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CONDUCTED BY

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EXPLANATION OF PLATE XVI.

A. *Microciona strepsitoxa.*

Figs. 1 & 2. Main skeletal spicules.
Fig. 3. Echinating spicule.
Fig. 4. Subclavate style.
Figs. 5 & 6. Long toxites.
Fig. 7. Smaller form of toxite.
Fig. 8. Long toxites; from a photograph, to show central twist.
Figs. 9 & 10. Isochelæ, front and side views.

[Figs. 1–7 magnified 260 diameters; figs. 9 & 10 magnified 850 diameters.]

B. *Trachytedania* (?) *echinata.*

Fig. 1. Main skeletal spicule.
Fig. 2. Echinating spicule.
Fig. 3. Tylote spicule.

[Figs. 1–3 magnified 260 diameters.]

XLIV.—*On a Method of Defence among certain Medusæ.* By J. Walter Fewkes *.

The Siphonophora, in common with other Medusæ, as is well known, possess a very powerful organ of defence in the stinging-cells, also called lasso-cells and nematocysts. There is reason to believe that there may be at least one other method of protection adopted by these animals. I propose this evening to lay before you the evidence of the existence of this second method of defence made use of by these animals, and to open the discussion of the homologies of the structures in which this new means of protection is lodged.

It may be well to anticipate what follows by the statement that the new method of defence is that of discolouring the water by the emission of coloured pigment from certain chromatic cells on the bracts, and that these cells bear relationships and perhaps are homologous with the nematocysts in

* From the Proc. Bost. Soc. Nat. Hist. vol. xxiv. pp. 200–208.

other genera of the groups in which they exist. The new method of defence is found, as far as known, only among the Siphonophores, and is limited to one or two genera.

Let us, on the threshold of our study, consider the history of the discovery of the structures in which this peculiar power is thought to be lodged.

In the year 1880, while engaged in the study of an *Agalma*, found at Villa Franca, South France, I noticed on the covering-scales certain coloured bodies which resembled in distribution in longitudinal rows the nematocysts which are ordinarily found on these structures. In the same year (1880) I described and figured these bodies, and called attention to the fact that when the covering-scale is broken from its connexion with the axis a coloured fluid is emitted from these organs. A covering-scale, ruptured from its connexion, was seen to pour out a considerable quantity of yellow fluid and to discolour the water in the immediate vicinity. When irritated, even while the bract is attached, the animal was supposed to discharge the colouring-matter in the same way although not in the same quantity. A similar phenomenon, connected with other organs, had already been described, for a discharge of colouring-matter from the tasters of *Forskalia* had been observed and mentioned by Kölliker; but, as far as known, no one had spoken of a like power of the chromatic "cells" or glands of the covering-scales of any Siphonophore.

My observations were not verified, or, at least, were not mentioned, by those who studied the Mediterranean Physophores up to the close of last year, when Dr. M. Bedot* again took up the subject, and from a study of what he regards a new species of *Agalma* (*A. Clausi*), possibly the same as mine, or, at least, found in the same locality, described and figured these glands again, generously quoting my description of eight years ago. His additions to our knowledge of the subject are so important that I have taken the liberty of quoting from his account somewhat at length.

Bedot says (p. 79):—"Ce qui donne un aspect particulier au bouclier, c'est la présence, à sa surface, d'un grand nombre de petites taches d'un rouge-carmin foncé (fig. 13, *gl*). Lorsqu'une de ces Agalmes est capturée, elle rejette une quantité très considérable de matière colorante d'un rouge jaune très intense. Pour l'observer facilement, on est obligé de changer plusieurs fois l'eau du bocal où elle se trouve. Au premier abord, j'ai cru que cette matière colorante provenait

* 'Tirage à part du Recueil Zoologique,' t. v. fasc. 1. "Sur l'*Agalma Clausi*."

des tentacles comme on le voit souvent chez les *Forskalia*. Mais j'ai pu me convaincre plus tard que ce n'était pas le cas. Cette couleur est produite par les boucliers ; les taches rouges qui se trouvent à leur surface sont des espèces de petites glandes, qui éclatent et laissent échapper la matière colorante.

