mesoglea lateral and ventral to the hydroecium. This account of radial fiber distribution applies best to the midbell region. In both nectophores, towards the ends of the subumbrellar cavity the fibers become shorter, and they disappear altogether at the very summit of the subumbrella (Fig. 8).

Two muscles are involved in swimming: the subumbrellar muscle (Fig. 9a) and the velar muscle. The subumbrellar muscle is a sheet of circularly oriented striated fibers in closely packed array, continuous around the entire subumbrellar circumference and extending from the subumbrellar summit to near the bell margin where a gap separates it from the circular striated muscle of the velum. There are no longitudinal fibers in the subumbrellar muscle such as were reported by MACKIE (1964) in *Nanomia*. The subumbrellar swimming muscle is anchored to the mesoglea around the entire circumference, not just along certain radii, as far as could be determined by numerous trials of carefully peeling the muscle sheet from the mesoglea. The velar muscle consists of a circular striated subumbrellar component, and a radial exumbrellar component. The thin mesoglea between the two is very rigid. The radial exumbrellar fibers are uniformly distributed around the circumference: no concentrations such as the fibers of CLAUS reported in *Nanomia* (MACKIE 1964) and other physonects (Fig. 9b) were discerned in *Diphyes*.

The nectosome of *Diphyes* is a rigid unit. A forward projecting process of the posterior nectophore is snugly seated in the hydroecium of the anterior nectophore so that the lateral ridges of the posterior one are confluent with the ventral ridges of the anterior. The anterior process of the posterior bell tapers to a narrow stalk of tough mesoglea by which the two bells are connected at the summit of the hydroecium. The anterior-posterior axis of the nectosome can be defined as the line transecting the apex of the anterior nectophore and the center of mass of the nectosome (as determined by suspending the nectosome from the apex of the anterior bell and describing a vertical line through it). The two nectophores are positioned such that their dorsal surfaces and the major portion of each subumbrellar cavity are on opposite sides of the main axis. The axis of each nectophore (the line running through the center of the subumbrellar cavity) is oblique to the main nectosomal axis by about 6–7°, but directed oppositely (Fig. 8). The nectosome is thus more or less bilaterally symmetrical with one subumbrellar cavity directed above the frontal plane and one below it.

Considered from an axial or cross-sectional point of view, the two nectophores of *Diphyes* function in a very similar manner, hence only the posterior nectophore will be considered here. The swimming muscle is anchored around the entire subumbrellar circumference by uniformly distributed radial mesogleal fibers. As the swimming muscle contracts, each of the four longitudinal creases, or joints, serves as a line of weakness or a fulcrum between the four relatively rigid units constituting the bell (i.e., one dorsal, two lateral, and one ventral unit; Fig. 9c, d). These exumbrellar joints allow for the bending of these four units around their apices by allowing the contract-

ing swimming muscle to straighten out between the regions underlying the longitudinal crests. In other words, as the swimming muscle contracts it tends to straighten out (in cross section) beneath regions where the overlying mesoglea is differentially weak, i.e., beneath the exumbrellar creases. On contraction the basal length of each of the four units of the bell (seen in cross section) is compressed; this causes the exumbrellar sides

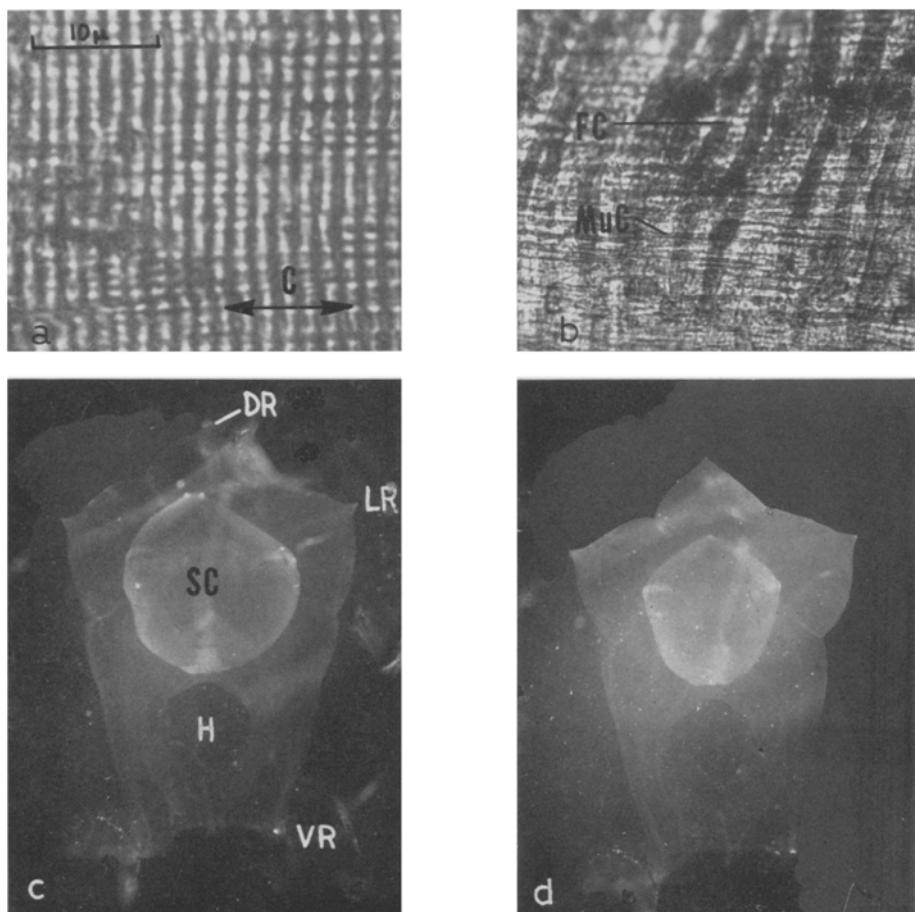


Fig. 9: *a* Subumbrellar swimming muscle of *Diphyes dispar*, showing alignment of striations of adjacent contractile processes. *C* = circular direction. *b* Fibers of CLAUS of an unidentified physnec siphonophore with the capabilities of both forward and backward swimming. *FC* = fiber of CLAUS, *MuC* = circular spinning muscle of the velum. *c, d* Axial view of the posterior nectophore of *Diphyes dispar*, in relaxed (*c*) and contracted (*d*) conditions. *DR* = dorsal ridge, *H* = hydroecium, *LR* = lateral ridge, *SC* subumbrellar cavity, *VR* = ventral ridge

of each unit to be pulled together, and increases the radial height of each unit. Due to the bending at the creases, there is only a 3 % decrease in the actual perimeter of the exumbrella, while the circumference of the swimming muscle decreases by 20 % (Fig. 9c, d). The large ventral region is deformed only slightly and remains essentially sta-

tionary with respect to the rest of the nectosome. Thus, the deformation consists essentially of the pulling in of the dorsal and lateral parts of the nectophore (Fig. 9c, d). This type of system allows for the development of very rigid mesoglea, which at least in the case of *Diphyes* has been an important factor in the development of very effective swimming.

The velum acts in the same way as that of other medusae on contraction; i.e., it contracts essentially simultaneously with the subumbrellar muscle and is pushed outward by the increased hydrostatic pressure within the subumbrellar cavity (Fig. 8).

Diphyes is propelled forward by contraction of either or both nectophores. The two swimming bells differ in rate and duration of the contraction cycle so that when both are operating together they have different periodicities and are out of phase most of the time (Fig. 10a). Average duration of the contraction cycle is shorter by several hundredths of a second in the anterior nectophore. This staggering of contractions in the two bells results in a very smooth locomotory pattern (Fig. 10b), for in the example shown the difference between maximum (11.7 cm/sec) and minimum (9.6 cm/sec) velocity during a series of swimming contractions is only about 20 %. Contrast this with *Polyorchis*, for example, in which the average difference between maximum and minimum velocity during swimming is 40–50 %. Even when only a single nectophore is operating in *Diphyes* this difference is only 25–30 % and the velocity is only about 10 % less than when both are operating; this is due primarily to the highly efficient streamlining of the rigid nectosome.

The swimming muscle in either bell decreases in circumference by 15–25 % on contraction. This brings about an expulsion of 25–45 % of the contained water in nectophores 2–3 cm long. Compare this with the average values found in other hydrozoans (Table 3). In *Polyorchis*, for example, there is an average decrease in circumference of 37 % and reduction in subumbrellar volume of 45–70 %. The velocities achieved by *Diphyes* are much higher than those in the other hydrozoans studied.

