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## Investigations on *Dorocidaris papillata* and some other echinoids of the Mediteranea

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*Prouho* *Laurent*

# THÈSES

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A LA FACULTÉ DES SCIENCES DE PARIS

POUR OBTENIR

LE GRADE DE DOCTEUR ÈS SCIENCES NATURELLES

PAR

HENRI PROUHO

INGÉNIEUR DES ARTS ET MANUFACTURES  
LICENCIÉ DE LA FACULTÉ DES SCIENCES DE PARIS  
PRÉPARATEUR AU LABORATOIRE DE DANYS-SUR-MER.

1<sup>re</sup> THÈSE. — RECHERCHES SUR LE DOROCIDARIS PAPILLATA ET QUELQUES  
AUTRES ÉCHINIDES DE LA MÉDITERRANÉE.

2<sup>e</sup> THÈSE. — PROPOSITIONS DONNÉES PAR LA FACULTÉ.

Soutenues le février 1888, devant la Commission d'examen

MM. HÉBERT, *Président.*

DE LACAZE-DUTHIERS, } *Examinateurs.*  
BONNIER, }

PARIS

TYPOGRAPHIE A. HENNUYER

RUE D'ARCADE, 7

1888

THESIS  
PRESENTED  
TO THE FACULTY OF SCIENCES OF PARIS  
FOR THE  
DEGREE OF DOCTOR OF NATURAL SCIENCES  
BY

HENRI PROUHO  
ENGINEER OF ARTS AND MANUFACTURING  
LICENCIATE OF THE FACULTY OF SCIENCE OF PARIS  
*PRÉPARATEUR* AT THE LABORATORY AT BANYULS-SUR-MER

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INVESTIGATIONS ON *DOROCIDARIS PAPILLATA* AND SOME  
OTHER ECHINOIDS OF THE MEDITERANEA

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Defended February 1888, before the Examining Committee

*Examiners*  
HÉBERT, *President*  
DE LACAZE-DUTHIERS  
BONNIEH

PARIS  
TYPOGRAPHIE A. HENNUYER  
RUE DARCEY, 7

1888

Translated by John M. Lawrence

Herizos Press, Tampa

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Henri Prouho

Henri Prouho was born February 12, 1854 at Rabatens-sur-Tarn in southwestern France. He received the degree of Engineer of Arts and Manufactures from the Ecole des Arts et Manufactures in 1874. He became a student of Henri de Lacaze-Duthiers at the Sorbonne in 1883. By 1885 he was a technician of Lacaze-Duthiers at Banyuls-sur-Mer. He received his doctorate from the University of Paris in 1888. Prouho took a position in the faculty of Lille in 1892. He retired in 1901 at the age of 47 because of ill health and returned to Rabatens-sur-Tarn where he died in 1921.

(from: J.L. d'Hondt. 2004. Un Zoologiste Tarnais méconnu: Henri Prouho (1854-1921). *Revue du Tarn* No. 194.)

## Translator's note

I have retained Prouho's anatomical terms that differ from contemporary ones. This was done partly to maintain awareness that this work is now more than one hundred years old. Although most terms are easily recognizable, I have listed some of them. Similarly, I have retained the species names used by Prouho. His names and the current names are given below.

Tentacles	tube feed
Echinids	echinoids
Conjunctive tissue	connective tissue
General cavity	coelomic cavity, perivisceral coelom
Genital glands	gonads
Ovoid gland, organ	axial organ
Radiole	primary spine

Prouho's name	Current name
<i>Strongylocnnetrotus lividus</i>	<i>Paracentrotus lividus</i>
<i>Echinus microtouberculatus</i>	<i>Psammechins microtouberculatus</i>
<i>Asterias glacialis</i>	<i>Marthasterias glacialis</i>

And, of course, the hero of the work:

<i>Dorocidaris papillata</i>	<i>Cidaris cidaris</i>
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whose name change was foreseen by Prouho.

This translation was made in 1982 when I was at the marine laboratory at Port-aux-Français on the beautiful Isles de Kerguelen, Southern Ocean.

**TO H. DE LACAZE-DUTHIERS**

**MEMBER OF THE INSTITUTE**

**FOUNDER OF THE ZOOLOGICAL STATIONS OF ROSCOFF AND OF BANYULS-SUR-MER.**

**DEAR AND HONORED MASTER,**

Since the day you were willing to admit me into your laboratory at the Sorbonne, your kind encouragements have not ceased to sustain me in the study of a science new to me, to which your attractive lessons had pulled me. Later, when I wanted to try my own efforts, you honored me with a high mark of confidence in attaching me to one of them.

I have been able, until now, to give you in return only my entire devotion: permit me to offer you today the dedication of my first work, which I ask you to accept as the gesture of my deep gratitude.

**HENRI PROUHO**

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STUDIES  
ON  
*DOROCIDARIS PAPILLATA*  
AND SOME OTHER ECHINOIDS OF THE MEDITERRANEAN SEA  
BY  
HENRI PROUHO  
Demonstrator at the Arago Laboratory.

INTRODUCTION.

How, after so many authors, have I been led to undertake new investigations on the anatomy of echinoids. I shall try to explain in a few words.

The types of urchins, whose organization has been delved into by my predecessors, are principally coastal species, i.e., those the naturalist can obtain easily. It is thus that Tiedemann, Valentin, Hoffmann, Perrier, Teuscher, and Koehler have addressed themselves by preference to genera more or less related to the present genus *Echinus*.

After all these works, it was natural to consider the organization of *Echinus* as being known. But it was all the more natural to wonder if there were not some new ideas to acquire by the anatomical study of a type belonging to a different and well characterized family.

The boats of the Arago laboratory often bring back from the open sea a cidaroid that my respected teacher de Lacaze-Duthier kindly brought to my attention. The conditions the laboratory offered me for the study of this beautiful echinoid were exceptional. I could not allow so favorable a condition to escape and I began my research.

Should I hope to collect numerous new and interesting facts from the study of this cidaroid? I did not concern myself about this. I did not think I would make a useless work in attempting an in-depth study of an organism insufficiently known from an anatomical point of view and which represented in our own seas one of the most ancient families of echinoids that was alive in geological times.

My first intention was therefore to publish a monograph on *Dorocidaris*, hoping the study of this single form would permit me to answer all of the questions I had the intention of approaching.

I could not limit myself to this plan and, as will be seen later on, I have had to apply myself sometimes to other selected genera among the echinoids. Moreover, I was led, so to speak in spite of myself, to occupy myself with a spatangoid the day when, wanting to verify to myself certain

facts stated by other authors, I had recognized inexact or incompletely observed facts.

The basis of this work will not remain less a nearly complete study of *Dorocidaris papillata*, the starting point of my studies.

I shall not devote a special chapter to the history of previous works.

A history should, in my opinion, be absolutely complete. Otherwise it has no longer a reason for being. Under this condition, it would be very long, tedious, and of dubious value.

Moreover, it should contain the account of the discussions and the debates the organization of the urchins has provoked in past years. This would necessitate the citation almost *in extenso* of the notes exchanged between the various anatomists. I believe it is possible for me to dispense with undertaking this task, reserving my criticism at the opportune times to those works related to the subjects of the different chapters of this memoir, at the front of which I shall place an outline of the echinoderm fauna of the coasts of Roussillon.

The generic or specific characters of the echinoids enumerated are extensively described in the works of A. Agassiz. It would be superfluous to reproduce them here.

#### ENUMERATION OF THE SPECIES.

##### STRONGYLOCENTROTUS LIVIDUS (BR.).

It abounds from 0 to 1 m depth (1) in the Bay of Banyuls. The Catalans call it *Engarotta*. They are very fond of it and consume large quantities of it. The animal nests in the holes made in the submerged schists of the cliffs.

Is it the urchin itself that makes its hole and, if so, how does it do it? Is it instead the hole that, by the continuous development of calcareous algae, grows little by little around the urchin that at first chose to live in a *preexisting* depression on the rock? No one that I know has responded to these questions in an irrefutable manner. As for me, I prefer to abstain for the moment.

##### SPHAERECHINUS GRANULARIS (A. AG.).

This beautiful urchin, which lives at the lower limit of the *Strg. lividus* zone, is in general a beautiful deep violet. One very frequently finds a white variety. The color of this variety is only due to the spines. The violet tint always persists on the tests, the tentacles, and the pedicellariae.

(1) These depths have and can have only a relative exactness.

## ECHINUS MICROTUBERCULATUS (DE BL.).

This little species occurs to 15 or 20 m depth and below. Very widespread on the bottoms that have been explored, it is difficult to assign a preferred habitat to it. The largest specimens I have had do not exceed 4 cm. The general tint is always greenish, with more or less apparent rose bands.

## ECHINUS ACUTUS (LAM.).

Begins at approximately 20 m and descends to 60 to 95 m depth, which should be a surprise as the *Challenger* collected it in 1350 fathoms (1).

*E. acutus* is very scattered on the coasts of Roussillon and one sees this. The depth at which it lives is very variable. It seems, moreover, to seek sandy shell-bottoms and flees the mud.

In this region of the Mediterranean, it shows well the characters assigned it by A. Agassiz (2), but it is necessary to stay on guard against those that refer to the form of the test for this is essentially variable. Sometimes it is, in the same region, almost completely spherical.

A character, very secondary without doubt but never wrong, is that the coloration of the test always has bands of more or less bright red.

The spines themselves are sometimes almost completely red, more often washed with yellow and a little green. They are always sharp, except on the oral pole where they are flattened at their end.

In the juveniles they are very long and attain a length nearly equal to the diameter of the test.

## ECHINUS MELO (LAM.)

It is near 45 m and deeper one finds this beautiful species, confused sometimes with *E. acutus*. It can be distinguished completely from the latter by characters of little value, it is true, but constant.

The test of *E. melo* is thicker and its tint is never as red as in *E. acutus*. Its form is generally more globose. The spines are always greenish, the primary being disposed in very distinct rows, which does not occur in *E. acutus*. The secondary spines are more numerous, as well as the pedicellariae, which results in the test being less naked than in the latter.

These characters serve well for the comparison of the two types which, examined side by side, cannot be confused.

(1) A. Agassiz, *Report on the scientific results of the Voyage of the H.M.S. Challenger*. (2) A. Agassiz, *Revision of the Echini*.

These few remarks agree with those Koehler (1) was led to make on the subject of these two species in the Gulf of Marseille. One can still affirm that there is reason for continuing to distinguish them on our littoral of the Mediterranean Sea.

*E. melo* is rare on the coast of French Catalonia. It has been fished at Cape Abeille at 45 m on a rock bottom. In contrast, it is frequent on the Spanish coast, where the laboratory boat has collected it at the end of Cape Creux at 90 m on a coralline bottom. In these areas, *E. acutus* is rarer than on the French coast. These two species apparently exclude one another.

#### DOROCIDARIS PAPILLATA (A. AG.).

It is often associated with *E. acutus* in the areas that have been explored, but as it never ascends as high, we place it last.

The fishermen of Banyuls know this beautiful echinoid very well. They call it *Courouno*, which means *crown, diadem*.

One encounters it off Banyuls from a depth of 60 m. However it is particularly on bottoms of about 100 m where it is abundant. There it lives either on a bottom of shell sand or on a coralline bottom.

The specimens brought back by the fishermen who drag the trawl are often in poor condition. The reason is that they dragged for hours, caught in the mesh of the net.

It is not the same for individuals brought back by the balancelle of the laboratory which, fishing with the aid of a mop, brings them back in a perfect state of preservation.

SPATANGOIDS. -- This group is represented by the following species.

#### ECHINOCARDIUM CORDATUM (GRAY).

This species has been collected at 2 m depth. One cannot say for certain the depth it reaches as it is very difficult to collect with the dredge. The only specimens I have had living have been taken in the Bay of Fontaule by my excellent friend Costes who took this good prize the first day he put on the diving suit.

Sometimes the waves throw numerous tests of this spatangoid up on the beach, but it is noticeable it is always during violent storms, which seems to demonstrate well they can embed themselves deeply in the fine sand where they live.

A. Agassiz distinguished *E. cordatum* from *E. mediterraneum*. I have had in my hands individuals that have shown me characters of this latter species but I have not been able to decide to separate it from *E. cordatum*.

(1) *Recherches sur les Echinides des côtes de Provence* (1883).

## SCHIZASTER CANALIFERUS (A. AG.)

The first specimen of this beautiful species, which has been brought back alive to the laboratory, was collected in the port of Port-Vendres by Pruvot in one of his numerous underwater excursions.

*Schizaster* lives there at 10 m depth in black mud of extreme fineness. Other specimens, similarly in very good condition, have been dredged since then at the entrance to the port at approximately 20 m.

## SPATANGUS PURPUREUS (LESKE).

One dredges it similarly at the entrance to the port of Port-Vendres in a bottom of sand at 10 to 20 m. This species lives at much greater depths where *Dorocidaris* lives. It is extremely abundant at 90 m.

*Spatangus purpureus* generally remains always noticeably smaller than those of the coast. Moreover, it is generally flatter and very deformed in bizarre manners. Otherwise, it does not show other distinctive characters.

## ECHINOCARDIUM FLAVESCENS (A. AG.).

It lives at approximately 30 m on shell and coralline sand, not far from the coast, to the southwest of the Bay of Banyuls. It is always of small size.

## BRISSOPSIS LYRIFERA (A. AG.).

The balancelle of the laboratory has collected it alive at the end of Cape de Cruex in Spanish waters at 90 m depth along with *E. melo*. This charming spatangoid assuredly exists to the east of Banyuls in French waters, as the traw or the dredge has often brought back tests without their spines.

All of the species I have listed have been collected alive and have survived in aquaria of the laboratory. There remains for me to mention the only echinoid I have never been able to have except in the spineless state.

This is *Echinocyamus pusillus* (Gray), uniquely representing clypeasters on the coast of Catalonia.

I have had the opportunity of observing it in the living state at Roscoff, where it inhabits a very characteristic shell sand. I have recovered this sand on certain points of the Roussillon coast. I am completely convinced *E. pusillus* will not be long in being brought back in good state by the boats of the laboratory.

## STUDY OF DOROCIDARIS PAPILLATA

One will find in this study not only the detailed history of a cidaroid, but additionally research on some echinoids made for the purpose of resolving certain interesting questions about the entire group of regular echinoids.

The usefulness of these investigations was indispensable every time *Dorocidaris* itself was not available in favorable conditions for observations.

### EXTERNAL CHARACTERS AND BEHAVIOR

I. -- *Dorocidaris papillata* has been illustrated frequently: Della Chiaji (1) has given a somewhat childish sketch of it; A. Agassiz (2) has published some excellent photographs. Muller (3) and especially Loven (4) have given some very good figures referring to the structure of the test. It would be superfluous to represent them again in this memoir.

We shall not discuss the characters of the sub-genus *Dorocidaris*. This would be to go beyond the limits we have set ourselves. One will find them indicated by Agassiz himself in his "Revision of the Echini".

We shall restrain ourselves by recalling briefly, and for the record, the principal traits of the structure of a test of *D. papillata*, remarking it can be taken as the type for the family of cidaroids, in which all true members show such a great conformity of structure that one is correct in wondering if it will not be appropriate to combine them all in the genus *Cidaris*, only distinguishing them by specific characters.

The interambulacral coronal plates are large and few in number. They have a single primary tubercle with the mamelon pierced by a hole (pl. XIV, fig. 1). The secondary tubercles are all situated around the scrobicular area.

The *interradii* of the largest ones I have observed do not have more than nine plates on the same meridional range or, if one prefers, there are never more than nine sets of interambulacral plates.

The number of these plates, needless to say, would not be characteristic. If I indicate it for *Dorocidaris*, it is to fix these ideas better. However, I do not believe there exists a real cidaroid in which the number nine would be exceeded. (5)

To the contrary, the ambulacral plates or radials are very small and very numerous, always simple, pierced with a single pair of pores and disposed regularly one above the other. They have small secondary tubucles.

The ambulacral pores of the test proper continue without interruption

(1) *Animali s.vert. d.regno di Napoli*, 1829. (2) *Revision of the Echini*, 1872. (3) *Über den Bau der Echinodermen*, 1853. (4) *Etudes sur les Echinoides*, 1874. (5) When I designate, without further explanation, a coronal plate by 1, the number refers to any one of the plates bordering the peristome; plate 2 comes next and thus up to the apex.

the peristomial membrane to its inner border. This membrane is covered with absolutely characteristic plates, having a completely different significance than the scales developed on some echinids: *Echinus spaera*, *E. microtuberculata*, etc.

These plates without doubt (1), at least for the radials are true ambulacral plates in cidarids, while those in the echinids have no morphological relation with those of the test itself.

To these characters of the first order, it is necessary to add one that is not of less importance. This is the complete absence of branchial gills on the border of the peristome.

The apical apparatus has a diameter at least equal to that of the peristome. The genital plates are all very nearly equal. The anal membrane is entirely covered with small plates; the anus is central (pl. xviii, fig. 1).

The spines of *Dorocidaris* are of two kinds. The *primary* ones are characterized, as in all of the cidarids, by a very hard cortical layer. They are carried only by the interambulacral plates on the primary tubercle with which they are articulated. Their ornamentation consists in a little roughness from saw teeth arranged in longitudinal lines that continue to the end of the spine.

In an adult, the radioles of interambulacral plates 1, 2, and 3 are more or less flattened, the oldest spine, i.e., that of plate 1, being the shortest, the thinnest, and the flattest. From the third on, the spines show a circular section, they are slightly conical, and their length increases up to the equator and decreases afterwards to the apical pole.

The length of the largest radiole in an intact adult is approximately two times the diameter of the test.

To the differences we just stated in the length and the forms of the radioles of the same individual can be added the differences of coloration.

Some are a beautiful red tint; others are only rosy; certain ones are red at the top, colorless at the base (pl. xv, fig. 14); others finally are completely colorless and are a dirty color. These latter are almost always invaded by a special fauna.

These are hydroids, serpulids, cirripedes (*Scalpellum* and *Alepas*) that most usually settle on the spines of *Dorocidaris* as they would have been able to do on all other supports.

Finally, I indicate a very original ornament that the radioles carry sometimes. It is a small valve of a lamellibranch, pierced by a spine and disposed at its base, no less a collar, as the guard of certain old rapiers. It is always on the spine of the oral hemisphere that one encounters the small shell of which I shall explain the presence in a moment.

The secondary spines, always lacking a cortical layer, are small, flat, and marked with a longitudinal striation. They are disposed around the primary spines, of which they scarcely overlap the bourrelet (pl. XV, fig. 6), in regular lines in the ambulacral zones, on the genital plates, ocelli, anals, and peristomials.

(1) LOVEN, *loc. cit.*

There is not a plate, as small as it may be, that does not carry at least one of these small spines whose mode of distribution corresponds to a very definite function.

Their color is always white, washed with pale-yellow. Together they give the general tint to the animal.

The pale-yellow tint very clearly is the indication of good health in a *Dorocidaris*; it is the normal color.

If an animal becomes brownish, it is a bad sign. If it develops green spots in places, it indicates that the urchin will be invaded by putrefaction before long.

II. -- Thanks to the exceptionally favorable conditions that occur at the Arago laboratory, it has been easy for me to observe if not completely, at least in part, the behavior of *D. papillata*.

Interestingly, of all of the echinoids listed at the beginning of this memoir, *Dorocidaris* is the one which adjusts best in captivity.

*Dorocidaris* apparently does not suffer from being transported quickly from a pressure of at least 7 atmospheres to a pressure of 1 atmosphere. It lives and eats in several centimeters of well-aerated water much better than our coastal species, and at that, not for several days but for three, four, and eight months. I find in my notes the following fact, which appears all the more astonishing as, above all, it concerns an animal used to great depths.

Some individuals were under observation in a tray of about 15 centimeters depth. One night, one of the cidaroids succeeded in escaping and fell on the floor where I found it the next morning. How long was it thus out of the water? I do not know, but it was nearly dry on the surface. For me, the animal was dead. There was no doubt. I do not know why I had the happy idea of throwing it back into the aquarium, and what was not my surprise to see, at the end of some minutes, this individual moving actively and showing all the characteristics of one in perfect health. The animal was very lively and remained in perfect condition until the moment I sacrificed it, i.e., 15 days later.

*Dorocidaris* appears thus indifferent to external pressure at least in the limits that I have just indicated. Moreover, it is a being to be added to the list of those that withstand great and sudden decompression without suffering.

My excellent colleague and friend, Doctor Joubain, has established an analogous fact in the cranies\*, which he has studied so well. Without making an enumeration of it, I shall say that the species producing observations of this general type at the Arago laboratory are numerous and varied. Hydroids,

\*Craniata: a group of gastropods. JL.



serpulids and cirripedes, which lived fixed on the radioles of *Dorocidaris* at 90 and 100 m depth, are very well satisfied with 10 cm of water.

Adult *Dorocidaris* move with the aid of their primary spines. The ambulacral tentacles are not locomotory organs for them.

Placed on a horizontal surface, the animal can move in any direction by using the radioles situated on either side of the plane in which it wants to move. These lateral radioles are then so many crutches that serve the cidaroid very adroitly. Those in front, immobile, seemingly reach out towards the goal.

The only spines that can serve in locomotion on a horizontal surface are situated on the oral hemisphere, the others are incapable of reaching the surface. In movement, one never sees the tentacles of the oral pole attach to the surface, particularly if the animal wants to move quickly.

But it is not only a horizontal surface that *Dorocidaris* trudges thus with great facility. It climbs the kinds of obstacles that are found in its passage. If the latter are very rough, then it relies on the ends of the locomotory spines.

There is more, and if I did not fear that the expression did not appear trivial, I would say that *Dorocidaris* excels at climbing the mast of *cocagne*\*. I have many times shown to travellers coming to the Arago laboratory in 1885, certain of these animals that, with the aid of their spines alone, had climbed the length of a glass tube of 1.5 cm diameter, placed vertically in the basin of the aquarium room. It is by tightly embracing the tube with their adoral spines that they accomplish this kind of *tour de force*.

In another circumstance, in which they had been placed in one part of the same basin, the *Dorocidaris* climbed the length of the trellis of iron wire that formed the barrier. It is from all indications, in each case, that the ambulacral tentacles cannot be any help.

The latter, we have said, are only accessory locomotory organs. This results from two principal causes. The first is that the terminal suckers are little developed. The second results from the ambulacral pores not being multiple on the oral surface by enlargement of the radial zone, contrary to that occurring in most other urchins in which the oral surface is flattest to to facilitate locomotion with the aid of the ambulacral tentacles.

A. Agassiz has indicated that *Arbacia* can move itself with the aid of its spines. I have not been able to observe this lively animal, but I do not doubt the observations of the wise professor of Cambridge. I even believe that one can add: "*All urchins* are capable of movement with the aid of their spines." But the movements thus realized are of little duration, and perhaps meaningless.

\*A pole up which men must shinny to obtain a bottle of wine at the top. JL.

In all of the latistellar\* echinids, the ambulacral tentacles are the true locomotory organs, the role of the spines is accessory.

In *Dorocidaris*, the radioles are the true locomotory organs, the role of the ambulacral tentacles is accessory.

The oral tentacles of an adult *Dorocidaris* are never very numerous nor sufficiently strong to develop an adherence that permits the animal to raise itself on a vertical plane. In juveniles of 1.5 cm diameter, it is not the same situation as the latter can easily support themselves the length of the wall of a jar.

The ratio of the force of adherence to the weight of the body decreases proportionally as the animal grows.

Now that we are acquainted with the fashion of movement of *D. papillata*, we can comprehend why one finds from time to time the small shell at the base of the adoral radioles mentioned above. *D. papillata*, we have said, frequently lives on sand bottoms. Now, among the numerous valves of lamellibranchs that are scattered on these bottoms, there are many that have been skillfully drilled by some carnivorous gastropods. It then happens sometimes that the cidaris, in trudging on the sand, engages the extremity of its locomotor spines in the hole of one of these shells that it carries with it.

In order to complete our observations on the locomotion of the urchin with which we occupy ourselves, take an individual with all of its spines intact and place it, mouth on top, on a horizontal surface. At the end of several minutes it will have righted itself and will have regained its normal position.

It is truly curious to see a *Dorocidaris* right itself this way with the aid of its radioles only (the ambulacral tentacles cannot be of any assistance since, as we shall see further on, they are only on the aboral hemisphere and completely absent ventrally).

One sees first of all the animal collapse its aboral spines, then explore the surrounding medium with its long rods, without doubt searching for an object that will singularly facilitate the task. Not finding this object, the *Dorocidaris* resolutely accepts its task and sets to work.

Then adroitly combining the play of its radioles, it succeeds after some efforts to give its equatorial plane an oblique position. The movement continues in the same manner and the plane is not long in becoming vertical. At this moment, the animal directs all of its radioles on which it is not resting towards its oral pole and by this maneuver it slowly but surely replaces completely its center of gravity by falling on its mouth. Certain primary spines join with the locomotor function another function no less evident. I want to speak of the flat radioles of coronal plates 1 and 2, which are incontestably organs of prehension. It is with them that

\*According to M. Jangoux, the adjective "latiselle" means literally "which looks like a widened star, and that Prouho's usage here presumably refers to the non-cidaroid regular echinoids (i.e. the euchinoids). The adjective seems redundant as "echinids" itself is used to designate the euchinoids.

*Dorocidaris* seizes and vigorously holds its prey. I have repeated this observation many times. Notice, moreover, that these spines of plates 1 and 2, and likewise 3, are very well disposed for serving this function since the direction of their tubercles orients them to incline themselves naturally towards the mouth.

Do not the radioles serve to protect the animals in addition? It would be unfortunately easy to defend the negative, and without doubt they should, in some case, hold certain enemies at a distance. But that which I can affirm is that these long spines are a very ineffective protection against young mullet (*Mugil*) and *Asterias glacialis*.

The former succeed by successive bits to remove all appendages, large and small, from the cidaris. The latter devours them in the space of two or three hours, after having tightly enveloped them in their arms without any care of the spines. I cite the observation:

In the month of March, 1883, I placed three *Dorocidaris* in a container where *Asterias glacialis* had lived for several months. A half-hour later, each urchin had become the prey of one or several asteroids and, when the latter had finished their repast, there remained only the tests of the cidaris as completely cleaned as if they had been in potassium hydroxide for several days.

The secondary spines are exclusively protective organs and they are admirably disposed in view of this function. The anal orifice, the genital pores, and the ocellar holes are protected by them. It should be mentioned in passing that it is exceedingly troublesome to observe the latter.

The ambulacral areas are formed from two rows of these small spines that, at the least excitation of the tentacles and when the latter are retracted, drop down in a fashion to mask them almost entirely. In the interambulacral zones, they are distributed all around the radioles, whose base they protect by lowering against them and thus forming a sort of conical palisade.

A *Dorocidaris* feeling itself protected from danger in well-aerated water trudges constantly from one side to the other, without doubt in quest of food. It shows then well-extended ambulacral tentacles and makes its long rods function as had been said. The secondary spines that surround the base of the radioles stay suitably straightened in order to allow a free functioning of the latter and those of the ambulacral areas are equally raised in order not to hinder the tentacles.

If one surprises the animal in this state of blossoming\* by slightly wounding it with a foreign object, one sees it immediately pull down its secondary spines, each on the organ that it has the mission to protect. The radioles stiffen themselves on their tubercles. The hedgehog of the sea forms itself into a ball.

The details I have just given appear perhaps a little long. I do not believe them useless in an age where it appears that one neglects to make the easiest observations.

\* Completely extending all of the tube feet. JL.

In 1838 L. Agassiz (1) said, after having reported that he had seen at the laboratory of Forbes an urchin climb the length of a vertical wall of a perfectly smooth glass bottle with the aid of its tentacles: "It remains to be known if, in the cidaris with long spines, these rods are not the principal organ of movement..."

I believe I have responded sufficiently to this question.

III. -- *Dorocidaris* feeds on animal material. In the region where I have collected them, it seems to feed particularly on sponges and gorgonians, of which the spicules abound in its excrements.

In captivity, I have seen it eat the most diverse animals: fish, annelids, sponges, and gorgonians on which it climbs completely at ease. It seems from these observations, therefore, that *Dorocidaris* is content with the food that it finds, provided that it is an animal. And, in this connection, it is well to note that urchins apparently can accommodate themselves with all diets.

*Strongylocentrotus* of our coast is considered, correctly, to feed on algae. Now when one places it in the aquarium and hunger possesses it, it is not rare to see it attack its equals. It chooses those that show an accidentally denuded surface on their tests and, little by little, gnaws all the epithelium of its victim.

*Dorocidaris* accidentally stripped of all its adoral primary spines is condemned to death of starvation. However, even under these conditions, it resists for a long time.

The experiment has been done, I must admit in spite of myself, in the aquaria of the laboratory where I had the imprudence of making live, at the same time as *Dorocidaris*, young mullet (*Mugil*). The urchins were, after a few days, completely stripped of their spines by the fish. I eliminated the latter and kept the *Dorocidaris* for observation. Six months later they still lived. After this time I placed one group in alcohol and continued to observe the other. After eight months of starvation and complete immobility, the latter were not invaded by putrefaction. They live still.

I believe to be able to confirm that an equal vitality has never been observed in any urchin of our coast. Adding to this that *Dorocidaris* resists more than all other urchins the action of corrupted water and that it survives for some time in an infested jar where *Strg. lividus*, *Sphaerechinus granularis*, *Echinus acutus*, etc. have resisted some hours with difficulty.

The prodigious vitality, for which the reason escapes us, has been observed also by all my colleagues who come to the laboratory. It is now well known to all the personnel at the station, and when one has been the attentive witness of it for three consecutive years, one is no longer surprised at the geographical and bathymetric distribution of *Dorocidaris*, nor of the conservation through geological time of a type that accommodates itself to the most diverse conditions and the most stressful of pressures, environment, and diet.

(1) L. AGASSIZ, *Monographies d'Echinodermes vivants et fossiles*. Neuchâtel, 1838.

IV. -- If now we compare a *Dorocidaris* to an urchin whose adoral ambulacral tentacles are provided with powerful suckers, besides being considerably multiplied by the enlargement of the radial zones towards the oral pole, we see both are found in very different conditions relatively to the external environment.

The one, the common urchin for example, adheres very strongly to the bottom on which it lives, to be able to establish itself in the zone constantly agitated by waves and again, for more security, it will establish itself in holes. The other, the cidaris, having a very weak force of adhesion will be obliged, under pain of being rolled without stop, to take refuge on the bottom where the action of the wave is insensible or very weak.

It is that, according to me, the only reason to invoke in order to explain the absence of *Dorocidaris* in shallow water.

We have said that this urchin acclimates very well in captivity under 10 cm of water. Why is it not acclimated on our Roussillonaise coasts at 10 cm of depth, for example? It would have found many places of the bottom convenient for its nourishment. The true reason appears to me to be that which I have just indicated.

When an urchin is provided with numerous ambulacral tentacles with powerful suckers, it can not only live on the coast, but moreover it will be able to descend to the calm bottoms to which *Dorocidaris* is condemned.

Meanwhile, it would not be possible to overgeneralize and make an absolute rule that no cidaroid can normally live in shallow water as, in spite of their structure so uniform, it is possible to have one better endowed than *Dorocidaris* in order to confront the action of the wave, either because of a more flattened form or because of their small size and that, moreover, there is always, as on the most exposed coasts, protected places able to serve as a refuge.

Whatever it may be, by its very structure, the cidaris type does not remain less a type of calm water and, consequently, of deep water.

#### MICROSTRUCTURE OF THE TEST

One knows very well since the work of Valentin (1), Hoffmann, and others, the intimate structure of the calcareous network that constitutes the plates of the test of the urchin. It is easy to study it by examining, under the microscope, thin sections of any part of the test, sections that one obtains without difficulty by grinding it very flat by friction on a simple rock.

The examination of these sections has shown me that the network of the calcareous skeleton of *Dorocidaris* shows nothing special. We shall not continue consequently, and pass on immediately to the study of the elements of an organic nature that enter into the composition of the test.

(1) Monograph on the genus *Echinus*, 1841.

The information the various authors give us is not very precise. Valentin teaches us that ,after treatment of the plates with hydrochloric acid, one obtains a "very delicate soft skeleton that, examined with a microscope, reflects in a manner more or less distinctly the contours of the calcareous network while showing a fibro-granular and membranous structure."

Hoffmann (1) said that, after the action of acid on the calcareous plates, an organic conjunctive structure remains that offers also a reticulated structure and consists of mixed fibers of cells and nuclei. The authors who have since studied the organization of urchins are not more explicit or have even completely neglected this histological point.

The expression of *soft skeleton*, which served Valentin, renders very well the impression one experiences when one sees a fragment of decalcified test. In order to obtain this soft skeleton in a condition that permits the study of the histological elements, it is well to operate in the following fashion:

The fragments of test, as small as possible, are first plunged in 45-degrees alcohol, then immersed into alcohol at the same concentration diluted with a tenth of the hydrochloric acid (if the objects are very small, one decreases the proportion of acid). The attack on the calcium carbonate begins immediately and one allows it to continue until it has entirely stopped, taking the precaution of often renewing the acidified alcohol. If the fragment is large, the operation will take a long time, and then it would be well to increase the strength of the alcohol and to use alcohol acidified to 60 degrees.

The bubbles of carbonic acid formed are not always successfully released. They are often found imprisoned in the matrix of the tissue. It is necessary at all costs to remove them as they delay, first of all, the attack on the calcareous particles they surround and, secondly, would be a serious inconvenience later on in embedding the tissue.

For this, it is necessary to subject the fragment immersed in the acidified alcohol to a weak vacuum which facilitates the release of the bubbles.

The decalcification being finished, the piece is washed carefully in 60-degrees alcohol, treated with successive alcohols until 100 degrees, and finally embedded in paraffin.

The thin sections prepared from a fragment of test thus treated are stained on a slide.

They show us: the organic network that fills up the mesh of the calcareous network, the skin that invests the test externally, and the membrane that lines it internally.

The organic network (pl. XIV, fig. 6; pl. XV, fig. 5) is constituted, as Hoffmann said, by a conjunctive weft, but the elements that form the mesh are not simple fibers. They are veritable anastomosed canaliculi whose extremely thin walls mold themselves on the calcareous network itself.

(1) *Zur anatomie der Echinen und Spatangen*, 1871.

In the interior of the canaliculi, one encounters numerous nuclei and also muriform ameboid globules whose presence and manner of occurrence in certain places leave no doubt of the canalicular nature of the network.

On the internal side of the test, the conjunctive substance that forms all of these small canals spreads out so as to constitute a very thin lining membrane that supports a ciliated epithelium.

Towards the exterior, the canalicular network similarly ends in a conjunctive layer that can be considered the deepest part of the wall (pl. XIV, fig. 6; pl. XV, fig. 5; pl. XVI, fig. 4). This presents diverse elements for consideration. We shall occupy ourselves first of all with those that form the support.

