

[*Discovery Reports.* Vol. XXX, pp. 301-408, Plates VII-XXVIII, August, 1960].

STUDIES ON *PHYSALIA PHYSALIS* (L.)

PART 1. NATURAL HISTORY AND MORPHOLOGY

By A. K. TOTTON

pp. 301-368

PART 2. BEHAVIOUR AND HISTOLOGY

By G. O. MACKIE

pp. 369-408

CONTENTS

	<i>page</i>
INTRODUCTION	303
ACKNOWLEDGEMENTS	303
MATERIAL AND METHODS	303
NON-TECHNICAL DESCRIPTION OF THE PORTUGUESE MAN-OF-WAR	306
APPEARANCE AND HABITS	307
Association with <i>Nomus</i>	309
Rolling or somersaulting behaviour	309
Floatation: Pneumatocyst or air-sac	310
Motion relative to wind and water	315
Stinging power and toxicology	322
Nematocysts	324
MORPHOLOGY	326
Historical	326
Polymorphism	328
Pattern of budding in the cormidia	328
Early larvae	342
Structure and development of the gonodendra	346
Jelly-polyps	351
Nectophores	352
Palpons	353
Ampullae	355
Gonophores	356
ORIGIN OF 'PHYSALIA' AND THE SIPHONOPHORA: THE PAEDOPHORE	
HYPOTHESIS	358
DISTRIBUTION	363
SUMMARY	365
REFERENCES	366

STUDIES ON *PHYSALIA PHYSALIS* (L.)

PART 1. NATURAL HISTORY AND MORPHOLOGY

By A. K. TOTTEN

British Museum (Natural History)

(Plates VII to XXV, text-figures 1-31)

INTRODUCTION

ALTHOUGH much of this story is technical, it is hoped that it may be of interest to laymen, seafarers and voyagers as well as professional zoologists. So it will be as well to explain that the Portuguese man-of-war is a sort of jelly-fish. People often ask 'why Portuguese?' It was the Portuguese, in the time of Henry the Navigator, who had fleets of the then curious, new, light ships called caravels. Between 1420 and 1552 they were exploring half the maritime world, and their characteristic fore-and-aft lateen sails were well known to all seamen. I think it must have been the possession of a fore-and-aft sail or crest, and the way in which *Physalia** heads into the wind, a fact which no sailor-man could fail to notice, but one which is certainly not observed in these days, that led seamen in the latter part of the fifteenth century to call these animals 'caravels' or 'Portuguese men-of-war'.† The seamen who took Sloane to Jamaica in 1687 were still doing so; but in these days of steam and diesel engines the name seems to be half-forgotten. Australians call the animals 'Bluebottles', and the Spaniards of the Canary Islands 'aguas vivas'.

ACKNOWLEDGEMENTS

I have to thank the Trustees of the Percy Sladen Trust for a grant which made my work at Arrecife possible. It was entirely due to the kindness and hospitality of the Administrator of the Parador Nacional, Señor Don José Juaréz Sanchez-Herrera, who showed keen interest in the work and went out of his way to satisfy every want, that a laboratory was arranged on his very convenient premises. It was one of the few places on the island where running water, hot and cold, and easy access to sea-water were available. Suitable boats were difficult to find, but Señor Don C. Martinez Cabrero was kind enough to lend his dinghy fitted with an outboard motor.

I also wish to thank Dr G. O. Mackie for his valuable co-operation in the field, and Dr Helene Bargmann for help in the arrangement of this report.

MATERIAL AND METHODS

The specimens, on which the morphological facts described in this memoir are based, derive partly from the Discovery Collections, but chiefly from those collected, anaesthetized and preserved in

* *Physalia* must not be confused with a smaller blue, floating, crested polyp *Vellela*, also very well known to seafarers, which is only two or three inches long.

† When I was trying to get permission to take some official photographs of the Portuguese man-of-war, so unfamiliar to the layman was this popular English name, that it was necessary to explain to the authorities that the object was of a zoological and not of a nautical nature.

formalin during a three-months' visit that I made in the spring of 1955 to Arrecife, Canary Islands. During part of this time I was fortunate enough to have the co-operation of Dr G. O. Mackie.

After having worked on these specimens, which range in size from 11 to 180 mm. in float-length, for two and a half years at the British Museum (Natural History), I heard that Miss Eleanor Dodge was preparing to work at Miami, Florida on the toxin of *Physalia*. I wrote to ask if she would be kind enough to secure me some larvae should they be available. On 14 January 1958 I received from her a most welcome series of young specimens measuring from 4 to 15 mm. in length. Miss Dodge was also kind enough to send me from Crandon Park Beach, Biscayne Key, off Miami, a second valuable collection of younger larvae measuring from 1·2 to 5 mm. in length, collected on 20 January 1958, which I received on 14 February 1958. I was thus able to figure and insert into the typescript, which I had already completed, information on those stages of development at which budding begins. In this way I have been able to complete the picture of the origin and pattern of budding in *Physalia*.

It is almost impossible to examine specimens fully until the air in the float has been displaced by fluid, or the float cut off. My most rewarding work has been done by combining successive dissections with photography. The methods employed had to be purely exploratory to begin with, because previous accounts of the arrangement of the groups of buds in *Physalia* were too superficial and illustrated either not at all (Schneider, 1896) or so inadequately (Steche, 1910; Okada, 1932, 1935) that they could not be checked and built upon. In fact it was necessary to start *de novo*. Now that some kind of pattern has been recognized it may be thought that the exploratory phase of the work was unduly long. The results must be published now before further refinements of the analysis can be made. But it is hoped that someone in the future will be able more quickly to examine a series of specimens (comparable with the young specimens to which I devoted much attention), and will find out to what extent there is variation of the pattern observed and illustrated in this memoir.

It is regretted that a better photographic technique was not available, but it was not possible to make repeated dissections in the photographic studio of the Museum. Also, the carrying of such dissections in dishes of formalin over long distances from laboratory to studio was found to cause too much disarray of the specimens through swirling motions of the liquid. Recourse was therefore made to dissection on the stage of a Bausch and Lomb binocular dissecting microscope set up on the base of an old Leica photocopier. The arm carrying the viewer, a Leica camera and lamps was swung to one side. When the dissection had been displayed, the body of the microscope was slid out and camera and viewer were moved into position.

A method of dissection that I would recommend to anyone wishing to examine the structure of *Physalia* for the first time is as follows: First remove the float, leaving the primary polyp and appendages of both oral and main zone attached to a narrow strip of the bladder-wall. Secondly, sever the oral zone at the basal internode from the main zone. Thirdly, sever the first two cormidia by a cut with fine scissors just to the oral side of the main tentacle. Then make a similar cut a little to the oral side of the chief tentacle of cormidium V. This will leave the three most representative cormidia attached to a strip of the bladder-wall, which can be turned about and folded to reveal the internodes between the three cormidia. A well-relaxed specimen about 4–5 in. in float-length would probably not be too complexly branched for recognition of the basic pattern of arrangement of branches, polyps, tentacles, and gonodendra. This basic pattern is described on page 328.

The structure of contracted specimens is exceedingly difficult, if not impossible, to analyse satisfactorily, so live specimens to be examined in this way should be carefully anaesthetized in magnesium chloride (7½% in fresh water) and fixed in formalin. It was found that expansion was aided by injecting with a fine needle both the magnesium chloride and the formalin into the gastrovascular space near the base of the chief tentacle. The muscular walls were found to be self-sealing. Air can

be drawn out from the float for sampling in the same way without loss, though it is better to cut out the complete air-sac.

The pneumatocyst can be quickly removed from a living specimen by making an incision with scissors down the wall of the pneumatocodon, while it is held by the crest in the air. Contraction of the outer muscular wall soon frees the sac, which can be tied off for safety short of the aboral valve before cutting off the remains of the pneumatocodon. Pressure can then be applied to the immersed sac (which of course floats) to dilate the dorsal processes until fixation is complete.

Physalia, it was found, could be handled by the float without fear of stinging, but a pair of plastic salad-servers, kept scrupulously clean, was used for handling the numerous laboratory specimens, and particularly for lifting them in a breeze from the sea into buckets. In this operation it was found imperative to avoid allowing the tentacles to touch either oars, gunwale or thwarts of the boat; tentacles adhere tightly to wooden objects and are almost impossible to remove. When lifted from the sea the tentacles may hang down for 5 or 6 ft. and need careful handling in a breeze.

The authorities at the Victoria Hospital at Las Palmas, where hundreds of stung patients are treated, advised the taking of an anti-histamine if badly stung, but there was no occasion to do so because the precautions outlined above were taken.

From my rough diary I see that specimens of *Physalia* were available at Arrecife, where we arrived on 18 February 1955, as follows:

- 4 March First specimens brought in by Señor Don Jorgé from Graciosa I.
- 10 Three right-handed specimens drifted in.
- 15 Wind S.E. all day, but dropping. At 5 p.m. numerous left-handed *Physalia* taken. Later when wind was S.W., many right-handed specimens taken.
- 20 Calculated that with present wind *Physalia* would pass 1 or 2 km. south of Arrecife, where in fact none came ashore. Drove to Caletta on north coast and picked up thirty-two.
- 4 April Many young specimens drifted on to beach on east side of Islote de los Ingleses.
- 9 One specimen, 4·5 in. float-length.
- 13 Strong N.E. trades. Many left-handed *Physalia*. First experiments on drifting.
- 15 A few *Physalia*. Second set of drifting experiments.
- 16 Sixty-five specimens brought in by boys. Third set of drifting experiments.
- 18 One young specimen.
- 21 A large sea-area covered by specimens, spotted through binoculars at 6.30 p.m. half-a-mile south of laboratory. Two dozen brought in.
- 6 May One young specimen from east side of Islote.
- 10 One young specimen.
- 12 Small specimens.
- 13 Three small specimens.
- 24 Departure.

I could get no reliable information in the Canaries as to periodicity of appearance of *Physalia*, except that at Las Palmas they were most noticeable up to June, after which they decreased in numbers. There was a common belief that they bred on a reef protecting El Canteras beach on the north side, and were washed off the reef into the bathing-area.

The Arrecife boys soon came to know that we were interested in 'aguia viva' as they called *Physalia*, and I used to issue buckets and a pair of plastic salad-servers to the best collectors, with a warning that only really fresh specimens, and particularly very tiny ones were needed. If specimens are to be kept in good condition for more than a day or so, very large vessels are required, such as the hatching-tanks used by Brooks and Conklin (1891).

The electricity supply at Arrecife used to be cut off at 1 a.m., after three warning flicks given a quarter of an hour previously. So it was always a race against time at the end of a busy day to transfer specimens to buckets and plastic bowls of fresh seawater; to get rid of stale water and moribund specimens, which I always deflated with a pair of scissors to avoid re-collection; and to reach one's bedroom and light a candle before the lights went out.

NON-TECHNICAL DESCRIPTION OF THE PORTUGUESE MAN-OF-WAR

For the benefit of the reader who does not wish to examine minutely the structure of *Physalia*, I will attempt to give in plain language a short account of its significant features with the least assumption of previous knowledge.

The conventional idea of a marine animal must be forgotten. *Physalia* is very simply organized, without head, tail, limbs, skeleton, mouth, alimentary canal, anus, gills, blood-vessels, body-cavity, kidneys, brain or one-way-traffic nerves. It is really an overgrown polyp-like* larva, belonging to the Cnidaria, the group which includes jelly-fish, corals and sea-anemones. It floats on its side and, without growing-up into a sexually mature animal itself, produces underneath as buds, innumerable similar daughter polyps—these too are really in the larval phase—which bud again and produce thousands of minute and not fully formed adults, having the essential structure of a jelly-fish or medusa, and which are called gonophores.† Though not fully formed like the usual jelly-fish, the gonophores represent the adult, sexual phase; and in any one specimen are all either male or female. The daughter polyps also bud off non-sexual simplified adults for propelling the broken-off branchlets which bear the true sexual adults.

So, in *Physalia*, we have two components to think of:

(1) The original polyp, hatched from the egg, which becomes a sort of nurse carrying about the innumerable buds to which it gives rise. An asexual larva itself, it not only buds off other larvae, but adults as well, both asexual and sexual. The larva is a hollow sac with a mouth at one end and only a single tentacle (Pl. VII, fig. 2); it develops from a fertilized egg and becomes very much enlarged and continues to float. The much enlarged original polyp itself extends from one end of the specimen to the other. One end is free of buds and has near its tip a pore communicating with the enormous air-sac, which as a small depression during the early development becomes pushed inside the float-end of the polyp. At the other end, the mouth, stomach and tiny tentacle of the original polyp soon become nearly hidden by all the daughter buds (Pl. VIII).

(2) We must consider these daughter buds: some of them take in and digest the food, some consist chiefly of a long stinging tentacle, others, the palpons, appear to be protective and sensory, and the remainder are the little imperfect sexual adults (the gonophores) and the asexual medusoids (the swimming bells or nectophores).

In no other cnidarian do we find such prolific budding as in *Physalia* (Pl. IX). After the original polyp has hatched from the egg and has assumed the horizontal position characteristic of the species, and the aboral float has begun to enlarge, the first buds begin to appear on the under-surface in the middle part of the polyp. Later buds arise in turn from the bases of the first buds which soon elongate, so that subsequent series of buds are borne on stalks or peduncles. The first series of buds is arranged in two major zones: an oral zone of at least five small peduncles separated by a gap, the basal internode, from a larger main zone of six or seven peduncles. As series after series of buds appear, each laterally

* A polyp has the shape of an elongated cylinder fastened at one end, with a mouth and one or more tentacles at the free end. The name is derived from the French word 'poulpe' meaning octopus with its mobile tentacles.

† I find that Leuckart (1851) had long ago come to the same conclusion.

on the peduncle of its predecessor, they gradually appear changed in character from the long feeding polyps (gastrozooids) to smaller protective palpons. The gastrozooids differ from those of related species in becoming separated from their tentacles. Each stinging tentacle itself is borne on an enlarged base (ampulla), which supplies stinging-cells (nematoblasts) to the long stinging tentacle. The palpons protect the even smaller, reduced, sexual medusoids or gonophores, which are the true adults. Probably the palpons have an anal function as well. There are intermediate stages between the first and last kinds of polyps.

The float is at first relatively small (Pl. VII), occupying the aboral end of the animal, but later on, greatly enlarged the float appears on top. On the inner wall of the air-sac of the float is a round pellucid patch, the gas-gland (Pl. VIII, fig. 5), which secretes air from the water into the air-sac. There is one common digestive and circulatory space, stretching also round the air-sac, with which all the daughter polyps and gonophores communicate, so that the products of digestion can reach all parts. Waste products can diffuse out through the fine tissues, through which oxygen also can be taken up from the sea; undigested refuse like fish-bones and scales can be got rid of again through the mouths of the gastrozooids.

The details of reproduction are still unknown, but probably terminal branches bearing the gonophores break off and are kept on the move by the asexual medusoids (swimming-bells). Fertilization probably takes place in the sea.

It was realized long ago that the long axis of *Physalia* takes up early in life a peculiar orientation in the water. Whereas most siphonophores have the oral-aboral axis vertical, the overgrown air-sac of *Physalia* topples over so to speak so that the long axis is horizontal. Circular and longitudinal sheets of muscle are developed everywhere, so that the animal can turn and twist about, lengthen and shorten its polyps and tentacles, and open wide and close its many mouths.

Physalia appears to be very successful in avoiding being eaten except in the juvenile stage. It needs no sense-organs to find food. Fishes as large as mackerel and flying fish bump into its tentacles and provide much more food than *Physalia* can digest. When the surplus is jettisoned, many of the attached feeding gastrozooids are lost, but this loss is quickly made good by the great proliferation of buds, a faculty which may have arisen in consequence of the abundant food.

Physalia is indeed an unusual sort of animal, an association of larval and adult individuals or persons—as opposed to organs—which have been budded from the parent larva but which have not become separated from it, the parent larva itself having developed a giant float to carry all these individuals at the surface of the sea.

APPEARANCE AND HABITS

Physalia's sky-blue, or light green, air-filled bladder with carmine-edged crest floats at the surface and the animal drifts in the wind. The float may reach a length of 10 or 12 in. and its deep-blue trailing tentacles, difficult to see when fully extended, can reach a length of 50 m. or more. The tentacles carry enormous numbers of stinging-cells or nematocysts.

The smallest specimens from Miami (Pl. VII) measured 1·25 mm. in length. This is less than the smallest, previously recorded by Huxley (1859), figured by him and probably taken in the spring of 1847 in the South Atlantic; it measured one-tenth of an inch (2·5 mm.) in length, though he gave it as measuring one-fifth of an inch. The Miami collection of about 100 larval individuals (1·25–5 mm.) was made on 20 January 1958 and reached me (in formalin) on 14 February. When the vial was opened the animals were a beautiful turquoise-blue all over and were uniformly covered with nematocysts. They were transferred to dishes of stock formalin neutralized with hexamine and covered with black paper after being examined with a tungsten ribbon lamp. But next morning little colour remained.

After another day there was practically none left. Agassiz and Mayer (1902) recorded traces of this blue colour in their figures of young individuals and also a plum-coloured pigment at the pore end. I have seen traces of this pigment too.

The first occasion when larvae were collected at Miami was on 21 October 1957. No more were seen until 8 November, and thereafter on 11, 13, 15 and 21 November; on the last date the first large accumulation of *Physalia* specimens was found. Further collections were made on 9, 12, 16 and 17 December and the last and most valuable, already mentioned, on 20 January 1958. The lengths of the larvae are given in Table 1.

Table 1

Date	Larval length (mm.)
8 November 1957	Under 30
11 November 1957	From 5 to 8, but mostly between 20–40
13 November 1957	From 19 to 59, but mostly between 30–50
21 November 1957	From 23 to 150, but mostly between 23–150
17 December 1957	Probably less than 15, mostly between 60–80
20 January 1958	From 1·25 to 5

Miss Dodge informed me that, though the large forms seemed more prevalent, the small ones could be found on certain (not all) days, and in large numbers if at all.

Physalia feeds on flying fish, mackerel and other surface-swimming fishes which collide with the tentacles, become immobilized by the nematocysts and are drawn up to the hundreds of feeding polyps, which lie on one side of the under-surface of the float. R. P. Bigelow has described (1891) how he was able to keep alive in large 'hatching-tanks', and study for a week or more, numbers of *Physalia* taken in the summer of 1889 in Vineyard Sound. His short paper is well worth reading. He reported that the pull of a live fish on a tentacle caused retraction, but contact—except by the mouth of a gastrozooid—with food or its close proximity caused no response. He noted the contrast between the erected crests—relaxed only for a short time—of animals seen in the Gulf Stream and the relaxed crests of specimens kept in the Woods Hole tanks. By directing a stream of air from a bellows on to relaxed specimens he obtained a general contraction of muscles and erection of the crest. He noted the shedding of gonodendra in the tanks and the detachment of gorged animals from the remains of the fish on which they were feeding. He also noticed that the palmar surface of the hand was not sensitive to the sting of nematocysts, which he likened to that of a bee when touched by the back of a finger.

In 1942 E. W. Gudger gave a résumé of recorded observations on the feeding habits of *Physalia*, from the time of Quoy and Gaimard's 1824 report on the voyage of 'Uranie' and 'Physicienne' onwards. In 1947 D. P. Wilson published photographs of a 5·5 cm. wrasse, *Ctenolabrus rupestris* (L.), in the process of being digested by a *Physalia* about 23 cm. in length.

Much light is thrown on the mechanisms in coelenterates by a recent paper by W. F. Loomis (1955) on feeding-reactions in *Hydra*, which are initiated and controlled by a hormone, reduced glutathione, released from the prey itself after penetration by nematocysts. If, as seems possible, the feeding-mechanisms of coelenterates generally is under some such hormone control, it becomes more easy to understand the method in *Physalia*. Very vast numbers of nematocysts would produce the discharge from the prey of large quantities of hormone and the feeding-mechanism would operate effectively. It may be that the often observed dropping of a half-digested fish is not a sign of repletion but of the autoxidation of the hormone, which, in *Hydra*, Loomis noted took place rather sluggishly. Since this report went to press, Lenhoff and Schneiderman* (1959) have published the results of experiments showing that reduced glutathione does induce a feeding response in *Physalia*.

* Tentacles are not lacking, as they state, but are partly separated from the fully grown gastrozooids.

ASSOCIATION WITH *NOMEUS*

The association with *Physalia* of the little purplish-barred stomateoid, the rudder-fish, *Nomeus gronovii* is interesting. It has long been known to shelter under *Physalia*, although I never saw one in the Canaries, and it was thought to lure other fishes into the reach of the tentacles; it was also considered to be immune from their stings. But Garman (1896) reported partially digested *Nomeus* attached to the tentacles, and an 18 cm. long specimen of a male *Physalia* taken by 'Discovery II' between stations when testing gear, on 29 December 1929, in a position $3^{\circ} 22' S.$, $32^{\circ} 25' W.$, is accompanied by a label in the handwriting of Dr Stanley Kemp, recording that 'twenty or more small *Nomeus* were seen swimming below the *Physalia* and in one dip the latter was caught as well as several of the fish. In the net the fish came into contact with the tentacles of the siphonophore and were immediately killed.' Kojiro Kato (1933) observed that *Nomeus* vigorously attacked *Physalia* from below, eating parts of it, including the tentacles. On opening the stomach of one fish as a check, he found unmistakable *Physalia* tissues inside.

I am indebted to Mr J. C. Natzio for a note on another stomateoid fish-associate. Natzio, a senior boy of Charterhouse School, sailed aboard R.R.S. 'Discovery II' to assist in the biological work of the spring cruise of 1958, and referred to the fish as *Lirus maculatus*. I understand that it is better known as *Schedophilus maculatus* (Günther), but I have found no reference to this association in the *Physalia* literature. On a few days following 17 March, when the ship was frequently stopped on station, the fishes were often seen to swim around and beneath tentacles of medium sized *Physalia*, and both animals were often taken together in hand-nets. On several occasions *Schedophilus* was noticed to swim from one *Physalia* to another. In an aquarium one of the fishes escaped after being entangled for about 10 min., and continued to swim around with apparently no ill effects. Mr Foxton, who was also on board, told me that another specimen of *Schedophilus* after being stung by *Physalia* towed the *Physalia* along the surface of a tank, later escaped, rolled on its side, but eventually appeared to recover. This fish, like *Nomeus*, is banded with blue, though the colour is not very conspicuous.

ROLLING- OR SOMERSAULTING-BEHAVIOUR (Pl. X, figs. 1-6)

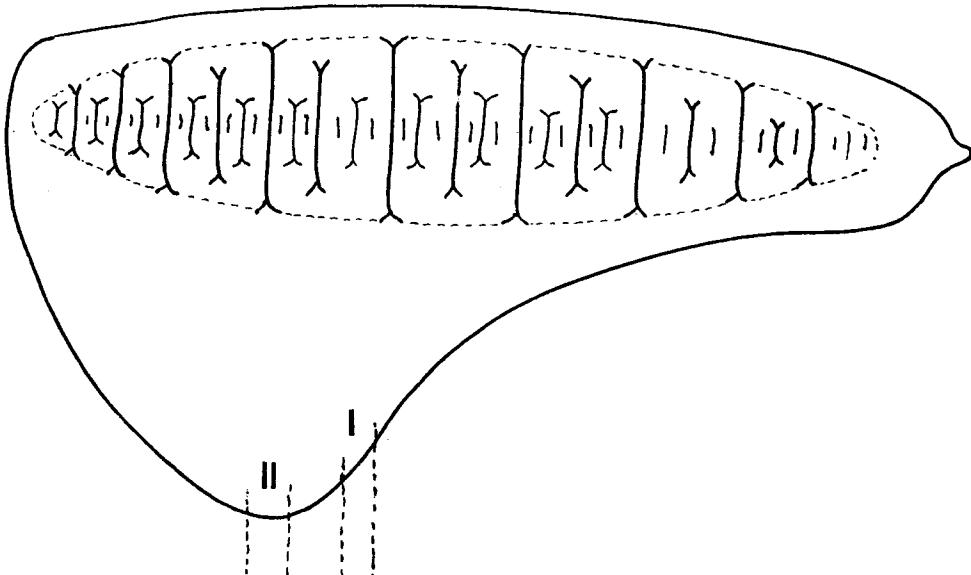
Much time was mistakenly spent at Arrecife watching rolling-behaviour, filming it and taking still photographs in the laboratory. It was only much later on, when the specimens were no longer available, that I realized that rolling takes place much more frequently in the still air of the laboratory than at sea in a good breeze. My tentative conclusion is that *Physalia*, when in a state of muscular tonus with crest erect, is in unstable equilibrium and is unable to remain upright without the aid of the force exerted by the wind. In the relaxed position, assumed after some time in the laboratory, it does remain upright but with the crest deflated, and the overall length increases, and the width decreases. In a note on sailing-experiment 3 (see page 318) I mention that specimen 1 fell over into the wind when the breeze dropped.

The older naturalists interpreted rolling-movements as change of 'tack', but the reason for it seems to be as follows: in the contracted, inflated condition with crest erect, *Physalia* is asymmetrical because most of the large tentacles, gastrozooids and gonodendra lie well out on the windward side, so that the heeling force thus set up prevents the animal from capsizing in a breeze. When the wind drops, the animal falls into the wind, and complicated muscular contortions are then needed to get back into the sailing position. This of course needs confirmation under conditions open to the wind, but I have certainly observed at sea in winds of force 3 or 4, a number of animals steadily drifting along without rolling; on the other hand I have not had an opportunity to watch them in a calm except under laboratory conditions. It is significant that Huxley (1859) in commenting on this somersaulting-

behaviour said, '... I have over and over again watched the operation going on with great vigour in a dead calm'.

FLOATATION: PNEUMATOCYST OR AIR-SAC

I was surprised, when I first dissected a live *Physalia* by making a vertical cut with scissors down the outer pneumatocodon wall, to see how quickly this muscular coat retracted and freed the pneumatocyst; and particularly to see the branching digitiform processes of the latter which fit into the pockets of the crest. Because little attention seems to have been paid to them, I give a photograph (Pl. X, fig. 7) of a fixed specimen. To obtain fixation of the extended air-sac, which is covered inside, except for the area of the gas-gland, by a thin chitinous layer, it is necessary to maintain pressure for some time on the sac while it is in the fixative. The raising and lowering of the crest evidently depends on muscular compression and relaxation of the float and the air-sac, as described by Leuckart (1851). Lesson (1843) gave a crude figure (*M*, pl. II).



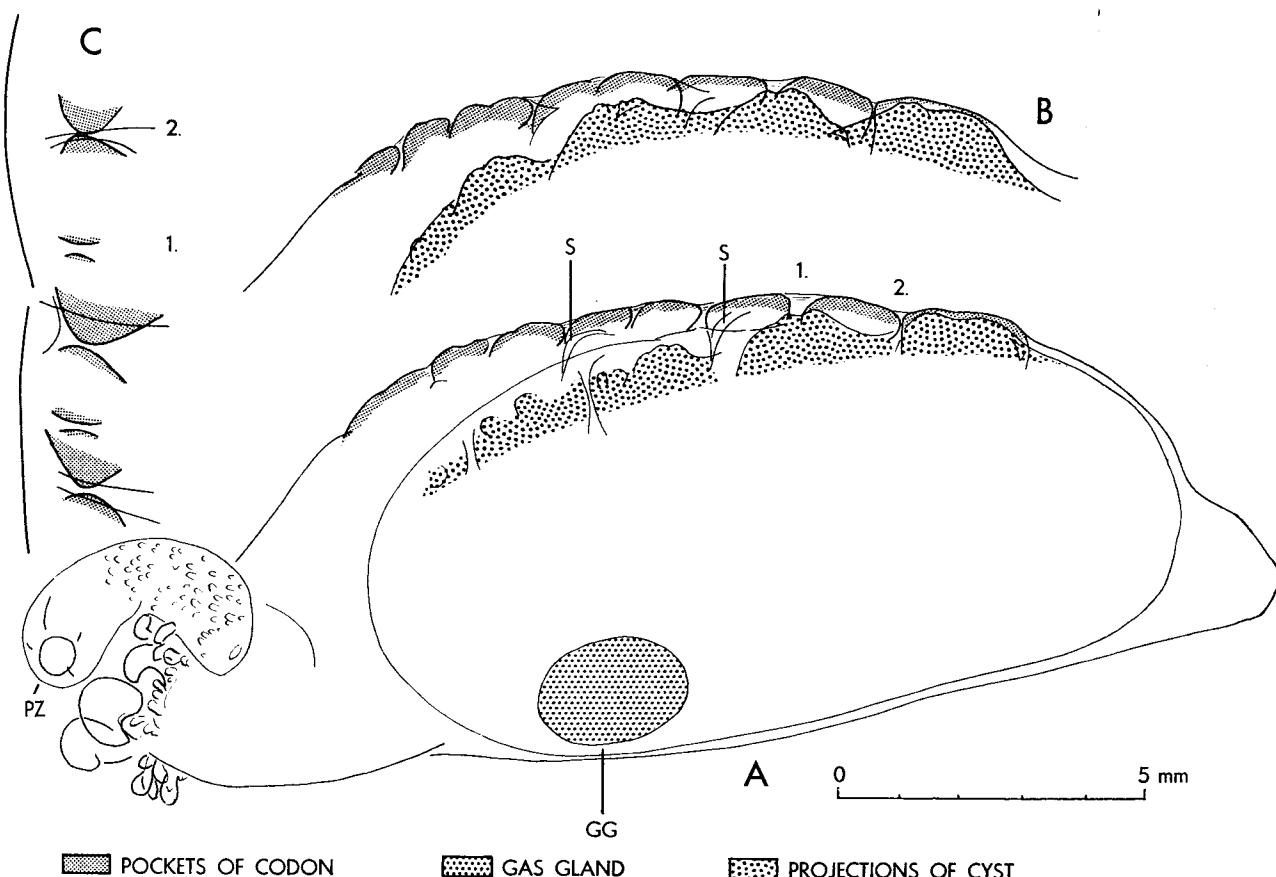
Text-fig. 1. *Physalia physalis*. A right-handed specimen, number 58, $\times \frac{5}{8}$ (Discovery St. 3255). Plan-view from above to show the septa of the crest. I, II = cormidia I and II (main zone).

The textbook account of *Physalia* by Delage and Hérouard (1901) contains statements—no authority quoted—about crest-structure which need correction. First of all I have never seen any sign of an internal longitudinal septum in the crest. Secondly there is no perforated septum joining the edges of the primary and secondary septa, and partially enclosing the outer pockets of the pneumatocodon. In consequence it is untrue to say that the finger-like processes of the saccus form horizontal pairs, one on each side of a longitudinal septum. The authors also wrongly describe the gas-gland as strip-shaped: it is nearly circular. Their diagram of the relationship between crest-pockets and saccus, shown in their pl. 28, fig. 4, is useful.

Here is a description of the crest of a specimen well preserved in an extended condition—specimen no. 58, taken by R.R.S. 'Discovery II' at St. 3255 on 13 June 1955 (in $41^{\circ} 08' N.$, $14^{\circ} 32' W.$), right-handed, of floatlength 16 cm., gas-gland diameter 45 cm. and pneumatocyst-capacity about 300 c.c. The first developed set of septa, ten in number, hang down some 3 cm. in the central region. The major pockets are subdivided three times, and rudiments of a fourth series are visible at the crest-margin. The secondary septa are 2.5 cm. deep, the tertiaries 1 cm. and the fourth series 0.5 cm. A view of the float and crest from above is given in Text-fig. 1.

From this figure it will be seen that the crest is of considerable thickness, and that there are depressions where the lower edges of the septa meet the sides of the float at the sites of the original fusion of pockets. For this reason the sides of the crest have not got plane surfaces.

The method of formation of the transverse septa which hang down inside the crest of the float can be deduced by seriating growth-stages. In a young specimen, No. Juv. 5 (Text-fig. 2), which has a float-length of 19 mm. (artificially stretched some 3 mm. by injection of fluids into the pericystic space), the upper surface of the pneumatocyst itself, now withdrawn from the crest, shows the beginnings of six dome-shaped pockets. At the apex of each pocket are the collapsed rudiments of later-developed twin pockets, themselves showing the beginnings of subdivision. Development of the crest is less marked at the ends than in the centre of the float.



Text-fig. 2. *Physalia physalis*. Young left-handed specimen, number 5, $\times 8$. Float-length 19 mm. To show origin of the crest as a fusion of crest-pockets. A, B from windward, C, from above. PZ = protozooid at oral end, GG = gas-gland, S = septum, 1 = before fusion, 2 = after fusion.

Part of the upper wall of the float is pushed out by the expanding muscular projections of the pneumatocyst, and the anterior wall of each pocket gradually fuses with the posterior wall of the adjacent pocket, forming a septum (Text-fig. 2), which grows deeper as the fusion-process proceeds with age. The secondary, tertiary and subsequent septa develop in a similar way as the finger-like projections of the pneumatocyst divide and push out smaller pockets at a higher level (Pl. X, fig. 7). The outer longitudinal muscles seem not to be involved in the fusion-process. A section of a septum shows a core of structureless lamella covered with gastrodermis. Leuckart (1851) stated that the septa were formed by the inner (gastrodermic) layer of circular muscles.

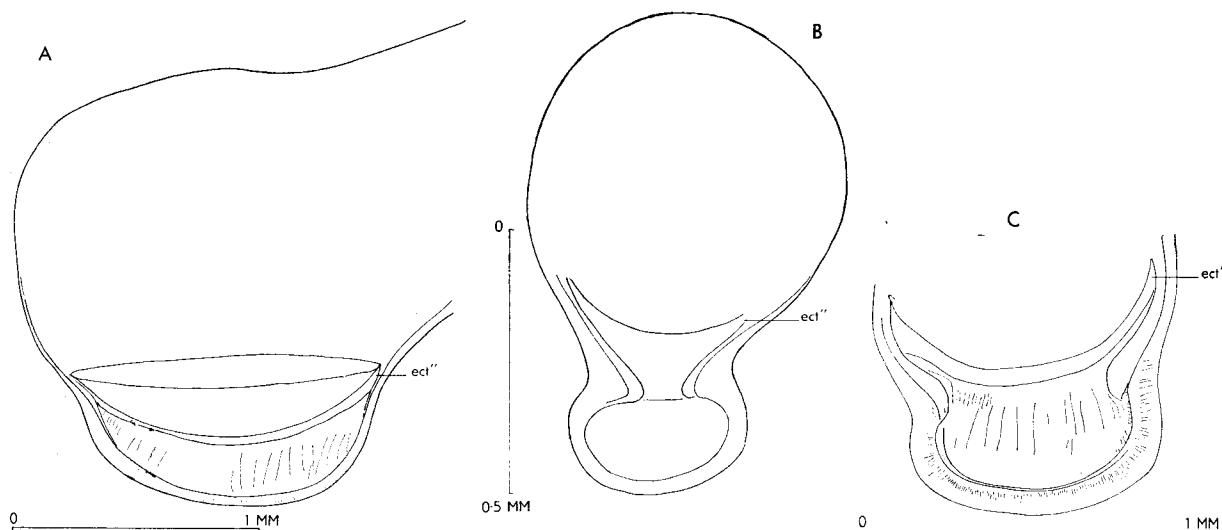
To obtain accurate data on the relationship between float-length, saccus-capacity and area of gas-

gland it would be necessary and far more easy to work on living material. However I have arrived at some rough conclusions after measuring material fixed in formalin. The relationship between float-length and capacity of a number of specimens was noted and a graph made.* Judging by the way in which the capacity-curve flattens out at the higher values, it might be supposed that the maximum float-length would not be more than about 23 cm. (9 in.), though Quatrefages's famous specimen (1854) measured 25 by 10 cm., or nearly 10 in. in length. I am indebted to Mr B. S. Kisch for a record of a 12-in. specimen washed ashore on 15 September 1957, at Errromardi, Bay of Biscay, at about the same time as the Channel swarm noted on page 315, but I have no data as to capacity in this specimen. When measuring the float-capacity of fixed specimens I withdrew and pumped back air several times with a hypodermic needle and syringe, but this method cannot be as satisfactory as working on living specimens. Even the measurement of float-length of fixed specimens cannot be made satisfactorily owing to frequent distortion due to preservation.

The relationship between the area of the gas-gland and the capacity of the air-sac appears to be roughly as shown in Table 2:

Table 2

<i>Area of gas-gland (mm.²)</i>	<i>Capacity of air-sac (c.c.)</i>
17	0.5
300	50
1000	150
1500	250-300



Text-fig. 3. *Physalia physalis*. Gas-glands of three larvae seen in optical section through the float-wall.
A, $\times 32$, B, $\times 70$, C, $\times 45$. *ect''* = secondary ectoderm.

In the early stages the gas-gland and the air-sac itself resemble those of physonect siphonophores. The secondary ectoderm forms a very deep layer which projects well into the air-sac itself as a solid plug (Text-fig. 3). A section of an 11 mm.-long specimen at this stage was published by Okada (1935).

It is remarkable that a simple epithelium can build up a gas-pressure. But *Physalia* is not alone in its ability to do this, for although in most fishes with a closed swim-bladder this build-up against a pressure-gradient is achieved by a counter-current capillary system—the *rete mirabile*—it has been shown by Sundnes, Enns and Scholander (1958), in at least three species of salmonid fish, that the pressure build-up of oxygen and nitrogen does not take place in the blood but is a function of the epithelium lining the swim-bladder.

* The data and graph, unfortunately, have since been mislaid.

After this larval stage has been passed through (Text-fig. 3) the gas-gland becomes a flattened disk on the lower part of the enlarged section of the float (Pl. VIII, figs. 1, 5). I made the following rough measurements, under one and the same set of conditions, of fourteen live specimens, whose horizontal length overall, omitting appendages, ranged from 35 to 60 mm. (see Table 3).

Table 3

<i>Float-length</i> (mm.)	<i>Gas-gland diameter</i> (mm.)	<i>Float-length</i> (mm.)	<i>Gas-gland diameter</i> (mm.)
35	10	50	10
40	8	50	10
40	9	50	15
40	10	55	12
40	10	60	10
45	7	60	11
45	8	60	13

Measurement of other specimens from various localities after fixation in formalin, some with and some without relaxation in magnesium chloride, are given in Table 4.

Table 4

<i>Float-length</i> (mm.)	<i>Gas-gland diameter</i> (mm.)	<i>Float-length</i> (mm.)	<i>Gas-gland diameter</i> (mm.)
2	0·8	50	9
4	1·0	53	11
11·5	2·5	65	12
20	2·5	85	16
22	3·0	92	18
26	5·0	140	35
32	7·0	188	45
38	7		

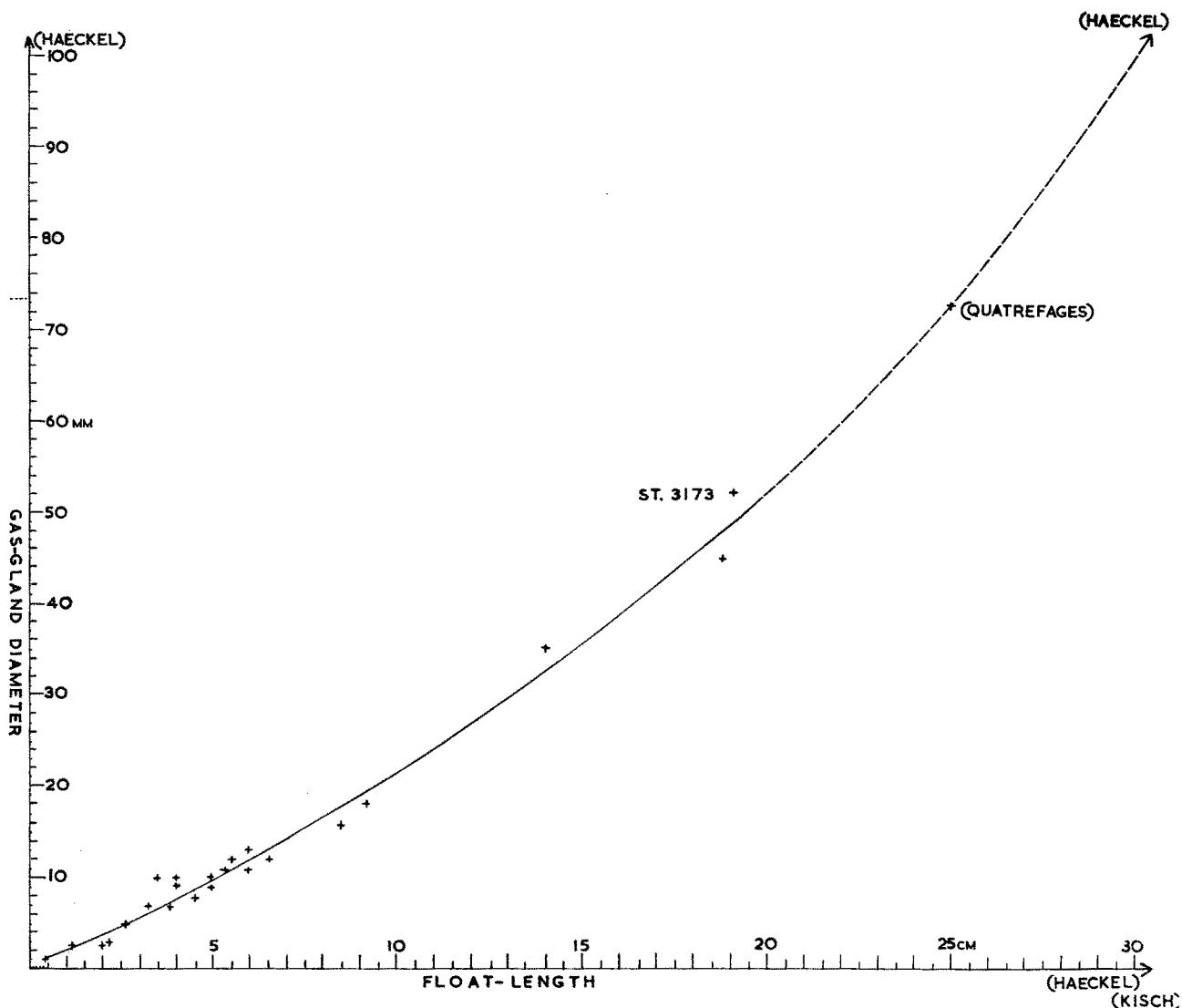
These data are shown in the form of a graph in Text-fig. 4, from which it can be concluded that Quatrefages's huge specimen may have had a gas-gland of diameter exceeding 70 mm. The largest known to me is that of a 'Discovery' specimen from St. 3173 ($42^{\circ} 35' N.$, $11^{\circ} 35' W.$), whose gas-gland measures 52·5 mm. Haeckel (1888) thought the gas-gland could reach a diameter of 100 or 200 mm.

Quatrefages (1854) described how a *Physalia* (right-handed and about 25 cm. in length) that he had been investigating at La Rochelle suddenly lost all its air and collapsed; and, having chanced to glance at it again a quarter of an hour afterwards, he was surprised to see it distended again, although a little smaller than before. He concluded that it must have taken in air through the pore. Haeckel (1888) stated that, by compressing the float voluntarily, the animal could extrude the included air through the apical stigma and sink down. After a short time had elapsed, he said it could rise again, secreting a great mass of air by the pneumadenia and refilling the float. He said he had often observed this process repeated in December 1866 off the Canary Islands.

I saw no sign of this behaviour at Lanzarote, nor did I succeed in squeezing the air out, owing to the slipperiness of the animal. Louis Agassiz (1862) who had observed thousands of *Physalia* alive recorded that he had never seen them emptying their air-sac and sinking under the surface of the water, even in stormy weather.

On the other hand, young specimens appear to act differently. Eschscholtz (1829) found, on irritating a *Physalia* five lines long (15–16 mm.), that it suddenly expelled all the air from its bladder and sank. Agassiz and Mayer (1902), who studied a number of young animals between 2 and 4 mm. in length taken by 'Albatross' in the autumn and winter of 1899, among the Paumotus and Society Islands, related that 'unlike the adult, these young individuals possess the ability to sink below the

surface; a feat which they accomplish by extruding a bubble of air through the pore of the float. In a few minutes the gas regenerates and then the animals rise to the surface'. A. Agassiz (1883) had already observed a young specimen of about 6 mm. 'swimming at various levels in the jar in which it was kept'. Miss Eleanor Dodge, writing from Miami, has kindly informed me that she has talked with people who have caught *Physalia* in plankton nets with their floats empty, but she did not refer to their size; it looks as if they must have been small, perhaps larval stages.



Text-fig. 4. *Physalia physalis*. The relation between the diameter of the gas-gland and the length of the float.

My companion at Lanzarote, George Mackie, made some experiments by withdrawing measured quantities of air from the pneumatocyst with a hypodermic syringe, but there was little subsequent change of volume.

Quatrefages seems to have been the first to have analysed the contents of the pneumatocyst; his results are given in Table 5:

Table 5
Percentage of

Specimen	Gas (c.c.)	O	N	CO ₂
1	45	17.7	82.2	0
2	72	17.2	82.7	0

On 25 September 1957 I removed the air-sac from a moribund, 7-in., right-handed specimen at Hastings—the last specimen of a swarm that began to come ashore in westerly winds on 10 September. About the same time, specimens were coming ashore also at St Jean de Luz, Bay of Biscay, and at Almunecar Granada in the Mediterranean. I took the excised air-sac, which I had placed unfixed in a jar of medicinal paraffin, to the Government Chemist's department on 26 September. On the next day, 27 September, Mr D. Green made the following analysis of the contents, whose cubic capacity he estimated at 200 c.c. The gas was liberated from the sac under brine and was found to contain carbon dioxide 0·5% by volume, oxygen 19·9% and nitrogen (by difference) 79·6%,* as compared with the average composition of atmospheric air: CO₂, 0·04%; O, 20·99%, and N plus inert gases 78·98%.

