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Fishing, Feeding and Digestion in Siphonophores

by

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6 Figures

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Introduction

There is no doubt that siphonophores are abundant enough in the plankton to play an important role in the economy of the sea, doubtless competing with Hydromedusae in many food chains. However, relatively little has been recorded of their feeding habits, and what is known is scattered through the literature and hard to locate. We here bring together the main facts concerning feeding activities in siphonophores, supplementing this information with material from our own studies.

In referring to « siphonophores » we exclude the pleustonic forms *Porpita* and *Velella* (O. Chondrophora, Totton 1954) which are morphologically and behaviourally quite distinct from true members of the O. Siphonophora.

One of us (D.A.B.) worked during January and February 1961 at the Stazione Zoologica, Napoli; the other (G.O.M.) worked at the Friday Harbor Laboratories of the University of Washington during May and June 1961. The work on *Forskalia*, *Stephanomia* and *Hippopodius* was carried on at Naples, the remainder at Friday Harbor [1].

Methods

Owing to their large size, excitability and powers of autotomy, the siphonophores are among the most difficult planctonic animals to maintain in captivity. However, given favourable conditions, the problems of maintenance can be overcome to a large degree and the colonies can be kept in good condition for periods of several weeks, during which time they feed, grow, mature sexually, etc. Some specimens of *Nanomia cara* Agassiz (Sub-Order Physonectae) were kept alive at Friday Harbor for up to 36 days.

Specimens should be taken from the sea with a pail or bowl; Köllicker (1853,

[1] We record with gratitude the assistance of the British Association for the Advancement of Science in making its Table at Naples available for this study, and of the National Research Council of Canada for providing an operating grant. We further wish to thank the Directors and staff of the two laboratories, who provided all possible aid and encouragement.

p. 11) long ago emphasized the futility of attempting to study siphonophores taken with a net. The transfer to the laboratory should be rapid and the specimens should at all times be protected from bright light, which excites them. A satisfactory culture tank was set up at Friday Harbor, in which the following important features were incorporated (Fig. 1):

1. Fresh sea-water (w) piped into the laboratory through glass was used.

2. The water was filtered (f) through Pyrex wool in a Buchner funnel before entering the tank. If the water is not filtered, sediment may accumulate in the

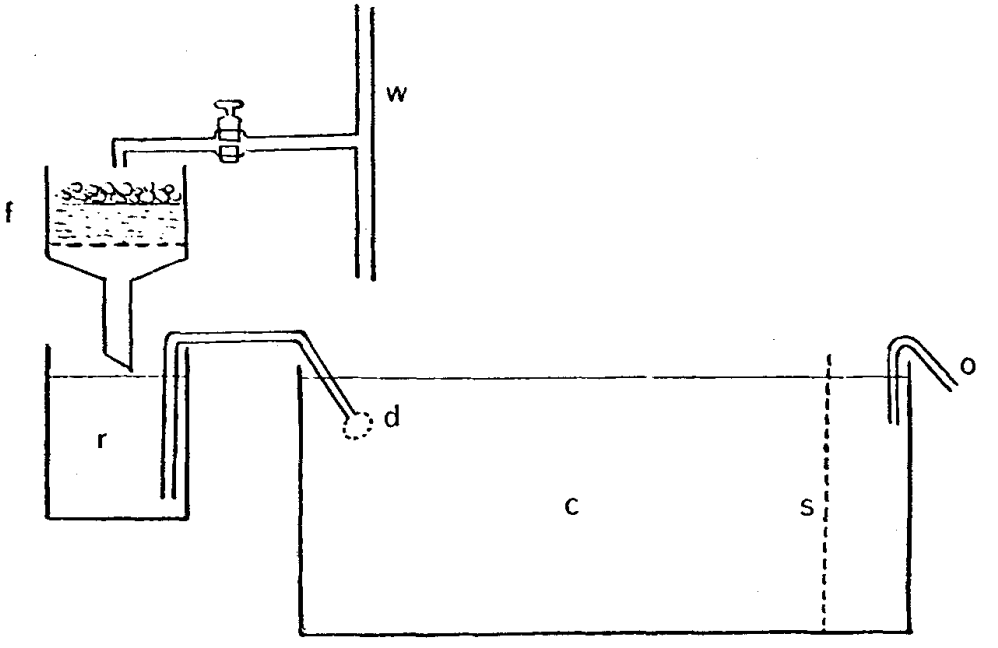

FIG. 1. *Culture tank for siphonophores. c, culture tank; d, diffuser; f, filter; o, outflow; r, reservoir; s, screen; w, water supply.*

culture tank. Particles of sediment adhere to trailing portions of the colonies, causing irritation and autotomy of parts.

3. The filtered water was allowed to collect in a reservoir tank (r) in which small air bubbles trapped during filtration are permitted to rise to the surface and escape. If these small bubbles enter the culture tank, they become lodged in the nectophores and in other regions of the siphonophore, irritating it.

4. The water was siphoned into the culture tank through a diffuser (d, a perforated ping-pong ball), so that turbulence of the inflowing stream was reduced to a minimum. The water flow should be sufficiently fast to prevent the water temperature in the tank from rising more than a few degress above that of the natural habitat. With the cool water (12-14°C) found at Friday Harbor during the period of study, aeration proved unnecessary.

5. The culture tank itself (c) was of 126 L capacity. The colonies of *Nanomia* were thus able to swim several times their own length in any direction from the centre without encountering obstructions.

6. The overflow siphon (o) was guarded by a screen (s) of sufficient area to ensure that colonies were not sucked up against it at any point. Plastic window screening was used for the screen.

At Naples, fresh sea water was not continuously available « on tap » and the colonies could only be kept in satisfactory condition for periods of a few days. Large tanks (75 L) were used. They were kept in a room maintained at 17-19° C. Water was brought in fresh from the sea in large containers, and aeration was employed. The animals were not used for experimental purposes after 48 hours, and they were abandonned earlier if they showed signs of deterioration.