These are elongated cells. The distal ends, pressed one against the other, support a cuticle that is always ciliated. The proximal ends attach themselves to the basal conjunctive layer that limits the canalicular network (pl. XVI, fig. 4). That which specially characterizes these cells is that, while they always touch one another at their upper part, they leave intracellular spaces below where new histological elements occur.

One finds there nervous tissue to which we shall return shortly. One meets also various free globules.

In the first place, it is necessary to report the mahogany-brown globules that give a red tint to certain points of the test. These corpuscles cannot be distinguished in the sections as their coloration disappears in acid (see the chapter on *perivisceral fluid*). In order to assure oneself of their presence, one should examine a scrap of the wall in a fresh state. One does not see, it is true, the intracellular spaces in this fashion. But as one is already convinced of their existence, one can conclude that the brown corpuscles occur within, as they would not be situated elsewhere.

One meets also in these intercellular spaces muriform corpuscles and masses of brownish granulations.

Never have I glimpsed glands there, either simple or compound.

The conjunctive canalicular network changes aspects at these suture lines of the plates. By the fact the small canals stop there, their lumen disappears, and their walls continue by the conjunctive fibrils that pass from one plate to its neighbor.

In *Dorocidaris*, the suture lines are always of an organic nature alone. The calcareous network of both neighboring plates do not knit. This explains why a test of a cidaris disarticulates so easily and spontaneously when all the organic substances have been destroyed.

The epidermal layer of the test continues on all its appendages, spines, pedicellariae, and covers similarly the ambulacral tentacles. The ciliated surface exists everywhere. The currents that it makes have not appeared constant in their direction, unless it is the length of the spine and on the peristomial membrane. The current follows the spines from the base to the summit. Those of the peristomial membrane goes as a confluent towards the buccal orifice.

## PERIPHERAL NERVOUS SYSTEM

The study of the peripheral nervous system is completely natural at this place, as it is included in the epidermal layer that has just been discussed. But it is not to *Dorocidaris* that one should address first of all in order to start this study well, because of the difficulties that they present in this animal.

*Echinus acutus*, to the contrary, shows favorable conditions. It is with it we shall begin.

I. -- J. Müller (1) stated that the ambulacral tentacles, the pedicellariae, and the spines receive nerves from the ambulacral nervous trunk, but he did not give any proof to support it. Hoffmann (2) tried to see this peripheral nervous system but did not succeed.

In 1874 appeared the beautiful work of Loven (3) on the structure of echinoids. At the same time that he discovered sphaeridea, he illustrated a nerve net on the test of a spatangoid *Brissopsis lyrifera*, which he was the first to demonstrate. It was then more and more probable that regular urchins should have a peripheral nerve net just as the irregular ones.

Meanwhile L. Fredericq (4) failed in his research and said in 1876: "It is in vain I have tried to prove anatomically the existence of this nervous plexus."

That was the situation when Romanes and Ewart (5) published in 1882 a memoir in which they described an external nervous plexus in urchins.

In 1883 Koehler (6) wrote: "I have not been happier than Fredericq, and it has been impossible for me to perceive this nerve net."

In my turn, I tried to discover this nerve net towards the end of 1885, and I had already obtained some results myself before I knew of the memoir of Romanes and Ewart.

The preparations I obtained agreed so little with the figures given by these authors that it was impossible for me to confirm their research. I stayed persuaded that the external plexus figured by them (fig. 15) (7) was formed solely by conjunctive cells.

It was at this moment, 14 December 1885, that a note of Sarasin (8) appeared in the *Zoologischer Anzeiger* dated from Trincomalie in which, regarding compound eyes the author had discovered in *Diadema*, was incidentally mentioned a question of a nerve plexus contained in the skin and transversed by so-called small vessels. Sarasin did no research to prove that the tissue in question was really a nervous tissue. Now, after the preceding historical glimpse, it was important to furnish this proof. I did not believe this should make me dispense with summarizing my research on *E. acutus* in some lines presented to the Academy of Paris, 22 February 1886.

(1) *Über den Bau der Echinodermen*, 1853. (2) *Zur Anatomie der Echinen und Spatangen*, 1871. (3) *Loc. cit.* (4) *Études sur les Echinides* (*Arch. zool. exp.*, v. V, 1876). (5) *Observations on the locomotor system of Echinodermata*, 1882. (6) *Loc. cit.* (7) *Loc. cit.* (8) *Über einen zusammengesetzten Augen bedeckten Seeigel*.



The Sarasins had no knowledge of this summary and did not cite it in their memoir (1) that had just appeared.

II. -- It is *Echinus acutus* to which I address myself for two reasons: First, the spines are sparse in the interambulacral area and one can easily remove very large scraps of skin. Second, this skin is almost colorless in this species.

So that those who will have an interest in verifying this research and will be able to do it without pain, I indicate in detail the following method.

It is necessary, first of all, to take an *Echinus* just collected that has not been rolled by the net. One cuts with scissors the fragments of the test of approximately one-half square cm, chosen from the middle of the interambulacral area, taking care to leave at least one spine from which the piece will always have to be held in the following manipulations.

One plunges the fragments into a solution of gold chloride (2%), and one lets them rest there until they have become very yellow. They are afterwards placed in distilled water with some drops of citric acid and exposed to a weak diffuse light. After several hours, the deposit of gold is produced. The piece of test takes a red-violet or bluish color. It is the latter that must be looked at preferentially as they will probably give a good result.

As soon as reduction has begun, one should from time to time examine with a microscope small scraps of skin that one removes from prepared fragments in order to follow the operation.

When the coloration is successful, one sees on the fragment of skin detached from the test with the greatest possible care and examined flattened either in glycerin or after mounting in balsam, numerous very apparent bluish lines running in the same direction and often anastomosed. Fig. 8 (pl. XVI) represents one of these preparations. These slate-blue trails thus indicated by the gold chloride are nothing other than the principal bundles of the nervous plexus sought.

In removing the scrap of body skin, one pulls out the external conjunctive layer that limits the calcareous network of the test. When one then examines the preparation, one sees before the eyes very variable histological elements in the midst of which it is difficult to orient oneself and that greatly hinder the observation of the bluish bundles that interest us. It is necessary to isolate them to see them better. One does this by treating the preparation with a brush.

One sees then that the bundles are fibrillar and that they are united by an innumeral quantity of extremely slender fibers that run in all directions (pl. XVI, fig. 9), but from which the network as a result limits the more or less irregular and always very small mesh. Nearly the largest I have been able to observe is approximately 0.013 mm.

One finds this fibrillar network especially at the periphery of the test. It is a question of ascertaining its nature.

It is necessary for this to begin the preparation again, but taking this time a fragment of the ambulacral area from which one removes a tentacle,

(1) DR. PAUL SARASIN, DR. FRITZ SARASIN, *Die Augen und das Integument der Diadematiden*. Wiesbaden, 1887.

respecting as much as possible the circumference of the corresponding pore-pairs.

That done, one notices on the adoral edge of the inner pore, the tentacular nerve net coming from the interior ambulacral nerve and that goes to the removed tentacle.

One should then carefully detach the skin that surrounds the pore pair and apply oneself at the same time to remove a fragment of the tentacle nerve-net. One observes it as before.

One perceives in this fragment of skin the fibrillar network described above with all of the same characters. One sees that it is reenforced at the border of the empty space corresponding to the tentacle removed by the largest bundles (pl. XVI, fig. 10) that surround the pore pairs.

These bundles, identical to those of the network shown in the first preparation (pl. XVI, fig. 8, 9) are in continuity with the fragment of tentacle nerve that stayed attached to the skin (pl. XVI, fig. 10, *nt*).

The reticulated tissue, with which we concern ourselves, is thus of the same nature. It is a nervous tissue.

Moreover, the fibrils that compose it are identical to those of the tentacle nerves and ambulacral nerves.

After becoming certain by this method that the reticulated tissue disclosed by gold chloride was composed of nervous fibrils, I have sought it on the normal sections of the test, and I found them without difficulty.

These sections show (pl. XVI, fig. 45, *np*), that the nervous plexus is situated above the conjunctive membrane limiting the canalicular net and, in the intracellular spaces left by the underlying cells, attached to the conjunctive layer below the nerve (*c*) crossing the mesh of nerve net.

It was of interest, after having established that the nervous plexus gives rise to the tentacle nerves, to see those that passed to the extremity of the ambulacral nerve itself. The sections made at the extremity of the radius gave the answer immediately.

The ambulacral nerve penetrates the pore, goes out to its surface and spreads out on the ocellar plate continuous with the peripheral nerve network (pl. XVI, fig. 2).

Thus is verified the conclusion I published in 1886: "*Echinus acutus* is entirely covered by a peripheral nerve net comparable to a kind of tulle woven with nerve fibers and in connection with the internal nervous system at as many points as there are ambulacral tentacles and ocellar pores.

III. -- Until now it has only been a question of nervous fibers. Where are the ganglionic elements found?

It is not possible to recognize with certainty an isolated nerve cell in echinoderms. Baudelot asserted this in his *Etudes general sur le systeme nerveux* (1), and I believe all those who have studied these animals have the same opinion. This difficulty will probably disappear one day. For the moment it exists. Neither the form, nor the dimension, nor the action of known reagents provide us a criterion. There is only a single case in which one will be able to assert that the cell is nervous. It is when one will

(1) *Archiv. zool. exp.*, v. I, 1872.

have established without possible error that it is in continuity of substance with a nerve fiber. Now, such a proof is very difficult to make, as the causes of error are numerous in the species.

When one examines a flattened scrap of skin in which the nerve fibers have been shown, one distinguishes various cellular elements there.

One sees first of all a conjunctive layer (that which lies immediately under the calcareous material) in which are found numerous muriform globules (pl. XVI, fig. 11, *gm*), curved calcareous spicules (*sp*), and cells with ramified protoplasm (*z*). These latter merit special attention, as one would be able to take them for nerve cells. They have large granular nuclei. They are uni-, bi-, and multipolar, and their extensions anastomose frequently. But one can never succeed in seeing one of these elements unite with a nerve fiber on which they are superimposed (pl. xvi, fig. 11, *np*). These are the conjunctive cells, and are those that in my view have been illustrated by Romanes and Ewart (1) (pl. LXXX, fig. 15) in which the fibrillar plexus appears to be unseen.

All these elements have been well examined. If one magnifies the objective of the preparation, one brings into focus the nerve plexus (*np*) itself and finally distinguishes below it a large number of nuclei that completely resemble those of the previously mentioned conjunctive cells and that are nothing other than the nuclei of epidermal cells (2).

It is in observing these isolated fragments of the fibrillar nerve net that one succeeds in seeing the cellular elements in connection with the fibrils. These cells (pl. XVI, fig. 7, 12), which to us represent the true ganglionic elements, are situated in the same layer as the bundles of nerve plexus. They are bipolar and elongated in the same direction as the fibers.

Does one seek to resolve the question by a section normal to the test surface? One still comes up against the great difficulties resulting from the diversity of elements that can be in contact with nerve tissue in the intracellular space. Nevertheless one succeeds in distinguishing the nuclei (pl. XVI, fig. 4) that are included in the fibrillar bundles and have the same significance as those observed previously by another method (fig. 7 and 12).

I cannot assert that, in addition to these ganglionic cells, there do not exist others similarly situated on the nerve plexus, but I do claim never to have made observations so free of causes of error to permit their illustration.

IV. -- How is the nerve plexus situated in relation to the epidermis? Where are the terminal nerves? It would be necessary, in order to approach this interesting question, to surrender oneself to a special study, to make it the subject of a memoir where one would not be content to say: "Here is the sensitive cell", but in which one would persevere above all to demonstrate it, after having made known the method employed. I have not

(1) *Loc. cit.* (2) These nuclei have not been represented so that the figure would be clearer.

approached these researches and am obliged to examine sections obtained as has been indicated. One sees in these sections numerous nuclei situated below the cuticle. A large number of these nuclei pertain to epidermal cells and *perhaps* in the number are some that pertain to the sensitive cells resembling those that Hamann (1) illustrated in his memoirs on asteroids (Sinneszellen) but I do not dare assert it.

The epidermal cells, as we have said, send out inferior extensions that cross the nerve plexus in order to go to join the subadjacent conjunctive layer, but in the same section. All these extensions of the supporting cells do not cross the nerve plexus through and through. There are some that, encountered by the razor in an oblique direction, stop on the plexus and appear to place themselves in contact with it. This is a cause of error that should be carefully avoided if one does not want to run the risk of describing a supporting cell of the body wall as a sensitive cell.

V. -- The Sarasins (2) have published a memoir on the integument of *Diadema setosum* in which is announced a fact that merits discussion, namely that the body wall of this urchin is crossed by an innumerable quantity of small vessels establishing communication between the external medium and the body fluid of the urchin. These small canals originate in a vascular space (*Gefässraum*) situated under the nerve plexus, and are directed towards the cuticle that is pierced by numerous pores.

The authors of the memoir do not tell us if they have observed these pores in the diademids and they do not illustrate them. They leave it up to what Ludwig (3) said on the subject of asteroids, in which there is a cuticle showing small openings and across which occur ciliated cells. Ludwig based this on the fact that the flat cuticle presents an appearance of fine points. One sees from this that it is regrettable that the Sarasins have not given us more details on this cuticle of the diademids. I have, myself, never observed similar perforations in the urchins I have had the opportunity to examine.

As for small canals that would come to open under this cuticle, it is similarly in vain that I have sought them in *Echinus acutus*, and I think all the tracts one sees in sections from the sub-neural conjunctive layer towards the cuticle are formed by extensions of epidermal cells that the Sarasins have not followed in their diademids (pl. XIV, fig. 6, *p*; pl. XVI, fig. 3, 4).

The sub-neural space the authors call *Gefässraum* seems to me to be formed by the most superficial layer of the canaliculi of the test. In *Echinus acutus*, it is often invaded by muriform globules. It is there that are found also the multipolar conjunctive cells and the spicules that already have been considered (pl. XVI, fig. 11).

(1) *Loc. cit.* (2) *Loc. cit.* (3) *Beiträge zur Anatomie der Asteriden* (*Zeit. f. Wiss. Zool.*, v. XXX, 1878).

It is finally at this place, under the nerve plexus, that all the canaliculi of the plate come to an end. That the amoeboid globules that go and aggregate there often in large numbers can remain in the intracellular spaces of the epidermis does not appear doubtful to me. But I can only admit that there are in *Echinus acutus* small vessels communicating with this sub-neural space, i.e., in short, the canalicular network with the exterior as, I repeat, it has been impossible for me to perceive them as well as the perforations of the cuticle. In addition, the figures given by the Sarasins in order to demonstrate the fact in a diademid do not seem to me to be sufficiently demonstrated. As to sensitive cells, these authors admit their existence, but do not demonstrate them. I maintain all the reservations that I have made previously.

VI. -- The nerve plexus innervates all the appendages of the test, and I have specially sought the manner in which it makes relations with the spines.

In following the plexus, either by the method indicated or by sectioning, one arrives at the conclusion that the peripheral nerve plexus forms a very evident nerve ring at the base of each spine, situated at a short distance from the point of inferior attachment of the motor muscles and resting directly on the latter.

One sees (fig. 4, pl. XVI) this ring is formed by the accumulation of nerve fibrils that, reaching this level, encircle the base of the spine in such a way that a section, crossing by the axis of the latter, cuts them all transversely, which gives the fine pointed characteristic of the transverse sections of echinoid nerves. But one sees also that the right section of this nerve is encircled by numerous nuclei of which a certain number show an extension evidently directed towards the fibrillar mass.

Here all mistakes are possible. These nuclei cannot be confused with the supporting elements of the skin. They must leave the nerve ring from which they accompany the fibers particularly at the periphery.

The presence of ganglion cells on the internal face of this ring is explained easily by the fact that the nerve ring is in reality formed of two layers (pl. XVI, fig. 3) of which the internal seems to result from a reployment of the external layer.

The nerve ring of the spines is very apparent in young urchins. Figure 5 of plate XVI represents a longitudinal section at the base of a spine pertaining to *Strongylocentrotus lividus* 4 mm in diameter. It shows (an) two very well defined islets that are the sections of the ring in question.

In ending this presentation of my studies on the integument of *E. acutus*, and in spite of all the repugnance that I feel in raising a question of priority from which science has never gained, I should recall that the Sarasins have indicated the nerve ring of spines in *Diadema setosum* in their definitive memoir (1887) and that I had described it in *Echinus acutus* on the date of 22 February (1886).

VII. -- *Dorocidaris papillata*. -- If one seeks to apply to *Dorocidaris* the methods of gold chloride that serve for *Echinus acutus*, one is soon stopped by insurmountable difficulties. In contrast, the method of transverse sections permits seeing the peripheral nerve plexus that one finds at the place where we described it in *E. acutus*.

When one examines the test of a cidaris stripped of all its spines and cleared of all organic material, one perceives in the interradial areas a quantity of small crossed furrows in the calcareous material that come from one plate to another in crossing the suture lines, running between the miliary tubercles and losing themselves on the circumference of the scrobiculair area (pl. XIV, fig. 1, *sn*).

One finds these furrows in the radial border of the interambulacral plates, where one sees them direct themselves towards the radial pores. They align with the suture of the ambulacral plates and each of them abuts a small groove cut in the aboral border of the internal pore of a tentacle. It is by this groove that the nerve net, coming from the internal nervous system and destined for the ambulacral tentacle, arrives at the surface of the test. At this point, it leaves a bundle that is in direct contact with the plexus and lodges in the furrow of which we just spoke.

All the fibrillar bundles coming thus to the surface by the grooves of the pores are directed by the furrows and go with them to the plate in order to innervate the appendages.

A section parallel to the direction of the radius and several interesting ambulacral plates shows these nerve bundles (pl. XIV, fig. 3, *sn*). It shows also that here, as in *E. acutus*, the base of the tentacle is surrounded by a true ring that we find again in section (*np*). Figure 12 of the same plate represents, greatly enlarged, the section of a furrow that has just been considered.

We thus arrive at the unexpected result: it is that a dried test of a cidaris carries the trace of the ensemble of the peripheral nerve net imprinted in cavities on the calcareous material. This trace is constituted by the previously described furrows. The latter are visible, not only on the tests of the present species, but also on numerous samples of species of fossil cidarids. One finds them figured with care on the illustrations published by Cotteau, and I am obliged to Munier-Chalmas for having been able to observe them myself on the test of divers molds.

Another interesting peculiarity of *Dorocidaris*: the nerve ring of the radioles is visible to the naked eye. It suffices in order to see it to put aside or pull out the secondary spines that hide the base of the radiole. One distinguishes very clearly in the body wall a circular line of which the contours are marked by a difference in coloration and which is nothing other than the nerve ring (pl. XV, fig. 5).

The peripheral nervous system of urchins, unknown for so long is thus partly visible to the naked eye in one of them, *Dorocidaris*, and one can follow the track of its principal bundles, not only on the dried tests of the present species, but also in fragments of fossil species.

## OCELLAR PORE

I. -- Although it is admitted today that the ocellar plate of an urchin does not have in its pore either an eye or an unpaired tentacle, it was of interest to examine anew the question in *Dorocidaris*, thus completing if it was possible the information furnished by authors who have studied it exclusively from the point of view of echinids.

Loven (1) has illustrated one of the ocellar plates of *D. papillata*, that allows me to give a new one of larger scale. These plates all have the same form and dimension (pl. XVIII, fig. 3, 4). They are cordiform, sprinkled with miliary tubercles that never touch the pore that is thus surrounded by a small, perfectly smooth zone. Their color does not show anything particular. One sees the body wall of the test is recurved, and there is neither an unpaired tentacle or any ocellary spot.

The sensitivity of the integument is very great in this region. Under the influence of the least excitation, the animal lowers its secondary spines that surround the pore in order to protect it. This sensitivity is not characteristic, as it is manifested at all other points of the test.

The ambulacral nerve, after having traversed the pore, spreads out on the ocellar plate. This disposition is represented (pl. XIV, fig. 4) in *Dorocidaris* and (pl. XVI, fig. 2) in *Echinus acutus* (2), which presents in addition a peculiarity relative to the internal nervous system that will be considered later. It is necessary to add that the superficial nerve plexus thus formed by this expansion is always very thick on the pore and around it on the ocellar plate. It often occupies a third of the total thickness of the body wall that is thicker in this region than anywhere else.

The histological constitution (pl. XIV, fig. 6) of the latter is always the same, with the difference that the cells are higher, more crowded together, and consequently their different nuclei are arranged in a large number of layers.

One can no longer distinguish the intracellular spaces. As for the sensitive cells that should be well developed here because of the importance of the plexus, I have not been able to separate them from the supporting elements.

In summary one sees that, in spite of the absence of a special sense organ situated on the ocellar pores, the latter have no less than five privileged points from the point of view of innervation. It would thus not be surprising that in a species of urchin still unknown one would find in these points really different sense organs. And these organs would in addition be better placed on these places on these plates called ocellar that, from the youngest age, are in their definitive place and no longer have to submit in their growth to modifications in dimensions.

(1) *Loc. cit.* (2) The supplement of *Jenaische Zeit. f. Naturwissenschaft*, V. II, 1886, contains a note in which O. Hamann confirmed several of my observations without any allusion to the note in *Comptes rendus de l'Académie des sciences de Paris*, 22 February 1886, where they are summarized.

II. -- In very young urchins, *Strongylocentrotus lividus* and *Echinus microtuberculatus*, 3 to 4 millimeters in diameter, the ocellar pores are constituted as in an adult except for dimensions.

#### REMARKS ON THE DEVELOPMENT AND REPAIR OF THE TEST.

In the present state of our knowledge, it is not possible to analyze the various phenomena that result in the deposition of the calcareous network of the test. All one can say is that the deposition is provoked by the activity of a special reticular tissue one finds everywhere in the interior of all the calcareous formations of the urchins.

This tissue, we have seen, is composed of fine canalicules in a plate already well developed, but if one considers either a bud developing on a portion of the test of a very young developing plate, one has difficulty in finding the canalicular nature of the organized network.

The latter appears in these young formations as constituted by conjunctive strands, very delicate, solid, and provided with numerous nuclei. It must be admitted that it is only later and little by little that these strands are transformed into canalicules.

Is it possible to ascertain the histological elements specially charged with calcium secretion?

One encounters, as we have seen, numerous muriform corpuscles in the network organized in the test. These cells in *E. acutus* are ordinarily numerous in the conjunctive layer situated below the body wall proper, and we shall see in an instant that one finds them in abundance in the canalicular network of the spines of *Dorocidaris*. It is thus natural to wonder if they are not the direct agent of calcium secretion.

In order to respond to this question, it suffices to examine a young plate in the process of development. If the muriform globule is the agent of calcareous secretion, one should encounter it in abundance in these young tissues. Now, not only does this form of cell abound in the plates in formation in young urchins, but they still appear to be completely exclusive. There is thus no reason to stop longer.

The formation of a young plate or of a bud of a plate already formed is always preceded by the appearance of nuclei, all similar, coloring strongly with dyes (fig. 13), showing a great resemblance with those of mesodermal cells of the larva and also with those of ameboid cells so widespread in the perivisceral fluid of urchins. These nuclei belong to the cellular formations that will form, little by little, the organic network of the young plate at the same time that they secrete calcium.

There does not exist a special cell type charged with this secretion outside of the net of which we just spoke.

A plate in the process of development increases at the periphery. The center of this plate will be thus always the oldest part. That where the tissue forms will be the first to become useless. In *Dorocidaris*, in which the thickening of the plates is considerable, this tissue does not disappear completely and it begins to undergo resorption. It does not persist less than the entire life of the individual.



II. -- We have seen that the membrane covering the test contains the peripheral nervous system. It is thanks to it that the animal receives at each instant the influences of the external environment. This role is of the greatest importance, but it is not the only one that the skin has to fulfill. It is that in fact which assures the preservation of the test.

The best means of proving it is to attempt the experiment of removing the skin on a certain portion in order to observe the results produced.

Now, this experiment has been done, without my consent, by the band of young mullets that have already been mentioned. These voracious companions of captivity of *Dorocidaris* were not content with pulling out the spines one by one, but removed the skin of certain of them on different parts of the test.

After some days, the regions thus stripped are clearly circumscribed and have been necromatized, while all around them the covering of the test preserves its ordinary aspect.

Some weeks later, all parts of the attainted test were rejected by a veritable exfoliation and it was truly curious to see the *Dorocidaris* wounded in the tanks of the laboratory thus exfoliate. One lost some interambulacral plates, another a part of the ambulacral zone, another finally rejected at once an entire interradial zone.

What had happened to it? There was formed little by little, under the denuded part and at the expense of the internal organic network, a membrane continuous with the external skin. The formation of this membrane limiting the necrosis had at the same blow brought a complete isolation and consequently, the exfoliation of the part of the test situated above it.

This partial destruction of the test always occurs if the denuded surface occupies a certain expanse. If, on the other hand, the wound is unimportant, then the skin has time to reform very early above the wound in order to prevent necrosis, and exfoliation does not occur.

That which happened to *Dorocidaris* in captivity in the aquariums of Banyuls happens sometimes to those that live freely on the bottom of the sea. They are wounded either by their natural enemies or by the devices of fish. Also it is not rare to capture some that are repairing their wounds as just explained.

The membrane that forms below the exfoliated part is always colored reddish-brown by the corpuscles of which we have already had the occasion to speak.

Besides there is no doubt that after exfoliation of the wounded part, the repair of the test does not operate in a complete fashion under this membrane, which is not long in becoming identical with the surrounding skin.

These few observations show very well that the preservation and the reproduction of the test are assured by the skin, whose existence is intimately tied to cells of the network that forms the test.

I have done nothing new to bring to the subject of growth of the test as a whole. One knows that the new plates grow around the apical rosette and not elsewhere. In a row, the oldest plate borders the peristome; the

youngest touches the apical rosette. The plates, once formed at the apical pole, are little by little driven back by those that form afterwards. They grow at the same time on their periphery and one understands easily how, this way, the whole of the test proceeds little by little towards its definitive size and form.

A *Dorocidaris* 11 millimeters in diameter has six interambulacral coronal plates in a row, and an adult of 52 millimeters has nine. These numbers show well the importance of the growth that can be called intercalary.

#### PRIMARY SPINES OR RADIOLES.

I. -- Valentin distinguished in a spine of the urchin the *rod*, which is the free part, and the *head* or *condyloid part*, which articulates on the mamelon of the tubercle. Between the two is the *collar*, terminated below by the *milled ring* (pl. XV, fig. 14).

The articulation of a radiole of a cidaris is made as in other urchins, with the sole difference that the articulating foyette of the spine is attached by its center to the mamelon with the aid of an elastic ligament. This character is a good characteristic of the cidarids, but it is not limited to the family. It is found also in the diademids.

The ligament is made of a bundle of elastic fibers formed from a part of the stroma organized from the corresponding plate. It penetrates very deeply into the mamelon that is consequently partly perforated after its disappearance. The radiole is, moreover, maintained on the mamelon by a conical trunk of very resistant elastic fibers, covered itself by a second cone formed of powerful muscle fibers. All of these fibers, elastic or muscular, are continuous with the stroma organized by the plate on one hand, and at the head of the spine on the other.

All is covered by the skin, which covers likewise the *collar*. The nerve ring has been described sufficient. We shall not repeat it.

The intimate structure of the radiole of a completely developed cidarid has been well known since the research of Stewart (1), A. Agassiz (2), and Mackintosh (3).

At the center, a *marrow* formed by a loose, not very firm calcareous tissue, then a zone where the small calcareous rods are more serrated and form a regular trellis whose aspect is freely rayed. This is the *middle layer*. Finally, an external layer or cortex that is very dense, very strong, and crossed by fine canaliculi formed at intervals from the middle layer.

This cortex characterizes the radioles of the cidarids (fig. 6), which Mackintosh (4) named the *Acanthostraca*. As for the organic tissue of the spine, it is identical to that which we described in the test itself. The illustrated elements contained within its canalicules are identical. The muriform corpuscles are never lacking.

- (1) *On the minute structure of Cidarid* (Quart. Journ. of micro. sc., 1871).  
 (2) *Loc. cit.* (3) *Report on the Acanthology of the Roy. Irish Academy*, 1883.  
 (4) *Loc. cit.*

II. -- *Development.* -- Development of the radioles of *Dorocidaris* must be followed on the young plates that circle the apical rosette.

It is interesting to note that the appearance of a radiole is always preceded by that of the secondary spines. These latter, as we have said, will have the mission to protect afterwards the base of the spine they surround. Now they have this protective role from the beginning. One can see them already, nearly completely formed themselves, bending together over the young, scarcely visible young radiole in order to form themselves as a tent under the shelter of which will occur the first stages of its development.

The center of the young plate that will produce a spine swells at first as a small round eminence that grows little by little and in which, at first, one distinguishes nothing other than the same elements of the plate on which it is a bud.

But soon the differentiation of the bud begins. It divides into two parts: an inferior one always part of the plate, the other superior. The first will form the tubercle. The second will differentiate to form the radiole. The skin covers everything. The new tissues are constituted below it.

From the beginning, the young bud is brightly colored red by the mahogany-brown corpuscles. These cells gather in great abundance in the skin and they are always apparent in the young tissue (the greater the number, the younger will be the tissue).

If one compares this observation with those reported for the healing of the test (p. 251), one comes to the conviction that the brown ameboid corpuscles have a role in the formation of adult tissue. One can however only make a hypothesis on the nature and the importance of their role.

Cannot one however consider these colored globules as responsible for provoking, in the points where they accumulate, a more intense local respiration required by the young tissue that they cover and that are unceasingly on the way to development.

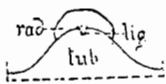


Fig. 1. -- *tub*,  
naisant tubercle;  
*rad*, naisant radiole;  
*lig*, ligament.

At this moment, the spine proper has become independent of the test (fig. 1), in the sense that it is already represented by a small dome of calcium covering the tubercle in formation and being attached to the latter only by organic tissue. It is very easy to separate this rudiment of the spine from the tubercle and, when the individual is dried, they separate by themselves.

A section, taken after decalcification on the axis of the future spine (fig. 2), shows us that the small dome is constituted by the conjunctive network that we recognize in the test itself. But these networks are looser

in the center (marrow) than at the periphery (middle layer). At the edge of the tubercle, consequently immediately under the spine, is a layer that begins to differentiate into elastic tissue. At the top of the tubercle, one perceives already a fibrous mass that is the ligament in process of formation. On the circumference also appear some muscular fibers as well as the nerve ring. Finally, over everything, is the skin.

In summary, we discover all the elements that enter into the constitution of the entirely developed spine, the cortex excepted. Here is how the course of its development goes.

The first part that definitely forms is the articulating part, the *head*. During this time the rod or stalk forms. It also is not slow in appearing directly under the milled ring. Figures 1, 2, 3, and 4 permit one to follow these transformations. Notice that, in figure 4, the tubercle has acquired if not its size, at least its definite form. The articulating base, nearly completely developed, already attaches to the powerful muscles and to the elastic ring not drawn on the sketches opposite (1). As for the rod proper, we see that it is still quite different from that which it will be later. Its structure is interesting to study at this time.

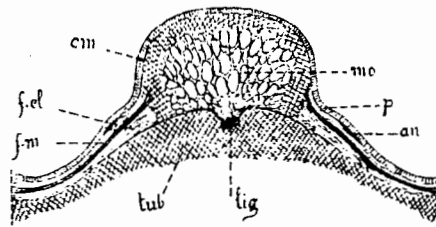


Fig. 2. -- Section passing through the axis of the tubercle of fig. 1. *tub*, tubercle; *lig*, ligament; *mo*, marrow; *cm*, middle layer; *fel*, elastic fibers; *fm*, muscle fibers; *an*, nervous ring.

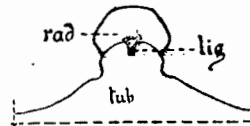


Fig. 3. -- *tub*, tubercle; *rad*, radiole; *lig*, ligament.

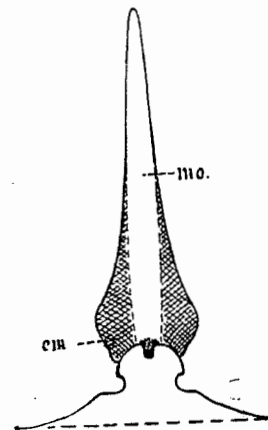


Fig. 4. -- Radiole whose articulating head is nearly entirely developed and whose young stalk is still made only by the marrow *mo* and the middle layer *cm*. The tubercle and the tissues of the articulation have acquired their definitive characteristics.

(1) These figures are only simple sketches to guide the reader and prevent ambiguity. All the details are omitted, but the outline is exact.

As for the rod proper, we see that it is still quite different from that which it will be later. Its structure is interesting to study at this moment.

From the beginning (fig. 2), we have seen apparently two types of calcareous tissue: that which shows the marrow of the adult and that of the middle zone. A section of the young radiole of figure 4

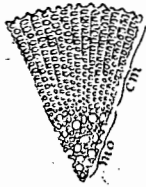


Fig. 5. --Sector of a transverse section of fig. XV, fig. 15).

4. *mo*, marrow;  
*cm*, middle layer.

The marrow is very developed and forms *by itself* the terminal part. The trellis-like tissue, which characterizes the middle layer in adults, forms here the periphery of the base, running the length of the stalk and disappearing before reaching the top.

This structure is going to persist for a long time yet, even though the radiole will be very elongated (pl. XV, fig. 15).

The collar is not distinct, the rod connects to the base by a simple concavity. It is smooth, marked only with fine stripes. But, growth continuing, the collar does not delay in differentiating and then one sees appear above it the small teeth that ornament the adult radiole (pl. XV, fig. 14). The alignment always continues to the summit and the small teeth that appeared first at the base (fig. 7.3) multiply in approximating more and more that which it finally attains (fig. 7.4). At this moment, the development of the spine is finished, its form and its size are no longer modified.

It is always entirely covered with colored skin because of the mahogany-brown globules, and possesses a very active ciliated lining on its surface.

A transverse section of the adult radiole shows us that the *cortex* has come to be added to the two pre-existing tissues, marrow and middle layer (fig. 6), and from a longitudinal section we learn that this cortex is terminated abruptly above the collar that it never invaded. The latter shows clearly delimited at the base of the stalk as soon as the cortex forms, i.e., when the ornaments of the base of the adult rod take their definitive characters.

One can summarize these various phases of development as follows:

- a) Appearance of a bud at the center of the plate;
- b) Division of the bud into two parts: tubercle and spine; appearance of the ligament, the elastic ring, the muscles, and the nerve ring;
- c) Differentiation of the tubercle and of the articulating base simultaneously with the appearance of the rod;
- d) Continued development of the rod;
- e) Appearance of the collar, brought about by the deposition of the cortical layer that forms the exterior ornaments of the radiole; complete differentiation of the cortex.

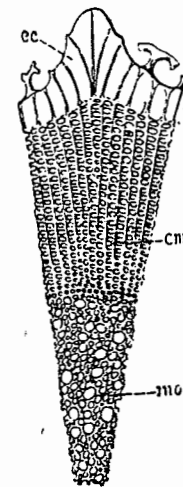


Fig. 6. -- Sector of a transverse section of an adult. *mo*, marrow; *cm*, middle layer; *ec*, cortex.