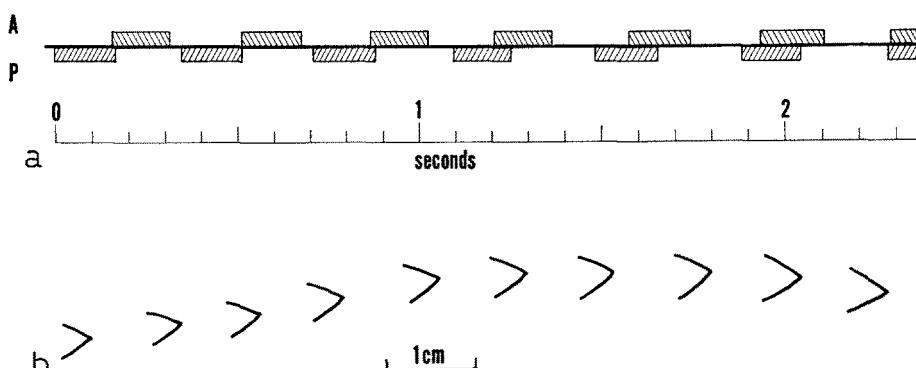


Fig. 10: a Timing of the contractions of the anterior and posterior nectophores of *Diphyes dispar* while swimming. Shaded areas represent the contraction phase. b. Change in position of the apex of the anterior nectophore of *Diphyes dispar* during swimming, showing the uniform high velocity made possible by streamlining and multiple swimming organs. Minimum velocity equals 9.6 cm/sec, maximum velocity equals 11.7 cm/sec, and average velocity equals 10.7 cm/sec. Time interval equals 3/32 sec; traced from cine sequence

Besides the rigid streamlining of the bell, part of this comparatively great effectiveness is due to the reduction of the area of the velar aperture by 80 % in *Diphyes*, making it a very effective nozzle (GLADFELTER 1972a).

Diphyes is capable of turning dorsally and ventrally; it was never observed to turn laterally but this possibility cannot be precluded. Turning is accomplished by the action of the velum. During straight swimming the velum contracts symmetrically. If a single nectophore is beating, a very slight turning can sometimes be discerned because of the oblique orientation of the two subumbrellar cavities with respect to the axis of the whole nectosome. On occasion, however, the radial velar muscles on the inside of either nectophore (i.e., the side of the velum near the nectosomal axis) are seen to contract, directing the jet of water obliquely toward the axis of the nectosome (Fig. 8), creating a net force on the outer wall of the nectophore, and causing the whole animal to turn in the opposite direction. Because of the long rigid configuration of the nectosome, however, even with a very pronounced asymmetrical contraction of the velum, the arc described by the turning animal is very broad. The mechanism of turning here is fundamentally similar to that seen in *Polyorchis* and different from that exhibited by the broader medusae (e.g., *Bougainvillia*, *Gonioemus*, etc.); that is, contraction of radial muscles causes the extended velum to be directed toward one side which becomes the inside of the turn. No fibers of CLAUS (see MACKIE 1964, and Fig. 9b) were found, and it is not known whether the velum can be displaced in any direction by the unilateral contraction of radial muscle fibers of the velum, or only in the direction of the nectosomal axis.

Rhopalonematidae

The bell of *Pantachogon haekeli* MAAS 1893 is about as tall as it is wide with sides nearly parallel, suggesting the anthomedusan form; however, the bell wall is very thin relative to the bell diameter, roughly 5 % of the latter. The mesoglea is nearly as rigid as that of *Diphyes*; when the bell is removed from water it does not collapse. The exumbrella is marked by a series of 32 equally spaced grooves which extend from the apex of the bell to the margin. The swimming muscle is highly developed, as indicated by the brilliant iridescence of the subumbrella regardless of the orientation of the medusa with respect to the light source and the observer. In the relaxed medusa the velum hangs downward as a great conical muscular curtain in which the relaxed velar aperture has an area only 25 % that of the cross-sectional area of the subumbrellar cavity at the base of the velum. The width of the relaxed velum is equal to nearly $\frac{1}{3}$ the length of the subumbrellar wall from margin to summit. The volume of water confined within the relaxed velum below the level of the bell margin is equal to nearly 25 % of the volume contained within the subumbrellar cavity above the bell margin.

On contraction the exumbrellar grooves operate essentially as do those of *Diphyes*, increasing in depth and allowing the exumbrellar surface to fold rather than simply to be compressed.

Pantachogon is an oceanic medusa from moderate depths (taken from 300 to 500 m). Unfortunately, only one specimen was brought to the surface in perfect con-

dition. It swam sporadically (with long periods of quiescence) for 24 hours after it was brought to the surface, but thereafter when an attempt was made to film its actions, no swimming occurred. Thus, all that can be said of swimming in this form is that it was the most powerful seen in any medusa (other than the siphonophores) and it would certainly reward the effort involved in procuring it in good condition to film this magnificent action. For example, with a single contraction, the initially motionless medusa (about 1 cm high) shot about 10 cm across the container.

The other rhopalonematid observed was *Aglantha digitale* (O. F. MÜLLER 1776), another form with a tall bell (height/width equals 1.2–1.5). The bell is thin-walled and is provided with rigid mesoglea and exumbrellar creases. The velum is level with the aperture of the bell, but very wide and well developed. Swimming was not analyzed in detail, but it involves a series of short contractions of moderate magnitude which propel the animal at a reasonably high velocity. An individual probed with a glass rod underwent a single strong contraction which carried it up to 8 cm or more at high velocity.

Narcomedusae: *Solmissus marshalli*
(AGASSIZ & MAYER 1902)

The order Narcomedusae, exemplified by *Solmissus*, includes forms whose bell is divided into two very distinct regions: a very rigid inflexible central disc and a thin, shirt-like lateral wall. The bell wall tapers to a very thin margin from which the velum extends. On contraction the circular swimming muscle of the lateral wall pulls the wall inward and upward toward the roof of the broad flat subumbrellar cavity. This upward bending of the lateral bell wall is unlike the action seen in any other medusae. The velum acts as an extension of the lateral wall, the curvature of the two being continuous till right near the end of the contraction. The exumbrella of the lateral wall is marked by a series of grooves which in lateral and axial cinematographic sequences were seen to act as joints during contraction. The action is similar to that in *Pantachogon*. During the recovery, however, the exumbrellar grooves became much more accentuated as the bell wall between grooves became strongly arched outward. Because of the inflexibility of the major bulk of the bell, swimming appears rather different from that in most medusae; it resembles the swimming of *Stomotoca* more than that of any other medusa studied. Turning is accomplished as observed in *Goniomedusus*, *Halistaura*, etc. The animal initially contracts the subumbrella and velar swimming muscle on one side, then strongly contracts those on the other side, creating a net force on the latter side and causing it to be on the outside of the turn.

THE SWIMMING MECHANISM OF SOME SCYPHOMEDUSAE

The scyphomedusae differ from the hydromedusae in several respects related to locomotion. First, scyphomedusae as a rule are considerably larger than hydromedusae; in each of the four orders with swimming medusae the average size of the full-grown

medusa is much greater than the average size of members of any hydrozoan order. Furthermore, in each of these four orders the largest members are considerably larger than any hydromedusan (see, for example, KRAMP 1961). Second, instead of a system of radial canals radiating out from a central junction or stomach, the scyphozoan gastrovascular cavity primitively consists of a central stomach and a series of broad radial pouches which extend nearly to the periphery of the umbrella and are separated from one another only by narrow radial lines of fusion of the roof and floor of the cavity. In one family of Semaeostomae (Ulmaridae) and throughout the order Rhizostomae, which on other grounds are considered to be the most highly evolved scyphomedusae (e.g., see HYMAN 1940, THIEL 1966), the broad radial stomach pouches have been replaced by narrow canals radiating outward from the central stomach toward the margin. A third feature related to locomotion which distinguishes scypho-

