A Note on the Occurrence of Nematocysts and Similar Structures in the Various Groups of the Animal Kingdom.

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With 8 Text figures.

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I. Introduction.

The number of groups of the animal kingdom in members of which Nematocysts have been described has not. I believe, been commonly recognised, since the references in the literature are very scattered, and in most instances have not found their way into the text books.

In this paper I have tried to put together all the references I could find to the occurrence of Nematocysts in various animals, and although this list is probably by no means exhaustive, still it includes representatives of no less than six Phyla (viz., Protozoa, Sponges, Turbellaria, Nemertinea, Mollusca, Chordata). In many of these instances the animals are so rare that it seems hopeless to delay publication until a personal examination has been made of each case, so that I have thought under the circumstances that the publication of a summary examination of the evidence even in these cases might not be without value.

The terminology of Nematocysts is in such a confused state that it will first be necessary to define clearly in what sense the various terms are used in this paper, since in most cases it seems quite impossible to harmonise the various usages to which these terms have been put by previous authors.

A Nematocyst in a Coelenterate consists of a capsule containing a rolled-up thread and an amorphus substance; the thread can be everted when the Nematocyst is placed under suitable conditions, and then remains attached to the capsule (distinction from the Spirocysts of Anthozoa).

A Nematocyst or Cnida is apparently always developed singly in a special cell, the Nematoblast or Cnidoblast. The word Nematoblast (= Cnidoblast) is here used for the cell which is about to form or has formed a Nematocyst. This seems to be the most

general usage of these terms, e.g. (Delage, Sedgwick, Bourne, Fowler, etc.) although Chun and Bedot have attempted to confine this word to that part of the Nematoblast cell which is actually converted into the Nematocyst, and Grosvenor has I think unfortunately used the word Nematoblast in Aeolids for the cells in the cnidosacs which ingest the Nematocysts (vid. p. 482 of his paper "On the Nematocysts of Aeolids"). —

"It is round this basal end of each enidoblast that the membranous cyst is first secreted; the cnidoblast itself is drawn away from this point towards the lumen of the cnidosac, and does not apparently take part in the secretion of the cyst, but in the meantime ingests nematocysts at its opposite end, which remains naked

and amoeboid."

It will not be necessary to give here a full history of the earlier theories of the mechanism of the Nematocyst explosion, as this has already been done by Lendenfeldt in his two valuable summaries of Nematocyst work published in the Biologisches Centralblatt for 1887 and 1897.

In nearly all these early theories the main cause of the explosion of the Nematocyst was thought to be a contraction either of a muscular wall surrounding the Nematocyst, e.g. Chun or of the capsule wall itself, and as Lendenfeldt remarks, p. 522, "Es ist selbstverständlich, dass alle diese Erklärungen der mechanischen Schussursache, eine Verkleinerung des Volumens der Kapsel beim Schusse, wie sie Zoja (s. o.) auch tatsächlich beobachtet haben will, voraussetzen."

Now it is the great merit of Iwanzoff, 1896, that he seems to have been the first to regard the Nematocysts as absolutely dead structures the mechanism of which could be explained on purely physical grounds. He was able to show quite clearly that Nematocysts could explode under conditions which absolutely exclude all possibility of a nervous, muscular or cytoplasmic factor (p. 141).

I wanzoff's explanation depends upon the fact that the cause of the expulsion of the thread is the entrance of water into the

capsule.

The whole of the factors involved in the discharge of a Nematocyst in a Coelenterate are not, yet I believe, satisfactorily accounted for. But the main fact that the process is, as far as the capsule is concerned, a purely physical one, is I think abundantly clear.

There seems to be no necessity to enter here into a detailed account of the work of later authors in this field, nor of the vast literature that has grown up on the subject of the development of the Nematocyst. There is however one point in the behaviour of Nematoblasts which I should like to refer to here, and that is their power of conveying in a hydroid the Nematocyst from the point

at which it is developed to the point at which it is used. This interesting subject was first opened up by the work of Hadzi, and the behaviour of the Nematoblast in these cases seems to present an interesting analogy to the behaviour of the Phagocyte cells in *Turbellaria*, which carry the ingested Nematocysts from the gut to their definitive position under the skin. To this point I will return in the conclusion of this paper.

In addition to the true Nematocysts referred to above, which are I believe only developed in and characteristic of the group of Coelenterates, certain structures have been described under the name of Nematocyst in other animals. For the purposes of this paper I have decided to divide all these structures into five

categories. -

(1) Autocnidae.

By this term I wish to imply that the Nematocyst has been developed singly, in a true Nematoblast within the tissue of its possessor. The Autocnidae are I believe confined to and characteristic of a single group of *Metazou* the Coelenterates.

(2) Cleptocnidae1).

Under this term I wish to include the Coelenterate Nematocysts which have been ingested with the food and are found in an unexploded condition in the tissue of their possessor (e. g. the Nematocysts of Aeolids, *Turbellaria*, etc.).

(3) Pseudocnidae.

Under this term I wish to include a number of structures which are almost certainly not homologous, and which have often been confused with true Nematocysts. This group is a very heterogeneous one, it includes on the one hand structure containing a spiral thread which can be discharged, e. g., the Nematocysts of certain Nemertines. Structures which can under certain conditions emit a thread, but in which the thread is not pre-formed within a capsule (e. g., The so-called Nematocysts of Epistylis and Otoplana) and a certain number of structures which have been described as Nematocysts especially amongst the Turbellaria, and in which no trace of a thread has been discovered.

(4) Polar Capsules.

These structures appear to be strictly analogous structures as regards development, structure, and mechanism, to the Nematocysts of Coelenterates, but they are confined to and characteristic of a single group of the *Sporozoa*.

¹⁾ For the suggestion of this useful term I am indebted to my former Tutor, Mr R. T. Günther, of Magdalen College, Oxford.

(5) Spirocyste		Anthozoa					201
(4) Polar Capsules	Cnidosporidea						
(3) Pseudocnidae	Epistylis umbellaria			Alaurina viridirostrum Polycystis Nagelii " mamertina Trigonostomum armatus Otoplana setosa (?) Anonymus virilis	Micrura purpurea " dellechiajei Cerebratulus urticans Lineus geniculatus		Appendicularia urticans
(2) Cleptocnidae	Polykrikos (?) Holophrya oblonga Kentrona Ophryodendron sertulariae		Renierina (?)	Microstomum lineare " rubroculatum " ingens Stenostoma sieboldii Peudostoma mollissima(?) Allostoma monotrochum Stylochoplana tarda		Aeolidoidae Tremoctopus microstoma	
(1) Autoenidae		Cnidaria					
1 Protozoa	(4) Acinetaria	II. Coelenterata	III. Porifera	IV. Turbellaria (1) Rhabdocoelida (2) Polycladida	V. Nemertinea	VI. Mollusca (1) Gastropoda (2) Cephalopoda	VIII. Chordata

(5) Spirocysts.