Colonies under culture were fed on particles of fresh crab meat or on small crustaceans such as *Artemia* nauplii, *Tigriopus* etc. Where crab meat was used, the particles were held with forceps and manoeuvred into the vicinity of the gastrozooids, which would then ingest them. *Nanomia* will live and grow on a mixed crustacean diet if each gastrozooid receives a full meal on the average once every three days. The state of distension of the palpons gives an indication of the animals' need for food: when they are filled out with a milky fluid contents there is no need to give further food. Growth of the colony is the best indication of a satisfactory regime, and may be measured by counting the appendages periodically. Under good conditions, a small *Nanomia* will add a new nectophore and a gastrozooid roughly every two days. The steady increase in size shown by carefully maintained specimens is always offset to some extent by accidental loss of parts; the faculty for autotomy is so well developed that one may suppose that shedding of nectophores and bracts (the members chiefly involved — SCHAEPPI, 1906) is probably as common in the natural habitat as it is in the laboratory. MOSER (1925) has pointed out that siphonophores have little regenerative ability. Local closure and healing rapidly follow any injury, but portions shed are not regenerated *in situ*, and badly mutilated members do not regain their proper form. In *Nanomia*, the only appendages found to possess regenerative ability were the palpons, which differentiate a new terminal bulb when the distal portion is amputated. The generally limited capacity for regeneration is doubtless offset by the steady production of new nectosomal and siphosomal members from the budding zones.

OBSERVATIONS

1. *Influence of light on activity*

Many of the free-swimming siphonophores appear to follow the vertical migration of the zooplanktonic organisms on which they feed (Dr. ANITA BRINCKMANN, personal communication, from observations at Villefranche-sur-Mer). More explicit evidence of vertical migration has come from recent studies by Dr. ERIC BARHAM who has descended several hundred fathoms into the water of San Diego Bay, California, in a bathyscaphe and has succeeded in marking correlations between the planktonic forms observed at particular depths and the deep scattering layers located by echo-sounding (BARHAM, *unpublished* [2]). These studies indicate that SIPHONOPHORA occur in sufficient abundance at certain depths to cause definable scattering layers, either by themselves or in association with euphausids or other planktonic organisms. Dr. BARHAM

[2] Since this paper went to press, Dr BARHAM's studies with the bathyscaphe « Trieste » have been published in Science **140**, 3568, 826-828.

has provided one of us (G.O.M.) with specimens for identification, which proved to be *Nanomia* sp. and *Lensia conoidea*. A note accompanying this sample states that the specimens were collected at 200 fathoms in a scattering layer « which descended from the surface at night time ».

Vertical movements of the zooplankton generally follow a 24 hour cycle, and are believed to depend to a large extent on the photosensitivity of the migrating organisms. Thus any ability which siphonophores may possess to respond to light will be of interest in the general context of vertical migration and predato-prey relationships among the migrants.

Experiments on *Nanomia cara* revealed a well-marked photosensitivity in this form. Colonies that had been kept in dim light or in the dark started to swim within 1.5 - 2.0 seconds (measured with a stopwatch) after illumination with a photoflood lamp. The actual incident light intensity was not determined. The burst of activity evoked subsided within half a minute in most cases, and thereafter the animal showed no more than normal activity. No comparable effect on behaviour was seen when illuminated colonies were suddenly plunged in darkness. In an attempt to determine the distribution of photosensitive areas of the colony, specimens of *Nanomia* which had been dark-adapted were illuminated at selected points by means of a microscope lamp focussed to a spot of diameter 3 mm. When the float and nectophores and connecting portions of the stem were illuminated, there was no swimming response. The stem in the posterior regions however, together with appended gastrozooids, palpons and their tentacles and tentillae all showed photoreceptive capacity, and illumination of them led to forward swimming. To produce swimming, the period of illumination had to be in the order of about two seconds. Shorter periods of illumination either produced no behavioural response, or produced local effects such as stem contraction and shortening of the tentacles. These local contractions sometimes preceded the swimming response. Light-depedent locomotory behaviour was also observed in *Stephanomia rubra* and *Forskalia edwardsii*. Again, the response was forward swimming. In *Forskalia*, dark-adapted animals exposed to daylight responded by swimming, but if the swimming animals were then illuminated by an intense articifical light (a 500 W photoflood at close range) they immediately ceased to swim. These observations are of considerable interest from the neurophysiological standpoint, but they are hard to interpret in terms of functional advantage in the life of the colonies in the natural environment. When considering the vertical movement of a siphonophore in the sea, it must be remembered that active swimming is not the only method by which the animal could control its position in space. In many physonects, adjustment of the volume of gas within the float may well be important in bringing about vertical movements. JACOBS (1937) has shown that expulsion of gas bubbles and their resecretion

by the float can lead to vertical movements in *Nanomia* (= *Stephanomia*) *bijuga*.

In the calycophore *Hippopodius hippopus* no sudden or dramatic response to light was observed, but it was found that colonies of this form collected in illuminated areas of the tank, along with other planktonic organisms. A tank kept under diffuse daylight from a west-facing window was blacked out except for a hole at one point. After an hour, all the specimens of *Hippopodius* had aggregated in this area. When the position of the hole was changed, the colonies moved to the new position. It is not at the moment clear what mechanism is responsible for this reaction. *Hippopodius* differs from the physonects in lacking coordinated locomotory movements; the nectophores are never seen to perform locomotory movements in strict concert together (although several may happen to be active at the same time) and in their responses to stimulation they behave independently. Thus, the aggregation in lighted areas can hardly represent behaviour organized on a colonial basis by the integrative action of the colonial nervous system, and we provisionally ascribe it to orthokinesis (FRAENKEL & GUNN, 1940), in which the nectophores, responding independently, show locomotory activity resulting in random movements of the colony; when these movements bring the colony into an area of a certain light intensity, activiy declines, so that the colonies tend to remain in this area. A mechanism such as this, though representing behaviour at a very elementary level, could be important in determining the organisms location in the water mass.

2. *Spreading of the fishing lines*

The surface-living siphonophore *Physalia* can elongate its tentacles to 8-10 metres and shorten them by coiling and contraction 12-15 cm (MACKIE, 1960). When the animal is being blown along by the wind the tentacles stream out for a considerable distance behind. No other « fishing » behaviour has been observed. Among the PHYSONECTAE, spreading of the fishing lines occurs during periods of general quiescence, that is, when locomotion is in abeyance, the stem is extended and the gastrozooids are not showing their « searching » behaviour. It is probably true that for most physonects, as for *Physophora* (VOGT, 1854, p. 48), full extension of the fishing filaments only occurs in still water.

