

A TWO-TENTACLED, COMMENSAL HYDROID FROM CALIFORNIA (LIMNOMEDUSAE, PROBOSCIDACTYLA)

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INTRODUCTION

The new hydroid, *Proboscidactyla* sp., which is the subject of this paper, was found living upon the tubes of a sabellid polychaete, *Pseudopotamilla ocellata* Moore, at Pacific Grove, California. The authors were able to collect and observe colonies during the summer of 1949 at the Hopkins Marine Station, and living colonies secured in September of that year were brought to Berkeley, California, for photography and further study.

The genus *Proboscidactyla* was established by Brandt (1834) for a new medusa, *P. flavicirrata*. Somewhat later Forbes (1846) described another medusa, *Willsia stellata*, for which he established the family Willsiadae. The generic name *Willsia* was changed to *Willia* by A. Agassiz (1862) because of an orthographical error on Forbes' part, and the family name then became Williidae. This family later came to include both *Willia* and *Proboscidactyla*. The Williidae were monographed by Browne (1904), who included six species of *Proboscidactyla* and two of *Willia*.

One of the most recent considerations of the family is that of Kramp (1940), who reviews the history of the Williidae and places this family with the families of Olindiidae and Moerisiidae in the suborder Limnomedusae, a group equal in rank to the Anthomedusae and Leptomedusae. Kramp defines the Limnomedusae as follows (p. 506):

"Hydrozoa with alternation of generations. The asexual generation is a sessile polyp with ability of asexual reproduction, with or without tentacles; the endoderm of the tentacles, when present, is in direct connection with that of the gastral cavity. The sexual generation is a velar medusa with hollow tentacles; gonads either on the walls of the stomach with perradial continuations along the radial canals, or on the radial canals alone; in the latter the umbrella-margin is provided with internal statocysts with an endodermal axis."

The suborder Limnomedusae was established by Kramp to include certain rather aberrant hydromedusans. This group seems to stem from both the Anthomedusae and Leptomedusae and may be polyphyletic.

Kramp (1940) also defines the family Williidae as follows (p. 509):

"Limnomedusae without statocysts; stomach with perradial lobes extending along the proximal parts of the radial canals; gonads surrounding the stomach and its lobes; radial canals branched; tentacular bulbs without ocelli."

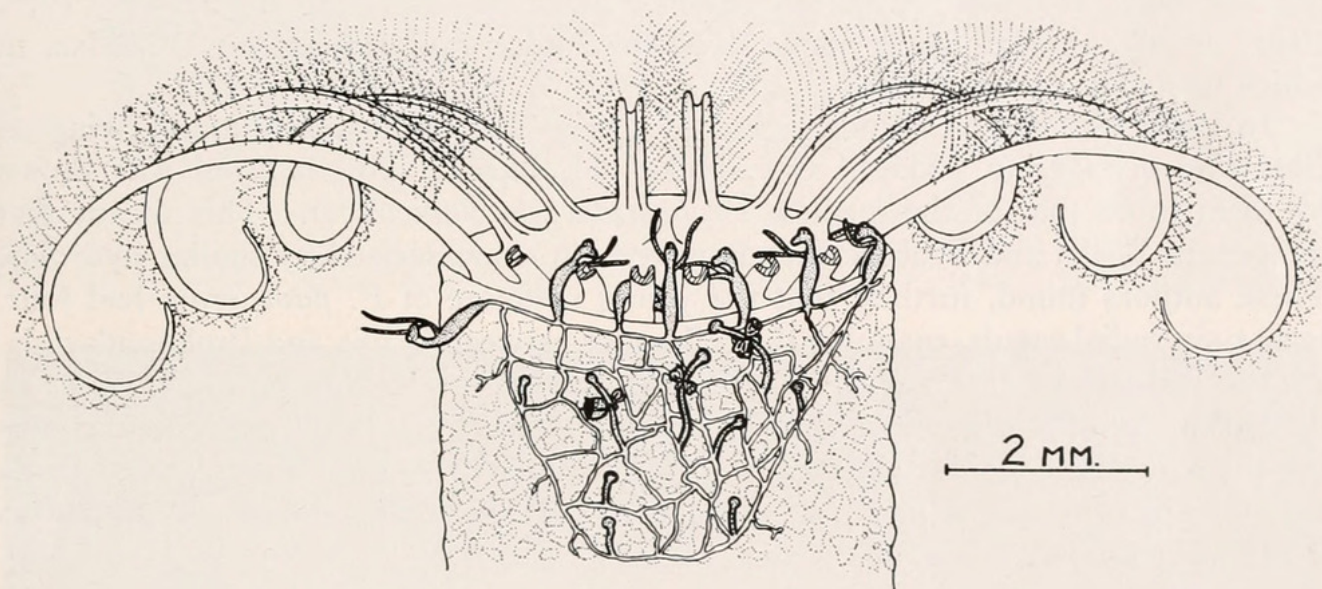
The two genera of the Williidae were initially separated on the basis of the number of primary radial canals; *Willia* having six and *Proboscidactyla* four.

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Some interesting information on the relationship of the above two genera was brought forth in a study of *Willia mutabilis* by Browne and Kramp (1939). In studying over 100 specimens they found 22 of these medusae with six primary radial canals and 41 with eight apparently primary radial canals. In the latter group, however, it was found that of the eight canals only four were truly primary, the other four arising not directly from the stomach but as branches of the primary canals, and thus being secondary in origin. Browne and Kramp also found specimens with 5, 7, 9, 10 and 11 apparently primary radial canals. The above data were taken by Browne and Kramp to mean that "The limit between the two genera *Willia* and *Proboscidactyla* is not so sharp as formerly supposed . . ." (p. 310), and that the species under study ". . . even tends to efface the limits of the two genera" (p. 302).

Until 1941 only two hydroids had been associated with the Williidae, and only in one case (*Willia stellata*) had the hydroid been shown to give rise to a specific



TEXT FIGURE 1. A colony of *Proboscidactyla* sp. in place upon a tube of *Pseudopotamilla ocellata*. Several of the worm's tentacles have been cut away, and the number of tentacles shown on the worm is reduced from the natural condition.

medusa of this family. This latter hydroid was first described as *Lar sabellarum* by Gosse (1857), who found it growing upon the tube of *Sabella vesiculosa* which he was keeping in his aquarium. According to E. T. Browne in "Plymouth Marine Fauna," 1931, *Lar* occurs on *Potamilla torelli*.