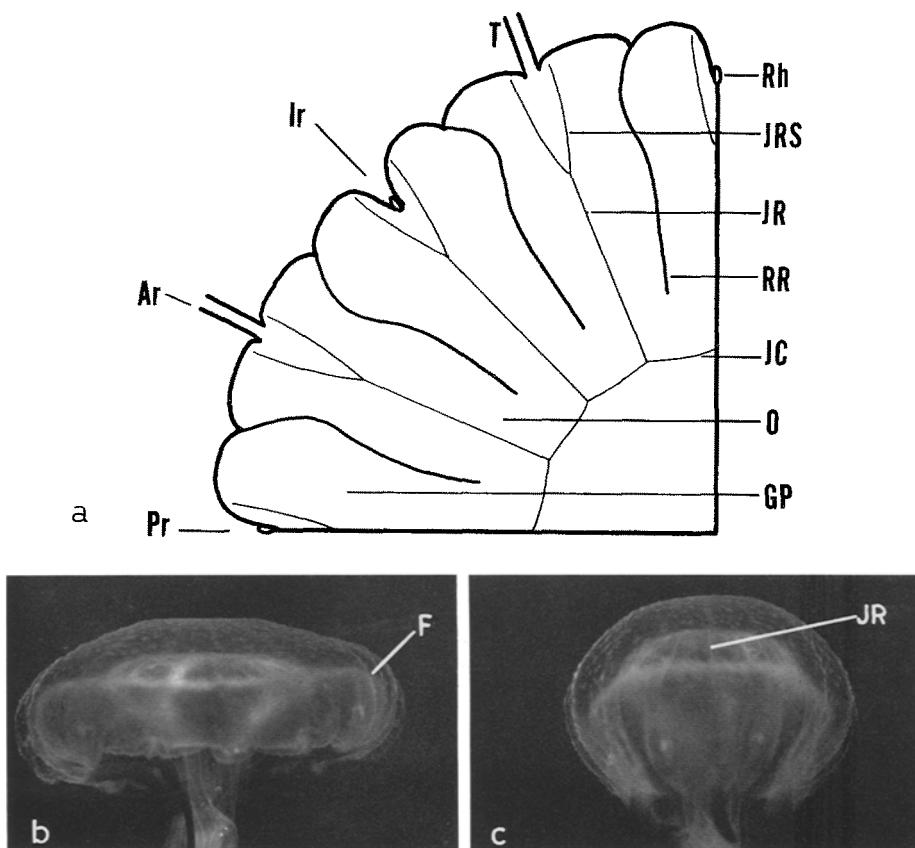


Fig. 11: a Oral view of one quadrant of *Pelagia noctiluca* showing basic components of the swimming apparatus. Ar = adradius, GP = gastric pocket, Ir = interradius, JC = coronal joint, JR = primary radial joint, JRS = secondary radial joint, O = opening to gastric pocket, Pr = perradius, Rh = rhopalia, RR = radial anchoring ridge, T = tentacle. Lateral view of young *Pelagia noctiluca* in relaxed (b) and contracted (c) conditions. F = exumbrellar folding of mesoglea near bell margin, JR = radial joint

medusae from hydromedusae is the absence of the velum in the former (though, as will be seen, an analogous structure has risen in the Cubomedusae). The locomotory system of the scyphomedusa *Cyanea capillata* has been treated separately (GLADFELTER 1972b) and can be used as a basis for comparison of the following species.

Chrysaora melanaster BRANDT 1838 and
Pelagia panopyra PERON & LESUEUR 1809

Both these jellyfishes are residents in Monterey Bay and at certain times of the year occur in relatively dense concentrations. The large purple and white *Pelagia* attains a bell diameter of about a meter, with the extended oral arms sometimes reaching more than about 5 m in length (L. TEPPLEY, personal communication and underwater movies); it has eight marginal tentacles. *Chrysaora* does not achieve quite so great a diameter; its umbrella is brown and the 24 marginal tentacles are red.

The locomotory systems of these two scyphomedusae are virtually identical and are considered together. The relaxed umbrella is broad and flat in young animals (those up to 15 cm in diameter) but unlike that of *Cyanea* the peripheral region of the umbrella is curled downward (Fig. 11b, c) even in anaesthetized animals, so that an actual subumbrellar cavity exists at all times. The primary difference related to locomotion between the two forms is that the umbrella of *Chrysaora* remains relatively flat throughout its growth, but that of *Pelagia* becomes considerably more dome-shaped and thickened along the oral-aboral axis.

As in the case of *Cyanea*, the gastrovascular cavity in these two species forms a flattened cavity on the oral side of the umbrella, bounded above by the thick umbrella proper and below by the thin subumbrellar sheet of mesoglea and muscle (Figs 11a, b, c, 12). The gastrovascular cavity consists of a broad central stomach and sixteen radially arranged pockets, which extend to the margin of the umbrella where the gastrovascular cavity continues into the tentacles. The pockets are all about the same width where they communicate with the central cavity but the per- and interradial ones are expanded toward the periphery and the adradial pockets are consequently narrowed in the same region (Figs 10b, 11a). The boundaries of these pockets are formed by radial anchoring ridges as in the case of *Cyanea*.

The mesoglea is segregated into two regions by the gastrovascular cavity, as was the situation in *Cyanea*: the thick exumbrellar mesoglea lies above the cavity and the thin subumbrellar mesoglea below it (Figs 12, 13a, b). These are connected along the anchoring ridges that form the boundaries of the pockets. However, in the case of *Chrysaora* and *Pelagia* the ridges are not composed of subumbrellar mesoglea segregated from the exumbrellar mesoglea by gastrodermis, but are radial thickenings of the exumbrellar mesoglea itself fused to the subumbrellar mesoglea via the fused gastrodermis between the radial pockets.

Medial to the opening of the gastric pockets into the central cavity, on the oral side of the exumbrellar mesoglea, there is a 16-sided coronal joint similar to that found in *Cyanea*. This joint marks the boundary between the two main functional regions of the umbrella: the central disc and the lateral region (there were four regions in *Cyanea*).

From the apices of this joint 16 radial joints course peripherally along the midlines of the gastric pockets. Each radial joint divides into two branches (secondary radial joints) near the periphery (Fig. 11a, b, c). In addition, 32 accessory radial joints are present, one along each side of each of the radial anchoring ridges in the proximal part of the gastric pockets (Fig. 12); these become less pronounced toward the margin. Large perpendicular fibers traverse the exumbrellar mesoglea from oral to aboral sides; they are especially well developed and concentrated along the apices of coronal, primary radial and accessory radial joints.

The subumbrellar mesoglea is very thin proximally (see discussion for the functional reason for this under *Cyanea*) except in the oral arms, but toward the margin it forms a thickened ridge, lens-shaped in cross section, under the radial joint. There is no system of circular and radial ridges of the subumbrellar mesoglea as was present in *Cyanea*, but in the peripheral region there is a series of fine radial ridges seen on the gastrodermal side of the subumbrellar mesoglea (Fig. 12c).

The swimming muscle is located on the subumbrellar side of the subumbrellar mesoglea and forms a broad annular region divided into 16 separate fields. The muscle fibers of each field terminate a short distance lateral to each radial anchoring ridge so that there is a narrow band of subumbrellar mesoglea on both sides of each anchoring ridge (Fig. 10b). Each muscle field extends from the level of the opening of the radial pocket to the margin of the umbrella. The structure of the swimming muscle has been described by KRASINSKA (1914); all contractile elements are circularly oriented. This arrangement of the swimming muscle in *Pelagia* and *Chrysaora* is very different from that seen in *Cyanea*.

Contraction of the swimming muscle results in a bending of the lateral portion of the umbrella inward and downward (i.e., orally) around the apex of the coronal joint, as in *Cyanea* (GLADFELTER 1972b). The large mesogleal fibers converging on the apex of the coronal joint serve to anchor this fulcrum to the exumbrella. In *Chrysaora* and *Pelagia* the umbrella lateral to the coronal joint consists of a single functional region, in contrast to *Cyanea* which shows a division of this part of the umbrella into coronal, lateral and marginal regions. Though the subumbrellar cavity is concave at the beginning of a contraction, the proximal part of it is nearly flat so that the force of contraction can be considered as horizontal (radial) and vertical (axial) components as in *Cyanea* (GLADFELTER 1972b); the horizontal component prevails initially, while the vertical component becomes increasingly important as the lateral region is bent downward. The central disc is slightly arched aborally on contraction and is compressed slightly in the radial direction.

As the lateral region is flexed inward by the contracting swimming muscle, the radial anchoring ridges are drawn together. This causes the surface of the umbrellar mesoglea on either side of the radial joint apex to be bent downward around the apex, which is serving as a fulcrum (or joint); that is, the exumbrellar mesoglea from the radial joint apex to the radial anchoring ridge is acting as a moment arm with its pivot at the joint apex and its force applied at the anchoring ridge (Fig. 13a, b, c, d). During this process the distance on the gastrodermal surface between the joint apex and the anchoring ridge (i.e., distance "a" in Fig. 13a, b) remains constant. Initially, the angle between the contracting force and the moment arm is small, so that a relatively great