During swimming, the tentacles and tentillae are contracted; in fact this general contraction is frequently a sign that swimming is about to take place. In *Forskalia*, net-spreading includes lateral extension of the long stalks (« pedicles » in HAECKEL's terminology) which carry the gastrozooids. It seems probable that elongation of the appendages is partly a passive process, representing relaxation of the longitudinal muscle systems and partly active, involving

contraction of circular muscle systems so that coelenteric fluid is forced out into the extremities. KÖLLIKER (1853, p. 7) notes that fluids stream down into

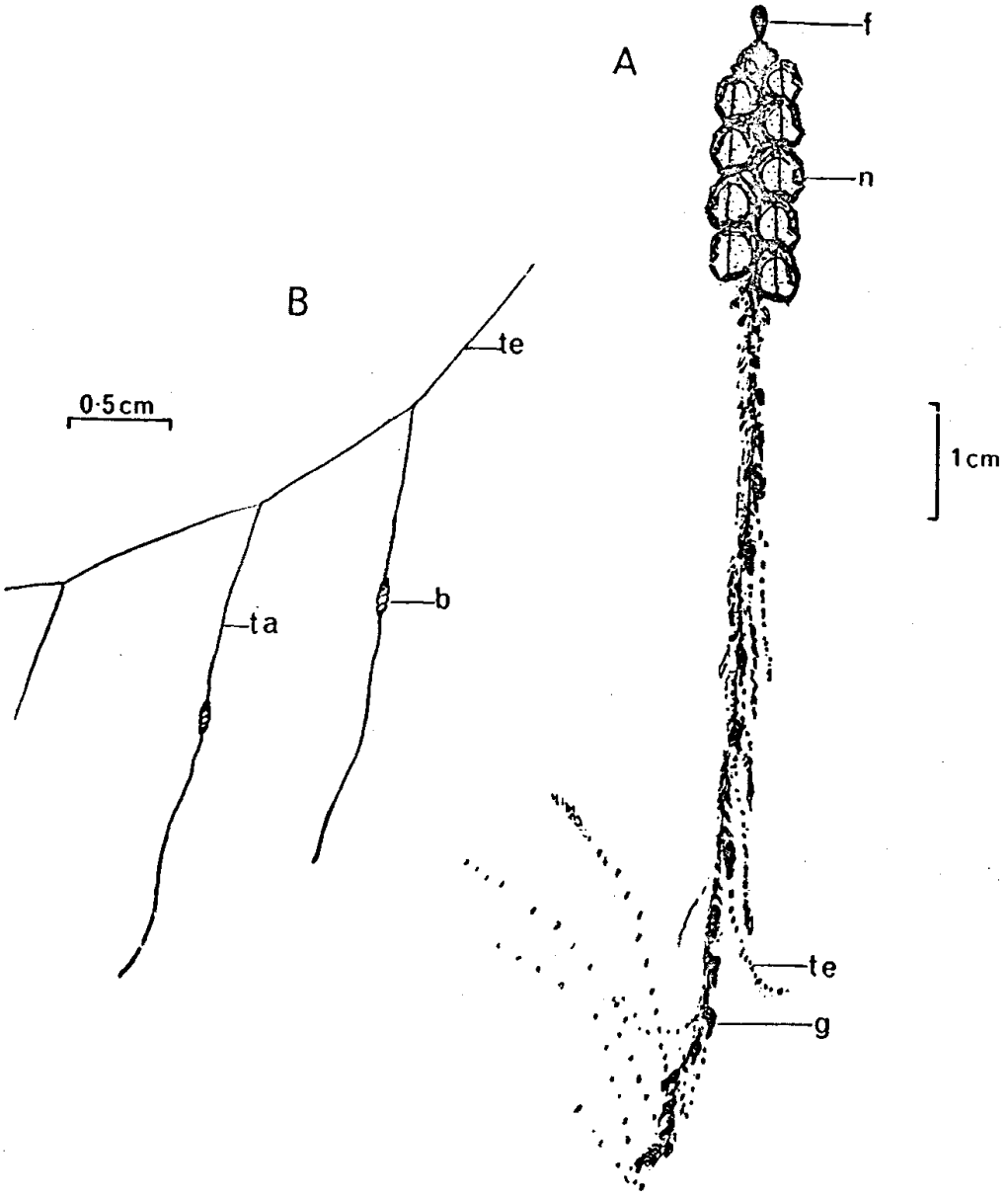

FIG. 2. *Nanomia cara, specimen with nine formed nectophores, illustrated in a natural posture, from a photograph. The siphosome and tentacles are not fully relaxed. B, part of an extended tentacle, showing two tentillae. b, erupting battery of tentilla; f, float; g, gastrozooid; n, nectophore; ta, tentilla; te, tentacle.*

the tentacles when they elongate. Observations on *Nanomia* (Fig. 2, A) in the sea suggest that the spreading is partly brought about by the slight swirling of the surrounding water, or by the residual momentum which carries the

trailing appendages outward after swimming has ceased. The final posture is very variable, and siphonophores may hang at any angle from the vertical to the almost horizontal, depending on the distribution of lighter and heavier parts (BERRILL, 1930; JACOBS, 1937). The siphonophore may hang in the water surrounded by a haze of its extended fishing filaments, or the latter may stream out in the water to one side, if there is a flow of water past the colony. We, like many other observers, have tried to draw or photograph the colonies in a way which would do justice to this remarkable sight, but with meagre success. For *Nanomia*, one of the smallest physonects, the following measurements were made on an extended individual:

Length of extended stem from float to lowest gastrozooid	11 cm
Number of gastrozooid tentacles	10
Av. length of extended tentacles	19 cm
Av. number of tentillae per tentacle	12
Av. length of tentillae, including terminal filament (Fig. 2, B)	2.5 cm
Combined length of all gastrozooid tentacles and their tentillae	490 cm
Number of palpon tentacles	36
Av. length of palpon tentacles	1.5 cm
Combined length of all palpon tentacles	54 cm
Total of all fishing lines	544 cm

For a much larger physonect such as *Stephanomia rubra*, who's stem measures over 1.5 m, the total length of all extended fishing lines would be in the order of 75 m, assuming that the bodily proportions are roughly comparable to those of *Nanomia*.