The generic name *Lar* was derived from the Roman "Lares" (household gods), and is particularly apt when one considers the oddly human appearance of this hydroid. Gosse noted that this hydroid had ". . . a most ludicrously-close resemblance to the human figure," and described its activities as follows (p. 113): "The head lobe moved to and fro on the neck; the body swayed from side to side, but still more vigorously backward and forward, frequently bending into an arch in either direction; while the long arms were widely expanded, tossing widely upward, and then waved downward, as if to mimic the actions of the most tumultuous human passion." Plate I, Figure 1 reproduces Gosse's figure of a colony of *Lar*

upon the extremity of a tube of *Sabella vesiculosa*; as will be seen later, this hydroid closely resembles the form to be described in this paper.

The production of medusae by the hydroid *Lar sabellarum* was described by Hincks (1872), who noted that the medusae produced were similar to *Willia stellata*. Browne (1896), in a thorough study of the growth of *Willia stellata*, was able to show clearly that the medusa of *Lar sabellarum* actually was *Willia stellata* and so *Lar sabellarum* became a synonym of *Willia stellata*. The family Laridae, which had been established for the hydroid Lar was thus invalidated, although Fraser (1918, 1946) continued to use Gosse's Lar and Laridae.

The second known hydroid of the Williidae was described by Mereschowsky (1877) as *Monobrachium parasitum*, for which he created a new family, Monobrachiidae. This hydroid differs from Lar in that it possesses but one tentacle, produces medusae with four primary radial canals and is found around the siphons on the shells of small subtidal bivalved molluscs. This hydroid is thought to be a Proboscidae because of the branching radial canals of its medusa, although it has not been associated with any specific adult medusa. Again Fraser (1918, 1946) recognizes the family name Monobrachiidae rather than the Williidae, of which he makes no mention.

In 1941, Uchida and Okuda described a new "Lar" which they found living on *Potamilla myriops* in Akkeshi Bay, Hokkaido, Japan. This hydroid was shown by them to be that of the medusa *Proboscidae flavicirrata*. This meant that the genera *Willia* and *Proboscidae* were both characterized by similar hydroids. These authors found, further, that the young medusae of *P. flavicirrata* had four, five or six radial canals, spanning the difference between *Willia* and *Proboscidae*. On the basis of the above evidence, plus the data of Browne and Kramp (1939) on the variability of *Willia mutabilis*, Uchida and Okuda united the two genera, adopting the name *Proboscidae* because of priority. Although not stated by Uchida and Okuda, the family name should accordingly be changed from Williidae to Proboscidae.