Schloesing and Richard (1896) gave the following analysis of float-gases shown in Table 6:

Table 6

Gas (c.c.)	O	N	Percentage of	
			A	CO ₂
410	15·1	82·02	1·18	1·7

Wittenberg (1958) has recently reported finding, in specimens taken at Woods Hole, a fifth component, carbon monoxide (traces to 8%). The majority of specimens contained from 1 to 5% CO, which accounted for all the combustible gas present.

MOTION RELATIVE TO WIND AND WATER

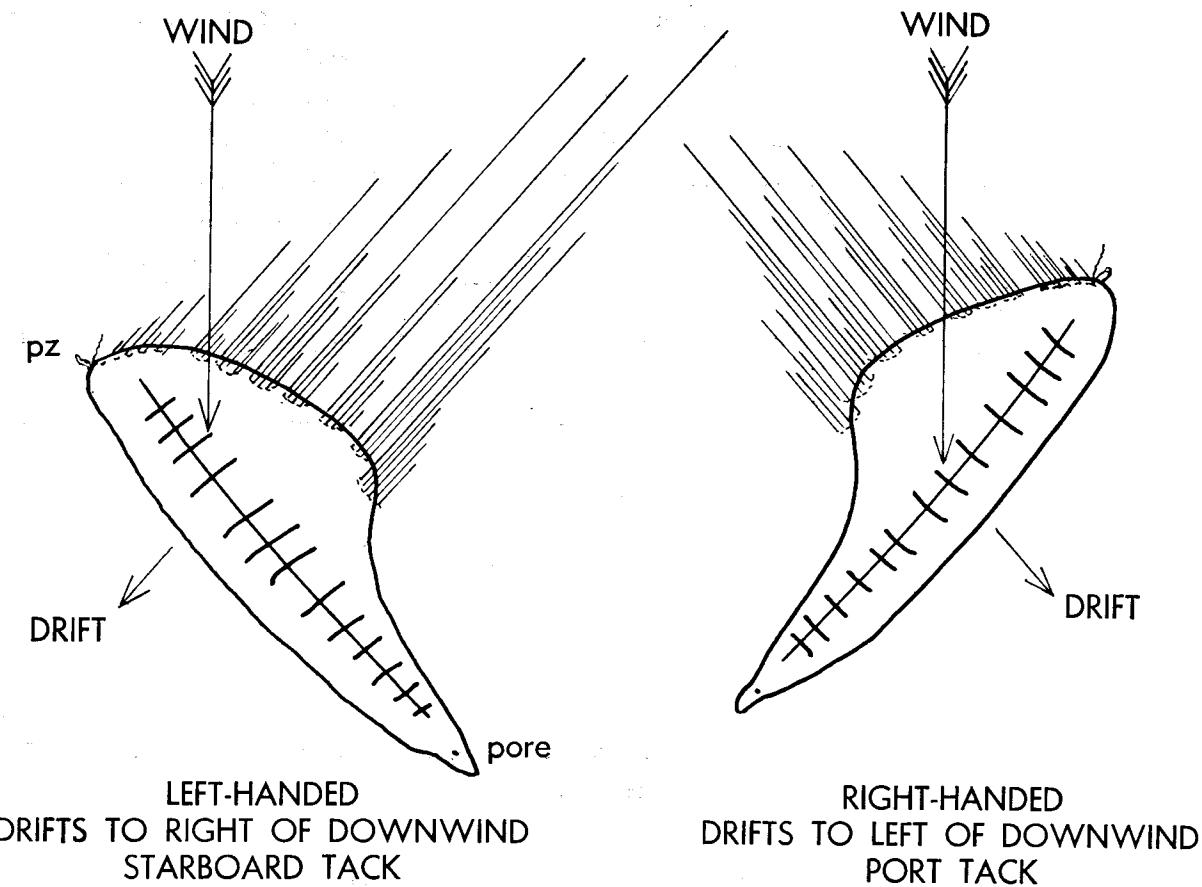
Physalia has a characteristic orientation relative to the wind. The aboral† half is free of appendages and the animal floats with its long axis at an angle of about 45° from the down-wind direction. The tentacles and appendages are borne on a bulge on the oral half of the animal, the tentacles streaming out on the windward side and acting as a drogue or sea-anchor. The bulge is situated either on the left or right side of the float (Text-fig. 5), and I think that left or right-handedness in a particular individual must be established on the first windy day that the larva keeps to the surface. The larval tentacle would cause a drag on the windward side, so that the float would be blown (so to speak) to leeward. As the new tentacles grow—and we know that their development is very precocious—this drag would be increased, and the part of the float from which they are budded would become bowed-out to windward as a bulge, resulting fortuitously in a left- or right-handed individual.

We may liken the steadily drifting *Physalia* to a sailing vessel hove-to on either the port or starboard tack. In life the oral end heads up to the wind, an important point to remember when observing the behaviour of living specimens in a breeze. Right-handed individuals appear to be on the port tack and left-handed ones on the starboard tack.

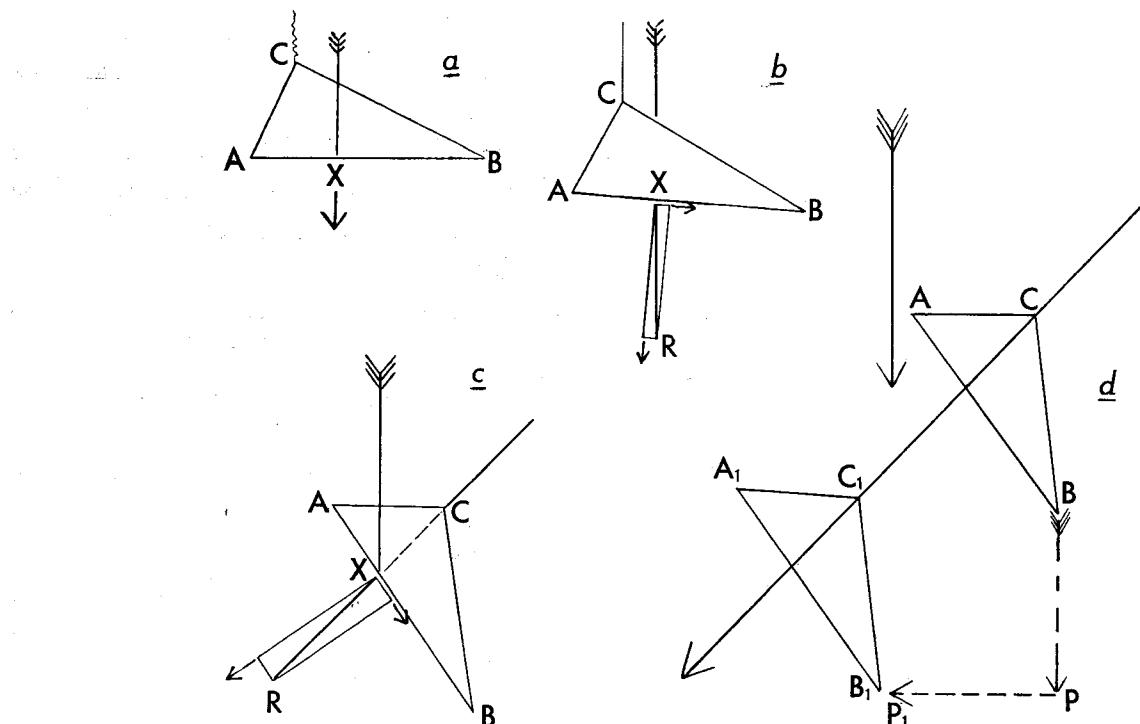
The animal, being asymmetrical, does not drift straight downwind. I have to thank Dr Henry Charnock, Reader in Oceanography at Imperial College, London, for a tentative explanation of its direction of drift. Suppose we consider a grossly simplified model of a left-handed animal seen from above, with a crest AB and the point of attachment of the appendages (the bulge) at C (Text-fig. 6a). In a given wind a force is exerted at X. This force has two components, one normal to the crest AB and the other along the crest; their resultant is R (Text-fig. 6b). After resting in this position during a

* Presumably this figure includes the inert gases.

† Huxley (1859), Haeckel (1888), Schneider (1898) and Okada (1932) all regarded, mistakenly I feel, the aboral (pore) end as anterior and the oral (protozooid) end as posterior.



Text-fig. 5. *Physalia physalis*. Angle of drift from the windward direction of left- and right-handed specimens. PZ = protozooid.



Text-fig. 6. *Physalia physalis*. Direction of drift. a, b, c, to show why the drift is not normally straight down-wind. d, to show an apparent movement into the wind caused by drift of the surface water to leeward.

calm, if caught by the wind the animal will be seen to rotate until *R* comes into line with *C* (Text-fig. 6c); it then drifts steadily, along a course at an angle of about 45° with the down-wind direction—to the right in this case because the specimen is left-handed. Rotation is very rapid, because the aboral half of the animal *X-B*, being free of appendages, only rests lightly on the surface.

The slight drift along the axis *AB*, which theory shows to be inevitable, I could not detect at sea. On the other hand there appeared to be a marked progression in the opposite direction, that is from *B* to *A*. No doubt this is accounted for by movement of the surface layer of water past *B* in the direction *BP*, and by a visual impression of movement of the animal across the wind from *P* to *P*₁ (Text-fig. 6d). The direction of drift of both right- and left-handed specimens is shown diagrammatically in Text-fig. 5.

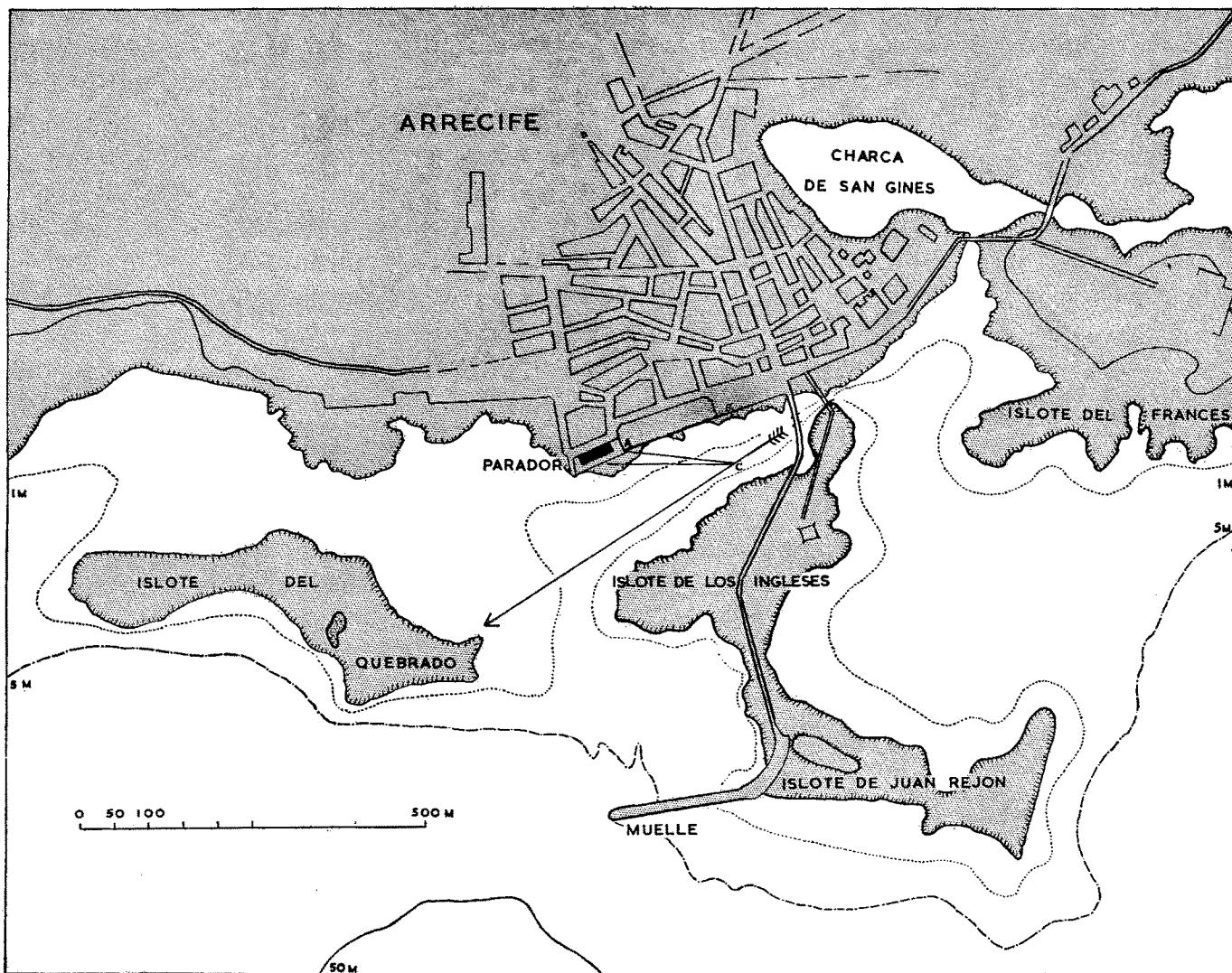
Woodcock (1944) was the first to draw attention to the motion of *Physalia* relative to wind and water. He cited observations on the asymmetry of 421 specimens in the North Atlantic and the Gulf of Mexico, and put forward a hypothesis to explain the advantages to specimens in the northern hemisphere of being driven consistently about 45° to the left of the down-wind direction. He also cited twenty-two preserved specimens from the southern hemisphere, most of which were mirror-images of the northern ones, and which would have been driven to the right according to his theory. But Fontaine (1954) noticed that forms driven ashore on the southern coast of Jamaica by prevailing east winds were left-handed, that is, they would have been driven to the right of the down-wind direction. I will not refer in detail to Woodcock's hypothesis because it need never, I think, have been postulated. My companion, Dr G. O. Mackie, and I (1956) found at Arrecife and off the island of Allegranza to the north of Lanzarote that both right- and left-handed specimens appear to be common in the North Atlantic. Chun (1887) had already recorded finding on the same day and in the same place in the Pacific Ocean thirty-two young specimens, of which eighteen were right- and fourteen left-handed. He also mentioned that both Eschscholtz and Leukart had referred to what he called this 'inversion'. We found that the type which comes ashore at any particular spot depends on the local wind. Indeed, on one particular day, 15 March 1955, a south-east wind had blown at Arrecife and was falling off at 18.00 hr., when I collected specimens that would have been driven to the left of the wind. An hour or two later, when the wind had shifted to the south-west, specimens of the other hand were taken. Winds from these two quarters were less likely to have driven in *Physalia* of the opposite hands, as can be seen from Text-fig. 7. Dr Mackie suggested to me that this disymmetry may have survival value, in that it obviates the stranding of the whole mixed population of *Physalia* in any one set of circumstances. No doubt it also ensures optimum density of the population in the most favourable environment. Woodcock had already suggested that motion either to the right or left of the wind would make it possible for *Physalia* to avoid remaining in the convergent zone caused by parallel, wind-induced surface vortices; as for example in the North Atlantic, where it could be fatally trapped by sargasso weed in those areas where the weed is common.

Wilson (1947) had accepted, as a working hypothesis, Woodcock's contention that movement will always be to the left of the wind-direction in the northern hemisphere, and suggested that though a fair breeze might give the full 45° inclination, a storm might tend to drive *Physalia* more directly before it.* His table vi assumed this last suggestion. He also thought that shoals of *Physalia* blown on to our coasts may have bred in latitudes higher than usual. If that were the case, one would expect the specimens to be small instead of exceptionally large.

After the preliminary experiments and observations on drifting *Physalia* made on 14 April 1955, at Arrecife, I carried out some further crude experiments on 15 and 16 April off the shore and inside

* Natzio's observations (see p. 322) tend to confirm this.

the mole and reefs, between the Parador and the bridge with specimens of float-length 18 cm. approx. Running in the direction of the wind was a measured distance of 150 m. between the wall *A* of the Parador forecourt and a second wall, *B* to the eastward near the bandstand (Text-fig. 7). The boat was taken up to a point marked *C* in Text-fig. 7 in line with wall *B*. A cross-bearing kept the outer or



Text-fig. 7. *Physalia physalis*. Chart of Arrecife, Canary Islands, showing position of drifting experiments.

Table 7

Run	Specimen	Time of start at C (hr.)	Time of finish at A (hr.)	Notes on 15 April
1	1	11.11	11.24	Not much crest up. A few minutes lost in 'rolling' at the start
2	2	11.33	11.41	Crest well up. Came right in to Parador wall
3	1	11.48	11.59	Crest well up at 11.50. At 11.58 breeze fell off and <i>Physalia</i> fell over into the wind. Arrived 50 m. out from wall <i>A</i>
4	3	12.25	12.30	No. 3 was used on 14 April. Crest was good but tentacles deteriorating. Arrived 30-40 m. from wall <i>A</i>
5	4	12.35	12.44	Another of yesterday's specimens, in similar condition. Arrived 20 m. out from wall

southernmost pier of the bridge in line with the pylon of the old drawbridge to the eastward of it. This conveniently gave the wind direction as well. Times of arrival of specimens opposite the Parador forecourt wall *A* were taken. Near here they were generally driven ashore. A spherical glass-float, which had been put over the side at *C* with the specimens, then had to be sighted, chased and its position approximately fixed by cross-bearings on shore marks. It consistently travelled down-wind. Five runs were made on 15 April towards the end of flood-tide between 11.11 and 12.35 hr. The times taken for *Physalia* to be driven from the starting-point *C* to the end of wall *A* were as shown in Table 7.

On this day, 15 April, the wind-velocity (?) at Airport was given by the kindness of the Meteorological Office, London, as 19 knots at 12.00 hr., direction 070°.

A second series of experiments was carried out on 16 April, at slack-water (low tide), when the velocity of the wind was less than on 15 April, perhaps 8 knots. No data could be given by the Meteorological Office, except that at 09.00 hr. the wind velocity was 8 knots, direction 120°. The results were as shown in Table 8:

Table 8

Run	Specimen	Start at C (hr.)	Finish at A (hr.)	Notes on 16 April
6	5	14.05½	14.11	A 'roll' at the start
7	6	15.23	15.32	Arrived 20 m. out from wall <i>A</i>
8	(4 together) 7, 8, 9, 10	15.40		
	7		15.49	Arrived close to wall <i>A</i> .
	8, 9			Picked up again (between extremes)
	10			Arrived 50 m. to east of wall <i>A</i> . Time lost through bad discipline of crew (2 boys)

No further opportunities for similar experiments occurred before I left Arrecife on 24 May.

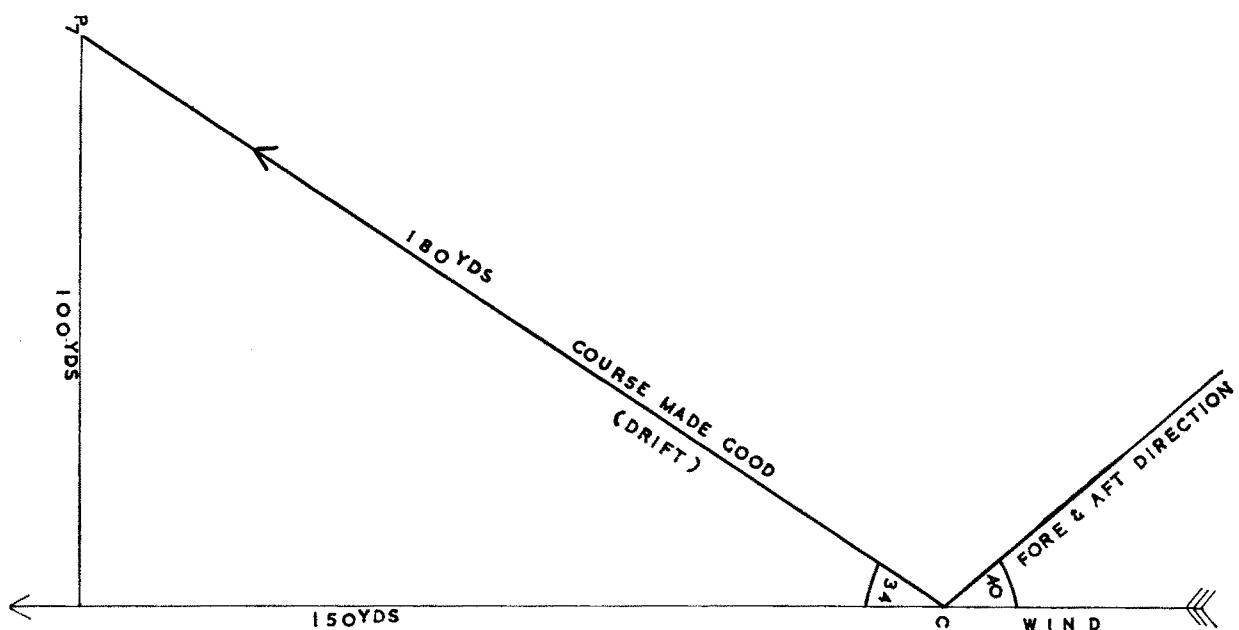
The direction taken by the long axis of *Physalia* relative to the wind is about 40°, estimated by holding close above the specimens a long pennant attached to the end of a bamboo.* It was not easy to have the boat manœuvred into the right position for close observation without blanketing the specimen or impeding its progress, and my notes were more than once blown into the water.

In order to get some idea of the angle of drift from down-wind direction at slack-water in a light breeze, I select the experiments on specimens 7–10. The course taken by no. 7 forms the hypotenuse of a right-angled triangle, of which the other sides are formed by (a) the distance (100 m.) from the end of the Parador wall *A* to the line-of-sight formed by the piers of the two bridges (direction of wind), and (b) the distance along the direction of the wind from the starting-point *C* to a point opposite the Parador wall *A*. This distance is almost the same as that between the two walls *A* and *B*. Measurement on paper of this triangle gives the angle of drift from the down-wind direction taken by no. 7 as 34° (Text-fig. 8); for no. 10 the angle was 42°.

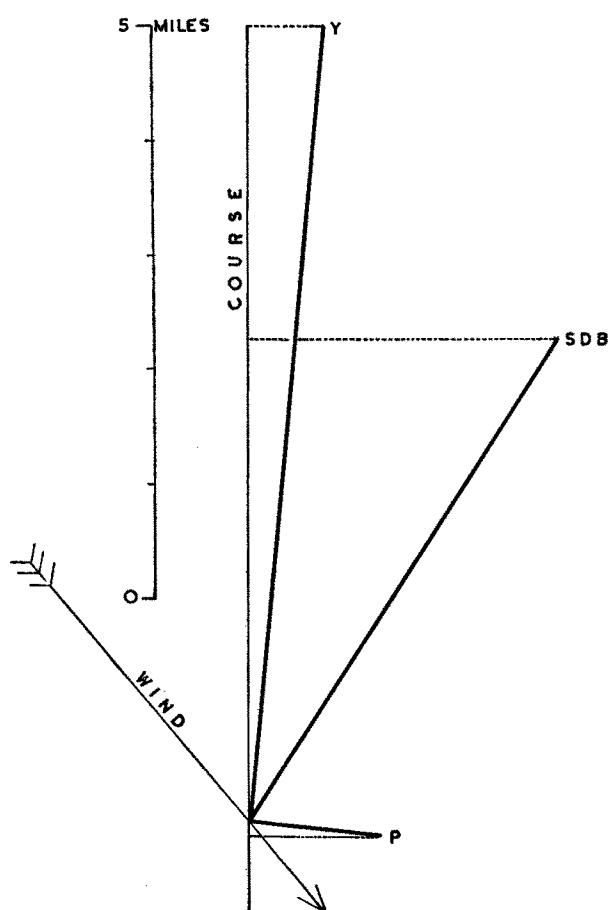
Plotting the result of the experiment on specimen 4 in the same way, I find that it drifted about 180 m. in 9 min., a speed of 20 m. a minute or 0.75 knots in a breeze of velocity rather less than 19 knots over the end of a flood-tide that can be ignored.† Specimens 6 and 7 made similar speeds, and specimens 2 and 5 were driven rather faster. These last four experiments were made under slightly different conditions. In Table 9 I suggest a comparison between boat performances and *Physalia* in 10–15-knot wind (see Text-fig. 9).

* The protozooid faces up-wind, the pore down-wind (see Text-fig. 5).

† Compare this with the estimate of Woodcock (1956) of 15.6 m. per minute in a breeze of 13 knots for a specimen of 17 cm. in length.



Text-fig. 8. *Physalia physalis*. Angle of drift in experiment number 7.



Text-fig. 9. *Physalia physalis*. Comparison between courses-made-good by a deep-keeled fast sailing yacht, Y, a shallow draft sailing boat, SDB and *Physalia*, P.

Table 9

	<i>Yacht, 50 ft., with much lateral resistance</i>	<i>Boat, shallow draft, 24 ft. × 8 ft. × 1 ft., canvas, 160 sq. ft.</i>	<i>Physalia</i>
Angle of fore-and-aft-line from the wind	40°	40°	40°
Course made good	45°	70°	146°
Leeway	5°	32°	95°
Forward speed, knots	7	5	—0.13
Sideways speed, knots	1	2.8	0.75

(It may be of interest to record here some observations that I made in May 1956 at Villefranche on the sailing-behaviour of *Velella*, about which little seems to be known. The observations were made from the causeway that links Le Port with La Darse. Small numbers of *Velella* were drifting slowly in the light breeze close into the rocks, so that I could look down on them at range of about 15 yards. After watching several individuals closely for 2 hr. or so, I came to the following tentative conclusions: *Velella* orientates its long axis to the wind in much the same way as *Physalia*. Having a rather short axis, it appears to be not very stable so that now and then it turns slowly, but eventually takes up its original orientation again at an angle of about 40° to the wind. Right- and left-handed forms occur as in *Physalia*, but no further opportunities arose, as I hoped they would, to continue a study of *Velella*.)

Since this report was begun, Woodcock (1956) published an interesting short article on 'Dimorphism in the Portuguese man-of-war', partly to give further details in support of his contention that, in the North Atlantic, the animal is consistently driven by the wind to the left of the down-wind direction. Whether Woodcock's figures would satisfy a statistician that left-handed individuals predominate there, and if so to what extent, it is not for me to say, but in view of the large population which must exist there I feel doubtful. I would agree that, supposing roughly equal numbers of the two kinds started off on their drifting-voyages round the average cyclonic wind-system of the North Atlantic, left-sailing *Physalia* might tend to sail away from the centre of the system, often in the direction of coastal waters. This was pointed out to me previously by Dr Mackie, but it would be a very big task to collect evidence of this. I have already started to fix the positions and tack of a few specimens observed at sea, in the hope that one day a meteorologist might be induced to work out the estimated positions of the same animals on a few days both before and after the time of observation. It is only in this way that I think we shall obtain data on their circulatory movements. It seems to me very improbable that ecological factors can act selectively for tack on each generation, or that dimorphism can be due to genetic differences. That anything like a 'tack'-change can be caused by 'migration of the tentacles on the pneumatophore' seems to me quite out of the question, although as the animal grows older, small branches of the cormidia do grow out to leeward. I very much like Woodcock's chart of the Kaiwi channel, which shows clearly the effect of a change of wind on the landfall of *Physalia*. His statement that off Deewhy Beach, Sidney, the right-sailers outnumber the others is interesting; but I doubt whether it will be confirmed, as Woodcock seems to hope, that most *Physalia* in the southermost hemisphere sail to the right.

But I can give him one more record of southern hemisphere specimens—sixty-seven 4-cm.-long *Physalia** collected by Prof. T. A. Stephenson at Muizenberg Beach, False Bay, S. Africa (prevailing winds in summer, south-east). Only one of these was right-handed.

For statistical purposes it is useless just to count animals of either tack from the southern hemisphere. Woodcock (1944) said 'of twenty-two south latitude animals preserved at the Museum of Comparative Zoology, Harvard University, and at the U.S. National Museum in Washington,

* B.M. Reg. No. 1934, 3.14.1.

nineteen were left-handed and three were right-handed, that is 86% of them were mirror-images of the animals from the northern hemisphere'. We must know whether and how frequently animals of either tack can in theory come ashore with winds that occur on beaches for which records are available.

Once more I have pleasure in acknowledging my indebtedness to Mr J. C. Natzio for reporting to me observations made aboard R.R.S. 'Discovery II' in the vicinity of $38^{\circ} 35' N.$, $20^{\circ} 13' W.$ in the middle of March 1958. The ship was frequently stopped and it was possible to keep *Physalia* individuals in view for some time. On a typical occasion the ship was lying-to with the wind north-west, force 2, on the port beam. The ship was drifting to leeward at about $\frac{1}{2}$ a knot and the speed of drift of *Physalia* specimens was estimated at about $\frac{1}{4}$ of a knot in a direction to the left of down-wind. The angle between the animals' course (drift) and the direction of this force 2 wind was about 40° , the maximum observed. In winds stronger than force 4 the line of the floats' crests was parallel to the wind's direction and the animals drifted straight down-wind. Natzio doubted whether *Physalia* drifted any faster under these conditions. *Physalia*, he said, is quite easily blown by a slight gust so that the blunter, oval end is temporarily ahead, and the animal may sail in this way for some little distance. He also reported that rolling appeared to be slow and deliberate in calm weather, while in a wind the animals seemed to be suddenly blown straight over until the crest was horizontal on the surface of the water. He got the impression that capsizing was caused by a sudden gust upsetting the stability of the float, and not as I suggested by a lull, for he observed a float to be blown apparently straight over on the water where it would remain for some seconds, after which it would flick back suddenly into the upright position again. In my opinion this behaviour does not constitute the rolling phenomenon. Natzio likened the appearance of *Physalia* to that of a buoy with a tide running past it, the tentacles functioning as the buoy's mooring cables; they have the same retarding effect as that of a sea-anchor.

During this spring cruise of 'Discovery II', Natzio reported, *Physalia* was seldom absent from view south of about $38^{\circ} 30' N.$ As a rule one specimen was not out of sight before others came into view. The maximum float-length observed would have been about 7–8 in. A swarm might consist of more than a hundred in an area of as many square yards, and the individuals in a swarm varied in size from the maximum down to as little as an inch or so. The average length was perhaps about 4–5 in. Very small ones could easily have escaped observation. Apart from the swarms, Natzio's impression was that *Physalia* was quite widely scattered.

STINGING-POWERS AND TOXICOLOGY

It appears from various published accounts that there is a complex mixture of pharmacologically active substances in the tentacles of the Cnidaria, not all of them necessarily confined to the stinging-capsules or nematocysts. It is not surprising, therefore, that the effects of being stung by these animals, or of injecting extracts, are varied. In addition some nematocysts have greater powers of penetration than others. Lane and Dodge (1958) report that tentacle-nematocysts of living *Physalia* may occasionally penetrate heavy-gauge surgical gloves. Attempts have been made to identify the substances which produce the stinging sensation and other effects, but until quite recently all the cnidarian substances used for experimental work have been obtained from crude tentacle-extracts. Fortunately new techniques are now available (Phillips, 1956; Lane and Dodge, 1958) for obtaining pure capsular contents.

As to the effects of being stung by *Physalia* I know of no records of fatalities, but as Elizabeth Pope (1953) has pointed out there has been some confusion in Queensland between *Physalia*, to which the name Portuguese man-of-war should be strictly confined, and a very dangerous Charybdeid jelly-fish

of the genus *Chiropsalmus*, to which some Queensland people have applied the same name. There is very good evidence that *Chiropsalmus* has caused the death of a healthy man aged 21 years within 3 min. of stinging, as well as a boy of 11 years in the Cairns swimming-bath. The toxin concerned must be far more deadly than the fastest-acting snake-venom. Very recently, Southcott (1958) has reviewed the subject of lethal stings by cubomedusan jelly-fish and has pointed out that it is still uncertain whether the cubomedusan responsible for deaths in northern Australian waters belongs to the genus *Chiropsalmus* Haeckel or *Chironex* Southcott. But Halstead (1958), who a month or two earlier discussed the subject of jelly-fish stings and their medical management, suggested that the species *Chironex fleckeri* Southcott might be identical with *Chiropsalmus quadrigatus*.

I have myself witnessed the effects of *Physalia* stings at Las Palmas, Canary Islands, where hundreds of bathers are treated at the Victoria Hospital. In one particular case I saw a girl being helped out of the water and up the beach with extensive urticarial weals all over her legs. She seemed in great pain. And yet I was told by a visitor to the Cape Verde Islands, that in one bay, João Devora, where he constantly met with *Physalia*, though it was absent in Bahia des Gates at Matiota, everyone was quite used to being stung and made no fuss about it. Again, I was told by an Australian that on the eastern beaches where *Physalia* is common, boys often pick up a specimen and creeping up behind a victim slap him on the back with the tentacles.

The obvious treatment for stings is the application of an anti-histamine cream or taking an anti-histamine by the mouth. First-aid treatment commonly given is the application of urine, picric acid or ammonia to the skin, and rubbing the skin with sand, though it is difficult to see how such methods could be effective.

Lane and Dodge (1958) report that nematocysts on laboratory surfaces or clothing retain their reactivity for at least two weeks, and that surfaces, clothing and skin can be decontaminated by the application of 95% ethanol. Although this treatment of the skin does not reduce the pain of the stings already received, Lane and Dodge consider that the local application of alcohol to the skin of a stung swimmer is an effective palliative measure, because the toxicity of the capsule contents of *Physalia* is reduced by such an organic solvent, which also inactivates adherent nematocysts.

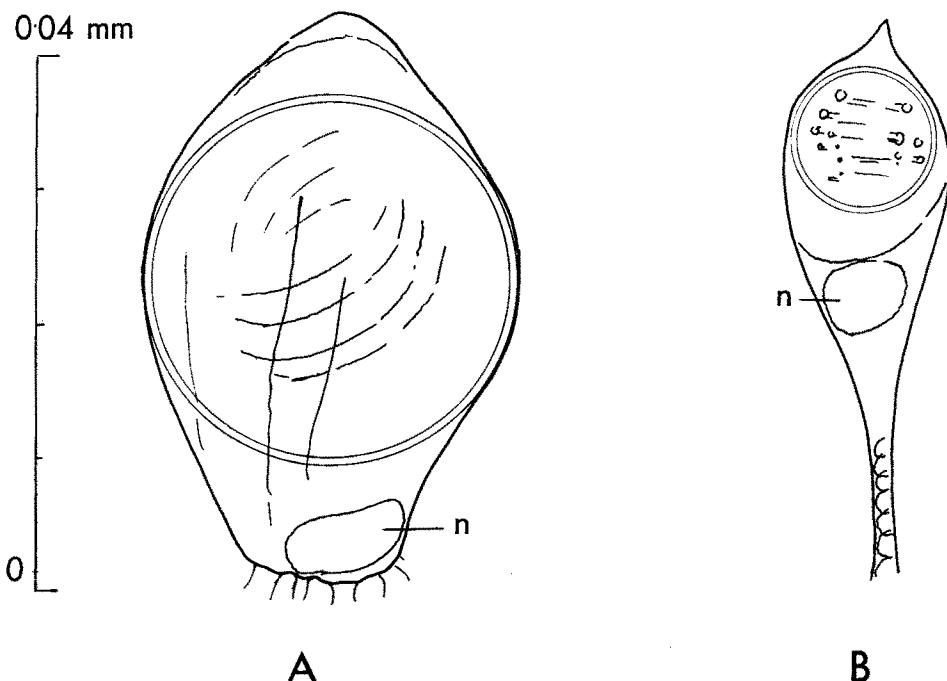
Some of the reactions to the injection of crude tentacle-extracts of Cnidaria in laboratory animals are: somnolence, paralysis, anaesthesia, digestive disturbances, prostration, respiratory interference, anaphylactic shock, and in small animals even death. But a distinction must be made between the injection of the crude extracts and being stung by the contents of the stinging capsules themselves. The effects of the latter are usually burning pain of varying degrees of severity at the site of contact, urticarial weals, pain in the lymphatic glands of groin or armpit, and perhaps shock.

Lane and Dodge (1958) have made a new and very different approach to the toxin problem, and one which pharmacologists appear to think is very promising, though perhaps it has not gone very far yet. They say that the nematocyst content appears to be a highly labile protein-complex. When tested in fish, frogs or mice it appeared to affect the nervous system, particularly the respiratory centres, before involving the voluntary muscles. The toxin elicited responses in the isolated heart of the clam which were similar to those caused by acetylcholine.

After intraperitoneal injection of mice with an appropriate toxin sample of pure *Physalia* capsule-content, Lane and Dodge report the following symptoms: increased activity and tremors probably due to local irritation. After 10 min. there were ataxia, decreased muscle-tone, flaccid paralysis, slowed and laboured breathing, defecation, aphrodisia, marked myosis, cyanosis, anoxic convulsions and death. Survival time was 1-48 hr. depending on the dose administered.

NEMATOCYSTS

We do not yet know the whole story of the development, transport and thread-devagination of the nematocysts of *Physalia*. There are two distinct types of nematocyst. Those found in the tentacles have globular capsules and tapering threads or filaments (Pl. XXV, fig. 4). The capsules are of two mean sizes, $26.8\ \mu$ and $11.3\ \mu$ in diameter (Lane and Dodge, 1958). That the threads taper can be seen both in optical section of the coiled-up threads and in devaginated ones. Pl. XXV, fig. 5 shows pads of these isorhizas round the mouth of a gastrozooid. Having no butt or hampe they should be referred to as isorhizas. Developmental stages can be found in the walls of the ampullae, from which they migrate not to the earliest formed pads or heads of the tentacle, but to those that have grown a little. They can be seen during passage in the ectoderm of the tentacle-tube or lamella. Will (1909) figured the cnidoblasts of this type of nematocyst, and although I could not resolve all the details of those I have examined, I can confirm his account of them in general (Text-fig. 10). The nucleus and



Text-fig. 10. *Physalia physalis*. Nematoblasts. A, from the ampulla, capsule diameter $27\ \mu$. B, from the ampulla, capsule diameter $11\ \mu$. n = nucleus.

nucleolus of the cnidoblast or mother-cell are clearly visible at the inner end. In immature cnidocysts there is a large, central, homogeneous, hyaline mass at the circumference of which the thread can later be seen developing. Surrounding this central mass is a clearer, transparent substance which presumably forms the capsule wall. In 1926 Will published, without figures, an interpretation of what he thought to be the earliest developmental stages, but there still remains doubt about the details.* Chun (1892) had published figures of immature, tentacular cnidoblasts which show the 'tube externe', a feature that was puzzling until Weill (1934) showed that it was only the prematurely devaginated thread of an immature nematocyst. In many immature cnidoblasts I have seen the thread of the nematocyst partially devaginated in coils in the body of the cnidoblast as figured by Chun. The thread of the nematocyst is frequently found in preserved material to be devaginated while

* In my opinion nothing is known yet about normal nematogenesis in any Cnidarian, except that the nematocyst originates as a homogeneous secretion-mass in an ectodermal mother-cell (nematoblast).

the capsule of the nematocyst is still retained by the cnidoblast. It is under these circumstances that fibrils of the cnidoblast-wall can best be seen.

The nematocysts of the tentacle of the protozooid appear to migrate into the tentacular heads from the ectoderm around its base. In mature specimens it is only in this region of the protozooid that any nematocysts can be seen, though the larvae are uniformly covered. It is a point of great interest that because the protozooid possesses only a relatively small tentacle, this never reaches that later stage in evolution found in secondary tentacles, where the much greater demand by these enormous tentacles for nematocysts has led to the development of hypertrophied basigasters called ampullae (see p. 355). In most siphonophores the basigaster of the protozooid is indeed smaller than those of the secondary gastrozooids, but in none of the other siphonophores is the contrast in size so great as in *Physalia*.

Neither my colleagues, Dr Evans and Mr Macfarlane, nor myself have been able to resolve the finer details of the threads of the nematocysts. There were certainly no spines as large as those indicated by Hardy (1956, fig. 24F) in any threads which we have examined. I was disappointed in an offer that was made to obtain pictures with an electron-microscope—the only satisfactory way of clearing up this point.

0 50 μ



Text-fig. 11. *Physalia physalis*. Nematocyst discharged from a palpon, to show butt or hampe. The spiral bands are not correctly represented. No spines were visible. $\times 575$.

The nematocysts of the palpons of *Physalia* appear to differ slightly from those found on the tentacles. I am again indebted to Miss Eleanor Dodge for a sample of nematocysts which she isolated from palpons. With the assistance of Dr Evans and Mr Macfarlane, I was able to measure and make a drawing (Text-fig. 11) of a representative capsule. It has a diameter of 20μ and, unlike those of the tentacles, possessed a butt or hampe at the base of the thread, the diameter of the butt measuring 3μ and its length 15μ . Although we examined nematocysts with a twelfth-inch objective in ordinary light as well as with phase-contrast and dark-ground illumination, none of us could resolve the finer details of the spiral bands on the everted thread. However it was quite clear that there were no large spines on the butt as illustrated by Weill (1934) in his fig. 343 b. Weill was not very precise about the place of occurrence of his 'sténotèles': he said that they came from the 'stolons gonozoidiques supportant les médusoides', but I can only suppose that he meant the palpons. I estimate that it would take nearly 80,000 of these capsules to inject 1 mg. of toxin into the prey, and about 24,000 of the tentacular capsules. The defensive role of the palpons in *Physalia* may be important because of the predatory habit of the associated fish, *Nameus gronovii*.*

Lane and Dodge found that nematocysts were still reactive after isolation from the tentacle-tissues and 20 weeks of frozen storage. They estimated that 1 g. of packed, wet, 'purified' nematocysts contained approximately 1,058,000 nematocysts.

* An article by Professor C. E. Lane (*Sci. Amer.* 202, 1960, p. 158) on nematocysts and their toxin, and on feeding reactions, contains some good photographs and a sketch of gastrozooids stimulated by glutathione. Unfortunately the article repeats some old morphological errors. Professor Lane demonstrates the relative immunity of the loggerhead turtle and of *Nameus gronovii*.

MORPHOLOGY OF *PHYSALIA*

HISTORICAL

So much has been written about *Physalia* that useful observations are likely to be overlooked. Many of the accounts are travellers' tales which have been shown to have no foundation. It would take too long and be too unprofitable to make a new summary, especially as five previous ones exist, namely those of Lesson (1843), Quatrefages (1854), Huxley (1859), Haeckel (1888), and Chun (1897b). Lesson, who had frequent opportunities to make observations on *Physalia* during the long voyage of 'Coquille' (1822/5) published an account of them in 1827 and 1838, and repeated these more fully with a survey of past observations in 1843.

I have come across no satisfactorily complete account of *Physalia*'s complicated morphology. Chun (1887) did once promise to deal with it thoroughly in a monograph on the Siphonophora but the work never materialized. Olfers (1832) gave a useful list of early references and names and figured the gonodendra. He mistook discharged nematocysts for Vorticellids attached to the tentacles. Olfers was of course writing before Wagner (1835) had published the first figures of nematocysts.* Trembley (1744) has figured what were probably the undischarged nematoblasts of *Hydra*, but it was Sir Joseph Banks's observations on *Physalia*, contained in his journal in an entry dated 12 April 1770 and seemingly entirely overlooked by Weill (1934), author of the first monograph on the subject, which provide our first knowledge of any nematocysts. I have to thank Dr A. M. Lysaght for drawing my attention to this entry: '...if touched by any substance they immediately exsert millions of exceedingly fine white threads about a line in length which pierce the skin and adhere to it giving very acute pain[.] When the animal exserts them out of any of the little knobbs or beads which are not in contact with some substance into which they can pierce they appear very visibly to the naked eye like small fibres of snow-white cotton.' Hooker published a shortened, rather dull and unscholarly version of Banks's Journal in 1896.†

On both 11 and 12 April, Banks noted that he had seen undoubted proof that the Albatross eat *Physalia*: 'April 11th....an Albatross that I had shot dischar[ge]d a large quantity[,] incredible as it may appear that any animal should feed upon this blubber whose stings innumerable give a much more acute pain to a hand which touches them than nettles.'

Banks also observed the 'kind of sail which he erects or depresses at pleasure'. But his other notes on trimming the sail and being able to sail 'in any direction he pleases' are not so trustworthy. The description of making it 'concave on one side and convex on the other varying the concavity or the convexity to which ever side he pleases for the convenience of catching the wind' is more likely a description of righting behaviour.

In the British Museum (Natural History) is a specimen, still well-preserved in alcohol, which must be one of Banks's (B.M. Reg. no. 1925.8.13.2). The label on the old 'surgeon's round' bears the names *Holothuria physalis* in much-faded ink. Its style, with a ruled line at top and bottom, and the handwriting corresponds well with that of labels on three bottles of fishes, *Serranus atricaudatus*, *Anthias sacer* and *Sebastes kuhlii*, all known I am told to be Banksian specimens. The Banksian *Physalia* has a float measuring about 7 cm. in length. It bears seven major tentacles and a number of gonodendra

* Wagner mistook the discharged nematocysts from the acontial threads of *Actinia holsatica* from Heligoland for sperms. Soon afterwards Ehrenberg (1838) published a large coloured plate of *Hydra vulgaris*, showing a number of irregularly discharged stenoteles, all with the tip of the thread still within the nematoblast, and the capsule at the outer end. He was under the impression that the capsules could be shot out and withdrawn again.

