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THE CRASPEDOTE MEDUSA OLINDIAS AND SOME OF ITS NATURAL ALLIES.

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I.

THE CRASPEDOTE MEDUSA OLINDIAS AND SOME OF ITS NATURAL ALLIES.

(PLATES I-III.)

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I. OLINDIOIDES FORMOSA gen. nov., sp. nov.

For some years past one species of veiled medusa, in particular, has been attracting the notice of the members of the Misaki Biological Station, by its large size, the beautiful variety of its colors, and some peculiarities in the form and arrangement of its tentacles. Attending, among other things, to the study of the veiled medusæ, my attention was naturally drawn to the above-mentioned species, and with the generous assistance of the Director of the Station, I have been enabled to collect enough material for study, the principal results of which are given in the following lines. It is a great pleasure to me to extend my best thanks to Professor Mitsukuri, the Director of the Station.

The medusa in question has proved on study to possess many striking points of resemblance to the Mediterranean species Olindias mülleri Haeckel; but for reasons which will appear farther on I have decided to form a new genus for it, and propose the name of Olindioides formosa for the species. Further, I have come to the conclusion that the genera Gonionema and Halicalyx are closely, and the fresh-water genera Limnocodium and Limnocnida more distantly, related to the new genus, and these relationships will be discussed.

There are some facts connected with the occurrence of the medusa that deserve notice. So far as my experience goes it is found only from December to June or July. The examples collected in December are all immature, with the diameter of the disk not over 20 millimetres or so, and although a few stragglers may be met with in July and August, they generally appear to be in a dilapidated condition. It must, however, be remembered that these limits are subject to variation from year to year. Another fact worth noting is that Olindioides formosa is a bottom species, and none but weakened or injured examples have been caught at the surface. The best season for collecting the medusa is March and April, when a large number of fishermen do trawling at various depths off the Station, and by sailing from one boat to another as the trawls are hauled in, one can, on successful occasions, easily get a few dozen specimens. The medusa appears to confine itself to the depth of from 20 to 30 fathoms, although my experience has not been varied enough to enable me to make any very positive statement on this point.

The umbrella is moderately high, measuring nearly one-half as much as its largest diameter, which is found slightly above the margin (Pl. I, Fig. 1); but in younger examples (Fig. 2) it is relatively higher, as in many other veiled medusæ. The jelly is thick and very consistent. The manubrium is quadrate with distinct lips, and when expanded hangs down into the umbrella cavity about two-thirds the height of the latter. Of some forty specimens that I have examined for the purpose, only three had four radial canals, and all the rest had six, so that there cannot be any doubt that six is the normal number for the species. Two of the canals start from two of the opposite corners of the manubrium, and of the remaining four two together from the other opposite corners. A comparison of a few examples is, however, sufficient to show that the number six is due to the bifurcation of two of the four original radial canals. This is easily seen on the apical view of almost any example, as shown in Figure 7, where two of the radial canals are seen to unite just before entering the central stomach, or as in Figure 8, where four of the radial canals forming opposite couples are seen to have a common root for each couple. Examples with two simple and two Y-shaped radial canals are not rare, and cases of five radia canals are also met with, though seldom.

The gonads are foldings of the subumbrellar walls of the radial canals, and extend the greater part of their lengths, leaving only a small proximal portion and a much smaller distal portion free (Fig. 6). In young examples these foldings are very simple and are clearly continuous (Pl. II, Fig. 13), but in older ones they become more complicated and are sometimes divided into numerous lobes, which are again subdivided into secondary lobes (Pl. I, Fig. 9). In the case of Y-shaped radial canals, the gonads extend upwards only as far as the point of division, and are therefore V-shaped. If the point of division lies very near the manubrium, however, the gonads leave a small proximal portion free, as in the normal case.

The endoderm of the radial canals presents different aspects on the oral and aboral sides. On the latter the cells approach nearly to the cubical form, and the cytoplasm is usually deeply stained and contains a comparatively small number of minute granules, while on the former the cells are tall and contain numerous large granules, which are probably a product of assimilation and form a reserve material. It must be remarked in this connection that the amount of these granules varies a good deal according to the nutritive condition of the example, and that in a specimen which in some way or other had lost its manubrium these granules were almost wholly absent. The endodermal lining of the gonads is composed entirely of these cells containing large granules.

The circular canal is very large, and the endoderm presents the same difference of aspect on the inner (oral) and outer (aboral) sides. On the former the cells are nearly cubical, stain deeply, and contain numerous fine granules, while on the latter side the cells are exceedingly tall and are at places almost clogged with large granules, which are exactly similar to those found in the lower walls of the radial canals (Pl. II, Figs. 15, 16; Pl. III, Figs. 17, 18). In some examples these cells are so tall as to project into and considerably narrow the lumen of the canal.

There are numerous centripetal canals of varying lengths in each sextant, lying, as in most other cases where these are found, close to the ectoderm of the subumbrella. They increase in number with the age of the medusa, and the longest lie midway between the radial canals, the next longest between the longest and the next radial canal, and so on. As the centripetal canals increase in number, however, this law is apt to be disturbed. In the specimen represented in Figure 6, for instance, this law holds good only for a short way; and even in small specimens the centripetal canals are not frequently found so regularly graded as in Figure 5. In one and the same specimen the number of centripetal canals varies from sextant to sextant, although within a limited range. To give only two examples, in a specimen with the disk of 75 millimetres in diameter, which is about full grown, the maximum number of centripetal canals was 23, and the minimum 18; in another of 15 millimetres in diameter the centripetal canals varied between 11 and 14; the total number for the former being some 120, for the latter 78.

The centripetal canals are, in structure, repetitions on a smaller scale of the radial canals, and their endoderm presents exactly the same features as in the former.