The immediate consequence is evident: in a radiole of *Dorocidaris*, the oldest part is the base, the youngest is always at the summit. It is no less evident that the deposition of calcium occurs constantly in the most external layer of organized networks found under the skin and that, in a transverse section, it is always the marrow that is the oldest.

These ideas moreover are clearly stated by W. Carpenter (1) who regarded the "organic substance of the of the external layer formed last, as the part essentially involved in the formation of these remarkable productions (echinoid spines).

At the point where we left, the radiole has finished its growth. It is mature. Its structure will no longer be modified, but its exterior aspect will be changed profoundly.

The progressive formation of the cortex involves the slow resorption of the skin and, at the same time, absolutely limits the development of the radiole since, as we have seen, this skin is indispensable to the life of the stroma underneath.

Stewart (1), of whom I shall have more than one occasion to refer to his accurate and precise observations, was therefore right when he said in regard to the spines of the cidarids that, probably in them, the marrow membrane that covers the test of all echinoderms dies after formation of the cuticle.

But the radiole does not lose this membrane simultaneously on all points of its periphery. It begins to be resorbed where the cortex is the oldest, i.e., immediately above the collar. Moreover, the disappearance of the skin involves colored cells. It is for this reason that the radioles begin to decolor. Then sometimes one observes some that present the strange aspect while it still continues to live at its summit, at the expense of the reserve material accumulated in that part.

Whatever happens, the skin is not slow in completely disappearing and the radiole, henceforth dedicated to the role of a wooden leg, is invariably invaded by those I indicated at the beginning of this memoir.

It is important to note that the collar *never* loses its skin, as it is never covered by a cortex and that is its essential character. Note in passing it is indispensable it should be thus in order to assure the preservation of the muscles and other tissues of articulation.

I have arranged the figure opposite (fig. 7), which permits following easily the single transformations of the rod. But in order to be complete, I should add there forms around the articulating pit a milled ring of cortex destined to reinforce the borders of this pit, and the tubercle encrusts itself also with a very strong and loose layer whose utility is evident.

(1) *Loc. cit.*

II. -- When a spine in the process of development is broken accidentally, it is repaired easily. The skin reforms over the break and produces at the center, corresponding to the marrow, a center of active development. One sees (pl. XV, fig. 6) appear then a small eminence (*b*) that elongates little by little and develops by passing through all the successive stages described above.

If the spine that had been broken already had lost its skin, it could not repair itself in the same fashion and here we have two cases to distinguish: first, where the break is produced towards the extremity of the spine; second, where this break has occurred not far from the articulating base.

In the first case, there is no repair. In the second, to the contrary, it happens very frequently the fragment of the rod remaining detaches itself from the articulating base because of the formation of a transverse membrane that, parting from the skin of the collar, crosses the spine in this region. The old trunk being rejected, a new radiole is born on the old articulating head. This mode of repair is very frequent. Nearly all the *Dorocidaris* collected show some examples.

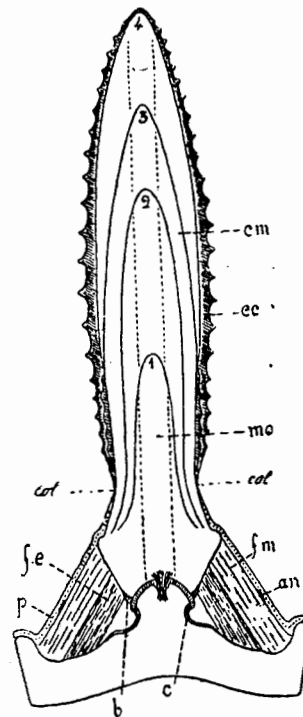


Fig. 7. -- 4 stages of development of a rod of cidarid numbered 1 to 4. *mo*, marrow limited by a dotted line; *cm*, middle layer; *ec*, cortex; *col*, superior limit of the collar; *b*, milled ring of the cortex reinforcing the edge of the cavity; *c*, crust of the adult tubercle; *p*, skin; *fm*, muscles; *fe*, elastic fibers.

If one can keep good count of that which has been said on the locomotion of *Dorocidaris* as well as the facts reported in the preceding lines, one will have the easy explanation of all the forms affected by the radioles in the same individual.

Consider an adult *Dorocidaris* with eight or nine interambulacral plates and suppose it intact. It shows from the peristome to the equator, radioles of progressing length. This variation in the length of the rod is due to the place occupied by the spine and not its age (as the oldest spines are the shortest). It results from the necessity of the animal being able to reach with all of the adoral radioles the ground on which it rests. Those spines carried by plates 1, 2, and 3 have a flat stalk, the normal adult form adapted for the function of prehension. (I do not show these diverse forms of the radioles. They are illustrated in the memoirs of A. Agassiz.)

The extremities of the radioles following are somewhat swollen and cut in bevels. This form is also normal and definitive. They characterize the essentially locomotor spine, with the extremity modified by contact with the ground.

From the equator to the apical pole, the radioles diminish progressively in length, and this variation is due to age, as well as the diverse forms that they take in this region. One meets there all the forms of the radiole in process of development on which we have insisted previously.

If the individual considered is not supposed intact from its birth, then we will find abrupt variations in the form of the radioles in all of the regions. The explanation for these variations is completely natural from what has been said on the subject of the repair of the spines after breaking.

As for the color of the rods, we have likewise seen the causes that make it vary.

All these considerations have a practical interest if one involves them in the determination of the species.

I have had in my hands an adult *Dorocidaris* with all of the radioles (except those bordering the peristome) in the process of regenerating on their articulating base. They were near stage 2 of figure 7. They were consequently a beautiful red, tapered, smooth, and without a collar. Very certainly, if I had not been forewarned by my previous observations, I would have believed I had a different species of *D. papillata* before me.

III. *General observations on the radioles of the cidarids.* -- After that which we have seen on the development of the cortex, one would be tempted to believe that it alone takes part in the formation of ornaments of the radiole. That is not correct. In *Dorocidaris*, one sees already the middle layer lay out slight longitudinal furrows on the stalk, but in the end it is the cortex that produces the characteristic teeth.

In the species that have very prominent and voluminous ornaments, *Phyllocanthus verticillata* for example, the middle layer forms a large part of their constitution, as one can assure himself by sections. In this case, and in all similar cases, the ornaments of the rod will be already well formed when the cortex comes to cover them.

It is the middle layer that gives the general form, the outline, of which the cortex finishes as the ornamentation.

A. Agassiz insisted very correctly on the different forms of radiole that one finds in the same species. Figures 21, 22, 16, 17, etc. of the first plate (1) give an idea of the variations in *Phyllocanthus annulifera* and *Phyllocanthus baculosa* (1). More recently, the same author returned on the same order of ideas on the subject of *Dorocidaris blakei*, which shows on one hand radioles very similar to those of *D. papillata*, and on the other hand, other radioles that, according to them, few paleontologists would have hesitated to report as the species *Rhabdocidaris remus* (Des.) of the Jurassic deposits. (2)

(1) *Revision of the Echini.* (2) *Reports on the results of Dredging by the "Blake", part I. Rep. on the Echini.* Cambridge, 1883.



Agassiz pointed out the danger that can result by determining a species by the simple examination of its radioles.

I completely share the ideas of the Cambridge echinologist, but I believe it is a type of error against which one can protect himself.

Being given any species of cidaroid, there are two reasons for which the form and dimensions of the radioles vary.

The first results from the place occupied by the radiole on the test. The example of *D. blakei* is striking and I scarcely see other means of evading the errors of determination that could come from the changing of form than by a comparative example of variations of an entirely known species.

The second is the consequence of development of the radiole. *Phyllocanthus imperialis* has large rods that are not completely clubs but approach it. Their extremity is large, rounded, and ornate with longitudinal projecting sides. At the middle of these rods I find one, as long as certain others, that is conical, pointed, and smooth. It is nearly certain that if one had to determine the two forms of radioles taken separately, one would not report them as the same species of cidaris.

It is this kind of error that can be avoided in most cases, if one can well admit that which has been said on the development of the radioles of *Dorocidaris* applies to all other members of the same family. And in reality, the identity of the structure of the radioles in all of the cidaroids, should involve necessarily the identity of their development.

In order to cover all the possibilities of our coasts, it is necessary (in the case where the test is absolutely unknown) to base an identification only on the adult radioles. It is necessary therefore to have a means of recognizing the latter.

For the living species, it is easy. It suffices to make a thin section. If the cortex is developed the entire length of the rod, the form of the radiole is definitive. But, for the fossil forms, it is necessary to have recourse to other means.

The first part to examine is the collar. Suppose it well developed. It can show two cases.

1st. The rod possesses ornaments, teeth, granules, etc. the entire length to the summit. In this case the radiole is adult.

2nd. The rod has ornaments only on the inferior part and is entirely smooth the rest of the length. In this case, the radiole is not adult, but it is not very far from its definitive state. It has reached very nearly its maximal dimension. Its general form cannot be very different from the adult form and one can have a very exact idea of what the radiole would become if its development had not been arrested by restoring the ornaments of the base to the smooth part.

In any case, one cannot assign as a distinctive character the absence of ornaments on the superior part of the stalk.

If the collar is not indicated, the radiole should be considered as a young form, dangerous to describe even if one already distinguishes traces of ornamentation as the modifications that the rod still has to undergo can be very profound.

If, at the same time, the articulating head is not very differentiated, one has a very young form.

In order to appreciate the age of a rod, it will not be necessary to trust the articulating head (the preceding case excepted) since, as we have seen, a very young rod can be borne on a very old head.

The conical, short, smooth forms, whether they possess a well-developed head or not, but without a collar, should be rejected absolutely, since they can appear in the most separated species and genera. It is thus that stage II of the scheme given above for the stalk of the radiole of *Dorocidaris* and that of a radiole of *Cidaris clavigera* will be, if my views are correct, nearly identical to each other.

#### SECONDARY SPINES

They are short with fine longitudinal striations. Their end is soft. The structure is very simple: there is no cortex at any point but only, as Stewart said, a "marrow passing gradually towards the periphery to a layer that corresponds to the middle layer of the primary spines".

These spines, lacking a cortex, remain thus always covered with skin, as in the echinids. Their articulation is made, as in the latter, without ligaments.

The tubercle is slightly prominent and carries a very small mamelon. As for the nerve ring, it is not differentiated. The muscles of articulation are simply innervated by the bundles of nerve fibers that pass between the tubercles.

I have drawn a transverse section of the superior region of these decalcified spines in order to show the organized network (pl. XV, fig. 17 and 18). One sees the small canalicules in which travel the muriform globules, and one notes that these epidermal cells are exclusively located in the superficial furrows. Between the furrows are found the calcareous rods *K* covered only by the cuticle. It often happens that these ameboid elements running in the network come to end in these small furrows between the cells (fig. 18, *gm*).

All of these secondary spines, when one observes them on an individual in good condition, show at the base a sort of white, transparent ampoule (pl. XV, fig. 6) situated on the side opposite to that on which the spine is inclined when it drops down in order to protect these neighboring parts.

These ampoules have been seen by O. Hamann (1) while I pursued my research. I had not judged it appropriate to report them in a preliminary note but I must say a few words today.

(1) *Loc. cit.*

O. Hamann wrote: "Each spine, from the longest and largest down to the smallest, carries glands at its base that are composed of large mucus-forming cells." Does the author mean to designate the radioles by *largest*, *longest*? I suppose so and, in this case, I cannot confirm his statement as it is the secondary spines *alone* that possess the basal ampoules.

As to their histological constitution, it seems poorly interpreted by O. Hamann.

To us, these ampoules (pl. XV, fig. 6e) are nothing but the puffs of the membranes that cover the spine, puffs filled with liquid and that collapse passively when one pricks them with a sharp needle.

The membrane that forms them is formed like the skin of the test, except that it is much thicker in this place and that the intercellular spaces between these supporting cells are enormous and very irregular. Observed alive, they offer in optical section the aspect drawn above (fig. 8). One can then very easily take them for vibratile cells while, in reality, these are simple intercellular alveoli containing muriform globules that, under slight compression, escape outside.

If one makes a section normal to this skin (fig. 9), after having treated the spine with dyes, one sees that these globules are contained in the spaces that separate the supporting cells disposed here as in the skin of the test, but much higher and very narrow. These cells, united by the ciliated cuticle, are grouped in a fashion to form the alveoli (fig. 10) into which slip the muriform corpuscles, all as we have seen before.

I have seen nothing that merits the name of glandular cell. The basal ampoules of the small spines no more contain glands than the rest of the skin, and I cannot understand to which histological element Hamann makes allusion when he speaks of *glandular cells* covered with vibratile cilia on their surface filled with granulations. Perhaps it is the muriform globule that the German the author has taken for these glandular cells making part of the membrane of the ampoule.

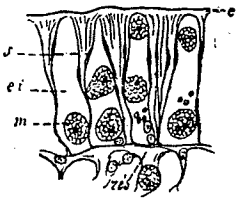


Fig. 9. -- Section of the membrane of an ampoule. *res*, connective mesh; *ei*, intracellular space; *s*, supporting cells; *m*, muriform globules; *c*, cuticle.

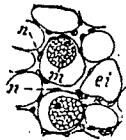


Fig. 10. -- Tangential section membrane of an ampoule; *ei*, intercellular spaces; *n*, nucleus of the supporting cells; *m*, muriform globules.

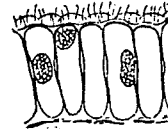


Fig. 8. -- Optic section of the membrane of an ampoule.

## PEDICELLARIAE

I. The pedicellariae of cidaroids have often been described and figured, those of *Dorocidaris papillata* in particular are found in the memoirs of Perrier (1), Agassiz (2), and Koehler (3)...where they are represented with more or less exactness. One knows that all these pedicellariae have their head directly articulated on a rigid stalk. Perrier distinguished two forms: the *thornless* pedicellariae and the *armed*. The first have narrow elongated valves adorned with very small teeth. Koehler correctly called them tridactyles. They correspond well, in fact, with those designated here in echinids.

The second (armed) have been well described only by Stewart (4), who has given an excellent figure of one of the valves. This author has indicated that the valves of this kind of pedicellaria are hollowed into a vast cavity communicating with the exterior by a large triangular opening bordered by teeth, as well as by a narrow canal dug into the terminal fang. These valves are always short and very swollen.

Stewart would be of the opinion of considering them as analogues of gemniform pedicellariae. I share his opinion, as I have found a gland in the cavity of the valves very similar to those of the geminiform pedicellariae of the echinids. When one examines one of these organs under the microscope in sea water fortified with alcohol, one very often sees welling up at its extremity a certain quantity of mucus. If one makes thin sections of the pedicellaria, one proves that the mucus is produced by three glands that fill the cavities of the three valves. I do not stop to study the histology of these organs, I give simply a sketch of a longitudinal section of a valve in order to show better the position of the gland and also to indicate that the large opening of the cavity of situated under the fang is not freely open to the exterior but is closed by the large cells with granular contents and provided with a well-developed ciliated lining. It would be quite possible that nerve endings are there. I have not pursued their study.

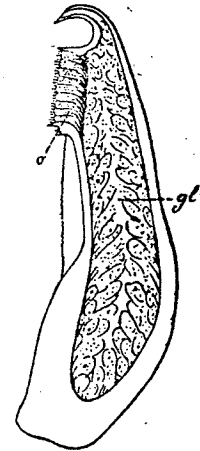


Fig. 11. -- Semi-schematic section of a valve of a glandular pedicellaria of *Dorocidaris*. *gl*, gland; *o*, cells situated before the triangular opening beneath the terminal hook.

(1) *Recherches sur les pédicellaires et ambulacres des Astéries et des Oursins*. (2) *Loc. cit.* (3) *Loc. cit.* (4) *On certain Organs of the cidaridre*, 1877.

If we compare a valve of a gemniform pedicellaria of *Dorocidaris* to the analogous organ of *Sph. granularis* for example, we see that their analogy consists of the presence of the mucous gland, but that this gland is differently situated in these two types in relation to the calcareous valves. In *Sph. granularis*, the gland is attached to the calcareous valve and supplied with powerful muscles. In *D. papillata*, it is contained in the valve itself and one does not understand easily how the product of its secretion is mechanically driven to the exterior as it does not seem provided with muscular fibers and, besides, the volume of the pocket of mucus is not susceptible to decrease since it is attached to the walls of a rigid chamber. One can only make hypotheses, but one must admit that the mucus is capable of escaping at the will of the animal, probably under the influence of the excitation of the cells that enclose the large windows of the glandular chamber.



Fig. 12. -- Transverse section of a valve of a glandular pedicellaria of *Dorocidaris*. *gl*, gland; *calc*, calcareous wall of the valve.

These glandular pedicellariae are large. Their head is frequently more than 1 mm long, but the stalk is always short.

There exists another kind of pedicellaria, much smaller than the preceding and that seems to be diminutive ones. In agreement with Koehler, I am of the opinion that one should consider them as definitive forms.

This form, very scattered nearly everywhere on the test, excludes the other two on the peristomial membrane. Now, O. Hamann (1) said he has found these glandular pedicellariae in *D. papillata* on the buccal membrane. Consequently, it is necessarily these that occupy us at this moment.

Without claiming that there never exists glands in this form intermediate between the tridactyle and the glandular pedicellaria with the big head, I certify that the glands have aborted in most of them and that the type of glandular pedicellariae remains that described by Stewart and in which I have observed, with a single exception, the presence of the mucus sacs.

These are encountered on the anal plate (a small number), the genital plates, the interambulacral area usually near the sutural lines. I confirm the observation of Stewart on the subject of the forms with four valves that he has found on the apical pole. This anomaly is very frequent.

As for the tridactyle pedicellariae, one encounters them around the radiole between the secondary spines and on the radial areas near the median suture.

(1) *Loc. cit.*

II. -- *Considerations on the functions and homologies of the pedicellariae.* -- Since O.-F. Müller has described the pedicellariae of urchins, it is not, so to speak, a hypothesis that one would give on the subject of their functions. It is certainly necessary to admit that all we still know today, after having acquired precise notions on their histology, is that the pedicellariae are neither parasites or embryos of urchins. The only hypothesis that can be accepted for the moment, based on the constitution of the head of these organs and on the fashion in which certain of them constantly try to bite, is that they are organs of defense.

It is necessary to add to this the presence in the gemniform pedicellariae of glands that, wrongly or rightly, have been considered as venomous glands.

However, it is to be remarked that the glandular pedicellariae are always the least mobile and the most unskilled in biting. It suffices, in order to be convinced of it, to observe on a *Sphaerechinus granularis* the gemniform pedicellariae that are well known and attain unusual proportions. One sees them shake maladroitly their large head on their rigid stalk, while all around them the trifoliated pedicellariae are twisting in all directions. Upon touch, they bite but if they do not seize the object they remain a long time before opening again. If the foreign body was seized, they seem incapable of getting rid of it.

Be that as it may be, the presence of glands attached to what one can call a *venom gland* and the fact that one finds very often gemniform pedicellariae either of *Sph. granularis*, or of all other species, attached to the integument of fish, molluscs, annelids, etc., permits hardly any doubt that it serves as an organ of defense.

One recognizes the observation reported by A. Agassiz according to which he regards the pedicellariae of the apical pole as charged with cleaning the test of excrements thrown out by the anus. I myself have never been able to verify this observation despite the considerable number of urchins I have observed.

Formerly other functions, which are not correct to us, have been attributed to the pedicellariae.

According to Romanes and Ewart, pedicellariae serve a locomotory function. It suffices to have observed some urchin at the sea shore to acquire the conviction that the pedicellariae can never serve in locomotion of these animals and that, if one sometimes sees *Echinus microtuberculatus* hanging on *Zostera* or other marine plants, it is by the aid of the ambulacral tentacles alone that they are attached there.

On the other hand, O. Hamann (1) said: "In *Echinus microtuberculatus*, the poison-containing pedicellariae occur most on the dorsal surface and serve, as I myself have been able to show on many occasions on animals held in the laboratory, to hold fast pieces of leaves, etc. with which the sea urchin in rest as in movement becomes masked. Here the slimy secretion of the glandular pedicellariae is of greatest use to them."

(1) *Loc. cit.*

Certainly, *E. microtuberculatus* often carries on its apex debris of algae or of *Zostera*, but it is with the aid of its ambulacra and not of its pedicellariae.

*Strongylocentrotus lividus* is still more skillful than the preceding in covering thus its anal orifice. The length of the coast of the Bay of Banyuls, when the water is calm and limpid, one perceives certain of these urchins immobile in their holes. They have all placed on their apical pole some foreign bodies, algal debris, fragments of crustacean carapaces, diverse shells, and often even the remains of their fellows. The idea never comes to the observer that these urchins retain these bodies with their pedicellariae. That would be perfectly impossible for them. Besides, it is easy to assure by simple observation that all of the diverse debris is held with the aid of the ambulacral tentacles.

One must therefore reject the opinions of Romanes, Ewart, and O. Hamann. Rather than attributing other peculiar functions to the pedicellariae. It is better to admit that the question is always open but that the sole reasonable hypothesis is the one that makes them protective organs of the test.

The study of the pedicellariae of *D. papillata* furnishes no clarification on the question. They are little formidable as organs of defense as they can move only in the very restrained limit around the point of attachment and that, in consequence, their zone of action is very reduced. They are, moreover, incapable of biting any enemy already fixed on the test because of the low mobility of their head.

III. -- Agassiz showed, by the study of the development of these organs in the asteroids and by interesting considerations that the comparison of the

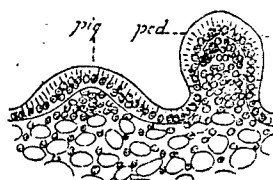


Fig. 13. -- Vertical section of two buds. One, *piq*, will form a spine, and the other, a pedicellaria.

diverse type of echinids suggested to him that the pedicellariae are the morphological equivalent of a spine. Here is what one observes in the regular urchins. The spine, we have said, appears from the beginning as a bud of the test. The first stage, before which nothing announces the appearance of the spine, is represented in the adjacent margin in a young *Str. lividus*. One sees a slight eminence that raises the skin more thickly at this spot (*piq.*).

Adjacent is found a second bud of the same plate (*ped.*) constituted as the first but of different form. The one (*piq.*) will form a spine. The other (*ped.*) will form a pedicellariae.

Follow the development of the latter: we shall see that its distal extremity rapidly differentiates into three lobes that are the first indication of the three valves of the pedicellariae, of which the muscles are not slow to form at the expense of the formative cells accumulated in the bud. There is thus formed a small head of a pedicellaria and at the same time the stalk appears beneath, clearly differentiated but short.

In the bud (ped.) of fig. 13, one sees already that towards the extremity, the formative cells group themselves in order to form the head. In a section of a new pedicellariae of adult *Dorocidaris* (pl. XV, fig. 5), one sees this head more clearly indicated by the grouping of cells at the extremity of the bud as well as by the differences of thickness of the skin that thins towards the top where is going to grow, little by little, the furrows limiting the three valves. The result of the preceding is that, in a pedicellaria, the part that develops first is the head or the summit.

This conclusion does not modify the morphological equivalence of the spine and of the pedicellariae. Both have the same origin, but it indicates to us an interesting difference in the mode of subsequent development of the two types of test appendages.

In a spine of *Dorocidaris*, the summit is the youngest part; in a pedicellaria, in contrast, it is the oldest.

IV. -- Recently, O. Hamann (1) described in *Sphaerechinus granularis* new organs encountered on the surface of the test, to which he gives the name *globifers* (globiferen). While the author still has made these organs known to us only by a short note, it is good to make some reservations here and now.

The *globifers* such as those described by Hamann exist in *Sph. granularis*. The question is knowing if they are organs really distinct from pedicellariae, and here is why:

One knows that there exists on the stem of all the gemniform pedicellariae of *Sph. granularis* three voluminous more-or-less spherical glands, each provided with an opening by which they release an abundant mucus. These glands have been described by Foettinger (2), then by Koehler (3), and are known to all those who have held a *Sphaerechinus* in their hands. Foettinger also observed similar glands in *Echinus melo* and *Echinometra subanularis*.

These glands have exactly the same characters as those assigned by Hamann to the three glands of *globifers* and present themselves in equal number. Suppose a gemniform pedicellaria of which the head has been detached, which is very frequent in *Sphaerechinus*. There remains on the test a stem carrying three glands and, if most of the portion of the shaft that extends beyond these glands is resorbed and disappears, which is very possible, one will have a perfect *globifer*. In this case, the *globifer* would be only a remnant of the pedicellaria. I do not believe that the skillful histologist of Gottingen has committed this mistake, but at least it has been good to discuss this embarrassing case.

Put aside this hypothesis and admit that the *globifer* has never had the head of a pedicellaria.

(1) *Loc. cit.* (2) *Structure des pédicell. gemniformes du Sphaerechinus granularis* (Arch. biol. v. II, 1881). (3) *Loc. cit.*



After what has just been said on the development of the latter organs, the globifer cannot be young pedicellaria as the head would be developed in the first place. This head has been aborted, and it is probable that one will find the globifers again only in the species that possess pedicellariae whose stem is provided with mucus pouches.

#### DIGESTIVE TUBE

I. -- When one describes the organization of an urchin, one generally supposes it is placed in its natural position, i.e., the mouth below. We will not adopt this orientation and will place *Dorocidaris* on its apical pole, the mouth above. This inversion of the urchin can, in the first approach, seem inopportune. Here are the reasons we have developed to legitimize it.

The day when competent authors agree, in order to establish the morphologies of the echinoderms, it will be necessary to adopt a single orientation. If one is to succeed in following the phylogeny of these beings, it is completely natural to think that the point of departure will be furnished by the crinoids.

Now, these have the mouth turned upwards in their normal position. One will have to, therefore, in order to facilitate comparisons, likewise place the mouth of asteroids, ophiuroids, and urchins upward. As for the holothuroids, this position will be found completely natural for a certain number of them.

This is certainly not giving a conventional orientation to a being that can modify the morphological value of an organ. But if this conventional position has a result the facilitation of comparisons, should not one adopt it?

One will object that, since the echinoderms having the mouth turned below are in the majority, it is more logical to change the position of the minority and that it is necessary, consequently, to turn over the crinoids and the holothuroids.

Such is not our point of view as, in placing the mouth of all echinoderms above, not only does one bear in mind the position of the primitive type, but further one conforms to a rule that one instinctively follows and that consists of placing the mouth above in all animals that one describes.

It has been a long time since de Lacaze-Duthiers set out the advantages of this rule, either in his works or to his hearers at the Sorbonne.

If one would want to force oneself to illustrate and describe each animal in its preferred position, one would reach in short order contradictions that would produce sometimes embarrassing descriptions.

When a zoologist illustrates a being whose normal position is unknown to him, either as he has not been able to observe it or as in reality any position is immaterial to the animal in question as is the case for certain pelagic forms, he does not fail to conform to the rule enumerated above and, if it is not made, those who come after him rectify the orientation by a common accord.

J. Müller, in his beautiful memoir on the larval forms of echinoderms, oriented all the *Pluteus* with the mouth below. Observers who followed him reversed this position of the larvae and they have done well. Although, if one places oneself in the point of view of the natural position of the *Pluteus*, there would be no good reason to fault Muller.

We shall place *Dorocidaris* with the mouth above, and as for its orientation around a ventral axis, we shall follow the view of Loven for whom radius III is anterior and the madreporite plate right anterior if the animal is placed on the mouth, left anterior if it is placed on its apical pole. The plate is part of interradius II.

I. *Masticatory apparatus and pharynx.* -- *D. papillata* possesses a masticatory apparatus or lantern, constructed on the same plan as that of other regular urchins. Without delaying for a detailed description of this apparatus, we shall recall some of the unique characteristics of cidarids and shall insist on the relations with the pharynx and the peristomial membrane.

The teeth of *Dorocidaris* are not keeled (*crista-dentilis*, Val.). Their inferior extremity or *plume* (in the echinoids) does not project outside the ensemble of the apparatus. There are no *dental* sacs.

The transverse arcs of the jaws are not fused. The apophyses of the test or *auricles*, on which attach the muscles of the jaws, are part of the interambulacral plates. It is fused two-by-two below the *radii* (1) only in old individuals.

The articulating pieces (scythes) show nothing unusual. The branches of the Y-shaped pieces (compass) are very short and bilobed. How is the peristomial membrane itself attached to the masticatory apparatus.

On the circumference of the buccal orifice, this membrane forms a circular lip lined with an epithelium that recalls by its color and form of its cells the superior extremity of the pharynx.

The five arcs of this lip, corresponding to the five jaws, are attached to the extremities of the latter (pl. XVIII, fig. 1, *i*) and the five parts corresponding to the radii fold up more deeply towards the interior in order to fuse to the pharyngeal wall in the interval of the two jaws (pl. XVIII, fig. 1). Moreover, the peristomial membrane is, in each of these intervals, solidly attached to the extremities of the jaws.

The part of the digestive tube included in the masticatory apparatus has been named the *pharynx*. Its general form is that of a right prism with a pentagonal base. The faces of the prism are opposed to the jaw and are

(1) The cases of fusing of the auricles are very frequent in *Dorocidaris* of great size. It therefore will be prudent, if one wants to preserve in the characters of the cidarids the independence of the auricles, to add that the character is only applicable to individuals still in the process of growing.

consequently interradiar, while the angles correspond to the ambulacral axes. Towards the buccal extremities of the pharynx, the angles increase in order to penetrate between the two contiguous jaws in the corresponding radius (pl. XVIII, fig. 1, ar; pl. XVII, fig. 1, ar).

The pharynx presents five lips situated vis-a-vis the teeth in the gutter where they are lodged (pl. XVII, fig. 1, l). Each of these is formed by a fold of the pharyngeal wall of which a section represents an S (pl. XVIII, fig. 1, l). At one of the bellies of the S corresponds the lip, while the other forms a bourrelet (b) projecting towards the interior. After being folded in this manner, the pharyngeal wall attaches itself to the interior of the corresponding jaw by a conjunctive membrane (g) (pl. XVIII, fig. 1; pl. XVII, fig. 2).

Five furrows alternate with the pharyngeal lips. At the base of the furrows, the peristomial lips (lp) are attached by joining to the epithelial layer of the pharynx.

All communication between the interior and the exterior of the test is therefore impossible around the teeth. It is important to insist on this point, as Steward (1) is of the opinion that it must exist.

The pharynx has with the masticatory apparatus firmer attachments than those of which we have just spoken. It is suspended by ten conjunctive lamina (pl. XVIII, fig. 1; pl. XVII, fig. 1, l, s), reinforced on their free edges by a muscular cord situated on all sides of the pharyngeal angles. These lamina are attached to the jaws, to the internal angles of their lateral faces, very close to the articulating pieces. They extend beyond as far as the membrane covering the entire apparatus, although towards the middle of the mouth they reunite by corresponding pairs to the faces of the pharynx and so form a bordering infundibulus of the lip (pl. XVII, fig. 1, s).

Also the pharynx is firmly attached to the jaws by five pairs of ligaments (t) that, rising from the pharyngeal wall, pass at right angles on the nerve ring and are attached at the interior of the jaw, the length of the tooth border (pl. XVII, fig. 1, 2).

III. *Peripharyngeal cavity*. -- The complete masticatory apparatus is covered by a membrane designated by Valentin (2) under the name of *lantern membrane*. This, attached all around the esophagus in the plane of separation of the latter and of the pharynx, molds itself on the jaws and their muscles and is continuous with the membrane covering the general cavity. It thus encloses the masticatory apparatus in a closed chamber without any possible communication with the rest of the peristomial cavity. It is important to be assured of this fact and this is easy. One reaches it either in proving that injections made into the interior of the cavity in

(1) *Loc. cit.* (2) *Loc. cit.*

question cannot penetrate into the general cavity, or in observing that the liquid contained in the masticatory apparatus cannot escape after one had colored all of the perivisceral fluid. Finally, careful dissection shows that, without exception, there is not the least disruption in the covering membrane.

The peripharyngeal cavity, isolated in the general cavity, presents five diverticula that correspond to five voluminous appendages formed by the covering membrane (pl. XVIII, figs. 1, 3, 5; pl. XIX, fig. 1, *st*). These organs, inflated by the peripharyngeal liquid, rise in the angle of the oblique ligaments. They are gracefully recurved in an arc and carry on the convex side two ranges of prominent mamelons. From each side of the Y-shaped pieces are found small bumps resembling those of the organs in question.

The membrane that forms these latter do not differ from that at all other points of the masticatory apparatus. Of a very delicate conjunctive nature, it contains numerous spicules and is invested on both faces with a ciliated epithelium.

It is interesting to remark that the spicules are lacking in the secondary caecum and that the membrane there acquires a much greater delicacy than the rest of the organ.

Stewart (1) was the first to make known these singular appendices of the lantern of *Dorocidaris* and, still now, one does not know of them other than in cidarids. The English author described and illustrated them exactly. But he expressed, on their functions, an opinion that we shall have to discuss further. For him, these appendages replace functionally the absent external gills. We say immediately that we cannot accept this point of view, that the name *gill* cannot be appropriate for these organs and that, not finding in the series of beings anything that can be compared to them, we propose to designate them under the name of *organs of Stewart*.

IV. *Esophagus and intestine proper*. -- Immediately after the pharynx comes the esophagus that empties into the intestine proper, after a more or less sinuous route (pl. XVIII, fig. 3, 4; pl. XIX, fig. 1, 6).

This presents the typical circumvolutions often described in the echinids.

*Dorocidaris* being placed on its apical pole, the radius III anterior, the intestine goes from left to right (in relation to the observer) and reaches the radius III which it does not cross.

This first circumvolution constitutes the first curve. It forms graceful festoons molded on the genital glands and extends from the region of the peristome to a short distance from the apical rosette (pl. XVIII, fig. 1, 3). There is no caecal stomach at the junction of the esophagus and the intestine. The color of this first curve, at first brown-violet as the esophagus itself, becomes little by little a brown-yellow that is maintained until radius III.

(1) *Loc. cit.*

In this region, the intestine reflects, running in the inverse direction (from the right to the left of the observer) and reaches thus the anal orifice by the intermediary of a short rectum (pl. XV, fig. 19; pl. XVIII, fig. 2, r). This second circumvolution is the second curve. Its developed length is much less considerable than that of the first although its angular route is in reality the same. It is distinguished in addition by the greater delicacy of the walls, narrowing (masked in fig. 2 of plate XVIII). It is entirely covered by the genital glands.

Fig. (2) of plate (XVIII) represents the ensemble of the two curves in *Dorocidaris* and can serve as a scheme for the description of the circumvolutions of the intestine of any urchin.

One sees that radius II, designated by Loven after a thorough study of the structure of the test, is distinguished from the others by this fact, that the intestinal circumvolutions do not cross it and that, in conclusion, it corresponds to an anatomically unpaired particularity that is found in radius III of spatangoids and clypeasteroids.