† The original is now in the Mitchell Library, New South Wales. A complete edition is to be published shortly under the editorship of J. C. Beaglehole.

which carry male gonophores. The specimen is right-handed and would have sailed to the left of the down-wind direction. It must be the specimen caught during Cook's first voyage, on 7 October 1768, south of the Cape Verde Islands, in latitude $9^{\circ} 42' N.$, and figured by Parkinson.

Huxley's (1859) observations, repeated from his 1855 communication, and his review of previous work are most useful. He longed for a Caliph Omar to straighten out the systematics, which, he complained, gave him an unpleasant vertigo. He made no proper distinction between palpons ('hydrocysts') and gastrozooids, and did not adequately describe the gonodendra ('gonoblastidia'), but to Huxley we are indebted for the first figure of a larva of *Physalia*.

Haeckel (1888) in his famous 'Challenger' report had to admit that physalids required a far more accurate anatomical examination than had been employed hitherto. He listed four genera and eleven species. He thought that there were four groups of species of *Physalia*, two with crested and two with non-crested floats. In each of these divisions there was a group with one and a group with several large main tentacles. I believe that all *Physalia* are crested in life, and that when fully grown they all have seven or more large tentacles. I have examined hundreds of living specimens of all growth stages in the Canary Islands, as well as preserved specimens from all oceans. I see no grounds for suspecting that there may be more than one species, which should bear the name *Physalia physalis* (L.). My field studies of Atlantic forms have provided answers to the two questions, which needed answering, before coming to this conclusion; (1) Are some of these animals crested throughout life while others are not, or is this only a matter of age and of degree of temporary inflation or deflation of the pneumatocyst? (2) Do successive growth-stages show (a) differing numbers of large (main) tentacles, and (b) a filling-up of the gap between the oral and main series of cormidia? The facts are that all *Physalia* are crested, that the number of large tentacles increases with age, and that the gap in question becomes relatively smaller and less conspicuous as growth proceeds.

Chun (1897b) and Bigelow (1911) both held the view that there were two and only two species, an Atlantic and an Indo-Pacific. But Bigelow assumed that, because up to that time none of the Pacific specimens examined had more than one large tentacle, it was evident that this was the final stage of development and that therefore the fully grown Pacific forms resembled an immature stage of the Atlantic *Physalia*. This argument has since been shown by Kawamura (1910) not to hold good. He found in fact later stages of development with more than one large tentacle.

The figures of *Physalia* drawn by Haeckel (1888) for pl. xxvi of his 'Challenger' report give no hint of the great complexity of budding. The only one of these figures which appears reliable is number 4. It is not a lateral view as stated, but a view from above of a right-handed specimen.* It shows very well the general shape of a relaxed specimen, although the basal internode is hardly visible, and the dorsal apical pore and ventral gas-gland cannot be seen. The protozooid is really in a terminal position (Pl. XI, figs. 1-3) and not in the subterminal one shown by Haeckel. Fig. 3 of Haeckel's plate showing a young specimen is misleading, because it shows the protozooid as having an ampulla and a gonodendron, structures never found in that position at any stage, and does not show the oral zone of appendages (see page 337). In fig. 3 (to which I refer again on page 339) and in fig. 6, Haeckel has simplified the structure of the gonodendron. Also the ampulla is always united along most of one side to the tentacle by the muscular fold which runs down the length of the tentacle. Haeckel's fig. 7 is valueless and fig. 8 is not at all accurate; fig. 5 is typical of a rather moribund specimen. I mention these points not to detract from the great value of Haeckel's pioneer work, but to help those who are not familiar with *Physalia*. Haeckel made the most of the specimens of the relatively few good species

* Brandt's generic name *Alophota*, used by Haeckel in explanation of the figure, refers to his idea that there were species of *Physalia* with no crest.

of siphonophores (thirty) which he included in his monograph, by making idealized coloured drawings, even when he was not sure of the details. It is greatly to his credit that he undertook the formidable task of making coloured sketches of living animals in the field, a task which would be quite impossible for me.

In 1932 G. H. Parker made some interesting experiments at Key West, Florida, on the neuromuscular activities of the tentacles. He also recorded the measured length of an extended tentacle as a little over 9 m., and stated that the tentacles can shorten to one-seventieth of their maximum length.

POLYMORPHISM

In *Physalia* there are three types of medusoid individuals all found on the gonodendra: (1) the reduced male and female gonophores, (2) the peculiar asexual nectophores, and (3) the jelly-polyps, which are probably vestigial nectophores.

Of polypoid individuals there are four types, as well as the unique protozooid with its small moniliiform tentacle: (1) the feeding gastrozooids which become separated from their tentacles, (2) the gastrozooids of group I of cormidia II-VII of the main zone and of all the cormidia of the oral zone, (3) the secondary and tertiary gonozoooids, which like those of (2) give rise by budding to the branches of the gonodendra; none of these have tentacles, and (4) the gonopalpons, which have no tentacles.

PATTERN OF BUDDING IN THE CORMIDIA

In spite of the large number of papers on *Physalia*, there is no good account of its gross morphology, especially of the cormidial groups of appendages and their development.

Anyone who tries to decide on the number and structure of these groups of buds will not be surprised to learn, I think, that so far no one has had sufficient patience to pursue the subject to a satisfactory conclusion. Without properly relaxed specimens, it was in the past a hopeless task; even today with better material to study, my conclusions must be of a tentative nature. In order to reach more definite results in the future, efforts should be made to anaesthetize and preserve in a thoroughly relaxed state the oldest as well as the very youngest stages of development. From a morphological point of view, the potential value of well-preserved, young specimens increases greatly for every millimetre below ten in float-length.

Previous workers on *Physalia* have tended, I feel sure, to simplify the problem by ignoring all except the largest branches of the cormidia. Accordingly, having had a great number of living specimens to deal with at Arrecife, on my return in 1955 I decided to make a completely fresh study of the structure and developmental sequence of the cormidia. My analysis is based upon detailed examination of some two dozen younger and three dozen older specimens, including those taken by R.R.S. 'Discovery', and has since been confirmed by examination of the lovely series of larvae, so kindly sent me from Miami by Miss Eleanor Dodge. Three years of laborious observation, dissection and photography have established a basic pattern of budding in the cormidia, a pattern which would have been less clear but for this opportunity of studying the early larval stages. The complexity of this pattern is illustrated by the series of growth stages shown on Pls. VII-IX. In some of the larvae examined (Pl. VII) very early indications of budding can be seen; others already carry several buds. The juvenile specimens shown on Pl. VIII vary in length between 12 mm. and 80 mm., and exhibit ever increasing budding, which culminates in the branching mass of cormidia typical of the adult *Physalia* (Pl. IX).

The cormidia are budded from a narrow tract of tissue lying along the under and windward side of the float extending from the protozooid (Pl. VIII, fig. 2) to a point half-way to the pore. This tract is divided by a gap—Haeckel's 'basal internode'—into two (Pl. XI, fig. 5), an oral zone and a main, aboral zone. The gap is particularly well marked in young stages. Specimens with float-lengths of

two or three centimetres show this division clearly. For study of the cormidia, I found it best to dissect off the whole of the budding-tract from the float and to examine the inner side first of all. In a well preserved, relaxed specimen a series of depressed openings, about a dozen in number, can be seen. Five or more in the oral zone are separated by the basal internode from the main series of seven in the aboral zone (Pl. XIII, fig. 1). The isolated first group of Cormidium I* opens separately into the pericystic space, as can be seen in specimen Lanzarote Juv B (Pl. XIII, fig. 4), so that although there are definitely only six cormidia in the aboral zone of this specimen, there are seven main openings into the pericystic space of the float, including two such openings in Cormidium I: they are the openings of the peduncles of the chief tentacles of each cormidium. Once the position of these peduncles has been found (Pl. XIII, fig. 1) it is possible, even in large specimens, to cut off each cormidial complex entire. The openings are clearly shown in the plate. Before cutting off the cormidia, it is essential to note their orientation, both with regard to the oral (protozooid) end of the float and to the leeward side, otherwise analysis of the pattern of branching becomes very difficult.

Steche (1910) and Okada (1932) numbered the cormidia of the main aboral zone starting from the aboral end; I have followed this method, both for the oral and aboral zones. In Pl. XI, figs. 4, 5, the ventral budding-tract removed from a specimen of float-length 10–11 cm. is shown with the cormidia clearly numbered. In this specimen there are at least six oral and six aboral groups; the seventh main aboral group is not developed. Seven is the maximum number of primary main-zone cormidia that I have found.

The branching-system of typical cormidia (III and VI of the main aboral zone, and 1 and 2 of the oral zone) of a specimen, number 25 from Lanzarote, were very carefully analysed. The results are shown in schematic drawings (Text-fig. 12), which not only give the correct proportions of the cormidia, but the exact number of groups on the related branches. Tables 10 and 11 (p. 338) give similar accurate analyses of the groups and branches of all the cormidia of both main and oral zones of specimen 25. This is the first time that such an analysis has been attempted.

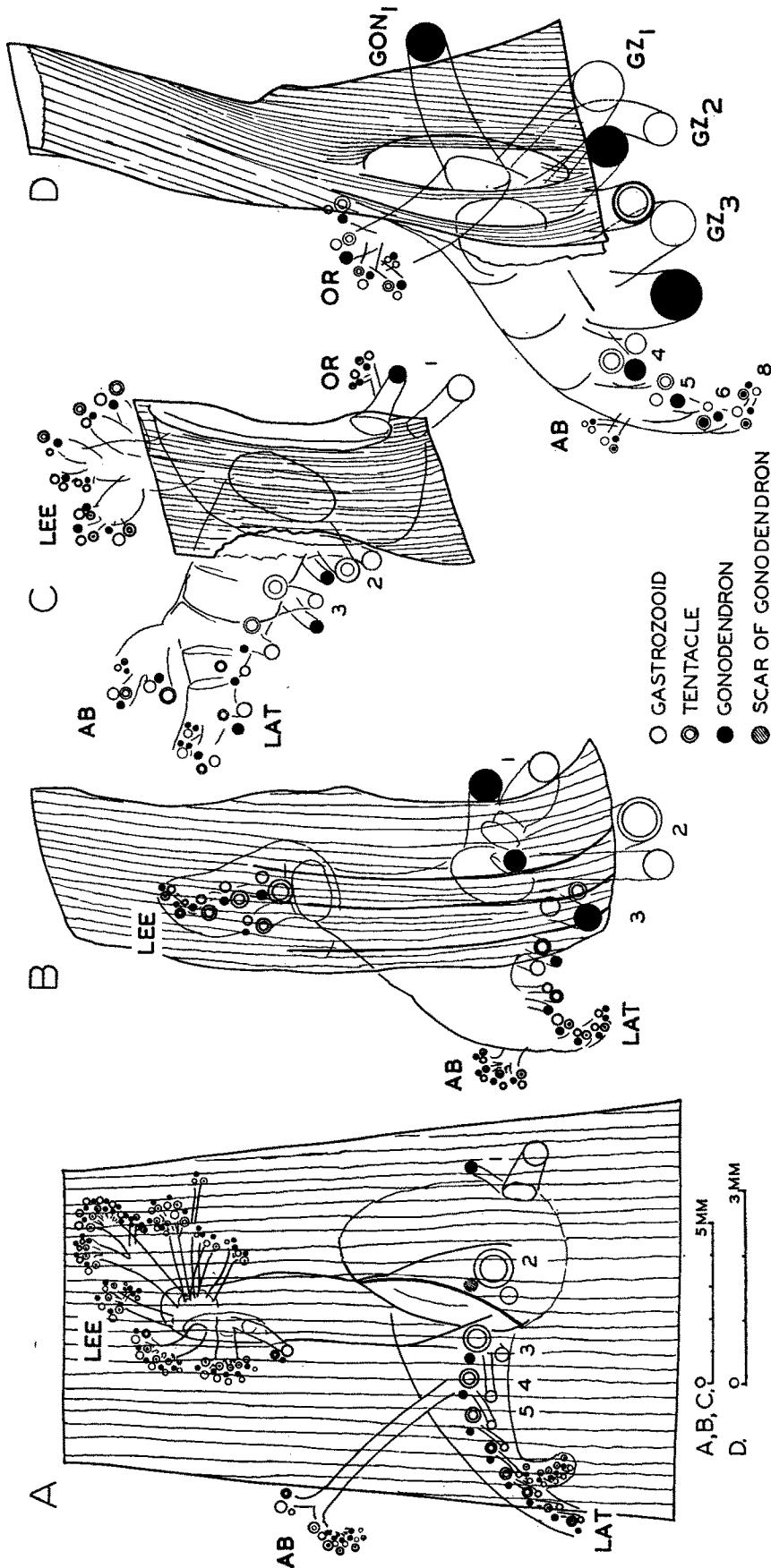
Comparison of the four drawings of Text-fig. 12 will at once make clear the main pattern of arrangement of groups in cormidia both from the oral and the main zone.

Main aboral zone (Pls. XII–XVIII)

In the main zone, the definitive number of cormidia cannot be determined in early stages; in specimens of from 1 to 2 cm. float-length there are often only five; in specimens of from 3 to 4 cm. float-length there may be six; even in a specimen with float-length of 17 cm., taken by R.R.S. 'Discovery II' in $3^{\circ} 22'$ S., $32^{\circ} 25'$ W., there are still only six cormidia in the main zone, although (as already mentioned) seven is the number usually found in the largest specimens. As in the oral zone, the smallest and presumably the youngest (VI or VII) lies at the oral end of the main zone.

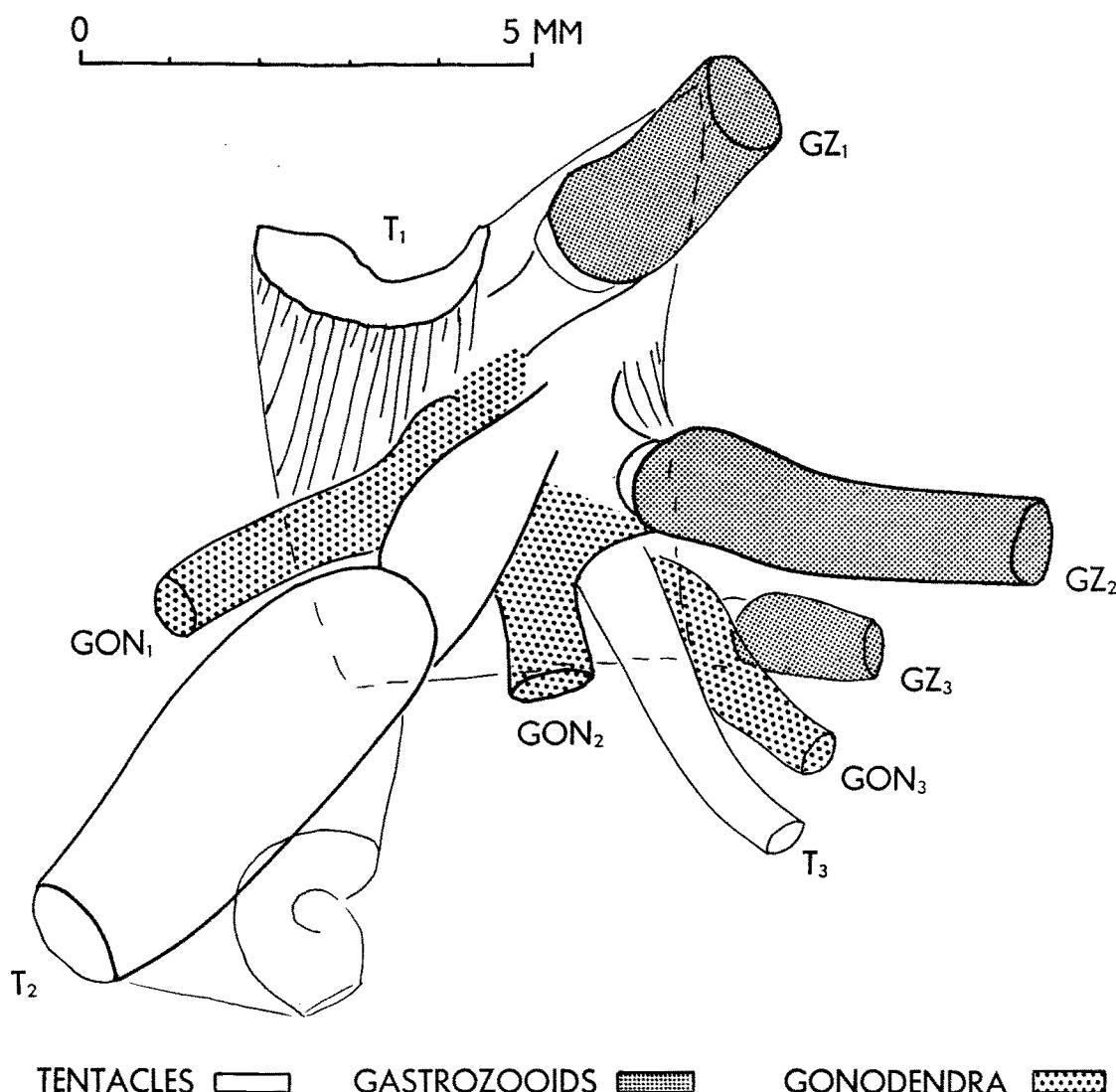
Careful examination of seven of the best preserved of my collection of younger specimens, measuring from 1·7 to 2·1 cm. in float-length, served to illustrate the early essential pattern of growth in the cormidia of the main zone (Table 10). There are three chief components of each cormidium: (1) a reduced group at the oral end consisting only of a gastrozooid with a peculiar gonodendron at its base, (2) a first tripartite group, or first lateral group, consisting of gastrozooid, tentacle and ampulla, and a gonodendron at the base of the gastrozooid, and (3) a further series of similar lateral tripartite groups, each growing from the base of its predecessor. This is the essential arrangement which visual analysis brings to light and which I have been able to record photographically. It is obscured only too soon by the development of (4) secondary series of branches (leeward, oral and aboral) from the bases of some of the lateral groups, bearing more tripartite groups (Text-fig. 12).

* Arabic numerals will be used for the cormidia of the oral zone and Roman for those of the aboral zone.



Text-fig. 12. *Physalia physalis*. Schematic drawings of separated cormidia of a left-handed specimen, number Lanzarote 25, cut from the lower part of the outer wall of the float. Float-length 18 cm., gas-gland diameter 2.5 cm., to show pattern of budding common to all cormidia. A, cormidium III (main zone) from above, $\times 4.5$. B, cormidium VI (main zone) from above, $\times 4.5$. C, cormidium I (oral zone) from above, $\times 4.5$. D, cormidium 2 (oral zone) from above, $\times 9$. AB = aboral branch, Lat = lateral branch, Lee = lee-branch, Or = oral branch. Tripartite groups numbered 1-8. Gz = gastrozooids of groups 1, 2, 3. GON = gonodendron of group 1. Note the common peduncle formed by the bases of groups 2 et seq.

(1) *Reduced group.* In cormidia III–VII prominent gastrozooids are found at the oral end of the cormidia, associated each with a characteristic, but atypical gonodendron (Pl. XII, fig. 4). In cormidia I and II on the other hand, each equally noticeable gastrozooid is linked both with a gonodendron and with a tentacle (Pl. XIII, figs. 3, 4), and lies on the aboral side of the tentacle. Thus in cormidia I and II the reduced group is missing and the first one is tripartite like all the other components of the cormidia (Text-fig. 13), whereas in cormidia III–VII the tripartite pattern of the first

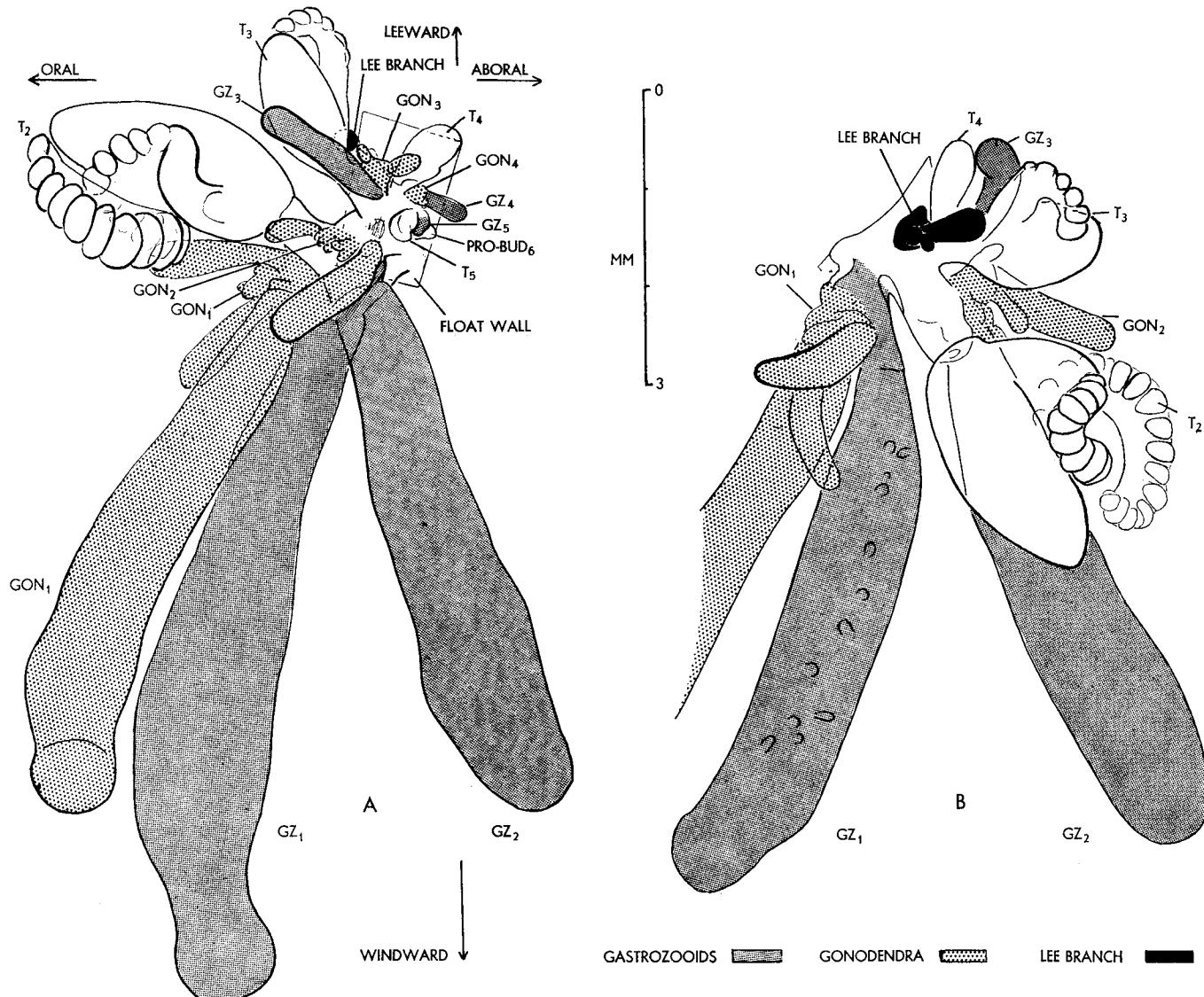


Text-fig. 13. *Physalia physalis*. Base of cormidium II (main zone) of a right-handed specimen, float-length 5 cm., from St. 403, to show the tripartite nature of the first three groups. In cormidium II, all the groups including group 1 are tripartite. $\times 11.5$.

group has been lost by the non-development of its tentacle. This pattern can generally be recognized even in old specimens when viewing them from the windward side. All seven cormidia open separately into the pericystic space. Both the gastrozooid and the gonodendron of the first groups (group 1) of cormidia III–VII appear to retain separate openings into the common atrium, or enlarged and subdivided base of each cormidium (Text-fig. 12B). But if early stages of their development are examined (Text-fig. 14A) it can be seen that the gonodendron is budded from the base of the gastrozooid as usual. It is only because of the subsequent broadening of its base and incorporation into the

growing and thickening wall of the float that the first gastrozooid's relationships become obscured in later growth stages (Text-fig. 12). The main foramen is that of the peduncle of the tentacle of group 2.

(2) and (3) *Tripartite groups,* first and laterals*. The general pattern of arrangement of the tripartite groups is easy to recognize once it becomes familiar (Pl. XIV, figs. 1-4). These groups were first described by Schneider (1898), who had only two specimens to work on, under the name of 'Urgruppen',



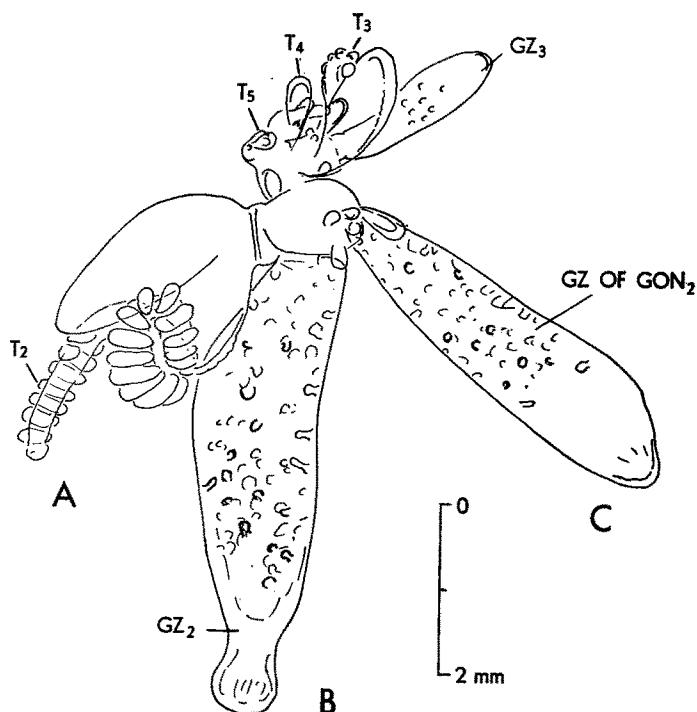
Text-fig. 14. *Physalia physalis*. Two views of cormidium VI (main zone) of a young left-handed specimen, number 11, to show stages in the growth of the lateral groups and lee-branches. A = oral view; B = aboral view. $\times 9\cdot5$. 1st group without a tentacle, GZ 1 and GON 1; lateral groups, gastrozooids GZ 2-5, gonodendra GON 2-5, tentacles T 2-5.

and although his account is difficult to follow without figures, it is a sound analysis of the tripartite groups and their subsidiary lateral branches. Each 'Urgruppe' (Text-fig. 15) consists of one polyp (gastrozooid), one tentacle and one genital cluster (gonodendron), all borne on a single peduncle (Pl. XIV, fig. 1). These simple 'Urgruppen' very soon become complicated, said Schneider, by the development of second, third and fourth 'Urgruppen' on similar peduncles, each arranged on one side of a thickened peduncle and separated from one another by lateral peduncles. Here he was probably referring to the relationship between the first tripartite group of a cormidium and the series (3) which

* The significance of these is explained on page 361.

I call lateral groups. Whether he was also referring to the series (4) arising from the bases of the lateral groups is not clear.

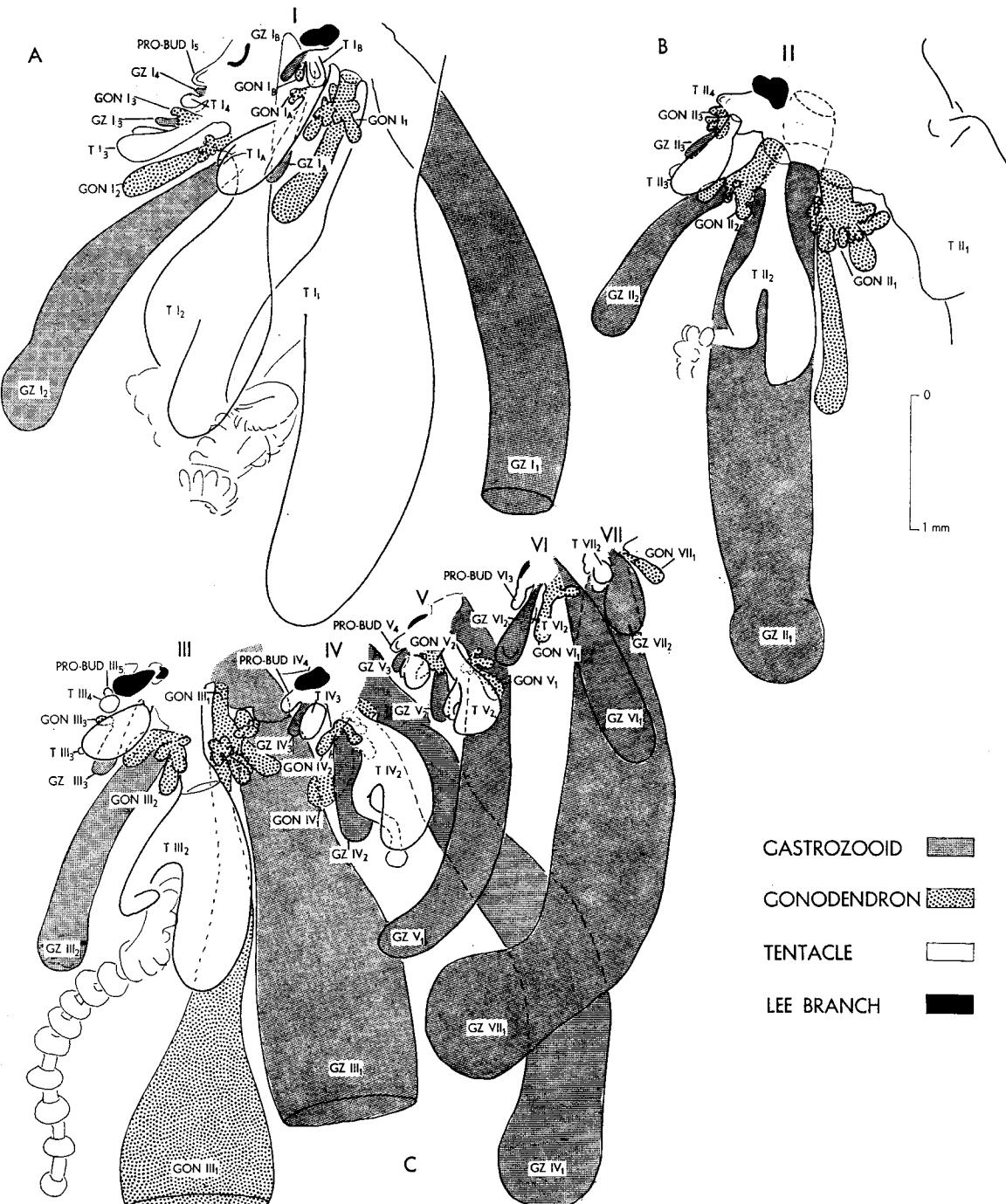
The development of group 2 and the subsequent lateral tripartite groups can best be seen in the aboral region of the main zone by examining cormidium I of a young specimen (Pl. XIV, figs. 2-3). This region looks very complicated in older stages (Pl. XIV, fig. 4); when mature it is almost impossible to analyse this first cormidium without knowledge of the younger stages. Cormidium I has room to expand because it lies at the aboral end of the main series, consequently the primary and lateral groups, especially the first, are better developed and more widely separated than those of the other cormidia. Its aboral end forms a projection (Pl. XIV, fig. 3) on which the youngest groups can be seen. Two



Text-fig. 15. *Physalia physalis*. Cormidium 5 (oral zone) of a young specimen number 11, less group 1, to show the three parts, A, B, C, of an 'Urgruppe'. Note the endodermal villi. GZ of GON_2 = gonozoid mentioned on p. 347. $\times 11$.

beautiful young specimens, measuring 2·9 and 8 cm. in float-length, show clearly that at this stage there are at least eight lateral groups in cormidium I. They decrease in size according to youth, so that the one at the aboral end is a very small bud (Pl. XIV, fig. 3). Each group consists of a gastrozooid, a gonodendron and a tentacle. They look as if they might be, and indeed at one time I thought they were, beginnings of new cormidia, but in each of the other cormidia of the main zone there is a counterpart of this series of lateral groups. As previously stated, there is evidence that the latest (youngest) cormidia to appear do so at the *oral* end of the budding-zone, whereas in the lateral groups the pattern of development is reversed, the youngest groups appearing at the *aboral* end of each cormidium. When fully developed, there may be from ten to twelve fan-shaped lateral groups (Pl. XV, fig. 4) in each main zone cormidium. They bud successively (Pl. XVII, fig. 4) each from the base of its predecessor and as growth proceeds they curl round (Pl. XV, fig. 6) so that the last small lateral of one cormidium can be seen lying to the *oral* side of the first and largest tentacle of the cormidium that lies at its aboral end.

(4) *Secondary basal branches*. These tend to occur wherever there is room for further growth and expansion, that is, on the *leeward* side of the float, at the *aboral* ends of the cormidia, and, in the case



Text-fig. 16. *Physalia physalis*. The cormidia of the main zone of a well-preserved, young, right-handed specimen K₂, float-length 11 mm., taken by Miss Dodge near Miami, to show the pattern of budding. A = cormidium I, B = cormidium II, C = cormidia III-VII. Group 1 of cormidium I is atypical in having lateral (I_A) and basal (I_B) buds. The arrangement of the parts for this drawing differs slightly from that in the specimen as photographed in Pl. VIII, fig. 5. $\times 20$. (From below, see Text-fig. 21 E.)

of cormidium VII, at the *oral* end of the cormidium. These secondary branches form a regular pattern and consist of later developed tripartite groups of appendages (Text-fig. 12). To *leeward* (Pl. XV, fig. 3) they arise from the base of the *second group*, which becomes incorporated into the ventral wall of each cormidial section of the float; *aborally* (Pl. XVI, fig. 3) they can spring from the peduncles of the *fourth lateral group et seq.* The branch at the oral end, when present, springs from the base of the gonodendron of the first group.

Some differences, not very great, exist between the seven cormidia of the main zone. It has already been pointed out that cormidium I is the most expanded (Pl. XV, fig. 4); cormidium II (Pl. XVI, fig. 4) is atypical because of the predominance of its main tentacle and in the absence of the reduced first group (see page 331) so characteristic of cormidia III–VII; cormidia III–V are the typical ones (Pl. XII, figs. 3, 4). In cormidium VII there is a secondary *oral* branch of groups at the base of group 1 as just mentioned. It is next to the basal internode between the two zones, where again there is room for the cormidium to expand, and it seems homologous with the regular series of secondary branches, met with in all mature cormidia (described under (4)), which spring normally from the bases of the peduncles of the second or third and fourth or fifth lateral groups. All these secondary branches of groups are shown in Text-fig. 12.

The degree of complexity which is brought about through the budding of secondary and subsequent series of *basal* buds is illustrated in Pl. XVI, figs. 1–4 of cormidium II of a left-handed 10-in. specimen, number Lanzarote 2. Figures 2, 4 are views from the aboral end. In figure 3 a black bristle indicates the position from which were cut the terminal, lateral groups 5–12, which curled over from left to right of the picture. Figure 1 is a view from the oro-lateral side of the cormidium. Before this photograph was taken a complex *basal* branch (Text-fig. 17A) had been cut off. This branch A consisted of six branchlets (Text-fig. 18). The first five of these were single tripartite groups, of which only the gonodendra remained. From the base of the fifth was budded a tertiary branch of five groups. The sixth branchlet (Pl. XVII, fig. 1) consisted of six groups. So that from this one *basal* branch A had been budded seventeen tripartite groups. After the photograph (Pl. XVI, fig. 1) had been taken a second basal branch was cut off (Text-fig. 17B). This branch B consisted of thirteen groups. Another branch C (Text-fig. 17) was left intact and bore nine groups. At the base of group 2 of the main series of laterals of this cormidium II (Text-fig. 17D) is another complex *basal* branch D, whose number of groups is at least 16; and from the base of group 4 of the same main series of laterals of cormidium II is a still further branch carrying six groups. Both group 4 and its basal branch are shown in Pl. XVI, fig. 3 to the left of the bristle, and lying on a small rectangular piece of black paper. The *basal* branch is the uppermost of the two.

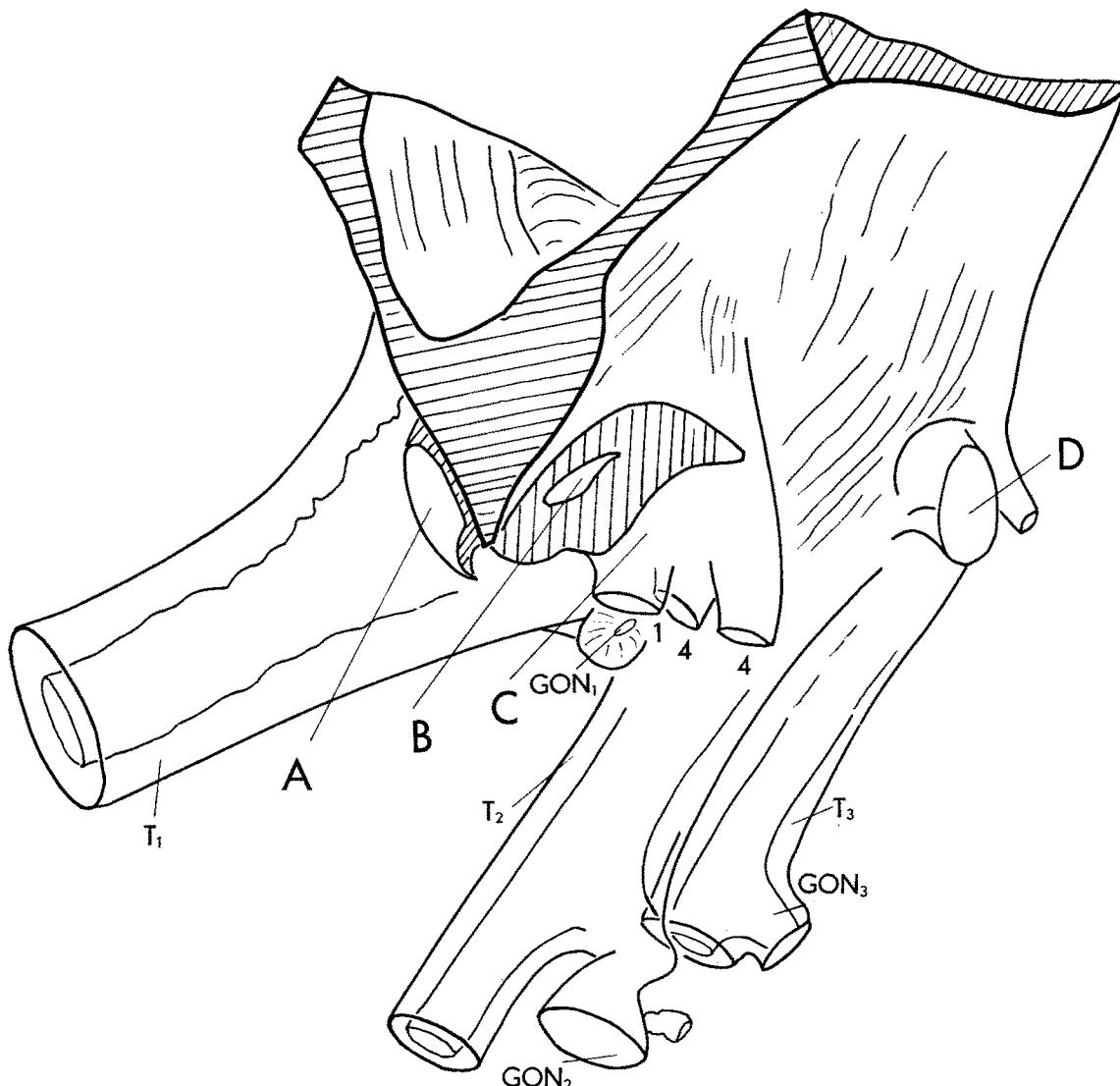
So the secondary and subsequent *basal* branches of cormidium II, which lie to *leeward*, had given rise by budding to at least sixty-one tripartite groups.

Further illustrations of this complex secondary cormidial budding will be found in the figures of cormidium III of the same specimen, Lanzarote 2 (Pls. XVII, XVIII). The first two (Pl. XVIII) show the cormidium viewed from opposite ends, and the rest show the severed branches, with indications of the positions from which they were cut. Figures 2 and 4 show the severed aboral branch and Pl. XVII, figure 3 shows the branches remaining *in situ* more clearly displayed. This photograph was taken after severing the terminal laterals 5–11, further magnified in figure 4.

A final re-examination was made of the two dozen young specimens measuring from 1 to 9 cm. float-length. They included a fine series of fifteen of the specimens sent me by Miss Dodge from Miami. The object of the re-examination was to make sure of the number of cormidia at the aboral end of the main zone. Some doubt had arisen whether there were two or only one anterior to the cormidium bearing the main tentacle, cormidium II, because of the condition found in one of Miss Dodge's specimens, number K 2 (Pl. VIII, figs. 5, 6, Text-fig. 19).

In every specimen of *Physalia* that I have examined, with the exception of K 2 just mentioned, it could be seen quite clearly that anterior to cormidium II there is a series of distinct tripartite groups, numbering in later stages a dozen or more, and that they obviously form a single cormidium, number I. The criterion is whether the first group of cormidium I is a simple tripartite, or whether it buds off a series of lateral groups.

In specimen K 2, which has a float-length of 12 mm. and is very well preserved, it appeared that there were lateral groups present in the first group of cormidium I. I therefore made camera-lucida sketches of both cormidium II and of group 1 of cormidium I of K 2. These are reproduced in Text-fig. 16. They show that group 1 has developed, beside a bud of basal leeward groups, at least two lateral groups, 1_A and 1_B . This condition is very exceptional.



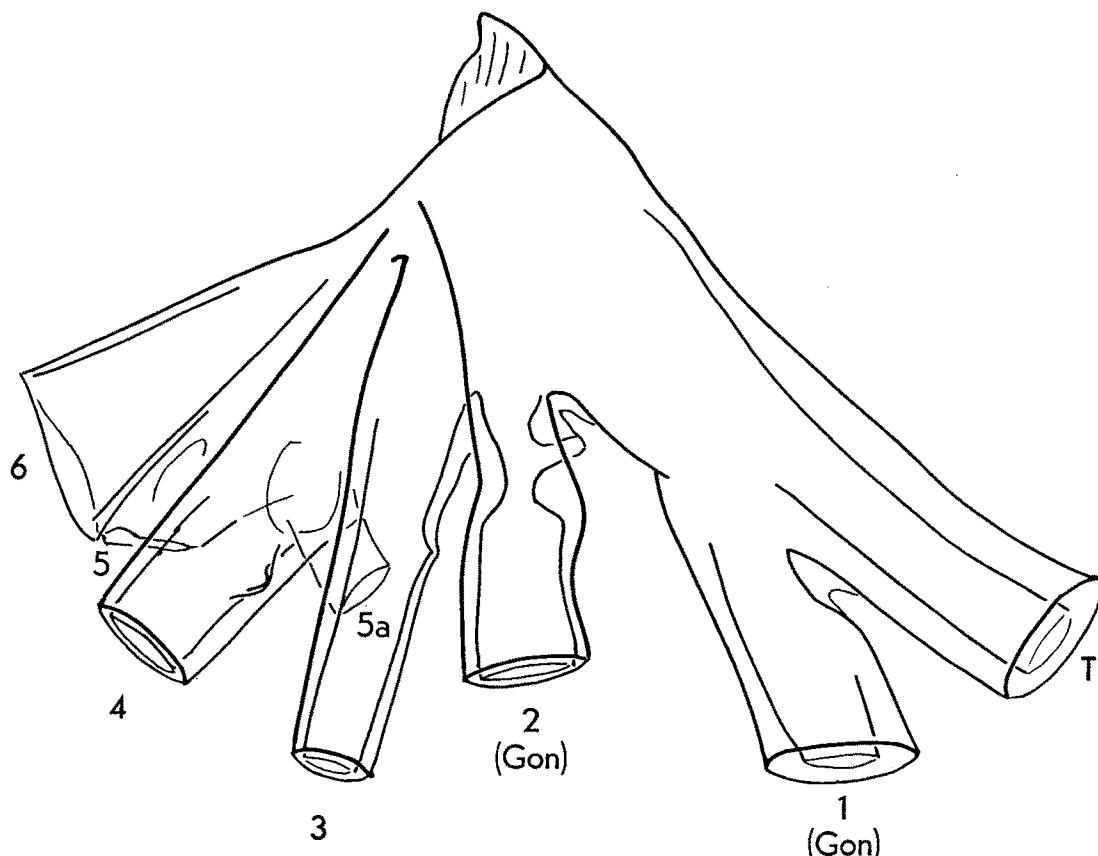
Text-fig. 17. *Physalia physalis*. Oro-lateral view of the base of cormidium II, specimen number Lanzarote 2, to show positions from which complex, secondary, basal branches were budded. Branch *A* was cut off and is shown in Pl. XVII, fig. 2. Branch *B* was cut off. Only the bases of branches *C* and *D* are shown. These four branches gave rise to 54 tripartite groups. A scar between the bases of tentacles 1 and 2 marks the position from which the gonodendron of group 1 was detached. The bases of gonodendra 2 and 3 are indicated, groups 4-11 are not shown; they would curl round to the left behind. $C_{1, 4, 4}$ = number of end-sections of branch *C* on three separate branchlets.

In the course of re-examination I confirmed that, in all other specimens, these branches of cormidium I originate from the compound joint pedicels of group 2 *et seq.*, and that group 1 is a simple, isolated tripartite group (see page 329). In K 2 on the other hand, group 1, though isolated, is exceptional in having rudiments of leeward groups and lateral groups. In all the other thirteen specimens of about the same age sent me by Miss Dodge this isolation of group 1 of cormidium I can be clearly seen. It was this isolation which led me to suspect the presence of two cormidia anterior to cormidium II bearing the main tentacle.