These structures, as far as I am aware, are confined to one group of the Coelenterates the *Antho:oa*. They are hollow capsules containing a solid spiral thread, in which the thread is discharged as a whole and is of course not everted. In the following table an attempt has been made to distribute the various structures which have been described as Nematocyts in the various animals into these five categories. The evidence on which this distribution is based will be found in a later part of this paper.

Part II. Nematocysts and Similar Structures in (1) The Protozoa.

In this part of my paper I do not propose giving any detailed account of the polar capsules of the Cnidosporidea, or the Trichocysts of Ciliates. On the other hand, I propose to discuss in some detail,

- (1) The Cleptocnidae found in certain Ciliates and Acinetaria.
- (2) The Cleptocnidae of the Dinoflagellate Polykrikos.

(3) The Pseudocnidae of Epistylis Umbellaria.

The polar capsules of the spores of the Cnidosporidea are small chitinous (?) pear shaped capsules containing a spirally coiled thread and developed singly in special cells, the Capsulogenous cells. The thread can under suitable conditions be everted in a manner absolutely analogous to that in the exploding Nematocyst of a Coelenterate, and probably serves for the attachment of the spore to the gut wall of the host, cf. Doflein, p. 861. As regards the development of these structures Awerinzew states on page 101 of his "Studien über parasitische Protozoen", 1909. —

"Obgleich es mir, infolge der unbedeutenden Größe des Objektes, nicht gelungen ist, die Bildung der Polkapseln in den Sporen von Ceratomyxa drepanopsettae in erschöpfender Vollständigkeit zu verfolgen, so erweist sich doch die Entwickelung dieser Kapseln nicht allein in ihren allgemeinen Zügen, sondern auch in allen Einzelheiten, als durchaus übereinstimmend mit der Entwickelung der Nesselorgane bei den Coelenterata (vgl. Iwanzoff, 1897)."

The Trichocysts of Infusoria have been defined by Doflein in the following passage, p. 285 of his "Lehrbuch der Protozoenkunde"

"Trichocysten sind im Kortikalplasma liegende, besonders bei holotrichen Infusorien weitverbreitete stäbchen- und spindelförmige Gebilde, welche durch ihre starke Lichtbrechung auffallen. Sie sind vielfach in kleinen Gruppen an verschiedenen Stellen im Körper angehäuft oder ziemlich gleichmäßig über dessen Oberfläche verteilt, zu welcher sie senkrecht stehen. Bei Einwirkung von chemischen Reizen oder von Druck werden sie ausgeschnellt, wobei sie zu langen Fäden werden, deren Enden bei manchen Infusorien

im Körper stecken bleiben (z. B. Lionotus), während sie bei anderen ganz ausgestoßen werden. Man hat diese Bildungen als Angriffsund Schutzwaffen gedeutet; doch ist diese Deutung unsicher, und es ist möglich, dass die Ausstoßung nur bei starken Reizen infolge von Quellungserscheinungen erfolgt."

The history of the earlier observations of these structures has been given by Bütschli in his account of the Protozoa in Bronn's Tierreich, p. 1459. From this it would appear that the discharge of these structures was first observed by Allmann in 1855. compared them to the Nematocysts of Coelenterates, but this view seems now entirely discarded. For example, Minchin in his introduction to the Study of Protozoa. 1912, p. 447, states — "Nor does there seem to be any ground for comparing it (the Trichocyst) to a Coelenterate Nematocyst or to a polar capsule of a Cnidosporidian spore".

More modern views on the structure and mechanism of Trichocysts can be found in the works of Schuberg and Khainsky.

In my paper on "Some Observations on Acinetaria, Part 3, The Dimorphism of Ophryodendron", Q. J. M. S., Vol. 53, Part 3, May 1909, I have already had occasion to refer to two cases of the presence of Cleptocnidae in the Ciliates in Kentrona and Holophrya oblonga.

The Kentrona in question were found crawling on rather moribund hydra, and were found to contain undischarged Nematocysts of the hydra in fair numbers.

In Naples, in the year 1908, I met with a large holotrichous Ciliate, which I am inclined to identify with Holophrya oblonga, crawling on the stalks of Eudendrium. The Ciliate was found to contain two kinds of Nematocyst absolutely identical with those of the Eudendrium. It also contained large numbers of chromatin granules, which I am inclined to derive from the partly digested nuclei of the Nematoblast cells of the hydroid. A direct proof of the origin of similar chromatin granules and Nematocysts in the case of an Acinetaria Ophryodendron abietinum has been given by me in my paper on this form in the Q. J. M. S., Vol. 53, 1909, -

"Ophryodendron abietinum was first discovered by Claparède and Lachmann in 1855 on Campanularia from the North Sea . . . "

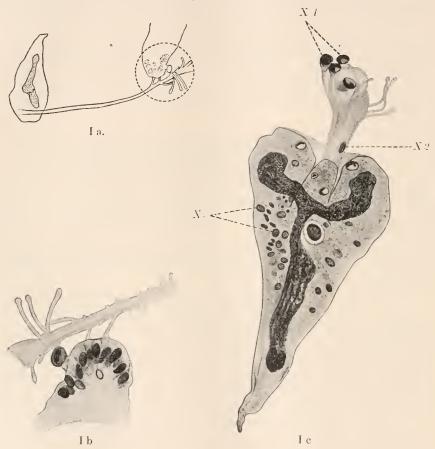
"They recognised in the interior of some animals both of the veriform and proboscidiform type small corpuscles 'tout a fait semblables aux organes urticants des Campanulaires' (p. 144), but as all their efforts to surprise the animal at the moment of feeding were vain (p. 145), they concluded that 'les corpuscles particuliers qu'ils renferment sont peut-être comparable aux trichocystes d'autres infusoires'."

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XXXIV.

On page 645 of the paper referred to above will be found an account of the method of feeding in Ophryodendron. –

"In an Ophryodendron abietinum which was drawn while feeding, it was noticed that the tentacles of the Ophryodendron were wrapped around the tentacles of the hydroid. After a short time the proboscis of the Ophryodendron was retracted, and the nematoblasts with their contained nematocysts could be seen sticking for some



time in the aperture of the tentacles, giving the tentacles a curious knobbed appearance. It is this appearance that is possibly responsible for the figures of knobbed tentacles in Ophryodendron.

The nematoblasts could now be seen passing down the proboscis into the body of the animal with a peculiar gliding motion. In the course of this passage the long axis of the nematocyst was always parrellel to the long axis of the proboscis; and when the nematoblasts passed simultaneously down the proboscis they followed parallel paths, thus indicating a feature that has already been

described in the sections of the proboscis, the prolongation of the tentacles as separate tubes down the proboscis. The first stage in feeding is shown in Pl. 15, figs. 1 and 2, in which one nematoblast has been pulled out of its position in the ectoderm of the hydroid, the later stage is shown in a drawing from a living specimen, textfig. 3, and from a stained preparation Pl. 15, fig. 3. It would seem that the size of the nematoblasts prevents their passage down the tentacles as long as the proboscis is in its fully extended condition.