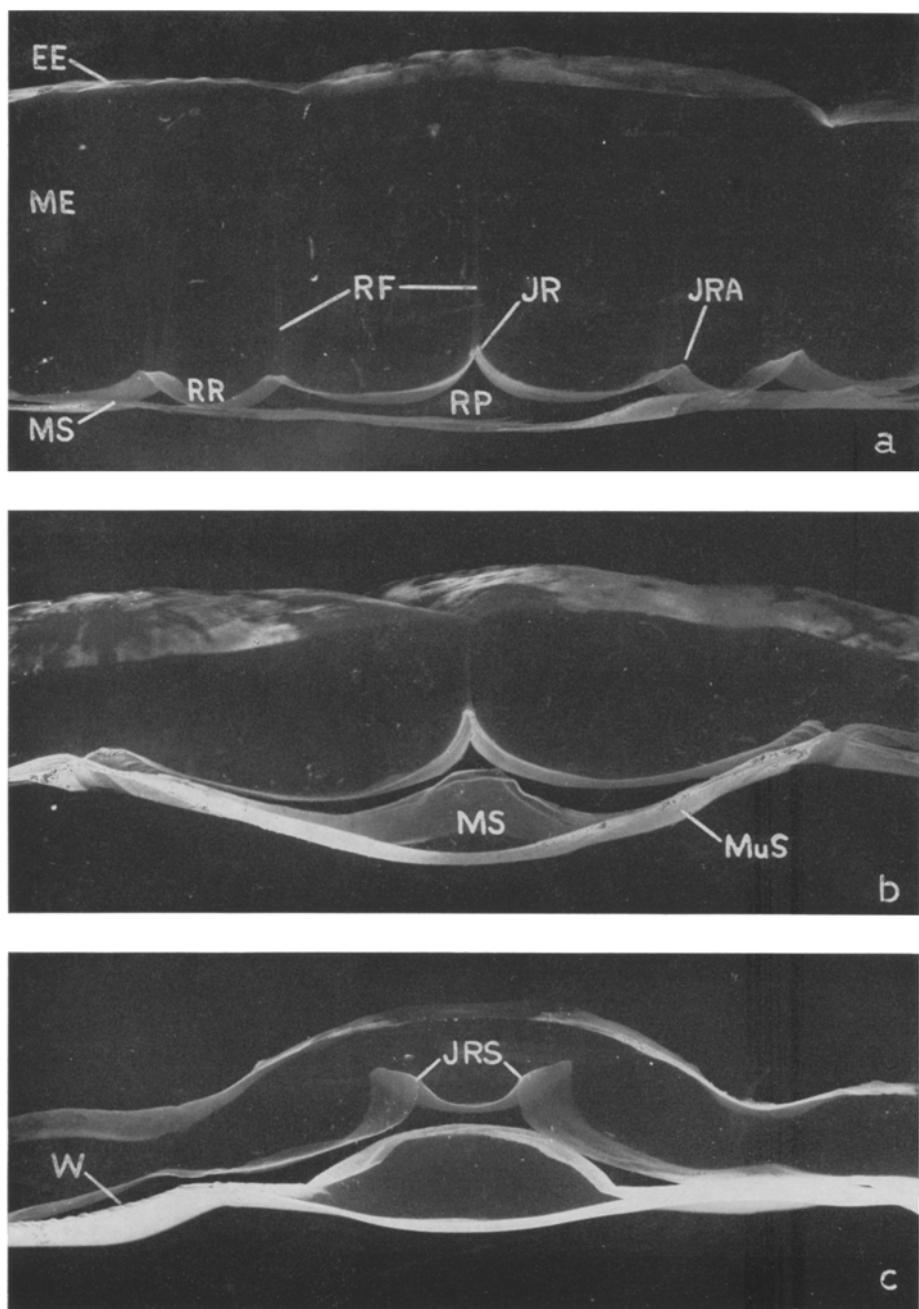


Fig. 12

amount of force is necessary to cause a given amount of angular displacement around the joint apex. As contraction proceeds, this angle becomes greater, and the applied force becomes more effective in bending the mesoglea around the joint apex.

Thus on the one hand, during contraction, the more that the elastic skeleton (i.e., the exumbrellar mesoglea) is deformed, the greater is the force required to effect a given amount of muscular contraction. On the other hand, the more the umbrella is bent downward from the horizontal and the more the sides of the radial and accessory radial joints are drawn together, the more effective becomes the actual muscular force being exerted. The relative contributions of these two factors in determining the rate and total amount of muscular contraction has not been measured, but the actual quantities are not required for an understanding of the system. The accessory radial joints permit slightly greater deformation of the exumbrellar mesoglea than would the radial joints alone.

The region of the umbrella near the margin undergoes the greatest amount of deformation between the maximum recovery and maximum contraction (Fig. 14a, b). Measurements taken from cinematographic sequences show that the decrease in diameter of the subumbrella at the point where the radial joints split is 35–40 %; about half way between this junction and the margin the subumbrellar decrease in diameter is about 50 % (45–55 %); and the same distance proximally the decrease is only about 25–30 %. The division of each radial joint into two branches allows for a much greater deformation of the exumbrellar mesoglea than is provided by a single primary joint (Fig. 13c, d). The greater degree of bending permitted by this double joint is reflected in the greater amount of folding of the exumbrellar surface nearer the margin (Figs 11b, c, 13c, d). The fine radial ridges seen on the gastrodermal side of the subumbrellar mesoglea allow for the relatively great shortening undergone by this region on contraction; they act in the same way as the radial ridges seen on the exumbrellar side of the velum in *Polyorchis*. In *Chrysaora* and *Pelagia*, as in *Cyanea*, the apex of each joint is anchored to the exumbrellar surface by large mesogleal fibers (Fig. 12). The support provided by these fibers allows the apical ridge of the joint to serve more effectively as a fulcrum for the bending of the umbrella on contraction.

During the early phases of contraction, as the lateral portion of the umbrella flexes around the apical joint, it is the proximal part of the region which contracts more strongly, changing the umbrella profile of this region from strongly convex to flat or even mildly concave (Fig. 14a, b). During this early stage the lateral part of the umbrella is actually thrusting backward against the water rather than forcing water out of the subumbrellar cavity; in fact, the volume of the subumbrellar cavity actually increases after this initial flattening of the lateral region (Fig. 14a, b). As the contrac-

Fig. 12: Tangential section through bell of *Chrysaora metanaster* (cross section through radial joint) at three levels. *a* Just periperial to opening of the gastric pocket. *b* Midway between coronal joint and the margin. *c* Near the margin. EE = exumbrellar epidermis, JR = primary radial joint, JRA = accessory radial joint, JRS = secondary radial joint, ME = exumbrellar mesoglea, MS = subumbrellar mesoglea, MuS = circular swimming muscle, RF = radial mesogleal fiber, RP = radial gastric pocket, W = wrinkles on gastric side of subumbrellar mesoglea

tion proceeds, the peripheral part of the lateral region contracts more strongly, so that after the initial flattening of the curvature of the sides of the subumbrella (as seen in the profile) the lateral region again becomes gradually more convex. The outer part of the region continues its contraction after maximum contraction has been reached in