The radial, circular, and centripetal canals are connected with one another and with the central stomach by the endodermal, or vascular, lamella. In younger examples this is a layer of strictly one cell in depth, but in a very large one of about 100 millimetres in diameter the nuclei lay without any order, forming irregular tiers across its thickness. The cell boundaries could not be detected usually, except in very young specimens. The endodermal lamella runs close to the subumbrellar ectoderm, but is separated from it by a thin layer of jelly, and meets the radial, circular, and centripetal canals along the line that separates the different kinds of endodermal cells described above.

There are two sets of tentacles different in structure and position, and presumably also in their main function. From their position I shall call them velar and exumbrellar; both are very numerous.

The exumbrellar tentacles may arise from the exumbrella at any level, from very near the apex to a short distance from the velum, but they are provided with endodermal roots, traversing the jelly and connecting them with the circular canal.

The majority of these tentacles arise just outside the velar tentacles, and in these the roots are very short; but several of them spring at various levels from the surface of the exumbrella (Pl. I, Figs. 1, 2), and in these the roots are not only correspondingly long, but are accompanied by streaks of thickened ectodermal cells loaded with ivory-black pigment granules. These streaks as well as the endodermal roots are narrow near the circular canal, but become broader higher up, and the black streaks are continued for some distance on to the free portion of the tentacles. In younger specimens these exumbrellar tentacles with long roots are very few, and there is no doubt that they increase with age; and the black pigment above mentioned appears to be developed always in conjunction with the union of these tentacles to the exumbrella; for those tentacles which arise a little above their fellows have their proximal portion tinged with black (Fig. 1). The ectoderm of these black streaks contains nettle-cells, and is the direct continuation of the marginal nettle-ring. There is no objection to calling these streaks "peroniæ." The number of exumbrellar tentacles in an example 15 millimetres in diameter was 72, and in one 75 millimetres in diameter 264.

The exumbrellar tentacles have numerous elongated warts arranged across their lengths, formed by tall ectodermal cells containing nettle-capsules. They are slightly enlarged at the tip, where there is an elliptical patch of mucous gland-cells. The terminal portions of the exumbrellar tentacles are slightly curved inwards in a characteristic way, and the glandular patch just mentioned may be found indifferently at the tip or on the oral or aboral surface of the tentacles. In the aquarium the medusa has been observed to anchor itself to the bottom by means of these glands, stretching out and using the exumbrellar tentacles very much in the same way as the tie-ropes of a half-filled balloon. As it is a bottom species there can hardly be any reasonable doubt that these tentacles are used in the same way in its natural surroundings. The tentacles that spring from well up on the exumbrella probably serve to fasten the animal to seaweeds or rocks lying over it.

The cells of the glandular patch above mentioned are very tall, and the cytoplasm contains numerous minute granules which stain well with hæmatoxylin (aqueous glycerin-alum solution after Rawitz), and the secretion is usually seen forming a row of rounded masses, each corresponding to a gland cell and connected with it (Pl. III, Fig. 20).

The endodermal roots of the exumbrellar tentacles lie directly underneath the exumbrellar ectoderm, to which they are closely applied. The cells are large and vacuolated, and are directly continued into the endoderm of the circular canal. On the inner side of these tentacle roots there is a layer of scattered ectoderm cells. The exumbrellar ectoderm lying about the tentacle roots is conspicuously thickened, and contains black pigment granules and nettle-cells.

The velar tentacles are very long, slender, and contractile when fully formed, but are found in all stages of development from a mere bulb to a long contractile filament armed with numerous stinging batteries. They are always found close to the base of the velum, and their endoderm is directly continued into that of the circular canal, without the intervention of what may be called "roots." In younger examples, of about 20 millimetres or a little more in diameter, the velar tentacles are all in the condition of bulbs, exactly like the basal bulbs of Gonionema; but in mature specimens (70 millimetres or more in diameter) some of the velar tentacles are exceedingly long and contractile, and are armed with numerous nettle batteries in the form of incomplete rings. These incomplete rings are arranged all with the open point turned towards the oral side, so that there is formed a longitudinal groove on the inner side of the filiform velar tentacle. The ectodermal muscle fibres of these tentacles are at least three times as thick as those of the exumbrellar tentacles and are cross-striped. This is in entire accord with their great contractility in life. These filiform velar tentacles are never very numerous, there being some ten or so in an example of about 60 millimetres in diameter. In the aquarium these tentacles are dragged along passively when the animal swims forwards, but when at rest they are loosely laid out on the bottom and occasionally contracted. I believe they are the principal organs for capturing prey. When strongly contracted, they tend more or less to form a spiral. In an example of 15 millimetres in diameter there were about 100 velar tentacles, all in the condition of bulbs, and in one of 75 millimetres some 325, of which a dozen or so were filiform.

The velar tentacles are very different in structure in the bulbular and filiform conditions. In the bulbular condition the ectoderm is so clogged with nettle-cells in all stages of development that it is hard to recognize the individual ectoderm cells. It is also to be remarked that none of the numerous nettle-cells are found fully developed. The endoderm is a direct continuation of the external part of the endodermal wall of the circular canal, with which it presents the same histological characters, and the mesoglœa is very thin. In the filiform condition the mesoglœa is tolerably thick, the endoderm cells are large and vacuolated, though less so than those of the exumbrellar tentacles. The stinging batteries contain numerous fully developed nettle-cells, and between the ectodermal cells close to the mesoglœa are found numerous nettle-cells in the later stages of development. These are placed with their long axes parallel or only slightly oblique to the length of the tentacle, and are, in my opinion, on the way to their destinations, the earlier stages having been passed in the bulbular velar tentacles. All suspicion that the bulbular and the filamentous forms may be fundamentally different has been dispelled by the presence of numerous intermediate stages. The bulbular velar tentacles as well as the ectodermal thickenings that connect them are then the nisi formativi of the stinging cells, whence they travel in opposite directions, up along the peronia into the exumbrellar tentacles, or down into the filiform velar tentacles. The wandering nettle-cells are much less numerous in the exumbrellar than in the velar tentacles.