After passing down the proboscis the ingested ectodermal cells may be found (Pl. 15, fig. 3) lying in the cytoplasm of the Ophryodendron, and in some cases the whole body is absolutely blocked by them. The cytoplasm of these cells seems to undergo fairly rapid digestion, but the nucleus is far more resistant; in early stages the nucleus retains its characteristic shield-shape and vacuolar appearance, but under the influence of the digestive enzyme its structure breaks down, and finally the only trace left of it is a

number of dots of darkly staining matter lying in small vacuoles dotted through the cytoplasm of the animal."

In all these cases of the presence of Cleptoenids in Protozoa, there is no evidence that these structures are of any value to the animals that contain them, and in this point these cases differ from the Cleptocnid in Turbellaria and Aeolids which are described below.





IIb.

There is one further case of the occurrence of Nematocysts in the group of Protocoa which I am inclined to place in this category, and that is the occurrence of Nematocysts in the Dinoflagellate Polykrikos. I have unfortunately never been able to obtain an example of this animal, and therefore it is impossible for me to arrive at a definite conclusion of this question.

These structures are fully described by Bütschli in his work

on Protosoa, Band I, p. 970,

"Zu den merkwürdigsten Erzeugnissen des Plasmas einer Dinoflagellatenform gehören die Nesselkapseln und sind in vieler Hinsicht beachtenswert. Einmal, weil sie unter den zurzeit bekannten Formen ganz unvermittelt bei der einzigen Gattung Polykrikos auftreten und weil sie viel höher entwickelt sind als bei sonstigen Protozoen. Wohl begegnet man ja bei Flagellaten und Ciliaten nicht selten den in mancher Hinsicht nesselkapselartigen Trichocysten, nur bei einer einzigen Ciliatenform aber (Epistylis flavicans) wurden echte Nesselkapseln beobachtet, die wir unter den Protozoen sonst nur noch bei den Myxosporidien finden. Doch ist die Ausbildung der Kapseln in den letztgenannten Fällen eine viel einfachere, während diejenigen der Polykrikos denen der Cölenteraten selbst in feineren Verhältnissen entsprechen.

Die Kapseln liegen in nicht gerade sehr erheblicher Zahl in der äußeren Plasmaregion des Körpers (55, 8; nh), dem Ektoplasma Bergh's, und treten, wie letzterer nachwies, in verschiedenen Entwickelungsstadien auf, wodurch der Einwand, dass sie nicht genuine Teile des Organismus seien, widerlegt wird."

The presence of developing stages of Nematocysts in an animal is no argument against their possible exogenous origin since it is just as possible for an animal to eat developing as mature Nematoblasts in its hydroid prey. The view that these Nematocysts of Polykrikos are of exogenous origin is by no means new, since Saville Kent had already formulated it in his Monograph of the Infusoria.

Personally as I stated above I am inclined to place these structures in the category of Cleptocnids, and if in the future this origin of the Nematocyst can be definitely proved it would le very temptingto regard the Micronuclei described by Bergh for Polykrikos and which are absolutely unique in the Dinoflagellates as the ingested nuclei of the Nematoblast cells.

The Pseudocnidae of Epistylis Umbellaria.

The history of these interesting structures is given in a concise form by Bütschli, page 1469, in his work on the *Protozoa*. —

"Die Entdecker der Organe, Claparède und Lachmann, bemerkten den Faden nicht und wagten kein Urteil über ihre Bedeutung. Auch Engelmann (1862, p. 26) kam nicht weiter. Erst Greeff entdeckte den Faden und das Ausschnellen. Dennoch zögerte er, sie bestimmt als Nesselkapseln anzuerkennen, da die Möglichkeit, dass sie von außen eingedrungen seien, nicht ausgeschlossen wäre."

Bütschli has also described the form and distribution of these structures in a passage on page 1468 of his work on *Protozoa*.

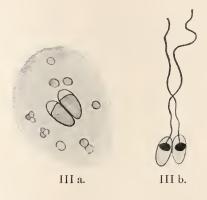
"Die Nesselorgane der Epistylis Umbellaria entdeckten Claparède und Lachmann 1858. Sie liegen ziemlich zerstreut in der Kortikalschicht, der Oberfläche parallel, nicht senkrecht zu derselben. Mit seltenen Ausnahmen (Claparède, Greeff) sind stets zwei der länglichen, etwas bohnenförmigen Kapseln paarweise zusammengestellt (74, 76, e) indem sie sich mit ihren geraden oder sogar etwas konkaven Längsseiten berühren . . . Die beiden Kapselpole sind mäßig zugespitzt; der eine ist etwas stumpfer und von ihm entspringt der in dem Kapselinnern aufgerollte Faden. Letzterer läuft, wie in den Kapseln der Cölenteraten, zunächst eine kleine Strecke in der Achse nach hinten und rollt sich hierauf in engen Schraubenwindungen auf. Hauptsächlich deshalb erscheint

wohl das stumpfe Ende hell, der größere Teil der Kapsel dagegen, welcher den dicht aufgerollten Fadenabschnitt enthält, dunkel. Die gleichnamigen Kapselpole sind gewöhnlich in den Paaren gleichgerichtet, zuweilen (Bütschli) schauen sie jedoch auch nach entgegengesetzten Seiten.

Spontane Entladung wurde bis jetzt nie beobachtet; doch kann man die Kapseln durch Druck leicht zur Explosion bringen. Der Faden tritt dann in etwa 8-10facher Länge der Kapsel hervor und die ziemlich derbe Wand der letzteren ist deutlich zu erkennen. Nach Greeff widerstehen die Kapseln der Einwirkung von Kali.

Dass die Gebilde echte Nesselkapseln sind und daher auch zweifellos wie solche funktionieren, ist nicht fraglich; ebensowenig jedoch, dass sie genuine Erzeugnisse der Epistylis sind. Schon die paarweise Vereinigung ist so charakteristisch, dass jeder Zweifel unmöglich scheint."

My reasons for placing these structures in the category of Pseudocnidae rest principally upon some observations on the living animal. The Pseudocnidae in the specimens I examined were found in pairs, and in the undischarged state they seemed to be elliptical capsules with a clear area at one pole and a rather darkly gelatinous content. In the unexploded condition, in spite of careful search I could find no trace of a preformed thread. In forms



treated with methylene blue in 1% acetic acid in distilled water a thickish thread was discharged from the clear pole of the Pseudocnidae. This thread could be traced back into the amorphous mass which remained in the capsule and which in the discharged Nematocyst was reduced to about one-third of its original volume. In sections of these structures I could find no traces of the thread.

I am inclined to regard these structures as highly developed Trichocysts, since the characteristic preformed thread of a true Nematocyst seems as far as my observations go to be absent.