DESCRIPTION

a. *Habitat*

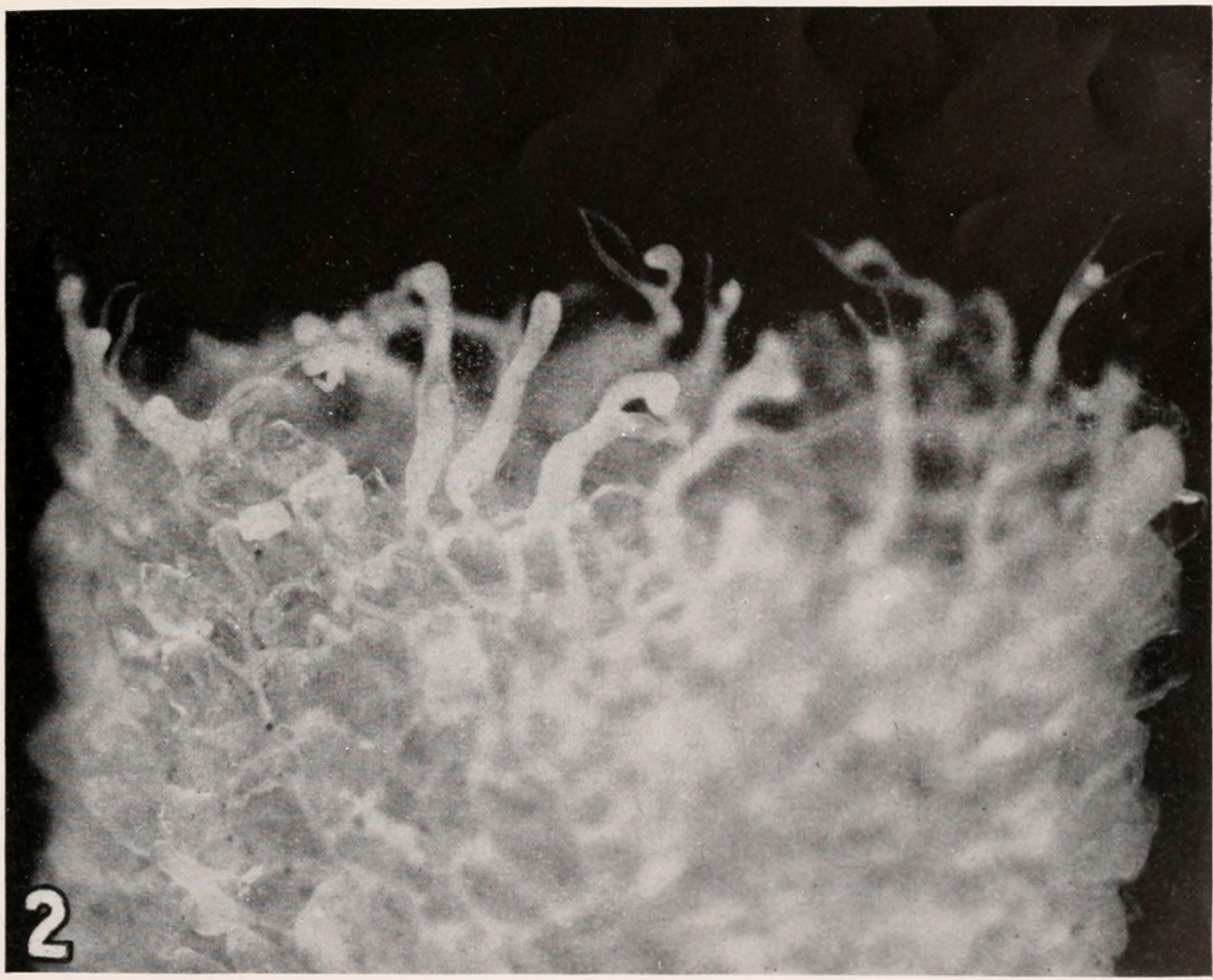
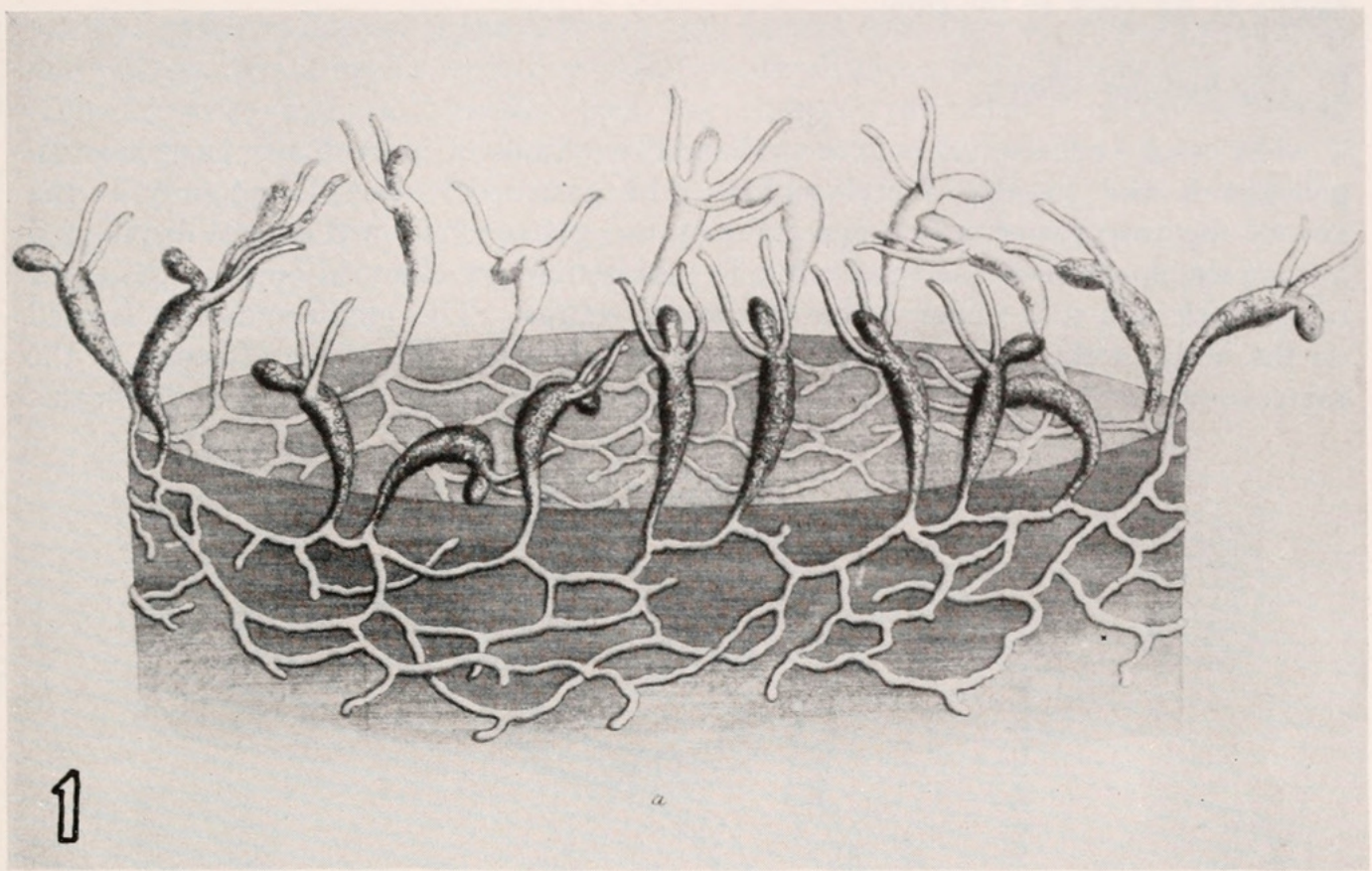
The new Californian hydroid is found growing upon the tubes of a sabellid polychaete, *Pseudopotamilla ocellata* Moore, and has been collected from several stations along the Monterey Peninsula from Carmel Cove to Point Pinos. The sabellid seems to be restricted to rocky areas of the intertidal zone around the mean lower low water line, where it lives in crevices and under or between rocks. The tube of the worm is of a parchment-like substance, richly embedded with sand grains, although the terminal free portion is frequently less sandy. The sabellid is free to turn within its tube. When the worm withdraws, the terminal portion

PLATE I

FIGURE 1. A reproduction of Gosse's (1857) figure of *Lar sabellarum* on the extremity of a tube of *Sabella vesiculosa*.

FIGURE 2. A living colony of *Proboscidae* sp. on a tube of *Pseudopotamilla ocellata* (ca. 25 ×).