Observations on the small calycophore *Muggiaca atlantica* in the tanks at Friday Harbor reveals a specialized type of net spreading behaviour, quite different from that which occurs in the physonects (Fig. 3). The stem is shortened and the tentacles are contracted before the movements begin (A). The nectophore then begins to perform a rapid series of swimming movements and simultaneously the stem and tentacles start to relax, the posterior ones first (B and C). The drag caused by the elongated appendages causes the nectophore to veer round in an arc of diameter 1-1.5 cm (D). The appendages are now fully relaxed and spread out centrifugally. Swimming abruptly ceases, and the bouyancy of the nectophore brings it round into the vertical position (E) dragging the upper part of the stem with it, but the greater part of the stem and appendages remain « frozen » in the position assumed during the preceeding movements. Gradually the weight of the stem causes it to sink more or less vertically below the nectophore and the configuration gradually dissolves (F). Water movements accelerate the process, but in still water the configuration (named the « veronica » after the bull-fighter's pass which it resembles) will be maintained for several minutes. The net-spreading mo-

vements themselves last only a few seconds. The activity is repeated fairly regularly by specimens in still water in the laboratory. Speciments sometimes dart around with shortened stem (as in A) for some distance before release of the net (B) ensues, but locomotion invariably ceases when the tentacles

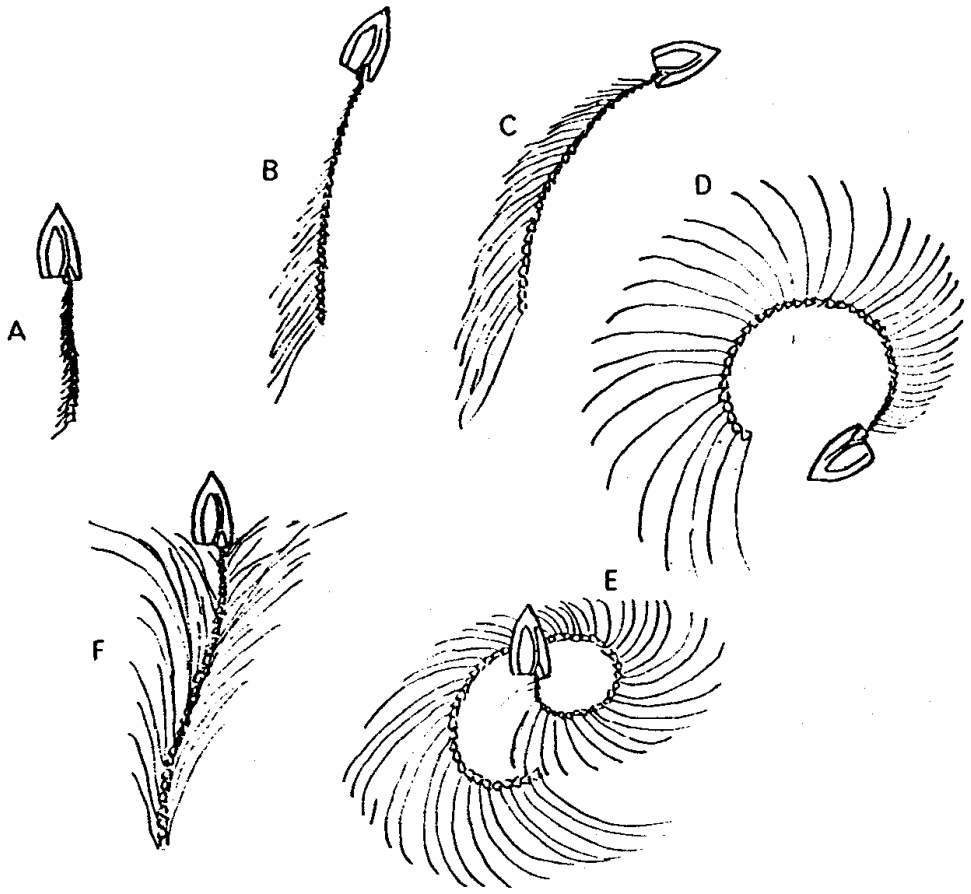

FIG. 3. *Spreading of the fishing filaments in Muggiaea (« veronica » display). For explanation see text.*

have extended to the degree shown in D. The movements may be executed in any plane, not just in the vertical plane as shown here.

Nothing exactly comparable to *Muggiaea*'s «.veronica» has been seen in other CALYCOPHORA, although a diphyid (*? Chelophyes appendiculata*) observed at Naples performed rather similar movements. Only the anterior of the two nectophores was active when the colony executed these movements.

3. *Capture and manipulation of prey*

Physonectid siphonophores spend long periods with their fishing filaments outspread, during which the only movements seen are local shortenings and

elongations of the tentacles and tentillae. KÖLLIKER (1853, p. 5) states that in *Forskalia* the gastrozooids writhe and twist in a variety of postures while the colony lies waiting for prey. However, this has not been our experience. Gastrozooid activity in *Forskalia* as in *Physophora* (KÖLLIKER p. 22) *Nanomia* and *Stephanomia* generally begins only when food has been captured. VOGT (1854, p. 52, 63) gives a vivid account of the regular changes in length of the filaments, which he likens to the casting of a fisherman's line. Similar movements occur in *Physalia* (BIGELOW, 1891; MACKIE, 1960), but they do not appear to occur in members of the CALYCOPHORA.

The actual capture of food has not often been described, possibly because specimens in captivity are usually too disturbed to feed. It is well known that *Physalia* feeds on fishes, often of considerable size, a process well described and photographed by WILSON (1947). For the much more delicately constructed planktonic siphonophores fishes are probably less used as food, although LEUCKART (1853, p. 13) provides a redevant note, of which the following is a translation: « In the gastrozooids of *Stephanomia* [*Forskalia*] *contorta* I have often found fish more than an inch in length, part of which protruded through the mouth opening, in spite of which everything was digested down to the skeleton ». In cases such as this, one suspects that several gastrozooids may have cooperated in the preliminary stages of digestion, as in *Physalia*, one of them being left with the skeleton after the others had detached. However, the individual gastrozooid has a surprising capacity for engulfing large objects (Fig. 6, H).