II. (2) Sponges.

In a paper on "Nesselzellen und Samen bei Seeschwämmen" in the Archiv für Mikr. Anatomie, Band VIII, Eimer has described Nematocysts in certain Sponges. On page 281 of this paper he states:

"Das wichtigste dieser Ergebnisse ist das, dass ich mehrere Arten von Kieselschwämmen mit Nesselzellen gefunden habe.

Die betreffenden Schwämme sind den Renierinen (O. Schm.) teils nahestehend, teils gehören sie in diese Familie."

As far as I can gather from the paper, which is not too clear, Eimer discovered Nematocysts in four distinct species of Sponge, none of which he names definitely.

As regards the description of the Nematocysts in the Sponge

itself, I shall merely quote a passage on page 282. —

"In diesem Gewebe liegen überall Nesselzellen zerstreut, einzeln oder in kleinen Häufchen, und zwar sehr zahlreich. Eine sehr bestimmte Anordnung zeigen diese Nesselzellen nicht. Sie liegen aber sehr oft um die Nadeln herum und umgeben am häufigsten die Einströmungsöffnungen in deren ganzem Verlauf. In besonders großer Menge aber kleiden sie die Magenhöhle des Schwammes aus; allein auch hier kommen sie nicht etwa in einer zusammenhängenden Lage vor, sind vielmehr zerstreut, wie im Innern. Da-

gegen scheinen sie auf der Oberfläche des

Tieres sich nicht zu finden."

Eimer gives two rough diagrams of the Nematocysts in their exploded condition which are copied in Text Figure IV.

Iwanz off on page 354 of his paper "Über den Bau, die Wirkungsweise und die Entwickelung der Nesselkapseln der Cölenteraten" states:

Ich untersuche einige von den von Eimer angegebenen Formen, doch konnte ich keine Nematocysten finden. Es ist sehr möglich, dass Eimer durch kleine im Leibe der Schwämme parasitierende Hydroiden irre geleitet wurde. Derselben Meinung ist auch Prof. Vosmaer, wie ich aus persönlichem Gespräche erfahren habe."

As far as I am aware these parasitic hydroids in Sponges are of a purely hypothetical nature, and until they have been adequately described I have felt that it would be safer to regard these Nemato-

cysts of Sponges as Cleptocnids.

IV a.

IV b.

It is important to note that these Sponges were attached to the carapace of a crab, and it would seem possible that occasionally the inhalant currents of the Sponge might carry Nematocysts from Coelenterates which had been torn up by the crab into the tissue of the Sponge, where they might be engulfed by Phagocytes. This hypothesis would appear to me to explain I wan zoff's failure to find Nematocysts in the Sponges which he examined, and also the remarkable resemblance of the Nematocysts of *Palythoa axinellae* as figured by I wan zoff to the second Nematocyst figured by Eimer.

II. (3) Turbellaria.

The references to the early literature on the occurrence of Nematocysts in the Turbellaria can be found in my paper "On the Nematocysts of Turbellaria", Q. J. M. S., Vol. 52, 1908.

In dealing with the group Rhabdocoelida in which the nomenclature appears to change in a somewhat kaleidiscopic fashion, I have decided in this paper to use the names given in von Graff's volume on the Turbellaria in Bronn's Tierreich. In some cases therefore the names in this list do not agree with the names given in my previous paper which were taken from von Graff's Monograph on the Turbellaria.

It appears to me that the Nematocysts described in the Rhabdocoelida can be treated in two categories, (a) Pseudocnidae,

(b) Cleptocnidae.

(a) Pseudocnidae.

Under this category I am inclined to place the cases described for the occurrence of Nematocysts in Alaurina viridirostrum, Polycystis Nagelii, Polycystis mamertina, Trigonostomum armatum, and Otoplana setosa.

I have given the evidence on which I am inclined to regard the so-called Nematocysts of Polycystis Nagelii and P. mamertina as rhabdites possibly specialized for prehensile purposes in my former paper. The Nematocysts described by Jensen in Trigonostomum armatum have already been placed by von Graff in the category Sagittocysts, though it is evident that he does so with

some feeling of reserve (see p. 2040).

"Ob diese, bei den Acoela (S. 1916) in so charakteristischer Ausprägung vorhandenen, spindelförmigen Körper mit einer in Flüssigkeit suspendierten Zentralnadel bei den Rhabdocoelida in derselben Weise ausgebildet sind, ist einstweilen noch fraglich. dessen gehören wahrscheinlich hierher die langen, hohlen, stabförmigen Körper von Trigonostomum armatus (Jens.), welche nach Jensen (335, p. 10; III, 15a, u. a., 19) in zwei, im Beginne der zweiten Körperhälfte anfangenden, die Mitte der Bauchfläche einnehmenden Straßen nach hinten ziehen, um nahe dem Hinterende nach außen abzubiegen und an die Hautoberfläche zu treten. haben eine Länge von 34, sind langgestreckt, in ganzer Länge gleich breit und an den Enden abgestumpft und jedes dieser Stäbchen soll einen feinen Zentralfaden besitzen, den jedoch Jensen niemals ausgestoßen sah."

In this category of Pseudocnidae I am inclined to place the oval bodies described by Mereschkowsky as Nematocysts in Alaurina viridirostrum. In none of these cases has the expulsion of the thread been described, but the state of affairs is very different

in the case of the Nematocysts of *Otoplana setosa* described by Du Plessis. Von Graff states on page 2042. —

"Dieselben bilden lange und dicke Bündel, deren Spitzen über die Oberfläche der Haut vorragen. 'L'animal peut comme les autres Monotes rejeter ces baguettes au dehors à volonté et sur les préparations colorées au bleu d'aniline on voit que de chacune de ces baguettes peut sortir un très long filament. Ce sont donc des vrais nématocystes' (Du Plessis)."

If this account is accepted it would appear that we have here a case precisely analogous to that of the Pseudocnidae of the Nemertinea which are described below.

(b) Cleptocnidae.

In this category I am inclined to place the instances of the occurrence of Nematocysts in *Microstomum lineare*, *Microstomum rubroenlatum*, *Microstomum giganteum*, *Microstomum papillosum*, *Stenostoma Sieboldii*, *Pseudostoma mollissima* and *Allostoma monotrochum*.

The clearest case of the occurrence of Cleptocnidae in the Turbellaria is that of the nematocysts of Hydra in *Microstomum lineare*.

"The Nematocysts of Turbellaria were probably first observed by Oersted (13) in *Microstomum lineare* but he failed to recognise their true character, and described them as 'krugförmige Drüsen'. They were subsequently examined by von Siebold (17) in 1848, and he leaves no doubt as to his recognition of their nature describing them as thread cells which 'denen der Hydra auf ein Haar gleichen sollten'."

It is probably to the occurrence of these true Nematocysts in Microstomum lineare that we owe the numerous accounts of Nematocysts in Turbellaria given above, since it seems to have been felt that the transitional stages between these true Nematocysts and the ordinary Rhabdites of Turbellaria should be found. The proof that these structures in Microstomum are Cleptocnidae depends mainly on the following observations (vid. Q. J. M. S., Vol. 52, 1908).