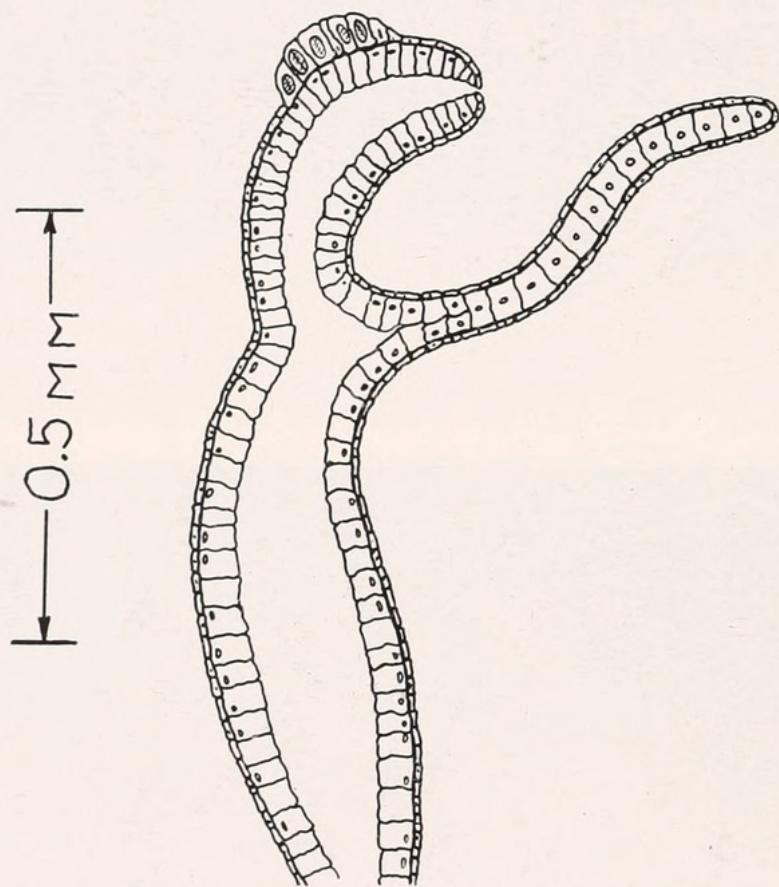
PLATE I



of the tube flattens and one edge folds over the other, thus covering many of the zooids at the edge of the tube.

b. *The hydroid colony*

The colony consists of two, or perhaps three kinds of individuals: gastrozooids, gonozooids and possibly dactylozooids. The gastrozooids are found only at the rim of the worm tube. In some colonies the gastrozooids are evenly distributed around the aperture of the tube, while in others they are clumped on the side of the tube which will fold under when the worm retires. The gonozooids are located on the body of the tube, apparently never on the rim. They are attached to the gastrozooids and to each other by an anastomosing system of naked hydrorhizae,

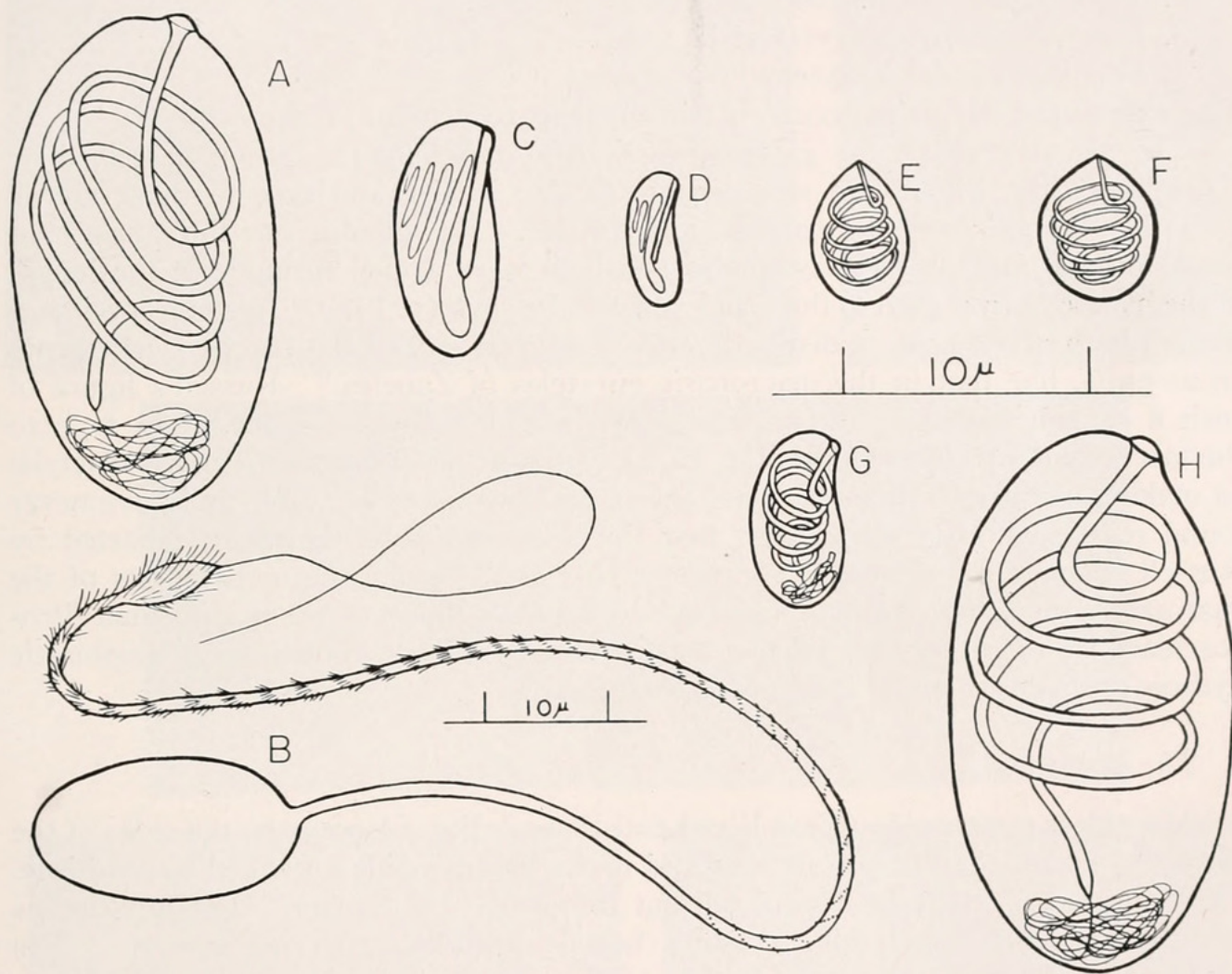


TEXT FIGURE 2. Diagrammatic longitudinal section through a gastrozooid of *Proboscidactyla* sp.

whereas the hydrorhizae of typical Anthomedusae always have a perisarc. The gonozooids, at the seasons we observed them, usually bore from one to four medusa buds in various stages of development. The whole colony may extend from the rim of the tube to a distance of 1.5 cm. down its length. At the edges of the colony farthest from the gastrozooids were found very short, capitate zooids which may have been dactylozooids, although their nematocysts are identical to the gonozooids, as is their appearance, except that they are smaller and lack medusa buds. Text Figure 1 represents a colony in place upon a sabellid tube. Several of the worm's tentacles are shown as cut away to allow a better view of the colony, and the number of tentacles represented on the worm is considerably reduced from the actual condition.