The intestinal circumvolutions are accompanied by two mesenteric lamellae, the one internal, the other external. The internal lamella seems to end with the esophagus on the membrane of the lantern but in reality it forms a complete ring around it, reappears in interradius 2, and runs again along the esophagus (*mo*) that it attaches to the ovoid gland. It reaches thus the underside of the apical rosette and forms there a pentagonal ring that binds between them the five genital glands (pl. XVIII, fig. 4). If one follows this internal mesenteric lamella to the rectum, one sees that it surrounds the latter, and at the same time attaches itself to the ovoid gland (pl. XV, fig. 19, *m*) and accompanies it to the lantern with whose membrane it merges.

As to the external mesenteric lamella, it is the one that attaches the intestinal circumvolutions to the test along their entire length. It surrounds the rectum and merges with the internal mesenteric lamella and, toward the esophagus, terminates in fusing the lamella (*mo*) (pl. XVIII, fig. 3) that binds the latter to the ovoid gland.

*V. Histology of the digestive tube.* -- We say immediately that, in *Dorocidaris*, the walls of the digestive tube are comprised of the same fundamental layers as in the echinids, namely: external ciliated epithelium, muscular layers with longitudinal and circular fibers, conjunctive layer, and finally internal ciliated epithelium.

The external epithelium is paved with small, polygonal cells. If one contents oneself with studying these cells in a cross section, one will have a false idea of their form. In fact, it happens that the action of the reagents causes the protoplasm of each of them to contract. This pulls the limiting membrane so it that molds itself exactly on the nucleus in such a way that the entire cell seems to be reduced to the latter, which remains attached to the underlying layer. It is necessary, to have an exact idea of this epithelium, to examine it flat after the action of silver nitrate.

The epithelial layer enveloping the intestine is continuous on all the organs and clothes all the internal surface of the test and preserves all the time the same characters.

We shall not stress the modifications of the muscular layer in the various regions of the digestive tube. We are content to say here that the longitudinal fibers are rare as in the echinids (1).

The conjunctive layer always contains throughout numerous calcareous spicules of various forms. In general, they amount to a small plate of irregular border and pierced with holes.

The pharynx has five longitudinal bands of triangular section, corresponding to the faces of the prism (pl. XIX, fig. 2, *f*). These bands lose themselves in the pharyngeal lips and are continuous, on the other hand, with the conjunctive tissue of the esophagus where the five layers are replaced by the much more numerous longitudinal and transverse folds.

At the first curve, this conjunctive layer decreases considerably in thickness and, always containing innumerable spicules at its periphery, presents toward the interior numerous small canals that constitute the network of the absorbing intestines. It preserves this character until a short distance from the rectum in the second curve. Then the lacunae of the network disappear and the conjunctive layer continues until the anal orifice where it continues with perianal membrane.

The three layers: external epithelium, muscular, and conjunctive of which we have just spoken take part in the formation of the mesenteric lamellae.

The internal epithelial layer is that of which the modifications are the most interesting to follow (2). A cross section of the pharynx shows that it presents at the interior five longitudinal folds produced by the conjunctive bands of which we have spoken above. The epithelium follows these folds quite naturally and forms on the cup a rose with five lobes that correspond as much to the furrows alternating with the folds. Now, the epithelial elements are different according to whether one considers them in the furrows or the folds.

On these latter are found long narrow cells, among which a large number show a calciform extremity releasing abundant mucus.

These cells are stained by hematoxylin. But the double stain of carmine-boric acid and methyl green is much more instructive. One sees, in fact, on the cups thus treated that these granular cells are of two kinds. They secrete two distinct types of mucus. One stains very strongly with carmine and is very clearly granular. That of the other retains exclusively methyl green and seems of homogeneous consistency.

In the furrows, these calciform cells are very rare and are replaced by shorter and more massive ones that contain fine granules and stain with methyl green and hematoxylin.

(1) Koehler, *loc. cit.* (2) I have not figured in detail the diverse forms of cells of this epithelial layer, not wanting to multiply the figures that are very numerous in this memoir. The typical form on which one can report is that of a long cell tapered at the base, which contains the nucleus, and swollen at the top.

At the base of the epithelial layer, on the entire periphery of the pharynx, exists also a continuous foundation of small pyriform cells whose role is difficult to comprehend. I shall willingly consider them as producing the brown-violet pigment that is often abundant in this region.

Finally it is necessary to indicate the mass of brown spheroidal granulations that, in old individuals, develop in abundance between epithelial cells where they very frequently release muriform globules.

Be that as it may, the pharyngeal epithelium is characterized by the presence of two types of mucus cells indicated in the preceding lines. These cells should play an important role in the preparation of food. They probably replace the absent salivary glands.

The epithelium of the esophagus is formed by cells identical to those of the furrows of the pharynx. There are no mucus cells.

In the living individual, the epithelial cells of the esophagus are clear or little colored.

It is not the same in the first curve, where they become opaque and take a very clear yellow color. These changes are produced by the appearance of numerous yellow granulations that fill the swollen extremity of each cell. Moreover, these latter are all identical, and differ from cells described in *Strg. lividus* by Koehler only in their dimensions. They are very clearly much larger.

From the second curve, the cells become much smaller, less rich in granulations, and finally in the rectum, they are completely clear.

From this rapid study, it follows that the different regions distinguished in the digestive tube of *Dorocidaris* are characterized not only by their form, dimensions, and respective positions, but more by the distinct characters of each of them furnished by the intestinal epithelium. It is certain that to each of these regions is reserved a special role in the phenomenon of digestion.

The food undergoes in the pharynx, then in the esophagus, a preparation that renders it ready to release the assimilable material that it contains during its stay in the first curve where absorption is most active.

This latter phenomenon continues equally in the second curve, but with less intensity, and it very probably ceases to take place in the latter portion.

All leads to the believe that it is in this part of the digestive tube that the excreta agglomerates in order to form the small balls that the urchins rejects by its anus, and that Rondelet compared to pills.

What mechanism affects the passage of alimentary material in the digestive tube? Direct observation is impossible here. One can only make hypotheses.

One understands without difficulty how the masticatory movements of the five teeth force the crushed particles to enter the pharynx. Having arrived in this first portion of the digestive tube, the food is conducted by successive contractions of circular muscle fibers of the intestine and also by the movement of vibratile cilia that cover all of the intestinal mucosa and produce a continuous current going from the mouth to the anus.

The feces accumulate thus little by little in the second curve, and encumber the rectum. The anal orifice, yielding under the pressure, opens in order to give passage to the excremental balls that escape to the outside.

VI. -- One will remark that until now there was no question of an organ well known not only in the regular urchins but again in the spatangoids where it was discovered first. Perrier (1), who studied it in many echinids, gave it the name of *intestinal siphon*. Later, Teuscher (2) described it anew and gave a section that fixes very exactly its relation with the digestive tube.

The intestinal siphon is a canal that "rises from the extremity of the esophagus near the point where the latter opens into the stomach sac, runs the internal border of the intestine, and opens anew in this organ very near its point of reflexion" (3). We know, in addition, by the studies of Teuscher and of Koehler, that the walls of this canal are clothed with an epithelium, presenting a great analogy with those of the intestine itself.

The intestinal siphon does not exist in *Dorocidaris*. It is easy to be convinced of this either by injections made into the digestive tube or by simple dissection. In all cases, examination of cross sections of the intestine just corroborates these first observations and is particularly instructive.

One sees in these sections that the internal mesenterial lamella is directly attached to the wall of the intestine itself and that this lamella does not contain in its interior a canal comparable to a siphon (pl. XV, fig. 8). But one sees in addition that immediately above the point of attachment of the mesentery, the mucosa of the intestine is sensibly modified and forms two folds much more developed than the neighbors, composed of cells very different from those that constitute the epithelium of the rest of the intestine. They are longer and narrower. Their less voluminous nuclei stain strongly with dyes, show no granules, and are placed at variable heights in the cell body. Finally, the distal extremities of these latter are clear, not swollen in mass, and deprived of yellow granulations.

If one examines now with the magnifying glass the internal epithelial layer of the intestine, one perceives distinctly all along the line of insertion of the internal mesenteric lamellae two more developed regular series of folds (those of which we just spoke). They are less colored than the neighbors and limit a sort of gutter that, commencing at the posterior extremity of the esophagus, follows the internal border of the first curve in order to terminate at the beginning of the second.

This gutter follows exactly the path that the siphon would follow if it existed. One does not find it in the urchins containing this latter organ and it seems logical to consider it as the first indication of the intestinal siphon in the echinids.

(1) *Loc. cit.* (2) *Loc. cit.* (3) Perrier, *loc. cit.*



But if this gutter can be considered as the morphological equivalent of the siphon, it would not be able to supply it with its physiological role, of such kind that we find present in regular urchins, in which all the phenomena depending on the existence of the siphon are supplied. It is true, as Perrier thought, that this organ assures in the second circuit a replenishment of water sufficient to permit an effect respiration of the perivisceral fluid in contact with the walls of the latter circumvolutions, the cidaroids find themselves, from this point of view, in a state of evident inferiority.

#### GENITAL GLANDS

As in the other urchins, each of them presents throughout an excretory canal with very numerous ramifications terminating in cul-de-sacs, in which develop the eggs and their spermatozoa.

No external character distinguishes a male gland from a female gland and the sexes of the individuals are not indicated by any particularity of form, of size, or of color.

The walls of the cul-de-sacs and ramifications are very resistant, and contain, as all other membranes of *Dorocidaris*, numerous calcareous spicules that have been described by Stewart (1).

Each gland is attached to the test by a membrane situated in its plane of symmetry and extends along the excretory canal, with the walls of which it merges.

In addition, the gland presents very numerous secondary attachments, either with the test or with the neighboring organs. These attachments are of small conjunctive straps formed from the walls of the gland and merged with the membrane covering the general cavity or with the walls of the digestive tube and is external mesenteric lamella.

The enormous development of the five glands is their most characteristic trait. They encumber the interambulacral area from the rectum to the region of the peristome. Toward the apical pole, their ramifications are so much developed (pl. XVIII, fig. 1) that the glands touch one another to cross the stays that support the second circuit. Thus it seems to have there, all around the anus, a ring constituted by a single gland. But it is not necessary to make a mistake. Despite their apparent confusion, the five glands always preserve their independence. Their cul-de-sacs touch one another, attach themselves one to the other by small conjunctive stays, but never fuse.

This remark leads us to insist on the independence of the excretory canals themselves.

(1) *Loc. cit.*

The five genital glands are linked by a pentagonal ring (pl. XVIII, fig. 4) surrounding the periproct and formed by a dependence of the mesenteric lamella that attach the esophagus to the ovoid gland. The membrane that forms this ring is continuous with the envelope of the glands, which is found therefore to be itself only a dependence of the portion of the mesentery mentioned above. In an adult it is not entire, but well reticulated as shown in Fig (4) of plate (XVIII), and is attached to the test only by its internal and external border. The space included between it and the test belongs to the general cavity.

We will have to return later to the genital pentagon, and we shall see that the membrane that constitutes it contains in its thickness an interstitial lacunar network belonging to the visceral lacunar (blood) system.

The extremities of the excretory canals of the genital glands are masked by the ring in question. But if one raises it after having conveniently cut it, one perceives the excretory canals penetrating the corresponding genital pores and one sees without any possible doubt that they are not linked together by a circular canal. They are independent. Each carries to the outside the products of its gland. It is impossible that an egg or a spermatozoan arising in one gland should be expelled by the pore of a neighboring gland.

It is thus not necessary that it would be necessary to understand the genital apparatus of *Echinus sphaera* according to Perrier.

This author, discussing the existence of the circular perianal canal mentioned by some of his predecessors said, "It is possible however to find a circular canal around the anus. It is necessary for that to insert the needle of a syringe into the excretory canal of one of the genital glands and to make the injection upward. One then sees it fill a circular canal and, beyond, ebb in part in the excretory canal of the four other genital glands and leave in part by the genital pores. This canal is therefore a dependence of the genital apparatus. It is there the excretory canals of the ovaries and testes open..." (1) The five excretory canals of the genital glands of an urchin open therefore into a common ring that, to him, would communicate with the exterior by the five genital pores.

Having stated that this manner of view was not the expression of reality in a cidaris, I have had to search to see if the genital apparatus of an echinid was otherwise disposed and I convinced myself that in *E. acutus* and all the urchins that I have been able to observe, including *E. sphaera*, the excretory canals of the genital glands are absolutely independent of each other.

The section represented (pl. XXII, fig. 10), representing *E. acutus*, indicates sufficiently the fashion in which an excretory canal terminates in the corresponding pore. It shows equally that this canal opens at the summit of a papilla that surmounts the pore.

This papilla exists in males and females. It is colored dark red-brown and is very developed at the age of sexual maturity.

(1) *Arch. Zool. exp.*, v. IV, series 11, 1875, p. 614.

## INTERNAL NERVOUS SYSTEM

I. -- In *Dorocidaris*, as in all the regular urchins, the nerve pentagon is applied on the wall of the pharynx at the level of the extremity of the jaws.

An careful dissection permits observing this pentagon in place (pl. XVII, fig. 1, N). Each of its sides furnishes a pair of cords ( $t$ ) that, at first view, could be taken for the nerves. But they are in reality very resistant ligaments attaching on the one hand to the jaws (pl. XVII, fig. 2,  $t$ ) and, on the other, to the walls of the pharynx that they support ( $t'$ ). They cross at a right angle the sides of the nerve pentagon and mix in passage with its envelope.

From each summit of the pentagon arises a nerve trunk (ambulacral nerve) that, in passing between the jaws, goes the length of the corresponding radius in following the line of the median suture of the ambulacral plates and penetrates, at its extremity, the ocellar pore. From its point of departure, i.e. from the summit of the pentagon, until the moment where it attains the border of the peristome, the nerve rests on a conjunctive membrane that is, in reality, a doubling of the peristomial membrane that limits a cavity communicating neither with the general cavity nor with the exterior (pl. XIX, fig. 1; pl. XVII, fig. 5, 6  $j$ ). If the ambulacral nerves rested directly on the peristomial membrane, they would be subject to the repercussions of all the deformations of this membrane whereas, this way, they are more isolated. Moreover, when one examines with attention the ensemble of the anatomical arrangements necessitated by the complexity of the masticatory apparatus, one finds quite naturally that there is thus formed a sort of bridge under each ambulacral nerve, in order to make up the difference in thickness between the test and the peristomial membrane and to facilitate the passage of the nerve to the peristome.

A cross section of the ambulacral nerve, made at a small distance from the auricles (pl. XVII, fig. 3), shows us that the nerve is not a simple nerve, but more a flattened tube in which one should distinguish two parts: one internal ( $n$ ), the other external ( $n'$ ), and between the two, the lumen of the tube ( $\omega$ ). The internal part is thick and contains the nerve elements, fibers, and cells. The external part ( $n'$ ) is uniquely conjunctive (in the preparation represented. It was invaded by pigmented granulations). But, although this latter does not contain nervous elements, we must consider it as making part of the nerve in the sense that it is formed by the neurolemma. Examining now the other sections of the same radius (pl. XVII, fig. 4-9), we no longer find the lumen ( $\omega$ ) of the tube. The two parts ( $n$ ,  $n'$ ) are joined and have obliterated it. There is consequently matter for discussion. Which of the two sections (3) (4) represent reality. Should one not admit that the space ( $\omega$ ) was accidentally produced by the reagents and that, in reality, the tube formed by the neurolemma is stopped by the joining of the walls? Whatever should be the interpretation adopted, it remains that the two parts ( $n$ ) ( $n'$ ) exist and that they include between them a space at least. We call this space *intra-neural space*, the space thus defined between the internal part and the external part of the nerve tube. Follow it to the pharynx.

The cross sections (4, 5, 6, 7), more and more approached by the latter, show us the nerve always divided in two parts ( $n$ ) ( $n'$ ), but a sole longitudinal sections is much more instructive. One sees in this section (pl. XIV, fig. 9) that the internal part ( $n$ ), which in reality contains the nerve elements, terminates in the wall itself of the pharynx and loses itself in the epithelial layer ( $ei$ ), while the external part ( $n'$ ) continues with the epithelium of the peristomial lip ( $ep$ ). The intra-nerve space ends therefore at the point where the two epithelia ( $ei$ ) ( $ep$ ) join, and if the lumen of the tube was not obliterated, it would open at the exterior in ( $w$ ). A section passing from the middle of one of the sides of the pentagon (pl. XIV, fig. 10) shows us that in this region, the nerve cord ( $N$ ) is likewise in continuity with the epithelial layer of the pharynx. One always finds the space ( $w$ ) between ( $N$ ) and ( $N'$ ) between the epithelium of the pharynx and that of the membrane ( $q$ ) that attaches the pharynx to the tooth.

This relation of the nerve pentagon with the pharyngeal epithelial layer being known, it is useless to search for special nerve cords placing it in relation with this part of the digestive tube as it is mixed, so to speak, with it all along its periphery.

We do not know how the nervous system develops in an urchin, but we propose a hypothesis for its constitution in an adult *Dorocidaris*.

The nerve ring of *Dorocidaris* is constituted as if it were developed in a circular invagination produced around the mouth, following the ideal line that separates the ectoderm from the endoderm. The ambulacral nerves are so made that they seem to come from five radial invaginations of this ring. The intranervous space that we have designated by ( $w$ ) in all the figures would be the vestige of the cavity of the supposed invagination.

From the summit of the nerve pentagon that gives it birth up to the ocellar pore, the radial nerve is covered for a distance by a conjunctive membrane filled with calcareous spicules, attached by its border to the network of the test, and forming underneath the nerve a closed tubular space (perineural space) isolated from the general cavity (pl. XVII, fig. 3-9). This space contains at the same time the radial dependencies of the water vascular system and of the visceral lucunar system.

The ambulacral nerve emits, on its route, lateral branches or tentacular nerves that penetrate the wall of each tentacle in passing by that of the two pores that is nearest the approach of the nerve or internal pore. These tentacular nerves are constituted as the trunk from which they emanate. They are the tubes into whose vent continue the intra-nerve space ( $w$ ).

The two parts of the ambulacral nerves contribute to the formation of the lateral branches. The external wall, which does not contain nervous elements in the principal trunk, acquires some from the very start of the lateral branch, of such kind that one cross section of them presents the nerve fibers all around the space ( $w$ ) (pl. XVII, fig. 11).

This section has been set in one of the neighboring preparations of section (7). In this region, the branches that detach from the ambulacral nerve should cross diagonally the perineural space in order to rejoin the pore to which they are destined.

Having reached the border of the internal pore of the tentacle that it must innervate, the nerve cord lodges in a furrow dug in the wall of the pore and coming out at the notch (*u*) (pl. XIV, fig. 2) visible at the exterior. It runs thus up to the surface of the test. A cross section in relation to the nerve, i.e. tangential to the test, made near the point of emergence of the nerve (pl. XIV, fig. 13), shows us that it has not lost its essential character during its crossing the pore. The nervous elements always enclose a space *w*. Examine now a cross section of the tentacle itself (pl. XV, fig. 10). The nerve has become a single cord. It has left en route its external part, which is spread on the surface of the test in order to constitute the superficial nervous plexus. The semi-schematic figure (pl. XVI, fig. 7) helps us understand this disposition.

The histological constitution of the ambulacral nerves and of the nerve pentagon of *Dorocidaris* does not differ from those that others have described in the echinides. The fibers are very fine, all run parallel in the direction of the nerve. The cells are principally situated on the external face of the internal part of the nerve tube. However one finds them in the mass itself of the nerve. It is crossed, normally to the surface, by numerous conjunctive tracts that attach to the envelope by small swellings (pl. XVII, fig. 10). This disposition is analogous to that which Teuscher (1) figured in asteroids and that to my knowledge has not been reported in the echinids.

If we unite that which we have just expressed with the facts established in the chapter where the peripheral nervous system was treated, we will have a nearly complete notion of the ensemble of the nervous apparatus. It remains to follow the tentacle nerves into the ambulacral tubes, that which will be done in regard to these latter organs. But before passing on, I should insist on an anatomical fact that the study of *Echinus acutus* has furnished me. I want to speak of the innervation of the genital glands.

II. *Innervation of the genital glands.* -- In *E. acutus*, the apical extremity of an ambulacral nerve is very curious to observe. One sees in the sections closer and closer to the ocellar pore that the little nerve band, raising its borders, transforms itself little by little in hollowing an internal cavity and finishes by forming a complete tube around the water vessel at a small distance from the pore (pl. XVI, fig. 4). This tube presents an enclosed part in a furrow of the test and an internal part covered only by the membrane lining the general cavity. The first part (*n*) sinks into the pore and resorts to the exterior in order to spread itself on the skin (pl. XVI, fig. 2). The second part (*n'*) remains under the membrane that covers it and furnishes the nerve fibers to a ring (*ng*) situated at the external border and below the membrane that forms the genital pentagon in

(1) *Beiträge zur Anatomie der Echinodermen.* Jena. Zeit. f. Natur., 1876.

following a little nearer the line of its connection with the test. This nerve ring is very apparent in a cross section (pl. XVI, fig. 6). One follows it consequently without difficulty. One can also see it after staining with gold chloride or by direct observation of the membrane of the genital pentagon. It passes under the excretory conduits of the gonads (pl. XXII, fig. 10) to which it furnishes nerve fibers. The fibrils that constitute it are identical to those of the ambulacral nerve. As for the ganglionic elements, I would not know how to affirm if it is necessary to consider as such the cells situated at the surface of this ring. Those who know what difficulty there is in proving the nervous nature of a cell in echinoderms will understand my reserve. Be that as it may be, we have established that *Echinus acutus* possesses a genital nervous ring linked to the apical extremities of the five ambulacral nerves.

I have sought this ring in *Dorocidaris* and I have not been able to find it. If one compares section (4) of plate (XIV) to the analogous section of *E. acutus*, one sees that in *Dorocidaris* the ambulacral nerves does not present at the entrance of the pore the particular disposition reported before. Is it necessary to conclude the genital glands of *Dorocidaris* are not innervated? Not at all. In *E. acutus* the innervation is made by the intermediary of a ring. It remains to discover how it takes place in other urchins. I have found the genital nervous ring in a young *Strongylocentrotus lividus* of 4 millimeters that I made a section of in order to study the development of the gonads (pl. XXII, fig. 1, *ng*).

#### PERIVISCERAL FLUID

The liquid that fills the visceral cavity of *Dorocidaris* is slightly reddish and turbid. Taken from an individual in perfect condition and placed in a watch glass, it is not slow in forming a clot (as Geddes (1) observed in the echinids), containing the major part of the formed elements that were previously free in the liquid. They are the elements that we have studied in the living state and after the action of dyes, in order to be able to recognize them in all the tissues where one encounters them. We have already reported several times the presence of certain of these coelomocytes in the tissues that have been studied until now. The method followed is most simple. It consists of observing the living formed element under the microscope, then to submit it, always under the microscope, to the action of the usual reagents. The changes of form, if there are any, as well as the particular colorations are followed with care. Finally the elements observed are shown in preparation in order to constitute an authentic model.

(1) *Observations sur le fluide périviscéral des Oursins* (Arch. Zool. exp., series 1, v. VIII, 1879).

The most abundant element is the *colorless ameboid globule with long pseudopods*. It is constituted (pl. XIX, fig. 7) of a mass of protoplasm containing a large, finely granular nucleus. This nucleus is not always visible in the living state. It is necessary, for it to appear, that the protoplasmic layer that masks it should be sufficiently thin by elongation of the pseudopods. I have never seen the pseudopods of the same ameba form the arcs as takes place in the echinids. These amebae, uniting, constitute the plasmodes that engulf, little by little, surrounding bodies and finish by forming the clot.

Treated with 45 degrees alcohol, the globules with long pseudopods are not sensibly deformed. Eosin stains them, as well as hematoxylin, which makes their nucleus very apparent (pl. XIX, fig. 8). This has a dimension that varies between 4-5 thousands of millimeters. It contains several nucleolar points. One recognizes easily the nuclei of corpuscles with which we occupy ourselves in the body of plasmodes by their aspect and to their size.

Besides the ameba with long pseudopods, one observes equally colorless ameboid globules, but whose pseudopods always remain very short and frothy. They contain large refringent granules pressed against one another, which gives them a very characteristic muriform aspect (pl. XIX, fig. 9, a). These muriform corpuscles, treated with 45 degrees alcohol, show a small nucleus of the same dimension as the grains of the globule and ordinarily their aspect is not modified. However, the refringent granules appear sometimes to be destroyed by the reagents. Picric-sulfuric acid and osmic acid fix them in a more regular manner.

Fixed by alcohol, they avidly take eosin and retain it. Hematoxylin colors them, but less vigorously. Carmine-boric acid colors only their nucleus. Osmic acid preserves their refringence. Whatever the reagent employed, the granules are preserved. One recognises these elements with the greatest ease wherever one encounters them (pl. XIX, fig. 9, a'; pl. XV, fig. 5, 18, gm). It sometimes happens that the muriform globule disintegrates under the action of the reagents. In this case, one finds in its place spherical granules originally contained in its ectosarc (pl. XIX, fig. 9, a'').

One recognizes, mixed with the preceding, ameboid corpuscles that are distinguished only by the much smaller size of their granules (pl. XIX, fig. 10, b). Alcohol makes them globular (fig. 10, b') and shows their limiting membrane by contracting the contents. At other times, it takes the aspect (b''). They color strongly with eosin.

The last formed ameboid element with which we have occupied ourselves is the *mahogany-brown colored ameboid globule*. This ameba presents in the living state the character that one can recognize in the other urchins and that have been well described by Geddes (1). The granulations that they contain are never larger than those of the muriform globule. They are a

(1) *Loc. cit.*

little near the size of the white corpuscles that have just been discussed. Forty-five degree alcohol renders them spheroid at first, then their pigment dissolves little by little and the granules disappear in large part at the same time that the nucleus appears. If the action of alcohol is of short duration, traces of the pigment remain. If it is prolonged, the pigment disappears entirely. The same thing occurs with rapidity if the alcohol is acidified with hydrochloric acid (pl. XIX, fig. 11, c'').

Thus transformed, the mahogany-brown globule is unrecognizable. It stains, moreover, with eosin like the white globule with small granules and, in a section of decalcified tissue, it is not possible to distinguish with certainty these two types of figured elements.

Finally, one finds in the perivisceral liquid of *Dorocidaris* very numerous spherical globules provided with a long vibratile cilium that moves very rapidly. When one places a certain quantity of perivisceral liquid in a watch glass, these globules, thanks to their rapid and constant movement, escape the grasp of the pseudopods of the plasmodium that forms in order to constitute the clot. They are contained in all of the liquid mass, but congregate principally at the border as would small ciliated larvae.

They stop when one submits them to the progressive action of alcohol. Their cilium, which was difficult to distinguish in the living state, becomes very apparent and a little nucleus appears (pl. XIX, fig. 12, d''). This aspect lasts only an instant. The action of the reactants continuing, the cilium disappears and the globule is reduced to a small sphere provided with a nucleus (fig. 12, d''). Hematoxylin colors this nucleus strongly, which is always smaller than that of the ameba with the long pseudopods, as one sees after comparing figures (8) and (12, d'') on the same plate.

If several of these globules are touching when the reagent seizes them, the small spheres, pressed one against the other, become polyhedral and their ensemble produces then the aspect figured (pl. XIX, fig. 13, 1'd'''; pl. XXI, fig. 7). In this state, it would be impossible to recognize the ciliated globules of the perivisceral fluid if one had not followed along the transformations the reagents made them undergo. This example is well made for us to be on guard against too prompt interpretation that can occur with the reading of a single histological section.

After this series of observations, it is interesting to examine the sections made through a clot of perivisceral fluid, treated as if it were a fragment of tissue. One finds there all the elements that we have just passed in review (pl. XXI, fig. 6): (*i*) ameba with long pseudopods, (*gm*) muriform globules, (*gv*) ciliated globules. Regarding *gm*', it is not possible to affirm if it represents a mahogany-brown globule or rather a white globule with small grains. This doubt results from that we observed above relative to the action of the reagent in the two forms.



All the formed elements that float in the general cavity are thus ameboid, with the exception of the ciliated form. These amebae are found in all the tissues of the individual, in all the mesenteric membranes, in the epidermal layer, in the network of the test and of its appendages, up to the extremity of the longest spine. The easiest to recognize in the sections is incontestably the muriform globule, and it is not possible to find in *Dorocidaris* a place where it would be absent.

It is by their own movement that the ameba move in the tissues in which they follow the interstices and which they can, in addition, cross easily by a true diapedis. Geddes says, in his memoir on the perivisceral fluid, "One finds everywhere all of the kinds of ameboid corpuscles. They pass easily across the tissues...". It seems good to me to state the fact *de visu*, that which does not otherwise present serious difficulties.

Take a fragment of internal mesenteric lamella and place it under the microscope with all the necessary precautions in order not to compress it and in order to be able to keep it alive as long as possible. We see in the fragment numerous brown corpuscles and numerous muriform globules that move slowly in the conjunctive tissue. It is necessary to observe by preference those that occur nearest the internal border of the mesentery, after being assured that these globules are indeed in the tissue and not at the surface, which one can do by a sufficiently careful observation. One sees certain of these globules pressed against the epithelial covering that they enter slightly, others that are already engaged in part or totally in the mass of this epithelial layer. One fixes his attention on these (pl. XV, fig. 3, a) and waits patiently. If one is favored by chance (because all the globules that appear to have to cross the epithelium do not do so), one will witness the exit of the muriform globule observed. The different phases of the phenomenon are represented (pl. XV, fig. 3, a, b, c, c, e). At the moment when the corpuscles become completely disengaged, it leaves behind it a slight depression that is not slow to disappear, and the epithelial layer conserves no trace of its passage. The brown globules lend themselves equally well to this kind of observation (pl. XV, fig. 4, a, b).

It is not doubted that the ameba with the long pseudopods can, as the preceding, cross the same tissues and the diapedis of these globules should probably take place easily. The direct observation is very difficult, as it is scarcely possible to be completely free of all of the causes of error. These living ameba allow very easy observation when they are free in a liquid. But when they are in a tissue that offers the same transparency, the same refringence as themselves, it should be almost impossible to distinguish them and especially to follow them during all the time that the phenomenon lasts. On the other hand, one can be fooled very easily by the ameba applied against the surface of the mesentery. However, one frequently sees forming, on the edge of the latter, small prominences from which leave small protoplasmic extensions, which elongate little by little and form a

small tuft in the middle of the vibratile cilia of the epithelium. These protoplasmic extensions cannot be other than the pseudopods of one or several ameba in the process of making a passage.

In the middle of all these formed elements of the perivisceral fluid, one meets brownish granulations, spheroids, of different sizes, sometimes sparse, sometimes agglomerated. It is not necessary to confuse these spheroids, which moreover are rare in the general cavity of *Dorocidaris* in good health, with the mahogany-brown globules. These are living cells; the others are waste products. Carmine and eosin do not color them. Hematoxylin renders them blackish and methyl green, a yellowish-green color.

These spherules probably become the muriform globules that absorb little by little the material excreted by the tissues they visit and end by disaggregating.

#### WATER APPARATUS

The madreporite plate of *Dorocidaris* has the same form and the same dimensions as the other genital plates. It presents numerous pores to the external surface, which are the orifices in the same number as all the conducting canals. There is a single orifice situated on the internal face (pl. XIX, fig. 3, *o*) from which arises the sand canal or water tube. This orifice is situated at the angle of a triangular concavity or madreporic cross (*cr*) bordered by a projecting crest. The plate thus is not riddled by pores at its internal surface on which, aside from the genital pore (*pg*) one distinguishes only the orifice of which we have just spoken.

The canalicules of the madreporite are lined by a ciliated epithelium continuous on the one part with the epidermal layer of the test and on the other part with the epithelium of the water tube. The cells that constitute it, long and narrow at the entrance to the canalicules, flatten little by little, becoming less pressed and preserve these characters until the entry of the water tube. There they resume their dimensions, taking that which they preserve the entire length of the tube and form a columnar epithelium identical to that which has been often described in the echinids.

The water tube is not the sole canal that opens into the internal pore of the madreporite plate. There is a second conduit, which we call the *annex water canal* (pl. XIX, fig. 5, *c'*), not presenting the columnar epithelium of the water tube strictly speaking and covered by a simply paved ciliated epithelium. These two canals run side by side but, while the lumen of the water tube preserves its first dimensions its entire route, the annex canal enlarges little by little and finally opens into the cavity of the ovoid organ (pl. XIX, fig. 5, 6).

When one makes an injection, applying the needle to the external surface of the madreporite plate, the colored material penetrates into the water tube and at the same time into the annex canal and goes on to fill the cavity of the ovoid organ. On the other hand, if the injection is made by the water

tube itself and directed towards the madreporite, one sees the colored mass leave by the water pores and at the same time ebb in a collateral conduit (annex canal) in order to spread into the cavity of the gland. Finally, by a series of transverse sections, one follows easily the two canals until their confluence in the internal orifice of the madreporite (pl. XX, fig. 1-8, c, c'). One sees in section (7) that the septum separating the two canals has disappeared in part and in section (8) that these have joined their lumens into only one. Examination of these sections does not allow doubt and one arrives at the same conclusion by the longitudinal sections, normal to the madreporite plate (pl. XIX, fig. 5).

There exists there, beside the water tube strictly speaking, an annex canal, which is the extension of the cavity of the ovoid organ and which, in the same way as the first, communicates with the exterior by the intermediary of the madreporite plate.

Follow now the water tube. It runs beside the ovoid organ and opens into a periesophageal ring supported by the membrane that covers the masticatory apparatus (pl. XVIII, fig. 3, 4, 5). This ring, very much larger than the water tube, presents five lobes more or less pronounced *vis-a-vis* the interradiar area. It is covered interiorly by an ordinary ciliated epithelium, the columnar epithelium of the water tube having disappeared at the meeting of the tube with the ring.

Five radial branches arise from the ring, engaging themselves between the articulated pieces and the intermaxillary muscles in order to resort to the surface of the covering membrane where they are reflected in order to run the length of the radii, paralleling the ambulacral nerves, one to the apical pole and the other towards the mouth (pl. XVII, fig. 1; pl. XIX, fig. 1). Each of these ambulacral vessels, which is supported by the membrane forming the perineural canal (pl. XVII, fig. 3-9), sends all along its path lateral branches to the ambulacral vesicles. These are flat and, as in the echinids, their cavity is subdivided by transverse septa that direct the circulating liquid to the interior. These septa do not reach the border of the vesicle, all around of which exists a continuous marginal canal. The walls of the ambulacral vesicles are formed by a thin conjunctive membrane provided with transverse fibers (muscular?), ciliated on its two surfaces and containing numerous calcareous spicules. At each vesicle corresponds a pair of pores. When one injects the system of the ambulacral vesicles, the colored mass follows the marginal canal of the vesicle, arrives in the external pore (the most elongated ambulacral vessel), by which it penetrates into the tentacle and at the same time, spreads between the septa of the vesicle (pl. XVIII, XIX, fig. 3, 1).