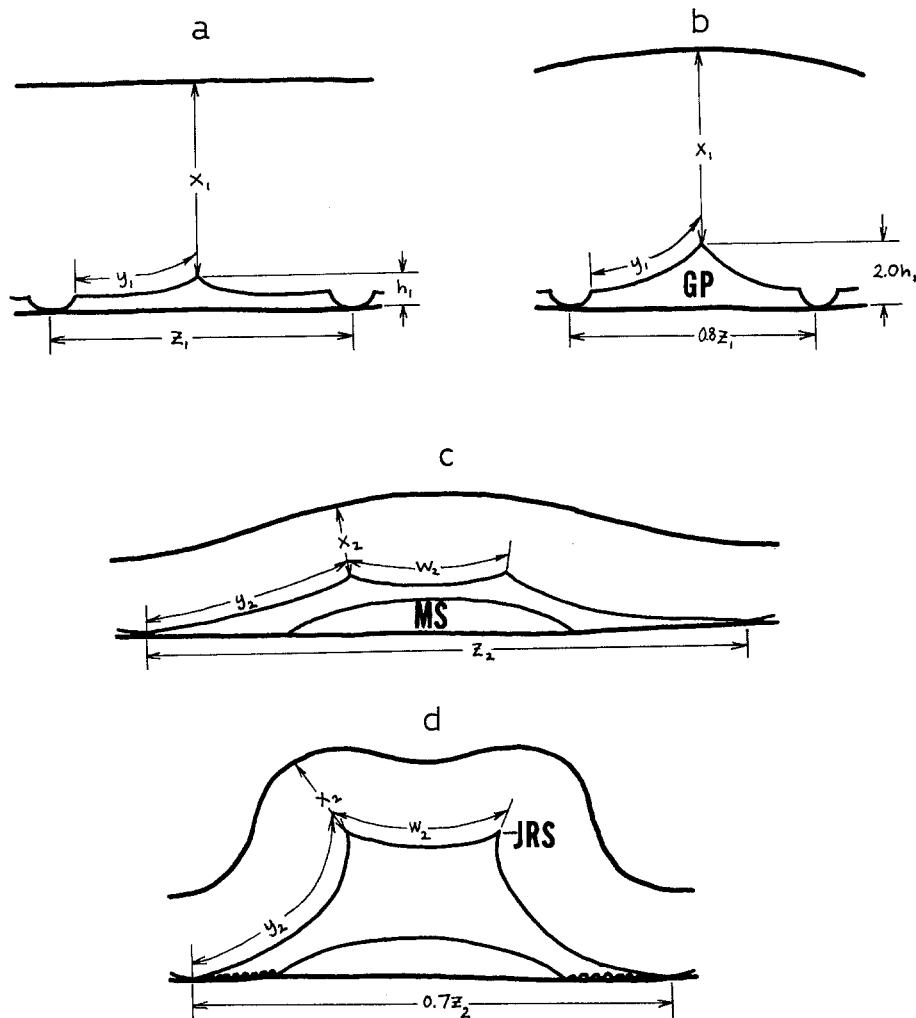


Fig. 13: Diagrams showing the action of the radial joints in *Chrysaora melanaster* and *Pelagia noctiluca* in relaxed (*a, c*) and contracted (*b, d*) condition; dimensions taken from cine sequences. Proximal region. x_1 = thickness of exumbrellar mesoglea above the apex of the radial joint, y_1 = length of the umbrellar mesoglea between the primary radial joint and the accessory radial joint, z_1 = distance between two adjacent radial anchoring ridges, h_1 = height of the radial gastric pocket at the apex of the radial joint, all in the relaxed condition, GP = gastric pocket. *c, d* Same as *a* and *b* but peripheral region. x_2 = same as x_1 , y_2 = same as y_1 , z_2 = same as z_1 , w_2 = distance along the roof of the gastric pocket between the two secondary radial joints, all in the relaxed condition, MS = subumbrellar mesoglea, JRS = secondary radial joint

the more proximal part. Recovery begins in the proximal region just as maximum contraction occurs near the bell margin. The whole contraction suggests a wave passing outward. Thus the sequence of profile changes occurring in the subumbrella closely resembles that of *Cyanea*, whose swimming mechanism was quite different. The actual contraction in a 7–8 cm individual lasts $\frac{1}{2}$ – $\frac{2}{3}$ sec and the recovery slightly longer. During recovery the umbrella gradually resumes its expanded condition due to elastic forces generated in the exumbrellar mesoglea during contraction.

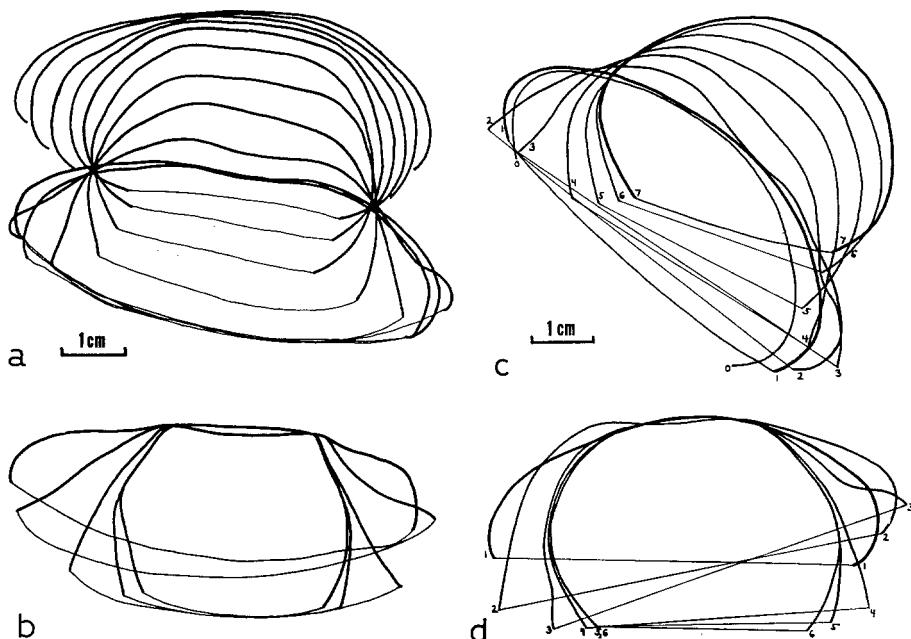


Fig. 14: Sequence of changes in the profile of the exumbrella and subumbrella of young *Pelagia noctiluca* during swimming; traced from successive motion picture frames. Time interval equals $1/8$ sec. *a* Exumbrellar outline showing actual change in position. *b* Subumbrellar outline, successive frames superimposed. *c*, *d* Sequence of changes in the exumbrellar profile of young *Pelagia noctiluca* while turning. Time interval equals $1/8$ sec; traced from cine sequence. *a* Showing actual change in position. *b* Successive stages superimposed to show asymmetry of contraction

Progression of the umbrella through the water is seen in Figure 14a. During the first $\frac{1}{4}$ – $\frac{1}{2}$ of the contraction much of the apparent thrust is due simply to elongation of the umbrella and the rest is due to the backward thrust of the lateral region on the water behind. During the remainder of the contraction, thrust is primarily a result of the extrusion of water from the subumbrellar cavity with a certain momentum (see GLADFELTER 1972a), which imparts an oppositely directed momentum to the umbrella. A maximum velocity of about 4 cm/sec is reached during this period. As recovery begins, deceleration is rapid and the central disc virtually ceases forward progress as the lateral region continues to move forward (Fig. 14a). Thus, though apparent progress

ceases, the center of mass of the umbrella continues to move forward till the end of the recovery. Before recovery is quite completed contraction begins again; that is, during swimming the umbrella never quite achieves the state of expansion seen in an anaesthetized animal. The average swimming velocity of the animal considered above was about 2 cm/sec over several contraction cycles.

Turning is achieved in a manner similar to that of *Cyanea*: during the initial stage of contraction one side of the umbrella contracts strongly with little effect in turning; then the other side contracts at a relatively greater rate, effecting a net displacement of that side with respect to the other, and an angular displacement of the whole animal (see GLADFELTER 1972b).

Charybdea rastoni (HAACKE 1886): a case of convergence

On the basis of multiplicity of morphological features, the cubomedusae must be considered scyphomedusae (HYMAN 1940a, KRAMP 1961, THIEL 1936, 1966). There are, however, certain striking similarities between cubomedusae and the hydromedusae. These similarities are presumed to have arisen after the historical separation of hydro- and scyphomedusan lines, and represent analogous developments resulting from convergent evolution.

The cubomedusae are moderate-sized scyphomedusae most being of the order of 100 mm in height but some achieving twice that height. They are actively swimming forms, usually found in relatively shallow coastal waters (BARNES 1966, BIGELOW 1909, CONANT 1898, personal observation). The sting of a few forms is lethal (BARNES 1966). *Charybdea rastoni* achieves a bell height of 35 mm (KRAMP 1961). It is fairly common in the kelp beds off Santa Barbara, California, in the autumn months and has been observed to feed on bottom-swarming mysids (J. CHILDRESS, personal communication).

Unlike the broad flat umbrellas of semaeostomes such as *Cyanea* and *Chrysaora*, the cubomedusan umbrella as seen in the lateral view is tall and bell-shaped with roughly parallel sides (Figs 15a, 16). Superficially it resembles an anthomedusan bell. The lens-shaped central, coronal or apical disc that forms the top of the bell is set off from the lateral portion by apposed sub- and exumbrellar grooves comprising the coronal joint. In cross section or polar view the bell is roughly square, with interradial vertices and slightly curved sides between. To either side of each interradius the bell is produced into two external longitudinal ribs which extend from the coronal joint to the bell margin. Between these ribs lies a deep external groove, the interradial joint. The ribs taper slightly in width toward the margin. The inside (medial surface) of each of these ribs bears a deep groove, the para-interradial joint. The gastrovascular cavity sets off the umbrella proper from the very thin subumbrellar sheet (Fig. 15b). A broad stomach underlies the apical disc; this communicates with the four broad perradial pockets by four narrow perradial gastric ostia. These perradial pockets extend nearly to the margin and are separated from each other only by narrow interradial strips where the exumbrellar and subumbrellar gastrodermal layers are fused. The exum-