Oral zone (Pls. XI, XIX)

The oral end of the float carries the protozooid (the primary gastrozooid) and ventrally five or more groups of cormidia arranged in oblique rows. The youngest cormidium lies nearest the protozooid (Pl. XIX, fig. 1).

Previous authors have mentioned the complexity of budding in the oral zone cormidia, but I know of no detailed analysis of their structure and development. In unrelaxed specimens, such analysis is well-nigh impossible, but among the few mature specimens that I have handled, specimen number 25 from Lanzarote, which had been specially relaxed in magnesium chloride, showed after dissection that



Text-fig. 18. *Physalia physalis*. Proximal part of basal branch A (see Text-fig. 17) to show bases of six branchlets described in the text. Scars could be seen at the bases of 2, 3 and 4 from which tentacles have been lost.

the pattern of budding is essentially the same as in the main zone, except that the first two groups of a cormidium, and sometimes the lee-branches as well, appear to open separately into the pericystic space. This multiplicity of openings makes it less easy to separate the oral cormidia from one another for individual examination. Five cormidia can be distinguished with certainty (Pl. XI, fig. 4), but my analysis of specimen number 25 (Table 11) (based on a unique well-relaxed animal, the only one ever examined) shows that most probably seven oral zone cormidia are present in fully grown *Physalia*. This will have to be confirmed by examination of additional relaxed specimens.

The whole *oral* zone appears to be somewhat reduced and growth is less profuse. None of the *oral* cormidia of specimen Lanzarote 25 has a tripartite group 1, and only two have a tripartite group 2. With the exception of cormidium 1, neither are lee branches present in group 2; on the other hand in group 1, *oral* branches occur more frequently in this group than in the main zone (cf. Tables 10 and 11).

The gastrozooids of the *oral* zone are definitely gastrozooids, not palpons, but they seem to develop slowly and in the early stages are not easily recognizable (Pl. XI, figs 1-3).

Table 10. Analysis of branching of cormidia of main zone of specimen Lanzarote no. 25

Aboral End							Oral End
Cormidia	I	II	III	IV	V	VI	VII
Group 1	Tripartite	Tripartite	Gz., Gon. (no tentacle)	Gz., Gon. (2 brs.) (no tentacle)	Gz., Gon. (of 7 sectns. Gz. and palpons, each from base of last). (No tentacle)	Gz., Gon. (no tentacle)	Gz., Gon. (no tentacle) [Oral br. of 6 groups]
2	Tripartite 5 Lee branches (1) 5 grps. (2) 4 grps. basal br. of 2 grps. (3) 5 grps. (4) 5 grps. (5) 1 grp.	Tripartite 3 Lee branches (1) 5 grps. and bud (2) 3 branchlets of 3, 4, 1 grps. (3) 1 grp.	Tripartite 3 Lee branches (1) 5 branchlets of 1, 5, 5, 3, 2 grps. (2) 3 branchlets of 4, 6, 2 grps. (3) 4 branchlets of 5, 1, 2, 2 grps.	Tripartite 1 Lee branch of 6 grps. from base of grp. 1 3 branchlets of 1, 4, 3 grps. From base of grp. 2 1 branchlet of 3 grps.	Tripartite 1 Lee branch of 7 grps.	Tripartite 1 Lee branch of 5 grps. from base of grp. 1 1 branchlet of 5 grps.	Tripartite 1 Lee branch of 5 grps. from base of grp. 1 1 branchlet of 1 grp.
3	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite
4	Tripartite (T. lost) [Aboral br. of 6 grps., 1 branchlet of 4 grps.]	Tripartite [Aboral br. of 1, 4 grps.]	Tripartite [Aboral br. of 6 grps.]	Tripartite [Aboral br. of 4, 2 grps.]	Tripartite [Aboral br. of 6 grps.]	Tripartite	Tripartite
5	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite [Aboral br. of 4 grps.]	Tripartite
6	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite
7	Tripartite	Tripartite	Tripartite Aboral branchlet of 5 grps. from base	Tripartite	Tripartite	Tripartite	Tripartite
8	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	End of branching
9	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	—
10	Tripartite	End of branching	Tripartite	Tripartite	Tripartite	End of branching	—
11	Tripartite	—	End of branching	Tripartite	End of branching	—	—
12	Tripartite	—	—	Tripartite	—	—	—
13	End of branching	—	—	Tripartite	—	—	—

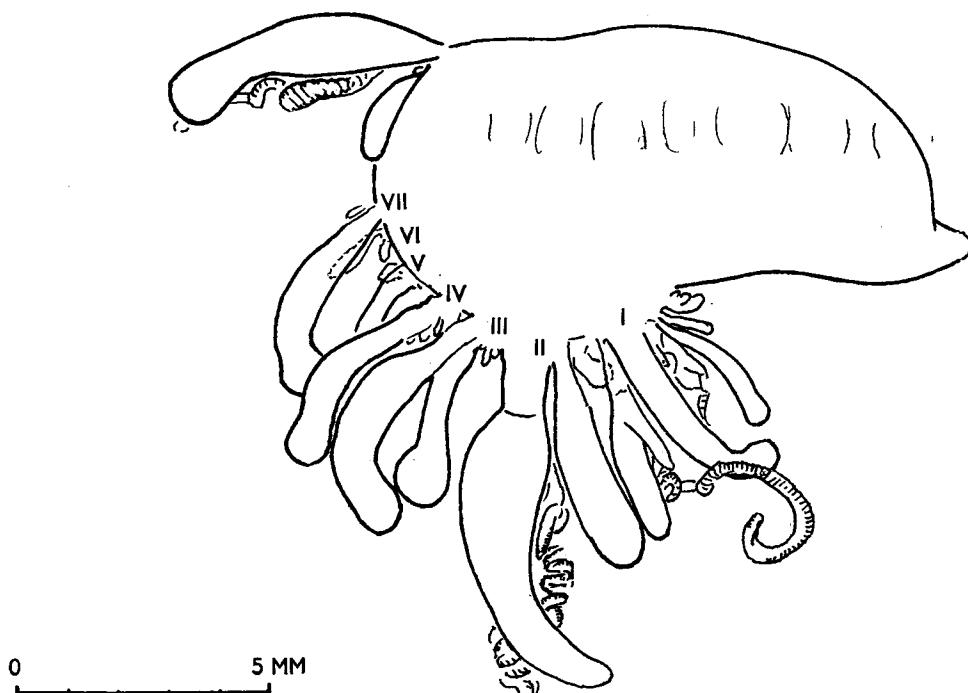
Br., Branch; Gon., Gonodendron; Grp., Group; Gz., Gastrozooid; T., Tentacle

Table 11. Analysis of branching of cormidia of oral zone of specimen, Lanzarote no. 25

Aboral End							Oral End
Cormidia	1	2	3	4	5	6	7
Group 1	Gz., Gon. (no T.) [oral br. 3 grps.]	Gz., Gon. (no T.) [oral br. 4 grps.]	Gz., Gon. (no T.) [oral br. 2 grps.]	Gz., Gon. (no T.) [oral br. 4 grps.]	Gz., Gon. (no T.) (no oral br.)	Gz., Gon. (no T.) (no oral br.)	Gz., Gon. (no T.) [oral br. 2 grps.]
2	Tripartite Lee br. of 5 grps. From grp. 3, 1 branchlet of 3 grps.	Gz., Gon. (no T.) (No Lee br.)	Gz., Gon. (no T.) (No Lee br.)	Gz., Gon. (no T.) (No Lee br.)	Tripartite (No Lee br.)	Gz., Gon. (no T.) (No Lee br.)	Gz., Gon. (no T.) (No Lee br.)
3	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite	Tripartite
4	Tripartite	Tripartite	Tripartite Aboral br. of 1 grp.	Tripartite	Tripartite (No aboral br.)	Tripartite	Tripartite
5	Tripartite Aboral br. of 3 grps.	Tripartite	Tripartite	Tripartite (No aboral br.)	End of branching	Tripartite (No aboral br.)	Bud (No aboral br.)
6	Tripartite	Tripartite Aboral br. of 2 grps.	Tripartite	Tripartite	—	End of branching	End of branching
7	Tripartite	Tripartite	Tripartite	Tripartite	—	—	—
8	Tripartite	(Bud)	(Bud)	(Bud)	—	—	—
9	Tripartite	End of branching	End of branching	End of branching	—	—	—
10	(Bud)	—	—	—	—	—	—

Br., Branch; Gon., Gonodendron; Grp., Group; Gz., Gastrozooid; T., Tentacle.

The second groups of all the main zone cormidia were tripartite, whereas this condition was found only in the first and fifth cormidia of the oral zone. Lee-branches were found only in cormidium I of the oral zone, the best developed, whereas they occurred in all the main zone cormidia. Aboral branches were absent from cormidia 4, 5, 6 and 7 of the oral zone, but all the cormidia except VII of the main zone had an aboral branch. Fewer lateral groups occurred in the oral zone than in the main zone. All the main zone cormidia consisted of at least seven groups, and one of them (I) had thirteen. In the oral zone all the cormidia had four groups at least and one of them (I) had ten.

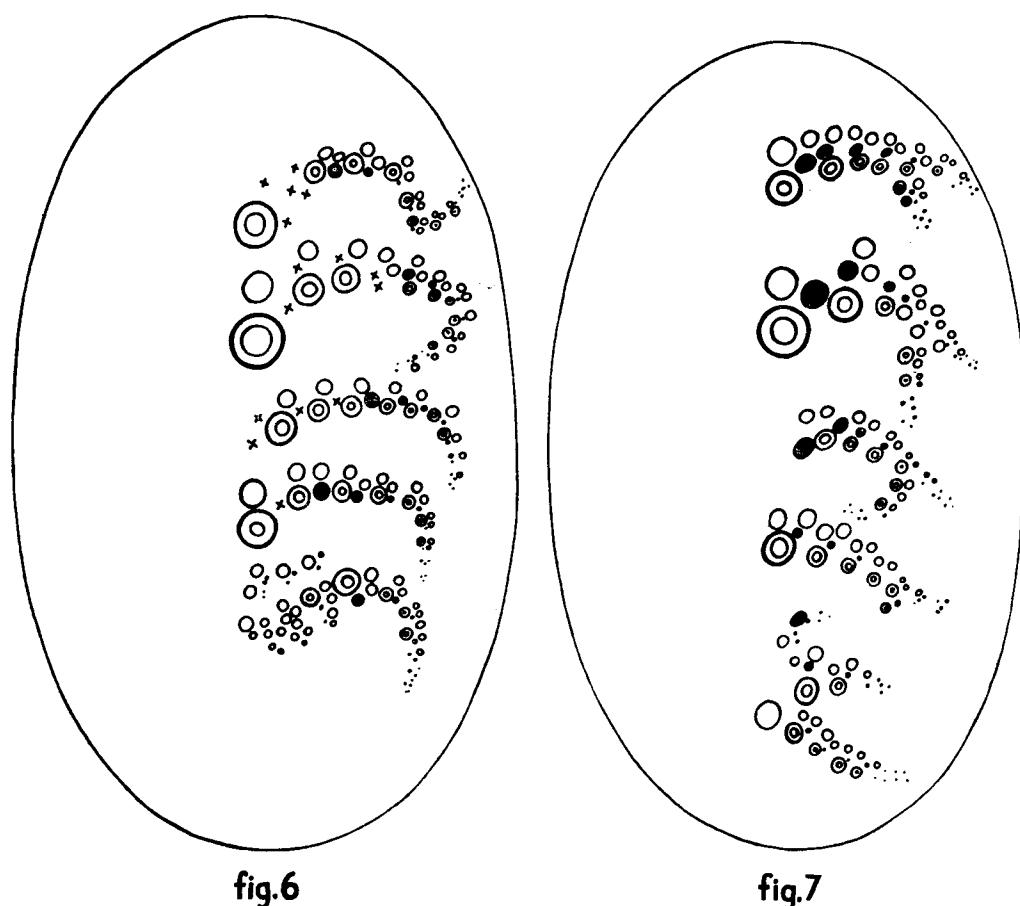


Text-fig. 19. *Physalia physalis*. Young right-handed specimen, K 2, viewed from above, showing the positions of the seven main zone cormidia.

Now that I have made a fresh study of *Physalia* I can in general confirm the facts given by Steche (1910, p. 361) about the main zone of cormidia in young specimens except that I find seven cormidia. This is the most valuable part of his paper, being an analysis of young specimens collected by 'Vettor Pisani' in the Pacific, Indian and Atlantic Oceans. The earlier part of the same paper dealing with still younger developmental stages was based on deductions made from figures by Huxley and Haeckel. This part, in my view, is not of much value because these figures themselves are not all of sufficient accuracy to be reliable. Haeckel's (1888) figures in particular are obviously simplified, idealized and, in some respects, erroneous as Steche suspected.* There is a further useful criticism I must make of

* For instance Haeckel's fig. 3 of a specimen purporting to be about 17 mm. in float-length was probably finished from a wrongly interpreted sketch. It shows a large ampulla at the base of the primary polyp where one never develops. In the original sketch, no doubt this was correctly meant to represent the oral end of the float, but in the finished drawing, a gap has appeared between this end of the float and the oral zone of cormidia which is labelled as a tentacle. The tiny tentacle so characteristic of the primary polyp can just be recognized at its base. It is shown clearly in Haeckel's fig. 4. His fig. 3 does show what might be taken to be five cormidia in the main zone as one would expect, but the gonodendra have been represented as too far advanced in development, and the ampulla of the cormidium at the oral end of the main zone appears to be unusually large. The muscular lamella uniting the ampulla to the base of the tentacle has been omitted, and the extent of the remains of the deflated crest is not properly indicated. All these points show that deductions made from this sort of figure are unreliable, although the figure does show correctly the first three large secondary gastrozooids to appear. I am a great admirer of Haeckel's industry and artistic ability and generally speaking his figures are a great advance on anything available in his day.

Steche's account. In explanation of his figs. 6 and 7 (reproduced as Text-fig. 20 here) the reader is not told whether the specimens were right- or left-handed, nor whether the viewpoint was from below or from inside the float (above). But by comparing Steche's figures with my diagrams (Text-fig. 21)—I dislike this form of representation but am obliged to use it for this purpose—it will be seen that Steche must have been representing left-handed forms from below. In my view, Steche lost his sense of orientation (a very easy thing to do when examining parts of *Physalia* under a lens), for he appears to have misrepresented the direction of the line of budding of the successive lateral groups of the



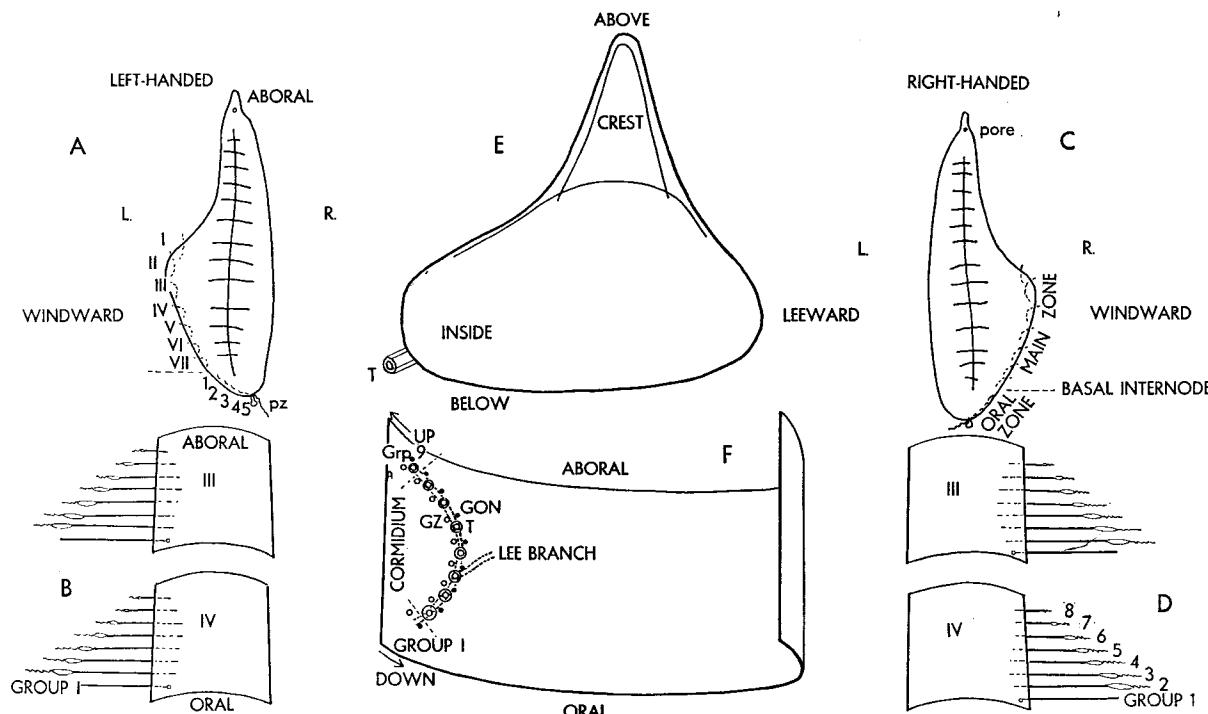
Text-fig. 20. *Physalia physalis*. Steche's (1910) schematic representation of the pattern of budding. Fig. 6 shows lateral groups (Gruppen, 2. Ordnung). Fig. 7 shows branches from laterals (Reihen, 3. Ordnung). Aboral end above. ⊙ = tentacle, ○ = gastrozooid, ● = gonodendron, × = lost appendage scar.

cormidium. As already stated, these bud from the base of the first or main group in any one cormidium, and subsequently from each other. Steche showed the line as extending first of all almost at right-angles to the main axis of the float, and then as curling round in the oral direction. Thus he represented the last lateral group of cormidium III for example as approaching the chief tentacle of cormidium IV, whereas in fact I find that it lies next to the chief tentacle of cormidium II. The budding line also does not run in the early part of its course as far down towards the lower part of the float as Steche showed it. Okada (1932) too has commented on this error of Steche's. Okada also correctly described the line of 'insertion' of the lateral groups as extending first obliquely downwards, and then upwards. These terms apply when looking down on to the animal as it floats on the water (Text-fig. 21).

Steche's elaborate diagrams of a two-dimensional arrangement of the cormidia do not in my view

give at all an adequate idea of the complicated sequence, which is three-dimensional. At any rate I failed to understand the later parts of his account.

Moser (1925), who had sixty specimens of *Physalia* taken by the 'Gauss' expedition to deal with, said that she had wanted to find an answer to the question whether certain alleged differences in origin and arrangement of the groups of appendages described by Steche had the significance given to them by him, or whether they were the expression of unending variation. But she had to confess that their study was so irksome and time-consuming that finally, without coming to any conclusion, she had contented herself with confirming the fact that there was great variation, and only exceptionally was there the regularity of arrangement found by Steche. I, like Steche, found a regular pattern of arrangement.



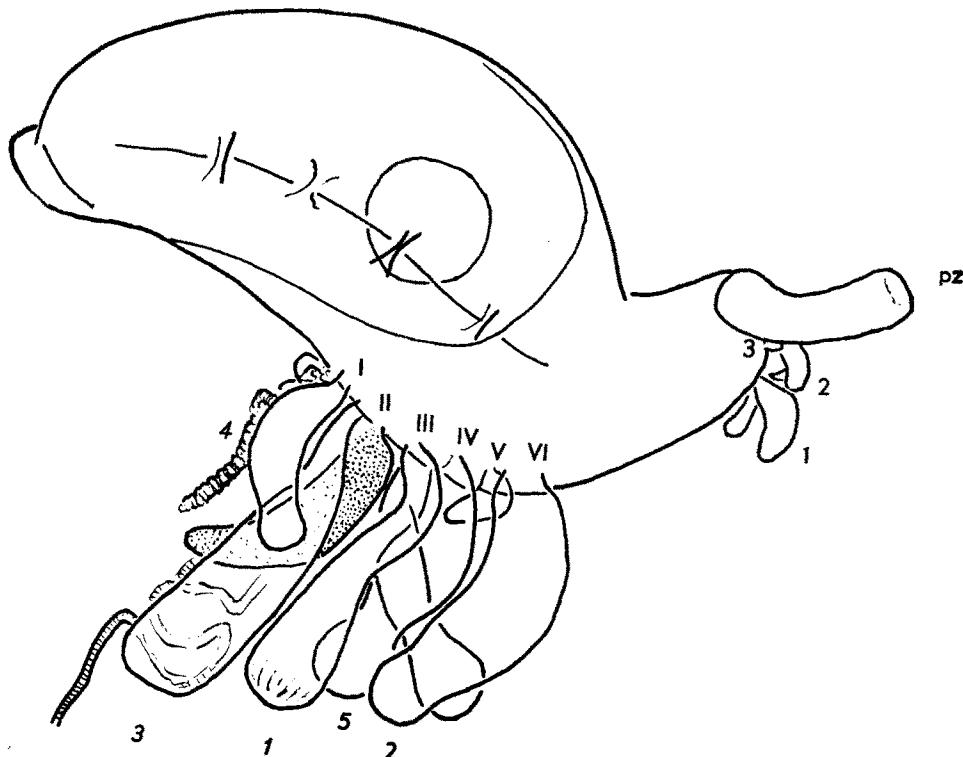
Text-fig. 21. *Physalia physalis*. Orientation of specimens, left-handed A, B, E and F, right-handed C and D. B and D = separated cormidia of left- and right-handed specimens: group I at the oral end is the oldest. Outline of A drawn from life at Arrecife. Other diagrams, schematic. F = part of a lower wall of a left-handed specimen showing a single cormidium and lee-branch.

In 1932 Okada repeated Steche's scheme of diagrammatic representation of the arrangement of cormidia, again with little success. Okada, who must have seen more of the very early developmental stages than anyone before him, said (1935) that a fairly large number occurred in the plankton taken at the Sete Marine Laboratory of Kyoto University in the spring of 1934, and that by comparing them with one another he could deduce the order in which the polyps and tentacles were budded. Unfortunately he did not enlarge on the subject in his short communication. The figures b, c and d of his fig. 1 are all labelled to show that gastrozooid number 1, the earliest to appear, lies on the oral side of the main tentacle, and gastrozooid number 2 on the oral side again of number 1. Okada's figures c and d both show gastrozooid number 3 on the aboral side of the main tentacle. In his 1932 paper Okada had indicated the same order of appearance, based on the degree of development of gastrozooids in a young specimen whose float-length was 2.5 mm. In addition, he indicated that gastrozooid number 4 appeared aborally to number 3, and that number 5 appeared between numbers 1 and 2.

The specimen shown (1935) in Okada's fig. 1d with a float-length of about 5·25 mm. still shows only the first three of the secondary gastrozoooids of the main zone. Until January 1958, I was unable to add any further evidence on this point because my specimens were too far developed, but since receiving Miss Dodge's material I have been able to clear up the sequence of the appearance and identity of these early buds.

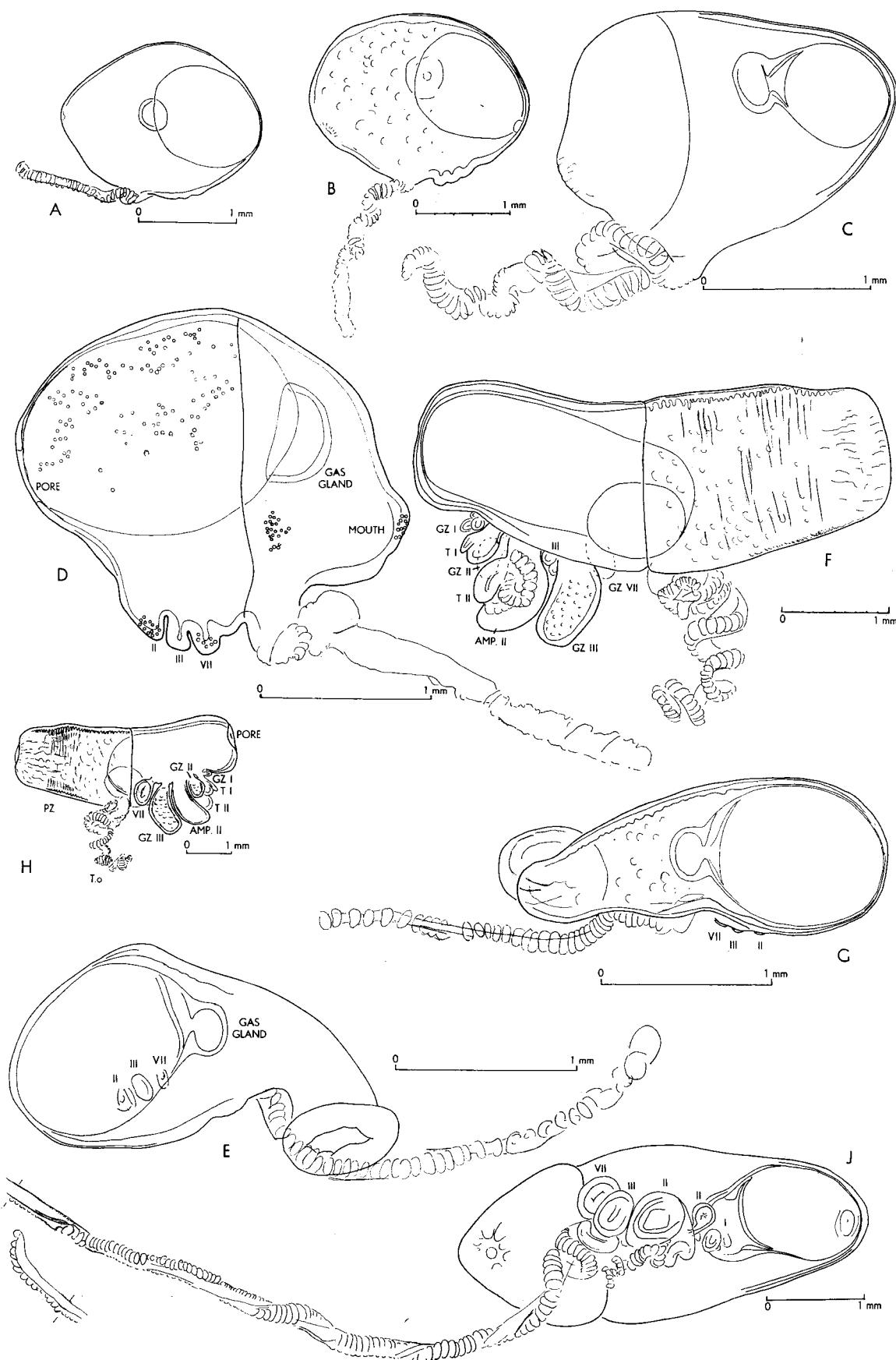
EARLY LARVAE (Pl. VII, Text-figs. 23-4)

Huxley (1859) was the first to figure the early larva of *Physalia*. He gave a figure of an individual taken probably in the spring of 1847 in the South Atlantic. It measures one-tenth of an inch (2·5 mm.), though he recorded it as one-fifth of an inch, in length. There is no sign in this figured specimen of secondary buds. Haeckel followed with one of his idealized figures (1888) and then Alexander Agassiz and A. G. Mayer (1902) gave two more interesting and convincing ones. Their specimens measured 2 mm. and 4 mm. in length and were found by 'Albatross' at the Fiji Islands, 1897-8, and on 5 and 7 September, and 4 November, 1899 and 22 January 1900, among the Paumotus and Society Islands. The smaller specimen was reported as having two very small evaginated protuberances from the ventral floor of the float.

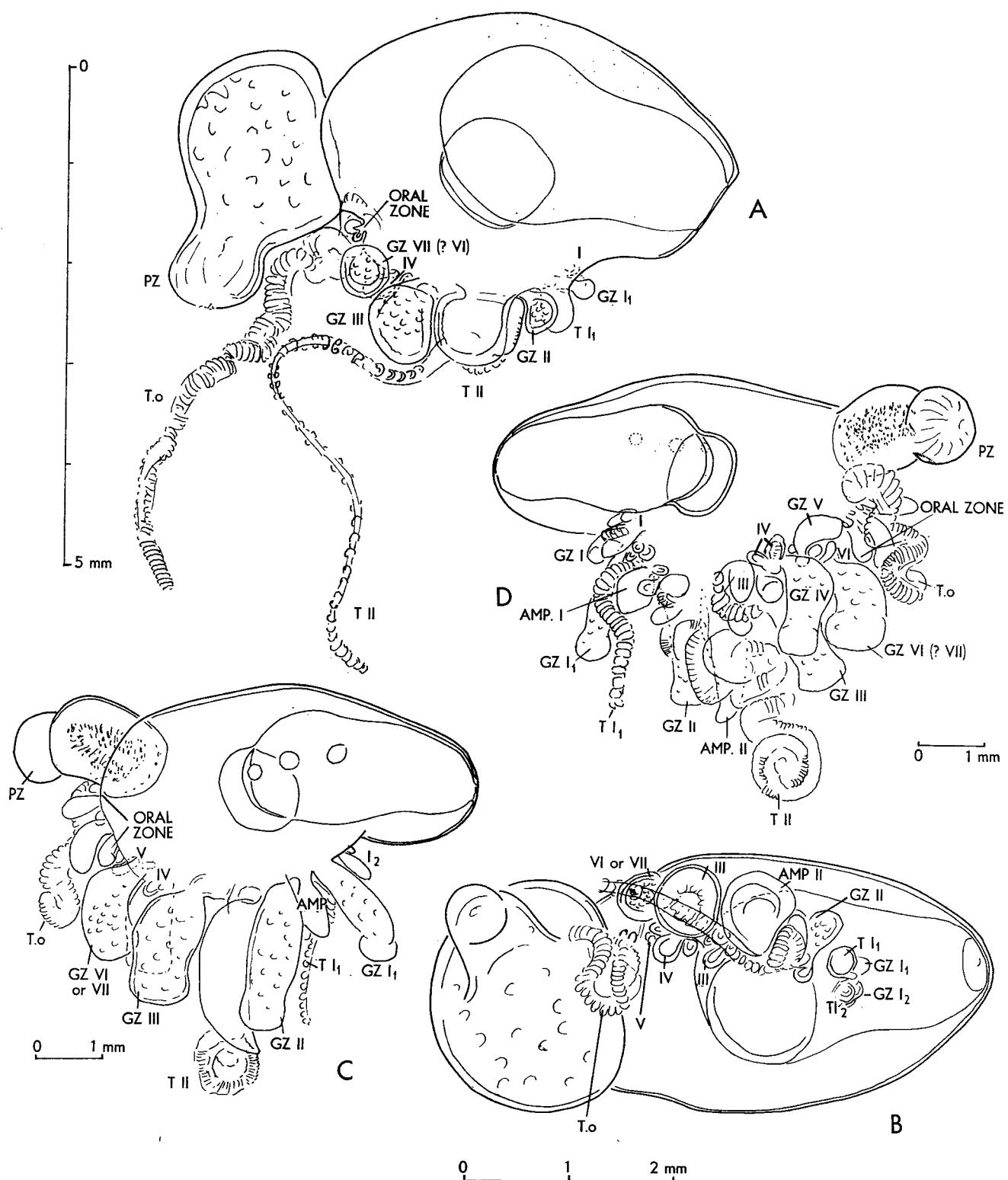


Text-fig. 22. *Physalia physalis*. Young left-handed specimen from Arrecife seen from above (overall length 22 mm.). Italic arabic numerals below show order of appearance of the first five gastrozoooids. Six cormidia are shown in the main zone and three in the oral.

The first of the secondary buds to appear in *Physalia* are those of the gastrozoooids of group number one of cormidia III and VII (or VI if only six cormidia are present) (Pl. VII, fig. 3, Text-figs. 23 and 24). These are closely followed by the bud for the ampulla of the main tentacle of cormidium II. Its gastrozoooid follows a little later from the same very short peduncle. Even at much later stages the first two precocious gastrozoooids (III and VII) are very noticeable and rather isolated (Pl. XIII, fig. 5). In Okada's (1932, 1935) notation they are P₁ and P₂ respectively, and the ampulla is ph ('phyllomeride').



Text-fig. 23. *Physalia physalis*. Larvae collected by Miss Dodge near Miami. All except D are right-handed. A, 2 mm. long, $\times 16$. B, 2.2 mm. long, $\times 15.5$. C, 2.05 mm. long, $\times 28$. D, 2.3 mm. long, $\times 28.5$. E, 2.25 mm. long, seen from below, $\times 30$. F, 4.75 mm. long, $\times 18$. G (larva E seen from above), $\times 28$. H (larva F seen from above), $\times 7.5$. J, 4 mm. long, seen from below, $\times 11$. AMP = ampulla of tentacle, GZ = gastrozooid, PZ = protozooid, T = tentacle.



Text-fig. 24. *Physalia physalis*. Older right-handed larvae collected by Miss Dodge near Miami. A, larva no. 24, 5·25 mm. long, seen from above, $\times 17$. B, no. 24 seen from to windward, $\times 18$. C, 7 mm. long, float-length 5·5 mm., seen from above, $\times 12$. D, the same, seen from below, $\times 12$. To = tentacle of protozooid. Other lettering as in Text-fig. 23.

The first three buds appear in surface view as short transverse folds (Text-fig. 23 A, B, D, E). On the sloping aboral side of the ampulla of II (Text-fig. 23, D) arises the gastrozoooid of cormidium II (P 3 in Okada's notation). From now on, the rate of growth of cormidium I is speeded up relatively, the gastrozoooid of its first group becoming Okada's P 4.

The identity of Okada's polyps, therefore appears to be:

- P 1 Gastrozoooid of cormidium III
- P 2 Gastrozoooid of cormidium VII or VI
- P 3 Gastrozoooid of cormidium II
- P 4 Gastrozoooid of cormidium I
- P 5 Gastrozoooid of cormidium IV (or V)

The points of interest that have come out of my examination of Dr Dodge's larvae are as follows:

(1) The final main pattern found in, say, a 10-in. specimen of *Physalia*, namely of buds arranged in seven main and five or more oral cormidia, each consisting of repeated triple groups of gastrozoooid, tentacle and gonodendron, does not arise regularly in orderly progression. As in other suborders of siphonophores certain buds develop precociously.

The first of these secondary buds to appear are three in number: the gastrozoooids of the main zone cormidia III and VII, and the ampulla of the tentacle of cormidium II, which forms the main tentacle.

(2) The fact that the oral zone of cormidia does not appear at first is due, probably to the fact that the first three precocious buds leave no room for it, so that its five, somewhat reduced, cormidia appear as an after-thought.

(3) Right- or left-handedness appears almost as soon as the first three buds, which are formed in the same longitudinal meridian as the larval (protozooid) tentacle. This larval tentacle must stream out to one side or the other as soon as the larva surfaces, and the three buds lie just below the surface on that same side (Text-fig. 23 A, B). The tentacles of early formed cormidia such as I and II, which soon follow, appear on the under side of the cormidal primordia, and the gas-gland very early takes up an asymmetrical position towards the under side. These two phenomena enable the observer to see whether an individual larva will become a left- or right-handed specimen, even where it measures only a couple of millimetres in length, and before there is any sign of the future crest.

(4) The first indication of the future crest is the appearance of two or three little dome-shaped projections from the upper surface of the air-sac (Text-fig. 24 C).

(5) The secondary buds can soon be seen to form an oblique line, the aboral one rather lower in the water than the oral one. The gastrozoooids of III and VII lie above the rudiments of cormidia IV and V. These are formed a little later and are not so easy to see because of being crowded out by the precocious ones III and VII (Text-fig. 24 A, B).

(6) The gastrozoooids of cormidia I and II can be seen quite clearly to develop on the aboral sides of their respective tentacles, whose formation tends to precede them (Text-fig. 24 C).

(7) There is often a quantity of dark pigment-granules in the endoderm of the air-sac. It surrounds the pore, but not symmetrically, and assuming that this pigmented area must be uppermost as in other siphonophores, it would seem that when the pigment is first formed the larva is orientated with its long axis neither vertical nor horizontal in the water, but at an acute angle to the surface. My belief is that this pigmented area round the pore of a siphonophore *saccus* in some way utilizes the light energy to control the contraction of the sphincter-muscle controlling the exit of gas according to the intensity of the light and the depth from the surface. The extent of the sphincter-muscle can be judged by its freedom from nematocysts which cover the rest of the larval body. In most of the specimens examined the pore was closed.

(8) I have examined early stages of the gas-gland only in optical section and as seen through the (cleared) pneumatocodon, so that I cannot add much to what Okada (1935, figs. 2 and 3) showed of it.

(9) It will be realized that because the oral half of the larva seems to be very muscular, the shape of the specimens varies a good deal with the state of contraction and content of food. The extent of the *saccus* too must vary with the content of gas at any particular time.

Physalia is distinguished from almost every other siphonophore by this complexity of branching by budding of the cormidia. Whereas in two sub-orders of siphonophores these cormidia bear bracts, and in one of them the terminal cormidia break off to lead a free existence and perform the function of reproduction, in the sub-order Cystonecta to which *Physalia* belongs there are no bracts and only the gonodendra break off. The most striking feature of the budding-pattern that distinguishes *Physalia* from its nearest allies, the cystonects *Rhizophysa*, *Bathyphysa* and *Pterophysa*, is that in them there is a single linear axial arrangement of successive tripartite groups (Urggruppen), namely gastrozoid, tentacle and gonodendron, the youngest group being nearest the float, whereas in *Physalia* each of the original tripartite groups gives rise to a series of up to a dozen lateral groups of the same kind, while still younger groups are budded from the bases of these.

In spite of the great complexity of growth, and in spite of the fact that, owing to varying stages of growth and states of contraction in the twenty young specimens from Lanzarote examined by me, no two look exactly alike, I have seen nothing in specimens from all oceans to make me suspect that I have been dealing with more than one species of *Physalia*. The view expressed by Steche (1910, p. 361) that there is one pattern of budding-characteristic of a species *utriculus* and another of a species *physalis* is not acceptable to me, particularly since Okada (1932) has demonstrated that the supposed characteristics of a Pacific *utriculus* are those of a juvenile specimen of *physalis*.

The only other siphonophore at all like *Physalia* is a remarkable specimen, now lost, taken by H.M.S. 'Challenger' and described by Haeckel (1888) as *Salacia polygastrica*. It was later renamed *Salacella* by Delage and Hérouard (1901) because the name *Salacia* was preoccupied. Haeckel not only named this delicate specimen—the stem measured only half a millimetre in diameter—which was 'much contracted in the spirit bottle', but he softened 'it gradually with water to make it so elastic that it could be extended to that degree which is figured in (his) plate xxv, fig. 1'. Haeckel's idealized figure shows a truly remarkable animal. No other specimen has ever been seen, but if such animals do exist they have many features in common with *Physalia*, from which they differ strikingly in the nature of their air-sac and by the fact that the cormidia are borne on a long stem. The existence of *Salacella*, if confirmed, would demonstrate conclusively that *Physalia* retains characteristics of larval forms such as are also found in physonect genera.

There is one striking morphological feature of *Physalia* which remains a puzzle, namely the arrangement of the cormidia in two zones, oral and main. It may be that one original complete series has become interrupted for some functional reason connected with the dynamics of orientation to the wind, but more probably precocious growth in some main cormidia left little space for the oral ones and so led to retardation in growth and reduction in complexity.

STRUCTURE AND DEVELOPMENT OF THE GONODENDRA

(Pls. XX–XXIII, Text-figs. 25–27)

Whereas in the cystonects, *Rhizophysa* spp. and *Pterophysa conifera*, a single gonodendron is budded out between neighbouring gastrozooids as a simple ovoid sac, which only subsequently develops terminal side-branches, in *Physalia* the gonodendra are much more diffuse structures.

In my completely fresh study of *Physalia*, the task of finding out how the gonodendra were constructed and developed was started in an exploratory way by examining the oldest and youngest stages that could be found. At Arrecife, I collected as many as possible of the large gonodendra dropped by live specimens in the laboratory tanks. Scars are often seen in places where there should be, but is not, a gonodendron (Text-fig. 17): this suggests that the dropping of a gonodendron occurs naturally. I soon found that the egg-shaped gonophores, hitherto supposed to be all male, were in any single gonodendron either all male or all female, and that the stalked medusoids, generally supposed to be female gonophores, were asexual nectophores and not gonophores at all, thus confirming Steche's view (1907).

Microscopical preparations were made of the young stages of the terminal branchlets of the genital clusters (which Schneider called 'Genitaltrauben'), and the growth-stages were seriated. Finally an attempt was made to work back from the oldest stages and forward from the youngest to a meeting-point which could be interpreted in terms of younger growth-stages and of mature structure.

Every primary gastrozooid develops a gonodendron at its base,* and the whole complex—gastrozooid, tentacle and ampulla, and gonodendron—is referred to in this report as a tripartite group.

A gonodendron develops when a main gastrozooid buds-off a number, varying from five to seven, of gonozooids (secondary gastrozooids) budding from one another and *lacking the characteristic type of tentacle*. The gonozooids bud from the base of a primary gastrozooid (Pl. XIV, figs. 1, 2) and the common base elongates to form a peduncle (Text-fig. 15), and the peduncles of the gonozooids elongate to form branches of the gonodendron (Text-fig. 25). The whole structure, somewhat resembling the wrist, palm and fingers of the hand, curls up as when the thumb and little finger are opposed, and eventually forms the globular gonodendron shown in Pl. XX, figs. 2, 6. The bases of the gonozooids give rise to the genital clusters, consisting of successively smaller palpons, and of gonophores, jelly-polyps, and nectophores (Pl. XX, figs. 3, 4). The gonophores represent the original, now much reduced, adult sexual phase of *Physalia*. The clusters branch and rebranch (Text-figs. 25, 26) and come to form the ultimate branchlets of the gonodendra (Pl. XX, fig. 5). At first they are short (Pl. XX, fig. 3), but they grow very much longer than the gonozooids, which finally appear to arise from the basal branches of a mature gonodendron (Pl. XVII, fig. 2).

The largest of the gonodendra which I preserved, a female one, was a globular mass of palpons and gonophores measuring 4 or 5 cm. in diameter (6 or 7 cm. when flattened in a dish), and consisted of seven main branches radiating out from its stem. Each main branch rebranched at least five times, so that there would be about 224 (7×2^5) terminal branchlets carrying 448 gonopalpons (two per branchlet), 224 medusoid nectophores and 2400 gonophores (ten per branchlet). Very many gonodendra were present in all but the very youngest stages of development, often five or more well-developed ones at a time. The potential number of gonodendra (Pl. XX, fig. 1) formed on the main zone of cormidia alone, based on an analysis of cormidium II of specimen no. Lanzarote 2, is about 500, and the number of gonophores, or adults, that they might bear would be at least a million.

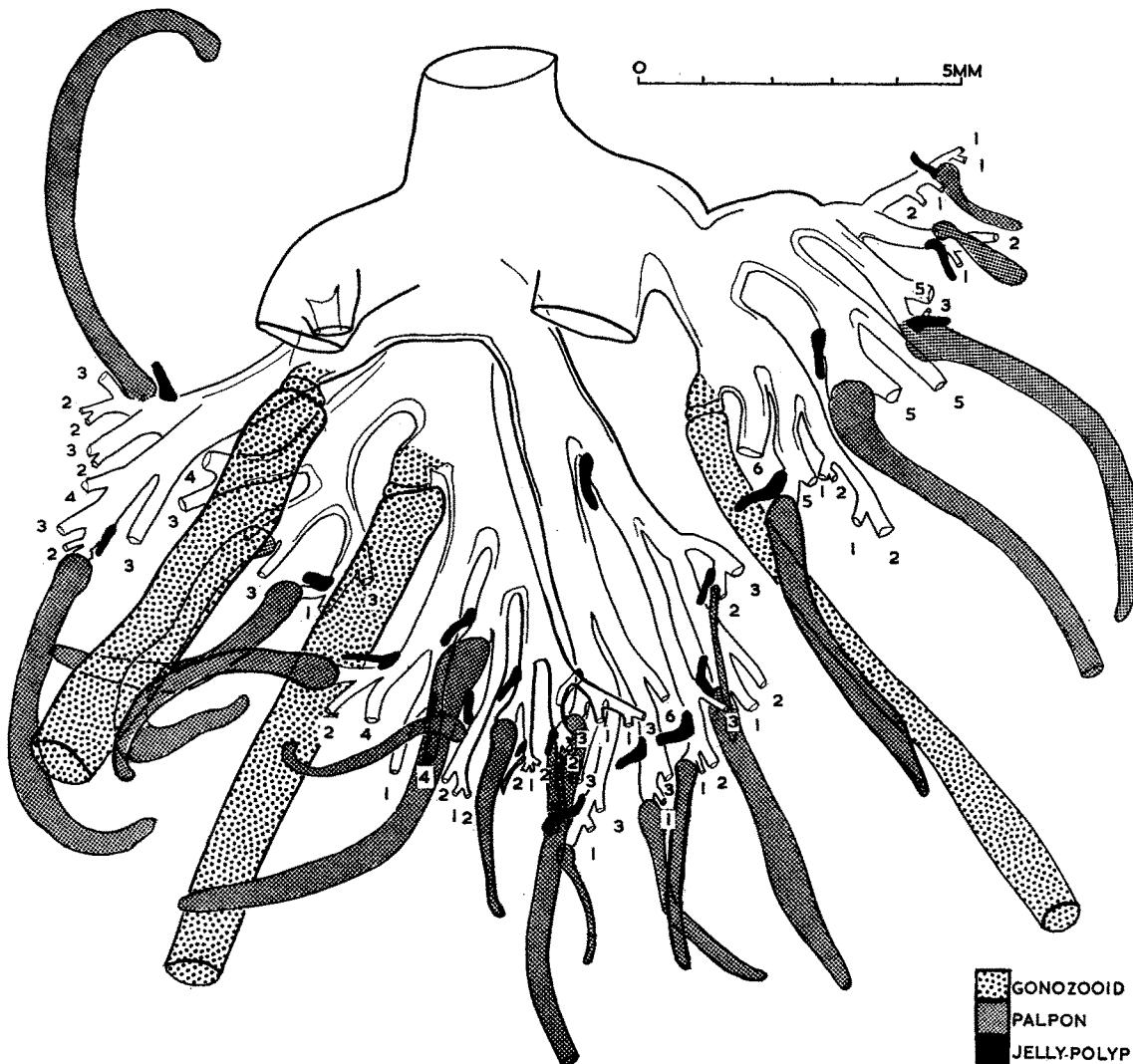
The muscular peduncle, or stem, and the branches of the gonodendra are highly contractile, but I have not noticed much sign of movement of the nectophores and palpons. I think it probable that whole gonodendra and perhaps later the terminal parts of the branchlets also become detached in the sea. Generally five or six gonozooids, from the bases of which the genital clusters grow, are found at the bases of the branches of these dropped gonodendra, but (as expected) never any tentacles.