The ambulacral vessel terminates in a cul-de-sac in the ocellar pore. As for the branch that is directed towards the mouth, it furnishes ramifications to the tentacles that surround the buccal opening. It is covered by the membrane that forms the perineural space that is well developed in this region (pl. XVII, fig. 5-7). Its ambulacral vesicles, still

preserving their ordinary characters, diminish little by little in size as they approach the mouth.

The system of ambulacral vesicles communicate with the exterior by the intermediary of the water tube and the madreporic plate. There exists no anatomical disposition capable of intercepting this communication. Its nature remains to be examined.

The mechanical causes that are able to provoke a current in the pores of the madreporite are the beating of the cilia and the changes of the total volume of the water apparatus. But it is necessary to add that no one has ever proven the existence of any current whatever across the madreporite of an urchin and that, on my part, I was not happier in studying *Dorocidaris*.

The direct observation being absent, we must study that which is most probable. Suppose the urchin blooms. If the cilia produce an effect from the interior to the exterior, the ambulacral system as well as the cavity of the ovoid gland would stretch to empty themselves. That is not possible. The volume of the water apparatus remaining the same, it cannot produce a current of exit without there existing at the same time a current of entry and visa versa. But in order for the two currents to exist simultaneously, it would be necessary that there would be in the madreporite two sorts of canals, one afferent and the other efferent. This is a disposition that all who have examined with care the structure of the madreporite will certainly refuse to admit.

It is probable that the beating of the cilia of the water pores tends to produce an effect from the outside to the inside. This effect will not be able, it is true, to provoke a current of entry as the interior pressure remains constant, but it will have as a useful effect maintaining the pressure needed in the water apparatus.

Suppose now that the tube feet originally extended come to contract. The vesicles enlarge in proportion and there will result an immediate pressure transmitted to the test and to all the viscera. This pressure will have two effects: the compression of the eminently deformable digestive tube and the extension of the flexible peristomal and anal membranes. These two effects will compensate largely the excess pressure that would tend to be produced in the perivisceral fluid following enlargement of the vesicles. The volume of the water apparatus will remain the same after as before the contraction of the tentacles, of which the play necessitates the production of no current in the madreporite.

However, if at a given moment the volume of the water apparatus is forced to decrease, the excess will escape outside by the water pores, and the cilia will serve then to clear the exit of formed elements that would be carried by the current. In this case, the madreporite will fill, according to the expression of Perrier, the role of a safety valve. But in short, it is not indispensable to the normal functioning of the tentacles.

If as we just saw, one cannot admit the existence of continuous currents in the canalicules of the madreporite, it is a phenomenon of accomplishment that nothing opposes. It is that of *simple diffusion* of ambient water into the cavities that communicates with these canalicules. One conclusion will be thus the following: The madreporic plate assures the penetration of the external medium into the water apparatus by *simple diffusion* and without currents.

II. *Ambulacral tentacles*. -- Their constitution varies according to the region of the test. Consider a tentacle situated in the adoral region. Its base is flat and it continues as a slender tube terminated by a sucker at the center of which one distinguished a conical prominence in the state of erection (pl. XIV, fig. 5). When the tentacle is retracted, the form represented is affected (pl. XVIII, fig. 3, *t*). A cross section of the basal region shows that the lumen is double (pl. XIV, fig. 8, *d*), formed of two canals, which contain the two ambulacral pores and are separated by a transverse septum. These two canals are not slow in fusing into a single one that forms the rest of the tentacle. The semi-diagrammatic figure (7) of plate XIV indicates the relations of the vesicle, the two pores, and the ambulacral tentacle.

The histological structure of the ambulacral tentacle does not differ essentially from that described in the echinids by Koehler (1) and Niemiec (2). The lumen of the tentacle is lined by a ciliated epithelium continuous with that which covers the interior of the pores, the vesicle, and the ambulacral canal itself. One distinguishes then a layer of longitudinal muscle fibers, a very developed layer of elastic fibers, a conjunctive layer, and finally an epithelial layer that is directly continuous with that of the test.

The conjunctive layer is remarkable for the calcareous spicules that it contains and that, when the tentacle is extended, gives it a ringed aspect. Separated from each other in the state of extension of the tube, these spicules touch each other in the contracted state. Their form, essentially irregular, cannot be characterized. They are arcs, simple towards the base of the tube, but complicated by external extensions in the upper part. These ramifications, always exclusively external, are moreover more developed than the spicules nearest the sucker (fig. 11). Examined either in living tissue or after the action of a weak solution of potash, these spicules appear disposed in such sort that they free a longitudinal band running from the notch of the internal pore to the sucker (pl. XIV, fig. 5). Immediately below this, the last site of spicules forms a complete ring (pl. XV, fig. 1') that surmounts the calcareous skeleton of the sucker, i.e. the rosette. The rosette is equally situated in the conjunctive layer and constituted of spicules of a very complex form whose ramifications in a bush radiate around

(1) *Loc. cit.* (2) *Recherches morphologiques sur les ventouses du règne animal* (Rec. zool. Suisse, 1886, v. II).

a central space corresponding to the extremity of the tentacle canal. It did not at all appear to us of a great interest to study, in the midst of all these spicules, those that represent the *cadre* of the tentacle of the echinids.

It is in the longitudinal band freed by the spicules that lodges the tentacle nerve (pl. XV, fig. 10, *nt*). It is enclosed in the thickness of the epidermal layer of the tentacle the entire length of its path. The conjunctive and elastic layers immediately below are reduced to a simple tissue. Arriving at the summit of the tentacle, the nerve swells a little (*n*) and terminates in the fascia of tissues encircling the base of the sucker that it innervates. This is filled with muscular fibers (*f*) independent of the longitudinal muscles, attached on side side at the center of the acetabular disc, and at the other to the walls of the tube.

There exists in the ensemble of the ambulacral system of an individual in good condition, a continuous pressure that, if the ambulacral tubes were deprived of contractile elements, would maintain it in a state of constant erection. Consider the water tube. It is erected because its muscle fibers are distended and because all its tissues depend of a common accord on the interior pressure to which the muscles of the vesicles resist. If all the fibers of the longitudinal muscles of the tube were in the same state of distension, they would be strong and immobile. But if certain of these fibers were to contract, the tentacle would obey their action and curve to their side. One understands how, in this manner, it can execute various movements.

We have said that the state of erection of the sucker presents a conical prominence (pl. XIV, fig. 5) at the center of the acetabular disc. What if the urchin wants to fix one of its ambulacral tubes? It applies the disc on the obstacle against which it is to be pressed in some sort of protruding cone. While the sucker is thus pressed against the surface to which it must adhere, the muscular fibers (*f*) attached to the summit of the cone contract and produce a depression there where they previously had a protruberance. The void tends to occur at the center of the acetabular disc and the adherence of the sucker is realized. This adherence is independent of the action of the longitudinal muscle fibers. The sucker adheres before they enter into play.

All that we have just said applies to the tentacles of the region that extends from the mouth up to the area of the equator, including those of the peristomial membrane (one knows that there exists nothing in cidaroids comparable to the ten buccal tentacles of echinids). We have insisted, at the beginning of this memoir, on the slight adherence that the suckers of *Dorocidaris* develops. One sees, after that which has preceded, that this is not caused by the imperfection of these organs, as they are as well

constituted as those of the latistellar echinids. Their weakness results only from their small size (1).

Examine now the tentacles from the equator to the ocellar plates. We see that they diminish progressively in length and that their sucker atrophies little by little so to disappear completely in the apical region. Figures (12) and (13) of plate XV represent the spicules of the extremities of the two tentacles. One (12) presented still a rudimentary sucker while the other (13), closer to the apical pole, was completely destitute. Its presence being linked to that of the rosette, the sucker is rudimentary in the first and nonexistent in the second. One observes its progressive formation in examining successively the tentacles of a radius, from the apical pole to the oral region.

The tentacles destitute of suckers are not capable of great extension. Their double basal part is very developed and the terminal tube is very short. It is probable that the absence of suckers at the extremity of the tentacles of the apical region is a trait common to all the cidaroids, but this is not a character peculiar to the family. We know in fact that we find it in the diadematids and the arbacids (2).

The liquid contained in the vessels of the water apparatus contains the same formed ameboid elements as the perivisceral fluid. It moves under the action of the ciliated epithelium that covers all the animal. It is easy to follow its movement in the tentacles of an animal in good condition thanks to the brown bodies that are never absent. One sees these latter arrive in the

(1) Here are some numbers that show the inferiority of *Dorocidaris* in this regard:

<i>Dorocidaris</i> of .....	40 mm	Diameter of suckers.....	0.40 mm
<i>Strg. lividus</i> of ....	46	-	..... 0.75
<i>Arbacia</i> of .....	42	-	..... 1.28
<i>Acrocladia</i> of .....	75	-	..... 1.96

(2) The genus *Arbacia* is separated from the cidaroids by some characters of the first order, among which it suffices to cite the structure of its peristome and of its peristomial membrane. This is however the second time that we are led to cite this genus in contrast to *Dorocidaris*. While preserving the powerful suckers of echinids on the oral region of the ambulacral zone, the mode of locomotion in cidarids borrows the aid of the spine (according to the interesting observations of Agassiz, *loc. cit.*), and all of the facultated locomotion being thus concentrated on the oral surface, the aboral ambulacral tubes have lost their suckers. This is equally a characteristic of cidaris. It is moreover interesting to certify with Mackintosh (*loc. cit.*), that the extremity of the locomotor spines of *Arbacia* are covered by a cortical layer analogous to those of the radioles of *Dorocidaris*.

tentacles by the external pore, reach the extremity of the tube, and descend in order to disappear in the internal pore. There is, between each tentacle and its vesicle, a veritable circulation. The current follows the same road as injected material.

Does there exist in the ensemble of the apparatus a true circulatory movement? Direct observation is not possible but such a movement is difficult to admit. It would be necessary, in order for it to exist, that there were in each canal making part of that apparatus, two currents in inverse direction. Now if one can, rigorously, admit them in the ambulacral vessels, it is difficult to understand that they cannot be produced simultaneously in the canals as small as the lateral branches destined to be tentacles. The currents that can be established between the vesicles and the ambulacral vessels will be intermittent currents and principally should erect or contract the tentacles. When the animal blooms, the only circulatory movements possible are, in our opinion, those established between the tentacles and the corresponding vesicles, independently of currents that can exist in the five ambulacral vessels, the esophageal ring, and the water tube.

There is not a true circulation in the water apparatus but rather a series of partial *vesicular-tentacular* circulations.

#### VISCERAL LACUNARY SYSTEM.

We shall describe, under this name, the apparatus very generally called in echinids: *systeme vasculaire sanguin*, *Blutgefasssystem*, *blood-vascular system*.

The first epithet, *vascular*, should be suppressed (at least in the cidarids) because the canals that constitute the system in question are not vessels, but simple interstitial lacunae, created in the conjunctive tissue. As for the adjective *blood*, it would seem preferable to us not to employ it, because the actual liquid to which one applies it, not being animated by a circulatory movement and not being charged with the transport of oxygen to the tissues, has not all the qualities required in order to merit the name of *blood*. H. Milne Edwards called this system of canals of echinoderms, *visceral vascular system*. We apply this name to it and modify the first adjective for the reasons that we indicated.

The study of this system presents difficulties that would be almost insurmountable if one were restrained exclusively to a single method of investigation. I employed the method of injection and that of sections, and whenever I could, I corroborated the results of one with those of the other. The colored solutions I used are: silver white (gouach) diluted in water, essence of colored turpentine, soluble blue prepared with gelatin or simply dissolved in distilled water. This latter material was always used when it was necessary to observe the injection in sections. Finally, a simple injection of air has given me very good results sometimes.



I have first of all researched the two marginal vessels of the intestine that are so easy to distinguish in echinoids. The sole one that it is possible to perceive in *Dorocidaris*, when one is not forewarned by previous researches, is the marginal external vessel (pl. XVIII, fig. 1, 2, 3, ve). On the internal border of the intestine, one sees a large mesenteric lamella, very resistant, crammed with calcareous spicules, often very strongly pigmented in brown. But one distinguishes nothing of resemblance to the internal marginal vessel of a *Echinus*. It is necessary therefore to attempt an injection by the external vessel. The operation is delicate as the diameter of this vessel is very small. It is however possible to succeed, and one sees then the colored material contained in a rich capillary network (pl. XVIII, fig. 3) that runs in the intestinal wall and attains the internal border of the intestine. Arriving there, the colored solution penetrates by short canalicules, into the interior of the internal mesenteric lamellae and spreads in outlining a sort of internal marginal vessel from which leave numerous and very irregular rammifications (vi).

A cross section of the intestine shows that the external marginal vessel is a dependency of the external mesenteric lamella (pl. XV, fig. 7, ve). When it is swollen, either by its natural contents or by the injected material, it is perfectly cylindrical and appears a true vessel. But as it is depauperate of an internal epithelium, one should consider it as a simple lacuna.

This external marginal lacuna is perfectly regular, well dammed, and isolated in part from the lamella in the interior from which it arises. It is all otherwise an internal marginal pseudovessel. This is contained in the thickness of the internal lamella (pl. XV, fig. 7, vi). Its lumen is irregular, poorly delimited in the middle of the conjunctive tissue. One cannot be mistaken there. This is nothing else than an interstitial lamella created in the internal mesenteric lamella. When at the capillary network that covers the intestine, it is composed of lacunar canalicules situated in the part of the conjunctive layer on which the epithelial cells attach.

Having thus, thanks to the first injections, found the internal marginal lacuna, injecting the needle into its interior that I have from this moment injected the visceral lacunar system. In order to have the chance of success, it is necessary to address an individual whose mesenteric lamellae are little pigmented (we shall see why further). A very successful injection shows us that the internal marginal lacuna continues on the second circuit until a short distance from the rectum. The external lacuna is ordinarily lost before the first, and the limit of the two lacunae indicates those of the intestinal capillaries. These extend from the region thus defined until the junction of the esophagous and the intestine. The network that it forms is very clear and perfectly outlined in all the route of the first circumvolution. Arriving at the second, terminal region one no longer distinguishes it with the naked eye. It becomes confused and the canalicules seem to lose themselves in a uniform lacunar lamella. This results in the

network being reduced little by little to its finest canalicules, and that they approach such a point that they appear to be mingled even under the magnifying glass.

The internal marginal lacuna runs the length of the esophagus (pl. XVIII, fig. 4, *vi*) and arrives thus on the internal border of the water ring where it forms a second ring joined to the first (pl. XVIII, fig. 4, 5; pl. XIX, fig. 1, 2, 4, 6). This periesophageal ring furnishes, from the one side, five branches to the mouth, and from the other, one to the apical pole.

This consists of a lacunar net which runs in the walls of the ovoid organ (pl. XVIII, fig. 3, 4, 1) and is directed with it to the apical rosette in order to extend into the thickness of the genital pentagon (*lg*) of which we have spoken before (p. 288). Before attaining this pentagon, the lacunae that follow the ovoid organ anastomose with a net arising from the extremity of the external marginal lacuna (pl. XVIII, fig. 3, 4, *rm*).

The five branches that the periesophageal ring send to the oral pole are formed of lacunae created in the five pharyngeal angles. In order to have a good idea of these, it is necessary to study cross and longitudinal sections. These sections inform us the pharyngeal angles are formed of a quantity of irregular conjunctive tracts anastomosed between them and attached to the walls of the pharynx (pl. XIV, fig. 9, *ar*). It is in the interior of the conjunctive tract that are situated the lacunae with which we occupy ourselves at this moment. I have succeeded several times in partially injecting them by making the injection by the internal marginal lacuna. One of these preparations is represented (pl. XIX, fig. 2). One perceives nearly regular canals, arising from the esophageal ring (*av*) and bordering the cutting edge of the pharyngeal angles. This aspect is illustrated by section (11) of plate (XIV) on which one finds at the top of the triangle (section right of the angle) the section of a sort of lacunar canal with a nearly circular lumen. This canaliform part of the lacuna disappears in the anterior part of the pharynx where it is transformed little by little into a lamella (pl. XVII, fig. 1) that recurves in order to pass under the intermaxillary muscles. When at the net formed by the tracts from the angle, it extends to the nerve ring (pl. XIV-XIX, fig. 9, 1). It was important to be assured of the existence of the pharyngeal lacunae. I have no longer any doubt of them when I am able to obtain a partial injection.

Each pharyngeal lacuna extends in the corresponding radius in a lacunar lamella that occurs between the nerve and the ambulacral vessel to which it is joined, and from the exit is found constituted five radial lacunae attached to the visceral lacunar system.

It has not been possible for me to inject at the radial lacunae and I had to study them only by the method of sections. This study should be made first in the peristomial region. A section, made nearly at the summit of the nerve pentagon (point that is not reached by the ambulacral vessel), we show the radial lacuna separated from the nerve by a perineural space (pl. XVII, fig. 8). On the following sections of (7) to (3), this lacuna (*lr*) is

applied against the ambulacral vessel (*aq*), previously injected with soluble blue. The section (4) is particularly interesting, as it shows a lateral branch (*lt*) detaching from the radial lacuna and accompanying the corresponding branch of the ambulacral vessel. In sections (6) and (7), the tentacle branches (*lt*) have been sectioned transversely, and one sees that each of them envelops the corresponding ramification of the ambulacral vessel.

It is thus well established: First, that there exists in each ambulacral zone a radial lacuna belonging to a visceral lacunar system, making a continuation of the pharyngeal lacuna emanating itself from the periesophageal lacunar ring. Second, that this radial lacuna sends, as the ambulacral vessel, a branch to each tentacle.

After having studied a radius in the peristomial region, one can understand a section of the same radius in any region of the test, near the equator for example. One finds there (pl. XVII, fig. 9) the nerve (*n*, *n'*), and the water vessel (*aq*). Between them a lamella (*lr*) in the thickness of which is the radial lacuna. All is covered by the membrane that limits the perineural space (*e*).

This space which one finds in all the sections, divided in diverse manners by the tentacle branches of the water and lacunar apparatuses, extends to the summit of the nerve pentagon where it appears to end in a cul-de-sac (pl. XIV, fig. 9, e). However I shall not affirm that it does not continue between the straps of the pharyngeal angles. What is very certain is that this perineural space does not accompany the nerve pentagon around the pharynx, and that in the adult there is no communication between the general cavity. The five perineural radial spaces are entirely closed and do not communicate with one another.

II. -- The liquid of the visceral lacunar system contains the same ameboid elements as the perivisceral fluid. But that which is essentially characteristic is the presence of a finely granulated amorphous material fixing well the colored material and which, in the individual preserved in alcohol, is perceived across the tissue thanks to its white-yellowish color and to its opacity. One does not meet this opaque content in the water vessels, nor in the clots of the perivisceral fluid. It is more or less abundant according to the conditions in which the urchin is placed and, although it fills completely the intestinal capillary network and its dependencies in those that have just been collected, one no longer finds it in *Dorocidaris* that have been starved some time in captivity.

The brownish spherules we have observed in the perivisceral fluid are met equally in the lacunae of the visceral system, and they are also more abundant in the older animal. In these large individuals, they are developed to such a point that the lacunae are nearly obstructed. The internal marginal lacuna is where accumulates a larger quantity of these granulations that sometimes color entirely in dark brown the corresponding mesenteric lamellae. Carried by the current of an injection, these granulations are now

slow to plug the lumen of the lacunae and are thus an insurmountable obstacle that stops the colored solution. It is in order to evade this inconvenience that one should address by preference little pigmented individuals of average or small size.

The content of the visceral lacunar system is not animated by a circulatory movement. It is not subject to any contractile organ nor of any ciliated epithelium. Meanwhile all evidence indicates that it should be displaced in order to move to the tissues where it is utilized. This movement is explained in the following fashion.

When the absorbents of the intestine function, they tend to fill more and more. This produces in this part of the lacunar system a pressure that determines a current towards the distal parts of the capillary net. Such a current can be only slow and its direction is constant.

III. -- While I was pursuing my researches on the visceral lacunar system and while I was trying to discover all of the extensions, a doubt occurred to me on their true nature. Did the various more or less poorly canalized spaces into which the injected material penetrated make part of an actual apparatus disposed in view of a physiological function, or were they interstitial spaces without importance, appearing in the tissues according to the caprices of a more or less penetrating injection?

Two principal arguments seem to us proper to eliminate this doubt:

First. The colored solution of an injection always follows the same trail in different individuals. This proves that its route is traced in advance in all, and that whatever be the material employed. The colored turpentine, the soluble blue, the gouache white, the diluted carmine, and air itself always follow the same road.

Second. No one has ever contested that the internal marginal vessel of an *Echinus* is a differentiated canal in view of a perfectly determined function. Now, we have seen that in *Dorocidaris* this vessel is replaced by an irregular lacunar space arising in the conjunctive tissue of the mesentery. We are obliged to attribute to the marginal lacuna an identical function to that of the very regular canal, well dammed up in *Echinus*. We cannot consider this lacuna as an accident produced by an injection. Ever since, we could no longer argue that the various networks of the visceral lacunar systems were formed by the more or less irregular interstices of the conjunctive tissue in order to refuse the true physiological functions. We cannot refuse to one the quality that we accord to the other.

IV. -- Examine now in what the way the lacunar system that we have just studied in *Dorocidaris* differs from the apparatus of others described in the echinids under the name of the hemal system and which are the new notions that resulted from this study.

Carl Vogt and Yung (1) thought it is not necessary to see in this system "a lacunar system of irrigation of a vascular form". These authors are, to my knowledge, the first who have raised doubts on the true nature of the canals ordinarily called vessels in the urchins. We have just seen that in *Dorocidaris*, the lacunar system is evident (2).

*Intestinal network.* -- The two marginal lacunae extend on the second circuit to a limit closer to the rectum than in the echinids, of such sort that the intestinal part, depauperate of capillaries, is, all proportions considered, less considerable in *Dorocidaris*.

The collateral vessel does not exist. The absence of this extension of the external marginal lacuna is without doubt interesting to verify in *Dorocidaris*, but it is not a character unique to cidaroids, as *Strongylocentrotus lividus* is equally depauperate.

*Periesophageal ring.* It has been known in the echinids since the researches of Teuscher and of Koehler. According to the latter, the hemal ring of *Sphaerechinus* sends a branch to each Polian vesicle. These organs are not distinct in the ring of *Dorocidaris*. They are represented only by the five lobes of the double esophageal ring.

*Network of the axial organ and the genital glands.* In *Sphaerechinus*, according to Koehler, a network distributed to the ovoid organ and linked to the esophageal hemal ring by a canal that runs along the sand canal (glandular canal). In *Dorocidaris*, there is no glandular canal as the extremity of the gland touches the esophageal ring itself. The network of the axial gland takes its source directly in this ring.

As for the network destined for the gonad and contained in the thickness of the genital pentagon, it remained unperceived to the day I reported its presence in *Dorocidaris* (3). Since then, O. Hammann (4) has found it, and I myself have confirmed its presence in *E. acutus* and *E. sphaera*.

In regard to this latter urchin, I shall remark that the system of tubes drawn by Perrier (5) on the mesenteric lamella that extends from the axial organ to the esophagous and described by him as a system of glands opening under the madreporite plate is composed, not of glandular tubes, but of lacunar canals belonging to a network continuous with that of the genital pentagon. There does not exist an excretory conduit opening under the madreporite. These supposed glands that are in reality nothing but a part of the lacunar system (*rm*) (pl. XVIII, fig. 3, 4) in *Dorocidaris*.

(1) *Traité d'anatomie comparée.* (2) I reported this character in *Dorocidaris* in a preliminary note (*Compt. rend. Acad. sci.*, 7 March 1887), but I still conserved a doubt on the subject of the intestinal capillaries that I consider today as lacunar, not having succeeding in certifying the presence of an epithelium. (3) *Compt. rend. Acad. sc.*, 15 June 1886. (4) *Vorläufige Mittheilungen z. Morph. d. Echiniden.* (*Jenaische Zeits. f. Natur.*, augegeben am 29 October 1886). (5) *Loc. cit.*

*Pharyngeal lacunae.* -- Teuscher reported that the esophageal hemal ring sends five vessels along the pharynx, but Koehler, not having been able to find these vessels, denied their existence. The conclusions of these two authors, relative to this point of anatomy, have been discussed by Herbert Carpenter who, taking the part of the opinion of Teuscher, thinks the proof of the absence of these pharyngeal vessels remains to be made.

As we have just seen, these vessels or better these pharyngeal lacunae exist in *Dorocidaris*, and this anatomical fact has not been previously reported by me, that it is found confirmed by Koehler himself in the following terms: "The existence of the five pharyngeal vessels having been much discussed, and their presence modifying the relations of the vessels in the urchins. I insist on declaring that I have found them in my turn". (1)

*Radial lacunae.* -- Authors are far from being in accord on the number and quality of the radial canals of an urchin. Perrier mentioned in his memoir on the *Appareil circulatoire des Ourisins* only a single radial vessel that is the ambulacral vessel. Koehler described two of them: the ambulacral vessel proper and a deep vessel that would be a subdivision of the first. They both would communicate with the water ring.

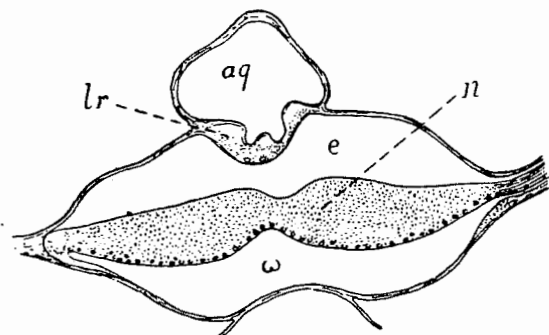


Fig. 14. Cross section of a radius of *Echinus sphaera*; *aq*, ambulacral vessel; *lr*, radial lacuna; *e*, perineural space; *n*, ambulacral nerve; \* , space corresponding to the intra-neural space of *Dorocidaris*.

Teuscher described two distinct vessels: one, the water and the other, hemal, called *nervengefass*, which contains the nerve and communicates with the periesophageal vessels.

The results furnished by the study of *Dorocidaris* does not agree with the descriptions of these cited authors. There is however, a correct idea in the point of view of Teuscher, who admitted in each radius of urchin an extension of the hemal ring. But the German author is wrong when he described as a hemal radial branch its *nervengefass*. Some researches on the echinids have convinced me of his error.

(1) *Compt. rend. Acad. sci.*, 5 July 1886.

The opposite sections made in a radius of *Echinus sphaera* shows that the radial lacuna is situated in the thickness of the membrane that separates the ambulacral vessel from the *nervengefäss* of Teuscher. It is easy to recognize thanks to the clot it contains. On the other hand, the perineural space which is the *nervengefäss* is not simple, but rather composed of two distinct parts and separated by the nerve itself. The space (e) corresponds to those

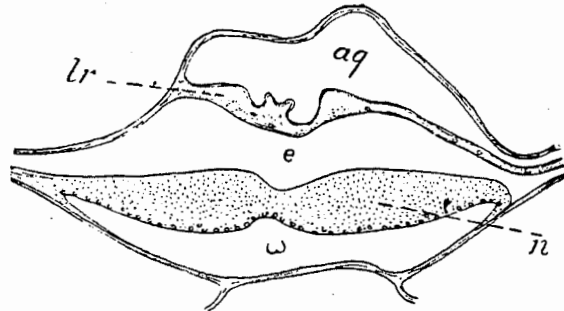


Fig.15. -- Cross section of a radius of *Echinus sphaera* at the level where the ambulacral vessel and the radial lacuna each emits a lateral branch.

we have designated by the same letter in *Dorocidaris* (pl. XVII). As for part (w) it seems to me to correspond to the interneural space of *Dorocidaris*, but I have not pushed very far my researches on *E. sphaera* in order to be able to affirm it.

Be that as it may, we find in an echinid as in a cidaroid, a radial lacuna belonging to a visceral lacunar system, situated between the ambulacral vessel and the perineural space. The two ambulacral vessels of which Koehler spoke are very probably the ambulacral vessels proper and the perineural space (e). The figure he gave (pl. X, fig.36) reproduced the aspect one obtains when one injects this space and the ambulacral vessel. I have at first supposed that the deep vessel of Koehler corresponds to our radial vessel, but this comparison is not possible as the canal to which the author alluded is "a deep vessel larger (than the superficial vessel), closely applied against the nerve". These characters are precisely those of the perineural space.

We have said that the space in *Dorocidaris* does not communicate with the general cavity. It is the same in the echinids. When one injects them, one sees the material penetrate to the pharyngeal angles where they stop. I have never been able to confirm that it escapes into the general cavity at the level of the auricles as Koehler claimed.

V. -- *Tentacle branches of the radial lacuna.* -- We have shown the existence of these tentacle lacunae, but we have not been concerned until now to follow them to the end. The question is difficult to resolve. It is necessary however to try. Here is what one observes in *Dorocidaris*:

In the cross sections made of the radius, one sees the radial lacuna, rather its lateral branches, applied against the tentacular branch of the nerve and accompanying it to the entrance of the pore. From this point, it is no longer necessary to think of the sections thus oriented, and one should address sections tangential to the ambulacral plates. One observes from

these sections that the tentacular nerve is accompanied during its transversing the test by a little canal (*7t*) situated to the interior of the pore (pl. XIV, fig. 13). This canal is found in the body of the tentacle itself (pl. XV, fig. 10, *vt*) always accompanying the nerve. Now, if we admit that the tentacle branch of the radial lacuna, after being joined against the nerve, accompanies it to the tentacle, it is precisely at the place of the little canal revealed by the sections that will have to be placed the lacuna that we seek to follow. It is thus very probable that it is itself that apparatus (*vt*). One can object that the canal (*vt*) could as well be the tentacle extension of the perineural space (*c*), but we can inject this space and we always see the injection stop before entering the pore in a cul de sac.

I believe thus it is necessary, until proof to the contrary, to conclude that the lateral branches of the radial lacuna extend into the tentacles, following the internal surface of the nerve.

VI. -- *Ovoid gland*. -- The ovoid gland of *Dorocidaris* extends from the madreporite plate to the esophageal ring, which it touches. It is supported by the portion of the mesentery (*mo*) that links the esophagus and the genital pentagon, and also by the lamella (*mir*) that extend the internal mesentery of the second circuit (pl. XVIII, figs. 3, 4, 5; pl. XV, fig. 19). Its form has nothing characteristic. I have represented it as faithfully as possible.

The organ in question is hollow. If one opens it by a longitudinal incision made the length of the water tube, one sees that its cavity is transversed by numerous tracts that detach from the wall, anastomose in an irregular fashion and limit the alveoli, anfractuosités of varied sizes and form (pl. XIX, fig. 6) of such sort that a cross section presents the aspect represented (pl. XXI, fig. 1). What is one examines comparatively the ovoid glands of several individuals? One sees the disposition of the tract varies infinitely, but one observes always without exception that they succeed in forming in the axis of the cavity a sort of very apparent cord directed towards the apical extremity (pl. XIX, fig. y, *cc*).

The cavity of the gland terminates in a cul-de-sac at its oral extremity, while it is extended to the apical pole by a canal collateral to the the water canal we have already mentioned and designated under the name of *water conduit annex*. It is this canal Perrier called the *excretory canal* in *Echinus sphaera*, and it is thus I have designated it in the notes that preceded this memoir in order to avoid the uncertainty. Such or such denomination means little, but we find ourselves facing a name that indicates a well defined function and should without any doubt be adopted if it were demonstrated that the ovoid gland is a gland of excretion. This demonstration not being made, it has seemed good to us no longer to employ the term *excretory canal*.

We have demonstrated by excessive sections that the *annex conduit* opens into the madreporite pores. These same sections and these same injections show that the conduit is the extension of the cavity of the gland (pl. XIX, fig. 5; pl. XX, fig. 1-8). The exterior water penetrates by diffusion into this cavity.



The axial cord mentioned above increases in thickness gradually as it approaches the madreporite. At some distance from this latter the peripheral tissue of the gland disappears, and it remains no longer a cord. This sometimes runs along the canal annex then, curving in, penetrates definitely into a space separated from this canal. At this moment the axial cord, which I shall call specially the *glandular process*, has acquired the greatest dimension and measures frequently 1 mm in diameter (pl. XIX, fig. 5, 6). It takes the form of a short club with a curved handle. The extremity of the club is not free and sends several conjunctive tissue extensions that attach to the test.

The space in which the glandular process lodges corresponds to the madreporite (p. 93) and is limited by a membrane that extends the envelope of the gland. This space is closed, without communication with the general cavity or with the pores of the plate. The membrane that limits it is profoundly modified in the part that confines the madreporite depression. In this region it is soft, delicate, and not filled with calcareous spicules, characters that under the magnifying glass serve to distinguish it immediately from the neighboring parts. When one tears it, one perceives in its thickness a spongy tissue, very soft, fleeing before the sharpest scapel.

*Histology.* -- The ovoid gland is lined by an epithelium that covers all the organs contained in the genital cavity. In a cross section one distinguishes, at first glance, the sand canal (c) (pl. XXI, fig. 1), the cavity of the organ (c'), and its own walls. The structure of these is difficult to analyse. It is necessary, in order to succeed, to apply to an individual placed in special physiological conditions that had brought previously a decrease in the number of cellular elements that ordinarily are present in this tissue. Prolonged starvation accomplishes these conditions well.

One recognizes then without difficulty that the substrate of the ovoid gland is loose conjunctive tissue with irregular alveoli directly continuous with that of the mesentery. The external peripheral zone is filled with calcareous spicules imprisoned in the conjunctive tissue element. It contains in addition the lacunae of the network that the injections have already made known to us (pl. XXI, fig. 1, 2, 7). Moreover, one sees in this zone the lumina of small canals lined by an epithelium resembling the external epithelium. These canals open onto the external surface of the organ (pl. XXI, fig. 2, q).

The conjunctive tissue stroma becomes looser in the internal peripheral zone. It forms numerous tracts and irregularities that one perceives when one opens the gland, and that are lined by a continuous epithelium presenting the same characteristics of the general cavity. Immediately under this internal epithelial covering, the conjunctive tissue alveoli are better delimited and a little more regular (pl. XXI, fig. 3, 4).

When one examines a section as that which has been represented (fig. 1, pl. XXI), one perceives the sections (*q*) of the external peripheral canals and also cells with numerous irregularities (*c'*) making part of the cavity intra-glandular. One distinguishes them easily thanks to the layer of alveoli that surrounds the latter (compare fig. (3) (*q*) to fig. 4, *c'*).

Numerous cellular elements are widespread in the alveoli of the conjunctive tissue.

The most abundant are characterized by a granular nucleus surrounded by a ramified protoplasmic zone. (The organ in section being that of a *Dorocidaris* starved for a long time, these elements are numerous. In an individual just collected, they encumber the conjunctive tissue). These cells (*i*) are nothing other than the amebae with long pseudopods identical to those we have studied in the perivisceral fluid after the action of the reagents. They have the same aspect and the same dimensions as the amebae imprisoned in a clot (pl. XXI, fig. 6, *i*).