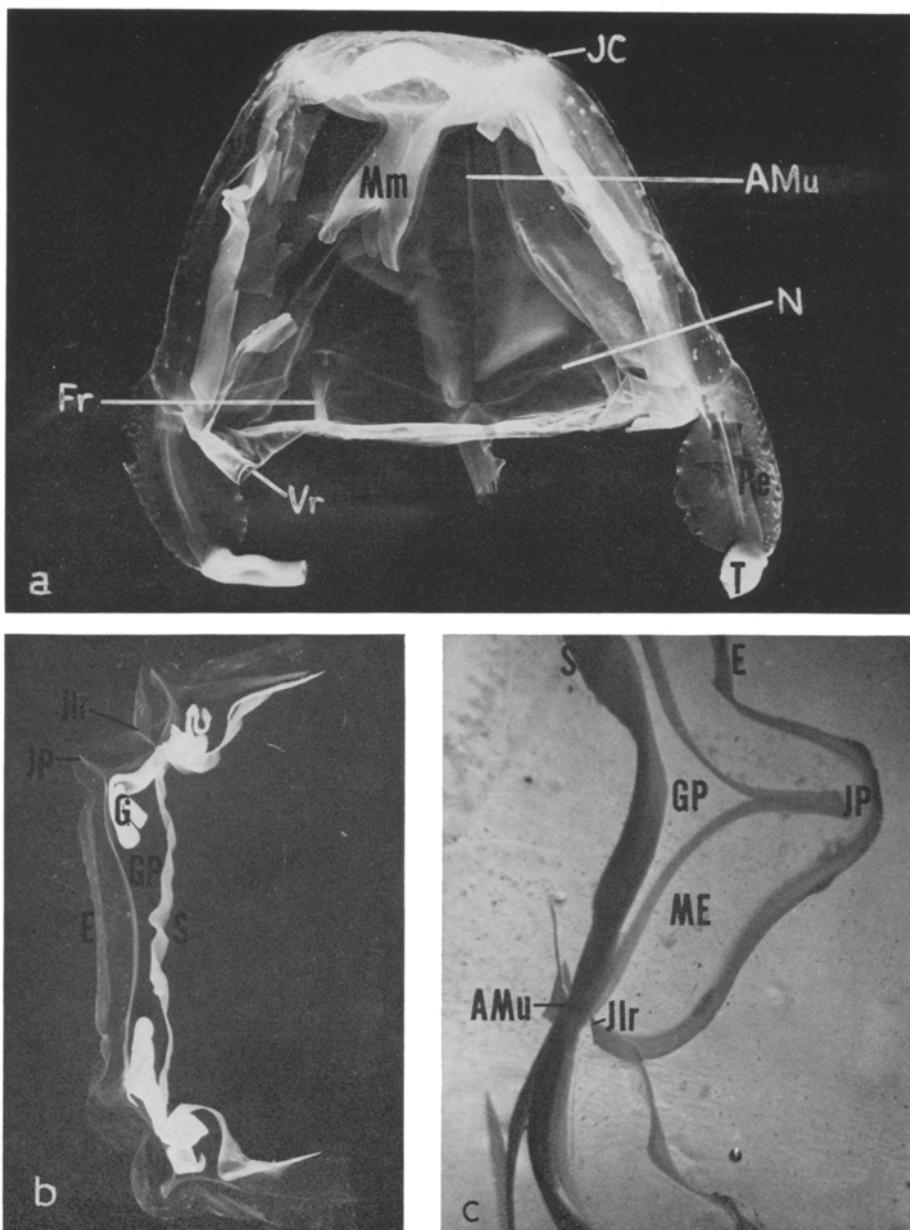


Fig. 15: *a* Structure of *Charybdea rastoni* as seen in an HCHO fixed specimen cut sagittally. AMu = line of anchorage of circular swimming muscle, Fr = frenulum, JC = coronal joint, Mm = manubrium, N = nerve ring, Pe = pedalium, T = tentacle base, Vr = velarium, *b* Cross section through one half of bell of *Charybdea rastoni* and *c* through interradial and para-interradial joints. AMu = anchorage of swimming muscle, E = exumbrella, G = gonad, GP = gastric pocket, Jlr = interradial joint, JP = para-interradial joint, ME = exumbrellar mesoglea, S = subumbrella

brellar mesoglea is tough and rigid, quite comparable to that of *Lensia* in this respect. Radial mesogleal fibers are densely arrayed throughout, with concentrations focused on the inter- and parainterradial joints. The swimming muscle is located just below the subumbrellar epidermis. It consists of a single sheet of fibers, all circularly arranged and extending around the circumference, anchored to the exumbrellar mesoglea only at the interradial and around the coronal joint and the bell margin. It extends from the coronal joint to the very margin, interrupted only by the festooned nerve ring (Fig. 15a). The margin of the bell is turned inward to form a thin horizontal annular shelf, the velarium, which bears a close superficial resemblance to the hydromedusan velum (Fig. 15a). However, the presence on the velarium of sixteen gelatinous lobes and a scalloped margin in relatives of *Charybdea* suggest that the velarium is a derivative of the marginal lobes such as are seen in *Cyanea* and *Chrysaora* (see CONANT 1898). Other differences between the velarium and the velum are as follows: canals of the gastrovascular cavity penetrate the velarium but never the velum; the circular muscle of the velarium is continuous with the swimming muscle of the subumbrella proper (it is interrupted only at the nerve ring, located a considerable distance above the margin, as shown in Fig. 15a); there are no radial muscle processes on the exumbrellar side of the velarium such as are present in a velum; and finally the velarium is supported perradially by four frenula or buttress-like projections of the umbrella which are confluent with the velarium. Four flattened blade-like pedalia project backward and outward at about 45° from the oral-aboral axis of the bell. These are extensions of the subumbrella; i.e., the mesoglea of the pedalia is continuous with that of the subumbrella and segregated from the exumbrellar mesoglea by the gastrodermal lamella (CONANT 1898). The pedalium consists of an outer thickened ridge and a medial thin blade-like portion (Fig. 15a). Epitheliomuscular cells cover the surface of the pedalium; the striated fibers of these cells fan out from the umbrella at the base of the pedalium over the entire surface of the blade. These fibers are arranged side by side and roughly parallel the long axis of the blade. The mesoglea of the pedalium is rigid and is traversed by numerous radial (with respect to the gastric canal running along its length) mesogleal fibers.

Thus while it is clearly scyphozoan in affinity, the cubomedusan system exemplified by *Charybdea* resembles the anthomedusan system in general configuration of the bell and in possessing a horizontal annular flap with circular swimming muscle around the inside margin of the bell. Functional resemblances to the semaeostome system include isolation of the swimming muscle on a thin subumbrellar sheet anchored to the exumbrellar mesoglea only along definite radii (and the margin) and the presence of a coronal joint and radial joints in the exumbrellar mesoglea. Unique features include the flattened, blade-like pedalia.

When the swimming muscle contracts there are three components of deformation in the exumbrellar mesoglea: (1) flexion of the lateral wall of the bell around the coronal joint, (2) a sharp flexion of the exumbrellar wall along the interradial and para-interradial joints, and (3) an inward bending of the relatively flat sides of the umbrella. When the lateral wall of the bell is flexed inward around the coronal joint there is no deformation of the lens-shaped apical disc (Fig. 16a). The effectiveness of this joint in providing for flexion of the lateral wall is due to the extreme thinness of

the mesoglea between the ex- and subumbrellar grooves comprising the joint. Contraction of the swimming muscle also exerts a pull on each of the four sets of interradial ribs to which it is anchored at the interradial joint. This draws the four sets of ribs together by causing the umbrella to bend sharply at the interradial and parainterradial joints. The para-interradial joints operate in a manner very similar to that seen in the peripheral part of the umbrella of *Pelagia* and *Chrysaora*, where two secondary radial joints lie between the lines of anchorage of the swimming muscle. As the four corners of the medusa are brought closer together on contraction, the four perradial surfaces of the (ex)umbrella become more flattened or slightly concave.

In *Charybdea* forward propulsion of the bell during swimming is provided for in the same way as was seen in the hydromedusae; i.e., as the subumbrellar cavity is laterally constricted, water is forced out through the aperture of the velarium, whose circular muscle is also contracting at this time. The basic temporal sequence is the same in *Charybdea* as in *Polyorchis*: the contraction begins slowly, during which time water is expelled slowly. As the contraction proceeds the rate of reduction of the subumbrellar circumference increases markedly, bringing about a greater rate of expulsion. Toward the end of the contraction phase the rate of expulsion diminishes (Fig. 16a, b). As the contraction proceeds, the hydrostatic pressure created within the subumbrellar cavity forces the velarium outward as in the case of the hydrozoan velum. The velarium, however, is buttressed to the subumbrellar wall at the perradii, so that it bows outward in the four quadrants but is stiffened at the perradii.

As can be seen in Table 3, swimming in *Charybdea* is quite effective when compared to that of the hydromedusae: high velocities are achieved (average velocity over several contraction cycles is about 6 cm/sec, with a maximum of over 9 cm/sec reached at the height of the contraction) with relatively slight expulsion of water (about 40 % of the water initially in the subumbrellar cavity is expelled). Probably responsible for this effectiveness are: (1) the rapid rate of discharge of subumbrellar water, (2) the moderately great narrowing of the bell aperture by the velarium, and (3) hydrodynamic properties of the bell which were not analyzed, such as its narrow elongate shape, the effects of the interradial ribs and finlike pedalia in streamlining, and the possession of only four simple tentacles.