"Lorsqu'on observe ces glandes au microscope, on voit (fig. 2, *gl*) qu'elles sont formées par une agglomération de cellules contenant un noyau et un protoplasme rempli de grosses granulations. Elles ont une forme sphérique ou allongée et sont implantés dans la substance gélatineuse, de telle sorte que la moitié de la glande, à peu près, dépasse la surface du bouclier. Elles sont recouvertes par l'épithélium. Lorsque le contenu de la glande s'est déversé au dehors, toute trace de cellule glandulaire a disparu et il ne reste plus, sur le bouclier, qu'une petite excavation entourée d'un léger nuage jaune.

"On remarque encore une quantité de petits corps sphériques qui forment une bordure autour de la gland et s'étendent ensuite en traînée jusqu'au bord du bouclier, parallèlement à son grand axe. Ces corps sphériques (fig. 14. 27, et fig. 2, *ct*) ne disparaissent pas après l'explosion de la glande (fig. 37). Ils sont formés d'une enveloppe creuse à paroi épaisse (fig. 14, *e*) et à l'intérieur se trouve un corpuscule également sphérique (*s*) accolé à la paroi. Sa structure est difficile à observer ; néanmoins on peut distinguer à l'intérieur une figure qui rappelle le fil d'un nematocyste. Ces corps se rencontrent sur les boucliers d'autres espèces de Siphonophores. Ils ont été déjà mentionnés comme étant des nematocystes, mais, je crois, sans qu'on en ait fourni la preuve, sans qu'on ait pu observer le fil déroulé. Il est très possible que cette opinion soit fondée, ou, tout au moins, que l'on ait affaire ici à une forme spéciale de cellule urticante. On les trouve souvent accumulés au bord du bouclier de l'*Agalma Clausi*, parfois aussi, ils y forment seulement de petits amas placés de distance en distance."

There is little doubt that while the bodies mentioned above have sometimes been mistaken for nematocysts, and while there is nothing to show that they have not in their interior the "fil d'un nematocyste," a distinction ought to be made between them and true nematocysts. We find similar rows of bodies not only among the Siphonophores, but also on the bell of many Hydromedusæ. It is doubtful, for example, whether the meridional lines on the external bell-walls of *Ectopleura* are rows of nematocysts, as they are generally considered, and the same is possibly true of the peculiar nematocyst-like bodies on the outer surface of the

bell of genera like *Gemmaria* and *Willia*. In *Athorybia* also the rows of so-called nematocysts on the outer walls of the covering-scales do not in many cases show the "fil d'un nematocyste," and therefore we may well question whether they are functionally nematocysts, lacking as they do this characteristic internal organization of these organs. Still the homology of these structures with nematocysts is an open question, and it remains yet to be seen whether they might not be regarded as lasso-cells in which certain parts have suffered a change in form.

There seems nothing to prevent our accepting the theory that the "corps sphériques" of the above description are homologues of nematocysts, and Bedot's figure, as far as it goes, does not disprove that they are these organs even if the central "thread" is absent.

Between these spherical bodies, however, and the pigment-pouches or glands Bedot thinks it necessary to recognize a distinction, and certainly their form is very different and justifies his views in this regard. Moreover the pigment-glands discharge their contents, whereas the spherical bodies do not have this power. Is there, however, anything to show that the pigment-glands are not more completely developed clusters of the so-called spherical bodies? and may not the pigment-gland be formed by an aggregation and maturation of the spherical bodies? Such an interpretation was given the coloured bodies when I studied them, and there is no new evidence to lead me to abandon my former opinion. The "pigment-spots" were at that time regarded as remotely represented in *Apolemia* "by elevations composed of *clusters* of cells on the surface of the tract." My use of the word cell with two meanings, one as a lasso-cell and the other as a histological cell, has led to a confusion and a just criticism by Bedot. I consider the pigment-glands to be formed of an aggregation of nucleated cells, and each pigment-spot to be comparable to a nematocyst (lasso-cell).