One meets also in the wall of the organ muriform globules and brown amebae, but these two elements are always less abundant than the first. In order to confirm the presence of the brown amebae, it is necessary to examine fragments of the organ in the living state as the reagents render them unrecognizable.

Finally, there exists in the alveoli of the tissue that we study brownish pigmented spherules, more or less abundant according to the age of the individual and principally confined in the zone of the peripheral lacunae. These grains of pigment are identical with those we have observed in the perivisceral fluid in the visceral lacunar system.

In examining the sections of the gland that, leaving its middle region comes nearer and nearer to the apical extremity, one encounters the progressive formation of the glandular process and of those of the submadreporite cavity (pl. XX, figs. 1-7, *e*). The process is formed by the tissue of the gland reinforced with thick conjunctive fibers scattered there and in its mass (pl. XX, fig. 11, *f*). It is lined with vibratile epithelium under which appears longitudinal muscular (?) fibers (*7*). In its entire route it is transversed by small canals (*d*) (figs. 9, 11, 12), some of which open on the wall but which mostly open at its apical extremity (pl. XX, fig. 10; pl. XXI, fig. 8, *d*). Between these canals, the conjunctive tissue contains those same cellular elements we found in the tissue of the organ itself. The process terminates in the madreporite depression, whose conjunctive tissue nets attach it to the plate.

The soft tissue of the membrane that covers the madreporite depression from the side of the anus (pl. XIX, fig. 5, *x*) is formed from kinds of vesicles with extremely thin walls, pressed one against each other, and containing most often globules with a long vibratile cilium that, when one places a fragment of the tissue under the microscope, escape in great numbers into the surrounding liquid (pl. XIX, fig. 14). Sometimes, however, I have happened to find these vesicles filled with muriform globules (pl. XIX, fig. 13). The fragment of section represented (pl. XXI, fig. 7) shows

the ordinary aspects of the contents of the tissue in question after the action of reagents. We have explained (see *perivisceral fluid*) how the globules with vibratile cila produced this appearance.

We have seen that the water system and the visceral lacunar system each form a periesophageal ring. The two rings are intimately linked. The one (external) is constituted by the extension of the water canal. The other (internal), by the extension of the internal marginal lacuna. When one injects this latter, one sees that it sends all around itself numerous ramifications that extend onto the water ring. This wall is thick towards the interior of the ring, and the conjunctive tissue that forms it is an annular extension of the tissue of the organ. It is necessary to remark however that the tissue of the ring is particularly the continuation of the peripheral lacunar part of the ovoid organ. One finds in the lacunae of this ring the ordinary formed elements, but I have never seen the amebae with long pseudopods there as abundant as in the gland. The double esophageal ring of *Dorocidaris* seems to me to be constituted on all its circumference as a *Polian vesicle* of the echinids. It is in order to recall this fact that I have called it the *Polian ring* in my previous notes (1). On the other hand, Carl Vogt and Jung (2) have remarked correctly, I believe, that the organs called *Polian vesicles* in urchins are very different from those that carry the same name in other echinoderms and, in that which concerns us, we renounced very willingly this denomination that we have transferred from an *Echinus* to a *Cidaris*.

VII. -- What are the functions of the organ we have just studied? The ovoid gland studied and named by Perrier in the echinids was considered by him an excretory organ. Later, Koehler showed that Perrier, decided by the regularity of alveoli of the conjunctive tissue that forms the substrate of the wall, had taken these alveoli for glandular cells. He never adopted the ideas of his predecessor on the excretory function of this organ.

M. H. Carpenter (3) was of the opinion that the ovoid gland must contribute to the production of brown bodies that are so known to all those who are occupied with echinoderms, and he means by that the brown amebae described by Geddes. These corpuscles are not at all an excretory product, but rather, with this pigmented state, have to play an active role (probably respiratory) in the economy of the urchin. There is thus in the point of view of H. Carpenter a new idea that consists of considering the axial gland of an urchin no longer as an excretory organ but to the contrary, as giving raise to young elements destined to live in the tissue of the animal.

The two kinds of pigment that one encounters most frequently in the urchins are essentially different from one another. One of these pigments makes part of a living ameboid cell. It is mahogany brown, soluble in

(1) *Compt. rend. Acad. sc.*, 15 June 1886. (2) *Loc. cit.* (3) *On Echinoderm morphology (Quart. Journ. of Micr. sc.*, 1886).

alcohol, and appears already in the larva. The other is an inert material, the product of waste not participating in the life of any cell. It is colored yellowish brown and is present in the form of granulations, sometimes isolated, sometimes grouped in mass (pl. XIX, fig. 15). They appear only in completely developed urchins, and it is probably the presence of the latter product in the walls of the ovoid gland that has led authors to attribute to this organ an excretory function.

Examine if the ovoid gland of a *Dorocidaris* plays a particular role in the production or in the elimination of this product of excretion:

One encounters these pigmented granulations in question not only in the gland, but especially also in the mesentery and it frequently happens that the ovoid organ of a *Dorocidaris* has none of them although they abound in the internal mesenteric lamella. It is very rare to see the gland of an individual of small or average size colored in brown by them. This is only in the largest and consequently the oldest *Dorocidaris*, which is strongly pigmented, but then the tissues of the animal are invaded in all parts by the pigmented granules.

These granulations are probably the result of the death of muriform globules that disaggregated after having absorbed the products excreted by the tissues in which they live. Now we have confirmed these globules in the ovoid gland as in the gonad, the walls of the tentacles, and even in the spaces of the intervals of the epithelial cells of the pharynx. Also one encounters especially the brown spherules that come from their disintegration. These spherules accumulate little by little in the mesentery and principally in the lacunae. It is thus quite natural to encounter them in the walls of the ovoid gland and this cannot be considered as specially charged with producing them. On the other hand, since the abundance of this product of excretion increases in proportion to its production in the tissue of an individual that ages, there exists no apparatus to eliminate it.

Must the ovoid organ give rise to brown amebae in order to function? I have no very precise observations, very free from causes of error in order to sustain the affirmative and cannot, consequently, adopt an opinion the support of which I have not carried any proof a very great distance. I must add, moreover, that the brown amebae are never more numerous in the walls of the ovoid gland than in the other points of the mesenteric tissue.

To the contrary, the colorless ameba with long pseudopodia are extremely numerous in the ovoid gland and more abundant than anywhere else. It is their presence that characterizes the tissue of the organ and the whole manner of explaining their accumulation in its walls is to admit that they really arise there.

Once formed, what becomes of these corpuscles? They move into the alveolar tissue of the gland and a great number, forcing their way across the walls, pass into the general cavity. The walls of the gland seem inappropriate for this diapedesis, as their external layer is always denser and reinforced by numerous spicules. These also exist a special disposition

that favors this migration of globules. I want to speak of the peripheral canaliculi that run in the alveolar tissue and opens at the surface (pl. XXI, fig. 2,9). These canaliculi constitute very easy points for the exit of amebae that find there a road all marked out in order to fall into the general cavity.

If the formed elements of the ovoid gland are destined to leave in order to be used elsewhere, it is evident that the walls of the organ will empty little by little when one suppresses the first material that feeds the proliferation of these elements, i.e., the liquid furnished by the absorbing intestine. It is also that which one observes.

When a *Dorocidaris* ceases to feed, the alveolar tissue of its ovoid organ empties little by little because the amebae with long pseudopods emigrate and are not replaced. This fact cannot be attributed to their resorption in place as the amebae that remain are as well constituted as those of a fed animal, and it is permitted to consider this observation as an indirect proof of the function we attribute to the ovoid gland.

Compare now the walls of the gland at any portion of the internal mesentery and see how these two tissues differ. From the histological point of view, the difference is of little importance. The walls of the organ can be considered as a simple hypertrophy of mesenteric conjunctive tissue. What does this mesenteric tissue thus lack so that it is found in the same condition as the walls of the organ? A single thing: contact with the external milieu, or at least contact with a liquid into which the milieu can diffuse. And we are thus led to conclude that the exterior water carries from its side an indispensable principle for the proliferation of the amebae (1). This appreciation of the conditions in which the ovoid organ is placed, leads us to think that the mesenteric tissue of an urchin becomes plastogenic when it receives on one hand the plastic material furnished by the absorbants, and that on the other hand it can realize from direct osmotic changes with the exterior water.

It is only in the cavities extending from the madreporic plate that the external milieu can diffuse. It is consequently within the walls of these cavities, irrigated by the visceral lacunar system, that shall be localized the phenomenon with which we occupy ourselves. The periesophageal ring is in these conditions. Also I am led to believe that the proliferation of amebae is accomplished in this part of the conjunctive tissue.

I have not been able to reach an opinion of the role of the glandular process and the sub-madreporic cavity in which it lodges. I have often found this extension of the gland filled with formed corpuscles that escaped from

(1) The function of the ovoid gland being thus understood, it is not possible to affirm that there is not produced in this organ a phenomenon of excretion that escapes us, but which would be the consequence of the plastogenesis itself.

that escaped from the walls and spread in mass in the sub-madreporic cavity. I have always observed the slow but very apparent contraction in its terminal mass. When one detaches it by cutting the conjunctive lines that link it to the internal surface of the plate, it retracts immediately and the corpuscles contained within its tissue spread around it.

As for the tissue limiting the sub-madreporic space towards the anus (pl. XIX, fig. 5), I have found it in numerous individuals, filled with a long vibratile cilium that, contained in the vascular alveoli of this strange tissue, become free when one places the fragment in a wet chamber. One sees them then swarm in the liquid of the chamber while some move about still imprisoned within the lobes of the tissue (pl. XIX, fig. 14). Having often repeated these observations, I have not been able to help considering it as a foyer for the production of ciliated globules of the general cavity. Some time after I found, in two individuals, the same tissue filled not with ciliated globules but with muriform corpuscles (pl. XIX, fig. 13). These bodies were equally abundant within the glandular process.

VIII. -- *Does the visceral lacunar system communicate with the water apparatus?* -- Communication between the apparatus described by authors in echinoderms under the name of the hemal vascular system and the water apparatus is one of the most ancient of controversial questions.

Agreeing with Agassiz and Hoffman, Perrier (1) affirmed the communication between the intestinal circulatory apparatus and the water system. He indicated a perfect continuity between the two: "These two parts of the circulatory apparatus communicate together by the intermediary of a vascular circle situated around the esophagus immediately above the lantern."

Teuscher (2) did not see this communication. Not being convinced by the researches of Hoffmann on this subject to which, he said, the author himself seemed to accord only little value. It awaited new observations on fresh animals. Not only did Teuscher not see the communication of the two systems, but he described the first and drew the two periesophageal rings, the one belonging to the water system, the other to the hemal vascular system.

Koehler (3), refining by injections the two rings of Teuscher, saw that they both send two ramifications into the Polian vesicles and he admitted that communication can be established between the two rings across the tissues of the vesicles. I have myself, in the course of my researches (4), said that exchanges between the two rings of *Dorocidaris* must occur without specifying the nature as I still have some doubts.

(1) *Loc. cit.*, *Arch. Zool. exp.*, 1875. (2) *Loc. cit. Beiträge z. Anat. d'Echinodermen (Jen. Zeit. f. nat.*, 1876) (3) *Loc. cit.* (4) *Compt. rend. Acad. sci.*, 15 June 1886. (4) *Memoire sur l'organisation et le développement de la Comatule de la Méditerranée*, 1886.

The work of Perrier on the *Comatule de la Méditerranée* having appeared, I found there the assurance that the sage professor of the Museum had not modified his point of view since his memoir of 1875. He said in fact (page 94): "For him (Koehler) as for me, the water apparatus and the vascular apparatus are only one" (page 215). "In the first (urchin) it (sand canal) communicates with the system of intestinal canals, all at the same time under the madreporic plate and by the Polian vesicles." Finally (page 266) "be that as it may, exclusive of some details of which the value remains to be determined, it is manifest that the system of irrigation of comatulids, such that we have just described, with all the connections that we have indicated, present numerous points of resemblance with the ensemble constituted by the ambulacral apparatus and the supposed vascular system of the urchins, systems that according to my research, confirmed and extended by the beautiful studies of Koehler, are in continuity with one another."

On the other hand, in a note to the Academy of Sciences of Paris of 17 January 1887, Perrier said: "The two systems (those with which we occupy ourselves) should communicate with one another by the intermediary of the Polian vesicles in the echinids, or by the anastomosing ring that, according to the similar researchs of Prouho, replace these vesicles in the cidarids. I have shown, a dozen years ago, to all the personnel of the laboratory of Roscoff, that an injection made into the system of ambulacral canals passed regularly into the system of absorbing canals."

Does the communication between the two systems exist in the echinids and in *E. sphaera* in particular? I have not made studies on this urchin but after the studies of Koehler on *Sphaerechinus*, it is very probable that there exists two perisophageal rings in *E. sphaera* itself, that these two rings send extensions into the Polian vesicles, and that their respective cavities are separated by the very tissue of these vesicles, which comes to say that they do not communicate. The results of the injections recalled by Perrier are not perhaps sufficient to conclude the identity of the two systems as these injections have not allowed him to see the two rings that Koehler was able to inject later.

As for *Dorociddaris*, the phrase of Perrier cited above does not translate exactly my thought, incompletely expressed in the note to which he made allusion. I must specify the nature of the only exchange that I believed possible between the two periesophageal rings. I wrote (1): "*An exchange of current between the two rings is impossible*". This cannot allow any doubt of my point of view, as two cavities that cannot exchange a current of their respective contained fluids do not communicate.

One arrives at this conclusion by the method of injection as well as by histological examination of the parts of interest.

I have made in the two rings double injections with the most varied material without obtaining a mixture of the two colors in the periesophageal

(1) *Compt. rend. Acad. sc.*, 7 March 1887.

collar. One of the injections was made into the internal marginal lacuna, the other by the sand canal itself. But, in my opinion, that which is still more probing is a simple injection of the lacunar system with a very penetrating material as turpentine. One can inject the entire lacunar system (the radial lacunae excepted) with this material without it passing to the water ring. If there were a communication canalized anywhere between the two systems, the water system would surely become colored in these conditions.

The figure (4, pl. XIX) represents the section of a collar of which the lacunar ring alone had been injected with soluble blue (in the figure the color has been changed in order to keep the conventional tint adopted and also I have colored the water ring which actually was not injected with the preparation). Microscopic examination of a series of parallel sections has not shown me a single particle of soluble blue in the water ring.

One can however succeed in making the material pass from a single injection into two rings. It suffices to augment sufficiently the pressure in the syringe. Such a conclusion should not weaken the conclusion stated above. It proves simply that the injections can sometimes be false and that it is necessary never to neglect the examination of the causes of error that surround an experiment.

When one tries to inject the lacunar system, it happens sometimes that the colored mass spreads into the intestine itself. Will it be necessary to conclude that the intestinal network communicates with the digestive tube? Obviously not. The fact proves simply that it has produced a rupture in the capillaries injected.

Finally, if these reasons are not sufficient to prove that the two esophageal rings do not communicate between themselves, one would be able to evoke the following easily made observation protected from all cause of error. One never meets in the water system the coagulated contents characteristic of the lacunar system.

The cross sections corroborate the results obtained by the injections. They indicate to us that the lacunar ring is sunk into the wall of the water ring and does not show us communication between the lumen of this latter lined by a continuous epithelium and the lacunae of the former.

*The communication between the two systems cannot be established by the intermediary of the ovoid gland.* -- This communication would be possible if the lacunar network distributed to the gland discharged into its cavity that, we have seen, is an annex of the water system. But as the lacunae of the glandular walls do not communicate with this cavity covered by a continuous epithelium, the visceral lacunar system and the water system cannot exchange a current of their contents.

We arrive thus at the following conclusion: not only do characters proper to each of the make the visceral lacunar apparatus and the water apparatus two systems with distinct cavities, but also these two systems are entirely separated from each other.



IX. -- Another question of at least equal importance is that the communication of the so-called hemal system with the exterior. This communication is admitted by Koehler. According to him it would take place by the intermediary of the ovoid gland and its excretory canal. Perrier willingly adopted this point of view that conformed to his general ideas on echinoderms.

It is certain that the excretory canal of the ovoid gland of *Dorocidaris* or our water canal annex communicate with the exterior, but it is less certain that the canal is not an extension of the visceral (hemal) lacunar system and that the contents of this system that reach into the walls of the axial gland cannot normally penetrate into its cavity. There would not exist at this level an exchange of current between the visceral lacunar system and the exterior milieu.

The liquid contained within the cavity of the gland and that of the lacunae of its walls do not communicate more with one another than the contents of the internal marginal lacuna, e.g., do not communicate with the general cavity. The cavity of the gland is not a lacuna belonging to a visceral lacunar system. It was important to insist on this point.

This is not special to *Dorocidaris*, and should be extended to echinids according to the studies of Perrier and Koehler themselves. In effect, if the cavity of the gland (or the excretory canal) were an extension of the so-called hemal system, Perrier would have injected the glandular canal of *Echinus sphaera* when he tried to discover the vessel that would end at the supposed heart. Instead of that, the author, taking all precautions necessary in order that the colored material did not ebb upward, has seen the cavity of the gland swell under the pressure of an injection, be distended, and the colored material refuses absolutely to leave (1).

On the other hand, if as Koehler said the glandular canal was the continuation of the *excretory canal* in *Sphaerechinus granularis*, it seems that it should suffice in order to inject it to make the injection into the excretory canal (or the cavity of the gland). Since then Koehler (2) has not been obliged to prick his needle as near as possible to the surface of the ovoid gland in order to inject the lacunae that end at this organ.

H. Carpenter was of the opinion that the so-called hemal system must not communicate with the exterior, but he declared he was ready to abandon his point of view when one demonstrates "The communication of the so-called excretory canal of the ovoid gland in an Urchin with the space beneath the

(1) *Loc. cit.*, *Arch.*, p. 612. (2) *Loc. cit.*

madreporite, into which the pore-canals and the water-tube both open" (1). We have demonstrated this communication by injections and by sections (pl. XX, figs. 1-8), but we have seen it carries nothing at all from the hemal system to the exterior. Consequently, despite the correctness of the anatomical fact that H. Carpenter dismissed in doubt, his ideas on the subject of the supposed communication are consistent with the truth. *The so-called hemal system (visceral lacunar system) does not communicate with the exterior.*

*Possible exchanges between the visceral lacunar system and the water system.*-- The exchanges that can take place between the two systems are on the one hand by osmosis and on the other by diapedesis of the formed ameboid elements. These exchanges are principally localized at the contact of the two esophageal rings and in the ovoid gland.

It is impossible to witness the phenomenon of diapedesis in these two regions. But after having seen the formed ameboid elements leave without difficulty from a mesenteric lamella, it is logical to admit that this phenomenon occurs there normally, as the amebae will have much more facility in crossing the less compact tissue limiting the two systems in the regions considered than those of the mesentery itself.

I have represented (pl. XV, fig. 2) a fragment of a cross section of the two esophageal rings, in order to show that if by the preceding one does not happen to detect the passage of globules from one ring into another, at least one can observe globules (*gm*) placed under the epithelium of the water ring in a situation such that they appear on the point of crossing it.

The normal phenomenon of diapedesis explains the presence, in the ambulacral liquid, of all the amebae that one encounters there.

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We have to try now to define the role of each of the three systems that we have previously studied. Namely: the visceral lacunar apparatus, water apparatus, general cavity.

The lacunar apparatus contains a liquid that the absorbing intestines draw from its source, in the walls of the intestine at the base of the epithelial cells. This liquid does not circulate (I mean by that that it does not return to its point of departure). It is simply guided by the lacunae in which it moves in obedience to the impulsion that imparts

(1) *On the vascular system of Urchins* (*Quart. Journ. of Micr. sc.*, suppl. 1885). The space to which H. Carpenter makes allusion does not exist. There is neither ampoule nor intermediary infundibulum between the water tube and the madreporite, but this changes nothing in the question.

to it a sort of *vis à tergo* coming from the repletion of the absorbants. It is utilized in the tissues that it reaches proportionally to its production, not crossing any respiratory organ and not taking consequently any part in the distribution of oxygen in the organism. It furnishes the plastic element and nothing more.

The perivisceral liquid circulates actively at the surface of the organs thanks to the movement of vibratile cilia. It receives on one hand the plastic element, under the form of formed globules that furnish specially the ovoid gland, and on the other hand, it takes oxygen to the ambulacral vesicles. It is permitted to think that the fluid is most particularly charged with furnishing this gas to the tissues that it bathes.

The liquid contained in the water apparatus is put in movement by a vibratile epithelium. It circulates in these respiratory organs (tentacles and ambulacral vesicles). It is it that, with the aid of the tentacles, brings oxygen from the external milieu in order to transmit it to the perivisceral fluid by means of the vesicles. This system of water canals irrigates no organ. It is an intermediary between the respirable milieu and the perivisceral milieu to which it gives oxygen that it has brought to the former. Incapable itself of leaving this gas in the tissues, it abandons to a liquid very well disposed for this since no organ escapes its contact. It is the agent of a *mediated* respiration.

The system of ambulacral vessels has thus two distinct functions, one of locomotion, the other of respiration.

The first function can disappear completely in a part of the ambulacral apparatus in cidarids, arbacias, diademas, and probably of still others that have not been observed from this point of view. *Echinus*, in contrast, *Strongylocentrotus*, and others have tentacles that are all simultaneously locomotory and respiratory.

For the second function to be accomplished in good conditions, it is necessary that the tentacles be extended. One would thus be able to believe that this is subordinate to the locomotory function. Such is not the case. An urchin placed in good conditions of milieu always presents its tentacles expanded, whether it be in movement or not. *Strongylocentrotus* of our coasts remains for the greatest part of its existence immobile in its hole and meanwhile its tentacles are constantly extended. *Dorocidaris* spreads out its aboral tentacles as soon as it has a feeling of security. A. Agassiz teaches us that those of *Arbacia*, equally destitute of suckers, attain a considerable length.

The regular accomplishment of the phenomena of which we have just spoken: transport of material absorbed by the intestine, circulation of perivisceral fluid to contact the internal organs, mediated respiration accomplished by the water apparatus liquid, do not necessitate in any fashion the entrance of a current of water by the madreporic plate.

The liquid of the lacunar system, which does not communicate with the sea water, moves without its intervention, the ambulacral liquid accomplishes osmotic exchange without needing to call a current from the exterior. The

penetration of water by diffusion to contact the tissues of the ovoid gland and periesophageal ring extension seems to be alone indispensable. We see further that in certain echinids (spatangids), the communication of the madreporic plate with the ambulacral system is suppressed and that the penetration of sea water to contact the glandular part of the lacunar visceral apparatus alone persists.

These conclusions to which we are led thus are in disagreement with those that Perrier formulated in the following fashion in his beautiful work on the *développement de la Comatule*: "in the comatulids (and we can add in all echinoderms whose organization is connected closely to that of crinoids) the external water enters freely and in a constant manner into the system of irrigation canals. It is called there incessantly by the movements of the vibratile cilia whose internal walls on one side at least of these canals are soft. Once in the canals, it continues to circulate there under the action of vibratile cilia and it takes charge of the distribution of nutritive material and of oxygen."

Return to the liquid of the general cavity. We know that it is divided into two parts, the exterior for the masticatory apparatus, the other contained in the interior of this apparatus in a closed peripharyngeal cavity. This latter part of the perivisceral liquid is not in contact with any ambulacral vesicle and the membrane that separates it from the exterior is very unfit for osmotic exchanges because of its thickness and its consistency. It is necessary however that it replenish its oxygen. Not being able to get it from the external milieu or the ambulacral liquid, it can take it from the surrounding perivisceral fluid. It is for this that the membrane of the masticatory apparatus is provided with five appendices that we have called *Organs of Stewart*.

These are admirably disposed in order to favor osmosis: their walls are very thin, their surface is multiplied by numerous ramified caeca whose delicateness is augmented by the absence of calcareous spicules. An active vibratile lining renews the peripharyngeal liquid of the interior and the perivisceral liquid of the exterior. In addition, by their radial situation, they are placed in the most oxygenated interior currents, i.e. those that are produced by immediate contact of the ambulacral vesicles. In summary, thanks to the exchanges that they provide, these remarkable organs maintain between the peripharyngeal liquid and the perivisceral fluid an equilibrium that translates it by equal distribution of the two, of all the principles that can be exchanged by the osmotic process.

(1) *Mémoire sur la Comatule, loc. cit.*

In the latistellar urchins, the peripharyngeal cavity is isolated from the rest of the general cavity as in *Dorocidaris*. But instead of presenting five appendices in the forms of gills floating in the perivisceral fluid, they possess ten true gills that spread into the external milieu. As a result the periesophageal cavity, instead of taking oxygen from the general cavity, can take it directly from the ambient water (1). The one essential difference between Stewart's organs of a cidarid and the external gills of an echinid (2) is summarized in the following table:

<i>Echinus</i>	<i>Dorocidaris</i>
External milieu	External Milieu
Gills	0
Peripharyngeal cavity	Peripharyngeal cavity
0	Organs of Stewart
General cavity	General cavity

#### LARVAL FORM OF DOROCIDARIS PAPILLATA

Does *Dorocidaris papillata* have a free larval form or better, does it develop without metamorphosis? It was permitted to ask these questions after the interesting observations of W. Thomson (1) on *Cidaris nutrix*. W. Thomson himself in search of the solution examined a large number of *D. papillata* in order to see if this urchin, as *C. nutrix*, sheltered its young on its test. He said that he never found a similarity to the *Cidaris of Kerguelen*. On my side, I have examined with care all the *D. papillata* that were brought to the Laboratory without being happier, waiting impatiently the period of sexual maturity of these beings in order to be able to resolve the question by performing artificial fertilization. This I have been able to do in the month of February 1885 thanks to the numerous individuals fished at this time who were not slow in throwing out abundantly eggs and spermatozoa.

(1) The authors who have studied the organization of urchins do not appear to have remarked that the external gills do not communicate with the general cavity and that they are unique diverticula of the periesophageal cavity. Moreover they do not indicate the independence of the two cavities.

(2) Stewart supposed that the external water is able to enter the periesophageal cavity of *Dorocidaris*. "...So that if the chamber (cav. periph.) communicates with the surrounding water, as it probably does near the tips of the teeth, water would then pass in and out of the space, and bathe the interior of the gills." If it were thus, these organs would serve respiration of the perivisceral fluid. We have seen that this penetration of water is not possible and that the role of Stewart's organs is otherwise.

*Dorocidaris* that expels the contents of its genital glands, remains immobile during the entire time the operation lasts. The papillae that surmount the genital orifices are then erected and there escapes a jet that reaches about 1 cm of height. The eggs fall back onto the test, but are immediately swept up by the vibratile movement of the surface and accumulate little by little around the urchin. As for the spermatozoa, they are dispersed into the ambient water as soon as they have been expelled.

The eggs are spherical, of a slightly transparent yellowish-white. Seen in mass they are frankly yellow. Their dimension varies from 0.16-0.18 mm. The spermatozoa present the characteristics of other urchins. They have a very tapered conical head and a very developed tail.

In order to obtain good fertilizations, it is necessary to have a very large number of individuals in order to be able to procure at the same time fresh eggs and spermatozoa, i.e. leaving the genital glands. As soon as an individual commences to spawn, one isolates it in a vessel that should be absolutely clean and collects with the aid of a pipet a certain quantity of eggs that one scatters in a crystal bowl. The eggs fall to the bottom and one takes the necessary precautions in order that they are dispersed in a single layer. That done, one isolates in the same fashion a male in the process of throwing out its spermatozooids. One takes a small drop of seminal fluid that one disperses in the bowl containing the eggs. The quantity of spermatozoa added should not cloud the clearness of the water. The results are certain if the operation is made in this fashion.

Segmentation begins approximately three hours after the spermatozoa have been placed in contact with the eggs (pl. XXIII, fig. 2). It is total, regular, and continues actively without presenting anything special. At the end of 24 hours, the egg has transformed into a blastosphere whose segmentation cavity is very apparent (fig. 6).

During the 80 hours following, most of the blastospheres acquire a ciliated covering and, escaping their envelope, become free. They swim rapidly then, coming to the surface and are not slow in crowding around the edges of the vessel where one collects them with a pipet in order to transport them to a second bowl. As for the eggs that have not transformed into a ciliated blastosphere after 48 hours, they should be thrown out. From the moment where the small larvae have hatched, they require careful attention. Twice a day I renewed the water, taking care, each time of carefully cleaning the bowls in which I raised them. This precaution is indispensable in order to prevent the larvae from clinging to the impurities that always settle more or less on the walls of the the container.

The ciliated blastosphere, once free, commences to transform into a gastrula. It flattens slowly at one point of its surface. The formation of this plane determines an axis of symmetry (diameter perpendicular to the

plane of flattening) at the extremity of which one distinguishes a crest of cilia longer than their neighbors (fig. 7). At the same time, the cells of the mesoderm (*m*) commence to form. Soon the flattened pole invaginates while the larvae elongates along its axis. The mesodermal cells bud to the summit of the invagination and become free between the ectoderm and the endoderm. 53 hours after fertilization, the gastrula is perfected (fig. 8).

The fifth day, the larva flattens parallel to its greatest dimension and incurves slowly. It loses thus its axis of symmetry that is replaced by a plane perpendicular to the flattened surface, containing the blastopore and the crest of cilia. At the same time, spots of mahogany-brown pigment appear in the thickness of the ectoderm.

The sixth day, the end of the larval intestine forms two diverticula (fig. 9, *v*) on either side of the plane of symmetry.

The pole corresponding to the blastopore becomes triangular little by little. On the eighth day one distinguishes, around the blastopore, three bumps (fig. 11) of which the median one corresponds to the inferior part of the anal lobe. The other latter two are the first indication of the posterior arms. The mesodermal cells are grouped in each of these latter lobes, and a calcareous spicule appears in the middle of each (fig. 10). Simultaneously, the larval intestine is incurved towards the concave surface in order to go to meet the ectoderm. Finally, the two diverticula are separated at the summit of the invagination in order for each to form a vaso-peritoneal vesicle (figs. 10, 11, 12).

The larva presents then a ventral surface, a dorsal surface, and an oral lobe and an anal lobe with a pair of arms. The end of the digestive tube opposed to the blastopore still does not open to the exterior. One perceives however an invagination (*b*) indicating the site where the mouth is going to form (fig. 11).

The tenth day, the posterior arms (*l*) are elongated, the mouth is opened and the digestive tube is divided into three lobes: an esophagous (*f*), a stomach (*d*), and an intestine (*g*). The blastopore has become the larval anus (pl. XXII, fig. 13).

From this moment we know *Dorocidaris papillata* has a larval form and that this larva is a pluteus. But the pluteus of ten days is too young for us to give an idea of that which should be the adult larva of our urchin. It is necessary to follow its development.

The fourteenth day, the three parts of the digestive tube are very accentuated. The mouth is wide open. The anus, in contrast, is reduced to a small pore. The arms are considerably elongated. The vibratile cilia have become scarcer on the surface of the larva. They are, so to speak, concentrated the length of a band that borders the oral lobe, the anal lobe, and the two arms (pl. XXIV, fig. 1). As for the spicules, figures (1) and (2) indicate their disposition. Consider one of them. One finds four principal branches leaving the same point. One serves to support the arms. It is rectilinear and formed of three calcareous rods bound together by small crossbars (pl. XXV, fig. 7). The others are simple, and among these we

distinguish: first an arched and ramous spicule that supports the cupola; second a spicule situated in the thickness of the anal lobe and that ends above the anus; third a spicule that penetrates into the oral lobe (2) and carries towards its base an arched branch situated in the cupola.

The vaso-peritoneal vesicles are very apparent. One of them (left vesicle) is placed in communication with the exterior by the *dorsal pore* (pl. XXIV, fig. 2, *vg*).

The pluteus no longer possesses only a pair of arms (posterior arms). During the following days, the lateral spicules of the oral lobe elongate and their extremities penetrate into two extensions that have developed on either side of the mouth and above it (pl. XXIV, figs. 3, 4, 5). These are the anterior arms that appear (2).

The posterior arms do not cease to grow. A lobe (7) appears above the anus and the larva remains in this state for about 15 days in accentuating its form little by little.

The cells of the mesoderm are scattered here and there in the body of the pluteus. Some, the most numerous, are colorous, ameboid (pl. XXIV, fig. 11) and offer all of the characters of the amebae with long pseudopods of the adult. Others, equally colorless but globular, are grouped at the extremity of the spicules (fig. 3). Finally some mahogany-brown amebae are dispersed a little everywhere. The pigment that colors these amebae has been produced from the fifth day in the ectoderm of the gastrula (pl. XXIII, fig. 9). The cells in which it is developed have become little by little ameboid and have emigrated into the mesoderm. It is necessary to remark moreover that, even after their emigration to the interior, these amebae stay preferentially applied against the ectoderm.

The esophagus possesses circular contractile fibers that produce at its surface an irregular transverse striation (pl. XXIV, fig. 3). It is covered interiorally with vibratile cilia inceasingly in movement. The stomach is distinguished by its yellowish color. It affects the form of an inverse crown. The food particles tumble in its interior under the action of its ciliated epithelium. The intestine is narrow and possesses few vibratile cilia. The vaso-peritoneal vesicles have enlarged, and each of them is divided into two lobes of which one is closely applied against the esophagus while the other is extended the length of the stomach (pl. XXIV, fig. 3, *vd*, *vg*). If this were the dorsal pore, the left vesicle would be identical to the right vesicle.

The larvae are too transparent to be studied directly in a water chamber. Nevertheless, I have believed useful to make thin sections of some.

The section (10, pl. XXI) passes by the plane of symmetry, climbs the three regions of the digestive tube. One sees that the esophagus and the stomach are separated by a sphinchter that ordinarily intercepts the communication between the two. When the pluteus wants to introduce into its



stomach alimentary particles previously drawn into the esophagus, the circular fibers of this latter contract quickly. There results a movement of swallowing that opens wide the lower orifice of the esophagus and pushes the foreign body into the interior of the stomach. The circular fibers immediately cease contracting and the esophageal-stomach orifice closes again immediately. Between the stomach and the intestine exists also a constriction, but which does not intercept the communication. The walls of the esophagus possess longer and more narrow cells than in the other parts of the digestive tube (fig. 7). The ectoderm is composed of a single layer of cells all alike. However, they become longer and more compressed along the ciliated bands (figs. 8, 9). The cells of the mesoderm are found, in these sections, disseminated a little everywhere. Finally, these sections teach us that the vaso-peritoneal vesicles are perfectly hollow formations (figs. 8, 9) and that the dorsal pore communicates with the left vesicle by a true canal (fig. 8, *pd*).

The pluteus represented (pl. XXIV, fig. 3) is 30 days old. At this moment two new formations appear. These are two bumps on the oral lobe, lateral and below (pl. XXIV, fig. 5) to the outside of which one distinguishes a little triangular spicule (3). These bumps are the rudiments of the third pair of arms that, at the end of the second month, have attained the proportions indicated in figure 1 of plate XXV. The spicule that appeared first is developed into a lattice rod, identical to those of the posterior arms. At the same time, the anterior arms are elongated. Finally a spicule appears at the summit of the cupola (fig. 1, *q*).