As seen in Figure 16c the velarium functions in the same capacity as the hydrozoan velum; it not only serves to narrow the aperture through which water exits from the subumbrellar cavity during contraction thus increasing its velocity, but it is also the primary agent in effecting turning. By stronger contraction of the circular (and only) velarial muscles on one side, the velarium on that side resists deformation by the hydrostatic pressure built up within the subumbrellar cavity. The other side of the velarium is forced outward and thus forms a nozzle as in the hydromedusae, directing a jet of water toward the side on which the velarium is contracted most strongly. Thus a net force is exerted on the subumbrellar wall of the side on which the velarium is less strongly contracted, forcing that wall outward so it becomes the outside wall in the turn.

Though the actual function of the pedalia remains uncertain, it has been suggested that they may play some role in turning. This role for them has been hypothesized by CONANT (1898); and HORRIDGE (1966) has observed that, "In turning they bend these

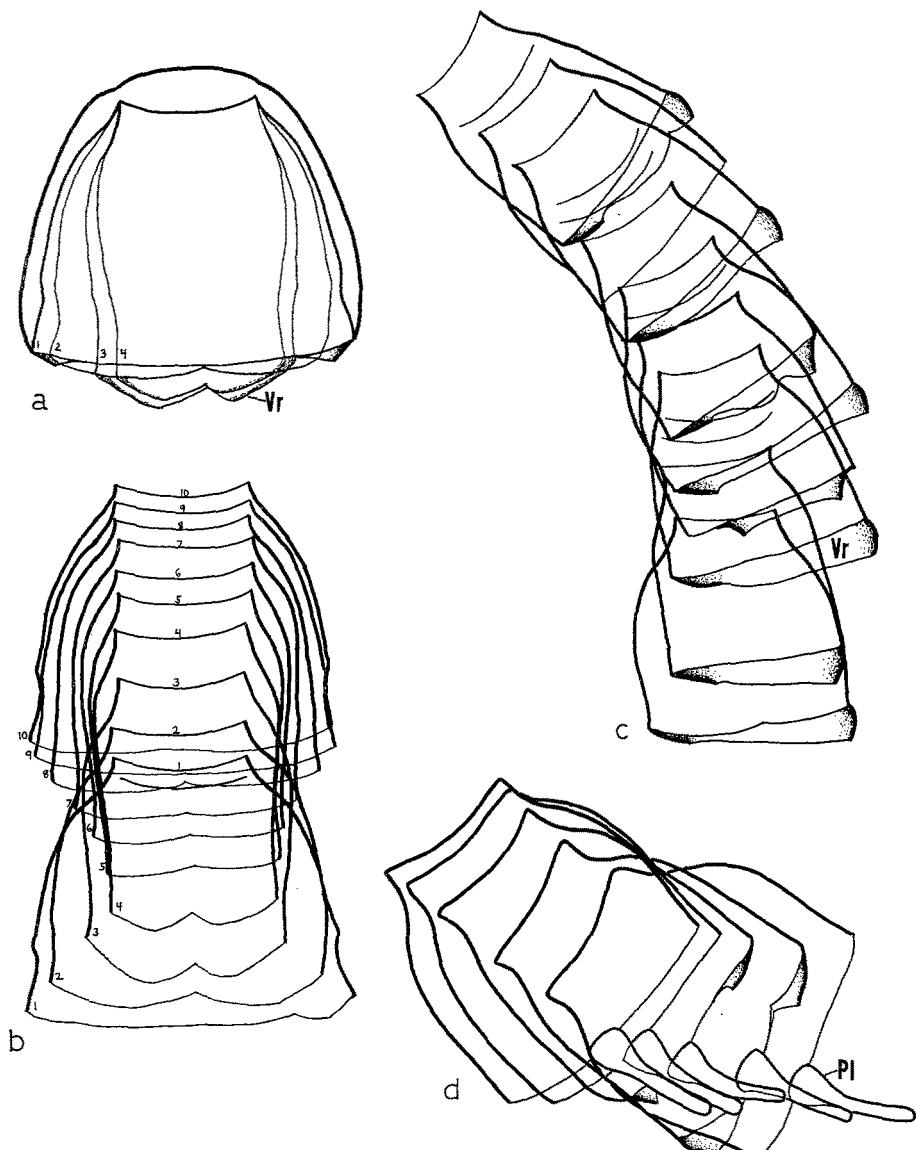


Fig. 16: Changes in the subumbrellar profile during contraction and recovery of *Charybdea rastoni*; traced from cine sequences. Time interval equals 1/12 sec. *a* Outlines superimposed. *b* Actual position. Vr = velarium. *c* Lateral view of the subumbrellar outline of *Charybdea rastoni* during turning, showing action of the velarium; traced from cine sequences. *d* Lateral views of the subumbrellar outline of *Charybdea rastoni* during turning, showing bending of the pedalia; traced from cine sequences. Pl = pedalium

large arm-like, flattened, blade-like pedalia laterally. As the bell pulsates the pedalia act as rudders." Both the above references apply to *Charybdea*. HYMAN (1940a) also makes the undocumented statement that removal of the pedalia in Cubomedusae destroys the turning ability of these animals.

Analysis of cinematographic sequences in the present study reveals that in fact the pedalia do bend during turning (Fig. 16d); they bend toward the inside of the turn. This action can be interpreted as being an active process, the pedalia acting as rudders to assist the velarium in effecting the turn. However, it can also be interpreted as a passive bending of the pedalia by increased water pressure on the outside of the turn (which is being effected solely by the velarium). Examination of cinematographic sequences suggests that the latter interpretation is the correct one, for it is in the second half of the contraction phase that the bending of the pedalia becomes most pronounced. That is, in *Charybdea* the pedalia are bent most during that period which in other medusae studied is the period of greatest turning and greatest lateral displacement (i.e., sliding), when the water pressure against the outside of the pedalia would be the greatest (Fig. 16d). Whether the bending of the pedalia during turning is a cause or a result, however, is still uncertain, and requires further investigation.

DISCUSSION

Having surveyed the locomotory systems of a variety of medusae of broad taxonomic representation, it is now clear that this system in general has a number of structural parameters which can vary through a whole spectrum of possibilities. These parameters are: (1) bell shape, (2) mesogleal consistency, (3) nature of the deformable skeleton (i.e., joints, etc.), (4) mesogleal fiber systems, (5) velar development, (6) muscle cell morphology, (7) muscle arrangement and (8) absolute size. There are also a number of functional parameters to be considered (e.g., see Table 3); the more important of these include: (1) maximum velocity, (2) average velocity, (3) acceleration and (4) turning radius. Because of the variability in determinations of functional aspects, only general correlations can be made between structural and functional aspects of the locomotory systems treated here.

Perhaps the most evident parameter of the locomotory system is bell shape. The forms we have surveyed display a spectrum of shapes from the broad, flat, even concave (ex)umbrella of *Cyanea* to the long, narrow and pointed nectosome of *Diphyes*. For the purpose of later discussion it is useful to establish three categories of bell shape (relaxed condition) for the forms studied: (1) tubular, in which the subumbrellar walls are more or less parallel in lateral view, (2) hemispherical, in which the subumbrellar walls diverge from the bell axis at roughly 45°, and (3) flat, in which the subumbrellar walls are horizontal, with essentially no subumbrellar cavity present. Those forms which are streamlined are often more effective swimmers than those which are flat (e.g., compare *Diphyes* and *Cyanea*, GLADFELTER 1972b), but as will be seen, it is generally difficult to correlate bell shape alone with swimming effectiveness.

Mesogleal consistency has not been quantified, but we can establish three categories of firmness which will be useful: (1) soft, (2) firm and (3) rigid. There is very

little known about the chemical or ultrastructural basis of this variability, in fact the mesogleal structure is only somewhat clear for a few anthozoans (*Calliactis*: CHAPMAN 1953, *Metridium*: GOSLINE 1971). In a general way it appears that rate of recovery of the deformed mesoglea to its expanded condition is related to firmness of the mesoglea, but a number of other factors are also important in this respect, such as bell shape, absolute size, the presence or absence of the velum (GLADFELTER 1972a, p. 68 and Fig. 8) and possibly a moderating action by the swimming muscle.