c. *The gastrozooids*

The gastrozooids are about 0.8 mm. tall, usually less than 0.1 mm. in diameter, and possess two tentacles located at about $\frac{3}{4}$ the distance from base to top. These tentacles arise from a common area but separate immediately upon becoming distinct from the body. They are highly extensible and may stretch to about 2 mm. in length. The tentacles are solid and their endoderm is in contact with the endoderm of the body. Text Figure 2 is a diagram of a longitudinal section through a gastrozooid showing the relationship of the endoderm of the tentacles and



TEXT FIGURE 3. Nematocysts of *Proboscoidactyla* sp.: a-e, of the gastrozooid; f-h, of the medusa. (a. unexploded macrobasic eurytele; b. exploded macrobasic eurytele; c. large microbasic eurytele; d. small microbasic eurytele; e. desmoneme; f. desmoneme; g. small macrobasic eurytele; h. large macrobasic eurytele.)

body. The "head" is separated from the "body" by a distinct "neck" and is capped by an oval battery of nematocysts. The "head" and "neck" are curved, making an arc of 90° , and the mouth is terminal, facing the side of the "body" on which the tentacles are located. The "body" is spindle-shaped, being largest at its mid-point and tapering at its lower end, decreasing to the size of the hydrorhizae, or about 0.03 mm. Plate 2, Figures 3 and 4, are photographs of living isolated gastrozooids. The gastrozooids are oriented around the top of the tube so that

they always face the tube opening. Plate 1, Figure 2, shows a living colony on a tube from which the worm has been removed.

d. *Nematocysts of the gastrozoid*

The types and approximate sizes of the nematocysts of the gastrozooids are given below. The measurements reported for these nematocysts and for the medusa are for discharged capsules. The gastrozooids possess (see Text Fig. 3a-e) :

1. Desmonemes : $8 \times 4 \mu$.
2. Telotrichous macrobasic euryteles : $22 \times 11 \mu$.
3. Large microbasic euryteles : $11 \times 4 \mu$.
4. Small microbasic euryteles : $6 \times 2 \mu$.

The macrobasic euryteles occur only in the nematocyst pad on the head.

The nematocysts of the gastrozoid of *Willia stellata* have been described by Russell (1938), who found nematocysts similar in size and type to those above, with the exception of the macrobasic euryteles. Russell did not find these, but found instead macrobasic mastigophores which were armed throughout the length of the hampe. In regard to the mastigophores he says (p. 145), "In some specimens treated with acetic acid or distilled water the distal end of the hampe swelled into an ampulla, like that in the macrobasic euryteles of *Zanclaea*." Russell's figure of such a capsule seems to illustrate a eurytele which appears identical in type to the macrobasic euryteles (Text Fig. 3a, b) found in the Californian *Proboscida*ctyla. In making our preparations of nematocysts we have used sea water and have never found mastigophores; we suggest that the macrobasic mastigophore reported by Russell is really a macrobasic eurytele. This would make the nematocysts of the gastrozoid of *Willia stellata* identical in type to those of the Californian *Proboscida*ctyla. Further, macrobasic mastigophores are not known for gymnoblastic hydroids other than as reported by Russell above.

e. *The gonozooids*

Mouthless gonozooids (Text Fig. 4 and Plate 2, Fig. 5) occur on the sides of the worm tubes, attached to one another and to the gastrozooids by naked hydrorhizae. They may occasionally be 1 mm. tall but frequently are shorter. The gonozooids are capitate, the distal sphere being heavily studded with nematocysts. The medusae are borne at about the middle of the gonozooid, and a maximum of four medusa buds may be present. These buds apparently arise successively, so that

PLATE II

FIGURE 3. Isolated living gastrozooids of *Proboscida*ctyla sp. removed from the colony shown in Plate I, Figure 2 (ca. $50 \times$).

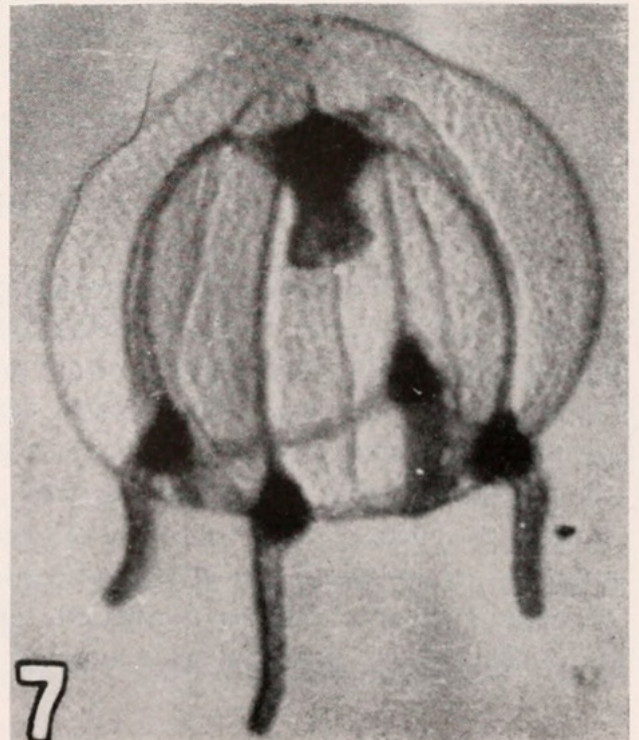
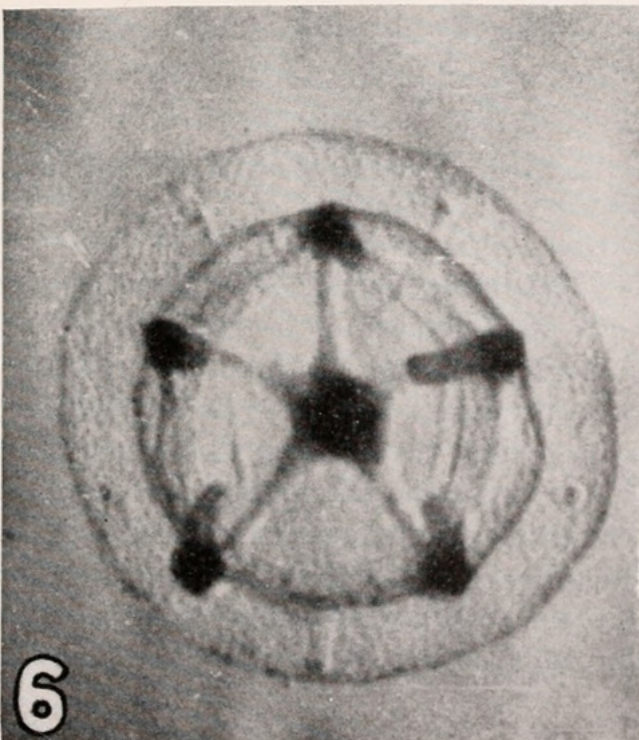
FIGURE 4. A single living gastrozoid of *Proboscida*ctyla sp. removed from the colony shown in Plate I, Figure 2 (ca. $50 \times$).