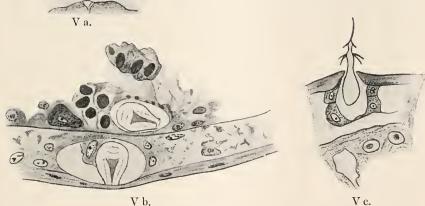
- (1) Microstomum lineare was seen to feed readily on hydra. Under these circumstances the three types of Nematocysts characteristic of Hydra were found under the skin of the Microstomum.
- (2) Some Microstomum which had fed upon *Cordylophora lacustris* were found to contain the characteristic Nematocysts of Cordylophora in place of those of Hydra.
- (3) In both these cases all the stages of the transportation of the Nematocysts from the lumen of the gut to their definitive position in the skin were found in sections of the worms.

- (4) Microstomum obtained from Scotch lochs at a depth beyond the region in which Hydra occurred were found to be free from Nematocysts. It is possible that this form had been previously described as a separate species under the name of Microstomum inerme.
- (5) The Nematocysts in Microstomum are found lying in vacuoles under the skin and no trace of a Nematoblast cell can be discovered in the sections. The Nematocysts usually lie singly in the vacuoles, but in some instances vacuoles have been found contain-

ing three to four Nematocysts, and in these cases the Nematocysts may be of

more than one type.

(6) Some Microstomum had been fed at 1 o'clock on Hydra stained intensely with Methylene blue. At 6 o'clock one of the Microstomum had a mass of blue material in its gut. Next day the colour had unfortunately faded during



the process of digestion, and only in one case was a Microstomum seen with the blue Nematocysts of the stained Hydra on which it had fed under the skin.

The instances of the occurrence of Nematocysts in Microstomum giganteum and papillosum have been dealt with in the paper referred to above. In May 1908 I found a Microstomum rubromaculatum on some weed to which was attached some colonies of Obelia. The Microstomum contained oval Nematocysts in packets of 3-4 under the skin, and singly in the gut. These Nematocysts emitted a thread on explosion, and appeared identical with the Nematocysts of Obelia. In the case of Stenostoma sieboldii I was able to infect the forms which I found at Naples with the Nematocysts of Eudendrium.

There are two other cases amongst the Rhabdocoelida which I am inclined to refer with a certain amount of hesitation to this category, and those are the cases of Nematocysts in *Allostoma monotrochum* and *Ulianinia mollissima*.

The Nematocysts of Allostoma monotrochum were described by

von Graff in the following passage. -

"Von Allostoma monotrochum Graff wurden (409, pag. 406, XIX, 19, b), zu je 3—4 in einer Epithelzelle eingeschlossen 3—4 w lange ovale Nematocysten bieschrieben, die einen spiral aufgerollten Faden zu enthalten scheinen. Doch bedürfen diese, wie auch die "Corpuscula bacillaria cava (organa urticatoria?) multa' des Provortex punctatus (Levins.) (368, pag. 179) erst noch einer genauen Untersuchung."

In this connection it is interesting to observe that Ritter-záhony in his "Beitrag zur Anatomie von Allostoma monotrochum" states on this subject. —

"Nesselkapseln (Nematocysten), die von Graff für A. monotrochum beschrieben worden sind (2, p. 406), vermisste ich jedoch."

On one occasion, in May 1908, I saw an Allostoma monotrochum crawling with its proboscis extended over a Campanularia, and in this case the Allostoma monotrochum contained Nematocysts which

agreed in appearance with those of the Campanularia.

The Nematocysts in *Ulianinia mollissima* were first described by Levinsen. In his Monograph on the Turbellaria, von Graff has renamed this form *Cylindrostoma mollissima* and therefore in his new nomenclature, I suppose the correct name would be *Pseudostoma mollissima*. I have not unfortunately been able to see the original description of this form, but von Graff states on page 2042 of his account of the Turbellaria in Bronn's Tierreich.—

"Nesselorgane gleich jenen des Microstomum lineare werden

für Ülianinia mollissima Levins. (368, p. 195) beschrieben."

and on the strength of this statement I am inclined to regard these structures as Cleptocnidae.

As far as I am aware there is no instance of the occurrence of Nematocysts in the Triclads and only two in the Polyclads, viz., in *Stylochoplana tarda* and *Anonymus virilis*. *Stylochoplana tarda* has as far as I know only once been found by von Graff, at Trieste. It is interesting to observe that it only differs from the common *Stylochoplana fusca* by its slightly smaller size, sluggish habits, and the possession of Nematocysts. The Nematocysts have not been figured, but are described as structures 0.01 mm long, with a thread 0.015 mm long, the base of the thread being covered with spines for a distance of 0.009 mm. This Nematocyst appears to be a very common type of Coelenterate Nematocyst, and it is tempting to regard these structures in *Stylochoplana tarda* as

Cleptocnidae. If this view be accepted, then the cases of Stylocho-plana tarda and fusca will present an interesting analogy to the cases of Microstomum lineare and inerme described above.

Anonymus vivilis has as far as I am aware only twice been found by Lang in the bay of Naples. The Nematocysts of this form are described as oval structures with a coiled thread, which lie in the parenchym and pass to the surface along special tracts. They have never been seen discharged. It seems possible from the pictures given of these structures that they are analogous to the Pseudocnidae found in Nemertines.

II. (4) Nemertinea.

The Nematocysts of Nemertines were first described by Max Müller in 1852 in a proboscis of a Cerebratulus urticans. The further literature on this subject can be found in Burger's Monograph on "Die Nemertinen des Golfs von Neapel" and his account of the Nemertines in Bronn's Tierreich, page 211. According to Burger the inner epithelium of the proboscis which of course on extrusion becomes the outer epithelium contains gland cells of many different kinds.

"Es gibt solche, die Bläschen, Stäbehen (Rhabditen), ja selbst Nesselelemente produzieren."

It does not seem necessary to go into the distribution of the proboscis on these structures here, as a very complete account is found in Burger; page 212. As regards the Nematocysts themselves Burger states on page 212. —

"Man hat zu unterscheiden zwischen Nesselzelle und Nesselkapsel. Jede Nesselzelle enthält immer mehrere Nesselkapseln von gleicher Größe. Die Nesselzellen des Rüssels von M. purpurea enthalten 4-5 Nesselkapseln. Die Nesselkapsel gleicht im ganzen dem Samenkorn mancher Umbelliferen, z. B. des Kümmels. Aber sie stellt ein meist etwas gekrümmtes Stäbchen dar, das an beiden Enden ziemlich gleich dick und abgerundet ist. Die Nesselkapsel ist hohl und es ist ein Faden in ihr aufgewunden, der die Nesselkapsel mehrmals an Länge übertrifft. Dieser Faden ist ebenfalls hohl und sitzt mit dem etwas dickeren Ende an dem einen Pole der Kapsel fest. Bei M. purpurea sind die Nesselkapseln nur leicht in der Zelle gekrümmt, bei M. dellechiajei und Cerebrutulus urticans dagegen bilden sie vollständige Haken (Taf. XII, Fig. 6). Das kommt daher, weil sie bei den letztgenannten Arten sehr lang sind und gestreckt keinen Platz in den Nesselzellen haben würden. Völlig gerade sind ferner die sehr feinen, ganz an größere Schleimstäbchen erinnernden Nesselkapseln der Nesselzellen aus dem Rüssel von Lineus geniculatus.