The marginal organs are all otocysts, and are present in large numbers, two at the base of the endodermal root of each exumbrellar tentacle. In younger examples they form a single row along the umbrella margin and are situated close to the circular canal (Pl. I, Fig. 3), but in larger ones they no longer keep the same front, and, generally speaking, the older ones are pushed up into the jelly of the umbrella (Fig. 4). They are either spherical or ellipsoidal, and some of the larger ones measure no less than 160 micra across. The vesicle is lined by a flattened epithelium, which presents a local thickening at a place turned towards the circular canal, where probably the sensory cells are found. The otolith is surrounded by some granular protoplasm containing nuclei, and is attached to the wall of the vesicle by means of a short stalk consisting of some granular, well-staining protoplasm containing nuclei. The otolith itself is highly refringent, and, when fully formed, consists of somewhat irregularly concentric layers arranged around a centre. It appears to be very hard and is apt to be detached from sections.

Haeckel says that the structure of the marginal vesicles of Olindias shows it to belong to the Trachomedusæ, but as both Olindias and Olindioides as well as the closely related genera before mentioned appeared to me to present several features which are not commonly met with among the Trachomedusæ, I have paid special attention to the development of the otocyst, which, in the absence of any knowledge of the life history, must be considered the most reliable criterion by which to decide the natural relationship of the veiled medusæ.

I have shown in Figures 15 to 19 (Pls. II, III) some stages in the development of the otocyst. The endodermal roots of the exumbrellar tentacles start from the circular canal at the place where the two kinds of endodermal cells already mentioned meet each other, and the first rudiment of the otocyst is seen in process of formation close to this root. It consists of a small segregation of ectodermal cells hardly distinguishable from the rest, closely applied to the endoderm of the circular canal at the point where the two kinds of cells meet (Pl. II, Fig. 15). At this stage it would be very apt to be overlooked, were it not for the presence of the root of a very young exumbrellar tentacle. There cannot be any reasonable doubt that the rudiment consists exclusively of ectoderm cells, since the boundary line between the two cell-layers is always distinguishable with a good objective (Zeiss apochromatic oil-immersion), and there is no sign of proliferation in the endoderm. On the contrary, the latter is usually found pushed in by the otocyst rudiment—just the contrary of what one would expect if the endoderm took part in its formation. The first rudiment just described forms, as will appear in the sequel, the otolith and the parts that directly surround it.

In the next stage (Fig. 16) the endoderm is generally found pushed in somewhat more by the otocyst rudiment, and around the latter on the outer side has been formed a cup-shaped cavity lined by a layer of cells, some of which are flattened, while others can hardly be distinguished from the surrounding ectoderm cells. This cavity is the beginning of the vesicle, and the layer of cells around it becomes its lining epithelium. In this stage the cells that formed the first rudiment are all alike.

The next change that takes place consists in the enlargement of the cavity and the differentiation of the central cells into two sorts, namely, those that are transformed into the otolith and those that form its investment and stalk. In the section reproduced in Figure 18 (Pl. III) this differentiation has hardly begun, and the deeply and faintly staining nuclei are found mixed together, although some of the more central ones are larger and clearer than others. It may also be noted that in this section many of the peripheral nuclei are vesicular in appearance. These differences taken by themselves appear to me to afford only a dubitable clue to the destination of the respective cells, depending as they do on the changing conditions of the nuclear substance. For example, even in one and the same otocyst some nuclei of its lining epithelium are clear and vesicular, while others are darkly stained. In a later stage the cells that are destined to be transformed into the otolith and those that remain as its investment and the stalk are clearly distinguishable, the central nuclei being generally larger, clear and vesicular, while the peripheral ones are deeply stained and are more or less flattened. It must be borne in mind, nevertheless, that these differences are by no means absolute. Sometimes, as is seen in Figure 17, the differentiation of the central cell mass appears to be effected at a very early stage, and in such a case the difference between the two kinds of cells is very striking.

In the last stage described the central cell mass was sessile, resting as it did directly against the endoderm of the circular canal by a broad base. If double staining is resorted to at such a stage, the cells that are destined to become the otolith stain of the same color as the endoderm, while the lining epithelium and the investing cells stain like the ectoderm; for example, with fuchsin and methyl green the endoderm and otolith cells are violet, and the epithelium, investing cells, and ectoderm are green.

And one is very apt to interpret such a different behavior towards stains as proving different origin. This is the fundamental principle of double staining, but if applied too liberally it is very apt to lead one into unwarranted conclusions. The researches of Fischer ('99) have taught us that this principle must be checked and rechecked constantly by other considerations to afford justifiable and reliable conclusions. The origin of a structure can be regarded as definitely proved only by being traced to its first beginning.

The cells that are destined to form the otolith gradually undergo histolysis; the cytoplasm becomes more and more attenuated, and the nuclei enlarge and become clearer and vesicular; finally they disintegrate and disappear, leaving in their stead a sparsely granular substance, which at first stains tolerably well, and in which small blocks of chromatin and some irregular fibres can be observed. At this stage the stalk is very distinct and consists of a deeply staining, finely granular protoplasmic mass containing several nuclei (Fig. 19). The otolitic substance gradually becomes more refringent, at the same time losing its affinity for stains, and finally comes to consist of numerous concentric layers. The otolith is surrounded by a nucleated protoplasmic investment to the last. In the stage shown in Figure 19, the lining epithelium of the otocyst is separated from the ectoderm only an exceedingly thin layer of mesoglœa; but in older stages the entire organ is pushed far into the jelly and has usually no cellular connection with the ectoderm. Exceptionally, however, such a connection persists through life. The otocysts are throughout life more or less closely applied to the endoderm of the circular canal, from which they are frequently separated by a very thin layer of jelly.