Analysis of the complexity of the gonodendra had been attempted in 1908 by Lens and van

* Delage and Hérouard (1901) show the gonodendron as arising from the pedicel of the ampulla—this is not correct.

Riemsdijk. They found that the ultimate branchlets consisted of two divisions, one bearing a jelly-polyp* and palpon, and the other a nectophore and palpon, and both bearing gonophores.

My study of the morphology and development of the gonodendra of *Physalia* substantiates the work of Lens and van Riemsdijk and amplifies it. I find that each normal final branchlet of the fully formed gonodendra consists of two sections, which are very likely homologous, each carrying one palpon and numerous gonophores (reduced sexual medusoids). The two sections can be distinguished from one another because the terminal one has a jelly-polyp (*jp*) at the base of the palpon (*pt*), whereas the



Text-fig. 25. *Physalia physalis*. A young gonodendron after removal of three branches. Specimen, Lanzarote no. 2. The numerals refer to the number of subterminal, nectophore-bearing sections (not shown) on each end branch. $\times 9$.

sub-terminal section has a long-stalked nectophore (*n*) in this position. The terminal palpons with their jelly-polyps are visible in the earliest growth-stages of the gonodendra (Pl. XXII, fig. 4); in well-developed specimens the oldest terminal palpons at the bases of the larger gonodendral branches reach a considerable size (Text-fig. 25).

No further budding occurs from a terminal section. Growth of the gonodendra proceeds by buds which develop on the sub-terminal sections and which give rise by dichotomy to a successive series of

* The jelly-polyp was called by Chun (1897a) and Steche (1907) the 'Gallert-polypoid'. It develops characters closely resembling in some ways those of the nectophore or asexual medusoid (see page 351).

terminal (final) sections and budding sub-terminal ones. The whole process was studied in the developmental stages now described and illustrated on Pls. XXI–XXIII.

I examined first the youngest stages found at the bases of the smallest gonodendra (Pl. XXII, figs. 1–3). These genital clusters arise opposite the basal jelly-polyps as innumerable small, laterally flattened, subdivided lobes, the pro-buds, arranged in many planes, and often look at first sight like trefoils. They bud and rebud several times to form the ultimate branchlets of the gonodendron (Pl. XXI, fig. 1), as distinct from its main branches, which are formed by the elongated peduncles of the gonozooids and first palpons, as described on page 347. The pro-buds of the genital clusters grow rapidly in length in an apical direction and produce sub-terminal buds on one side, so that the apex becomes bent to the other side. Each of these little lobes thus comes to appear bi-lobed (Text-fig. 27A and B). These two stages have not been specially identified, and are hypothetical. One half, really the faster growing terminal end, can soon be recognized as the rudiment of a palpon and a jelly-polyp; the sub-terminal part is a new pro-bud, *B* (Text-fig. 27B). As a result of further budding, pro-bud *B* develops secondary dichotomies, and the new pro-buds *B*₁, *B*₂, (Text-fig. 27D) each become transformed into replicas (Text-fig. 27E) of the previous stage, shown in Text-fig. 27C. The terminal part of each successive pro-bud grows faster than the sub-terminal part to form a new terminal palpon and jelly-polyp, while the sub-terminal section can either end by becoming the palpon and nectophore, or go on developing and dividing into another terminal and sub-terminal section. We are now at stage *D* (Text-fig. 27) where there is a major dichotomy between the left '*B*'-side bearing pro-buds *B*₁ and *B*₂ and the right '*A*'-side bearing the terminal palpon and pro-bud *A*₂. The two halves are essentially alike, but one is farther advanced in growth than the other, for on the '*A*'-side we can soon recognize the rudiment of another palpon and jelly-polyp pro-bud *A*₂¹⁴ (Text-fig. 27F). As a result of repeated sub-terminal budding and dichotomy we get a series of terminal sections—palpon and jelly-polyp—alternating with sub-terminal pro-buds. These developmental processes which I have postulated would account for the origin of the final branchlets of the whole gonodendron (Text-fig. 26). Having followed the development of one of the branchlets as far as the last dichotomy, we can see what is the destiny of the final sub-terminal pro-buds: * they divide for the last time to form the rudiments of the sub-terminal nectophore and palpon of the sub-terminal section (Pl. XXI, fig. 3).

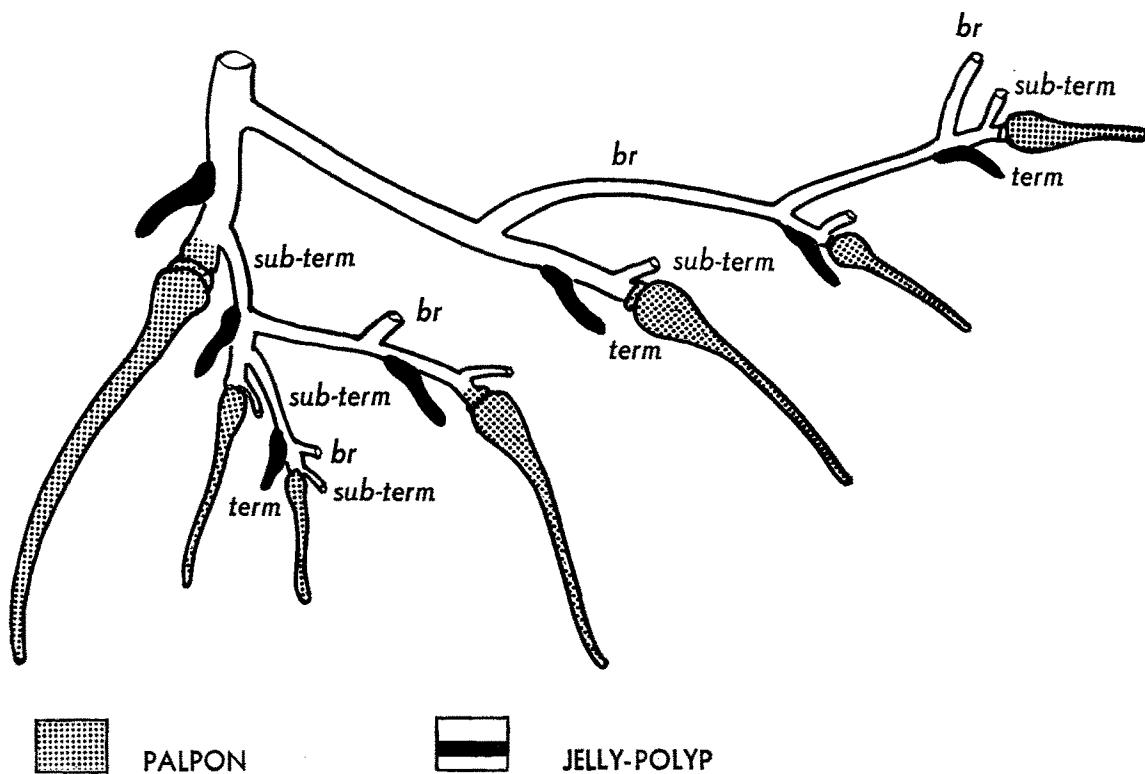
In some cases a final sub-terminal pro-bud is not developed: that is, the final palpon and nectophore are not budded off, then the branchlet ends in a terminal section only, consisting of a palpon and jelly-polyp. Pl. XXI, fig. 7 shows a pair of final branchlets, the right with two terminal sections and the left with two terminal and a final sub-terminal section. Normally there is a matching pair of final branchlets with sub-terminal sections.

I must now describe in greater detail how the middle growth-stages of the genital clusters (Schneider's 'Genitaltrauben') develop into the final branches of the fully grown gonodendra. I have not determined whether there is a definite number of new buddings and dichotomies which might fix the amount of branching. But if we take the hypothetical stage shown in Text-fig. 27F as the starting-point of the next stage, it can be seen at once, on comparison with Pl. XXII, fig. 4, that the whole of the right side of Text-fig. 27F as well as the whole of the left side—the major dichotomy is between pro-buds *A*₂ and *B*₁—can develop into something similar to what is shown in Pl. XXII, fig. 5. In both figures the larger palpon (*p.st*) and the jelly-polyp (*jp*) form a terminal section; and the sub-terminal pro-bud (*pr. A*₂²) above it in Text-fig. 27F has given rise in Pl. XXII, fig. 5 to a smaller terminal section and a new sub-terminal one. From the latter arise (1) the nectophore (*nect*), and (2) the palpon of a

* Such as *A*₂², Text-fig. 27F. Pl. XXII, fig. 4 is the equivalent of the '*B*'-side of Text-fig. 27F.

final branchlet. In Text-fig. 27F the second pro-bud A₂ of fig. D has developed into similar terminal and sub-terminal sections (A₂^{1B}, A₂¹⁴).

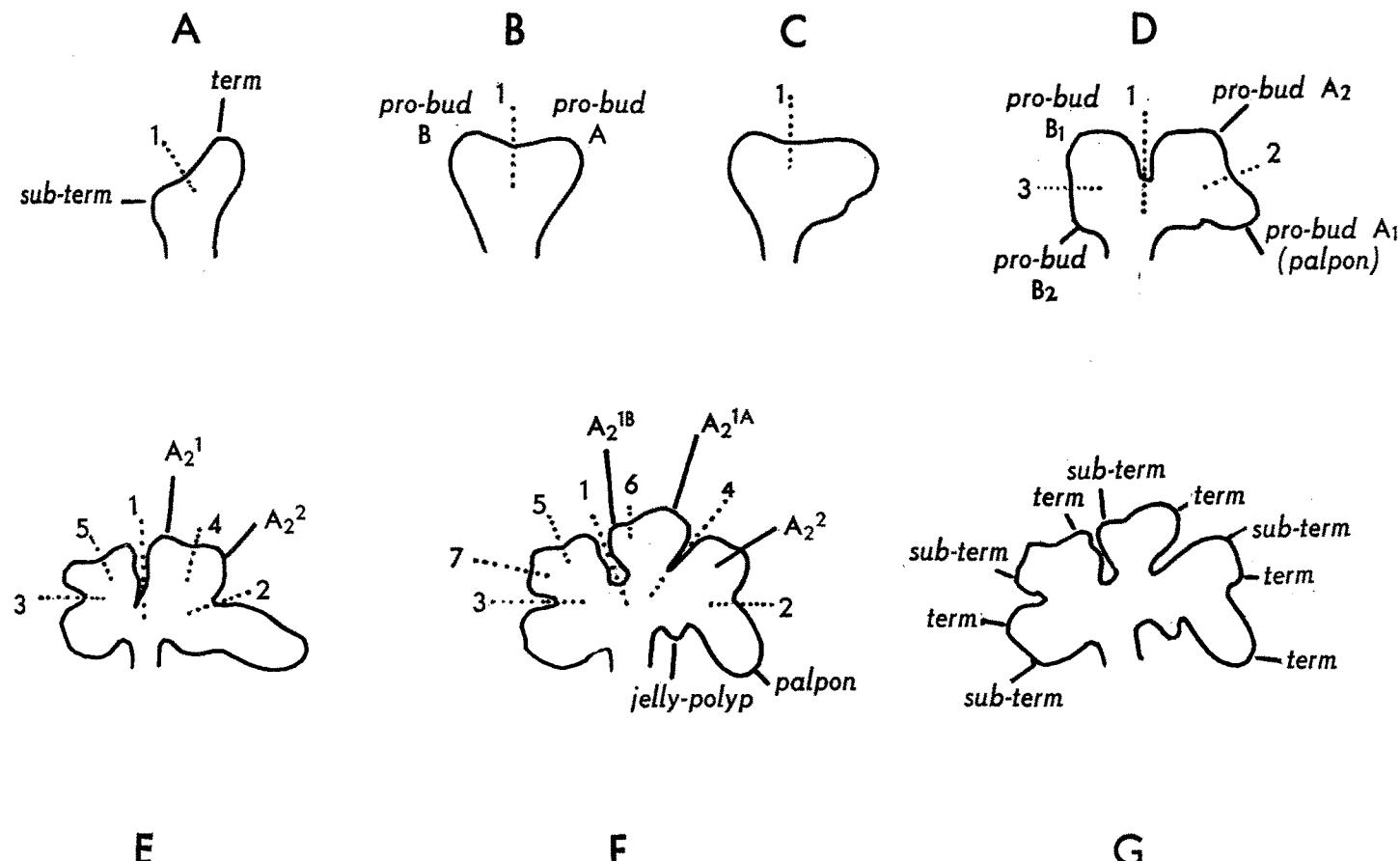
New pro-buds always arise sub-terminally, and as a rule at a point opposite a jelly-polyp. Sometimes they form terminal-type, sometimes sub-terminal-type sections. Pl. XXII, figs. 6 and 8 show slightly later stages of development that might have been reached later on by the specimen shown in Text-fig. 27F. The first palpon, which is morphologically the terminal part of the branchlet, has grown very much more rapidly than the sub-terminal parts. Pl. XXII, fig. 11 shows how complicated the young genital clusters look when the branchlets lie side by side. Those shown in Pl. XXII, fig. 8 have been separated, flattened out and mounted on a microscope slide.



Text-fig. 26. *Physalia physalis*. Schematic drawing of a branch of a gonodendron to show repetitive pattern of growth.
br = branch, sub-term = sub-terminal section, term = terminal section.

It will be noticed at this stage, which I call the Key-stage from a fancied resemblance to the lever-steps of a simple key, that the buds of both terminal and sub-terminal sections stand out more or less at right-angles to the long axes. In the next stage (Pl. XXIII, fig. 2) they are more or less parallel to one another and stand at an angle of 45° to the common axis. The jelly-polyps are no longer little conical projections but have become more cylindrical; and the nectophore bud shows its medusoid nature. The gonophores are now conspicuous objects. Pl. XXIII, fig. 2 (right) may usefully be compared with its earlier counterpart shown on the right-hand of Pl. XXII, fig. 4. Stages of growth intermediate between those shown in Pl. XXIII, figs. 1 and 2 may be seen in Pl. XXII, figs. 10, 11. The most mature stage of growth of branchlets of the gonodendron that I have seen is shown in Pl. XXI, fig. 3, which shows clearly (1) the jelly-polyp (*jp*) of the palpon (*pt*) of the terminal section, (2) the asexual nectophore (*n*) and palpon (*ps.t*) of the sub-terminal section, and (3) a number of female gonophores. A rather less mature stage is shown in Pl. XXI, fig. 2, where the mesogloea of the stalks of both

nectophore and jelly-polyp is less well-developed, and their endodermal canals are relatively larger in diameter and still open. Pl. XXI, fig. 4 shows the last four dichotomies of part of an immature gonodendron spread out on a microscope slide.



Text-fig. 27. *Physalia physalis*. Early growth stages (hypothetical) of branches of a gonodendron. A later growth stage of fig. F (cf. Pl. XXII, fig. 2) is shown in Pl. XXII, fig. 5. *sub-term* = sub-terminal section, *term* = terminal section, 1, 2, 3 etc. = successive dichotomies, A_1 , A_2 , A_2^1 , A_2^{1A} , etc. = successive budings.

JELLY-POLYPS

(Pl. XXI)

As stated on page 348 there is at the base of each terminal branchlet a palpon which has at its base a jelly-polyp. These are well shown in Pl. XXI, figs. 1, 2, 6, 7. It is necessary to understand the regular type of branching just described in the gonodendra in order to demonstrate that the jelly-polyps are not vestigial stalks left after the nectophores have dropped off, an erroneous interpretation put forward by Huxley, Haeckel and Chun.

In the older growth-stages, both jelly-polyp and nectophore-stalk look much alike (Pl. XXI, fig. 3). This resemblance of the oldest known growth-stage of these two buds is due to the fact that in each the endodermal lumen becomes relatively reduced at the same time as the mesogloea becomes very much thicker (Pl. XXI, fig. 3). In both cases the endodermal canal—now almost occluded—comes to lie on the abaxial side, next to the ectodermal fold (Pl. XXI, fig. 6) except sub-terminally, where it lies centrally to link up with the sub-umbrella of the nectophore and the tip of the jelly-polyp. This structural resemblance between the basal parts of these two kinds of buds—one a medusoid and the other, once thought to be a polyp, but now shown to be a reduced nectophore—was for long inex-

plicable. No wonder that the jelly-polyp was mistaken for the stem of a broken-off 'female medusoid'. The jelly-polyp seems to be in fact a reduced nectophore. Both have the frenum-like longitudinal muscular lamella referred to above as the ectodermal fold.

One morphological feature of the gonodendra, common to those cystonects whose gonodendra are well enough known to me for comparison, namely *Physalia physalis*, *Rhizophysa eysenhardtii*, *R. filiformis* and *Pterophysa conifera*, is that in all of them the final sections of the branchlets consist of a group of three kinds of bud: (1) a terminal gonopalpon without a palpacle (reduced tentacle), (2) a sub-terminal nectophore (asexual medusoid bud) [(1) and (2) together forming what I have described, in *Physalia*, as the sub-terminal section] and (3) male or female gonophores. But in *Physalia* alone there is, proximal to these three structures, another palpon with a jelly-polyp (a reduced nectophore), these two structures forming the terminal section, which is developed first and which gives rise by budding to the sub-terminal section (carrying the nectophore and palpon). The sub-terminal section is budded out (Pl. XXI, fig. 3) from the base of the palpon at a point opposite to its jelly-polyp.

The difference between the gonodendra of *Physalia* and those of the other cystonects is that in *Physalia* there are multiple-terminal as well as sub-terminal sections, whereas in the other cystonects there is a single sac-like terminal section from which the multiple ones are budded. The sub-terminal sections in all cystonects are clearly homologous. The arrangement in *Physalia* is the most complex and so is probably the most highly evolved. These comparative morphological details form a key to understanding the relationships between the various cystonects.

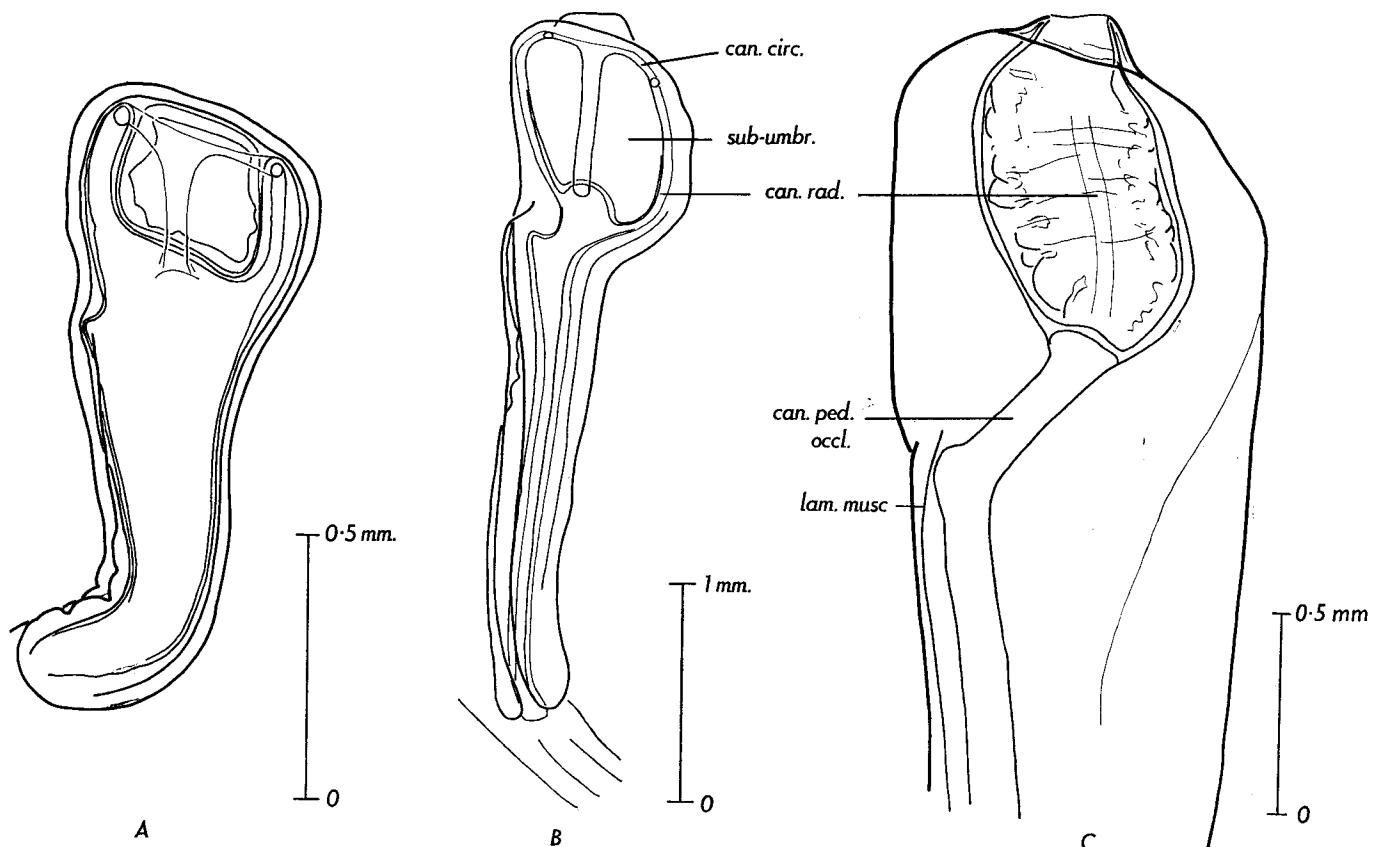
Long ago, sketches of a terminal branchlet of a young gonodendron were published by Chun (1897a, fig. 26b), and of an old as well as of a very young stage of the same by Richter (1907, figs. 7 and 8). Richter referred to four types of buds: (1) palpon, (2) male medusoid, (3) female medusoid (i.e. nectophore), and (4) 'Gallertpolypoid' (that is, jelly-polyp, interpreted by Haeckel as the 'pedicels' of detached female medusoids). Richter's figures, though incorrectly labelled, are basically sound and may be compared with my photographs. Libbie Hyman (1940) in her indispensable book of reference gave a figure of part of a gonodendron (fig. 155B) which is unfortunately misleading. She seems to have mistaken palpons for jelly-polyps in both this and fig. 155A. The latter figure in other respects gives a good representation of an early stage of development of three gonodendra; but the characteristic arrangement of palpons, gonophores, jelly-polyps and nectophores is not correctly shown in her fig. 155B.

NECTOPHORES

(Pl. XXIV)

The best criterion for judging the degree of development of a gonodendron is the state of development of the nectophores (Pl. XXIV, figs. 5-7). In early stages I find that the coelenteron of the nectophore pedicel is spacious and the mesogloea thin. In the most advanced stages I have seen the mesogloea is very thick and the coelenteron of the pedicel occluded (Text-fig. 28). Huxley (1859), Haeckel (1888) and Chun (1897b) all regarded the nectophores as female medusoids, which they thought probably became detached and produced ova as free-swimming Anthomedusae. Chun even suggested that they might develop into the *Amalthea amoebigera* of Haeckel (1879) (a doubtful synonym of *A. sarsi* Allman, *fide* Kramp).

The nectophore of *Physalia* has no manubrium and no germ-cells have been seen at any stage of its development. Moreover, the occlusion of the endodermal canal in the nectophore-stalk would probably prevent later entry of ova in any way similar to that described by Brooks and Conklin (1891) for *Rhodalia*. The secondary ectoderm of the sub-umbrella is peculiar in having folds of the mesogloea supporting it, figured by Goto (1897, figs. 8 and 9). What Goto called the manubrium is in my



Text-fig. 28. *Physalia physalis*. Three nectophores at different growth-stages. In A the gastrovascular space is wide open; in C occluded. A, $\times 70$, B, $\times 29$, C, $\times 53$. can.circ. = circular canal, can.ped.occl = pedicular canal (occluded), can.rad = radial canal, lam.musc = muscular lamella.

view nothing more than the irregular folding of these tissues at the point where the radial canals arise from the pedicel in the most advanced growth-stages that we know. It seems probable that the nectophores must function as swimming-bells.

Judging by the undoubtedly breaking-loose of the terminal branchlets, consisting of terminal gonopalpon, nectophore and sexual medusoids, of *Rhizophysa*, I think it likely that the equivalent sections in *Physalia* may do the same thing. In *Rhizophysa*, nectophore and palpon are orientated in a peculiar way, axes in line, as if to balance each other when detached and swimming. In *Physalia* I have seen some very expanded gonodendra in which the stalk separating this part of the branch from the basal section—gonopalpon and jelly-polyp—is very fine. These terminal sections of the gonodendra, when detached, are probably kept on the move by pulsations of the nectophores. It may be that the final branchlets become freed at some particular stage of growth, or at a certain season of the year, but I must say that I have seen no specimens in which the nectophores are missing from the normal position in which they first appear as very small buds very early in the development of the gonodendron.

PALPONS

(Pls. XX, XXV)

Besides the gonophores and nectophores, the final parts of the gonodendra in *Physalia* are made up of palpions (Pl. XX, fig. 4). The normal sub-terminal ones have at their base an asexual nectophore; the palpions of the terminal sections have at their base a jelly-polyp ('Gallertpolypoid' of Chun, a reduced nectophore). None of the palpions have palpacles (simple tentacles).

There appears to be no recent summing-up of our knowledge of the homology and functional morphology of palpons and it will not be out of place to consider the subject briefly here. We have to go back to Haeckel's great 'Challenger' report (1888) to find anything of the sort. Haeckel set great store on allowing the empirical and speculative methods of research to converge. Nevertheless, while I am a sincere admirer of his prodigious pioneering work, I always regret that Haeckel allowed so much hypothetical interpretation and terminology to colour his observational records, because a great deal of it now seems to be quite mistaken. It is a pity also that he should have idealized his finished figures in order to make his preliminary sketches complete and attractive. But these are trivial criticisms of his painstaking work in general.

What he has to say about palpons is contained in four sections of his general introduction, under the headings: (1) palpons or 'tasters', (2) cystons or anal vesicles, (3) palpacles or 'tasting' filaments (the German word 'tasten' meaning to touch) and (4) gonostyles or reproductive stalks. Haeckel, while agreeing that palpacles were only the tentacles of palpons and not a separate sort of bud, contrasted palpons with cystons, saying that palpons were mouthless and had no glandular villi, whereas cystons could empty fluid and excretions from the canal system through a terminal opening which was to be regarded as an anus. He used Allman's term 'gonostyles' or 'blastostyles' for what he called the 'sexual palpons', frequently branched, whose sole function was to produce gonophores. A subsidiary title for his section 4 is 'Blastostyles, Gonoblastidia, Gonodendra, Klinozooids'. The term gonodendra he specifically applied to large clustered masses of gonophores attached to branched gonostyles, which last he regarded as secondary polypoid individuals. He mentioned that palpons are found generally distributed in the physonects and cystonects, but not in the calycophores.

As a result of my own observations on living and preserved material of physonects and cystonects, I conclude that there is no real distinction between palpons and cystons. Terminal openings may suddenly appear where there has been no previous indication that such a thing is possible. I cannot now find my field notes on the subject, but I think that it was in *Nanomia bijuga* that I first observed (at Villefranche) the flattening-out of palpons in a progressive peristalsis followed by an opening-wide of the tip of the palpon and the ejection of particles. In some species of *Forskalia*, for example, the Mediterranean species with the lemon-coloured spot on the velum that I call *edwardsi*, I have often observed the well-known ejection of an orange-coloured liquid from the tip of a palpon. I have observed palpons opening in other species too. In one particular preserved specimen of *Physalia physalis* many of the palpons were fixed in the act of opening (Pl. XXV, figs. 2, 3) and in others there is a collection of dark matter, usually distributed over the villi, near the tip as if about to be ejected. It appears to me that the palpons are to be regarded primarily as reduced secondary polyps budded from the bases of replicated gonozooids. Secondarily, they may become separated from the gonophores and gonodendra. This can be very clearly seen in a small specimen of *Athorybia rosacea*, taken by 'Discovery II' in September 1955, off Lanzarote at St. 3308, and brought to me by Dr Kramp. It can also be clearly seen in *Forskalia edwardsi*, and I have illustrated it in a figure of *Marrus antarcticus* (Totton, 1954, fig. 21). In *Physophora hydrostatica*, where the palpons are very large, this relationship is not apparent in mature specimens, which represent the condition found in the post-larva developed to a higher degree. In the physonect *Nanomia bijuga* a bunch of male and a bunch of female gonophores is budded from the pedicel of each palpon. I think it probable that some palpons have come to act as food-reservoirs for the growing gonodendra—in *Pyrostephos antarcticus* they are usually full of liquid fat or oil—as well as organs of defaecation. In *Physophora*, *Forskalia* and *Athorybia* they are particularly active sensory organs. In *Apolemia uvaria* there is a kind of palpon, few in number, that is brown and heavily armed with nematocysts. The palpons of *Physalia physalis* have a beautiful pad of nematocysts on one side of the tip and on the tip itself. In this species all

stages of regression from gastrozooid to gonopalpon (non-feeding gonozooid) can be seen when tracing the development of a gonodendron by successive budding or replication.

All palpons, it would seem, are reduced secondary gastrozooids (gonozooids), specialized for purposes other than feeding. It is in *Apolemia uvaria* that they most nearly resemble gastrozooids, because in this species the tentacle of the gastrozooid is unbranched and looks like a palpacle. The repeated sac-like protuberances from the stem of *Rhizophysa*—the buds of the gonodendra—show little similarity to palpons, though the side branches terminate in palpons; but the intricately branched gonodendra of *Physalia* clearly originate from the peduncles of secondary gastrozooids.

It has always been a puzzle to understand the appearance of a partial ring of palpons round the base of the protozooid at an early post-larval stage in the development of physonects. But in the light of what has now been learned about the branching system in *Physalia*, it has become easier to homologize the process of budding of successively more reduced daughter polyps from the bases of the gastrozooids in *Physalia* with the phenomenon to which I have just referred, namely the budding of a partial ring of palpons. In *Forskalia* the whole gonodendron buds from a basal palpon; in *Marrus* it probably does so as well; in *Athorybia** there is a palmate arrangement of eight or nine palpons arising from the pedicels of the gonodendron, but it would be necessary to study growth-stages to determine the minute structure.

AMPULLAE

Haeckel (1888)—to whose account of *Physalia* most students hitherto have been likely to refer—used the same term for true palpons and for the basal ampullae of the tentacles. For a long time I have held the view that these ampullae, containing as they do in their walls innumerable nematoblasts, were homologous with basigasters or nematoblast-nurseries—otherwise missing in *Physalia*, except in the protozooid—which have become separated from the gastrozooids, just as the tentacles have. Schneider (1898), I find, came to the same conclusion. But for a time I had to modify my interpretation because on two occasions I found young growth-stages of ampullae with papillae inside, and a terminal part that resembles a gastrozooid instead of the tip of an ampulla. My final conclusion is that an ampulla is simply the hypertrophied basigaster of a gastrozooid. This is the sort of condition found normally in the young growth-stages of gastrozooids of all siphonophores, where the basigaster is relatively enormous, and the as yet undeveloped terminal part appears only as a slight projection from it.

At the proximal end of a tentacle, particularly a young one, it can be seen that the last few nematocyst-'heads' budded contain no nematocysts. In this region, nematocysts can be seen in the ectoderm of the muscular lamella where it connects the ampulla to the tentacle: these nematocysts appear to be migrating to the 'heads'. There is in this region a sudden transition between 'heads' devoid of nematocysts and 'heads' well armed with them. As the ampulla and tentacle increase in size the 'heads' become bigger. Migration of nematocysts into the 'heads' takes place only in the restricted area already described. The original tip of a tentacle has, naturally, small 'heads'.

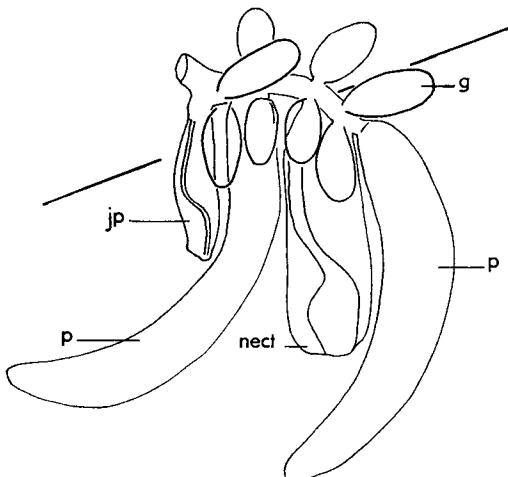
A fact of great evolutionary interest is that the protozooid which has only a small tentacle, has no ampulla, but instead a very inconspicuous basigaster of a generalized type. We have here then an evolutionary phenomenon, found also in physonects like *Agalma elegans*, where the protozooid and its basigaster remain at an earlier phylogenetic level, while the basigasters in the secondary gastrozooids are more highly evolved. Instead of being able to deduce the evolutionary steps from a study of fossils, we can do so, in bud-colonies of this sort, from a study of successively produced buds.

* These palpons do not open directly as stated by Haeckel into the common stem cavity. It is necessary to anaesthetize the delicate creatures to cause relaxation of the muscles before one can really observe their structure. Even so, the air in the float, which always rises to the surface, makes it almost impossible to observe the under-surface until the air has been replaced by liquid. Today of course we have what Haeckel had not—binocular dissecting microscopes.

GONOPHORES

(Pls. XX-XXIV, Text-fig. 29)

Two of those who in the past have done the most detailed work on the gonodendra are Richter (1907) and Steche (1907). By one of those strange but not infrequent coincidences, these two men appear to have been working simultaneously but unknown to each other, the one at Leipzig and the other at Strassburg.



Text-fig. 29. *Physalia physalis*. End branchlet of a mature gonodendron shown in section in Pl. XXIV, fig. 3. The plane of section is indicated by a line. Two gonophores that lie on the underside and appear in the plate are not shown in the drawing. *g* = gonophore, *jp* = jelly-polyp, *nect* = nectophore, *p* = palpon.

Prior to the work of Steche, Huxley (1851, 1859), Haeckel (1888), Brooks and Conklin (1891) and Goto (1897) all regarded the gonophores as male organs. Huxley and Haeckel thought that the ova developed later on the stalked 'female medusoids' (now known to be nectophores) after becoming freed from the gonodendra.

Richter (1907) also regarded the gonophores as being male organs and his whole account of their development is most unusual, as he himself admitted, and is in my view unacceptable. In fact I think that Richter reversed the proper sequence of events in the various growth-stages.

Steche (1907) demonstrated for the first time the existence in *Physalia* of two kinds of gonophores, female as well as male, and stated that each gonodendron was wholly of one sex only. Even now Steche's work is not well known, and this is the first occasion on which his observations have been confirmed. Curiously enough Steche himself stumbled quite accidentally across the fact that some of the gonophores were female, when he was investigating the 'Glockenkern' (entocodon) of various hydroids and siphonophores during the winter of 1905. In some sections of the nectophore of *Physalia* he had fortunately included a large specimen of the real female gonophore growing from its base. He recorded how surprised he was to find a single layer of unripe germ-cells instead of the thick spermarium he had expected to see. He described and figured in longitudinal section a developmental phase in some ovoid medusoids, in which the spadix of giant 'multinucleate' cells was capped by a single layer of what he called female germ-cells (Taf. X, fig. 26). I have a section which confirms his figure (Pl. XXIV, fig. 3). Text-fig. 29 shows the plane in which the section was cut.

Richter wrote an addendum to his paper in which he commented on Steche's work published while his own manuscript was in the printer's hands. Most of the addendum is concerned with relatively unimportant differences in their two papers, but Richter also remarked that 'Steche made some very

interesting observations on older examples of *Rhizophysa* and *Physalia* which apparently lead to an explanation of the place of origin, previously unknown, of the female germ-cells. According to him the structures previously regarded as male gonophores are undifferentiated germ-tissue, which only later, and in different specimens, develop into male and female germ-cells. In my oldest examples these transformations minutely described by Steche were not observed'. Actually, Richter figured (Taf. XXVIII, fig. 25) what is obviously a section of one of these female gonophores, that he took to be a stage in the development of a male gonophore. Richter rather ungraciously added that Steche had made no new contribution to the subject of the gonodendron and its appendages.

Perez (1929) published good figures of the endodermal cells of the spadix of the male gonophore, and drew particular attention to the division of many of the nuclei into two, three or more parts, and to the physiological significance of this phenomenon, namely the control of a 'flux metabolique' between the coelenteron and the developing germ-cells. He gathered together many other instances of this phenomenon, of which the multilobate nuclei of the *rete* on the ventral radial canal of the young nectophore of Hippopodiids is another.

Although the complete story of the method of reproduction in *Physalia* is not yet and perhaps never will be known, some progress has been made, and I have been able to substantiate Steche's work and to extend it. Having cut sections of gonodendra to elucidate morphological points, I found two quite distinct types of gonophores, which matched those sectioned and figured by Steche in 1907. I then examined dozens of gonodendra of all sizes which had been dropped by my laboratory specimens at Lanzarote. I found that I could soon distinguish these two types of gonophores, very often without clearing and mounting stained specimens, and from surface inspection in the light of a tungsten-ribbon lamp, or in optical section only.

One type (Pl. XXIII, fig. 5), evidently the male, had a thick cap of germ-cells borne by a relatively less capacious endodermal spadix. The walls of this spadix were relatively thin and not at all or only a little lobulated. The cap of germ-cells, situated as usual in the secondary ectoderm formed by the entocodon ('Glockenkern') and covering the spadix, consists of very numerous small cells which presumably are spermatogonia. I have not made a cytological study of them.

The other type of gonophore, which can be recognized at all stages of growth, is presumably the female (Pl. XXIV, fig. 3). Its endodermal spadix has much larger cells than those of the male type, about 7000 in number, and the whole ectoderm of the spadix becomes lobulated. In place of the thick cap of spermatogonia there is a very thin layer of germ-cells in the secondary ectoderm. Selecting one of the largest female gonodendra, I managed to cut one of the small gonophores in half transversely and then, after removing the outer membranes, to dissect out the endodermal spadix, leaving the mesogloea and the thin layer of secondary ectoderm with its germ-cells intact. When stained with Ehrlich's haematoxylin and cleared, I found to my astonishment that the germ-cells formed a continuous, narrow, sinuous band, one cell thick and two cells broad, running over the surface (Pl. XXIII, fig. 4). Rapid inspection of a whole mount showed that the cells had large nuclei containing stained chromatin particles. The polygonal cells measure about $13-14\mu$ in diameter and contain vacuoles. The nuclei are about $11-12\mu$ in diameter. The female gonophores measure up to 1.7 mm. in length and 0.85 mm. in diameter.

In the latest stage of development, in both male and female gonophores, I find that the whole manubrium (with the exception of the outer membranes with the pair of linked and branched radial canals) may be drawn out, often inside out, into the lumen of the branchlet (Pl. XXIII, fig. 6). These masses, curious to relate, circulate freely in the branches and the cavities of the palpons. I have observed this in living gonodendra.* It was this sequence of events that Richter misinterpreted, reversing the

* I have already mentioned (page 354) that the palpons can open their tips.

order in which they occur; nor did he state how he deduced his sequence. In the legend to his text-fig. 7, he stated that in the *youngest* stage of development of the male gonophore, the germ-cells lie inside the branchlets and he indicated schematically certain opaque bodies filling the lumen of the branchlets. The pedicels of the nectophores shown in Richter's fig. 7 have little mesogloea, and on this criterion alone (see page 352), apart from my observations on living material just described, I believe that this figure represents an advanced but not final stage in the development of the male gonophore. Richter described a complicated sequence of developmental events. In the youngest stage of the male gonophore he showed the conventional medusoid bud, an outgrowth of ectoderm, mesogloea and endoderm with a small 'Glockenkern' (entocodon). He described how the growth of the 'Glockenkern' downwards pushes the endoderm, ectoderm and 'Glockenkern' into the lumen of the branch, and subsequently, how the lower ectodermal layer of the 'Glockenkern' pushes up again into the half-emptied gonophore. This he appears to have thought resulted in the condition shown in his fig. 25, Taf. XXVIII, which he regarded as the *penultimate* stage of development of male germ-cells, but which I regard as an early stage.

Examination of several of my specimens that bore at least ten large gonodendra showed that all the gonodendra of one specimen were either all male or all female. Ripe eggs have never been seen. Haeckel said that *Physalia* specimens which he observed in the Bay of Algeciras on his way home from the Canaries in March 1867 bore ripe sperm, but he did not state whether the sperms were motile. Because we find ripe eggs neither on the bud-colony nor shed in surface waters, it is probable as Steche (1907) said that they undergo development in the depths, as in *Velella*.

ORIGIN OF *PHYSALIA* AND THE SIPHONOPHORA: THE PAEDOPHORE HYPOTHESIS

The evolution of *Physalia* and the other siphonophores seems to be linked with that of certain cormorphine, myriotheline and margelopsine hydroids; with *Pelagohydra* and with the so-called Disconantha (*Velella*, *Porpema*, *Porpita*).

Hadži* (1918), like Chun (1897a) before him, suggested the derivation of physonect siphonophores from the floating hydroid *Margelopsis gibbesi* (fig. 8 and legend); also of the Chondrophora (Disconantha) from cormorphine hydroids (fig. 9 and legend) and of both physonect and calycaphore siphonophores from simple hydroid corms of the *Myriothela*-type (fig. 10). Garstang (1946), who I think cannot have known of Hadži's paper, also drew attention to the similarity between disconanths and cormorphines, and between physonects and myriothelines. A review of work on the phylogeny of siphonophores and disconanths may be found in a paper by Leloup (1954).

I suggest that all these comparable forms, cormorphine, myriotheline and margelopsine† hydroids as well as *Pelagohydra* and the disconanths and siphonophores, are themselves derivatives of comparatively lately evolved and new types of animal organization—tentaculate actinula larvae, and that it is through the adaptive radiation of such larvae that these neotenic groups have arisen. The new tentaculate actinula larva must not be confused with the conception of the actinula of Brooks's (1886) hypothesis. Brooks's hypothesis satisfactorily accounts for the origin of the Hydrida, from which stock the precursors of the paedophores must have arisen in the following way: Certain early hydroids tended to retain their larvae which hitherto had been released early as eggs or free-swimming ciliated planulae. We can see this sort of trend in some bougainvillid hydroids today. These retained larvae must have been comparable on release with the actinulae of present-day myriotheline hydroids.

* So far I have only a translation of some of the figure subscripts in this paper, which is in Serbo-Croat.

† These subfamily names have been used by evolutionists in a general way and are so used without precise restriction here.