In some genera irritation of the animal leads to a change in colour of the covering-scale, which may be akin to the discharge of pigment from these bodies. This phenomenon seems also to be connected with pigment-cells in the organs, although the character of these structures has not been fully described.

Dr. Carl Chun mentions a change of colour of the covering-scales in *Ceratocymba spectabilis* from the Canaries. He speaks of this phenomenon in the following manner:—

"Sehr eigenthümlich verhält sich das Deckstück bei stärkerer Berührung, insofern auf einen Reiz hin zuerst in der

Umgebung der beiden hornförmigen Canäle des Oelbehälters und späterhin auch von den Ecken beginnend in der gesammten Gallerte eine weissliche Trübung auftritt. Dieselbe beruht auf dem Erscheinen ausserordentlich feiner Körnchen, die wieder (nach etwa einer halben Stunde) verschwinden, wenn die Eudoxie der Ruhe überlassen wird. Die eigenthümliche Trübung erinnert an eine analoger Erscheinung bei Hippopodius nur dass hier die auf einen Reiz erfolgende und später verschwindende milchige Färbung an die Ektodermzellen der Schwimmglocken gebunden ist. In gewissem Sinne muss selbst die structurlose Gallerte des Deckstückes einem Reize zugänglich sein, wie das allmähliche Auftauchen und ebenso langsame Verschwinden einer ziemlich intensiven Trübung beweist."

We might possibly compare this phenomenon with the cutaneous circulation and change of colour in pelagic fish-embryos and in Cephalopoda; but we know so little of the organs by which it is produced that one can as yet hardly venture an explanation.

The excretion and discharge of a coloured fluid from those organs which are known as "cystons" or tasters with a terminal opening has been noticed by several authors. Both Kölliker and Leuckart speak of it, although they seem to regard the discharge as due to a rupture of the wall rather than [as taking place] through a normal terminal opening. Kölliker says, "Ohne Zweifel ist diese Substanz ein Excretionstoff, doch wird ohne genauer Kenntniss ihrer chemischen Beschaffenheit nichts Näheres über ihre Bedeutung beizubringen sein."

Hæckel describes the structure of these Cystons or "anal vesicles," showing that they are excretory organs with a terminal anus and glandular walls often highly coloured. They are, according to him, confined to the Physophores, mainly to the Apolemidæ, Agalmidæ, and Forskalidæ.

The "cystons" or hydrocysts with "mouths" in the Agalmidæ are often, according to Hæckel (*op. cit.* p. 219), coloured red or brown, and "the fluid secretion, or the pigmented granular or crystalline masses secreted by it, are ejected by the distal mouth, or, rather, the anal opening, which is closed by a muscular sphincter." In the genus *Forskalia* the same author says, "When a quietly floating *Forskalia* is touched it suddenly discharges the contents of the chromadenia [pigment-glands] and makes the surrounding water dark and intransparent."

Hæckel offers the following explanation of the phenomenon in *Forskalia*:—"The excretion of the pigment-masses and

the darkening of the water by it have probably the same physiological function as in the Cephalopoda—to protect the attacked animal from its persecutors and facilitate the capture of food-animals."

The character of the "cystons" in a genus of Apolemidæ called *Dicymbia* is described by Hæckel. Each "cormidium" or cluster of the stem is said to have in this genus a single deep-red cyston, and the secreted pigment is accumulated in a "head-like terminal expansion of the distal proboscis, and thrown out by a small terminal opening, the anus."

In *Apolemia uvaria* *, which often reaches a great size, I have repeatedly observed the so-called "cystons" in specimens from Villa Franca. Hæckel simply mentions the fact that each cormidium of this genus has several cystons, but gives no special description of them.

The cystons of *Apolemia* are brick-red in colour and easily distinguished from the remaining appendages of the cormidium. Their general relationship to the covering-scales may be seen in my figure of the axis of the well-known *A. uvaria* from the Mediterranean. I have not seen them discharge their excretions †, but the intensity of their colour varies in different individuals and in different cormidia on the axis. Although I have repeatedly watched the well-known "lana di mare" *Apolemia*, I have never been fortunate enough to discover one which ejected colouring-matter from these reddish bodies, and have not been able to produce it by an irritation of the animals.