The colors * of the medusa are as follows: for the tips of the exumbrellar tentacles a beautifully transparent, shining lilac, for the next adjoining portion a shining smaragdine-green, and for the peronia and the basal portion of those exumbrellar tentacles that arise some way up the umbrella ivory-black, the latter thinning out and passing into the green portion or separated from it by a short colorless stretch; for the radial and circular canals a deep scarlet, and for the centripetal canals a lighter scarlet. There is also a small smaragdine-green triangular area at each corner of the base of the manubrium, on either side of which is a lilac area of the same color as that of the tips of the exumbrellar tentacles; there is in addition one or two somewhat irregular longitudinal streaks of lilac along the middle of each side of the manubrium. The tips of some of the filiform velar tentacles are occasionally just tinged with green and lilac. The gonads are egg-yellow. In small specimens the more axial portion of the manubrium is egg-yellow, but in larger ones it is almost entirely colorless.

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* The names of the colors used in this description are in accordance with the system proposed by Saccardo ('94).

Some histological notes other than those mentioned heretofore may now be added.

The velum is very strongly developed, its mesoglœa is very thick in full-grown examples, and on the subumbrellar side is thrown into numerous vertical folds, forming muscular lamellæ. The subumbrellar musculature is also vigorously developed, and there is a special muscular ring just inside the base of the velum, adjacent to the nerve-ring. This is due to a special development of the muscular lamellæ, which are here very numerous and closely set, and are also exceptionally tall. The muscular lamellæ are found here and there in all parts of the subumbrella, but they are inconspicuous elsewhere.

The nettle-cells are exceptionally large and cylindrical, and are in general form like those of many actinians. When fully formed they are as large as 30 micra by 7 micra, and the protoplasmic mantle and the nucleus can always be distinguished very clearly. The latter is usually found near the more slender end of the organ and is frequently horseshoe-shaped. When the nettle-cells are placed in their definitive position this slender end is invariably directed inwards, being the closed end of the urticating vesicle.

As before mentioned, the nettle-cells are comparatively few in the exumbrellar tentacles, but are especially numerous in the ring-shaped warts of the velar tentacles, and in these they are imbedded between exceedingly tall ectodermal cells, which are very conspicuous in sections even under a low power. These ectodermal cells are provided with very long stalks which stain deeply with hæmatoxylin, are more or less undulating, and are attached below to the mesoglœa. The body of the cell consists of a granular or a somewhat fibrous cytoplasm with a distinct membrane and a deeply staining nucleus situated near the centre. Under ordinary objectives the transition between the stalk and the body of the cell appears sudden, but with a high-power apochromatic system it is seen to be more gradual. These stalks were at first suspected to be muscular in nature, but further observations revealed many transitional forms between these and the ordinary tall ectodermal cells; and further, these stalks look very different from the muscular fibres lying immediately below. It is evident, however, that the protoplasm of the stalks of these cells has undergone a special modification, but its nature has so far remained obscure to me. These cells with deeply staining stalks are also present in the warts of the exumbrellar tentacles; but they are less numerous there and the stalks are shorter.

Olindioides formosa has been observed in the following localities: Misaki; Kanagawa (practically identical with Yokohama, Prof. Mitsukuri); Bay of Tateyama, southeastern extremity of the Bay of Tokyo (Dr. Oka).

II. GONIONEMA DEPRESSUM sp. nov.

This is a pretty species common among the eel-grass growing within the wharves of Yokohama, and specimens can easily be obtained at any hour of the day by towing in such situations by means of a weighted net. I have never seen the medusa on the surface of the water during the daytime. The Woods Hole species, for which Mayer has recently proposed the name of G. murbachii, is stated to come to the surface at night, and the towing for the medusa appears to be performed there only in the evening; but it is probable that the animal never quits the eel-grass entirely, since it is known that the grass grows rank in the eel-pond, where it is always hunted for. The Yokohama species has a rather shallow open umbrella, which may measure 20 millimetres by 8 millimetres or a little more. The smaller examples have the umbrella relatively deeper; one of 4 millimetres in diameter measures just as much in height. The jelly is only moderately thick. The swimming movements are vigorous, but only a few pulsations are made consecutively at a time, after which the animal slowly sinks with expanded umbrella and outstretched tentacles until it touches some object, when it attaches itself to it by means of the adhesive disks of the tentacles. The manubrium is quadrate with distinct lips, and hangs down close to the level of the umbrella margin. The radial canals are four, and the gonads are developed on their lower walls along nearly their entire lengths, leaving only a small proximal and an equally small distal portion free. In very young examples the gonads are simple thickenings of the wall of the radial canals, but in larger ones they are thrown into folds which are arranged alternately on either side of the canal. These folds remain, however, very simple, and, so far as I have observed, are never divided into lobes (Pl. II, Fig. 13).

The tentacles are numerous; in an example of 18 millimetres in diameter there were 59, and in another of 4 millimetres there were 32; 64 was the largest number of the tentacles I have observed so far. They are very flexible, but are not as contractile as the velar tentacles of Olindioides; they are armed with incomplete ring-like warts, in which the nettle-cells are found. The most characteristic feature of the tentacles, however, is that they bear at some distance from the tip each an adhesive disk, by which the animal can securely attach itself to any external object. When the tentacles are expanded, these disks are nearly flat and elliptical, but in contracted tentacles they are more or less saucer-shaped, and are compressed along the length of the tentacle (Pl. II, Fig. 11; Pl. III, Fig. 21). They consist of tall cylindrical cells very similar to those of the adhesive disks of Olindioides, and the secretion can be observed almost at any time, forming rounded or elongated masses each corresponding to a mucus cell. The cells stain well with hæmatoxylin, but especially so near their free ends. These disks have been described as "sucking," but a study of their structure reveals nothing capable of exercising a pumping action. In all the known species of Gonionema these disks are situated on the inner side of the tentacles, and cause the characteristic angular bend, which has given rise to the generic name.