Eine Nesselkapsel aus dem Rüssel von *C. urticans* ist 0.1 mm lang, aber nur 0.002 mm breit. Ihr Faden erscheint auch bei mittleren Vergrößerungen noch haarfein "

Unfortunately I have only had one opportunity of examining these Nematocysts in Micrura purpurea and Cerebratulus urticans, and my attempts at obtaining further examples of these animals have failed. In both these cases I can feel little doubt from the examination both of fresh material and of sections that we are dealing here with capsules containing a pre-formed thread which is everted in a precisely similar manner to that of a Coelenterate Nematocyst. In the case of the Nematocysts of Micrura it was however interesting to observe that the thread swelled up and disappeared within 10 minutes of the explosion. It is perfectly clear that these cases of the occurrence of Nematocysts in Nemertines cannot be regarded as Cleptocnids, and these structures seem to differ essentially from the true Nematocysts of Coelenterates only in two points (1) in their development in packets in a single cell. (2) in the case of Micrura in the disappearance of the thread shortly after explosion.

II. (5) Mollusca.

In the group of Mollusca there are two instances of occurrence of Nematocysts.

The first is the well-known case of the Nematocysts of Aeolids which has been so brilliantly worked out by Grosvenor.

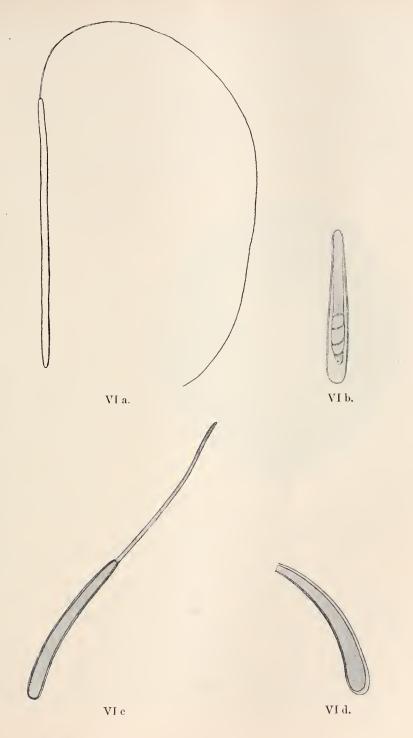
The second is the rather obscure case of their occurrence in a Cephalopod, *Tremoctopus microstoma*.

Cleptocnids in Aeolids.

It is to the work of Grosvenor that we owe the present acceptance of the view that the Nematocysts in Aeolids are derived from their Coelenterate prey. In his paper on the Nematocysts of Aeolids (Proc. Roy. Vol. 72) Grosvenor gives a short historical account of the origin of this view. From this it appears that the Nematocysts of Aeolids were found by Alder & Hancock who however in their first paper formed no very clear view as to the nature of these structures. Grosvenor the states n. that

"By the time of writing the 'Monograph of British Nudibranchiata', Alder and Hancock had arrived at a true conception of the nature these bodies.

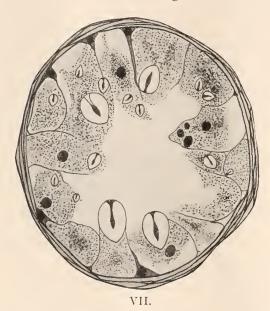
In December, 1858, T. Strethill Wright read a paper before the Royal Physical Society of Edinburgh, in which he maintained that the cnidae, or thread cells of the Aeolidae, were derived from the Hydroids on which they fed. He mentions that the same idea had previously occurred to Huxley and Gosse, and that the latter had suggested the method of proving its correctness."



As an example of the evidence which Strethill Wright was able to bring forward in support of his view, we may give the fourth observation cited by Grosvenor from Strethill Wright's work.

"An E. Drummondii, found on *Tubularia indirisa*, had nematocysts of the four kinds. found in the latter. Having fasted for 'a long time', this specimen was fed on *Coryne eximia*. Next morning its papillae and alimentary canal were crowded with the cnidae of *Coryne mixed* with those of Tubularia."

These observations were unfortunately completely overlooked, with the result that Bergh in 1861 described the Nematocysts in



Aeolids as being secreted in the Cnidosac, and this view was further developed by later workers, whose papers have therefore now only a historical interest.

Grosvenor summarizes the result of his own work on page 483 of his paper. —

"The facts brought forward as evidence that the nematocysts of Aeolids are derived from their prev are as follows:

> (1) Not only are nematocysts of Aeolids and Coelenterates identical in plan of

construction and mode of discharge, but each of several distinct types occurs in both groups.

- (2) A single type of nematocyst does not occur uniformly throughout a species, but different individuals of the same species may have quite different nematocysts; moreover, a single individual may have nematocysts of several different types, found in as many distinct species or groups of Coelenterates.
- (3) When it is known on what Coelenterate an Aeolid has recently been feeding, the nematocysts of the two are found to be identical. Also the nematocysts from the faeces of an Aeolid, which are generally admitted to be derived from their food, are always identical with at least some of the nematocysts from the enidosacs.

- (4) Those Aeolids (Janidae, Fionidae and Calma glaucoides) which habitually feed on animals other than Coelenterates have no nematocysts.
- (5) Though several have tried, no one has succeeded in giving even a plausible account of the development of nematocysts in Aeolids.
- (6) This view affords a satisfactory explanation of the function of the ciliated canal through which nematocysts and other indigestible bodies have been observed to pass from the gastric diverticulum of the cnidosac.
- (7) A repetition of Strethill Wright's experiments gave entirely confirmatory results. In one case three R. peregrinas, having only small pip-shaped nematocysts in their cnidosacs, were fed on Pennaria Curolinii, the nematocysts of which, after a month, had almost entirely replaced the original pip-shaped ones."

Grosvenor's results have been amply confirmed by Cuénot. In the case of the Cleptocnids of Aeolids it is interesting to note that these structures are undoubtedly used defensively by their possessor. Grosvenor stated on page 476.—

"In this way a fish which had snapped at the cerata, the loss of which, as is well known, does not seem to inconvenience the Nudibranchs at all, would receive a discharge of nematocysts into its mouth, where they would probably act with the greatest possible effect. This is in complete agreement with Garstang's view as to the meaning of certain features in the coloration of Aeolids. He suggests that the localisation of the bright colours in the cerata 'serves to direct the experimental attacks of young and inexperienced enemies to the non-vital papillae and away from the vital and inconspicuously coloured parts of the body', and 'at the same time gives them (the enemies) the needful experience of the unpalatable nature of their intended prey' ([9] p. 175). The erection and elongation of the cerata conduce to the same result (i. e. make them the most probable mouthful for an enemy), even when the bright colours are absent or otherwise disposed."