FIGURE 5. A living gonozooid of *Proboscida*ctyla sp. bearing several medusa buds (ca. $35 \times$).

FIGURE 6. A living pentamerous medusa of *Proboscida*ctyla sp., oral view, one day after release (ca. $50 \times$).

FIGURE 7. A living tetramerous medusa of *Proboscida*ctyla sp., one day after release (ca. $50 \times$).

PLATE II

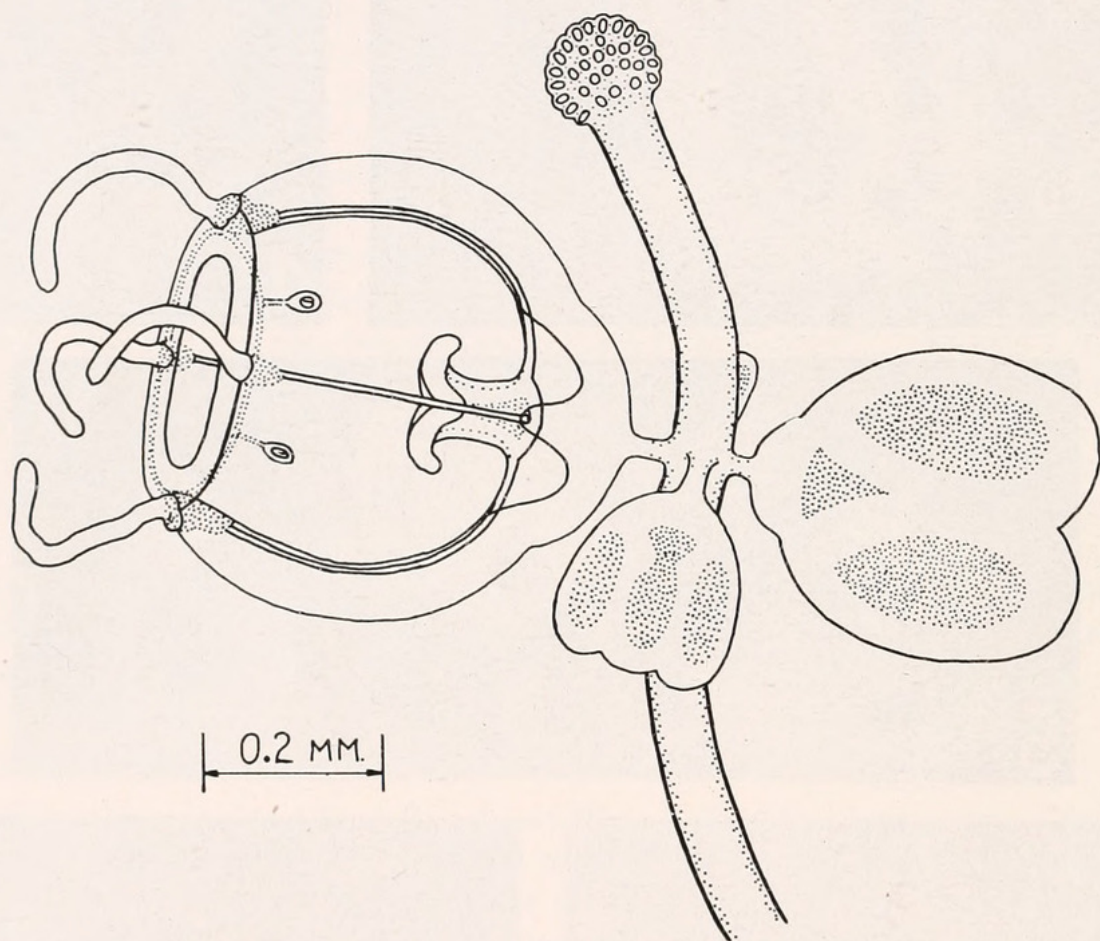


if four are present there are always a large one and three successively smaller ones arranged as in Text Fig. 3. In our specimens the larger medusa buds were seen to pulsate vigorously for a day or two before they were released. Many of the gonozooids possessed 1, 2 or 3 immature buds with no pulsating medusae.

The nematocysts of the gonozooids are the same as those of the gastrozooids except that no small microbasic euryteles are present.

f. *The medusae*

In the course of this study we have seen 25 released medusae. With a single exception, each medusa possessed four primary radial canals, the exception having



TEXT FIGURE 4. A gonozooid of *Proboscidactyla* sp. bearing medusa buds in different stages of development.

five. Plate 2, Figure 6, is a photograph of the living, one day old, pentamerous medusa, and Plate 2, Figure 7 illustrates one of the tetramerous specimens. The medusa possessing five canals was noted before its release and occurred on a gonozooid which also bore normal tetramerous buds. Text Figure 5 shows a medusa as it appears shortly after release, at which time the medusae are about 1.3 mm. tall and 1.0 mm. in diameter. There are four interradianal cnidothylacies (nematocyst sacs) which contain large and small macrobasic euryteles, and four tentacles possessing desmonemes and small macrobasic euryteles. The medusa with five radial canals had five tentacles. In no case in the immature medusae which we observed did we find any sign of branching of the radial canals. The ring

canal is represented by a solid cord, to which each of the interradial nematocyst sacs is attached by a strand of endodermal cells. The tentacles are hollow, inserted into the bell by means of large orange-brown pigmented endodermal bulbs, and are marked by nearly regular circular ridges which contain nematocysts. The stomach is four-lobed, each lobe leading into a radial canal. The manubrium is also four-lobed and hangs free under the bell. No statocysts or ocelli have been observed.