On a cursory observation, the tentacles appear to arise from the margin of the umbrella, but a closer inspection shows that they spring always from the exumbrella at a short distance from the margin, just as do the exumbrellar tentacles of Olindioides; and one can easily observe the endodermal tentacle roots traversing the jelly to join the circular canal. In Gonionema these roots are very short, and as a consequence the peronia do not come into view, although the ectoderm lying over these tentacle roots is slightly thickened.

On the inner side of the tentacles, close to the base of the velum, are the basal bulbs of the tentacles, exactly corresponding both in position and number to the former. These bulbs are exactly similar in structure to the rudimentary velar tentacles of Olindioides, that is to say, they contain hollow prolongations of the endoderm of the circular canal, and the ectoderm is clogged with developing nettle-cells. In Gonionema these bulbs never become elongated and filiform, but there is no doubt that they are the homologues of the velar tentacles of Olindioides.

The marginal organs are all otocysts, and are present two at the base of each tentacle. In structure they are also exactly like those of Olindioides; they are, however, generally smaller, a fully developed vesicle measuring only 75 micra in diameter. Again, the majority remain close to the marginal ectoderm containing the outer nerve-ring, and retain a cellular connection with it; but some of the oldest otocysts are pushed far into the jelly, and the cellular connection with the ectoderm disappears. They remain, however, more or less closely appressed to the endoderm of the circular canal (Pl. III, Fig. 22). The otolith, when fully formed, shows a radial arrangement of its constituent pyramids.

The endodermal lamella remains one-layered throughout life, and joins the circular and radial canals along the line that divides the two kinds of cells as in Olindioides. It is separated from the subumbrellar ectoderm by a thin layer of jelly.

The coloration of the medusa is as follows: radial canals, basal bulbs, and the adhesive disks of the tentacles a transparent chestnut-brown; tentacles, gonads, the larger part of the manubrium, and the circular canal a lighter brown, marginal area of the manubrium pale green. At the very base of each tentacle there is a speck of shining emerald-green, of the same color as the green portion of the exumbrellar tentacles of Olindioides. These are not eyes.

The musculature is well developed, but less so than in Olindioides, and the muscular lamellæ are confined to the subumbrella. There is, however, a strong muscular ring exactly in the same position as in Olindioides, namely, near the base of the velum, just internal to the inner nerve-ring. Here the mesoglœa, or, as it may be called, the supporting lamella, is thrown into extensive irregular folds, on either surface of which the muscular fibres are closely arranged in a row.

III. REMARKS ON OLINDIAS MÜLLERI HAECKEL.

There are some points in Haeckel's description of this medusa that require comment. The following remarks are based on an examination of an excellently preserved museum specimen of about 50 millimetres in diameter from Naples, that has been in the possession of this school for several years, and of a few examples that have recently been obtained from the Naples Zoölogical Station, fixed according to my directions. The latter material is, so far as I have examined, in a rather unsatisfactory condition histologically, due, as I believe, to histolysis having set in before fixing. But so far as the general structure is concerned, these specimens can be safely depended on, the more so as there is the perfect specimen as a control.

The general form of the medusa is very well represented in Haeckel's figure, but the filiform velar tentacles (Fangfäden) are too numerous. In the perfect specimen above referred to there were only some 35, irregularly distributed along the entire margin, and these are of very unequal length and thickness. There can also be observed various stages in their development from the bulbular to the filiform condition, the bulbular forms being about four or five times as numerous as the filiform ones. Haeckel ('79) also speaks of numerous ocelli situated between the velar tentacles, which, according to him, appear to contain a biconvex lens. These so-called ocelli are nothing but the bases of the exumbrellar or of the filiform velar tentacles, which contain a red pigment in the endoderm, and the supposed biconvex lens is simply the axial cavity of the tentacle viewed in optical section.

The exumbrellar tentacles are armed with incompletely ring-shaped or horseshoe-shaped nettle-warts, and are provided each with an adhesive patch of mucous cells at the tip. The patch extends on the inner side more than on the outer. The endodermal roots of the tentacles are not very long, but are quite conspicuous.

In the fully developed condition the gonads consist of numerous lobes, each of which looks somewhat acinous, but a closer examination shows that these lobes are continuous with each other; and a comparison with the lobed condition of the gonads of Olindioides already described leaves no doubt that each gonad of Olindias must have been formed as a single continuous thickening of the subumbrellar wall of a radial canal and became lobed only secondarily. An examination of Haeckel's figure ('79, Pl. XV, Fig. 10) of a young example of about 8 millimetres in diameter bears out this view.

As to the habitat of Olindias mülleri, I have not been able to ascertain it. Haeckel ('79, p. 253) says that it appears to be rather rare, or perhaps to be confined to certain localities, and I am informed by the authorities of the Naples Station that it occurs especially in the months of October and November and then disappears. Considering that the exumbrellar tentacles are provided with adhesive disks, and judging from analogy, it is very probable that Olindias mülleri is a bottom species like Olindioides; and its comparative rareness must at least in part be attributed to this peculiar habit. It appears, however, that the medusa can be obtained without difficulty at the Naples Station in the proper season. The material lately sent me appears to have been collected late in August or very early in September.