There is a peculiarity in the tasters of the genus *Nanomia* which would seem to have a bearing on the discussion of the pigmented bodies of the cystons.

A. Agassiz, in his description of *Nanomia*, called attention to the pigment at the base of the taster of this genus, which he designated as an "oil-globule." He supposed that this body formed the float of the young *Nanomia* which budded from the parent. From a comparison of this oil-globule with the float of the adult I have shown that a derivation of the young from the adult by budding is improbable. Still oil-globules are very conspicuous structures on the stem of the *Nanomia*, and have not been observed by me in other genera. Consequently, although the tentacular knobs and most of the

* The existence of what I have called "nectotasters" or tentacular appendages to the nectostem in *Apolemia* is not mentioned by Hæckel (*op. cit.*), although it is an exceptional feature in *Apolemia*. These appendages and the stem which bears the nectocalyces of *Apolemia* are easily seen and have been figured and described. Kölliker speaks of them as the "Fuhler zwischen den Schwimmglocken."

† Bull. Mus. Comp. Zool. vol. viii. no. 7.

other structures of *Nanomia* are identical with those of *Agalmopsis pictum*, a genus to which I formerly referred *Nanomia*, the exceptional character of the cystons seems to me to separate it from Sars's genus.

The "oil-globule" forms a swelling at the proximal end of the "cyston," and was not observed to be ruptured. There seems, in point of fact, to be no opening through which it can be discharged. Its regular form, its constancy, its position, all stamp it as an organ of some kind. If we regard it as a float of a new individual it differs very greatly from the adult float of *Nanomia*. If we consider it a pigmented accumulation of excretory matter we disregard completely its character as far as the examination which has been made goes. It seems as if it should be regarded as connected in some way or another with the function of the cystons, but how I am unable at present to say.

Reviewing the data which have been brought forward, we have the following facts bearing on the discharges of a coloured fluid from organs of the body or the modification in colour due to irritation in Siphonophores.

1. Certain Agalmidæ, Forskalidæ, and Apolemidæ discharge a coloured fluid from their cystons. This fluid is regarded as an excretion and is supposed by Hæckel in one case to be the means of protection, as the sepia of the Cephalopoda.

2. A typical genus of Agalmidæ (*Agalma*) has pigment-glands on the bracts which discharge their contents when the covering-scales are broken from the stem. This discharge probably takes place on simple irritation.

3. Certain Hippopodidæ and a single known monogastric Calycophore change colour somewhat on irritation (see Chun's description above).

4. *Nanomia* has a prominent pigmented "oil-globule" at the base of the cyston, which has never been seen to discharge its contents.

What conclusions may be drawn from the above statements? Are we dealing here with phenomena of a similar character, or have we organs with two or three different functions? Are these discharges when they occur simply the throwing off of excretions, or do they also serve for protection of the Medusa from its foes?

It seems not improbable that the physiological function of certain of the tasters, which are known as cystons in *Forskalia*, is that of excretion. This power of throwing off excretions may also serve for protection. Yet it must be borne in mind that all the Calycophoridæ, the Pneumatophoridæ, and Hippo-

podidæ have no cystons or similar excretory organs, nor has the function of excretion yet been referred in them to any special organs. Is it possible that the discharge of coloured matter from the pigment-cells of the bract of *Agalma* is also a method of excretion? and is it the same as that of the cystons of *Forskalia*? It seems to me improbable that we have to deal with excretions only in this case, although we may have an instance of a novel means of protection, which is in part accomplished by the discharge of the excretion in *Forskalia*. Upon this theory, however, we need much more light, which can best come from more observation.