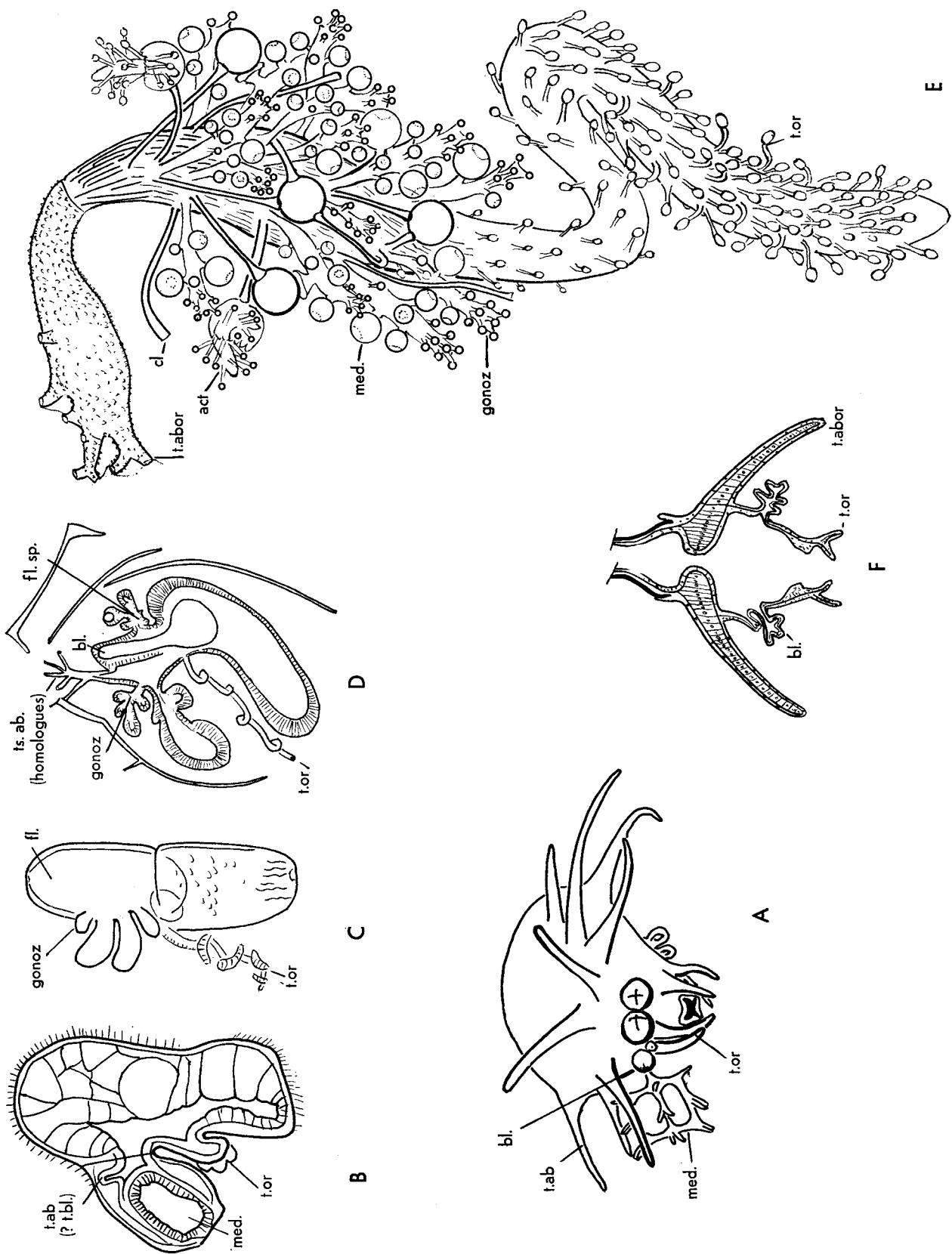
At first, no doubt, the actinulae swam by means of tentacles, as suggested by Garstang (1946), before settling down on the substratum and budding-off the sexually mature medusae. Soon asexual reproduction or budding took place during the prolonged, free-swimming larval phase, and finally the sexual adult stage was budded from the daughter polyps (gonozooids) of the still free-swimming actinula, originally a larva but now a neotenic, mature animal of a new type. So now the parent zygote (oozoid) has become an asexual carrier of the offspring (gonozooids) that I call a *paedophore*.

I do not propose to try to suggest all the detailed steps that must have followed one another in the course of the origin and adaptive radiation of this new type of organism, the paedophore. But some of the animals evidently remained entirely free-swimming and emerged as disconanths, *Pelagohydra* and some of the margelopsines, while others took to the bottom and emerged as loosely attached myriotheline and corymorphine hydroids. The great interest of *Margelopsis haeckeli* (Werner, 1954) is that it is planktonic for most of the year. During this time the larvae are retained until they develop into actinulae, which are then set free to become free-swimming hydroids; but the autumnal eggs develop into stereoblastulae, which pass the winter on the sea-bed. This life-cycle indicates how an entirely free-swimming hydroid may have arisen from a fixed precursor as a neotenous larva.

The essential structural organization of the new type of actinula is the possession of two sets of larval tentacles, oral and aboral, together with daughter polyps in the region between. These daughter polyps either have functional mouths and are called gonozooids, as in the disconanths, or the mouths are lacking although the polyps have tentacles and are obviously reduced polyps, as in *Myriothela penola* Manton. Again, the daughter polyps may be so reduced as to form scarcely recognizable stalks which bear the medusae, as in *Margelopsis haeckeli* Hartlaub.

In siphonophores generally, these reduced gonozooids are difficult to identify because often there is a replication accompanied by successive reduction. This can be seen in *Physalia*, where each gastrozooid except the protozooid may be regarded as the first of a series of groups (cormidia) of gonozooids, the last gonophores and nectophores being produced on the last few of the series of replicates called palpons.

Garstang agreed with Schneider who, in 1896, expressed the view that the siphonophore somatocyst was homologous with a bracteal canal. These canals Garstang showed to be homologues of tentacles. Leloup in 1954 suggested that a siphonophore tentacle was homologous with an oral tentacle of an actinula. Neither of these zoologists pursued the subject to the conclusion at which I myself have arrived. In fact Garstang still thought that the nectophore of a siphonophore represented the caudine gonophores of a stalked hydroid, and not those of hydroids like the corymorphines that bear them on the hydranth. In my view it is with the gonophores of the hydranths that the nectophores are to be homologized. We can in fact put the figure of a swimming margelopsine hydroid, *Climacocodon* or *M. gibbesi*, which is really a neotenous actinuloid nurse-carrier, side by side with that of either a calyconula or a physonect larva of a siphonophore and show correspondence of essentials (Text-fig. 30). Although *Climacocodon* has radial symmetry and many tentacles arranged in two groups, oral and aboral, and produces sexual medusae, while the calyconula has only one of each group of tentacles and a single asexual medusa arranged on a single meridian, Garstang has provided an explanation for this difference in symmetry. Bilateral symmetry in the calyconula was due, he pointed out, to the presence of a great deal of yolk which restricted the delamination of tissues to a single meridian. The calyconula, no doubt, is not very like the larva of the ancestral siphonophore, which probably had a float as does the larva of the cystonects, the group which includes *Physalia*. Garstang showed how the calycones had lost this float. Like the larva of the cystonects, the calyconula has a precocious nectophore, which the cystonula larva of *Physalia* has not.



Text-fig. 30. *Physalia physalis*. Some siphonophoran and other Paedophores, to demonstrate homologies. A, *Climacocodon ikarri* Uchida (after Uchida 1924, $\times 37$). B, Calyconula larva of *Sulculeolaria quadrivalvis* Blainville (after Metchnikoff, 1874), $\times 20$. C, larva of *Physalia physalis*, $\times 95$. D, larva of *Agalma elegans* (Sars) in section (after Totton, 1956), $\times 43$. E, *Myriothela purpurea* (Gosse) (after Allman, 1876), $\times 4$. (There are difficulties in determining the prior name of this intertidal species from the Dorset coast. 'Arum cockii' Vigurs' (Cocks, Ann. Rept R. Corn. Poly. Soc. for 1849, p. 90 (published 1850)) is a nomen nudum. The same name on p. 34 of the Report for 1853 of the same society (published 1854) is antedated by *Spadix purpurea* Gosse (Ann. Mag. nat. Hist. Vol. XII, p. 125) published in July 1853. The prior generic name is *Myriothela* Sars 1849, if *Lucernaria* Fabricius 1780 is excluded.) F, *Tubularia larynx* (after Leloup, 1954), $\times 10$. *bl* = position of blastostyle (hidden), *fl* = float, *gonoz* = gonodendron, *med* = gonod = gonoz = gonozooids (homologues), *med* = medusoid, *t.ab* = aboral tentacles, *t.bl* = oral tentacles of blastostyle, *t.or* = tentacle of blastostyle.

It is in this context that we may look for the meaning of the tripartite groups of *Physalia*, about which I said so much earlier on when describing the pattern of budding in the cormidia (pages 328 ff.). Each tripartite group is the homologue of an asexual replicated gonozooid of *Velella* and of a blastostyle* of *Climacocodon*, with which I have just compared a siphonophore actinula larva. The difference is that the *Physalia* polyp, or gastrozooid, is very much elongated, the aboral tentacles of the *Physalia* nurse-carrier are absent, and its oral tentacles reduced to a single one, and the single gonozooid complex, the gondendron, has replaced the simple gonozooid or blastostyle.

If early larvae of *Physalia* are compared with those of the other two groups of siphonophores, namely the calyconulae of Calycophora and the physonulae of Physonectae, both resemblances and differences will be noticed at once; the large air-sac and tentacle in *Physalia*, the large nectophore and small tentacle in the calyconula, and the air-sac, tentacle and bracts of the physonula (Text-fig. 30).

Had it not been for comparison of the cystonect cystonula larva of *Physalia* with the physonect larva and with the calycophore calyconula, it would have been more difficult to speculate about the ancestry of *Physalia*. As it is, it seems possible that *Physalia*'s ancestor arose by neoteny after the first appearance of actinula larvae in hydroids, and that it proved advantageous to develop an enormous float, to bud extravagantly and precociously, and to develop bigger and better tentacles with very numerous nematocysts for the capture of the comparatively large fish with which the animal came into contact so effortlessly.

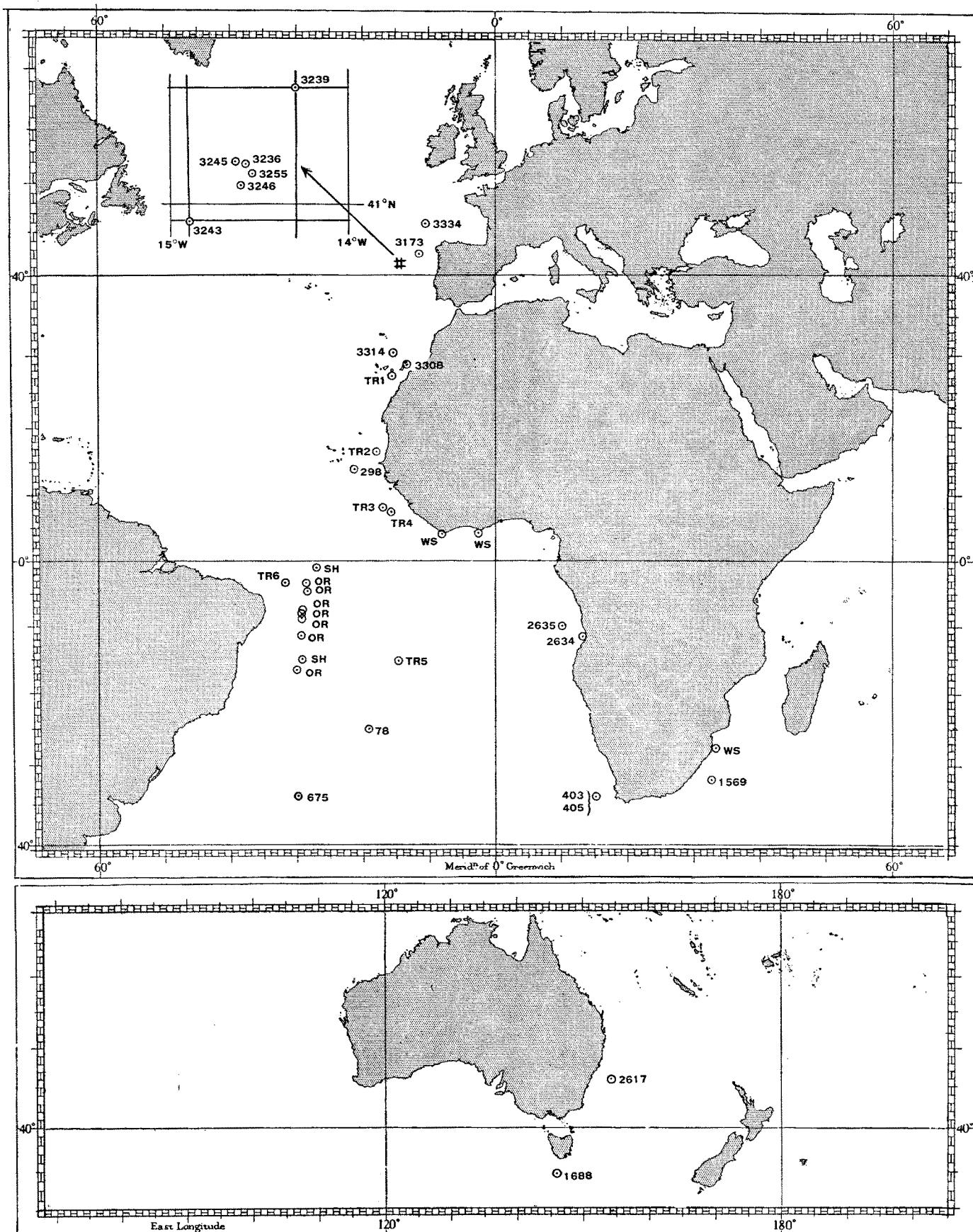
Thus evolution for *Physalia* has consisted, I think, partly in its ability through the ages to improve its adaptation to catch and devour fishes at the surface of the sea and to live in a stormy environment. In this respect it may be contrasted with the deep-sea calycophore species of *Chuniphyes* which have particularly small polyps and no floats. On the other hand the floats of even deep-sea cystonects are large. *Physalia* is also obviously adapted to drift at an angle of about 45° to the right or left of the down-wind direction. Because this angle increases† as the waterline lengthens, it looks as if this adaptation has evolutionary value. If the process of being drifted on to a lee-shore is the analogue of being captured by a predator, the future of *Physalia* may lie in the direction of improvement in this adaptation. Herein may be part of the significance of the great size of the float in *Physalia*, and a rapid growth-rate would help in this respect. The apparent neotenic character of *Physalia* lends cogency to these considerations.

We do not know that right- or left-handedness is affected by natural selection, and it is difficult to see how one tack can be more advantageous than the other. I do not think that Woodcock's suggestion of advantages to be gained by one tack in feeding is a good one, though the theory of wind-induced vortices no doubt is sound. But it is quite certain that the tack of an individual is fixed from a very early phase of its life-history. The future tack of any individual larva can be recognized already when only the rudiments of secondary buds are becoming visible and the length of the larva is still less than 1.5 mm. The gas-gland itself, even at that age, does not lie symmetrically in the axial line. Because, by custom, we call the meridian in which the tentacle and secondary buds lie ventral, the dorso-ventral plane early comes to lie almost parallel to the surface of the water. The gas-gland itself, while still located at the oral end of the air-sac, then lies asymmetrically, somewhat on the underside. I am of the opinion that right- and left-handedness arises fortuitously when the larva surfaces. Perhaps there is a slight bias of which we know nothing, but the tentacle must come to lie either to the right or to the left, and henceforward the tack is fixed.

I think the predominance of one tack would be disadvantageous because the maintenance of both

* Present but not shown in the original figure.

† Woodcock (1956) stated that the young specimens drifted at a smaller angle. I can well believe this, but have not checked it.



Text-fig. 31. *Physalia physalis*. Chart to show the distribution of specimens recorded by members of the staff of the National Institute of Oceanography in the Atlantic, and in Australian waters.

forms obviates the danger of the population being swept out of its optimum environment by the wind. The mere fact of being drifted by the wind at 20–30 m. per minute must be of great value in food capture and must aid maximum distribution.

DISTRIBUTION

It does not seem an adequate treatment of this subject to deal merely with such observations as may be recorded in the literature. It is hoped to make a special study of the question later on, basing it on replies to a questionnaire circulated through appropriate channels to seafarers.

The potential value of ships' logs is shown by the following extracts provided by the Marine Superintendent of the Meteorological Office from meteorological log-books of various ships:

(1) *M.V. San Veronico* (Eagle Oil and Shipping Co.)

Captain S. Miller, O.B.E. Curaçao to Rotterdam.

13 May 1957, at 12.00 G.M.T. in 36° 30' N., 36° 24' W. While the ship was stopped for engine repairs many Portuguese Men-o'-War were observed. They consisted of.... The bladder size varied up to about 8 in. in length. On puncturing the bladder of one caught in a bucket (see photograph) it was observed.... [A note on 'deflation' and subsequent 're-inflation' follows, but is not precise enough for evaluation at present.]

(2) *S.S. Loch Garth* (Royal Mail Lines)

Captain G. S. Grant. West coast of North America.

30 May 1957, at 39° 50' N., 124° 32' W.

At 17.40 G.M.T. the ship passed through a line of small Portuguese Men O'War formed in a direction N.E.–S.W. The line approximately a quarter of a mile in length and 50 ft. in width, was of a dark green appearance. [Query: were these *Velella*?]

(3) *S.S. Tekoa* (New Zealand Shipping Co.)

Captain F. C. Taylor. Curaçao to London.

(a) 15 June 1957, at 19.00 G.M.T. in 36° N. 43° 20' W. passed through numerous Portuguese Men O' War (*Physalia*) and By-the-Wind Sailors (*Velella*). These siphonophores are usually seen when entering the Gulf Stream, but they have been sighted this time without the usual accompanying rise in sea temperature which generally ushers you into the Gulf Stream.

(b) 16 June 1957. Vessel still passing many of the above....

(4) *S.S. Orion* (Orient Line)

Captain J. O. Birch, D.S.C., R.D. Honolulu to Vancouver.

25 August 1957 in 44° 18' N., 132° 06' W. The sea was observed to be thickly speckled with transparent colourless jellyfish, circular in shape and about 2–4 in. in diameter. When viewed through binoculars a dark centre could be seen and also what appeared to be a small vertical fin. No tentacles or feelers however could be seen and the observer therefore is not definitely sure as to whether they were Portuguese Men O' War or not. The sea continued to be speckled with these jellyfish until dusk, sometimes lying in bands down-wind. The vessel therefore has passed through a field of these marine creatures at least 164 miles wide. Wind N. × W. Force 3. Ship's course 048°, speed 17·8 knots. [Internal evidence seems to indicate that what Captain Birch saw were specimens of *Velella*.]

(5) A note headed *Physalia* appeared in *The Marine Observer's Log*, vol. IX, 1932. It was an extract from the Meteorological Log of *S.S. Niagara*, Captain T. V. Hill. Auckland, New Zealand to Victoria, B.C. 'At 4.0 p.m. 19 May 1931, large numbers of *Physalia*....' [Once more the evidence pointed to a mis-identification, but similar logs must contain a wealth of useful information.]

To the Hydrographer of the Navy, Rear-Admiral K. St B. Collins, O.B.E., D.S.C., I am indebted for supplying the following information in response to a request for observations to be made if possible by ships of the Fleet during a cruise in the West Indies at the beginning of the year 1958.

Portuguese Men-o-war were sighted from *H.M.S. Delight* between 13.00 and 15.30 on 5 February 1958, off Havana, Cuba. The ship was steering course 260° speed 14 knots, and the men-o-war could be

DISCOVERY REPORTS

seen at ranges up to three hundred yards. Density: individuals over 500 yards apart from 13.00 to 14.00 (i.e. dispersed over 14 miles). Large shoal at 15.00, extending for 3 miles with individuals about 200 yards apart. Type: all appeared to be left-handed on starboard tack. Meteorological conditions: Wind from 120°, 10 knots; sea temperature 79° F. The Gulf Stream in this locality was flowing at two knots.

This must be the first recorded occasion on which the tack of specimens has been noted at sea. Observations or collections made by 'Discovery' and 'Discovery II' or members of the staff travelling in other ships are recorded in Table 12.

Table 12

Position	Station	Date	Tack of specimen
<i>R.R.S. 'Discovery' and 'Discovery II'</i>			
27° 15' N., 15° 32' W.	Testing gear	21 October 1925	1 R
16° 19' N., 18° 24' W.		26 October 1925	1 R
8° 06' N., 17° 06' W.		1 November 1925	2 L
7° 17' N., 16° 19' W.		2 November 1925	1 L (2)
25° 5' S., 15° 17' W.		28 November 1925	1 L
25° 47' S., 14° 48' W.		29 November 1925	1 L
3° 22' S., 32° 25' W.		29 December 1929	1 L (2)
35° 18' S., 19° 01' 10" W.	78	12 June 1926	1 L
13° 01' 45" N., 21° 34' 45" W.	298	29 August 1927	1
34° 14' S., 15° 01' E.	403	24 May 1930	1 R
34° 16' S., 15° 02' E.	405	4 June 1930	1
34° 08' S., 29° 50' 2" W.	675	26 April 1931	3 R
31° 50' 3" S., 32° 20' 5" E.	1569	12 April 1935	—
45° 10' 8" S., 146° 04' 6" E.	1688	6 March 1936	1 L
12° 17' 4" S., 13° 31' 3" E.	2634	10 April 1939	1 L
10° 19' S., 09° 36' 4" E.	2635	11 April 1939	—
34° 02' S., 154° 16' E.	2717	8 October 1950	2 L, 1 R
42° 35' N., 11° 35' W.	3173	22 November 1954	1 R
42° 02' N., 13° 16' W.	3235	18 May 1955	—
41° 11' N., 14° 34' W.	3236	19 May 1955	1
41° 30' N., 14° 17' W.	3239	24 May 1955	1 R
40° 56' N., 14° 53' W.	3243	26 May 1955	2
41° 10 1/2' N., 14° 38' W.	3245	27/28 May 1955	2 R (3)
41° 05' N., 14° 36' W.	3246	30 May 1955	1 R
41° 08' N., 14° 32' W.	3255	11/13 June 1955	2 R
28° 49 1/2' N., 13° 40 1/4' W.}	3308	19 September 1955	1
28° 49 3/4' N., 13° 37 3/4' W.}		21 September 1955	—
30° 08' N., 15° 53' W.	3314	13 October 1955	1 R
45° 44 1/2' N., 10° 48' W.	3334		
<i>R.S.S. 'William Scoresby'</i>			
27° 52' S., 33° 05' E.	—	8 August 1950	1
04° 25' N., 02° 46' W.	—	27 October 1950	2
04° 26' N., 08° 17' W.	—	27 October 1950	1
<i>'Southern Harvester'</i>			
15° 05' S., 29° 22' W.	—	5 May 1948	1
01° 11' S., 27° 17' W.	—	8 May 1948	1
<i>'Orwell'</i>			
16° 12' S., 30° 11' W.	—	25 January 1954	1
11° 37' S., 29° 40' W.	—	26 January 1954	1
09° 03' S., 29° 22' W.	—	27 January 1954	1
08° 18' S., 29° 15' W.	—	27 January 1954	1
07° 40' S., 29° 07' W.	—	27 January 1954	1
04° 21' S., 28° 44' W.	—	28 January 1954	2
03° 47' S., 28° 35' W.	—	28 January 1954	2

All these positions are shown in Text-fig. 31.

Information is required on the following points.

- (1) Where is the animal most commonly met with?
- (2) Does it occur at sea in vast shoals or isolated or both, and under what meteorological conditions?
- (3) *Physalia* occurs in two forms, right- and left-handed: are both forms equally common and do they occur together?
- (4) Is it difficult for an observer on shipboard who is familiar with boat-sailing to distinguish the right- from the left-hander by the way it is orientated to the wind? (The right-hander appears to be hove-to on the port-tack and drifts to the left of the down-wind direction, and vice versa, the tentacles acting as a drogue.)
- (5) Fixes are required for animals definitely observed to be right- or left-handers with a record of wind-force.
- (6) In a wind does the animal drift along steadily? In a sudden lull does it fall over into the wind? Subsequently, and in a flat calm, does the animal roll about and somersault to right itself?
- (7) Is *Physalia* ever observed in long parallel wind-rows?
- (8) Records of recollection of previous observations on *Physalia* in any oceans are needed.
- (9) Precise records are needed of the effects of stinging by *Physalia* (identified as having a bladder that rests on the surface).

SUMMARY

1. There is only one species of Portuguese man-of-war, *Physalia physalis* (L.), though it occurs everywhere in two forms, the so-called right-handed and left-handed. Both forms were found together in the Canary Islands. The question of right- and left-handedness is discussed.

2. Observations from a boat were made at close quarters on left-handed specimens drifting in a moderate breeze at slack tide. The angle of drift from down-wind direction was measured, and the rate of drift determined.

3. The well-known somersaulting phenomena were studied in open water. They were seen generally in a calm and followed loss of equilibrium in the absence of a breeze.

4. Specimens ranging in float-length from 11 to 180 mm. were anaesthetized and fixed for morphological study.

5. The animal is shown to consist of a hypertrophied asexual larva acting as nurse-carrier for other larvae, the polyps, and adults, the medusoid gonophores.

6. The pattern of budding has been determined. There are two budding-zones on the under and windward side of the oral half of the float, separated by a gap into a main zone and a reduced oral zone. The budding system is basically the same in both.

7. The single cormidia of a number of specimens, both young and old, have been compared with one another on the same specimen and from specimen to specimen, and photographic records made from several angles.

8. The general pattern of budding in a single cormidium shows a series of about a dozen tripartite groups, consisting each of a single gastrozooid and its associated tentacle and nematocyst nursery (the ampulla) together with a complex gonodendron, each group budded from the base of its predecessor with the youngest group formed at the aboral end. Secondary branches and branchlets carrying still more series of tripartite groups are produced from the bases of certain groups of the first series, and tertiary ones from the bases of some groups of the secondary series. A well-marked series of these branches is formed to leeward of the main series.

9. Full details of sexual reproduction are unknown and ripe ova have never been observed. *Physalia* is dioecious. Some of the so-called 'male' gonophores are female.

10. There is no evidence that the so-called 'female' medusoids are shed and that the jelly-polyps (*Gallertpolypoide*) represent their stalks, as has been suggested. The 'female' medusoids are nectophores, not concerned with sexual reproduction.

11. The jelly-polyps, the 'Gallertpolypoide' of Chun, found on the branches of the gonodendra, are vestigial nectophores. In the early stages of their development there is no sign of a 'Glockenkern'.
12. The basal ampullae of the tentacles are homologous with the basigasters of gastrozooids of other siphonophores. Their walls are filled with nematoblasts.
13. The gonodendra and tentacles are more complex and so probably more highly evolved than in other cystonects. Their growth-stages and the structure of their asexual nectophores and jelly-polyps were studied. Early egg-cells were located in bands in the ectoderm of female gonophores. Photomicrographs of early growth-stages of the gonophores are given.
14. A brief review of the literature, including the pharmacology of stinging is given.
15. A list is given of points upon which further information about the living animal is desired.

REFERENCES

- AGASSIZ, A., 1883. *Explor....Gulf Stream....The Porpitidae and Velellidae*. Mem. Mus. Comp. Zool. Harv. vol. VIII, 2, p. 8.
- AGASSIZ, A. and MAYER, A. G., 1902. *Reports Sci. Res. Albatross. III. Medusae*. Mem. Mus. Comp. Zool. Harv. vol. xxvi, 3, p. 139.
- AGASSIZ, L., 1862. *The genus Physalia and our Physalia arethusa*. Contr. Nat. Hist. U.S.A., Boston, vol. IV, p. 335.
- ALLMAN, G. J., 1876. *On the structure and development of Myriothela*. Phil. Trans. R. Soc. vol. CLXV, p. 549.
- BIGELOW, H. B., 1911. *The Siphonophorae*. Reports Sci. Res. Exped....Albatross, vol. XXIII.
- BIGELOW, R. P., 1891. *Notes on the history of Caravella maxima, Haeckel* (*Physalia caravella Eschscholtz*). Johns Hopk. Univ. Circ. vol. x, p. 90.
- BROOKS, W. K., 1886. *The life-history of the Hydromedusae: A discussion of the origin of the medusae and of the significance of metagenesis*. Mem. Boston Soc. Nat. Hist. vol. III, p. 359.
- BROOKS, W. K. and CONKLIN, E. G., 1891. *On the structure and development of the gonophores of a certain siphonophoran belonging to the order Auronectae (Haeckel)*. Johns Hopk. Univ. Circ. vol. x, p. 87.
- CHUN, C., 1887. *Zur Morphologie der Siphonophoren. 2. Ueber die postembryonale Entwicklung von Physalia*. Zool. Anz. vol. x, p. 574.
- 1892. *Die Canarischen Siphonophoren in monographischen Darstellungen. II. Die Monophyiden*. Abt. Senck. Nat. Ges., Frankfurt, vol. XVIII, p. 57.
- 1897a. *Ueber den Bau und die morphologische Auffassung der Siphonophoren*. Verh. dtsch. zool. Ges. vol. VII, p. 48.
- 1897b. *Die Siphonophoren der Plankton-Expedition*. Ergebn. der Plankton Exp. vol. II, K. b.
- DELAGE, Y. and HEROUARD, E., 1901. *Les Coelenterés. Traité de Zoologie concrète*. Paris, vol. II, pt. 2.
- EHRENBERG, C. G., 1838. *Ueber das Massenverhältnis der jetzt lebenden Kiesel-Infusorien und über ein neues Infusorien-Conglomerat Polirschiefer von Jastraba in Ungarn*. Abh. ph. kl. K. pr. Ak. Wiss. 1836, vol. CIX, Taf. 2.
- ESCHSCHOLTZ, FR., 1829. *System der Acalephen*. Berlin.
- FONTAINE, A., 1954. *Some observations on Physalia, the Portuguese man-of-war*. Notes Nat. Hist. Soc. Jamaica, no. 64, p. 61.
- GARMAN, S., 1896. *Report on fishes collected by the Bahama Expedition of the State University of Iowa, under Professor C. C. Nutting in 1893*. Bull. Labs Nat. Hist. Univ. Ia, vol. IV, p. 81.
- GARSTANG, W., 1946. *The morphology and relations of the Siphonophora*. Quart. J. Micr. Sci. vol. LXXXVII, pt. 2, p. 103.
- GOTO, S., 1897. *Die Entwicklung der Gonophoren bei Physalia maxima*. J. Coll. Sci. Tokyo, vol. X, p. 175.
- GUDGER, E. W., 1942. *Physalia, the fish-eater*. Bull. N.Y. Zool. Soc. vol. XLV, 3, p. 62.
- HADŽI, J., 1918. *Shvačanje sifonoforá [Understanding siphonophora]*. Rad. jug. Akad. Znan. Umj. vol. CCXIX, p. 195.
- HAECKEL, E., 1879. *Das System der Medusen, Atlas*. Denkschr. med.-naturw. Ges. Jena, vol. I.
- 1888. *Report on the Siphonophorae*. Rep. Sci. Res. H.M.S. 'Challenger', Zool. vol. XXVIII.
- HALSTEAD, B. W., 1958. *Jelly-fish stings and their medical management*. South African Practitioner, April-May 1958, p. 43.
- HARDY, A. C., 1956. *The Open Sea*. London: The New Naturalist.
- HOOKER, Sir J. D., 1896. *Journal of Sir Joseph Banks*. London.
- HUXLEY, T. H., 1851. *Ueber die Sexualorgane der Diphyiden und Physophoriden*. Archiv. Anat. Physiol. 1851, p. 380.
- 1855. *On the anatomy and physiology of Physalia, and its place in the system of animals*. (Huxley, William (sic).) Proc. Linn. Soc. vol. II, p. 4.
- 1859. *The Oceanic Hydrozoa*. London: Ray Soc.
- HYMAN, L. H., 1940. *The Invertebrates: Protozoa through Ctenophora*. New York: London.
- KATO, K., 1933. *Is Nomeus a harmless inquilinus of Physalia?* Proc. Imp. Acad. Japan, vol. IX, 9, p. 537.
- KAWAMURA, T., 1910. *Rhyzophysa and Physalia*. Dobutz Z. Tokyo, vol. XXII, p. 445.

- LANE, C. E. and DODGE, E., 1958. *The toxicity of Physalia nematocysts*. Biol. Bull. vol. cxv, p. 219.
- LELOUP, E., 1954. *A propos des Siphonophores*. Vol. jubilaire Victor van Straelen, Bruxelles, vol. II, p. 643.
- LENHOFF, H. M. and SCHNEIDERMAN, H. A. 1959. *The chemical control of feeding in the Portuguese Man-of-War*, *Physalia physalis L.*, and its bearing on the evolution of the Cnidaria. Biol. Bull., vol. cxvi, p. 452.
- LENS, A. D. and RIEMSDIJK, T. VAN, 1908. *The Siphonophora of the Siboga Expedition*. Siboga Exped. vol. IX.
- LESSON, R. P., 1827. *Considérations nouvelles sur la grande Physalie, la Caravelle, la grande Galère des tropiques*. Bull. Sci. Nat. vol. xi, p. 163.
- 1838. *Voyage de la 'Coquille'*. Paris, Zool. vol. II, pt. 2, 2^e div.
- 1843. (Roret's Suite à Buffon.) *Acalèphes*. Paris.
- LEUCKART, R., 1851. *Ueber den Bau der Physalien und der Röhrenquallen im Allgemeinen*. Zeit. wiss. Zool. vol. III, p. 189.
- LOOMIS, W. F., 1955. *Glutathione control of the specific feeding reactions of Hydra*. Ann. N.Y. Acad. Sci. vol. LXII, 9, p. 209.
- METSCHNIKOFF, E., 1874. *Studien über die Entwicklung der Medusen und Siphonophoren*. Zeit. wiss. Zool. vol. xxiv, p. 15.
- MOSER, F., 1925. *Die Siphonophoren der deutschen Südpolar Expedition, 1901–3*. Dtsh. Südpol Exped. vol. xvii, Zool. IX.
- OKADA, YŌK, 1932. *Développement post-embryonnaire de la Physalie pacifique*. Mem. Coll. Sci. Kyoto, B, vol. VIII, p. 1.
- 1935. *Les jeunes Physalies. Note supplémentaire sur le développement post-embryonnaire de la Physalie*. Mem. Coll. Sci. Kyoto, B, vol. X, p. 407.
- OLFERS, J. F. H. von, 1832. *Ueber die grosse Seeblase (Physalia arethusa) und die Gattung der Seeblasen im Allgemeinen*. Abh. Akad., Wiss. Berlin, 1831, p. 155.
- PARKER, G. H., 1932. *Neuromuscular activities of the fishing filaments of Physalia*. J. Cell. Comp. Physiol. vol. I, p. 53.
- PEREZ, C., 1929. *Division directe des noyaux dans la spadice des gonophores chez la Physalie*. Arch. Anat. micr. vol. XXV, p. 548.
- PHILLIPS, J. H., 1956. *Isolation of active nematocysts of Metridium senile and their composition*. Nature, Lond., vol. CLXXVIII, p. 932.
- POPE, E., 1953. *Marine stingers*. Aust. Mus. Mag. vol. XI, p. 111.
- QUATREFAGES, A. DE, 1854. *Mémoire sur l'organisation des Physalies (Physalia)*. Ann. Sci. Nat. Paris, Ser. 4. Zool. vol. II, p. 107.
- QUOY, J. R. and GAIMARD, P., 1824. *Voyage de l'Uranie et la 'Physicienne'*. Zool. pt. 2 and Atlas, p. 377, Paris.
- RICHTER, W., 1907. *Die Entwicklung der Gonophoren einiger Siphonophoren*. Z. wiss. Zool. vol. LXXXVI, p. 557.
- SCHLOESING, T. and RICHARD, J., 1896. *Recherche de l'argon dans le gaz de la vessie natatoire des poissons et des physalies*. C.R. Acad. Sci., Paris, vol. CXXII, p. 615.
- SCHNEIDER, K. C., 1896. *Mittheilungen über Siphonophoren. II. Grundriss der Organisation der Siphonophoren*. Zool. Jahrb. anat. vol. IX, p. 571.
- 1898. *Mittheilungen über Siphonophoren. III. Systematische und andere Bemerkungen*. Zool. Anz. vol. XXI, p. 172.
- SOUTHCOTT, R. V., 1958. *The Cubomedusae—lethal jellyfish*. Discovery, vol. XIX, p. 282.
- SCHECHE, O., 1907. *Die Genitalanlagen der Rhizophysalien*. Z. wiss. Zool. vol. LXXXVI, p. 134.
- 1910. *Die Knospungsgesetz und der Bau der Anhangsgruppen von Physalia*. Festschr. . R. Hertwigs, Jena, vol. II, p. 355.
- SUNDNES, G., ENNS, T. and SCHOLANDER, P. F., 1958. *Gas secretion in fishes lacking rete mirabile*. J. exp. Biol., vol. XXXV, p. 671.
- TOTTEN, A. K., 1954. *Siphonophora of the Indian Ocean together with systematic and biological notes on related species from other oceans*. Discovery Rep. vol. XXVII, p. 1.
- 1956. *Development and metamorphosis of the larva of Agalma elegans (Sars) (Siphonophora: Physonectae)*. Pap. Mar. Biol. and Oceanogr., Deep-Sea Research, suppl. to vol. III, p. 239.
- TOTTEN, A. K., and MACKIE, G. O., 1956. *Dimorphism in the Portuguese Man-of-war*. Nature, Lond., vol. CLXXVII, p. 290.
- TREMBLEY, A., 1744. *Mem. Hist. Polypes d'eau douce*. Leide.
- UCHIDA, T., 1924. *On a new 'pelagic' hydroid*. Climacocodon ikarii, n.gen., n.sp. Jap. J. Zool. vol. I, p. 59.
- WAGNER, R., 1835. *Entdeckung männlicher Geschlechtsteile bei den Actiniens*. Arch. Naturgesch. vol. II, p. 215, Taf. 3.
- WEILL, R., 1934. *Contribution à l'étude des Cnidaires et de leurs nématocystes. I. Recherches sur les nématocystes (morphologie, physiologie, développement)*. Trav. Sta. Zool. Wimereux, vol. X.
- WERNER, B., 1954. *Ueber die Fortpflanzung der Anthomeduse, Margelopsis haeckeli Hartlaub durch Subitan- und Dauereier und die Abhängigkeit ihrer Bildung von äusseren Faktoren*. Ver. deutsch. zoolog. Gesellsch. Tübingen, 1954, p. 124.
- WILL, L., 1909. *Ueber das Vorkommen kontraktiler Elemente den Nesselzellen der Coelenteraten*. S.B. naturf. Ges. Rostock, N.F., I, p. 48.
- 1926. *Die Bildung der Nesselkapseln von Physalia*. S.B. naturf. Ges. Rostock, vol. III, Folge I, p. 70.
- WILSON, D. P., 1947. *The Portuguese man-of-war*. *Physalia physalis L.*, in British and adjacent seas. J. Mar. Biol. Ass. U.K. vol. XXVII, p. 139.
- WITTENBERG, J. B., 1958. *Carbon monoxide in the float of Physalia*. Biol. Bull. vol. cxv, p. 371.
- WOODCOCK, A. H., 1944. *A theory of surface water motion deduced from the wind-induced motion of Physalia*. J. Mar. Res. vol. V, 3, p. 196.
- 1956. *Dimorphism in the Portuguese man-of-war*. Nature, Lond., vol. CLXXVIII, p. 253.

PLATE VII

Post-larvae of *Physalia physalis* collected by Miss Dodge
near Miami, Florida.

- Fig. 1. Early stages showing the formation of cormidia II, III and VII are seen in the lowermost two larvae (cf. Text-fig. 23D). Cormidia I and IV can be seen as buds in the top right specimen (cf. Text-figs. 23J and 24, A and B). $\times 7\cdot3$.
- Fig. 2. Two of the earliest stages of development of cormidia II, III and VII (cf. Text-fig. 23B, D, E and G). $\times 16$ approx.
- Fig. 3. The lowermost specimen shows buds of cormidia I, II, III and VII. The square-shaped bud is the ampulla of II group₁, and is separated by its tentacle from the gastrozoid of II group₁. The uppermost specimen shows the extent of the pneumatocyst (cf. Text-figs. 23J and 24A and B). $\times 11\cdot4$ approx.
- Fig. 4. The four buds seen clearly in the centre and lower right specimens are those of gastrozoid II, ampulla II, gastrozoids III₁ and VII₁ (cf. Text-figs. 23J and 24A and B). $\times 7\cdot3$.

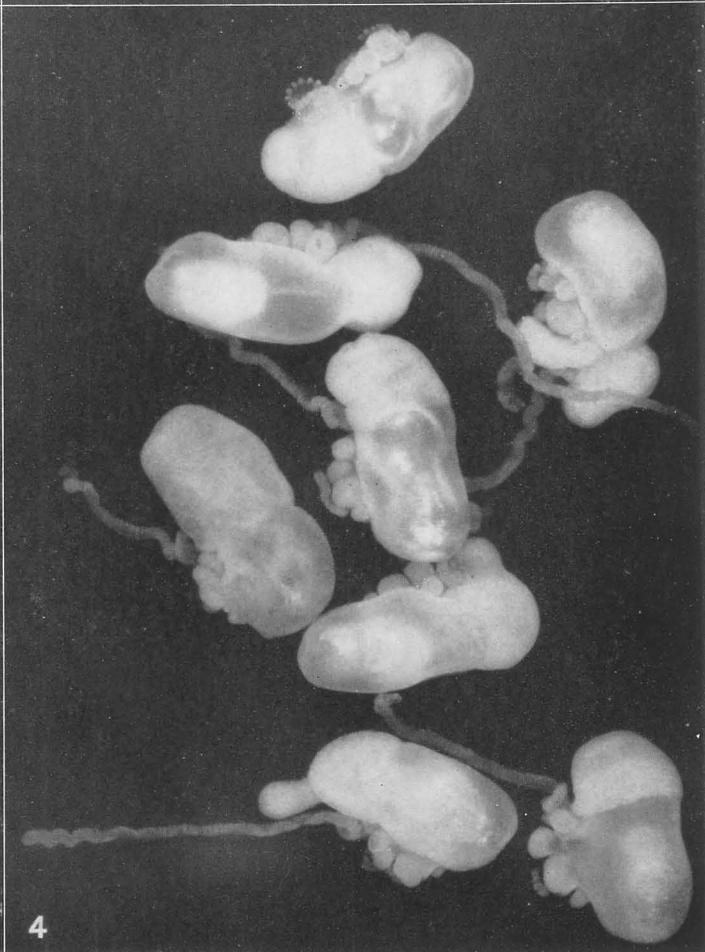
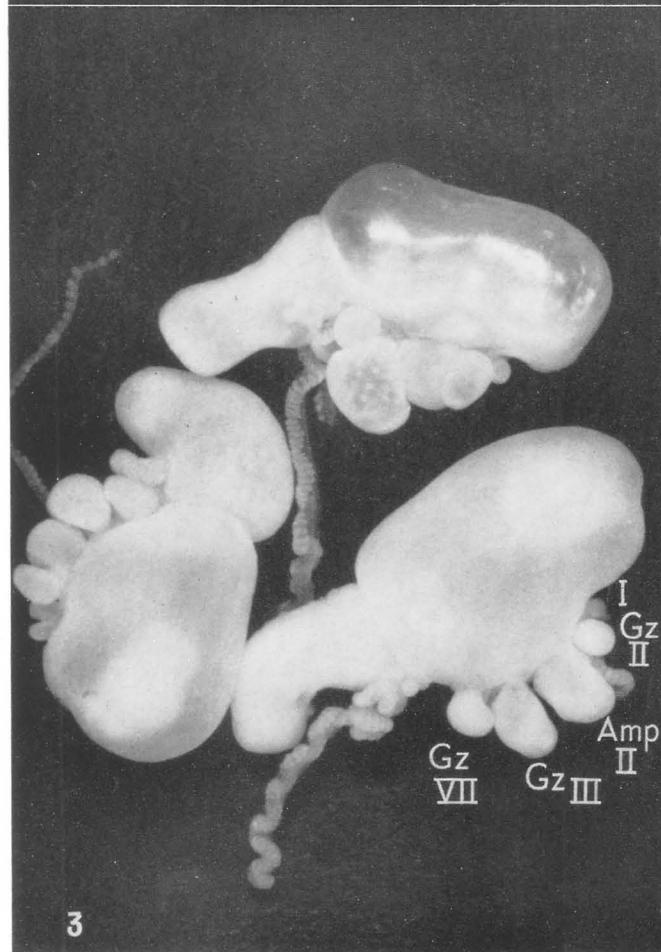
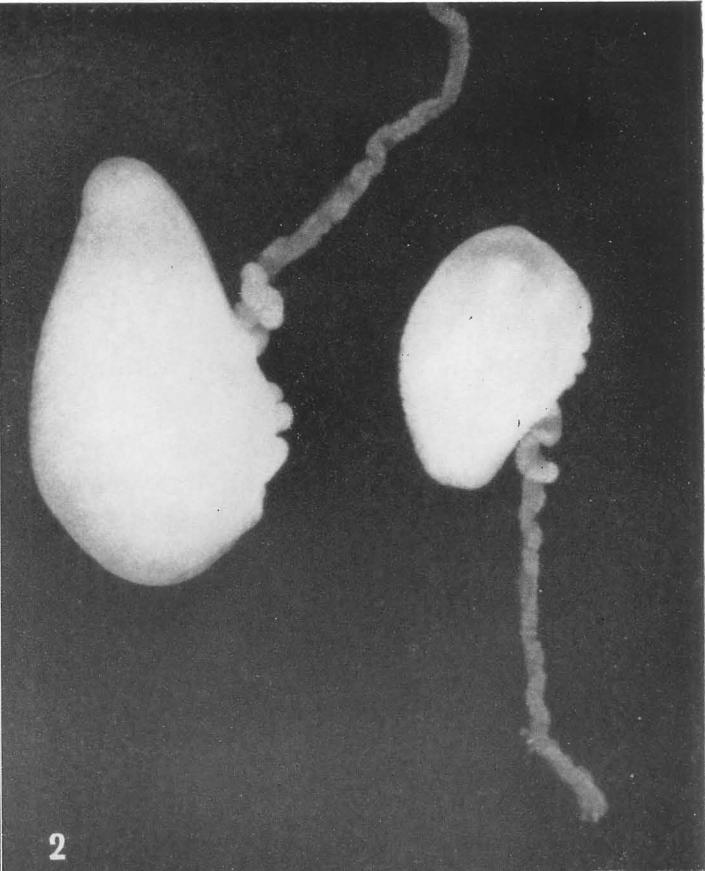
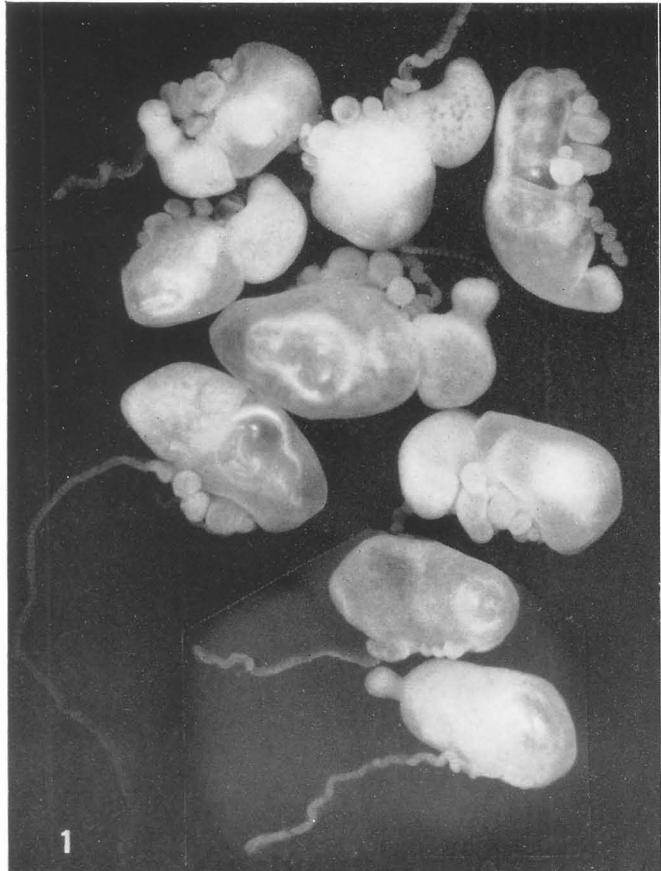


PLATE VIII

- Fig. 1. A young left-handed *Physalia* from Arrecife, specimen Juv. 12, float-length 2·9 cm., showing crest, gas-gland, basal internode, main tentacle (cormidium II) and individual groups of cormidium I. $\times 1\cdot9$.
- Fig. 2. A young right-handed *Physalia* from Arrecife, specimen Juv. 8, float-length 3 cm., viewed from above, showing early stages of crest-development, oral zone and main zone of six cormidia separated by the basal internode. The limits of cormidium III can be seen extending from the oral side of the main tentacle (II) to the large gastrozoid of its group 1 on the other side. $\times 2$.
- Fig. 3. A left-handed young specimen from Arrecife, Juv. 5, float-length 19 mm., viewed from the leeward (under) side. There are six cormidia in the main zone and five in the oral. $\times 4\cdot7$.
- Fig. 4. The same from the windward (upper) side. At this stage some main zone cormidia bear a larger windward gastrozoid (group 1) and a smaller leeward one. In the oral zone two gastrozoids of groups 1 and 2 predominate (cf. Text-fig. 22). $\times 4\cdot7$.
- Fig. 5. A young right-handed *Physalia*, K 2, float-length 12 mm., gas-gland diameter 2·5 mm., taken by Miss Dodge near Miami, Florida, viewed from the leeward (under) side. There are seven cormidia in the main zone. $\times 5$. (For details see Text-fig. 16.)
- Fig. 6. The same specimen from the windward (upper) side. Cormidium VI is partly hidden by VII (cf. Text-fig. 19).