An important component of the diet is undoubtedly crustacean microplankton, which several authors name as the chief food. VOGT (1854, p. 52) states that small medusae are also consumed. The same author further records (p. 64) that he kept *Stephanomia rubra* for two or three days and fed them on small crustaceans. In our own studies we have found that *Forskalia* will capture and consume *Artemia* nauplii. Larvae coming in contact with a tentillum are immediately paralysed and held to the tentacle, which then undergoes stepwise shortening in the region proximal to the point where the prey is attached. Before the prey has come within reach, the gastrozooid begins to elongate and to writhe around in all directions (Fig. 6, E). As soon as contact is made, the prey is rapidly ingested. In *Stephanomia*, *Artemia* were transferred in a similar manner, but often continued to struggle, even while entering the mouth. It was also observed in this form that transfer of prey from tentacles to gastrozooids was apparently aided by discharge of nematocysts from around the oral region of the gastrozooid. Many physonects, and *Physalia* (HUXLEY, 1859) possess nematocysts in this region. *Nanomia* catches *Artemia* larvae, but only with the small tentacles of the palpons; transfer to and ingestion by the gastrozooids are, however, accomplished perfectly efficiently. *Muggiaea* avidly accepts the small copepod *Tigriopus*.

Close observations on *Nanomia* show that the writhing (searching) action of gastrozooids can be elicited in two ways, tactile and chemical. Electrical stimulation of a tentacle will cause eruption of adjacent nematocyst batteries. This

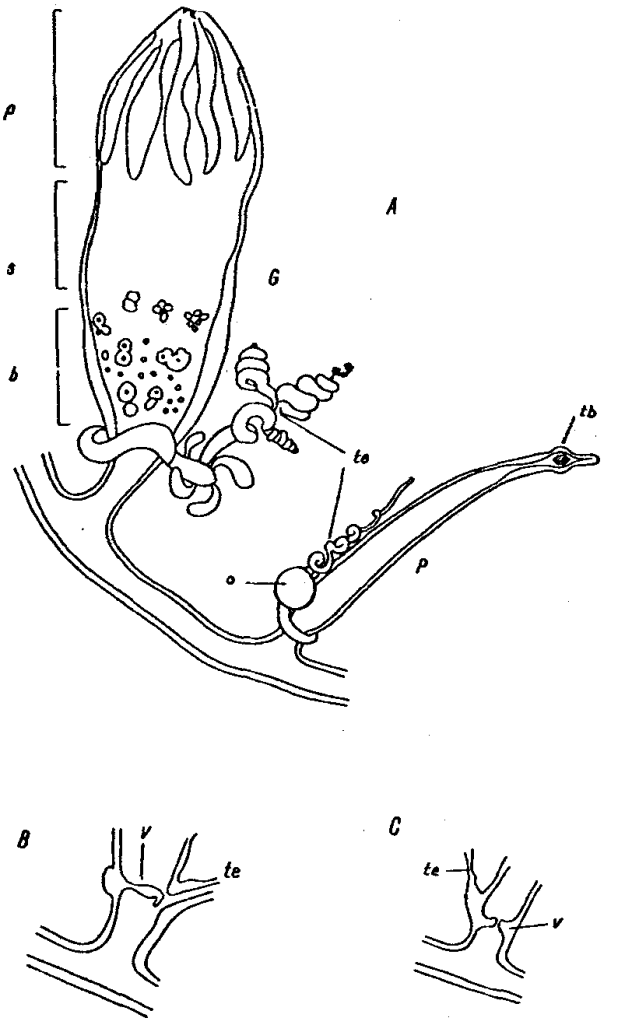

FIG. 4. *A. Portion of stem bearing a gastrozooid (G) and a palpon (P). B. optical section of base of gastrozooid, to show valve. C. similar view of palpon. b, basigaster; o, oil-filled vesicle; p, proboscis; s, stomach, tb, terminal bulb; te, tentacle; v, valve.*

is followed by shortening of the tentacle and, after one or two seconds delay, by the writhing behaviour of the gastrozooid to which the tentacle is attached. The excitation spreads along the stem to a variable number of gastrozooids on either side. Alternatively, the searching activity can be elicited chemically by putting fresh crab tissues or body fluids into the water. Low concentrations

of reduced glutathione are also effective as LENHOFF & SCHNEIDERMAN (1959) showed for *Physalia*. In the natural state both mechanical and chemical stimuli are doubtless involved in eliciting the response. The process of ingestion itself appears to be largely or wholly mechanical for in the physonects as in *Physalia* excited gastrozooids will spread out their mouths and attempt to engulf, often with success, wholly unsuitable objects with which they come in contact. *Nanomia* under the influence of crab body fluids was once observed to ingest a large bunch of its own tentacles; the latter were not damaged by this tretment but, passing through the stem canal, entered a neighbouring palpon and from there began to emerge once more to the outer world, via the terminal orifice. Occurrences such as this lead some to speak of the siphonophores as « unintegrated », but one cannot generalize from laboratory freaks and, in fact, the colony in very far from unintegrated, particularly where locomotion is concerned (MACKIE, in press).

FIG. 5. *Caught in the terminal filament, a copepod (Calanella) hangs transfixed by nematocysts from the erupted battery of Stephanophyes superba (after* CHUN*). b, battery; e, elastic band;* ta, tentilla; tf, terminal filament.

Outstanding problems face students of the SIPHONOPHORA in the field of nematocyst function. The nematocysts are not only widely distributed in the general ectoderm of many regions, but in the PHYSONECTAE and CALYCOPHORA they are also found in large batteries (Fig. 2, B) mounted on the tentillae, in association with an elaborate and largely mysterious system of elastic bands and muscle strands capable of rapid uncoiling and elongation. Thus, in the tentillae, we are concerned not simply with nematocyst discharge but also with the often simultaneous, but quite distinct, eruption of the supporting apparatus of the battery as a whole. Similar but simpler erupting mechanism seems to occur in the marginal cirri of certain LEPTOMEDUSAE (Fam. MITROCOMIDAE). It should be noted that the so-called « batteries » found on the tentacles in *Physalia* [1], *Gonionemus* etc. are not true erupting batteries, but are simply large aggregations of nematocysts.