Cleptocnids of Cephalopods.

The only other instance as far as I am aware of the occurrence of Nematocysts in the Mollusca is that in a Cephalopod, *Tremoctopus microstoma* which is described by Bedot in his "Note sur les Cellules Urticantes" in the Rev. Suisse de Zool. et Ann. Mu. D'Hist. Nat. Geneve, Tome III, page 538.—

"Troschel a décrit chez le *Tremoctopus microstoma* Reynaud (*Philoxenis microstomus* Troschel) un fait très curieux. Des cylindres transparents, garnis des cellules urticantes, sont fixés par les

ventouses aux bras de l'animal. Cette observation a été confirmée dernièrement par Joubin qui a donné une excellente figure montrant le mode de fixation du cylindre à nématocystes sur les ventouses. Mais il n'a pas pu se rendre compte du mode de développement ou de la provenance de ces cylindres.

Il m'a été possible d'étudier un exemplaire de Tremoctopus microstoma Reyn. de la Méditerranée et, en examinant de coupes du cylindre à nématocystes, je suis arrivé à cette conclusion que, très probablement, il ne s'agit pas d'un organe spécial du Tremoctopus, mais simplement d'un tentacule de Méduse que l'animal

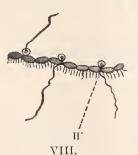
s'est approprié.

En effet, on retrouve sur une coupe transversale du cylindre (fig. 10) une disposition des tissus qui concorde absolument avec la structure typique des tentacules de Méduses. A l'extérieur se trouve un épithelium ectodermique (Ect.) renfermant de nombreux cuidoblastes pourvus de tiges qui viennent se fixer sur la lamelle de soutien (1). Celle-ci envoie dans l'ectoderme des prolongements assez épais. Sa face externe est tapissée d'une couche musculaire longitudinale (m). Au-dessous de la lamelle de soutien se trouve une couche entodermique (ent.) composée de cellules rondes. L'axe du cylindre est creux."

It seems quite clear from Bedot's work that in this case we are again dealing with Cleptocnids, though it is interesting to observe that this is the only case of a Cleptocnid, as far as I am aware, which is not first swallowed by its host before being made use of.

II. (6) Chordata.

The only case in which, so far as I am aware, Nematocysts have been described in a Chordate, is that of Appendicularia urticans described by Fol in his "Études sur les Appendiculaires du



Détroit de Messine" in Mémoires de la Société de Physique de Genève, Tome XXI, page 480. —

"L'ectothélium présente une modification singulière; partout, excepté dans l'intérieur du capuchon, il se compose de deux espèces de cellules, les unes étoilées, les autres, urticantes. Les cellules étoilées (Pl. IX, fig. I, 4) sont de petits amas aplatis de protoplasme, dans lesquels l'acide acétique fait apparaître un nucléus. Les cellules urticantes (u), plus nombreuses, renferment une vésicule ovoïde,

longue de 0.012 mm et large de 0.008 mm. Dans cette vésicule se trouve un globule fortement réfringent, d'un diamètre de 0.004 mm; il suffit d'ajouter une goutte d'eau douce pour voir ce prétendu globule se dérouler en un long fil, qui sort de la vésicule, et atteint une longueur de 0.1 mm (Pl. IX, fig. 1). C'est aux cellules urticantes des tentacules de Cydippe, que nos cellules ressemblent le plus."

In this instance I am inclined to regard these structures until further evidence is forthcoming as Pseudocnidae.

III. Conclusions.

If all the instances of the occurrence of Nematocysts in various animals mentioned above were true Nematocysts developed by their possessor the presence of these structures in such isolated instances in the various groups would, I believe, present great difficulties to an evolutionist. It seems to me that if this view were accepted there would be only two possible explanations to be offered

- (1) that these structures are homologous, i. e., they have been derived from Coelenterate ancestors possessing these structures
- (2) that these structures are analogous and have been evolved afresh in each instance.

The first explanation would appear to lead at once to insuperable difficulties. As I have already stated in my earlier paper on this subject it would involve the acceptance of the view that the Microstomum which contained Cordylophoran Nematocysts must be traced back to a Cordylophoran line of ancestry, whereas the commoner type of Microstomum with Hydra Nematocysts must be traced back to a Coelenterate of the Hydra type with its three distinct forms of Nematocysts. In the case of the Aeolids the acceptance of this view would lead to even more startling results. If on the other hand the Nematocysts in all these instances are explained as analogous structures due to convergent evolution, the isolated appearance of these structures in one or two species in each group would again appear to strain this hypothesis to the breaking point, and it appears to me that even without the experimental evidence given above as to the origin of these structures in some animals, the conception of Cleptocnids must have forced itself on the mind of the observer as the only explanation of the curious distribution of these structures in the animal kingdom. On the other hand it must be admitted that the polar capsules of Sporozoa, the Pseudocnidae of the two species of Nemertinea and possibly of the Turbellarian Otoplana setosa and the true Nematocysts of the Coelenterates afford a most amazing instance of what is apparently convergent evolution. In these cases in which apparently all possibility of an explanation based on homology is excluded, we find different animals all of which have developed a similar though not identical complicated mechanical structure.

In conclusion I should like to draw attention to a curious feature in the behaviour of wandering cells carrying Nematocysts.

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As is well known from the researches of Hadzi and Boulenger, the Nematoblasts have the power of carrying the Nematocysts from the point at which they are first laid down to the point at which they are used and there arranging the Nematocyst so that finally the pole of the capsule from which the thread is to be discharged always points towards the periphery. The same phenomenon is shown by the wandering cells which carry the ingested Nematocysts of Microstomum from the gut to their definitive position under the skin, cf. Martin, "The Nematocysts of Turbellaria", Q. J. M. S., Vol. 52, 1908. —

"At a later period nematocysts can be found lying just outside the gut, sometimes free, but usually surrounded by three or four cells. These cells seem to be mesenchymatous phagocytes, though I am not quite sure whether it is not possible for the cells of the gut itself to become free and take up a wandering existence in the body cavity. Finally the nematocyst is transported to a position directly under the ectoderm; here it lies in the vacuole (vide. figs. 2-4) (which is not an artifact, since it can be seen in the living animal) surrounded by about six cells. The wall of the vacuole after a time becomes thinner and denser. There is one point of great interest as regards the orientation of the nematocysts under the skin. The large barbed nematocysts in their final position, always lie so that the thread, when it is discharged, will pass out of the animal, although they may lie pointing in any direction while they are still in the gut cells of the body cavity. This rule does not seem to hold good in the small cylindrical nematocysts, which, as far as I can see usually lie almost parallel to the surface."