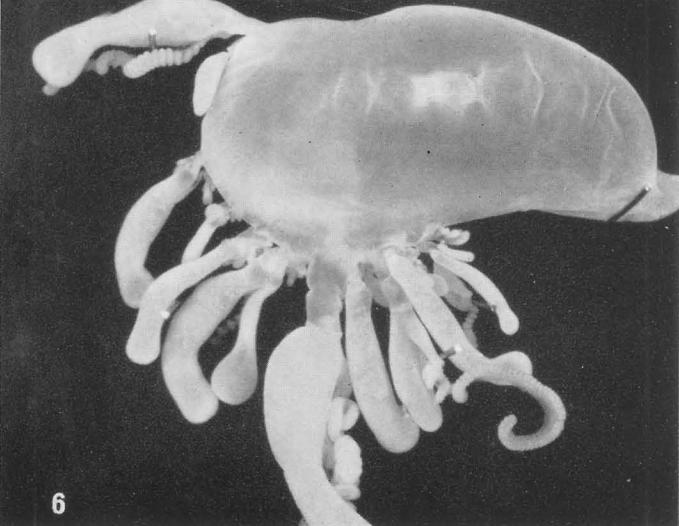
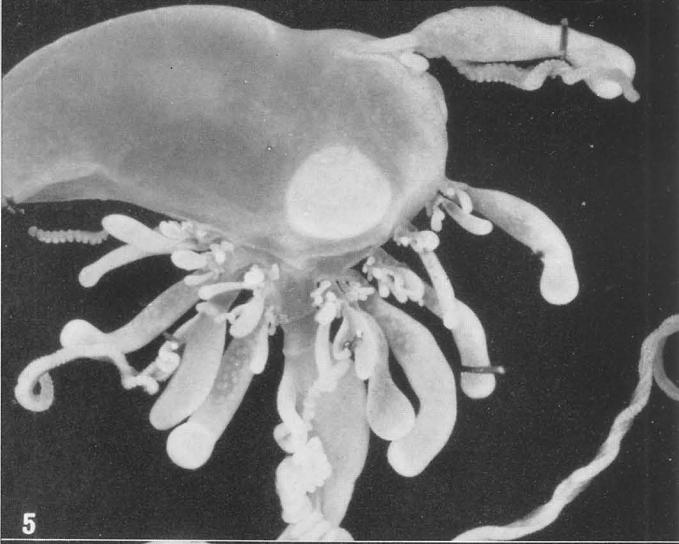
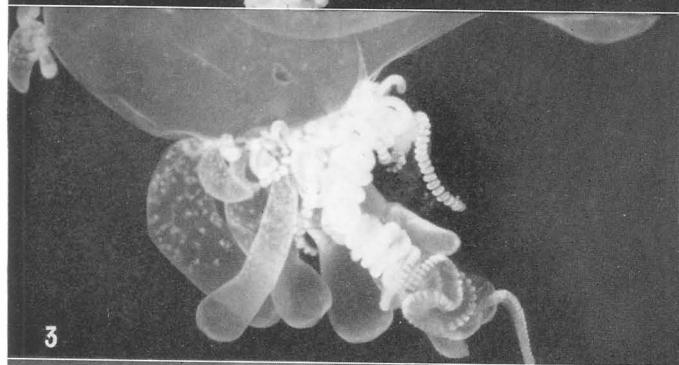
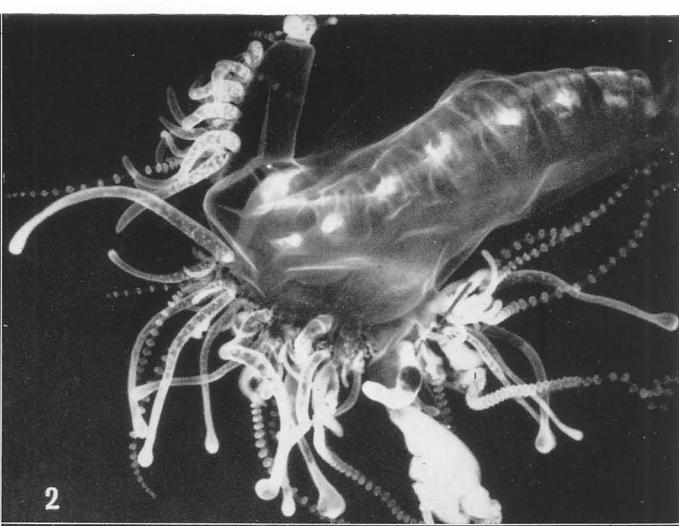
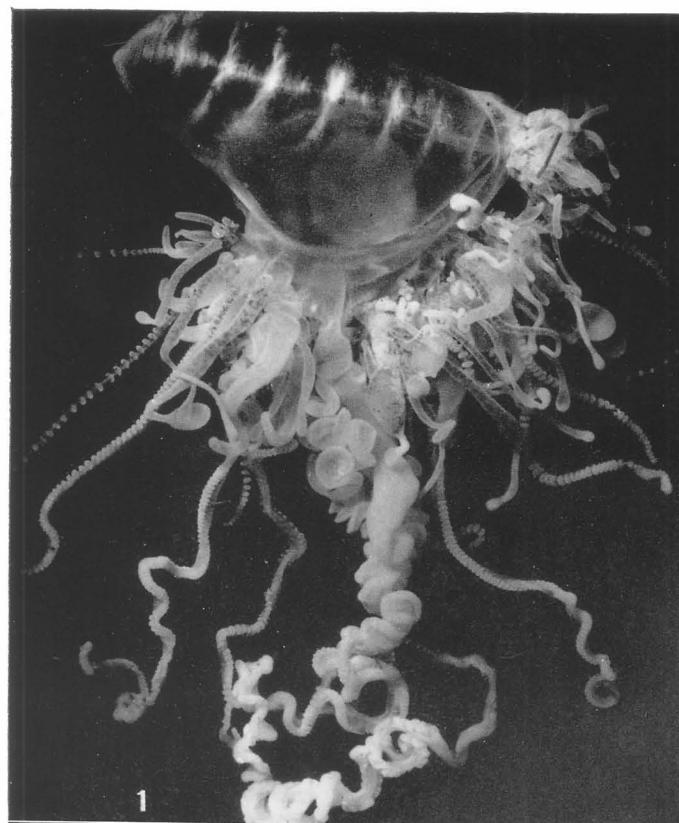


PLATE IX

Fig. 1. A medium sized, right-handed, living specimen in a tank at
Miami Marine Laboratory. By courtesy of Dr Charles E. Lane.

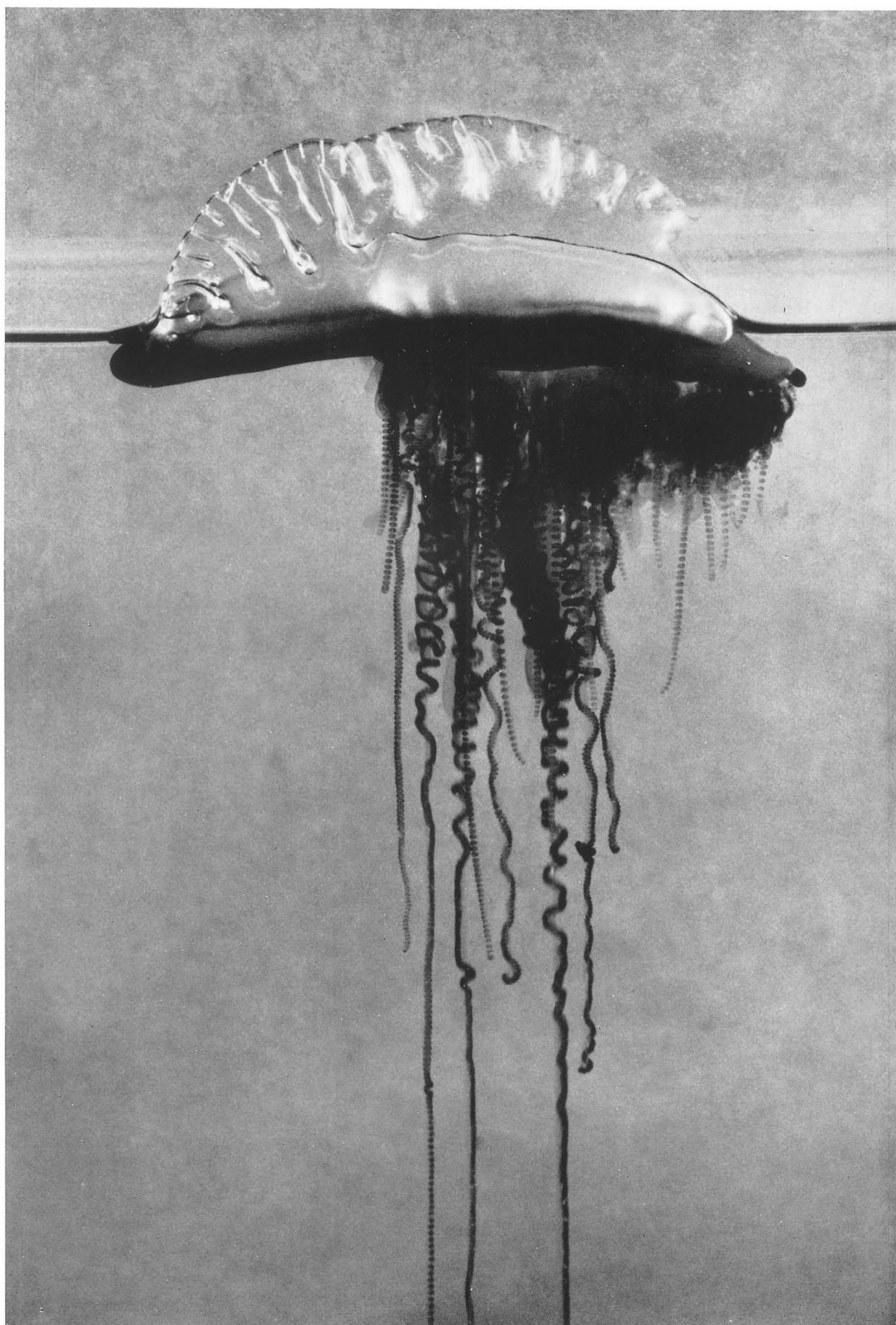


PLATE X

Figs. 1-6. Living *Physalia* rolling in a laboratory tank at Arrecife.

Figs. 2, 3 and 5 show phases of the righting motion. The aboral end is raised as in figs. 2 and 3, and after twisting movements falls over as in figs. 4 and 6. The gas-gland can be seen in figs. 1 and 3.

Fig. 7. Air-sac of *Physalia* dissected out and fixed in a state of artificial compression (tied off near pore) to show partially inflated dorsal processes, and the disk-shaped gas-gland. $\times 1.25$.

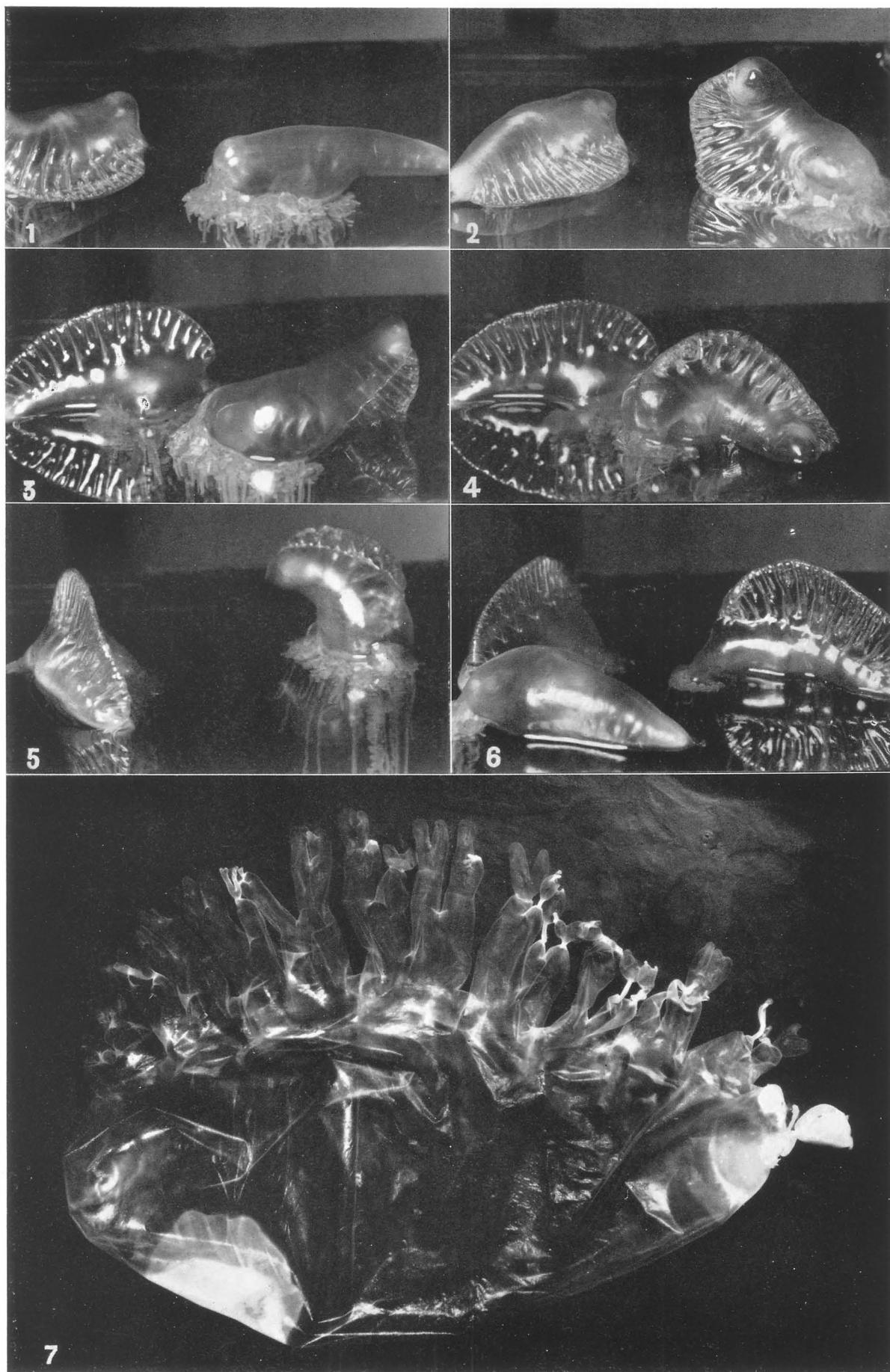


PLATE XI

Figs. 1-3. Oral end of a young left-handed *Physalia* from Arrecife, float-length 16 mm., to show terminal position of the protozooid, the incomplete septum across its base and the larval tentacle.

Fig. 1 view from leeward side, fig. 2 from below, fig. 3 from windward side. The largest polyps will become the gastrozoooids of the first groups of the five oral cormidia.

Fig. 4. A right-handed specimen from Arrecife, Lanzarote, no. 24, float-length 10.5 cm., gas-gland 2.3×1.9 cm. Oral zone of the ventral tract seen from the windward (upper) side. Tentacles and gastrozoooids as well as palpons are present. The figure shows the protozooid (bottom left), six cormidia and the basal internode (a black gap at top centre). $\times 1.8$.

Fig. 5. Ventral tract of the same specimen seen from the windward side. Cormidia I-VI of the main zone (on right) separated by the basal internode from five cormidia of the oral zone (on left). The protozooid is at the top, left. $\times 0.8$.

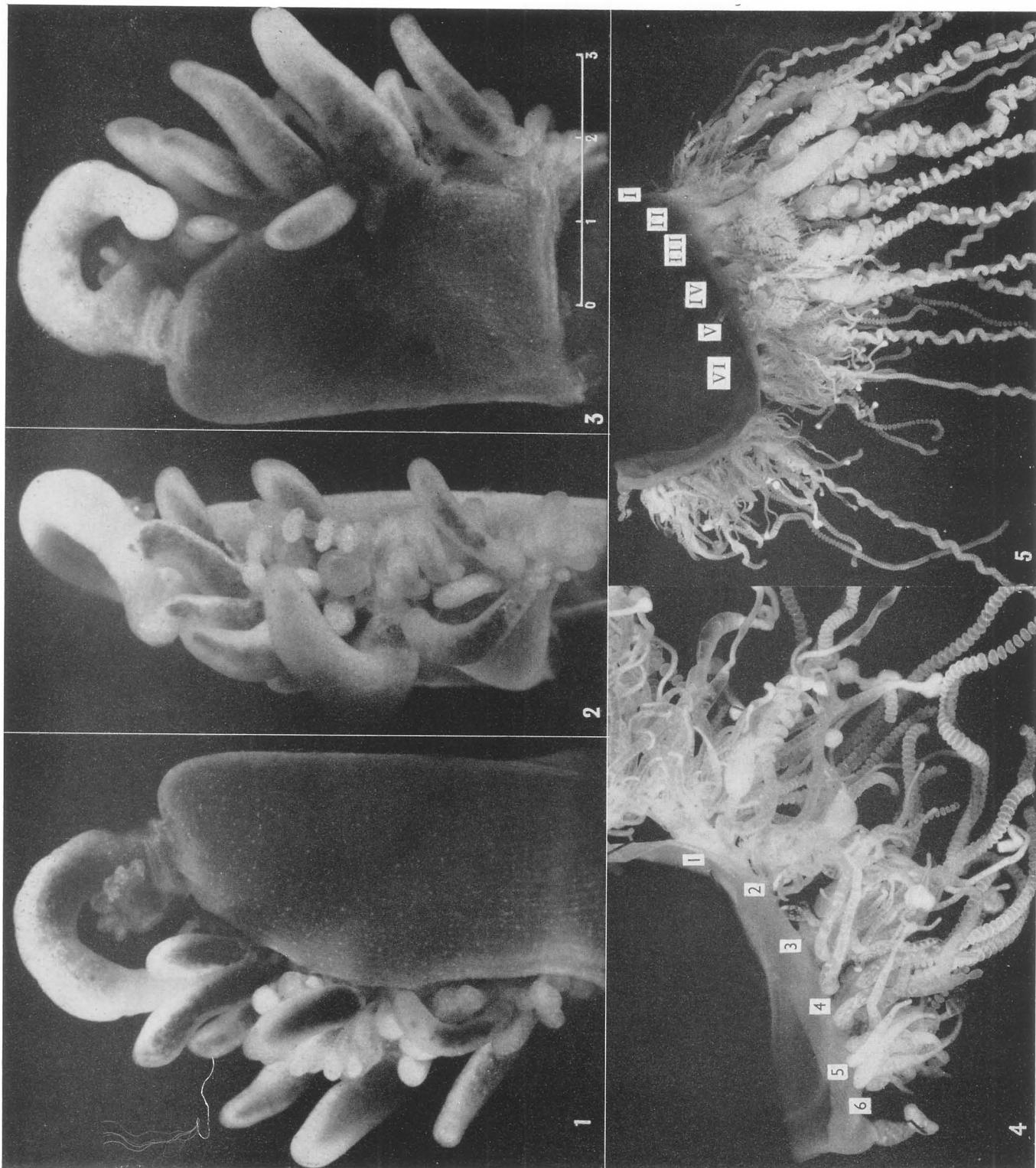


PLATE XII

Figs. 1-3. A left-handed specimen from Lanzarote, no. 3, float-length 9 cm., gas-gland diameter 2·3 cm. Cormidia IV, III, and II seen from the aboral end to show similarity of pattern of all cormidia, and acceleration of growth in those at the aboral end. Terminal lateral groups at top right, lee-branches on left and aboral branch in centre. $\times 1\cdot3$.

Fig. 4. The same specimen as in figs 1-3. Cormidium IV seen from the oral end to show the characteristic gastrozooid and gonophore of group 1 (black background). $\times 2\cdot2$.

Fig. 5. The same specimen as in figs. 1-3. Cormidium II seen from the aboral end to show lee-branches (top left), terminal lateral groups (top right), aboral branch (centre, black background) and gonodendron of group 1 (main). $\times 2\cdot6$.

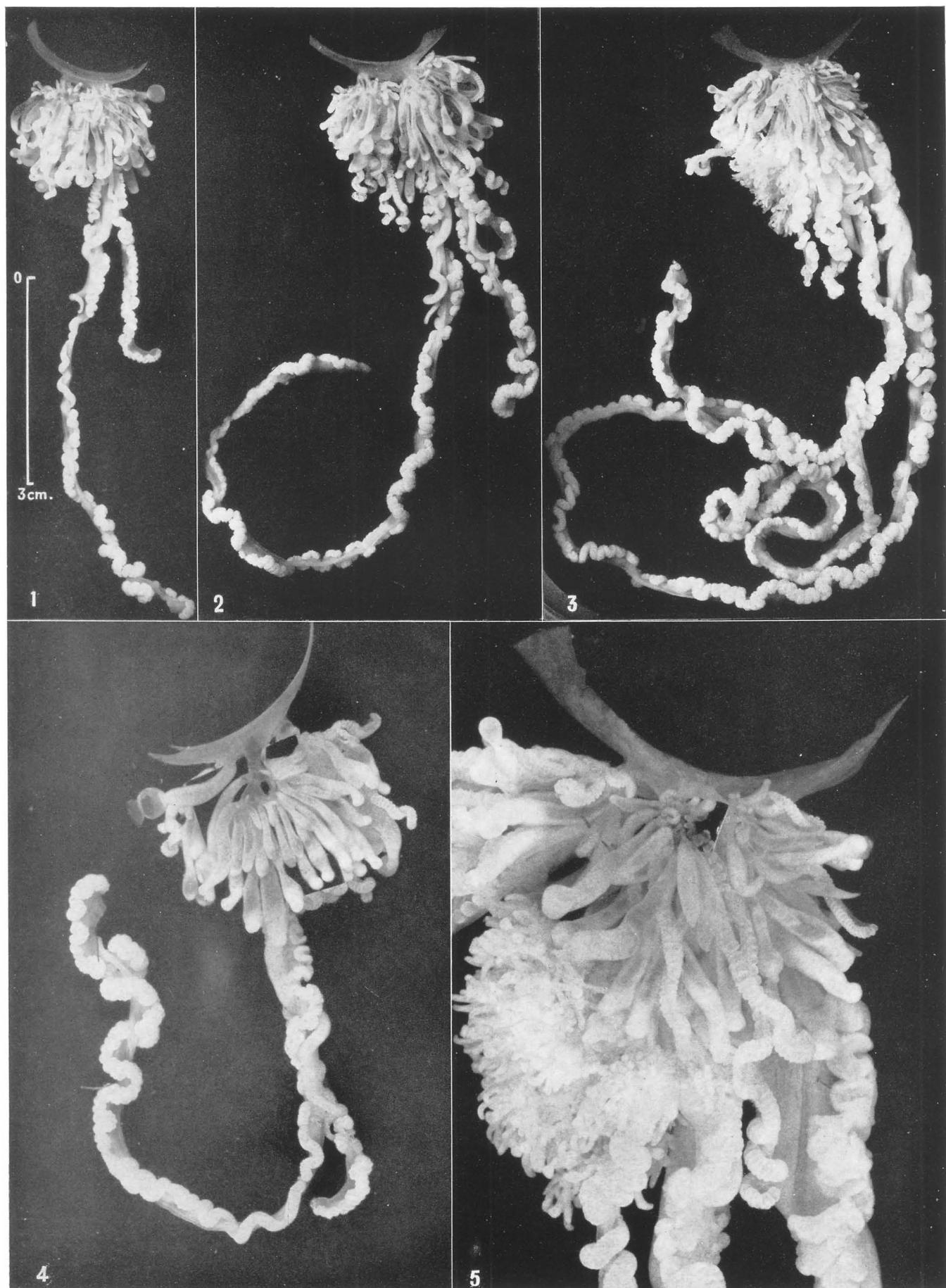


PLATE XIII

- Fig. 1. A left-handed specimen from Lanzarote, no. 25. Ventral tract seen from inside the float (above), oral end to the right after injection of black gelatine into cormidia (except I). $\times 1\cdot3$.
- Fig. 2. A young left-handed specimen from Lanzarote, no. Juv. B, float-length 8 cm., seen from above or windward side. The distinctness of the groups of cormidium I can be seen at the aboral end (left). The largest ampulla is that of group 2 of cormidium II. Parts of cormidium I and II are obscured by the black background inserted under the groups of cormidium I. The other side is shown in fig. 4. $\times 2$.
- Fig. 3. The same specimen. Cormidium II from the windward side. At top left (aboral end) appears the precocious gastrozooid of group 1, and below its point of attachment is the slender peduncle of its gonodendron. Its (main) tentacle and ampulla lie to the right. $\times 5\cdot7$.
- Fig. 4. The same specimen. Cormidium I seen from below or the leeward side. The other side is shown in fig. 2. The tentacle of group 1 is on the left. $\times 5$.
- Fig. 5. The same specimen. Cormidia III, IV, V and VI. Main tentacle of II on the left. Note the four prominent gastrozooids of the first groups (which do not bear tentacles) that grow directly from the bladder-wall, and are some of the earliest buds to appear. The large horizontal gastrozooid is part of group 1 of cormidium III. The vertical two gastrozooids at a lower level are parts of groups 1 of cormidia IV and V. The horizontal gastrozooid at a higher level (right) is part of group 1 of cormidium VI. $\times 5\cdot7$.
- Fig. 6. The same specimen. Cormidium III seen from the windward side (oral end to the right). Gastrozooid and gonodendron of group 1 on the right. Terminal lateral groups on the left. This stage of development is rather later than that shown in the figures of specimen K.2. $\times 5\cdot7$.

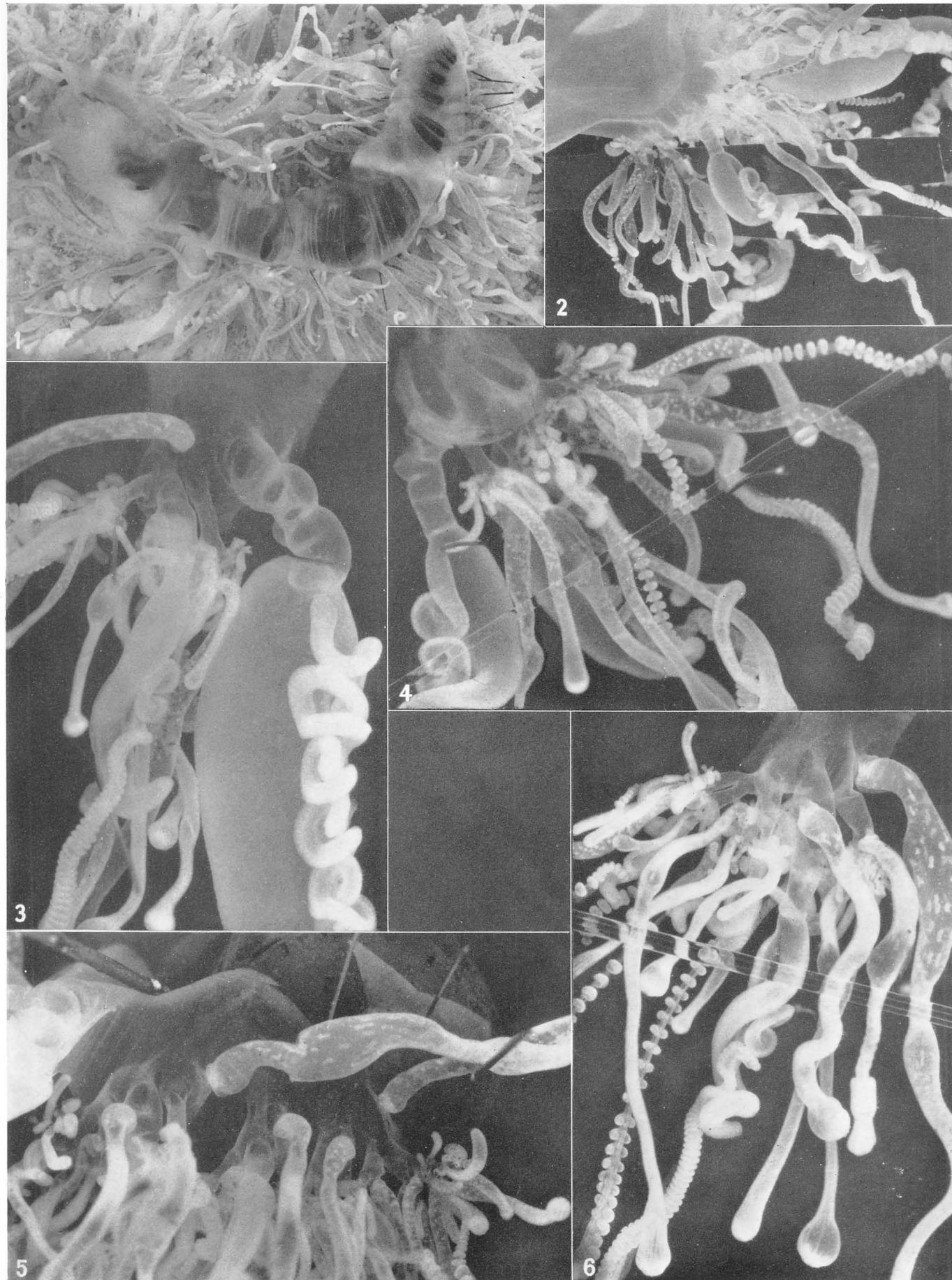


PLATE XIV

Fig. 1. Cormidium IV of a young left-handed specimen from Lanzarote, no. Juv. 11, to show stages in the growth of the tripartite groups. Group 1 (bottom) has a gastrozooid and gonodendron, but no tentacle. Group 2 (right and centre) is tripartite, but the gastrozooid has been lost. Group 3 (top, left and right) is tripartite. Group 4 (left and across to top right) is tripartite. $\times 8$. For drawing of a comparable cormidium of the oral zone see Text-fig. 15.

Fig. 2. Part of cormidium I of specimen no. 5 from Lanzarote to show an early growth stage of a tripartite group (black background below) gastrozooid, tentacle and ampulla, and gonodendron. $\times 6.5$.

Fig. 3. A young left-handed specimen from Lanzarote, no. Juv. 12 (cf. Pl. VIII, fig. 1), float-length 2.9 cm., gas-gland diameter 7 mm., seen from the upper or windward side to show eight individual groups of cormidium I, on the left; main tentacle (cormidium II) on the right, with lateral groups on its left; tentacle (ampulla) and gastrozooid of groups 1 of cormidium I (gonodendron underneath) in centre; tentacle (gonodendron lying over it, gastrozooid missing) of group 2 of cormidium I; groups 4-8 of cormidium I at top left. There are no nematocyst heads yet developed on the tentacles of groups 5-8 (see Pl. XV, fig. 5 for more mature state of the projection carrying the terminal laterals of cormidium I). $\times 5.5$.

Fig. 4. A right-handed specimen from Lanzarote, no. 5, float-length 11.5 cm. Cormidium I viewed from windward and slightly above to show: main series of groups (eleven), oldest on the left, youngest curling back almost to meet it; lee-branches at top left and right; aboral branch just under a horizontal tentacle of lee-branch at right indicated by a white pointer; scar of gastrozooid of main group at right base of its peduncle; gonodendron of main tentacle to left of its peduncle. Tentacles of groups 6, 7, 8, and 9 lie on the top of those of 2 and 3. $\times 2.3$.



PLATE XV

Fig. 1. A young left-handed specimen from Lanzarote, no. Juv. 12, float-length 2·9 cm., gas-gland diameter 7 mm., seen from leeward (under) side to show early growth stages of lee-branches (on black background) at base of cormidium III (five groups to the left, two to the right). All three parts of a young group can be seen in the left-hand branch (oral end) of group 1 at base of cormidium III (on right-hand black background), tentacle, gastrozoooid and gonodendron (reading from right to left). $\times 4$.

Fig. 2. Specimen Juv. B. Cormidia V and VI before separation (oral end to the right) seen from to windward. Cormidium VI is seen partly from the aboral end. The figure shows the conspicuous, precocious gastrozoooid of group 1 of V and of VI (right), and the peculiar gonodendron; the lateral groups of VI (bottom centre); on the left, the gastrozoooid and gonodendron of group 1 of VI (above), and lateral groups (below). $\times 5\cdot3$.

Fig. 3. A left-handed specimen from Lanzarote, no. 25. Cormidium III seen from above (inside float) to show lee-branches (top right). The main series of lateral groups is at the bottom, group 1 to the right. $\times 1\cdot6$.

Fig. 4. A left-handed specimen from Lanzarote, no. 2, float-length 10 cm., Cormidium I to show individual groups (sixteen). The gastrozoooid is on the aboral side of each group; the gonodendron is hidden underneath (except that of group 2). The bases of the peduncles were cut in dissection. $\times 1\cdot5$.

Fig. 5. A right-handed specimen, B.M. Register no. 26.3.6.1, float-length 18·5 cm., taken by R.R.S. 'Discovery' on 21 October, 1925, in $27^{\circ} 15' N.$, $15^{\circ} 32' W.$ Cormidium I viewed from aboro-windward side to show the projection formed by the younger lateral groups of I (to which all these tentacles belong). For an earlier stage of development of this area, see Pl. XIV, fig. 3. $\times 1\cdot4$.

Fig. 6. A left-handed specimen from Lanzarote, no. 16, float-length 12 cm. Cormidium I to show curled-up terminal, lateral groups, fourteen in number. $\times 5$.



PLATE XVI

Fig. 1. Cormidium II of a left-handed specimen from Lanzarote, no. 2, float-length 10 cm., seen from the oral end, an oro-lateral view, showing: basal lee-branches *B*, *C* and *D* of Text-fig. 17 at top right after removal of lee-branch *A* (see Pl. XVII, fig. 1). $\times 1.1.$

Fig. 2. Same specimen, cormidium II, aboro-lateral view. The aboral branch is turned up (top right) and its pedicel lies next to the V-shaped cut. Also shown are the large tentacles of groups 1-4 (bottom right to centre left); lee-branches top left; terminal lateral groups curling round again to the right to lie under the aboral branch as viewed. Natural size.

Fig. 3. Same specimen, cormidium II, from the windward side and a little aborally. Groups 5-12 have been cut off (see bristle). Shown are: groups 1-4 and aboral branch (to left of bristle); gastrozoooid of group 1 lying on top of the ampulla of the main tentacle; the gonodendron is represented by a scar found to the left of the stalk of the tentacle, but not visible in the photograph; group 4 (lower on black background) with stout peduncle; aboral branch (black background) above group 4. $\times 1.3.$

Fig. 4. Same specimen, aboro-lateral view. The first seven groups are numbered 1-7. *Br* = aboral branch. $\times 2.2.$

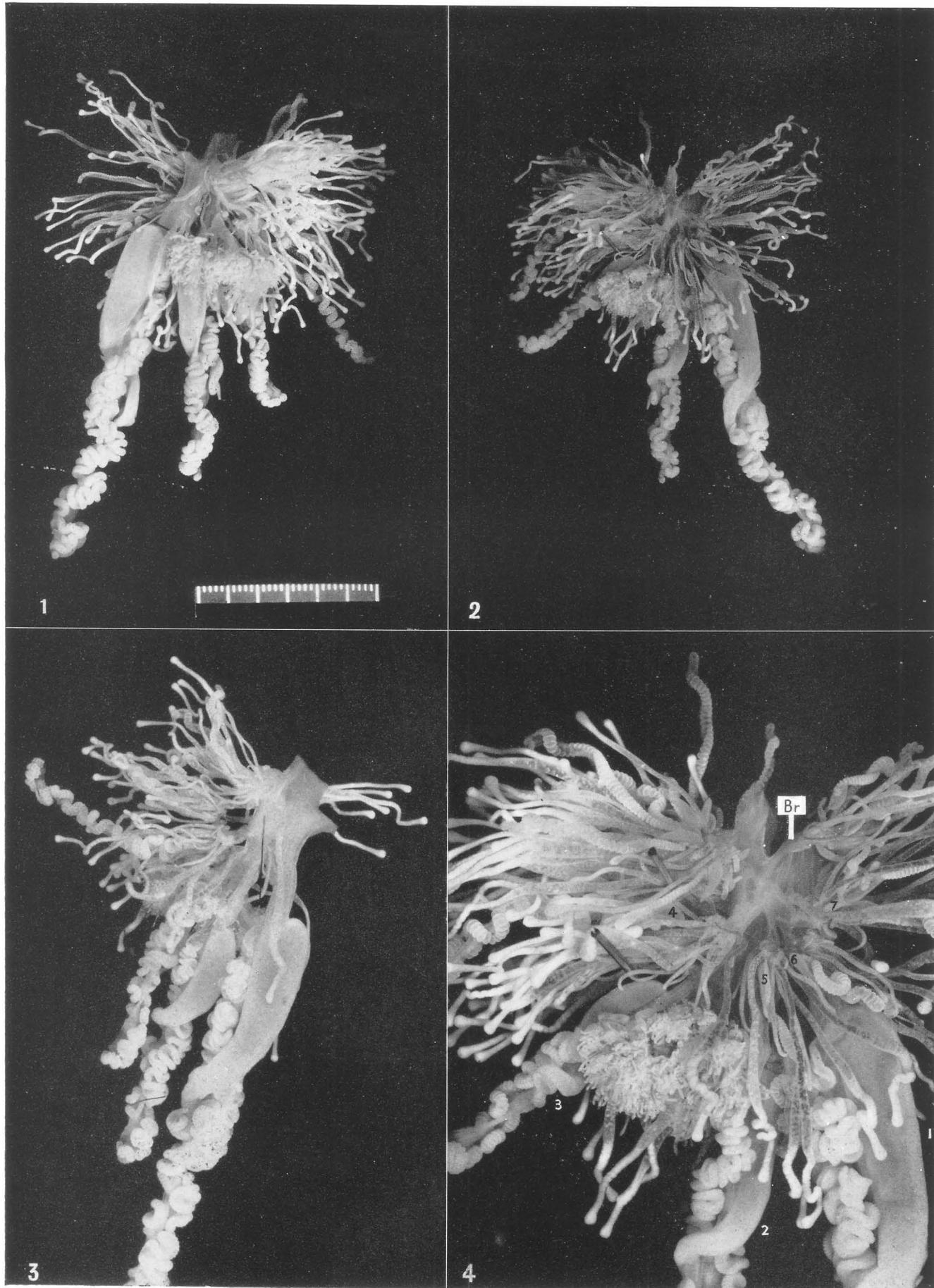


PLATE XVII

- Fig. 1. Part of cormidium II of specimen Lanzarote no. 2. Separated branchlet 6 of the lee-branch figured in fig. 2. $\times 2\cdot6$.
- Fig. 2. One of the basal lee-branches (see Text-fig. 17A) cut from cormidium II, consisting of six branchlets representing the remains of tripartite groups 1-5, or subsidiary basal branches, 5a and 6. Branchlet 1 has lost its gastrozoid; branchlets 2-5 are gonodendra only; 5a and 6 consist of five and six groups respectively (for branchlet 6, see fig. 1). $\times 1\cdot3$
- Fig. 3. Cormidium III of specimen, Lanzarote, no. 2, seen from the aboral end after cutting off the terminal lateral groups 5-11 which are pinned out to the right (top). Shown are: lee-branches, top left; tentacle and gonodendron of group 1 (largest); tentacle and gonodendron of group 2, between T_1 and GON_1 ; gastrozoid₄, tentacle₄ and gonodendron₄ between T_1 and several laterals; T_3 and GON_3 between lee-branch and GON_1 ; bristle marks the spot from which lateral groups were cut. $\times 1\cdot8$.
- Fig. 4. The same cormidium showing terminal laterals 5-11, group 5 on the left (group 11 is very small) and a subsidiary basal branch of two groups from the base of group 6 at the top. The divisions between the groups, except 9 and 10, are marked. $\times 5\cdot4$.

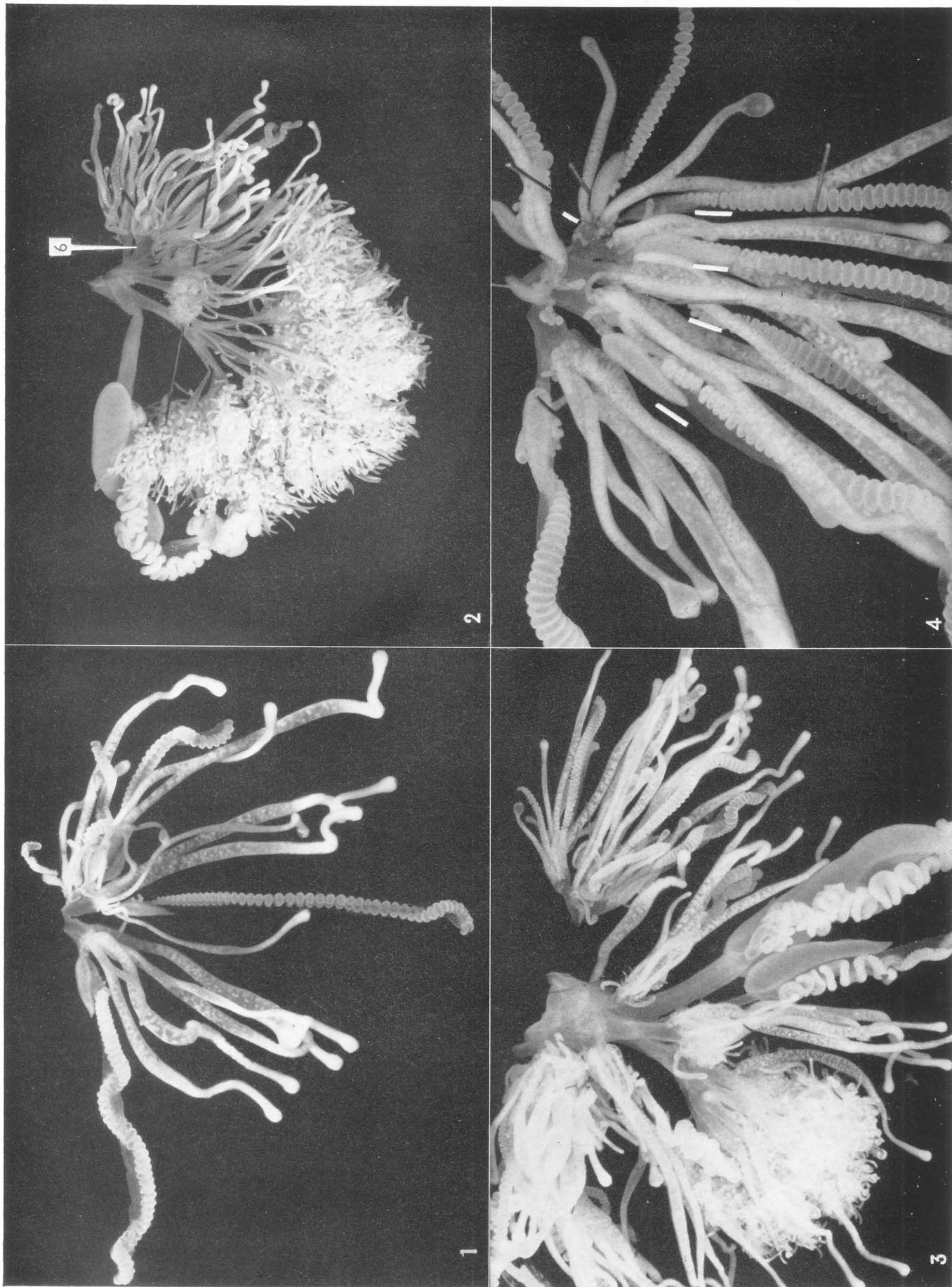


PLATE XVIII

Fig. 1. Lanzarote specimen, no. 2. Cormidium III (less group 1) seen from the oral end to show: *GZ*, *T* (main tentacle) and ampulla, and *GON* of group 2; lee-branch, top right; and the series of lateral groups, bottom left. $\times 1.8$.