The appearance of a spicule always occurs in the middle of a small mass of mesodermal globular cells (pl. XXV, fig. 6, 4). These cells accompany likewise the extremity of a spicule in the process of formation during its growth. It is thus logical to consider them the formative elements of calcareous rods.

While the antero-lateral arms elongate, a trifurcated spicule appears on the dorsal surface very near the pore (this spicule has been omitted from figure 1, pl. XXV). It is represented alone in fig. (4)). It develops little by little and its two lateral branches fit into the two small mamelons (4) situated between the anterior arms (fig. 2). These two mamelons and the corresponding spicules represent the antero-internal arms.

Other changes occur at the same time in the larva in consequence of the formation of lobes all along the ciliated band. The posterior lobe (7), already formed in the pluteus of 30 days stands out as figure 3 of plate XXV indicates. Two lobes (7'') are developed on all sides of the cupola between the two pairs of arms with latticed spicules. Finally two lobes (7''') (fig. 2) stand out in the dorsal ciliated band. Three months after fertilization, the pluteus has acquired the form represented (pl. XXV, fig. 2).

The pluteus of *Dorocidaris* lacks ciliated epaulettes. Thus its movements are slow. It floats with difficulty, despite the vibratile movements of the ciliated band that appears especially destined to maintain the alimentary currents.

My observations were extended still another month during which, hoping all the time to be present at the formation of the young cidaris, I redoubled the care and attention. Unfortunately, my hopes have been disappointed, and the last pluteus resulting from a fertilization done on 14 February died in the month of June without anything indicating the formation of a juvenile.

Is the pluteus of three months the definitive adult form of *D. papillata*? There is reason to think so since after having attended its successive transformation after fertilization, slow but continuous transformations, we have seen the larva keep this form for 30 days more without modifying its characters. If the juvenile has not begun to develop during this lapse of time, it is because it has not been possible to place the adult pluteus in the environmental conditions and food they would have found in the free state.

Among the numerous larvae that J. Müller illustrated, there is one that the author collected a single time at Messine and which he described in a chapter titled: *Über eine Larve mit Gitterstäben, auricular Fortsätzen und Wimpeln des Schirms* (1). J. Müller did not know to which urchin to assign this pluteus. However, he was disposed to consider it as a larva of *Echinocidaris (Arbacia)*.

The relative length of the four pairs of arms, the great development of the lobes of the ciliated band, the latticed spicules are many of the characters that lead me to believe that the larva of Messine is nothing but a pluteus of *Dorocidaris papillata*. There is however a character that, if it really exists, does not permit making this identification. The latticed spicules of the Messine larva carries small spines, while those of the pluteus of *Dorocidaris* are absolutely smooth. These spines exist on the latticed spicules of all the other larvae drawn by Müller, and it is possible that the author has drawn them inadvertently on those of larvae of Messine.

The details that I have just given on the development of the pluteus of *Dorocidaris papillata* will permit, I hope, its recognition with certainty at its different ages, wherever one will encounter it.

Amidst the numerous plutei of *Dorocidaris* that I have raised in order manage better these researches, I have had a small number of monstrous larvae. Two among these merit being reported. One (pl. XXV, fig. 8) showed between the two posterior arms, a pair of supplementary arms (*x*) developed at the expense of the lobe (*l*). The other (fig. 9) is of particular interest since it possesses the unpaired arms (*sp*) characteristic of spatangids. These two larvae were aged thirty days, and their internal organization presented nothing abnormal. However they did not continue to develop and died a little later.

(1) *Über die Gattungen die Seeigellarven*, 1885.

## STRONGYLOCENTROTUS LIVIDUS

### DEVELOPMENT OF THE GENITAL APPARATUS

In a note to the Academy of Sciences (17 January 1887), Perrier recalled he had written in number 194 (1885) to the *Zoologischer Anzeiger*: "The dorsal organ of crinoids has often been compared to the ovoid gland or supposed heart of urchins and sea stars. There is reason now to investigate if this problematic body has not some role to play in the formation of the genital glands of echinoderms". He added: "I announced I shall count on undertaking researches in this direction. No one until now had expressed a parallel opinion on the role of the supposed heart of echinoderms. The first idea of these researches and the method to follow in order to carry them out better, as I have done for the comatulids, thus belong to me."

Nothing is more just than this claim. For my part, I must declare that the researches of Perrier on the comatulids have engaged me to study the development of the genital apparatus of the urchin. Having been able to collect very young *Strongylocentrotus lividus* at the beach at Banyuls, I have tried to resolve a part of the question that has just been emphasized.

In that, I do not believe to have overreached my rights, and I am certain that Perrier has not had, for a single instant, the thought that I have the intention of appropriating to myself the *original idea* of these researches.

The youngest *Strg. lividus* I have been able to study had a size of 1.5 mm. At this age, the apical rosette is constituted as Loven (1) has described. The five genital plates and the five ocellars surround the central disc. The anus and the genital pores are not yet formed. If one sections an urchin of this dimension, one confirms that the madreporic plate is pierced by two of these pores that lead into a well developed water-tube. One perceives all along this tube an elongated body in which one distinguishes a glandular substance containing numerous nuclei. This formation is the nascent ovoid gland. It extends until below the madreporite and is enveloped by a delicate membrane that attaches it to the esophagus. There are not traces of the genital gland.

Examine now serial sections on the axis of a young *Strg. lividus* of 3 mm. We confirm that the genital plates are not perforated and no particular formation exists in their area. As previously, we find that the sand canal and the rudimentary ovoid gland end in a space (e), the sub-madreporic space (pl. XXII, fig. 4). But, on either side, we distinguish a formation (g) that did not exist in the younger urchin. One of these formations (g) is immediately attached to the test. The other is joined to a thin membrane that envelops the ovoid gland and the sand canal. Study the serial section in both directions from section (4). In one direction, the formations (g) disappear (fig. 3, 2). In the other, to the contrary, they increase in importance (figs. 5, 6, 7, 8), while the water tube and the gland disappear in their turn. In section (8), the two formations (g) soon touch. In the following section, they merge and further on one no longer finds them. One

(1) *Loc. cit.*

arrives thus, keeping in mind the orientation of the sections, to find that the body (*g*) has the form and situation represented in diagram (9).

Enveloped by a thin membrane, which extends the mesenteric lamellae binding the ovoid gland to the esophagous, this formation is characterized by the nucleiform cells it contains (fig. 7). These large nuclei have a very prominent contour. They are generally ovoid and possess a very apparent central nucleolar point. Their dimension is 0.006-0.008 mm.

In order to ascertain the nature of the formation that interests us, it is necessary to study older individuals. In a *Strg. lividus* of about 6 mm, one notices five small blind sacs (one in each radius) applied against the internal surface of the test under the genital plate. They are united by a membrane that surrounds the periproct and continues with the mesentary that supports the ovoid gland. These are the five nascent genital glands. Now, these five interradiial tubes contain nucleiform cells indentical to those we found in the formation (*g*) of *Strg. lividus* of 3 mm. This is nothing other than the genital bud.

Having ascertained the true nature of this bud, it is necessary to examine the manner of its relation to the ovoid gland. If it were formed by it, there would be a continuity of substance between the two. Moreover, one would encounter nucleiform cells at least in the part of the gland giving rise to this bud. Now, the bud is completely exterior to the gland. It ends in a taper on the extension of its envelope that lines the submadreporic space. It has not been possible for me to confirm within the gland the presence of a simple nucleiform cell that characterizes the genital bud.

In the note cited above, Perrier wrote: "As this body and the ovoid gland it nearly touches are both the product of the membrane on which they rest, one can say that the results obtained by Prouho, if all is as they are defined, do not differ as much as he seems to think from these that I have just recalled and thus the agreement should invite him to new studies."

I can only repeat that which I have said in my note of 3 January 1887: "If the genital bud of *Strg. lividus* emanates from the gland itself, the development of the genital apparatus of the urchins is accomplished by a procedure analogous to that which Perrier described in the comatulids. One could say that the nascent ovoid gland of the young echinoid is or contains a genital stolon just as the dorsal organ of the young comatulids. My observations do not permit me to make this conclusion." The conclusion to which these observations lead us is the following: the primitive genital bud of *Strongylocentrotus lividus* belongs to the mesenteric lamellae linking the esophagous to the ovoid gland and it arises independently of the latter.

The primitive genital bud we have observed in a juvenile of 3 mm develops little by little proportionally as the animal grows. It advances first under the madreporic plate and then, extending from one part and the other under the genital plates, grows around the priproct and, at the same time, grows a blind extension in front of each interradius. While the bud develops in this manner, it remains attached at its point of origin, but the nucleiform elements move into the most distant points of the primitive center, i.e. within the five radial caeca.

It follows that soon one no longer meets them either in the area of the ovoid gland or in the membrane that the bud has formed behind it as it encircled the anus. This membrane is attached to the test by the two lateral borders. There is consequently, between it and the test, a perianal annular space (pl. XXII, fig. 1, *h*). In most adult urchins this space is placed in communication with the general cavity because of perforations that are produced in the membrane that lines it (see the genital pentagon of *Dorocidaris*).

The young urchin possesses thus at this moment five genital buds united by a pentagonal membrane that is the continuation of the mesentery. If one had not observed the single primitive bud produced under the madreporite, one would be tempted to believe that the five buds have each arisen independently under each genital plate.

Each of these buds elongates little by little by its adoral extremity, while its apical extremity penetrates into the corresponding genital plate (fig. 1), which is not slow to be completely perforated. Thus are constructed the five genital pores. While this perforation is accomplished, the buds, which until then were simple cords, begin to produce lateral ramifications. It is then easy to see directly the five nascent genital glands of *Strg. lividus* of 7-8 mm with the aid of a strong microscope. I was not preoccupied with following their ultimate development and I have not studied the evolution of nucleoform cells.

Finally, I report the presence in a *Strg. lividus* of 6 mm of the genital nerve ring (fig. 1, *ng*) at the plate where we encountered it in the adult *Echinus acutus*.

### SPATANGUS PURPUREUS

#### INVESTIGATIONS ON THE WATER SYSTEM AND THE LACUNAR DEPENDENCIES OF THE INTESTINAL ABSORBING SYSTEM

There exists on the internal surface of the apical pole of *Spt. purpureus* two calcareous lamellae that unite between them the four genital pores (pl. XXVI, fig. 16) and are in life covered by the membrane that links the four genital glands (pl. XXVI, fig. 2, 1). These two plates enclose between them a space occupied in part by a soft spongy tissue that abuts a cord that comes out from the ovoid gland (pl. XXVI, fig. 1, *p*). According to Hoffmann (1), the beginning of the sand canal is situated between these two plates. It is probable the author has taken for the sand canal the cord of which we just spoke.

Koehler designated this extension of the ovoid gland under the name

the name *madreporic canal* and as he considered it as either the excretory canal of this latter or as the end of the sand canal. He admitted that it communicates with the exterior by the intermediary of spongy tissue. That, according to my research, is not at all correct. In *Spt. purpureus* not a single water pore opens between the two subapical plates where is found the spongy tissue and the madreporic canal (of Koehler). This latter is homologous to the glandular process of *Dorocidaris*. It is not consequently either the sand canal or the excretory conduit of the ovoid gland. The space included between the two plates corresponds to the submadreporic space and the spongy tissue represents very probably the tissue that in *Dorocidaris* borders the madreporite cavity.

But since the water pores do not exit between the two apical plates and the madreporite canal or rather glandular process is a structure absolutely different from the water-tube of regular echinoids, where then is the canal that represents the latter in *Spatangus*?

Teuscher is, to my knowledge, the only author who has had a presentiment of the true water tube. He indicated it clearly in these terms: "Der Steincanal welcher an seinem Cylinderepithel leicht kenntlich ist, liegt dem Herzen auuserlich an, aber naher, als bei den Echinea" (1). Unfortunately, the author has not given the explanatory figures and besides Koehler (2), making allusion to this canal, said "Never in the sections of the gland, does one find traces of a canal that would be joined to it as Teuscher said." There has resulted an uncertainty and a confusion that H. Carpenter was not slow to reveal in one of his arguments (3).

The discovery of the true water-tube of a spatangoid is however easy to make. It is simply a matter of following the water-pores of the madreporite, which can be done either with the aid of injections or by sections. When one injects the madreporite by applying the needle to the external surface, one sees that the colored mass penetrates into a canal (pl. XXVII, fig. 1) situated at the end of the right subapical plate. If one breaks this plate with care, one perceives it is perforated with longitudinal canals filled with the injection. These canals are the direct continuation of the water pores. Transverse sections confirm the fact with the greatest conspicuousness and shows us the canals of the sub-apical plate are lined with a vibratile epithelium analogous to that which characterizes the sand canal of urchins. A section taken in the region where the plate in question or madreporic apophysis stands out from the test proper (pl. XXVI, fig. 7) passing through ( $\beta$ , fig 16), one sees these canals have penetrated into the apophysis (*am*). One perceives also the left plate (*pl*) and, between the two, the sub-madreporic space (*e*) containing the process (*p*) and the spongy tissue (*sp*). Continue the sections progressively from the madreporite. We see the cavity in which is sunk the madreporic apophysis take shape little by little to form a regular canal that would appear if the sections had passed the end

(1) *Beiträge zur Anatomie der Echinodermen (Spatangus meridionalis)*, *Jenaische Zeits. f. Nat. wiss.*, 1876. (2) *Loc. cit.* (3) *Notes on Echinoderm morphology (Quart. Journ. of micr. sc., October 1883).*

of the apophysis (pl. XXVI, fig. 9, c). This canal is the water tube provided with its characteristic columnar epithelium and it is this that Koehler has believed to see lose itself in the conjunctive tissue of the genital membrane.

The water tube of spatangoids is thus a canal with columnar epithelium that opens at the posterior end of the madreporic apophysis. Up to now, except for the form and dimensions, the analogy with *Dorocidaris* is complete. There remains to be found the water canal annex. This canal forms in the depths of the cavity of the ovoid gland. It is easy to follow by a series of cross sections. In section (9), it (c') is still in touch with the rest of the tissue of the gland and joined to the sand canal (e) (compare this section with that of plate XX, fig. 5). We again find it (fig. 14) always separated by this latter. Finally (fig. 8, 15) the septum that separates the annex canal from the water tube has disappeared and the two canals open at the end of the madreporic apophysis (diagram, fig. 3, c, c').

Having advanced further the study of the water system, it is indispensable to examine closer the lacunar branches that belong to the absorbing system.

When one makes an injection by the internal marginal vessel, the material passes into the so-called *communication branch* (Hoffmann), from there into a peribuccal ring (av) in order to go on the one hand into the five radii and on the other into a canal (cg) (pl. XXVI, figs. 3, 5) that

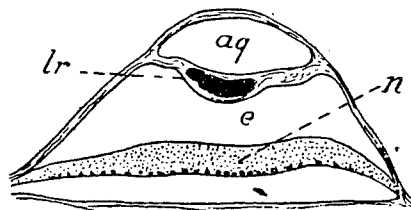


Fig. 6. -- Transverse section of a radius of *Spt. purpureus* injected by the internal marginal vessel: aq, ambulacral vessel; lr, radial lacuna; e perineural space; n, ambulacral nerve.

follows the path assigned by the authors to the sand canal.

Examinations of the sections made of the injected pieces teach us that the colored mass has penetrated into a lacunar ring joined to the ambulacral ring independent of the perineural space, and this ring furnishes five lacunae (fig. opposite, lr) running the length of the radius under a canal that, we shall see further on, is the ambulacral vessel. The lacuna thus injected represents in spatangids the radial lacuna of regular echinoids. It allows itself to be injected here without difficulty, probably because the resistance created by the pharyngeal lacunae of the Regularia does not exist. This lacuna is, as in the Regularia, situated in the membrane that separates

the ambulacral vessel from the perineural space.

Make now a cross section of the branch that comes loose to follow the sand canal (of the authors). This section is represented in the memoir of Koehler (pl. V, fig. 34). It shows the lumen of two canals (C, C') and there is the marked canal (C) our injection has followed (pl. XXVI, figs. 5, 3, cg). Never have I seen the colored mass penetrate into the canal C' of Koehler, designated by va' in our drawing. We follow the canal cg until the ovoid gland. Having reached this point, it furnishes a lacunar network (l) to the gland. Then the injection reappears at the other end of the gland and forms a network (lg) within the membrane of the genital apparatus (pl. XXVI, figs. 1, 2). The canal (cg) is represented in the latistellar urchins by the lacuna Koehler has named *glandular canal* in *Sph. granularis* and in *Dorocidaris* is not differentiated because of the contact of the ovoid gland with the lantern.

There thus exists in the spatangids, a peribuccal ring belonging to the visceral lacunar system that furnishes five radial lacunae, also a lacuna (glandular canal) irrigating the walls of the ovoid gland and the genital gland (fig. 3).

Return to the water system. An injection made by the madreporite penetrates as we have said into the water tube (c), but it does not stop there. It fills a canal with small lateral ramifications (fig. 3, l) that crosses the ovoid gland and continues the length of the glandular canal until a short distance from the esophagus. This ramified extension of the water tube no longer possesses a columnar epithelium. This disappears little by little in the same region where appear the first ramifications of the ovoid gland. After having passed the latter, the ramified canal joins intimately to the glandular canal but does not merge with it. The injections are indispensable in order to be assured of this fact and their results are constant. An injection made by the internal marginal vessel fills the glandular canal and never passes into the ramified water canal (fig. 13). Inversely, an injection made into the water tube never penetrates into the glandular canal.

In the regular urchins, when one injects the water tube, the mass penetrates into the ambulacral vessels. Here, the thing has never taken place. The colored material stops at the end of the ramified canal, i.e. a small distance from the esophagus. This is because this canal ends there in a cul-de-sac. If one makes a section 1-2 mm from its end, one now finds only that the lumen of the glandular canal becomes single.

However, in the section of a radius taken higher, there exists a vessel (ap) situated as the water vessel of a regular urchin. It seems that in the spatangids, this vessel should be likewise in relation with the water tube. Inject it directly. We see the injection penetrate into the ambulacral vesicles and fill a ring that follows the lacunar ring. From there, it enters into a wavy canal (figs. 5, 3) (it is the canal marked (C') in fig. 34 of Koehler). This wavy canal ends in a cul-de-sac some distance from the end of the ramified water canal. There is no continuity between the two.



This study indicates that in the spatangids, the apparatus called the water system in the regular urchins is separated into two parts. First an apical part that is actually the water system, including the madreporite, the water tube proper, the annex canal, and the ramified water canal. Second an ambulacral adoral part composed of the wavy canal, the peribuccal ring, and its five ambulacral vessels.

H. Carpenter (1) stated doubts on the connections of the *communication branch* that Hoffmann and the subsequent authors considered as establishing a communication between the system of the intestinal vessels and the ambulacral vessels. He asked for new studies in order to establish "the connection of the intestinal vessel of *Spatangus* with both the oral rings". The doubts of H. Carpenter are justified. The so-called communication branch of Hoffmann is related only with the peribuccal lacunar ring (pl. XXVI, fig. 4,av) and not at all with the ambulacral ring (aa'). It is incontestable that if this branched communication (vi) bifurcates at its end in order to open into the two rings, one could inject them simultaneously by making an injection by the internal marginal vesicle. Now it is always the lacunar ring that is injected with the radial lacunae and never the ambulacral rings and vessels. But in order to be assured of this fact, it does not suffice to examine under the microscope. It is necessary, moreover, to make cross sections of the radii and the peribuccal rings thus injected. Without this one is liable to confuse the ring and the ambulacral vessels with the lacunar ring and the radial lacunae. Hoffmann ignored the presence of the radial lacunae and, when making an injection into the vessels of the intestine, he saw the material penetrate into the radial areas. He believed he had injected the ambulacral vessels (*Wassergefasscanale*).

I did not at first realize the separation of the two parts of the water apparatus. Thus I did not report it in my preliminary note of 21 June 1886 (*Comptes rendus de l'Academie des sciences*).

Never having been able to succeed in injecting the ambulacral vessels and the wavy canal by making the injection by the water tube, but persuaded that in the spatangids as in the regular urchins the ambulacral system showed communication with the madreporite, I attributed the negative results I obtained to an insufficient penetration of the injections and I did not doubt that the ramified water canal does not join the wavy canal. In this, we have just seen, I committed an error that is found corrected in the preceding lines and into which I would not have fallen if I had not suspected the value of the injections that warned me of an interesting and absolutely unexpected anatomical fact.

(1) *Loc. cit.*

We have seen that in *Dorocidaris* the ovoid gland possesses a circular extension (periesophageal lacunar ring) that, thanks to the circular extension of the water tube (periesophageal water ring), is in contact with the external environment that diffuses into this latter ring. In spatangids, the tissue of the gland is continuous the length of the glandular canal, and it is found likewise in contact with the external environment thanks to the ramified extension of the water tube. There is thus an analogy of the structure between the double ring of *Dorocidaris* and the part of the so-called canal of the authors that spreads from the ovoid gland to the end of the ramified water canal.

In summary, in spatangids the external environment can diffuse solely by contact with the tissue of the ovoid gland and its extension. As for the ambulacral system that in *Echinus* communicates with the exterior, it has become a closed cavity. But it always remains suited to maintain respiration of the perivisceral fluid thanks to the tentacles and vesicles of the petals. This system stays likewise fit to aid locomotion since, as we have seen in a preceding chapter, communication with the exterior by the intermediary of the madreporite is not an indispensable condition for the functioning of the tentacles. If, however, this condition is favorable, it would be very interesting to be able to study a species of spatangid presenting better developed and more active ambulacral tentacles in order to see if the rupture of the water system into two parts exists. But it would be of much greater interest still to study, from this point of view, very young individuals. It seems probable to me that the separation of the two parts of the water system should take place some time after the formation of the young spatangid.

#### SUMMARY

*Dorocidaris papillata*. -- After having given a view of the echinoderm fauna of the coast of Roussillon, we have studied the habits of *Dorocidaris papillata* and ascertained the role of the spines.

The development of the radioles has been followed from their appearance until the definitive form and this study, joined to some observations on the mode of repair after breakage, has given us useful information for the determination of the species.

*D. papillata* possesses glandular pedicellariae of which each calcareous valve contains a mucous sac.

The role of the pedicellariae remains unknown.

The principal bundles of the peripheral nervous plexus are lodged in special grooves hollowed in the calcium at the surface of the test. The nature of these grooves known in some fossil species is thus discovered.

The peripheral nerve plexus forms at the base of each radiole a nerve ring visible to the naked eye.

The ambulacral nerves are tubular forms presenting a virtual intraneural space that ends between the epithelium of the pharynx and that of the peristomal lips. The internal part of the ambulacral nerve tube forms a peribuccal nerve ring that is continuous with the epithelial layer of the pharynx.

The digestive tube lacks an intestinal siphon. This character is not found in any of the echinoids studied to date.

The water pores of the madreporic plate communicate with two distinct canals: the water tube (sand canal) and the annex canal (excretory conduit of Perrier). This latter is the extension of the cavity of the ovoid gland.

The entry of water by the madreporite occurs by simple diffusion.

The system of ambulacral canals differs from that which is in the echinids only in the peristomial region (absence of buccal tentacles).

The ambulacral tentacles are of two kinds. One appropriate for aiding in locomotion is provided with suckers (adoral hemisphere). The other kind, deprived of suckers, is exclusively respiratory (aboral hemisphere).

The functioning of the sucker is explained by the play of muscle fibers independent of the longitudinal muscles.

The visceral lacunar system (hemal system of others) is solely composed of lacunae hollowed in conjunctive tissue of the mesenteric lamellae. The absorbing capillary network ends in two marginal lacunae: one external, the other internal. A collateral vessel does not exist.

The internal marginal lacuna leads into a periesophageal ring hollowed into the internal wall of the water ring. This lacunar ring furnishes: 1, a network distributed to the ovoid gland and continued into the genital pentagon; 2, five pharyngeal lacunae from which rise five radial lacunae joined to the external surface of the ambulacral vessels. The lacunae give off lateral branches for the ambulacral vessels. The lacunae give off lateral branches for the tentacles.

There are no differentiated Polian vesicles of the esophageal ring.

The visceral lacunar system does not communicate with the exterior. The ring belonging to the visceral lacunar system does not communicate with the water ring. The only exchanges possible between the two take place by osmosis and diapedesis.

The two systems, lacunar system and water system, do not communicate with each other under the madreporic plate.

The visceral lacunar system is thus an apparatus completely separated from the water system.

The ovoid gland is the place of formation of the white amoeboid globules with long pseudopods that are strewn in the perivisceral fluid, the ambulacral canals, and in all tissues. The esophageal lacunar ring is an extension of these walls of the gland.

The role of the three distinct cavities: general cavity, lacunar system, water system, has been studied in a special chapter.

The general cavity includes two parts not communicating with each other: the general cavity proper and the pharyngeal cavity.

This latter is not provided with external branches, contrary to those that occur in echinids. It possesses five internal appendices (Stewart's organs) destined to favor the osmotic exchange between the peripharyngeal liquid and the perivisceral liquid.

The larval form of *D. papillata* is a pluteus with four pairs of arms of which two present latticed spicules with smooth rods. These are the posterior arms and the antero-lateral arms. The anterior arms and especially the antero-internal arms are short. The cupola is flat and presents two lateral lobes. There are in addition other very developed lobes the length of the ciliated fringe. The ciliated epaulettes are lacking.

*Echinus acutus*. -- Its study has permitted us to show there exists in urchins a peripheral nerve system situated in the epidermal layer of the test constituted by a reticulated plexus in touch with the internal nervous system, by the tentacular nerves, and by the apical end of five ambulacral nerves.

This plexus forms at the base of each spine a nerve ring rich in ganglionic elements.

Also we have discovered in this *Echinus* a genital nerve ring in touch with the five ambulacral nerves.

*Strongylocentrotus lividus*. -- In studying the very young individuals of this species, we have observed the development of the genital apparatus.

The five genital glands come from a single primitive bud, developed at the expense of the mesentery.

The ovoid gland is not a genital stolon.

*Spatangus purpureus*. -- The madreporite presents an external apophysis at the end of which ends the water tube (canal with columnar epithelium) and the annex canal. The ovoid gland sends between the madreporic apophysis and the left subapical lamellae an extension that is homologous to the glandular process of *Dorocidaris*.

The internal marginal lacuna furnishes a branch that forms a peribuccal lacunar ring. This ring gives off from one part five radial lacuna and on the other, a lacuna (glandular canal) that reaches to the ovoid gland, distributes itself in its walls, and ends in a network within the membrane that links between them the four general glands.

The apparatus called water in the regular echinoids is in spatangids divided into two parts that do not communicate with each other: first the water tube proper extended by a ramified canal that borders the glandular canal and dead ends toward the esophageal region; second the ambulacral system including five radial vessels, a peribuccal ring and an undulating canal applied against the part of the glandular canal that borders the esophagus and deadends there.

The visceral lacunar system does not communicate with either of these two parts.

The so-called branch of communication empties only into the peribuccal lacunar ring and not at all into the ambulacral ring that accompanies the latter.

The lacunar visceral system does not communicate with the exterior.

#### APPENDIX

The studies that have just been described were entirely finished when O. Hamann (1) published the definitive results of his work on the histology of echinoderms. Without having intention of giving here a complete analysis of this memoir, which concludes an important series of studies on a group of animals that I myself have studied only a part, I shall restrain myself to the following remarks:

O. Hamann confirmed the observations that I summarized 22 February 1886 (2) relative to the existence of the peripheral nerve plexus of *Echinus acutus* and of the mode of innervation of the spines by this plexus (basal nerve ring of the spines).

He reported the presence of a hemal nerve ring (*anale Blutlakunenring*) situated in the thickness of the membrane that forms the genital pentagon. I made known the existence of the perianal lacunar network in *Dorocidaris* on 15 June 1886 (3).

The German author seemed to attach a great importance to the presence of an annular space contained between the genital pentagon and the test (*Schizocölring*). This space does not exist before the genital bud has encircled the periproct. It is the consequence of the development of the bud behind which it is constituted, little by little. And if this annular space is a closed cavity in the young urchin, it communicates broadly with the general cavity in the adult. It is moreover completely separated from the submadreporic space that seems to have remained unperceived by Hamann, and which itself is a closed cavity in which the ovoid gland ends.

Is this perianal space of real morphological importance? The question seems debatable and one should not forget that it is, in the adult urchin, a simple extension of the general cavity.

O. Hamann has not observed that the cavity of the ovoid gland communicates with the exterior by means of the annex canal. For him, this gland is an organ in which the useless formed material is separated from the blood. It will be thus an organ of excretion without an excretory duct. The conclusions to which the study of *Dorocidaris* has led are completely different.

(1) *Beitrage zur histologie der Echinodermen* (*Jen. Zeits. f. Nat.*, v. XXI, 1887). (2) *Compt. rend. Acad. sci. Paris*. (3) *Compt. rend. Acad. sci. Paris*.

We agree with the German author in regard to the separation of the two esophageal rings, but I give to him the responsibility of his hypothesis when he considers the Polian vesicles as respiratory organs.

O. Hamann has not seen the radial lacunae of regular urchins. I have not studied them in *Sphaerechinus* or in *E. acutus*, but having found them in *E. sphaera*, I do not believe I go too far in saying that these lacunae exist in all urchins. It is in the thickness of the membrane that separates the canal *W* from the space *Sch* (1) (memoir of Hamann, pl. XIV) that one must search to discover the radial lacuna. Moreover, the existence of these lacunae has been misunderstood by Hamann in *Spatangus purpureus* itself, where however it is easy to inject by making the injection by the internal marginal lacuna.

In the second part of the memoir, dedicated to irregular urchins, I found (p 223) the following phrase: "Dass der Steinkanal nur von der madreporenplatte bis zur Druze reicht und hier in ein Gefassgeflect mündet, ist ihm (Teuscher) wie allen folgenden Beobachtern, auch Koehler, entgangen." Hamann would not have written this phrase if he had known of my note of 21 June 1886 (1).

The conclusions of the German author relative to the structure of the so-called sand canal of the authors, which he called *Gefassgeflect*, are essentially different from mine. For Hamann, all the cavities that compose the *Gefassgeflect* communicate with each other. To me, two sorts of distinct cavities exist, one belonging to the visceral lacunar system, the other to the water system. But in order to discover the independence of the two sorts of cavities, it is not sufficient to make transverse sections of the *Gefassgeflect*, it is necessary to have previously injected it with soluble blue. If Hamann had not neglected the method of injections, he would have been able to make the following observations:

By injecting the internal marginal lacuna, he would have seen the colored material pass into the lacunae marked *Bl* and *Kl* in fig. 8, pl. XVII, in his memoir, without ever penetrating into the lacunae marked *K*. He would have concluded *Bl* and *Kl* do not communicate with *K* and these cavities belong exclusively to the visceral hemal lacunar system. With the same stroke He

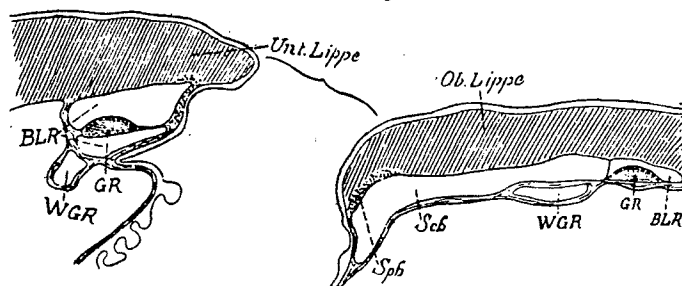


Fig. 17. -- Vertical section of the mouth of *Sptg. purpureus*, according to Hamann. *GR*, nerve ring; *WGR*, water vascular ring; *BLR* and *Sch*, hemal lacunar ring; *Sph*, sphincter.

(1) *Compt. rend. Acad. sc. Paris.*

would have injected the walls of the gland, the genital membrane, and the colored material would not have penetrated into the water tube.

To the contrary, if he had made the injection by the madreporite, he would have seen the colored mass penetrate into the tentacles, from there into the cavities K of the figure in question, and finally into the lacunae B1 and K1. At the same time he would have confirmed the injection did not penetrate into the radial areas.

These two injections, the one by the madreporite, the other by the internal marginal lacunae, would have shown the skillful histologist of Gotingen that there is, in the part of the sand canal of the authors with which we occupy ourselves, two categories of cavities that do not communicate with each other.

According to Hamann, the hemal lacunae that accompany the esophagus empty into a peribuccal ring containing the nervous system, and from this ring (*Schizocölringkanal*) leave five hemal lacunae in which are lodged the five radial nerves. Koehler has already pointed out, very correctly, that the spaces in which are lodged the nerve trunks of a spatangoid are not these vessels. And if Hamann had sectioned pieces previously injected with soluble blue he would have reached conclusions very different than those he has published.

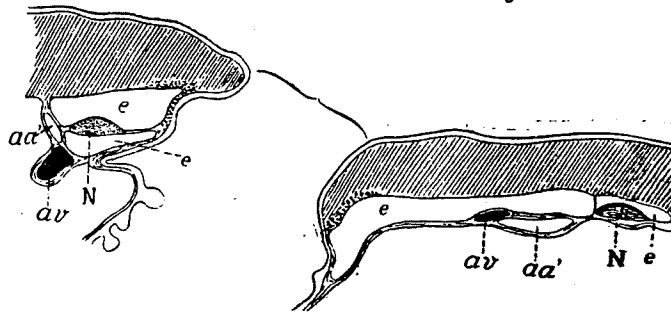


Fig. 18. -- Same section as fig.17, in which an injection by the internal marginal lacuna demonstrates the true ring *av* of the visceral lacunar system; *aa'*, ambulacral ring; *N*, nerve ring; *c*, perineural spaces. Hamann has not seen the lumen of the lacunar ring *av* (upper lip) and he has attributed to the water ring the lumen *av* (lower lip) whereas it belongs in reality to the lacunar ring. In addition, he has not shown the true lumen *aa'* (lower lip) of the water ring.

I have reproduced opposite (fig. 17) the section of the mouth of *Spatangus purpureus* given by Hamann (pl. XVII, fig. 3) and beside it (fig. 18), the same section after injection with soluble blue by the internal marginal lacuna. The comparison of these two figures replaces advantageously the most minute description, and one should conclude that the author whose memoir we discuss in part has not observed the true peribuccal ring of the visceral (hemal) lacunar system. This ring *av* (fig. 18), as well as that of the radial lacunae that leave it (fig. 16, *lr*) are in communication with the absorbing intestinal system that have no relation with the *Schizocölbildungen: Langskanäle* and *Schlundsinus* of O. Hamann.

## PLATE LEGENDS

## PLATE XIV.

*Dorocidaris papillata.*

Fig. 1. Fragment of the test (interambulacral area); *m*, mamelon of the primary tubercle; *t*, secondary tubercle; *sn*, groove of the peripheral nerve net. Size. 2 d.

2. Four ambulacral plates and part of the neighboring interradiar plate; *p*, ambulacral pores; *u*, notch in which is lodged the tentacle nerve; *r*, tubercles of the pedicellariae; the other letters as before. Size. 9 d.