All medusae examined were very immature, and neither sections nor microscopic examination of the whole medusa showed any signs of the location of the gonads.

g. *Nematocysts of the medusa* (Text Fig. 3f-h)

1. Desmonemes: $6 \times 5 \mu$.
2. Large telotrichous macrobasic euryteles: $25 \times 11 \mu$.
3. Small telotrichous macrobasic euryteles: $8 \times 4 \mu$.

No microbasic euryteles were found in the medusae.

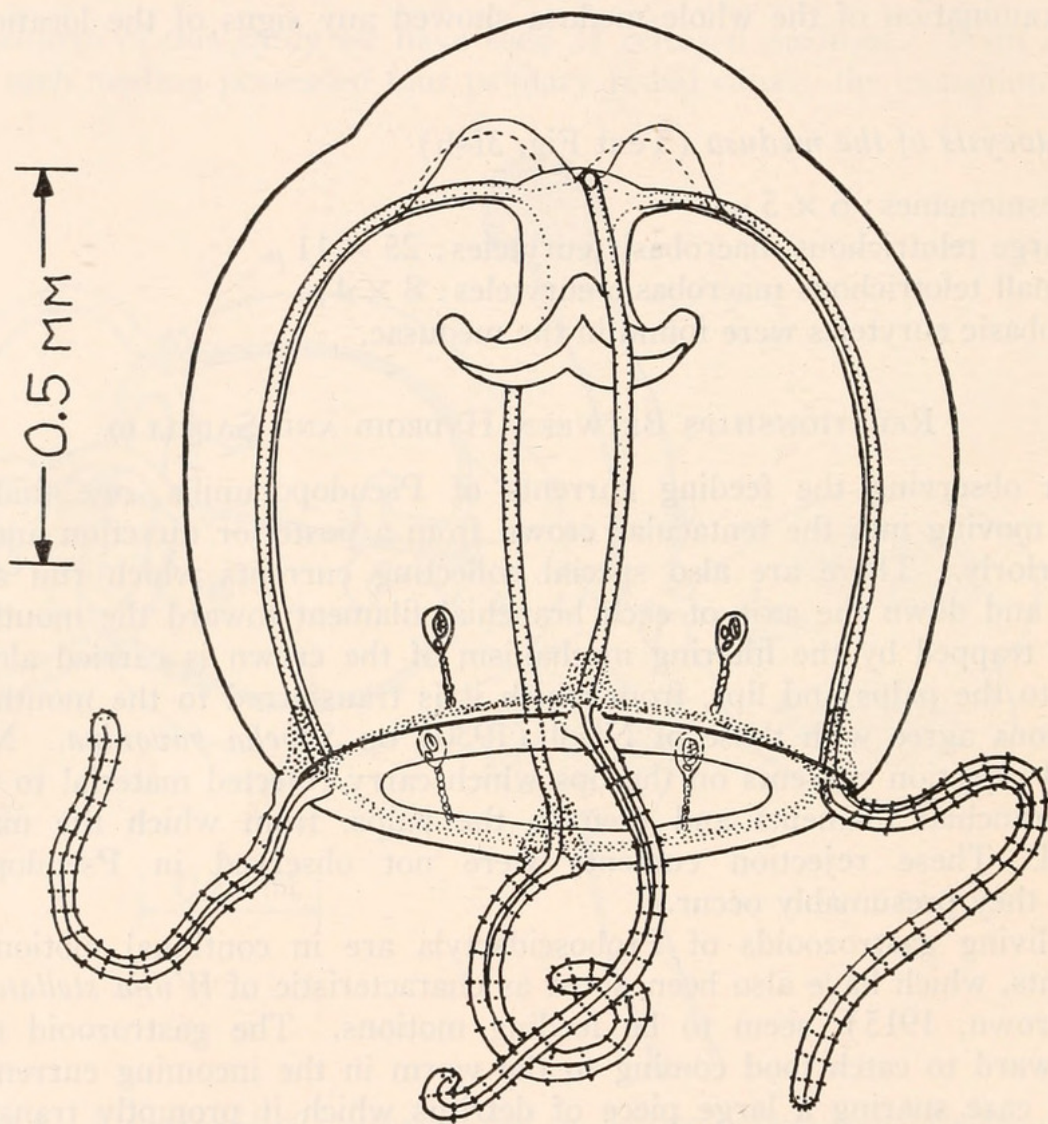
RELATIONSHIPS BETWEEN HYDROID AND SABELLID

Upon observing the feeding currents of *Pseudopotamilla*, one finds strong currents moving into the tentacular crown from a posterior direction and passing out anteriorly. There are also special collecting currents which run along the pinnules and down the axis of each branchial filament toward the mouth. Food which is trapped by the filtering mechanism of the crown is carried along these paths onto the palps and lips, from which it is transferred to the mouth. These observations agree with those of Nicol (1930) on *Sabella pavonina*. Nicol also described rejection currents on the lips which carry rejected material to the bases of the branchial filaments and then to the palps, from which the material is discarded. These rejection currents were not observed in *Pseudopotamilla*, although they presumably occur.

The living gastrozooids of *Proboscoidactyla* are in continual motion. These movements, which have also been noted as characteristic of *Willia stellata* (Gosse, 1859; Brown, 1915), seem to be feeding motions. The gastrozooid may lean far backward to catch food coming to the worm in the incoming current, in one observed case snaring a large piece of detritus which it promptly transferred to its mouth. The gastrozooids also lean forward, sometimes embracing the bases of the branchial filaments with their tentacles; in other cases they lean far into the aperture of the tube and quickly move their tentacles over the surfaces of the lips and palps of the worm. In the cases where the gastrozooids embraced the branchial filaments they were observed actually to remove particles of food, which the worm had collected, from the groove in the axis, which food they promptly devoured. In other cases they searched the surfaces of the lips and palps, and seemed to be gathering food from the currents there. The gastrozooids swing their bodies and tentacles in movements which apparently cover every available area in search of food particles. The rejection currents also presumably carry food to *Proboscoidactyla*, which is in an ideal position to reach into these currents; certainly the area where the rejection currents occur are well covered by the gropings of the

tentacles. Thus this hydroid, living as it does on a host which possesses strong ciliary feeding currents, is able to utilize these currents to supply food for itself.