Fig. 2. The same cormidium seen from the aboral end to show: lee-branches top left; terminal lateral groups right; middle lateral groups centre; aboral branch severed, on black background, after lowering from base of laterals. $\times 3$.

Fig. 3. The same before cutting off branches. Lee-branches are shown at top left. $\times 1.8$.

Fig. 4. The aboral branch from the base of group 5 of cormidium III of the same specimen to show: three groups, the largest, no. 1, on the right, smallest at top left; subsidiary basal branchlet of two groups from base of 1/2. The first has a light ampulla, the second is small (top right). $\times 3$.

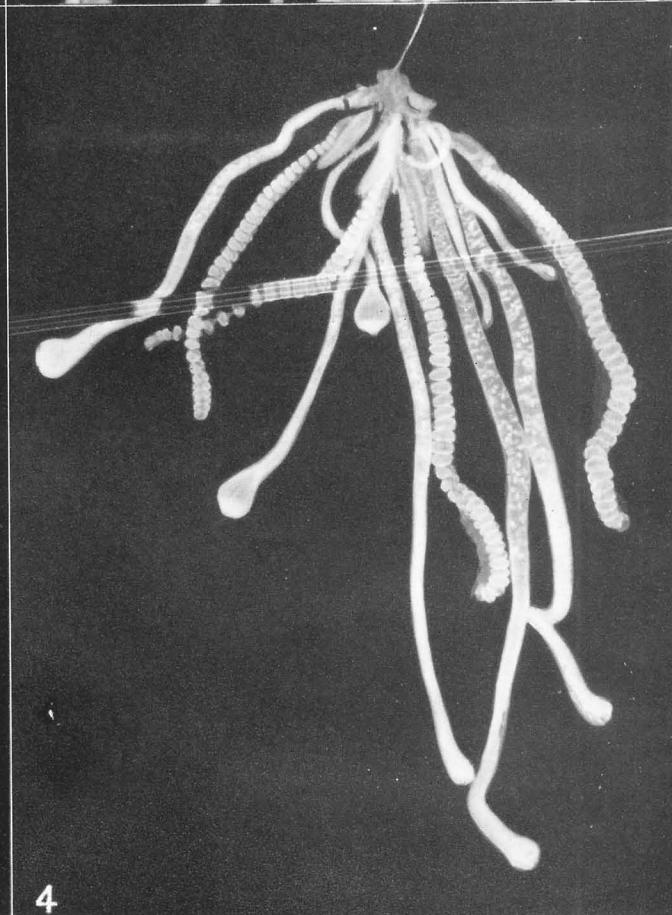
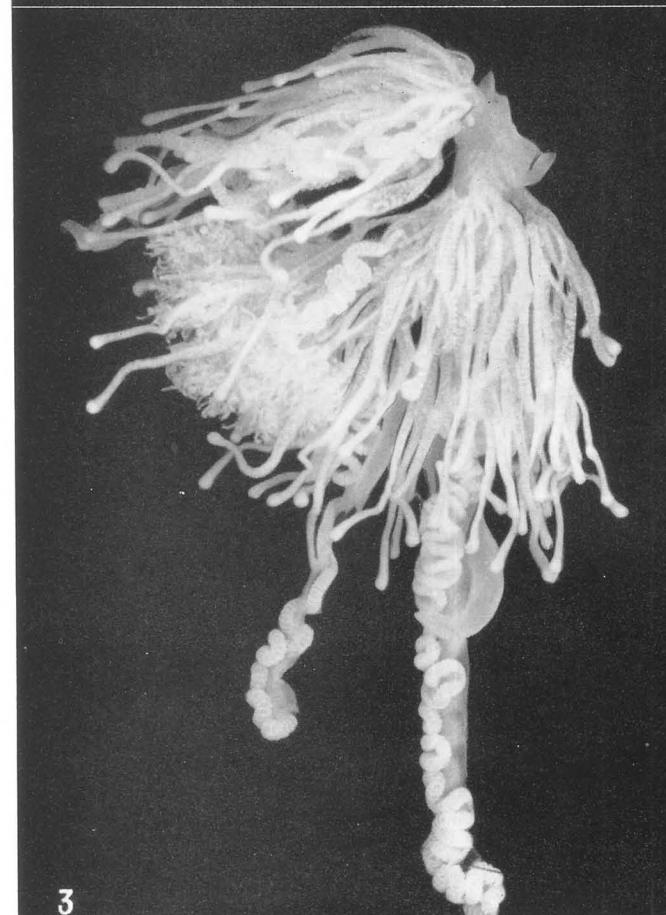
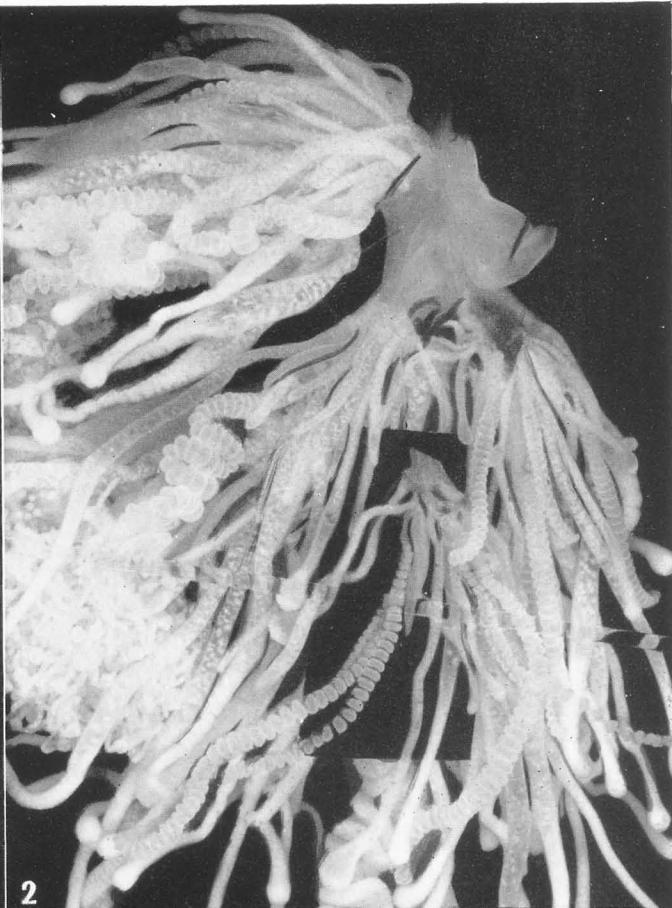
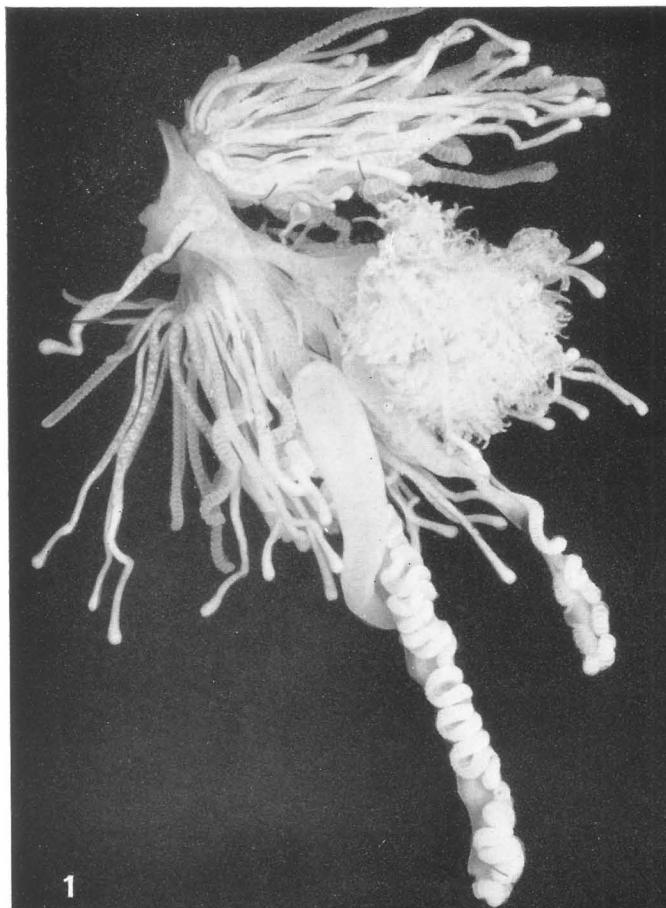


PLATE XIX

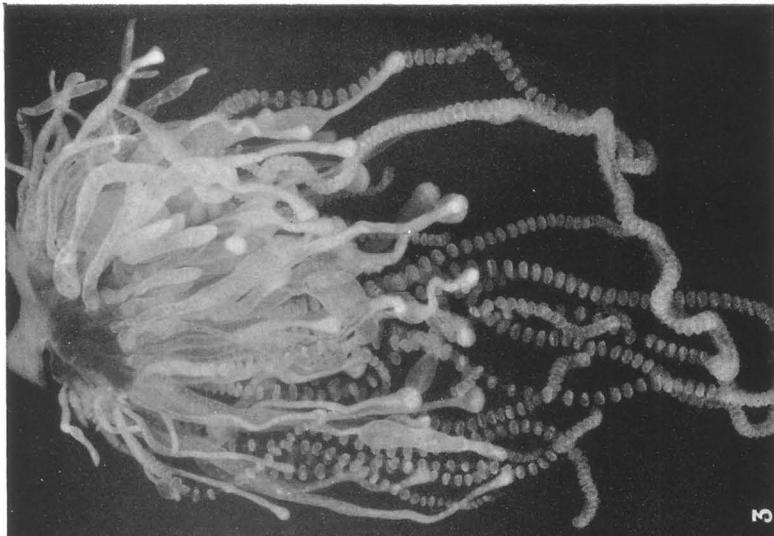
Fig. 1. A young right-handed specimen from Arrecife, no. Juv. 8, float-length 30 mm., gas-gland diameter 5 mm., to show: oral zone with five cormidia; the basal internode between the oral and main zones; the large gastrozooid of group 1 of cormidium VII; and the protozooid and larval tentacle. $\times 3\cdot8$.

Fig. 2. Part of the oral zone of a left-handed specimen, Lanzarote, no. 25. Cormidia 1 and 2 seen from above. The finger-shaped projection (left centre) is the main series of lateral groups (axis filled with black gelatine). See schematic drawing, Text-fig. 12C, D. $\times 1\cdot8$.

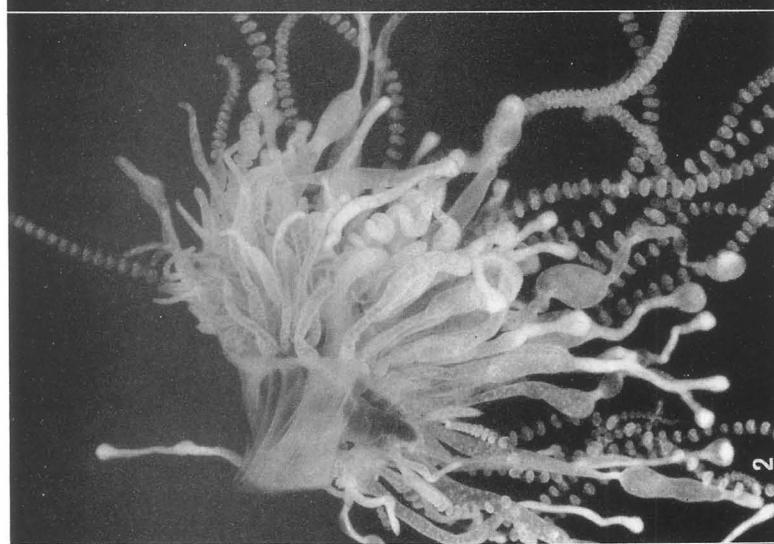
Fig. 3. The same specimen seen, tilted back, from the aboral end and windward side to show: main series of lateral groups of cormidium 1, filled with black gelatine; lee-branch of cormidium 1 top left; aboral branch of cormidium 1; the peculiar gonodendron of group 1 of cormidium 1 top right; gastrozooid of group 2 of cormidium 1 overlying large ampulla of tentacle 2; gastrozooids of groups 3–6 of cormidium 1, bases filled with black gelatine; tentacle₈ of cormidium 1, just left of GZ₆; ampulla of tentacle₇, just to left of T₈. $\times 1\cdot8$. See schematic drawing, Text-fig. 12C.

Fig. 4. Specimen Lanzarote, no. 25. Oral zone of cormidium 1 seen from the aboral end, showing: GZ₁ top right; series of lateral groups, right top centre to left centre foreground; lee-branch top left; aboral branch left centre. $\times 5\cdot4$. See schematic drawing, Text-fig. 12C.

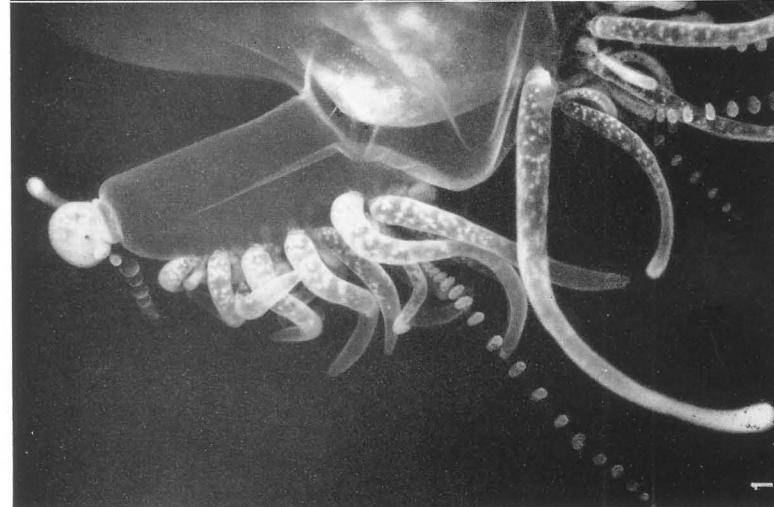
Fig. 5. The same cormidium seen from the oral end to show: GZ₁ top left; GON₁ left; lee-side of lateral groups centre; lee-branch right. $\times 5\cdot4$.



3



2



1



5



4

PLATE XX

Fig. 1. A large, preserved right-handed *Physalia*, float-length 20 cm., from Villefranche, Mediterranean, by permission of Dr G. Tregouboff, Museum, Station Zoologique, to show gonodendra of a mature specimen. Cormidium I on the right. $\times 0.6$.

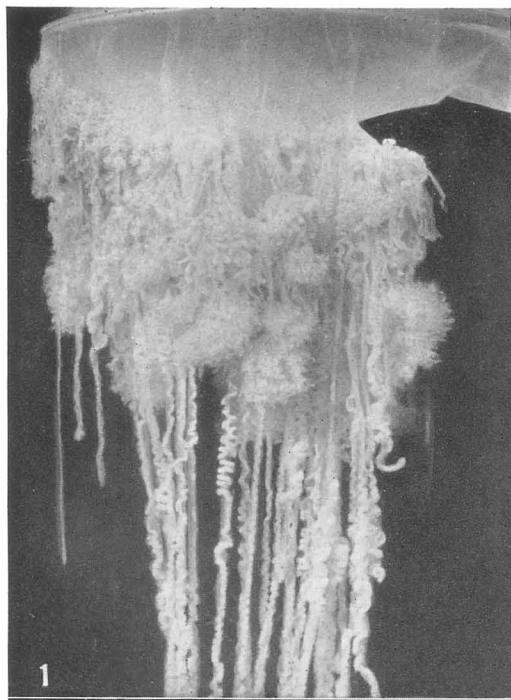
Fig. 2. A mature gonodendron dropped by a living specimen in a laboratory tank at Arrecife. Photographed (as in life) after anaesthetization in $MgCl_2$ and fixation in formalin, and seen from above. $\times 1.3$.

Fig. 3. One tripartite group of a cormidium of specimen Lanzarote, no. 2. Of the eight gastrozooids, number 3 with a prominent kink is probably the original one of the whole group, associated with the tentacle; numbers 2, 5, 7 and 8, which are gonozooids without tentacles, were budded from its base. The genital tufts (palpons, nectophores, gonophores and jelly-polyps) are budded from the bases of the gonozooids. For details, after removal of three branches, see Text-fig. 25. $\times 1.1$.

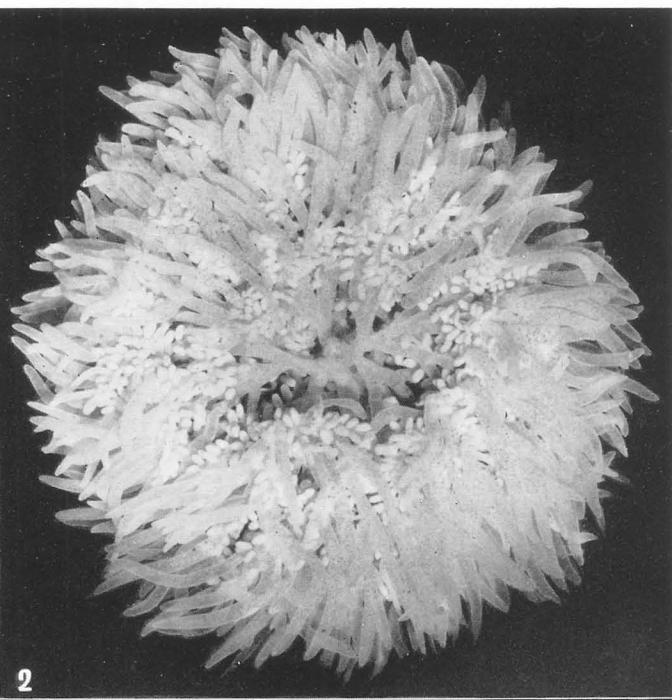
Fig. 4. A young gonodendron from specimen Lanzarote, no. 2 from basal branch A (branchlet 3) of cormidium II. The polyps whose tips can be clearly seen are palpons; the long polyps are gonozooids (with no tentacles). $\times 4$.

Fig. 5. A gonodendron not fully developed. $\times 8$.

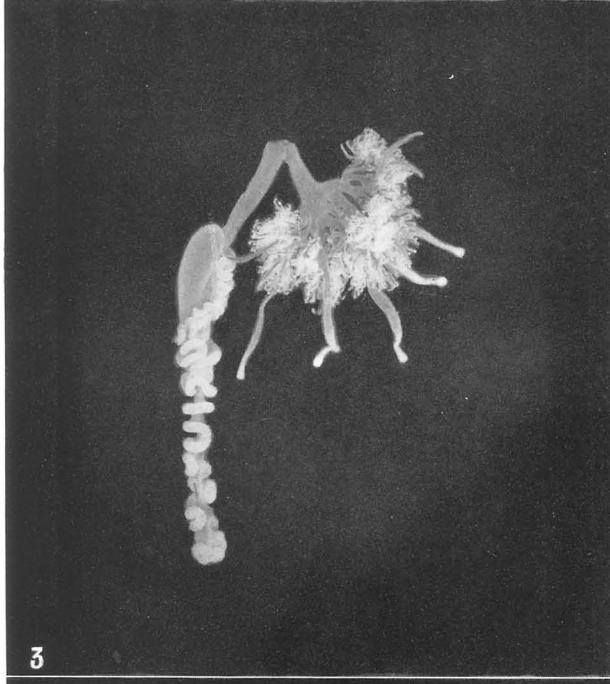
Fig. 6. A mature gonodendron dropped by the same living specimen shown in fig. 2, seen from the side. $\times 1.5$.



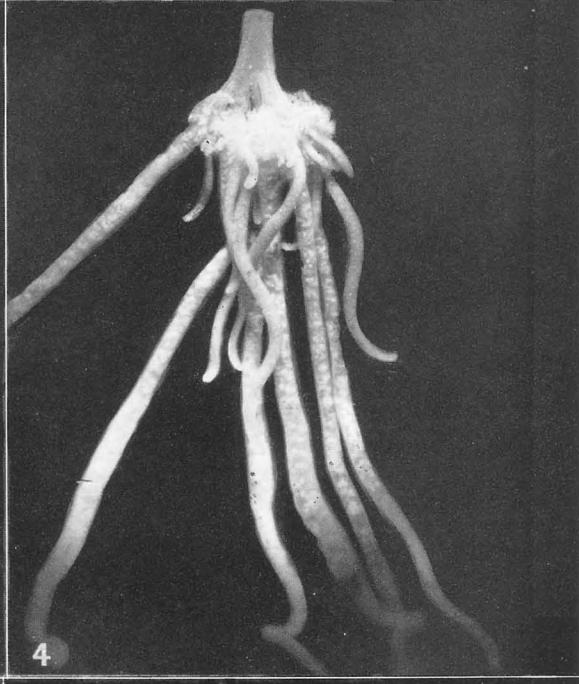
1



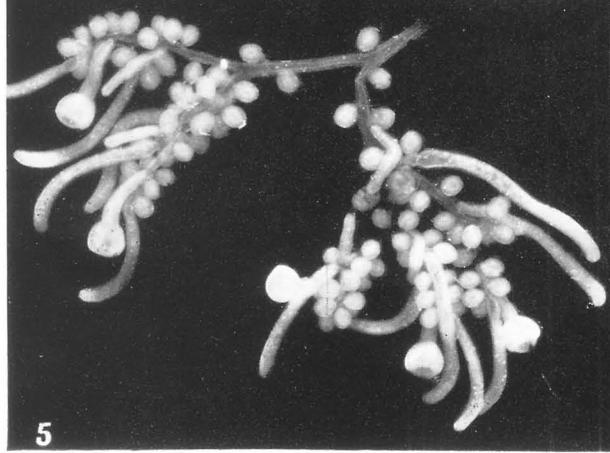
2



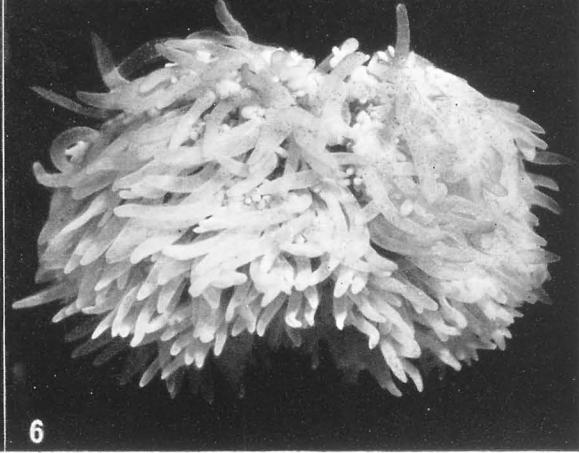
3



4



5



6

PLATE XXI

- Fig. 1. End branchlets of an immature gonodendron to show the pattern of arrangement and the open endodermal canals in the stalks of the nectophores. $\times 5$.
- Fig. 2. One end-branchlet of an immature gonodendron, enlarged. $\times 8\cdot7$.
- Fig. 3. Part of a gonodendron to show a fully developed end-branchlet consisting of a terminal section (jelly-polyp and terminal palpon) and a sub-terminal section (nectophore and palpon). Several female gonophores are visible. The endodermal canal of the nectophore is now occluded and the mesogloea hypertrophied both in the nectophore and jelly-polyp. $p.st$ = sub-terminal palpon, n = nectophore, $p.t$ = terminal palpon, jp = jelly-polyp. $\times 7$.
- Fig. 4. Part of an immature gonodendron of a female specimen from the Scilly Isles, kept for a time in a tank in the Laboratory, Plymouth, in November 1954. There are two end-branchlets lying partly on top of each other, so that the jelly-polyp of the right-hand branchlet is almost hidden by the shorter, central palpon. The proximal gonophores are more fully developed than the distal ones. The lumen of the endodermal canal of the stalk of the nectophore is still open. $\times 16$.
- Fig. 5. An end-branchlet of a gonodendron in a middle stage of development. The jelly-polyp is seen as a hollow, finger-shaped process next to the palpon of the terminal section. At this stage of development the endodermal canal of the stalk of the nectophore is wide open. $\times 31$.
- Fig. 6. Part of a branchlet of an immature gonodendron which has lost the sub-terminal palpon and most of the gonophores. Jelly-polyp on the left, terminal palpon at the bottom, nectophore and gonophore. The radial and circular canals of the nectophore can be seen in optical section, and also the muscular lamella on the stalk of the nectophore. $\times 25$.
- Fig. 7. The Plymouth specimen (see fig. 4), showing a pair of end-branchlets of a maturing gonodendron. That on the right differs from the usual type (on the left) in having two terminal sections instead of one terminal and a sub-terminal section, and so in being without a nectophore. Each section on the right has a jelly-polyp, terminal palpon and gonophores. $\times 10\cdot3$.

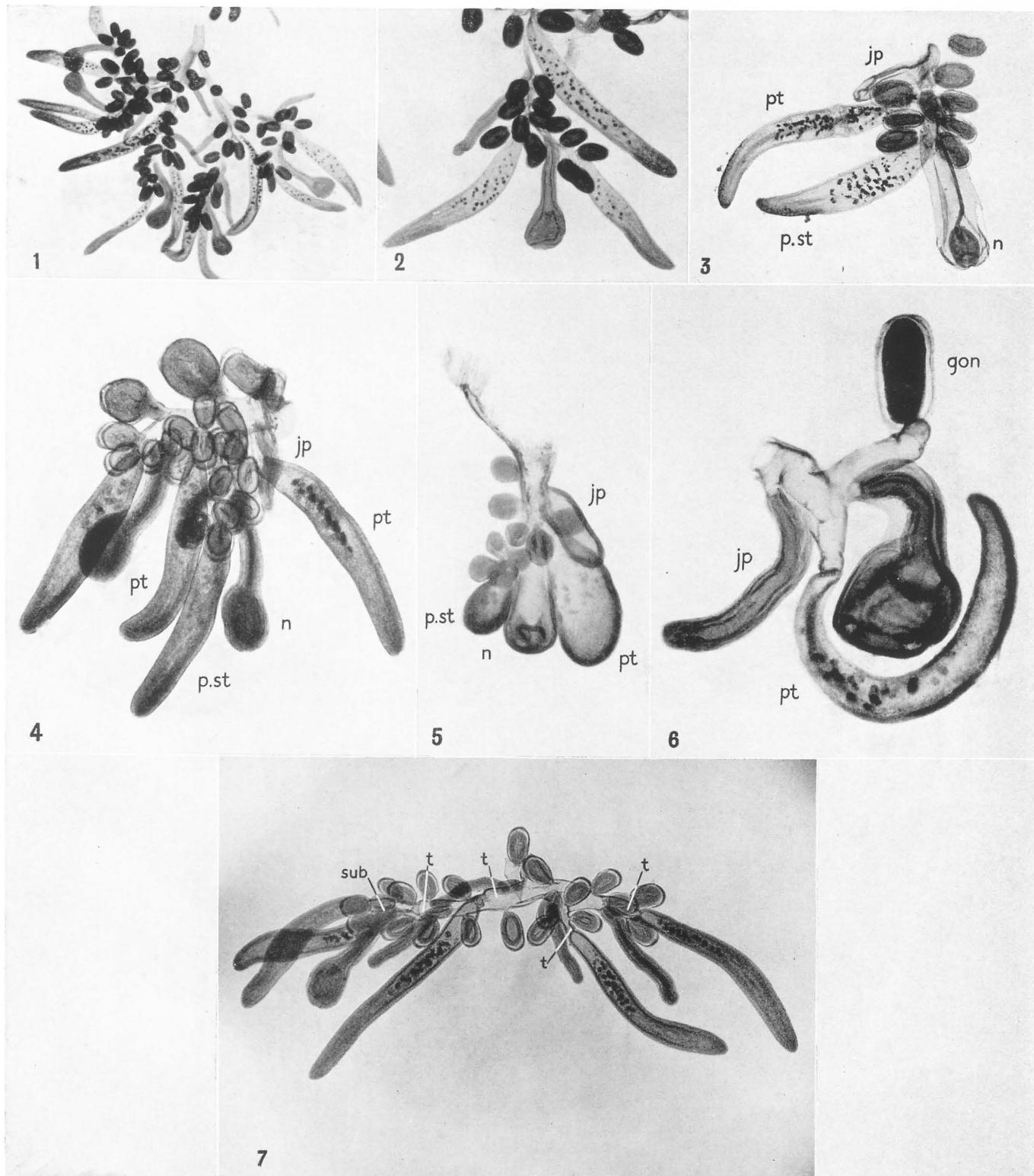


PLATE XXII

Genital tufts of gonodendra

- Figs. 1, 2, 3 and 7. Early growth stages (cf. fig. 2 with Text-fig. 27G).
Fig. 1 \times 36, fig. 2 \times 70, fig. 3 \times 76, fig. 7 \times 65.
- Fig. 4. Terminal and sub-terminal sections of end-branchlets. \times 60.
- Fig. 5. Middle stage of development of an end-branchlet (cf. Text-fig. 27G for an earlier stage of the same). \times 55.
- Fig. 6. (In the 'key' stage of development) showing two branchlets growing out sub-terminally from the large palpon. The smaller one consists of only the usual two end sections, terminal and sub-terminal; the second itself bears a similar branchlet growing out sub-terminally opposite its larger terminal palpon. The left-hand part of this specimen was removed for the sake of clarity. \times 40.
- Fig. 8. (Cf. with fig. 6) showing rapid growth of the terminal palpon, on the tip of which can be seen a heavy armature of nematocysts. Its jelly-polyp can be seen below the palpon. \times 30.
- Fig. 9. A 'key' stage showing how a sub-terminal section buds from a terminal one. \times 79.
- Fig. 10. Showing a branchlet 'dividing' three times; three end sections on the right, three on the left and numerous gonophores. The tips of the palpons are heavily armed with nematocysts. The right side is comparable with fig. 8. \times 36.
- Fig. 11. Showing how complicated the genital tufts look when lying side by side. Here two tufts, partially separated, have been flattened in one plane on a microscopical slide. \times 37.

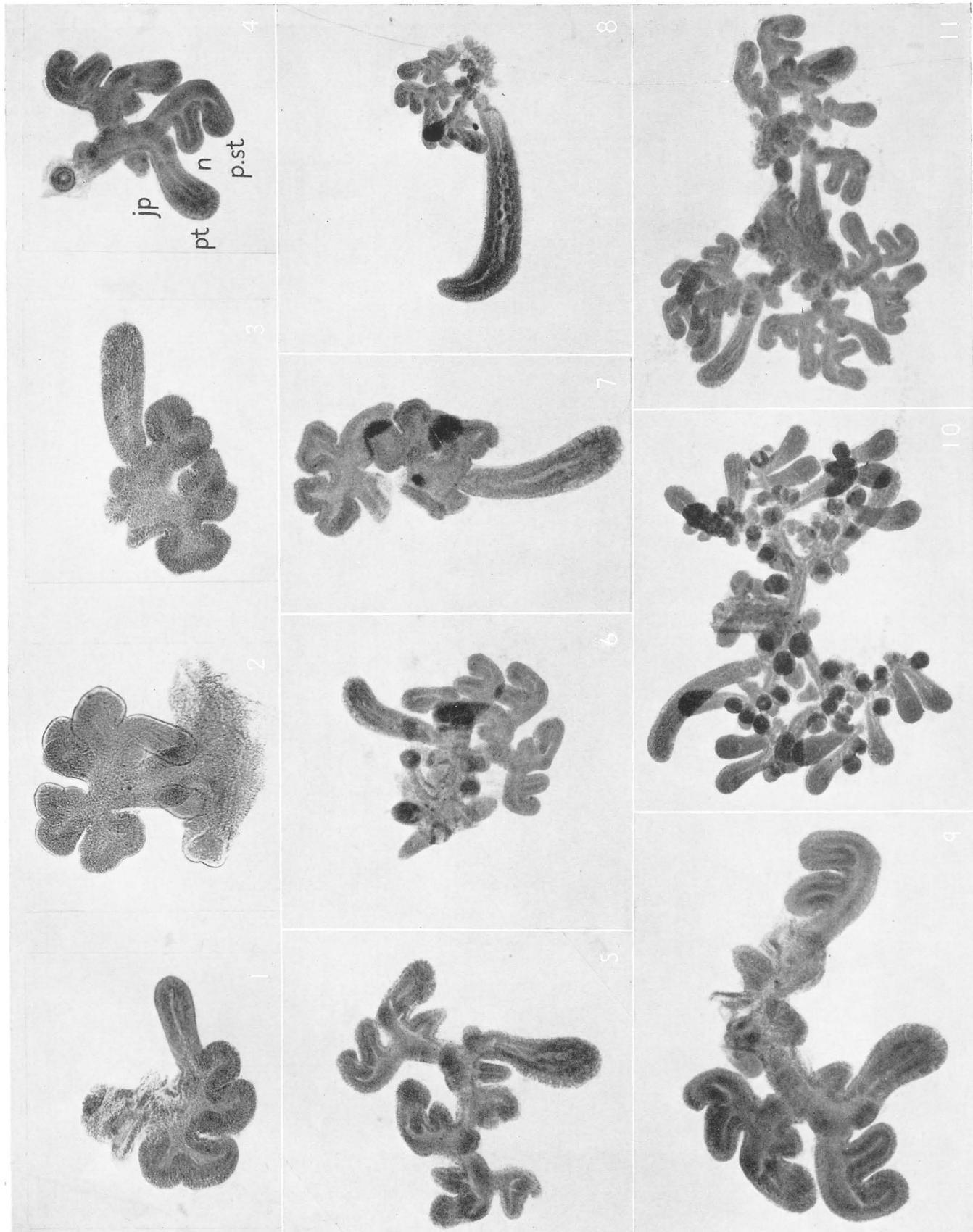


PLATE XXIII

- Fig. 1. Young stage of development of a genital tuft of a gonodendron of the Plymouth specimen. $\times 55$.
- Fig. 2. Part of an immature male gonodendron, middle stage of development of an end-branchlet, showing its origin as a sub-terminal bud growing out opposite a jelly-polyp of a terminal palpon. The terminal section on the left (jelly-polyp and palpon) has not developed a sub-terminal pro-bud, which might have given rise to a pair of similar end-branchlets. $\times 40$.
- Fig. 3. Part of an immature gonodendron of the Plymouth specimen. Passing from below round to the top right three typical end-branchlets at an early stage of development can be seen. Each consists of a terminal section (appearing to be basal and consisting of jelly-polyp and terminal palpon) and a sub-terminal section (top right) consisting of nectophore and sub-terminal palpon. Rudiments of gonophores are visible. One gonophore always appears at the base of the terminal palpon. $\times 55$.
- Fig. 4. Part of the ectoderm of a female gonophore freed from the endoderm and the covering exumbrella of the medusoid, to show the sinuous band of oogonia. $\times 15$, further magnified on the right.
- Fig. 5. Fully grown male gonophores. Inside the thin outer membranes can be seen the cap of spermatocytes, completely surrounding the spadix. $\times 17$.
- Fig. 6. Part of a female gonodendron from specimen Lanzarote, no. 25, dropped in the laboratory, to show the endoderm of the gonophores drawn inside out into the lumen of the branch of the gonodendron. $\times 15$.

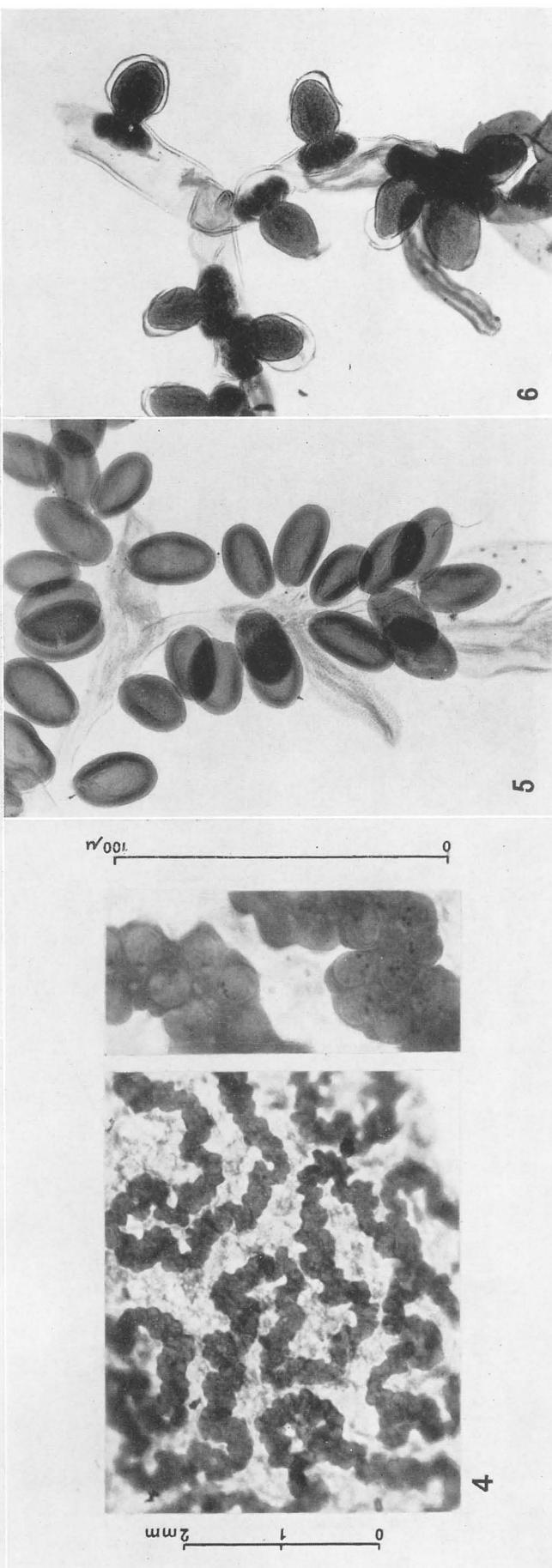


PLATE XXIV

Female gonophores

Figs. 1 and 2. Young growth stages in transverse section. The radial canals are visible in the endoderm of the outer wall and the oogonia in the ectoderm of the spadix. $\times 242$.

Fig. 3. Transverse and longitudinal sections in an end-branchlet of a gonodendron. The section passes through the bases of a nectophore and jelly-polyp (left and right centre), but below the bases of the two palpons of the terminal and sub-terminal sections of the branchlet. A terminal palpon is visible, bottom right. Similarity in structure is shown in the nectophore and jelly-polyp—type of ectoderm hypertrophied mesogloea, occlusion of canal and muscular lamella. $\times 38$. (See Text-fig. 29.)

Figs. 4–7. Growth of the nectophores (seen in optical section). In fig. 5 the perforation of the velum is visible; in fig. 6 the endodermal canal is occluded; in fig. 7 the gastrovascular space of the stalk is wide open, and the ectoderm can be seen cupped in the endoderm. Radial and circular canals are visible in optical section. Fig. 4 $\times 50$, fig. 5 $\times 55$, fig. 6 $\times 50$, fig. 7 $\times 219$.

Figs. 8–15. Young male gonophores (seen in optical section). Photomicrographs to show stages in the growth of the entocodon which gives rise to the cup-shaped mass of spermatocytes that later covers the spadix. The smaller gonophore (fig. 13) shows the earliest stage, comparable with the entocodon of the much larger nectophore that grew alongside it (fig. 7) and measures 0·1 mm. in diameter. In the larger gonophore (fig. 13) the base of the entocodon has started to grow over the spadix, and the primary endoderm has become reduced in thickness though it contains vestiges of two or three radial canals. $\times 270$.

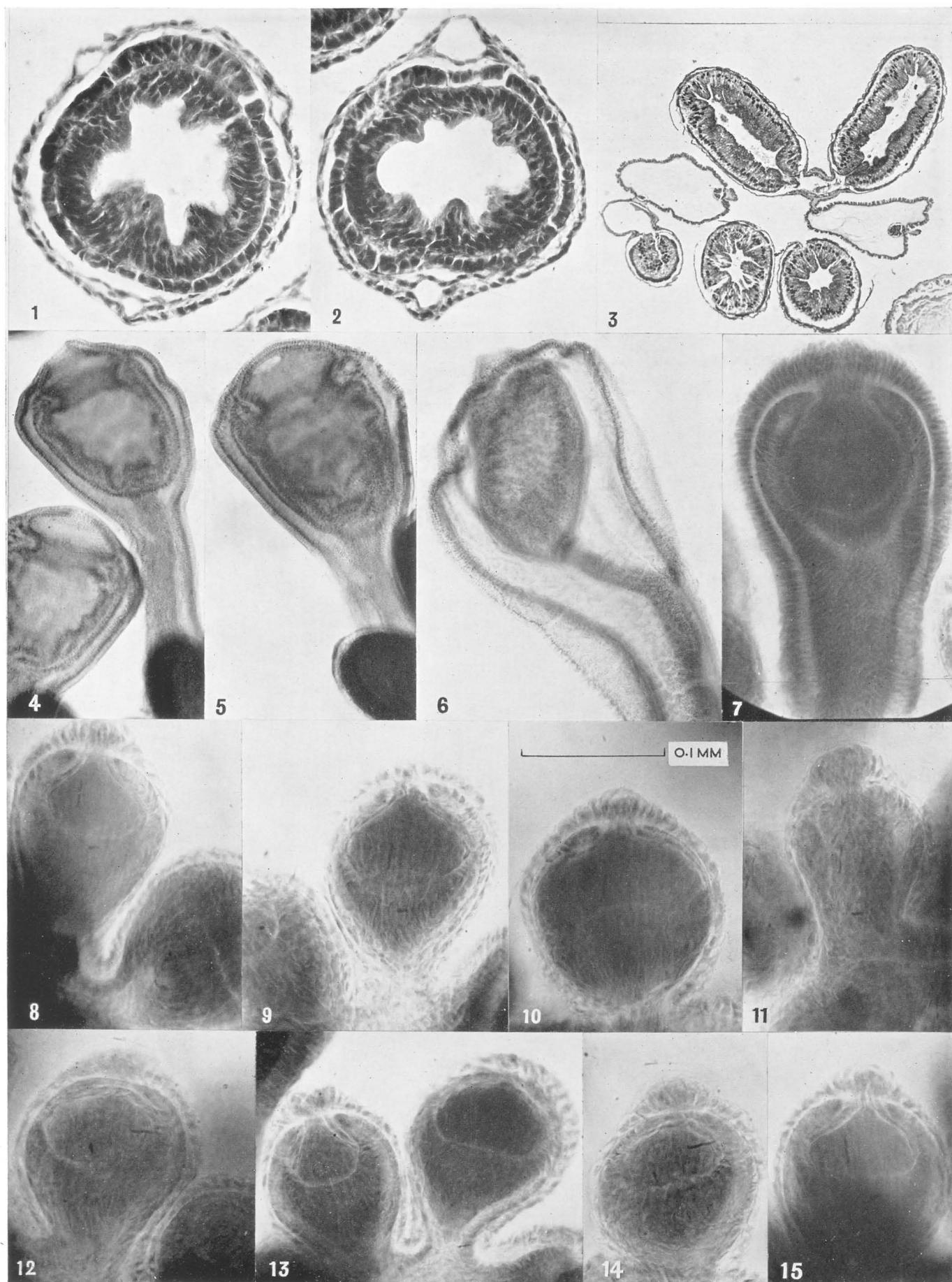


PLATE XXV

Fig. 1. Part of a small tentacle from a basal branch of cormidium II of specimen Lanzarote, no. 2, to show the longitudinal muscular lamella and nematocyst heads, each containing about 600 nematocysts (0.027 mm. or $\frac{1}{1000}$ inch in diameter). $\times 30$.

Figs. 2 and 3. Palpons of a specimen from Chesil Beach, Dorset, B.M. Register no. 1954.10.9.1, to show apical opening of palpons, analogous to an anus. Fig. 2 $\times 29$, fig. 3 $\times 25$.

Fig. 4. Living and still reactive tentacular nematocysts of *Physalia* (by courtesy of Dr Charles E. Lane, University of Miami). The two size groups average $11.5\ \mu$ and $26.8\ \mu$ in diameter. Optical sections of the coiled-up threads show that the threads taper towards the tip (anisorhizas). The point of emergence (*P*) to which the base of the thread is attached is indicated in this photograph by a dark prominence. $\times 1500$.

Fig. 5. Oral end of a gastrozooid to show apical pads of nematocysts and meridional striae. Both of these features are absent in the palpons. $\times 32$.