Something of the same kind has been observed by Grosvenor in Aeolids, p. 474, Proc. Roy. Soc., Vol. 72, "On the Nematocysts of Aeolids". —

"The arrangement of the Nematocysts within the enidosac seems to indicate that they are used as weapons, for they usually lie with the aperture, through which the thread will be everted, turned towards the periphery of the 'cnidoblast'. It is true that the 'round Turbellaria-like nematocysts lie much more indiscrimately, and that even the long Actinian nematocysts are sometimes reversed, but as a general rule the arrangement is as described'."

It is very hard to see how this arrangement of Nematocysts can be effected. Probably in the case of the Cleptocnids the original efforts of the animal were directed towards the expulsion of a mass of undigestible capsules through the skin. Only two possible explanations of the arrangement of a Nematocyst have occurred to me

(1) that the Nematocysts exercise a stimulus on the cell containing them, which in some extraordinary way compels that cell

to so arrange the Nematocyst under the skin that it points in the right direction,

(2) or the explanation may be a simple mechanical one, viz., that the structure and the shape of a hydroid Nematocyst will always set it a certain angle under certain conditions of pressure, and that the resultant of these forces leads to the Nematocyst under the skin always pointing in the right direction. One cannot help feeling however that this problem of the arrangement of Nematocysts is one which should appeal to physiologists.

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Text Figures.

- I. (a) Diagram showing proboscidiform individual of Ophryodendron abietinum with extended proboscis feeding on a tentacle of an Obelia. 4 comp. oc. + 4 mm apochr.
 - (b) Details of the same preparation; one cell has just been dragged by the tentacle of the Ophryodendron out of its position in the ectoderm. 6 comp. oc. + 2 mm apochr.
 - (c) Later stage in the feeding of an *Ophryodendron*; the proboscis is now retracted and carries at the end of some of its tentacles ectodermal cells from the *Obelia* (X 1).

X2 = an ectodermal cell on its way down the proboscis.

 $X\beta$ = ectodermal cells of the hydroid in various stages of digestion. 6 comp. oc. + 2 mm apochr.

- II. Cleptoenidae of *Polykrikos* (after Bütschli, *Protozoa*, Bronn's Tierreich, Pl. LV, fig. 8 c).
 - (a) Nematocysts unexploded.
 - (b) Nematocysts exploded.
- III. Pseudocnidae of Epistylis umbellaria,
 - (a) unexploded condition,
 - (b) exploded condition after addition of dilute acetic and methylene blue.
- IV. Cleptocnidae (?) in *Porifera* (after Eimer, Nesselzellen und Samen bei Seeschwämmen. Archiv f. mikr. Anat., Bd. VIII, 1892, p. 283); the full length of the thread shown in the original figure of Nematocyst B is not reproduced here. NB. The original figures in this case are very rough.
 - V. Cleptocnidae in Microstomum lineare,
 - (a) exploded hydra Nematocyst lying in its vacuole under the skin of *Microstomum lineare*,
 - (b) part of a section through a *Microstomum* showing an unexploded *Hydra* Nematocyst in the gut and in a vacuole under the skin,
 - (c) exploded Cordylophoran Nematocysts lying under the skin in *Microstomum lineare*.
- VI. Pseudocnidae of Nemertinea,
 - (a) Pseudocnidae of *Cerebratulus urticans* in the exploded condition. 4 comp. oc. + 4 mm apochr.,
 - (b) Pseudocnidae *Micrura purpurea* in an unexploded condition. 6 comp. oc. + 2 mm apochr.,
 - (c) Pseudocnidae Micrura purpurea immediately after explosion showing the thread. NB. The full length of the thread is not shown,
 - (d) Pseudocnidae of Micrura purpurea after the disappearance of the thread.
- VII. Cleptocnidae of Acolids (after Grosvenor, "On the Nematocysts of Acolids", Fig. 13, "Transverse Section through middle of a Chidosac of R. Peregrina,

fed on *Pennaria Cavolinii* for one month. Some of the cnidoblasts are already surrounded by membranous cysts, while others are still ingesting nematocysts").

VIII. Pseudocnidae in Appendicularia urticans (after Fol, Études sur les Appendiculaires du détroit de Messina, Génèva 1872). W = cellules urticantes.

Karl Dietze. Biologie der Eupithecien.

II. Teil. Text. 172 Seiten Großquart. Mit 4 Tafeln Abbildungen in Lichtdruck, Berlin 1913. Kommissionsverlag von R. Friedländer u. Sohn.

Der starke Band enthält folgende Abschnitte:

I. Ein kurzes Vorwort.

Wir erfahren hier von dem Autor in dem ihm eigenen, liebenswürdigen Erzählerton, nicht ohne romantischen Einschlag, einiges über Genesis und Ausarbeitung seiner bewunderungswürdigen Biologie der Eupithecien.

II. Allgemeiner Teil.

Er macht uns zunächst mit dem dem dritten und Hauptabschnitte bei der Anordnung der Arten zugrunde liegenden, leitenden Gedanken bekannt. Sie wurden möglichst ihrer Blutsverwandtschaft

nach zusammengestellt.

Einer kurzen Orientierung über die wesentlichen Charaktere der Eupithecien und ihre Stellung in der großen Familie der Geometriden schließen sich dann weiter sehr eingehende Erörterungen allgemeiner Natur über die vier Stadien Ei, Raupe, Puppe und Falter an.

III. Besonderer Teil.

Dieser Hauptabschnitt führt uns in die Kenntnis aller der in ihren verschiedenen Entwickelungsphasen bisher bekannt gewordenen 93 Arten der paläarktischen Fauna und der zu ihnen gehörenden Formen (Subspezies, Varietäten etc.) ein. An diesem "Bekanntsein" kommt selbstverständlich weitaus der Löwenanteil unserem Autor zu.

IV. Schlusswort.

Der erste Plan war, die Eupithecien der ganzen Erde zu bearbeiten. Dafür reichten Zeit und Kraft nicht aus. So entstand eine Beschränkung auf die paläarktischen Arten, von denen nur die eingehend behandelt wurden, deren Lebensgeschichte genauer bekannt war. Daher der Titel: "Biologie der Eupithecien". Gewissermaßen als Gratisbeilage sind die übrigen paläarktischen Arten als Falter in Lichtdruck hinzugefügt worden.

Die Farbenlichtdrucke von Martin Rommel in Stuttgart geben die in ihrer Schönheit und Naturwahrheit entzückenden Originalbilder der Raupen und ihrer Nährpflauzen des künstlerisch hochbegabten Verfassers oft bis zum Verwechseln ähnlich wieder.

Weiter folgen dann ein: "Alphabetisches Verzeichnis der Namen aus Teil I und II, nebst Angabe der Urbeschreibung", ferner ein:

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

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