The structure of the tentillar batteries was explored in detail by LEUCKART (1853) and by others both in that prolific decade and since, the more recent being KOROTNEFF (1884), CHUN (1891) and SCHNEIDER (1892). In spite of the mass of information obtained the process of eruption is still not understood. The

[1] LANE & DUDA (1958) provide a toxicological study of the *Physalia* nematocysts.

batteries are said to contain nerve cells, but to suggest that these elements have anything to do with eruption of the battery or with discharge of the nematocysts would be entirely speculative. In our own studies, we have noticed that batteries erupt under electrical stimulation, but that this is not necessarily accompanied by discharge of more than a few of the nematocysts. CHUN states that once a battery has been erupted (Fig. 5) it cannot be coiled up and used again. If this is true, it is hard to explain the fact that in dozens of specimens of *Nanomia* examined at Friday Harbor, none were found with gaps in the row of tentillae such as one would expect to find if these structures are abandoned after use. Obviously much remains to be discovered regarding the role of the batteries in feeding. *Stephanophyes superba*, studied by CHUN, has two distinct sorts of battery, each with its own characteristic cnidome. In the main batteries, there are at least 1164 nematocysts, representing four different sorts. *Nanomia*, collected at Friday Harbor and studied by phase contrast microscopy, proved to have six different types of nematocyst on the tentillar battery, including a large eurytele which discharges a filament 6 mm long. In addition, hook-like attachment structures, not previously described, occur in one part. As reported above, attempts to get *Nanomia* to catch food with its tentillar batteries were unsuccessful, although the small tentacles of the palpons were used to catch *Artemia*. The palpon tentacles contain only one sort of nematocyst, a small isorhiza. It is puzzling to find that identical isorhizas occur in several other parts of the colony, such as the bracts and nectophores, where they cannot possibly play any part in food capture.

Under what conditions *Nanomia* employs its tentillar batteries and their formidable armament is a problem calling for careful study, using well-maintained specimens. The extreme morphological complexity of the structures implies the existence of a mechanical performance of equal elegance and intricacy.

4. *Digestion*

The histology of the digestive organs in siphonophores was studied intensively by the nineteenth century workers but in only one case (WILLEM, 1894) do we find what would now be regarded as a functional or physiological approach to the process of digestion. The matter has fared little better in the present century and a thorough histo-physiological investigation is still needed. *Physalia* (CYSTONECTAE) has attracted more attention than other members of the Order (reviewed by MACKIE, 1960) and Dr. CHARLES LANE and associates at the University of Miami are now engaged in general biological studies on *Physalia* which will certainly throw new light on digestive processes. We will confine ourselves therefore to discussion of the PHYSONECTAE and CALYCOPHORA.

(a) PHYSONECTAE. Two of the polymorphic components of the colony are

involved, the gastrozooids and the palpons (Fig. 4, A). Both are polypoid in origin and are equipped with tentacles, but ingestion is carried on solely by the gastrozooids. HAECKEL (1888) distinguished two types of palpons, those with terminal openings which he called « cystons », reserving « palpons » for those

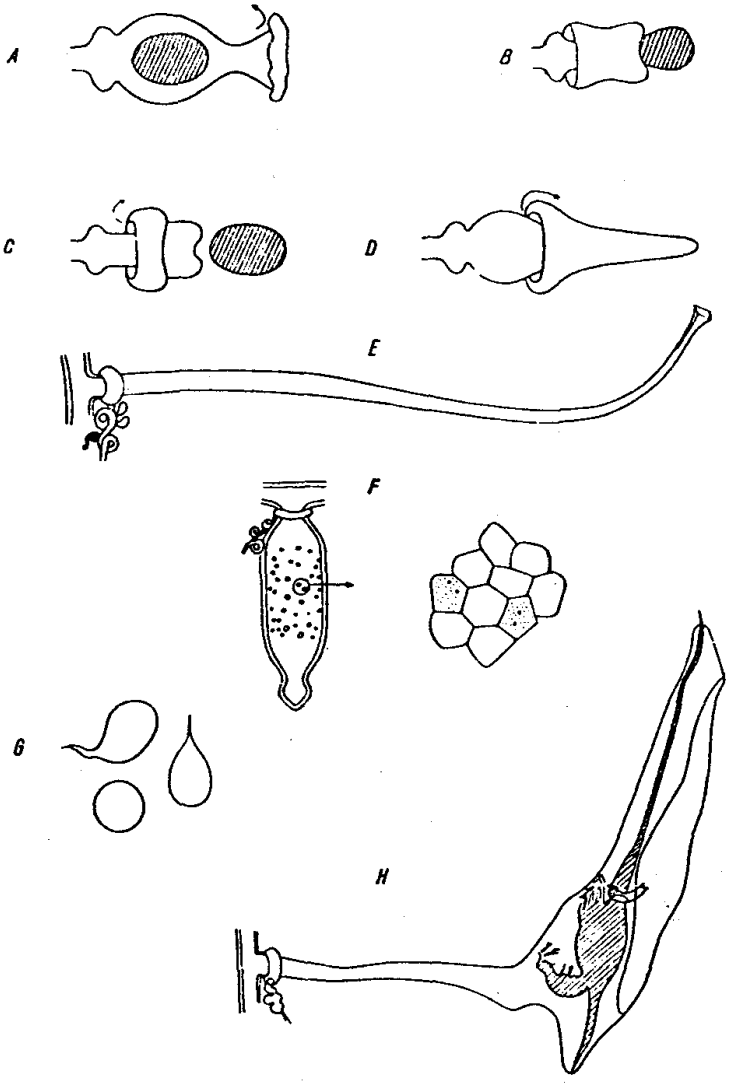

FIG. 6. *A-D, stages in egestion of food bolus from gastrozooid (explained in text); E, elongated gastrozooid, as in « searching » behaviour; F, scattered cells in the palpon endoderm which take up carmine particles; G, holocrine secretion bodies from palpon endoderm; H, gastrozooid engulfing a zoaea larva (sketches from life).*

without such openings, but as CHUN notes (1889-1897, p. 289) nearly all of these structures have since been found to have openings, and are in fact « cystons ». For some reason, however, HAECKEL's word « cyston » has not been generally adopted although it would have the attraction that, unlike « palpon », « Fühler », « taster » etc., it carries no implication that the organ is primarily concerned

with the reception of tactile stimuli, which is certainly not the main function in most cases.