IV. NATURAL RELATIONSHIPS OF THE DESCRIBED SPECIES.

On looking through the published descriptions of the veiled medusæ it will at once be evident to any one that the genera Olindias, Halicalyx, and Gonionema, and the new genus Olindioides must be put together into a natural group, for which we may adopt the name Olindiadæ used by Haeckel. The common characters are very simple and clear: jelly tolerably consistent, radial canals four or six, manubrium well developed and quadrate, with distinct lips, velum well developed, gonads originally a continuous fold of the subumbrellar wall of the radial canals, which may secondarily become lobed, with two sets of tentacles, the velar and the exumbrellar, with an adhesive disk somewhere on each exumbrellar tentacle, at the base of which there is a pair of otocysts. The exumbrellar tentacles are provided with endodermal roots, which more or less traverse the jelly to join the circular canal. Bottom species or living among seaweeds.

The genus Halicalyx, with one species, H. tenuis, was originally described by Fewkes ('82) and recently redescribed by Mayer (:00), who says that it is closely allied to his genus Gonionemoides, but that it differs by the absence of "suctorial" disks on any of the tentacles. I may, however, be allowed to suggest that the exumbrellar tentacles (stiff tentacles standing out sharply at right angles to the bell and sprinkled over with wart-like protuberances of a deep purple color) will probably be found on a closer examination to be provided with an adhesive disk near the tip. The mucous glands in similar positions of Olindias have been overlooked.

Haeckel says that he at first placed Olindias in the Æquoridæ, but that the structure of the marginal vesicles shows it to belong to the Trachomedusæ. Mayer ('99) also regards Gonionema as a trachomedusan; but Murbach ('95), who has studied its development, says that there is true alternation of generations, the larva passing through a hydrula stage. Haeckel places Gonionema in his leptomedusan family Cannotidæ, which is characterized by the absence of marginal vesicles, the possession of four- or six-branched, forked or pinnatifid radial canals, in the course of which the gonads lie. On the systematic position of Halicalyx neither Fewkes nor Mayer says anything.

It is evident from a perusal of their works that Haeckel and Mayer have been led to regard Olindias and Gonionema as belonging to the Trachomedusæ by the structure of the otocysts, and the only peculiarity of these organs that could have impressed them appears to me to be that the otolith is provided with a stalk, by means of which it is attached to the wall of the vesicle. But the presence of a stalk taken by itself seems to me to be of no systematic importance, since, in all the Leptomedusæ thus far described or observed by me, the otoliths are attached to the wall of the vesicle, and it is simply a question of the comparative length of the intervening portion that determines the presence or absence of the stalk. Further, if one compares the stalk of the vesicle of any of the medusæ above mentioned with that of such undoubted Trachomedusæ as Glossocodon or Liriope, there are some differences, which, taken in conjunction with the observations on the development of the otocyst, point to a fundamental difference between the two. The otolithic stalk in Glossocodon and Liriope is very distinctly set off both from the protoplasmic mass surrounding the otolith and the wall of the vesicle; but in all the genera of Olindiadæ the stalk passes on gradually into the periotolithic mass on the one hand and the vesicle wall on the other. We have also seen that in Olindioides the endoderm takes no part in the formation of the otocyst.

Among the differences set up by the Hertwigs ('78) for the two types of otocysts, one characteristic of the Trachylinæ and the other of the Leptolinæ, is one of innervation. According to the observations of the two brothers, the otocyst is innervated in the former group by the upper (outer) nerve-ring, and in the latter by the lower (inner). In Olindioides and Gonionema the otocysts appear to be supplied from the outer nerve-ring; but this coincidence with a character of the Trachylinæ must be due to convergence, and the difference of innervation must not be regarded as absolute for the two types of otocysts. In Olindioides, moreover, the two nerve-rings are seen in several places to be directly continued one with the other through breaks in the mesoglœa separating the two.

The presence of centripetal canals is another point of resemblance between Olindiadæ and some Trachomedusæ; but it is evidently of no systematic moment, since these canals may be present or absent in closely related genera.

I have spoken of the marginal nettle-ring; but it must be borne in mind that it is unlike the nettle-ring of the genuine Trachomedusæ. For, while in the latter the ring is a very distinct structure continuous throughout, in the Olindiadæ it is brought about merely by the close proximity of the velar tentacles, and in such a form as Gonionema, where the intervening spaces are wider, the ring tends to become more or less discontinuous, and in some sections through such a space the nettle-cells are totally absent. We must also remember that in some Leptolinæ there is a well-developed nettle-ring, as in Laodice (Brooks, '95).

The presence of endodermal tentacle roots in the Olindiadæ is another feature of resemblance to the Trachomedusæ, but we must also remember that these structures may be present in forms which undoubtedly belong to the Leptolinæ (Brooks, '95).

The unsatisfactoriness of Haeckel's system of the medusæ has been pointed out by Brooks ('86, '95), but accepting it we must place the subfamily Olindiadæ in the Leptodmedusæ. It is impossible to put it under the Cannotidæ, to which Gonionema is referred by Haeckel. It appears, to me that it comes with least violence under the Eucopidæ, where our medusæ may find their temporary resting-place.

The genus Gonionemoides formed by Mayer (:00) is evidently nearly related to our genera, but less so than these are among themselves, and it will perhaps be found advisable to place it in a distinct subfamily.

The fresh-water medusæ Limnocodium and Limnocnida have not found a satisfactory place in the system. Allman ('80) and Fowler ('90) think that Limnocodium should be placed in the Leptolinæ, while Lankester ('80) and Günther ('94) bring it under the Trachylinæ, in which the latter also places his genus Limnocnida from Lake Tanganyica. It appears to me that these genera present some features which point to their affinity to the Olindiadæ, near which they can, in my opinion, be placed most naturally. But as I am not able to examine any material of these medusæ, I shall confine myself to some critical remarks on the statements of previous authors concerning points of fundamental importance.