Many individual gastrozooids were observed whose bodies were distended with food particles as in Plate 2, Figure 3. When such individuals were sectioned, the contained material appeared to be eggs in various stages of digestion. Uchida and Okuda (1941) reported that *P. flavicirrata* readily ate the eggs of its host, *Potamilla myriops*, as the worm spawned. We do not know the source of the



TEXT FIGURE 5. A medusa of *Proboscidactyla* sp. shortly after release.

eggs contained by the Californian *Proboscidactyla*; perhaps they were the eggs of the host or perhaps they were foreign.

The two-tentacled condition of *Proboscidactyla* seems to fit it well for its way of life as a commensal. These tentacles are unusually maneuverable and active for a hydroid, and their location on the gastrozooid enables it easily to lean between the branchial filaments, whereas a larger number of tentacles might be a handicap by becoming entangled with the worm. Also the great length to which the tentacles can extend allows the hydroid to cover more territory and thus increases the amount of food it can capture. We have never found this hydroid associated with any animal except *Pseudopotamilla ocellata*.

DISCUSSION

The hydroid described in this paper is similar to those of *Proboscidactyla stellata* and *P. flavicirrata*, but differs from them in that the Californian *Proboscidactyla* apparently never has gonozooids arising from the gastrozooids. Uchida and Okuda (1941, p. 435) report for *P. flavicirrata*, "The blastostyles are sometimes branched off from the gastrozooids," and Brown (1915, p. 167) says of *P. stellata*, that in the colonies he observed one gonozooid arose "... from the base of each polyp at the back," although Hincks (1872) figures gastrozooids and gonozooids arising separately in that species. In all other features of their morphology these three hydroids apparently are remarkably similar. We have found no gastrozooids bearing more than two tentacles, although Brown (1915) and Uchida and Okuda (1941) report occasional individuals with three or more tentacles.

The habitats of all three hydroids also show remarkable similarities, *P. stellata* living on *Potamilla torelli*, *P. flavicirrata* on *Potamilla myriops* and the Californian *Proboscidactyla* on *Pseudopotamilla ocellata*.

As for the immature medusae described by us, there is little or no way to distinguish them with certainty from other species of *Proboscidactyla*. The young medusae of *P. stellata* are predominantly hexamerous, although an occasional pentamerous one is found, while those of *P. flavicirrata* vary from tetramerous to hexamerous. *P. mutabilis* is also highly variable. In the Californian form we have found mostly tetramerous medusae as mentioned above. There is an important difference, however, between the Californian species and *P. flavicirrata*. Uchida and Okuda (1941) described the presence of minute eye-flecks on the abaxial faces of the tentacle bases in immature *P. flavicirrata*. These eye-flecks become obscure or are lost in the adult. We have found no such eye-flecks in the Californian material, nor have such flecks been reported for any other member of the family. The presence of these eye-flecks in *P. flavicirrata* necessitates a change in the family definition, which we suggest should read as follows:

Proboscidactylidae:

Limnomedusae without statocysts; stomach with perradial lobes extending along the proximal parts of the radial canals; gonads surrounding the stomach and its lobes; radial canals branched in the adult; interradial cnidothylacies present; tentacular bulbs usually without ocelli except in young stages of certain species.

Just where Mereschkowsky's hydroid, *Monobrachium parasitum*, fits into this group is not known. Unfortunately, the descriptions of the medusa of *Monobrachium* are very incomplete, and beyond the fact that the radial canals branch little is known of it. If *Monobrachium* is a true *Proboscidactyla*, then we would have a rather striking example of divergent evolution among the hydroids of the genus, some of them being specialized for life as commensals with sabellids and others specialized to live with clams. The hydroid of *Monobrachium* differs from that of *Proboscidactyla* in lacking the pronounced "neck" and in possessing but one tentacle. Also the medusae in *Monobrachium* arise directly from the hydrorhizae rather than from gonozooids so it is possible that *Monobrachium* will prove not to be a *Proboscidactyla* and may not even belong to the Proboscidactylidae. But

it will be interesting, should *Monobrachium* be shown to be a true Proboscidae, to see whether this rather unusual hydroid also has a medusa which is divergent, or whether the medusa is of the normal pattern while the hydroid generation alone has diverged.

The specific identification of our Californian hydroid must await further information. Only one Proboscidae, *P. occidentalis*, a medusa, has ever been reported from Californian waters. This was described by Fewkes (1889) from Santa Cruz Island. There is nothing in Fewkes' description which enables us to identify our form with his. This is not unusual when one considers the generalized characters of the immature medusae of this group; indeed, our form could be identified with almost any other Proboscidae as readily as it could be with Fewkes' species. The closeness of the localities (Monterey Peninsula and Santa Cruz Island) suggests that the Californian Proboscidae described by us may be identical with *P. occidentalis*, but until further stages in the development of our form are known this identification must remain speculative.

There still remain species of Proboscidae for which no hydroid stages are known, among which one American form merits attention. This is *Proboscidae* (= *Willia*) *ornata* (McCrady), a medusa which has been reported from the Woods Hole region. Hargitt (1904, p. 40) reports it as, "More or less common at irregular intervals. Occasionally taken in numbers in the Eel Pond and in the tow of the harbor." There are also at least two sabellids (*Parasabella microphthalmia* (Verrill) and *Pseudopotamilla oculifera* (Leidy)) in the Woods Hole area which would seem to be possible hosts for the "Lar" stage of *P. ornata*. The authors hope that the attention of biologists at Woods Hole may be attracted to this problem, and that the hydroid of *P. ornata* will not long remain unknown.

SUMMARY

1. The history of the Proboscidae is summarized and changes are suggested in the definition of the family.
2. A new Californian hydroid is described as *Proboscidae* sp. This hydroid may be that of *Proboscidae occidentalis* Fewkes.
3. The new hydroid lives as a commensal upon the tubes of a sabellid polychaete, *Pseudopotamilla ocellata* Moore.
4. The commensal relations of the hydroid to the host worm are described, especially the utilization by the hydroid of the feeding currents produced by the worm.
5. The relationship of Proboscidae to *Monobrachium parasitum* is discussed.

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