In a form such as *Nanomia*, and probably in all Physonects, digestion involves two phases: Phase 1, in which the food, taken into the gastrozooid, is broken up extracellulary, and Phase 2, where particulate matter is taken up by cells in the palpons and gastrozooids and is subjected to intracellular digestion. The products of the second stage of digestion appear to be returned to the gastrovascular fluid, by means of which they are dispersed all over the colony. WILLEM (1894) gave the first and only published experimental evidence for these two aspects of digestion, using food soaked in Indian ink to facilitate observation. Siphonophores are so transparent that the movement of coloured objects inside the gastrovascular system can be followed easily and without damage or disturbance to the colony.

The disposal of waste materials is carried out in two ways. Large objects which resist the preliminary extracellular digestion are egested through the mouth. Disposal of smaller particles that get into the general circulation occurs by way of the palpons. Such particles, e.g. pigmented matter from the eyes and chromatophores of prey, discharged nematocysts taken in with the food etc. accumulate by ciliary action in the terminal bulb of the palpon (Fig. 4, A. *b*) and are discharged through the terminal orifice. CHUN (1889-1897, p. 315) cites METSCHNIKOFF as the first to observe this phenomenon, but KÖLLIKER (1851, p. 8) describes it in *Forskalia* and correctly comments « Ohne Zweifel ist diese rothe Substanz ein Excretionsstoff » (see also LEUCKART, 1853, p. 17). The role played by cilia in the digestive processes has never been studied in detail. The very abundant and strong cilia of the buccal region of gastrozooids probably assist in the engulfment of food, and the ciliary accumulation of excretory particles in the palpon tips has been mentioned. All other parts of the endoderm are ciliated, and it is quite possible that the ciliary beat is regionally polarized as in the radial canals of some HYDROMEDUSAE (e. g. *Gonionemus* — MACKIE & MACKIE, in press) in such a way that a single tube can have particles moving in opposite directions on the two sides.

The sequence of events during digestion was studied in a specimen of *Nanomia*. The specimen was kept in a large finger bowl. It was examined continuously over the first hour, and at frequent intervals thereafter. When not being examined, it was kept cool on the water table. The observations are given here as they were recorded at the time.

Time (minutes)

0 Carmine-infiltrated crab muscle fed to one gastrozooid.
1 food ingested.
3 food in basigaster beginning to disintegrate.

5 rhythmic pumping movements of the gastrozooid begin, and some of the food matter is flushed out into the stem canal, through the open basigastral valve (Fig. 4, B).

10 palpons in the vicinity of the fed gastrozooid begin to show rhythmic flushing movements, similar to those of the gastrozooid. The particles of carmine and food matter can be seen passing to and fro between the gastrozooid and various palpons, via the stem canal. The gastrovascular canals throughout most of the colony are now coloured pink with carmine.

25 within the space of a few minutes, three palpons discharge carminé particles from the terminal orifice.

35 the gastrozooid starts to eject the food bolus (Fig. 6 A-D). Its basal valve is shut and the rhythm is in abeyance, but the palpons continue to show rhythmic movements.

45 the gastrozooid, having ejected the bolus, is active again, flushing at its original frequency. Five palpons have now eliminated matter.

50 carmine is observed to have accumulated in the cytoplasm of certain cells in the endoderm of the palpons (Fig. 6, F) and gastrozooid. No carmine uptake is visible elsewhere, although some free carmine is still present in the coelenteric fluid. (No further event of importance was recorded until three hours later).

240 A number of cells in the endoderm of both palpons and gastrozooids are now visibly refringent and distended. They detach from the epithelium and float away free in the enteric fluid (Fig. 6, G) where they disintegrate within about half a minute. These are not the same cells which had taken up carmine particles.

270 The cells which had accumulated carmine now also detach and disintegrate. Carmine is loose once more in the coelenteric fluid and is accumulating in the terminal bulbs of the palpons. The rhythmic movements continue.

Next day, after sixteen hours, the palpons were still visibly distended with a fluid of a slightly milky appearance, and traces of carmine were visible in the palpon tips.

These observations confirm the role of the palpons as accessory digestive organs and as organs of elimination. The terminal bulb is clearly a region specialized for the accumulation of waste matter. The rhythmic movements seen throughout the main course of digestion serve to mix and distribute the matter undergoing digestion. The rhythms of the various members differ. The gastrozooid in the study quoted above showed a filling phase of 20-25 seconds, and an emptying phase of 9-16 seconds. The palpons possessed their own inherent rhythmicities, but those in the immediate vicinity of the gastrozooid were observed to fall under the latter's influence, emptying when it filled and filling when it emptied. Members can withdraw from the communal flushing activity by closing their basal valves. They do so when they are eliminating wastes. Elimination of waste matter from the palpon occurs by a modification of the filling and emptying cycle, in which the basal valve (Fig. 4, C) is shut during « filling », opening during emptying. After a few such cycles, nearly all the fluid has been pumped back into the stem canal. A peristaltic ripple then runs down the palpon from base to tip, and the waste matter is expelled. The basal valve

of the palpon then relaxes, and the normal flushing rhythm is resumed. Gastrozooids expel large boluses (Fig. 6) by folding back the buccal fringe over the basal part, simultaneously contracting the base (A, B). When the bolus has been expelled the lip region begins to move back again in the distal direction (C). For a time the wall of the organ is doubly flexed (C, D). The uptake of carmine by certain cells presumably occurs by phagocytosis. The observation that the stomach region of the gastrozooid has this ability is interesting in view of CLAUS' finding (1878, p. 37) that discharged nematocysts are sometimes found in the endoderm cells of this region. Claus deduced that the nematocysts had come in with the food and had then undergone phagocytosis. In *Apolemia*, CHUN (1889-1897, p. 114, pp. 312-313) and WILLEM (1894) have described a remarkable type of cell in the palpons which possesses a ciliated funnel capable, according to WILLEM, of accumulating particles into cytoplasmic vacuoles. One must suppose that the phagocytosed food continues to undergo digestion by a rather slow process of intracellular enzymatic breakdown. Electron micrographs of the palpon endoderm show disintegrated matter in intracellular vacuoles. The cells in question possess a very rich endoplasmic reticulum of the « rough » type (having abundant ribosomes lining the membranes) reminiscent of other zymogen cells such as the acinar cells of the pancreas. The detachment of cells from the endoderm evidently constitutes a form of holocrine secretion by which the products of intracellular digestion reenter the enteric fluid. The tadpole shape of the newly extruded cell (Fig. 6, G) is brought about by pressure from the surrounding cells during expulsion.