The point of greatest importance in determining the position of these medusæ is of course, in the absence of a definite knowledge of the life history, the origin of the otolithic cells, which, according to Lankester ('80) and Günther ('94, '94a), are produced from the endoderm of the circular canal. Lankester made his observations on the marginal vesicles exclusively by means of optical sections, and it is no discredit to the author to say that none of his figures touching the point in question can be considered as decisive. Günther ('94), on the other hand, carried on his observations on actual sections prepared from materials killed with osmic acid, and by means of the best optical appliances, and he reproduces several figures intended to show the endodermal origin of the otolithic cells. It must, however, be remarked that the figure (Fig. 1) he gives us of the earliest stage that came under his observation in the development of the otocyst represents a somewhat advanced stage, when its constituent parts have all been formed, and these parts have only to enlarge, multiply, and undergo a little differentiation to arrive at the definitive condition; and it is exceedingly improbable that any additional endoderm cell should at this stage wander out to reinforce their precursors, even if these were derived from that source (compare Figures 17 and 18 in the present paper). The absence of the intervening mesoglœa must not be taken by itself as a proof of the morphological continuity of the two cell layers, and it is necessary to exercise constantly self-criticism not to be misled into taking appearance for reality. The question of morphological continuity or discontinuity in such a case comes very near to splitting a hair, and it is only by the closest scrutiny that one can draw a safe conclusion.

It may be added in passing that the structure of the otolith which Lankester and Günther regard as unique represents only a developmental stage in other forms, and it is possible that these authors have observed only comparatively young otocysts, and that in older ones the otolith loses its cellular structure. Should the ectodermal origin of the otolithic cells be granted, the structure of the marginal vesicles of Limnocodium and Limnocnida is exactly like that of the same organs of the Olindiadæ, except for the peculiar prolongations into the velum of the vesicles in the first-named genus.

The presence of tentacle roots, though of secondary importance, is another feature common to the Olindiadæ and the two fresh-water genera.

The young stages of Limnocodium described by Lankester ('80, '81) are supposed by him to have developed from the egg-cell, although he did not observe any mature females, but only males. On examining them, however, one is struck with some features in their anatomy that point strongly to their origin as medusa buds either from a hydroid stock or, more probably in this case, from young female medusæ.

the presence of a closed subumbrellar cavity, a manubrium, and the radial canals at a stage corresponding in other respects to that of the Trachomedusæ, in which there is as yet none of these parts, is a point that seriously interferes with the supposition that the young medusæ studied by Lankester were derived from the egg-cell (Brooks, '86). Some leptoline medusæ proliferate by budding when young, and produce ova when older.

As to the hydroid described by Parsons, Bourne, and Fowler, it is not known for certain whether it is a member in the life-history of Limnocodium, although this supposition must be allowed to be very probable. Some light will perhaps be thrown on this point by the French naturalists who have recently observed the medusa in a lily tank in the Zoological Garden of Lyon (Vaney et Conte, :01), or by the collection from Mr. Moore's expedition to Lake Tanganyica.

Any one who is acquainted with the Narcomedusæ, and especially with their marginal sense-organs, will hardly agree with the proposal of Günther to place Limnocnida, even provisionally, in that group.

In conclusion I shall add a synopsis of the Olindiadæ, which will bring forth their distinctive characters and their natural relationships more clearly, though necessarily in a schematic way.

Subfamily: Olindiadæ.—Eucopidæ with two sets of tentacles, velar and exumbrellar, the former springing close to the base of the velum, and the latter at variable distances from it, but always from the exumbrella and connected with the circular canal by endodermal roots. Marginal vesicles numerous, two on either side of the base of the exumbrellar tentacle. Manubrium well developed and quadrate, with distinct lips. Radial canals four or six. Gonads primarily continuous folds of the walls of the radial canals. With an adhesive disk on each exumbrellar tentacle.

SYNOPSIS OF THE GENERA.

1. Velar tentacles just as numerous as the exumbrellar.................. 3.
2. Velar tentacles more numerous than the exumbrellar.............. 5, 6.
3. Velar tentacles all rudimentary, in the form of basal bulbs....Gonionema.
4. Velar tentacles all filiform...................................Halicalyx.
5. Radial canals four...Olindias.
6. Radial canals six..Olindioides.

Gonionema (= Gonionemus) A. Agassiz.

Agassiz, '62, p. 350. Haeckel, '79, p. 146.

G. vertens A. Agassiz.
    Agassiz, '62, p. 350. Haeckel, '79, p. 147.
G. murbachii A. G. Mayer.
    Murbach, '95. Mayer, :01, p. 5. Morgan, '99.
G. suvaënsis A. G. Mayer, '99, p. 164.
G. aphrodite A. G. Mayer, '94, p. 237; :00, p. 62.

The last two species belong in my opinion to Gonionemoides, since they posesss only four otocysts in each quadrant.

Halicalyx J. W. Fewkes.
    Fewkes, '82, p. 277. Mayer, :00, p. 63.
H. tenuis J. W. Fewkes.
    Fewkes, '82, p. 277. Mayer, :00, p. 63.
Olindias F. Müller.
    Müller, '61, p. 312. Haeckel, '79, p. 252.
O. sambaquiensis F. Müller.
    Müller, '61, p. 312. Haeckel, '79, p. 254.
O. mulleri E. Haeckel.
    Haeckel, '79, p. 253.
Olindioides S. Goto.
    O. formosa S. Goto.

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EXPLANATION OF PLATES I–III.

ABBREVIATIONS.

can. crc.	Circular canal.
ec'drm.	Ectoderm.
en'drm.	Endoderm.
gl. muc.	Adhesive mucous gland.
go.	Gonads.
ot'cys'.	Otocyst.
rx. ta.	Endodermal tentacle roots.
ta. ex'ubr.	Exumbrellar tentacle.
ta. vel.	Velar tentacle.