A number of medusae have a structural provision for mesogleal deformation which reduces the force required to effect a deformation of a given magnitude (see GLADFELTER 1972a). The presence of at least the more elaborate of these "joint systems" must be explained on historical as well as functional grounds. For example, all tubular forms have such a structural provision, but only among the Anthomedusae is the elaborate system such as occurs in *Polyorchis* to be found. Such a system is found in all Anthomedusae examined which fall into the tubular category but not in those which are not tubular (viz. *Stomotoca*). On the other hand, simpler provisions such as permanent exumbrellar creases are found in several orders: Trachymedusae (*Pantachogon*), Siphonophora (*Diphyes*) and Anthomedusae (*Euphypha*). All the tubular Anthomedusae have bell mesoglea that can be categorized as soft or firm, whereas those tubular forms with only permanent exumbrellar creases are rigid. The other elaborate type of joint system is that found in most of the scyphozoans studied, and has undoubtedly been in the group for a long time. However, where the gastrovascular system has changed, as in the Ulmaridae (*Aurelia*, *Phacellophora*), the basis for the joint system has disappeared, and these forms lack the elaborate provision of other Scyphomedusae; yet no difference in other parameters of locomotion, structural or functional was evident.

The role of radial mesogleal fibers has already been discussed by GLADFELTER (1972a, b). In summary, within a particular species their distribution coincides with those regions of the bell which are deformed during contraction. Their concentration is greatest at joint apices in the Anthomedusae and Scyphomedusae, and along these lines thickening of the mesoglea during contraction is at a minimum. Elsewhere in the bell where there is a differential concentration of these fibers, the thickening of the bell is inversely proportional to the fiber density (see GLADFELTER 1972a, Table 1). This suggests that the fibers act as tensile agents and increase the radial integrity of the bell. Among different species fibers are usually best developed in more active, strongly swimming forms.

The function of the velum was clearly demonstrated in *Polyorchis* (GLADFELTER 1972a) and supporting evidence has been presented in the present paper for *Euphypha* and *Diphyes*. In these tubular forms the velum narrows the aperture through which water leaves the subumbrellar cavity, acting as a nozzle and increasing the momentum of the discharged fluid. In addition, when it contracts asymmetrically it is the primary agent effecting turning. In broader forms, including even some of those classed as tubular (e.g., *Bougainvillia*) the velum may still play an important role as a nozzle (see especially *Gonianemus*) but is of reduced importance during turning, asymmetrical contraction of the bell margin playing an important role as well. There is a good direct correlation between the degree of development of the velum and swimming effec-

tiveness, culminating in the great parabolic velum of the trachymedusan *Pantochogon*. In forms with flatter bells, where a velum could not effectively function as a nozzle, it is quite weak or even absent, as in the flat *Obelia*. There are probably historical and functional reasons for the absence of a velum in the Scyphomedusae. Functionally there is a limit to the effectiveness of such a thin flap of tissue in either a relatively flat or a large medusa. In fact it was shown in *Polyorchis* that the velum was less effective as a nozzle in larger individuals (GLADFELTER 1972a, Table 4). As an animal increases in size the volume of water expelled from the subumbrellar cavity increases as the third power of the diameter, whereas the cross-sectional area of muscle containing this water increases only linearly. In the tubular Cubomedusae an annular, centripetal flap, the velarium serves the same functions as the velum, though it is independently derived as discussed above. The existence of this structure is a striking example of evolutionary convergence: a similar structural response to similar functional demands in phylogenetically separate groups. Turning effectiveness is greater in the broad, flat forms such as *Halistaura* (Fig. 6e) or *Chrysaora* (Fig. 14c, d) than in tall forms. The former virtually rotate around a point during turning, whereas the radius of the turning arc generally increases with the height/width ratio: in *Polyorchis* it is at least one bell height, and in *Diphyes* it is much greater.

The morphology of individual epitheliomuscular cells of the swimming muscle is quite variable, but in general the degree of development of the contractile processes is well correlated with swimming effectiveness. The swimming muscle processes vary from a thin filament in the base of the epithelial cell as in *Phialidium* or *Stomotoca* (L. FRASER, unpublished electron micrographs) to ribbon-like processes as in *Polyorchis* (GLADFELTER 1972a) or *Gonianemus* (FRASER 1962) to thick spindle-like processes as in *Pelagia* (KRASINSKA 1914). The arrangements of these contractile elements vary from a very loose mesh as in *Phialidium* or *Obelia* (CHAPMAN 1968), to a fairly well-defined sheet of parallel fibers in *Polyorchis*, to a very tightly structured sheet of fibers with aligned striations in *Diphyes* (Fig. 9a), to a stratum highly convoluted in *Cyanea* (GLADFELTER 1972b). The contractile effectiveness of the swimming muscle is probably a direct function of its cross-sectional (radial) area, and a definite increase in this parameter can be seen in going from loosely spaced cord-like elements (*Phialidium*, Fig. 6c, d), to closely spaced band-like elements (*Polyorchis*, *Gonianemus*, *Liriope*), to very tightly spaced band-like elements (*Diphyes*), to thick closely spaced cord-like elements in very convoluted array (*Cyanea*, GLADFELTER 1972b). Beyond this stage, an increase in cross-sectional area can be achieved by gross folding of the subumbrellar mesoglea parallel to the muscle processes as was seen in an incipient stage in *Scrippssia* and in a more elaborate condition in *Cyanea*. Increase in muscle cross-sectional area is necessitated by one or more of the following if constant locomotory efficacy is to be maintained: (1) Increased size. As the bell increases in diameter its bulk increases as the third power but the amount of swimming muscle only as the second power (cross-sectional area increases only linearly). It was seen in the case of *Cyanea* that in going from small to large individuals the muscle cross-sectional area was increased both by increase in convolution of the muscle stratum and increase in size of the gross mesogleal folds (GLADFELTER 1972b). (2) Increased mesogleal rigidity appears to be an index of increased elastic modulus, hence requires better developed swimming muscle to achieve

a contraction of similar magnitude and duration to that in a softer form. (3) Increased strength of contraction also requires a better developed swimming muscle.

Another response of the swimming muscle to the structure of the whole system is the presence of radially arranged striated fibers in flat bells (*Obelia*: CHAPMAN 1968, *Cyanea*: GLADFELTER 1972b). The functional necessity for this arrangement was discussed by GLADFELTER (1972b).

The role played by absolute size in the swimming effectiveness of medusae has been discussed by GLADFELTER (1972a) and above. In tubular forms, in which the velum has an important role as a nozzle, it has been shown (GLADFELTER 1972a) that smaller forms are much more effective swimmers relative to their size, and that the velum becomes more effective as a nozzle. The ratio of muscle area to mass also increases with decreasing size within one species. This relationship is less clear in other forms, especially very broad or flat ones: young *Cyanea* and the ephyrae of *Aurelia* actually achieved negative velocity toward the end of recovery, whereas this does not occur in the adults.

The structure of the locomotory system imposes the operating limits on swimming ability, but it is the latter on which natural selection operates. At the present time it is not clear what the precise selective agents acting on the locomotory system are, however, the ecological needs for a swimming system are several-fold:

(1) Many forms are slightly negatively buoyant, and some locomotory ability is necessary to maintain the animals in the water column.

(2) It is undoubtedly important for animals to be able to change their position with respect to possible food sources in the surrounding water; the most dramatic example of this is probably the dramatic diurnal vertical migrations undergone by some medusae, probably correlated with optimizing feeding stations.

(3) The ability to escape from a predator may be important, at least to some species. *Aglantha* (Trachymedusae) for example gives a single powerful contraction in response to a probe, which is considerably more effective than the normal type swimming contractions.

(4) Benthonic forms such as *Gonianemus*, *Vallentinia* and *Cladonema* which are adapted to living much of the time attached to benthic vegetation are all very powerful swimmers. Though at first appearing enigmatic, this is obviously important for a form which must retain its station in a fairly restricted stationary environment in the course of strong water movements.

SUMMARY

1. The locomotory systems of forty-two genera of hydro- and scyphomedusae, representing nine orders, were surveyed, to serve as a basis for generalizations about medusan locomotion. The more pertinent of these have been discussed. The comparisons are based on previous studies of *Polyorchis montereyensis* and *Cyanea capillata* (GLADFELTER 1972a, b).
2. The bell ranges from broad and flat to long, narrow and pointed; the mesoglea ranges from soft to rigid. Radial mesogleal fibers are distributed in the regions of

- the bell deformed during contraction, and are most densely arrayed along joint apices. A variety of "joint systems" is present, from none or temporary creases, to permanent exumbrellar creases, to elaborate systems in most Anthomedusae and Scyphomedusae: a classification of mesogleal skeletons was erected.
3. The contractile elements of the swimming muscle vary from widely spaced cord-like elements in weak swimmers to tightly packed ribbon-like processes with aligned striations in small strong swimmers, to thick cord-like elements in closely spaced, highly convoluted array arranged on larger mesogleal folds. Radial swimming muscles are present in flat forms.
 4. The velum (Hydromedusae) or its analog, the velarium (Cubomedusae) is important in forms with strongly arched bells, where it functions as a nozzle during straight swimming and turning. It is less important in broader bells, which, however, can turn in a smaller radius than tall forms.

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