The details of the intracellular stage of digestion are still somewhat obscure, and the process of absorption of the final breakdown products has not been studied. Presumably the cells of the endoderm in all the non-digestive organs are capable of absorption from the enteric fluid. Visible particles in the fluid can be seen moving around in all parts of the colony. Several of the earlier workers saw globules and particulate matter moving in the canals and VOGT (1854, p. 81) was able to detect a regular surging to and fro of material, doubtless caused by rhythmic flushing movements of the feeding appendages. However, there is no evidence that particles or globules are taken into the cells in regions other than the gastrozooids and palpons, and it may be assumed that only dissolved material can be absorbed in most regions. It is uncertain what capacity the siphonophore has to store material, either intracellularly or extracellularly. Oil drops derived from the food accumulate in a vesicle near the base of the palpon in *Nanomia* (Fig. 4, A) but in no other form. It is possible that they serve for buoyancy rather than as a food reserve. The vesicles may contain much, little or no oily matter, probably depending on the type of food recently consumed.

(b) CALYCOPHORA. We have made no detailed observations on digestion in this group and previous studies have left considerable areas of uncertainty.

In contrast to the PHYSONECTAE, the CALYCOPHORA lack palpons. It is very possible that they have an accessory digestive organ in the « somatocyst » (ROSE, 1931) but there are several different sorts of « somatocyst » and other possible functions have been proposed. Presumably the gastrozooids are the main digestive organs, as in the PHYSONECTAE. METTEY & HAMON (1949) studied the cytology of the gastrozooid in *Abylopsis*. In the buccal region they found gland cells, believed to produce a viscous material serving for the agglutination of prey. A variety of cell-types occur in the middle, or stomach, region, which the authors believe to represent a single basic type of cell seen in various stages of a secretory cycle. Both holocrine and merocrine modes of secretion are described. In the basigaster, the cells appear to be absorptive rather than secretory. METTEY & HAMON do not state whether their observations were made on gastrozooids that had been starved or fed recently, and they did not follow the process of digestion *in vivo*. Thus it is not easy to interpret their cytological and cytochemical findings in terms of digestive physiology. They make no reference to intracellular digestion in *Abylopsis*, but cite observations by EHLE describing the phenomenon in *Hippopodius* and *Praya*.

We have observed *Muggiaea* ingest food. The process is similar to that described in PHYSONECTAE and CYSTONECTAE. METTEY & HAMON note for *Abylopsis*, and we have observed in *Muggiaea*, that the gastrozooids at times adhere to inanimate objiects by their probosces. We have seen rhythmic passage of fluids up and down the stem canal in *Muggiaea*, and attribute this to the activity of the gastrozooids.

SUMMARY

Siphonophores were observed in carefully maintained culture tanks in a study of activities related to feeding. In several forms behavioural responses to light were also noted. Like the crustacean microplankton on which it feeds *Hippopodius* aggregates near illuminated windows in a darkened tank. In a fully extended *Nanomia*, the combined length of all fishing filaments is estimated to be nearly fifty times the lenght of the stem. In *Muggiaea*, spreading of the fishing lines is achieved by a series of precisely executed movements having the character of a specialized behaviour pattern. Capture and manipulation of prey were observed and are discussed. Both chemical and tactile stimuli are effective in evoking feeding behaviour in the gastrozooids of *Nanomia*. In the same form, digestion of food was studied, using carmine as a tracer. After a preliminary extracellular digestion in the gastrozooid, food matter is pumped rhythmically in and out between palpons and gastrozooids, during which intracellular uptake of particles by cells in both types of nember occurs. Subsequently, cells detach from the endodermal lining and disintegrate, this being interpreted as a form of holocrine secretion in which intracellularly digested material reenters the enteric fluid for final absorption elsewhere in the colony. Particulate wastes are expelled from the palpon tips.

Zusammenfassung

Siphonophoren wurden zur Untersuchung ihres Fütterungsverhaltens in sorgfältig unterhaltenen Kulturgefässen beobachtet. In einigen Arten wurden auch Reaktionen auf Lichtreize untersucht. Ebenso wie das Crustazeen-Mikroplankton, das seine Nahrung bildet, versammelt sich *Hippopodius* im sonst verdunkelten Behälter an der Fensterseite. In einer voll ausgestreckten *Nanomia* wurde die kombinierte Länge aller Fangfäden auf das fast 50fache der Stammlänge geschätzt. In *Muggiaea* wird die Ausstreckung der Fangfäden durch eine Reihe genau abgestimmter Bewegungen vermittelt, die den Charakter eines spezialisierten Verhaltensmusters aufweisen. Fang und Verarbeitung der Beute wurden gleichfalls beobachtet und werden beschrieben. Chemische wie auch Tastreize sind an der Verursachung des Fütterungsverhaltens der Nährpolypen von *Nanomia* beteiligt. In dieser Art wurde auch die Verdauung der Nahrung untersucht, unter Verwendung von Karmin als Markierung. Nach einer extrazellulären Vorverdauung im Nährpolypen werden die Nahrungsstoffe rhythmisch zwischen den Tastern und Nährpolypen hin- und hergepumpt, während gleichzeitig intrazelluläre Aufnahme von Partikeln durch die Zellen der beiden Polypensorten stattfindet. In der Folge lösen sich Zellen von der Entodermschicht ab und desintegrieren. Dieser Vorgang wird als eine Art holokriner Sekretion betrachtet, indem intrazellulär verdautes Material wieder in die Leibeshöhlenflüssigkeit eintritt, um schliesslich anderswo in der Kolonie absorbiert zu werden. Partikuläre Abfallstoffe werden an den Spitzen der Taster ausgeschieden.

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