It is legitimate to conclude that the discharge of a highly coloured fluid by the scales of *Agalma* is in part a means of protection for the Medusa, and it would seem natural to connect it with the function of excretion; but we know so little about the character of the excretions and the manner in which they are produced in Medusæ, that at present we can hardly definitely ascribe the special function to these glands. Possibly similar glands are found in other Physophores, and the excretion has not been recognized from the fact that it is not so highly coloured as in *Agalma Clausi* and *Forskalia*. The discharge of this fluid from a living animal, if it take place without rupture of the wall of the scale, would imply special excretory openings somewhere on the bract; and one is tempted to search for such openings, if they exist, on the distal tip of the scale, when they would be homologous with the excretory openings known to exist on the bell-margin of certain Hydromedusæ, as Metschnikoff and others have shown.

If we accept the theory that the discharge of a coloured fluid is a method of defence, the question arises, How is that defence accomplished? Does the fluid darken the water in the immediate vicinity of the Medusa which possesses this power and in that way conceal it from its foes, as in the case of the Cephalopoda? or does it serve, as is possibly the case with the rattle of the rattlesnake, to warn away its enemies? May it not even bewilder its prey and thus be rather a means of capturing its food than of self-protection? Has it possibly a poisonous nature fatal to its prey or foes? Our knowledge of its nature is all too small to give us an answer to these questions. Its bright colour would indicate that even if it is poisonous this is not its only property, or its sole function that of killing its enemies or prey. The ability to change the colour mentioned in *Ceratocymba* by Dr. Chun might come in the same category as a similar power in fishes and Cephalopoda. In that case we might have a kind of cutaneous

pigment-circulation. The discharge of pigment, however, is something different and possibly capable of a very different interpretation.

Is the discharge normal or abnormal? Is it a result of extraordinary conditions under which the animal is placed in confinement in our aquaria, or is it an habitual mode of protection? It seems to me that the latter interpretation will best satisfy our limited knowledge; and although when the bracts are broken the discharge is more voluminous, since the glands are wholly emptied of their contents, the method of its discharge shows it to be a function which is perfectly normal.

It seems to me that we have in these "glands" the homologues of nematocysts, the thread of which is wanting and the cells of the interior of which have degenerated or rather specialized into pigment-bodies, instead of functioning as an urticating-thread. These modified nematocysts throw off a coloured fluid which, while it serves in a similar way in protection or in killing its prey, bears little morphological likeness to the well-known lasso-cell.

XLV.—*On the so-called Cretaceous Lizard*, Rhaphiosaurus.

By A. Smith Woodward, F.G.S., F.Z.S., of the British Museum (Natural History).

In 1840 Prof. Sir Richard Owen described a small portion of mandible from the Lower Chalk of Cambridgeshire under the name of *Rhaphiosaurus* *, regarding the fossil as referable to a Lacertilian Reptile and provisionally associating with it a series of undoubted Reptilian vertebræ from the Lower Chalk of Burham, Kent. Ten years later the vertebræ proved to pertain to a distinct generic type named *Dolichosaurus* †; and the original jaw thus remained as the sole evidence of the existence of *Rhaphiosaurus*. In 1865 Prof. Seeley ‡ stated incidentally that the specimen so determined probably belonged to a fish; and still more recently the genus has been recorded § as one requiring further elucidation.

* R. Owen, "Description of the Vertebral Column &c. of a small Lacertine Saurian from the Chalk," Trans. Geol. Soc. [2] vol. vi. (1840) p. 413, pl. xxxix. fig. 3. *Rhaphiosaurus subulidens*, Owen, Brit. Assoc. Rep. 1841, p. 190. *R. lucius*, Owen, in Dixon's 'Geol. Sussex' (1850), p. 385, pl. xxxix. figs. 1–3. *R. subulidens*, Owen, "Foss. Rept. Cret. Form." (Pal. Soc. 1851), p. 19, pl. x. figs. 5, 6.

† R. Owen, "Foss. Rept. Cret. Form." (Pal. Soc. 1851), p. 22.

‡ H. G. Seeley, Ann. & Mag. Nat. Hist. [3] vol. xvi. p. 145.

§ Smith Woodward, "A Synopsis of the Vertebrate Fossils of the English Chalk," Proc. Geol. Assoc. vol. x. (1888) p. 281.