PLATE I.

Olindioides formosa.

Fig. 1. Adult medusa in natural colors; diameter 55 mm.
Fig. 2. Young medusa in natural colors; diameter 15 mm. at mouth of umbrella.
Fig. 3. Portion of umbrella margin; diameter of umbrella 30 mm. Exumbrellar view; × 27 diameters.
Fig. 4. Portion of umbrella margin; diameter of umbrella about 100 mm. Exumbrellar view; × 13 diameters.
Fig. 5. One sextant with manubrium; diameter of umbrella 15 mm. Subumbrellar view.
Fig. 6. One sextant with manubrium; diameter of umbrella 75 mm. Subumbrellar view.
Fig. 7. Apical view of radial canals; diameter of umbrella 10 mm.
Fig. 8. Apical view of radial canals; diameter of umbrella 15 mm.
Fig. 9. Portion of gonad, showing three lobes which are subdivided into lobules; diameter of umbrella 90 mm.

PLATE II.

Gonionema depressum.

Fig. 10. Adult medusa in natural colors; diameter 18 mm.
Fig. 11. Portion of tentacle, showing the adhesive gland disk. ×54 diameters.
Fig. 12. Portion of umbrella margin including a radial canal; diameter of umbrella 18 mm. ×13 diameters.
Fig. 13. Radial canal with gonad and manubrium; nearly adult.

Olindioides formosa.

Fig. 14. Terminal portion of a longitudinal section of tentacle, showing the adhesive glandular patch; diameter of umbrella 60 mm. ×54 diameters.
Fig. 15. Portion of a radial section of umbrella margin, showing the first traces of otocyst; diameter of umbrella 10 mm. ×570 diameters.
Fig. 16. Portion of a radial section of umbrella margin; diameter of umbrella 10 mm. ×420 diameters.

PLATE III.

Olindioides formosa.

Fig. 17. Portion of a horizontal section of umbrella margin; diameter of umbrella 10 mm. ×420 diameters. On one side of the tentacle root the otocyst is just cut tangentially.
Fig. 18. Portion of a radial section of umbrella margin. ×420 diameters.
Fig. 19. Otocyst in a later stage of development. ×420 diameters.
Fig. 20. Portion of adhesive glandular patch; diameter of umbrella 10 mm. ×730 diameters. The mucus is seen as exudations at the free ends of the cells.

Gonionema depressum.

Fig. 21. Portion of a longitudinal section of tentacle, showing the adhesive disk. ×240 diameters.
Fig. 22. Otocyst fully developed; diameter of umbrella 18 mm. ×420 diameters.


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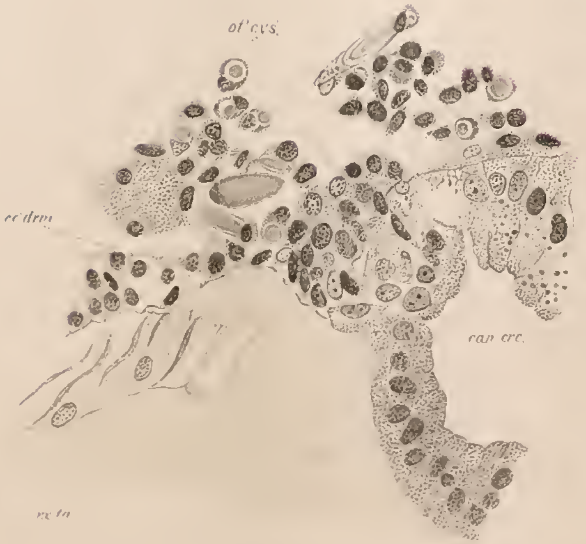

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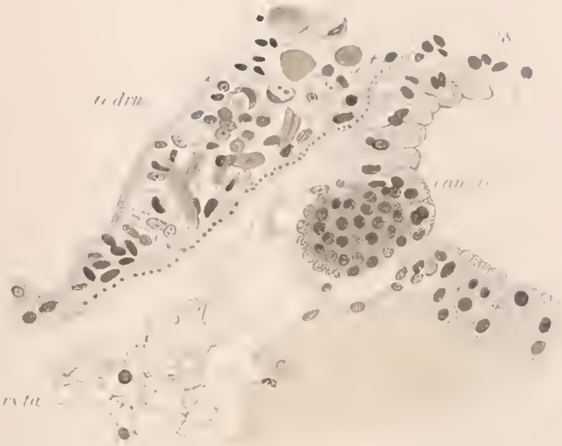

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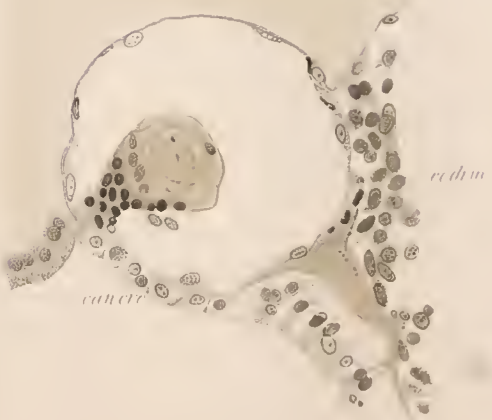

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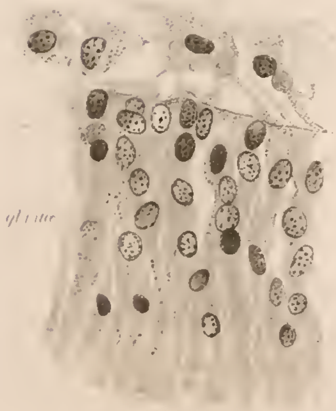

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