3. Longitudinal section of an ambulacral zone near the ocellar pore; *va*, ambulacral vesicles; *s*, suture line; *t*, tentacles cut obliquely; *sn*, section of the nerve fascia lodged in the grooves *sn* of the preceding figure; *np*, section of nerve fascia surrounding the tentacle. Size. 25 d.

4. Longitudinal section of the extremity of a radius and of the ocellar pore; *aq*, ambulacral vessel; *a*, ocellar pore; *o*, ocellar plate; *np*, peripheral nerve net; *n*, ambulacral nerve. Size. 25 d.

5. Ambulacral tentacle sectioned near its attachment to the test; *n*, tentacular nerve. Size. 8 d.

6. Fragment of section (4) near the border of the ocellar pore; *ep*, nucleus of the epidermal cells; *p*, extension of these cells to the nerve plexus, *np*; *c*, conjunctive membrane limiting the test network, *rc*; *k*, spaces occupied by calcareous material; *gm*, muriform globule. Size 460 d.

7. Semi-schematic section taken transversely to a radius; *ta*, retracted tentacle; *va*, corresponding unsectioned vesicle; *sp*, calcareous spicules; *p*, ambulacral pores; *aq*, ambulacral vessel; *lr*, radial lacuna; *e*, perineural space; *n*, ambulacral nerve; *np*, peripheral nerve plexus; *nt*, tentacular nerve.

8. Transverse section of a tentacle following ( $\omega$ ) (fig. 7); *d*, partitions that divide its lumen into two parts. Size 45 d.

9. Longitudinal section passing by a median plane to a pharyngeal ridge; *ei*, pharyngeal epithelium; *ep*, epithelium of the peristomial lip; *ar*, tract of the pharyngeal ridge, in which are hollowed the lacunae; *lr*, radial lacuna; *e*, perineural space; *n*, ambulacral nerve; *N*, nerve ring;  $\omega$ , point where the virtual intra-nerve space opens. Size. 25 d.

10. Section of the nerve pentagon *N*, in an interradius; *N'* corresponds to the part *N'* of the nerve tube (pl. XVII);  $\omega$ , groove that continues the virtual intra-nerve space; *q*, membrane that is attached to the tooth. Size. 25 d.

11. Transverse section of a pharyngeal ridge; *ar*, tract of the ridge; *c*, coagulated contents in the lacunae of the latter; *ei*, epithelium of one of the grooves of the pharynx colored with methylene green. Size. 115 d.

12. Section of a groove of the test; *sn*, nerve fiber; *ep*, epidermal cells. Size. 265 d.



Fig. 13. Tangential section taken near the point of emergence of a tentacle nerve; *nt*, tentacle nerve; *g*, nerve cells;  $\omega$ , intraneural space; *lt*, little canal that accompanies the nerve; *fm*, muscle fibers of the corresponding tentacle. Size. 265 d.

## PLATE XV.

*Dorocidaris papillata.*

Fig. 1. Transverse section of the periesophageal double ring; *aq*, water ring; *av*, ring belonging to the visceral lacunar system. Size 45 d.

2. Part of fig. 1; *gm*, muriform globule, some of which are situated immediately below the epithelium; *ef*, formed elements contained in the water ring; *sp*, location of the dissolved calcareous spicules. Size. 265 d.

3. *a, b, c, d, e*, muriform globule crossing the epithelial layer of the internal mesenterial lamella, observed *in vivo*. Size. 385 d.

4. *a, b*, muriform globule, *m*; and brown globule, *gb*, crossing the same membrane.

5. Section of the newly formed pedicellaria; *ep*, epidermal layer *f*, forming cells; the head begins to differentiate; at the upper part, it is separated from the stalk by a foundation of more strongly colored nuclei; *r*, canalicular network of the test; *c*, membrane that limits it. Size. 265 d.

6. Base of a radiole in repair, stripped in part of secondary spines that surround it.

7. Two portions of a similar transverse section of the first intestinal curve; *e*, epithelium of the intestine; *gt*, groove; *vi*, internal marginal lacuna sunken in the mesenteric lamella; *ve*, external marginal lacuna. Size. 25 d.

\*

9, 10. Longitudinal and transverse section of tentacle of the adoral hemisphere; *ep*, epidermal layer; *c*, conjunctive layer containing the spicules and consequently the rosette; *sp*, spicules of the basilar region; *el*, elastic layer; *m*, longitudinal muscular fibers; *nt*, tentacular nerve; *n*, enlargement of the nerve that forms below the sucker a ring whose section is met again in *n'*; *f*, true muscle fibers at the sucker; *vt*, canal that accompanies the tentacular nerve. Size. 115 d.

11. Calcareous spicule of a retracted adoral tentacle, drawn in place; the anterior half of the rosette is elevated; one sees the space left free by the spicules in which would be located the tentacular nerve. Size. 180 d.

12. Calcareous spicules of the extremity of a tentacle located in the aboral hemisphere next to the equator; the rosette is rudimentary. Size. 80 d.

13. Calcareous spicules of the extremity of a tentacle of the apical pole. Size. 80 d.

14. Adult radiole whose summit is still covered by the epidermal layer of the test; *t*, articulating head; *a*, bourrelet; *c*, collerette. Size. 1 d.

\* (no legend given for fig. 8. JL)

Fig. 15. Younger radiole.

16. Still younger radiole.

17. Transverse section of a secondary spine, above the ampoule, after decalcification.

18. Detail of the same; *r*, canalicular network; *K*, free space left by the calcareous baguettes of the periphery; *ep*, epidermal cells lodged in the striations of the spine; *gm*, muriform globule. Size. 460 d.

19. Section of the apical pole following a distance from the apical rosette; *a*, anus; *r*, rectum; *p*, genital pore; *G*, genital plate; *g*, bit of genital gland; *ag*, genital pentagon; *O*, ocellar plate; *po*, ocellar pore; *ov*, ovoid gland; *mi*, mesenteric lamella going from the rectum to the lantern along the ovoid gland; *c*, water tube. Size. 2 d.

#### PLATE XVI.

##### *Echinus acutus.*

Fig. 1. Transverse section \*\* (fig. 2); *aq*, ambulacral vessel; *n*, ambulacral nerve; *ep*, epidermal layer of the test; *np*, peripheral nerve plexus. Size. 65 d.

2. Longitudinal section of the ocellar pore; *a*, ocellar pore; *n*, ambulacral nerve; *n'*, a part of the ambulacral nerve that furnishes the nerve fibers to the genital ring *ng*; *np*, nerve plexus; *ep*, epidermal layer; *O*, ocellar plate (the tinted plate replaces the test network). Size. 45 d.

3. Basilar nerve-ring of the spines transversely sectioned; *an*, nerve ring; *g*, nerve cells; *ep*, epidermal cells; *p*, their extensions; *e*, intercellular spaces. Size. 460 d.

4. Portion of a longitudinal section of another spine. Same letters. *np*, peripheral nerve plexus; *z*, conjunctive cells; *gm*, muriform globules; *m*, muscular fibers of the motor fibers of the motor muscles of the spine. Size. 460 d.

5. Longitudinal section of the base of a spine (*Echinus* of 4 mm). Same letters. *el*, elastic fibers; *T*, tubercle; *t*, articulating head. Size. 115 d.

6. Transverse section of the genital nerve ring; *ng*, nerve ring; *lg*, lacunae of the genital pentagon. Size. 460 d.

7. Fragment of a nerve fascia of the peripheral plexus; *g*, nerve cells. Size. 460 d.

8. Fragment of the epidermal layer of the test seen horizontally; *np*, principal fascia of the nerve plexus stained with gold chloride; *sp*, calcareous spicules; *k*, empty space corresponding to the attachment of a pedicellaria. Size. 115 d.

9. Portion of the isolated nerve plexus. Size. 460 d.

10. Fragment of the epidermal layer surrounding a pair of pores; *nt*, remainder of the detached tentacular nerve in continuity with the fibers of the plexus, *np*; *k*, location of a pedicellaria. Size. 25 d.

Fig. 11. Epidermal layer of the test seen by the surface that rests on the calcite and in which the epidermal cells where supports have been omitted; *z*, conjunctive cells; *gm*, muriform globules; *sp*, calareous spicules; *np*, nerve fibers of the plexus (colored with gold chloride). Size. 460 d.

## PLATE XVII.

*Dorocidaris papillata.*

Fig. 1. Buccal extremity of the pharynx; *c*, extremity of a tooth (in place); *m*, fragment of the neighboring jaw, likewise in place (the intermaxillary muscles have been raised); *ph*, lumen of the pharynx; *ar*, pharyngeal ridge; *s*, conjunctive lamellae; *n*, nerve pentagon; *t*, *t'*, ligaments; *l*, pharyngeal lips; *b*, bourrelets; *q*, membrane that attaches to the jaws; *aq*, water vessel; *va*, ambulacral vesicles.

2. *d*, tooth in place within a fragment of its jaw; the side *m'* has been sectioned in a fashion to show the ligament *t*.

3. Section of a radius, passing in ( $\xi$ ) of figure 1. *aq*, water vessel; *lr*, radial lacuna; *e*, perineural space; *n*, internal part of the nerve tube; *n'*, external part;  $\omega$ , intra-neural space. Size. 65 d.

4. Section ( $\delta'$ ), same letters. *lt*, tentacular lacuna. Size. 65 d.

5. Section ( $\gamma$ ); *j*, cavity that accompanies the nerve while it crosses to the peristome (see pl. XIX, fig. 1).

6. Section ( $\beta$ ). Size. 25 d.

7. Section ( $\alpha$ ); the water vessel *aq* touches at its end; it is bifurcated *nt*, departs from a tentacular nerve.

8. Section ( $\theta$ ); the water vessel no longer exists.

9. Section of a radius within the locality of the equator; *s*, suture of the ambulacral plates. Size. 65 d.

10. Part of a transverse section of the ambulacral nerve; *f*, nerve fibers; *g*, nerve cells; *c*, conjunctive tracts attaching to the nerve envelope. Size. 460 d.

11. Transverse section of a tentacle nerve; *n*, nerve fibers;  $\omega$ , intra-neural space. Size. 265. d.

12. Portion of a transverse section of the ambulacral nerve, showing the origin of a tentacle nerve *nt*. Size. 215 d.

Letters common to all figures of plates (XVIII to XIX):

<i>M</i> , madreporic plate.	to the lantern and along the ovoid gland.
<i>C1</i> , first intestinal curve.	<i>mo</i> , mesenteric lamella connecting the esophagus and the ovoid gland.
<i>C2</i> , second intestinal curve.	<i>oe</i> , esophagus.
<i>G</i> , genital plate.	<i>ov</i> , ovoid gland.
<i>g</i> , genital gland.	<i>c</i> , water tube.
<i>vi</i> , internal marginal lacuna.	<i>c'</i> , water canal annex.
<i>ve</i> , external marginal lacuna.	<i>p</i> , glandular process.
<i>l</i> , lacunae distributing themselves to the ovoid gland.	<i>e</i> , sub-madreporic space.
<i>av</i> , periesophageal lacunar ring.	<i>ar</i> , pharyngeal ridge.
<i>lph</i> , pharyngeal lacunae.	<i>r</i> , rectum.
<i>aa</i> , water ring (ambulacral)	<i>st</i> , Stewart's organs.
<i>va</i> , ambulacral vesicles.	<i>aq</i> , ambulacral vessel.
<i>mi</i> , internal mesenteric lamella.	<i>y</i> , Y-shaped ossicles.
<i>me</i> , external mesenteric lamella.	<i>pa</i> , articulating ossicles.
<i>mir</i> , mesenteric lamella going from the rectum	

Note. -- The ambulacral and interambulacral areas are numbered according to the nomenclature of Loven.

PLATE XVIII.

*Dorocidaris papillata*.

Fig. 1. *Dorocidaris* with the test raised, with the exception of the genital plates and the anal membrane. *a*, anus; *pg*, genital pores; *d*, membranous lamella that attaches each genital gland to the test; *f*, partitions of the mesenteric lamella of the second intestinal curve covered by the genital gland. Size. 1 d.

2. The two curves of the intestine, of which the two marginal lacunae are colored red; the injection of the capillaries is omitted and the transverse dimensions of the intestine are a little reduced in order to make the figure clearer. Size. 1 d.

3. Injected *Dorocidaris* (lateral view); the genital glands 1 and 2 are raised, as is a part of the intestine. *T*, test stripped of its appendages; *m*, primary tubercle; *ps*, secondary spines; *o*, ocellar plate; *L*, masticating apparatus; *t*, tentacles; *au*, auricles. Size. 2 d.

4. Apical rosette and genital pentagon seen from the internal surface; the ovoid gland the esophagus are pressed down. *lg*, genital lacunar network injected (by the lateral marginal lacuna); *b*, hole of the membrane of the genital pentagon. Size. 2 d.

5. Masticating apparatus of which the covering membrane has been raised in part; *cph*, peripharyngeal cavity; the articulating ossicle that covers the ambulacral vessel *aq* has been raised. Size. 2 d.

## PLATE XIX

*Dorocidaris papillata*

Fig. 1. Reconstituted section of the masticating apparatus and the peristome; *ph*, pharynx; *m*, jaws (the intermaxillary muscles are raised, the right jaw is sectioned following its plane of symmetry); *d*, tooth; *r*, membrane that covers the masticatory apparatus; *u*, muscles that connect between them the Y-shaped ossicles, transversely sectioned; *s*, conjunctive lamellae; *c'*, cavity of the ovoid gland; *lr*, radial lacuna; *n*, ambulacral nerve; *N*, nerve ring; *l*, pharyngeal lips; *b*, pharyngeal bourrelets; *q*, membrane that attaches to the tooth; *lp*, peristomial lips; *i*, attachment of the peristomial lips with the jaw; *e*, perineural space; *j*, cavity formed by a doubling of the peristomial membrane. Size. 2 d.

2. Esophageal extremity of the pharynx and periesophageal pharynx seen from their internal space; the Y-shaped ossicles have been cut and the covering membrane cut all around the rings. It resulted in the contraction of the muscles that connect the Y-shaped ossicles to produce the reversing of the membrane such as represented in the figure. The pharyngeal ridges *lph* have been injected by the internal marginal lacuna and the water ring by the sand canal. Size. 6 d.

3. Madreporic plate seen from its internal surface; *pg*, genital pore; *o*, orifice where the aquifer pores open and the water tube and the annex canal come to open; *cr*, madreporic cavity. Size. 2 d.

4. Transverse section of the periesophageal double ring; the lacunar ring *av* has been injected only by the internal marginal lacuna. Size. 45 d.

5. Figure reconstituted with the aid of sections to show the annexes of the madreporite; *x*, tissue limiting the space *e* towards the rectum; *paq*, aquifer pores. Size. 15 d.

6. Ovoid gland opening longitudinally; *cc*, axial cord; *rm*, lacunar network that was visible without injection thanks to its opaque contents; *g*, excretory conduit of a genital gland; *ag*, genital pentagon. Size. 2 d.

7. Ameba with long pseudopods, living. Size. 460 d.

8. Ameba with long pseudopods fixed in 45 degrees alcohol and stained with hematoxylin. Size. 460 d.

9. *a*, ameboid muriform globule; *a'*, fixed by alcohol; *a''*, disaggregated. Size. 460 d.

10. *b*, ameboid globule with small grains; *b'*, *b''*, after the action of alcohol. Size. 460 d.

11. *c*, *c'*, mahogany-brown ameboid globule; *c''*, after the action of alcohol. Size. 460 d.

12. *d*, living ciliated globule of which the cilia, slightly visible have not been drawn; *d''*, the same immediately after the action of alcohol; *d'''*, after staining with hematoxylin. Size. 160.

Fig. 13. Vesicles of the tissue (x, fig. 5), filled with muriform amebae. Size. 125 d.

14. Vesicles of the same tissue, from where escape the ciliated globules that surround them. Size. 125 d.

15. Pigmented granulations distributed in all tissues of old individuals. Size. 460 d.

PLATE XX.

*Dorocidaris papillata.*

Fig. 1. Transverse section of the ovoid gland not far from the place where the processes detach; c, water tube, c', cavity of the gland; p, origin of the glandular process; g, peripheral tissue of the gland. Size. 35 d.

2. Section closer to the madreporic plate; same letters; e, sub-madreporic space. Size. 35 d.

3, 4, 5, 6, 7, 8. Sections or portions of sections still closer to the madreporic plate. One sees the processes form there and enlarge the sub-madreporic space e; section (7) shows the communication of the two canals, c, c', that mingle in section (8). In section (7), space e is limited by soft tissue x, and the apical extremity of the glandular process is indicated in dots. Size. 35 d.

9. Transverse section of the glandular process showing the canalicules that cross it. Size. 115 d.

10. Section of the apical extremity of the process showing a network of canalicules. Size. 115 d.

11. Portion of a section of the process next to the periphery; h, ciliated epithelium (the aspect of this epithelium is accounted for by the reasons given in the text, p. 281); l, longitudinal fibers (muscular?); d, lumena of the canalicules; i, nuclei of the amebae with long pseudopods; f conjunctive fascia cut transversely. Size. 460 d.

12. Portion of another section taken in the central part. Size. 460 d.

PLATE XXI.

*Dorocidaris capillata.*

Fig. 1. Transverse section of the ovoid gland in the middle region; c, water tube; c', cavity of the gland; q, peripheral canalicule; l, lacunae injected by the internal marginal lacuna. Size. 45 d.

2. Portion of a transverse section of the gland taken at the periphery; e, external epithelium; sp, spaces left by the dissolved spicules; gm, muriform globules; y, pigmented granulations; q, peripheral canalicules in which the external epithelium extends; the nuclei dissiminated in the conjunctive stroma belong to the ameba with long pseudopods. Size. 215 d.

3. Portion of a transverse section of the gland taken at the internal periphery; e, internal epithelium; i, ameba with long pseudopods; q, lumen of a peripheral canalicule. Size. 460 d.

Fig. 4. Section of a sinus *c'* of the intra-glandular cavity. Size. 460 d.

5. Detail of the portion *x* of section (1); *i*, ameba with long pseudopods; *e*, epithelium of the intra-glandular cavity. Size. 460 d.

6. Section in a clot of perivisceral fluid; *i*, ameba with long pseudopods; *gv*, ciliated globules; *gm*, muriform globule; *gm'* is probably a brown ameba modified by the reagents. Size. 460 d.

7. Portion of a section in the soft tissue (*x*) that borders the madreporic cavity (pl. XIX, fig. 5) in order to show the aspect produced by a mass of ciliated globules after the action of the reagents. Size. 460 d.

8. Detail of section (10, pl. XX) in order to show the termination of the canalicules *d* of the glandular process.

#### PLATE XXII.

##### *Strongylocentrotus lividus.*

Fig. 1. Longitudinal section of a genital bud (*Strg. lividus* of 6 mm); *g*, genital bud; *v*, nucleiform cell; *pg*, genital pore in process of forming in the corresponding plate; *r*, organic network of this plate; *ng*, nerve ring; *ag*, membrane of the genital pentagon; *h*, space found between the latter and the test. Size. 460 d.

2, 3, 4, 5, 6, 7, 8. Successive sections normal to the madreporic plate of *Strg. lividus* (3 mm). *M*, madreporic plate; *c*, water tube; *ov*, ovoid gland; *ov'*, apical extremity of gland; *e*, sub-madreporic space; *g*, original genital bud; *v*, nucleiform cells; *p*, water pores; *mo*, mesenteric lamella connecting the ovoid gland to the esophagus. Size 460 d for sections 3, 4, 7; 115 d for sections 2, 5, 6, 8.

9. Apical rosette of *Strg. lividus* (3 mm) seen from the internal surface on which are represented schematically the original bud *g* and the five radial buds 1, 2, 3, 4, 5 that arise when the urchin reaches a size of 4-6 mm. Line \*\* indicates the direction of the sections represented previously.

10. Section of the genital pore of an adult *E. acutus*. *G*, genital plate; *dg*, excretory canal of the gland; *ng*, nerve ring, *pg*, pore; *m*, genital papilla. Size. 25 d.

11. Detail of the preceding section to show the nerve ring *ng*; *l*, lacunae of the genital pentagon. Size. 265 d.

#### PLATE XXIII..

##### *Dorocidaris papillata.*

Fig. 1. Fertilized egg. Size. 107 d.

2, 3, 4, 5. Successive stages of segmentation. Size. 107 d.

6. Blastosphere; *c*, segmentation cavity seen by transparency. Size. 107 d.

7. Free blastosphere presenting a flattening of the site where the

invagination goes; *m*, first mesodermal cells (seen in imaginary section). Size. 215 d.

Fig. 8. Imaginary section of a gastrula of four days; *a*, blastopore; *e*, ectoderm, *i*, endoderm; *m*, mesodermal cells. Size. 215 d.

9. Imaginary section of a larva of six days. Same letters *v*, diverticula destined to form the vaso-peritoneal vesicles. Size. 215 d.

10. Imaginary section of a larva of eight days; *vi*, right vaso-peritoneal vesicle; *vg*, left vesicle; *t*, larval intestine; *i*, spicules of the forming posterior arms. Size. 107 d.

11. The same larva seen from the ventral face; *b*, depression of the ectoderm where the mouth will open. Size. 107 d.

12. The same larva seen from its right side; *V*, ventral surface, *D*, dorsal surface; *Lo*, oral lobe; *La*, anal lobe. Size. 107 d.

13. Pluteus of ten days; *a*, blastopore that will become the anus; *f*, esophagus; *d*, stomach, *g*, intestine. Size. 107 d.

#### PLATE XXIV.

##### *Dorocidaris papillata.*

Fig. 1. Pluteus of fourteen days; *b*, mouth; *a*, anus; *f*, esophagus; *d*, stomach; *g*, intestine; *vd*, right vesicle; *vg*, left vesicle; *l*, posterior arms; *2*, spicules of the anterior arms. Size. 115 d.

2. Dorsal surface of a pluteus of fifteen days; same letters. *pd*, dorsal pore. Size. 115 d.

3. Pluteus of thirty days; *2*, anterior arms; *m*, mesodermal cells. One sees on the esophagus the striations produced by the circular contractile fibers. Size. 115 d.

4. The same seen from three-fourths; *Lo*, oral lobe; *La*, anal lobe.

5. Left section of the dorsal surface of a pluteus of thirty-five days; *3*, mamelon indicating the origin of an anterior-lateral arm; appearance of the corresponding spicule; *pd*, dorsal pore. Size. 115 d.

6.  $\alpha$  Section ( $\alpha$ , fig. 10); same letters as preceding. Size. 115 d.

7.  $\beta$  Section ( $\beta$ , fig. 10); *e*, ectoderm; *Lo*, oral lobe; *La*, anal lobe; the other letters as preceding. Size. 115 d.

8.  $\gamma$  Section ( $\gamma$ , fig. 10); same letters; *m*, mesodermal cells. Size. 115 d.

9.  $\delta$  Section ( $\delta$ , fig. 10); same letters. Size. 115 d.

10.  $\omega$  Longitudinal section following the plane of symmetry of the pluteus ( $\omega$ , fig. 8); same letters. Size. 115 d.

11. Two living mesodermal cells. Size. 385 d.

12. Two mahogany-brown amebae of the pluteus. These are those that produce the spots of the larvae. Size. 385 d.



## PLATE XXV.

*Dorocidaris papillata.*

Fig. 1. Pluteus of two months; 1, posterior arms; 2, anterior arms; 3, antero-lateral arms; *q*, spicule forming at the summit of the cupola; *pd*, dorsal pore. Size. 57 d.

2. Pluteus of three months seen from the dorsal surface; same letters as preceding; 4, spicules of the antero-internal arms merging in *k*; *l''*, *l'''*, lobes of the ciliary fringe. Size. 115 d.

3. The same reversed, the mouth below, in order to show the lobes *l*, *l'*, *l''*. Size. 65 d.

4, 6. Forming spicules enveloped by globular mesodermal cells. Size. 115 d.

5. Fragment of a spicule of the posterior arm showing two ramifications in the process of growing. Size. 115 d.

7. Extremity of a lattice-like spicule. Size. 870 d.

8. Monstrous pluteus of *Dorocidaris* of thirty-six days; *x*, supplementary arms. Size. 57 d.

9. Monstrous pluteus of *Dorocidaris* of thirty-six days; *sp*, unpaired supplementary arm characteristic of larvae of spatangids. Size. 57 d.

## PLATE XXVI.

*Spatangus purpureus*

*Letters common to all the figures of this plate.*

*M*, madreporite.

*am*, right sub-apical calcareous plate or madreporite apophysis.

*pl*, left sub-apical plate.

*pa*, water pores.

*pg*, genital pores.

*ov*, ovoid gland.

*p*, glandular process.

*sp*, spongy tissue.

*c'*, annex canal.

*c*, water tube.

*e*, sub-madreporic space.

*lg*, lacunar network destined for the genital glands.

*l*, lacunar network sunken into the walls of the ovoid gland.

*mg*, membrane that connects the four genital glands.

*d*, fragment of the diverticulum.

*oe*, fragment of the buccal extremity the esophagus.

*va*, ramified water canal.

*cg*, glandular canal.

*av*, lacunar ring belonging to the visceral lacunar system.

*lr*, radial lacunae.

*vi*, branch coming from the marginal internal lacuna (communicating branch of Hoffmann).

*va'*, undulating canal.

*aa'*, ambulacral ring.

*aq'*, ambulacral vessels.

Fig. 1. Apical pole of *Spt. purpureus* seen from the internal surface; the membrane *mg*, which binds the genital glands, has been cut in order to show the sub-apical plates. Size. 1.5 d.

2. This preparation differs from the preceding in that the membrane *mg* has been kept in place and the ovoid gland turned up.

3. Scheme showing in *Spt. purpureus* the annexes of the madreporite, the central part of the visceral lacunar system and the separation of the two parts of the so-called water system in the regular urchins. The peribuccal rings have been pressed down towards the top of the plate around *xy*;  $\gamma$ , region in which the glandular canal exists alone.

4, 5. Left and right parts of the peribuccal rings, injected. Size. 2 d.

6. Following section ( $\alpha$ , fig. 16). Size. 6 d.

7. Following section ( $\beta$ , fig. 16). Size. 6 d.

8. Transverse section passing by the extremity of the madreporic apophysis. Size. 6 d.

9. Following section ( $\delta$ , fig. 1); *g*, commencement of the tissue of the ovoid gland. Size. 25 d.

10. Portion of a transverse section in the apical region of the ovoid gland in order to show the water tube *c*. Size. 25 d.

11. Portion of a section nearer the adoral extremity of the gland; the water tube *c* is transformed into a ramified canal *va*. Size. 25 d.

12. Transverse section of the ovoid gland in the region where the properly-called water tube is entirely replaced by the ramified water canal *va*; *c*, cavity of the gland.

13. Section of the so-called sand canal of the authors, following ( $\gamma$ , fig. 3).

*Note.* -- Sections 10, 11, 12, 13 have been made on pieces previously injected by the internal marginal lacuna.

14. Part of a transverse section taken right next to the extremity of the madreporic apophysis in order to show the two canals *c*, *c'*. Size. 65 d.

15. Detail of section (8); the two canals *c*, *c'* communicate. Size. 65 d.

16. Sub-apical calcareous layers. Size. 1 d.

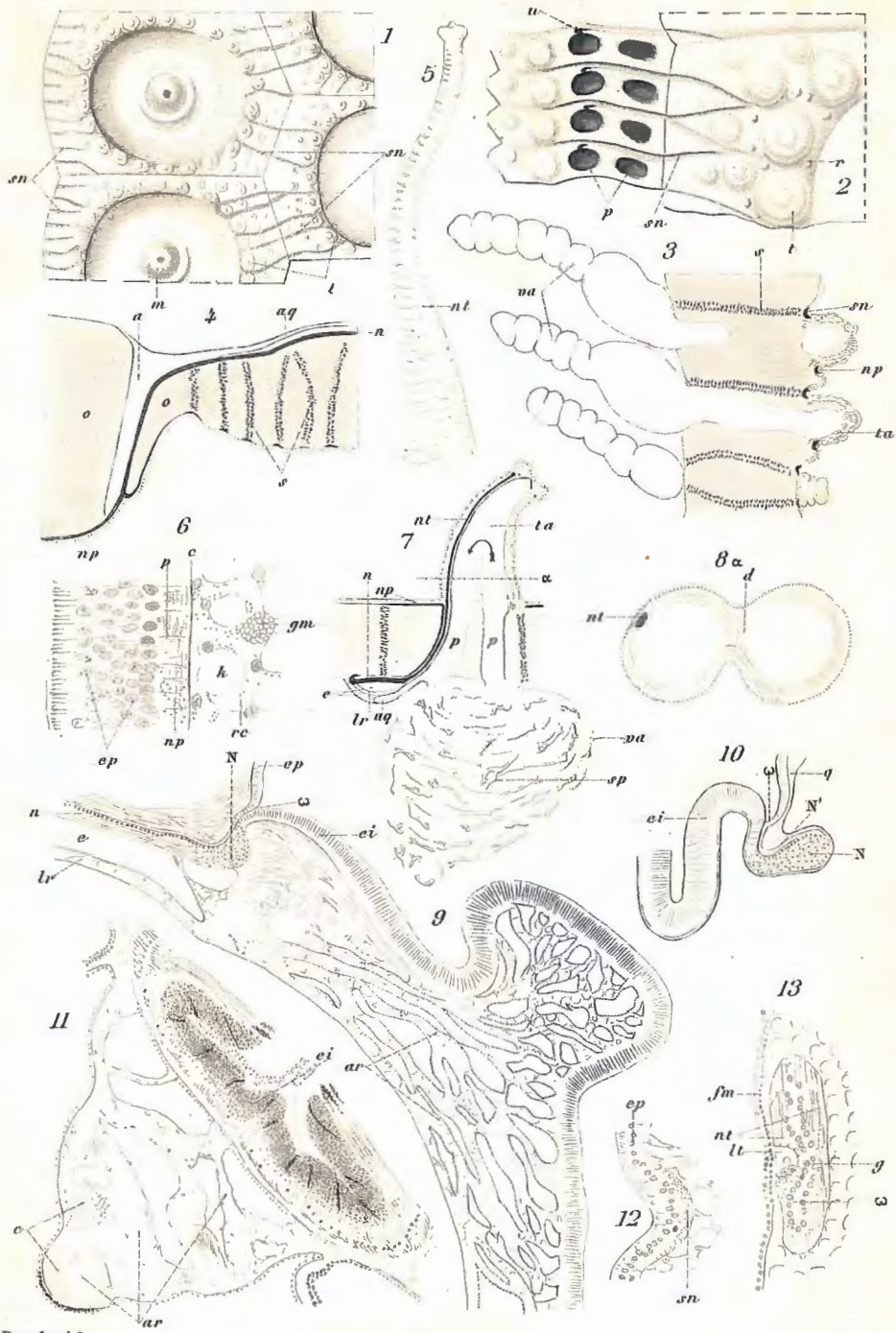
17. Scheme of the madreporic annexes, central parts of the visceral lacunar system and water system in *Dorocidaris*; *aa*, water ring; *aq*, water vessels; *lph*, pharyngeal lacunae.



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Dujour. sc.

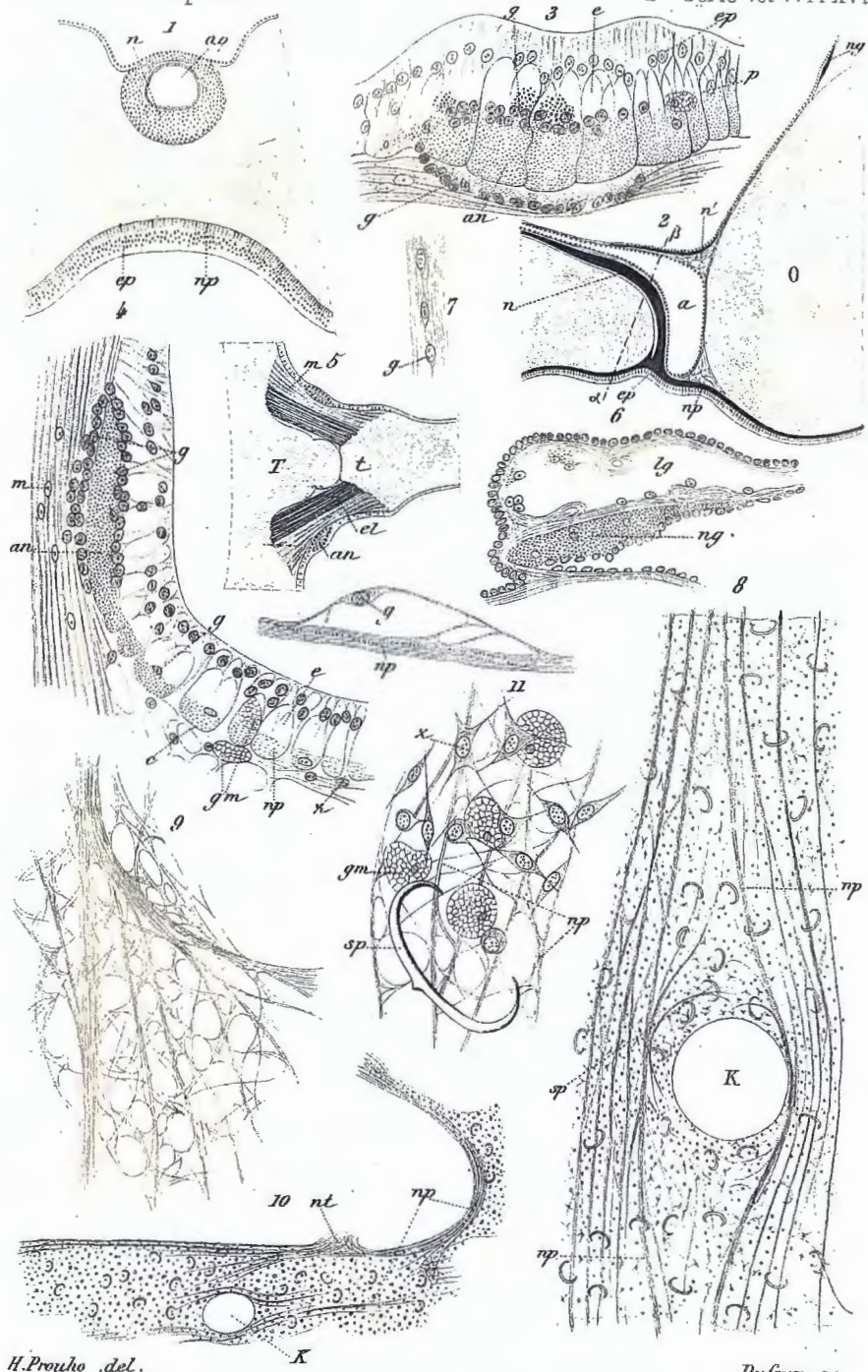
DOROCIDARIS PAPILLATA



H. Prouho del.

Himly sc.

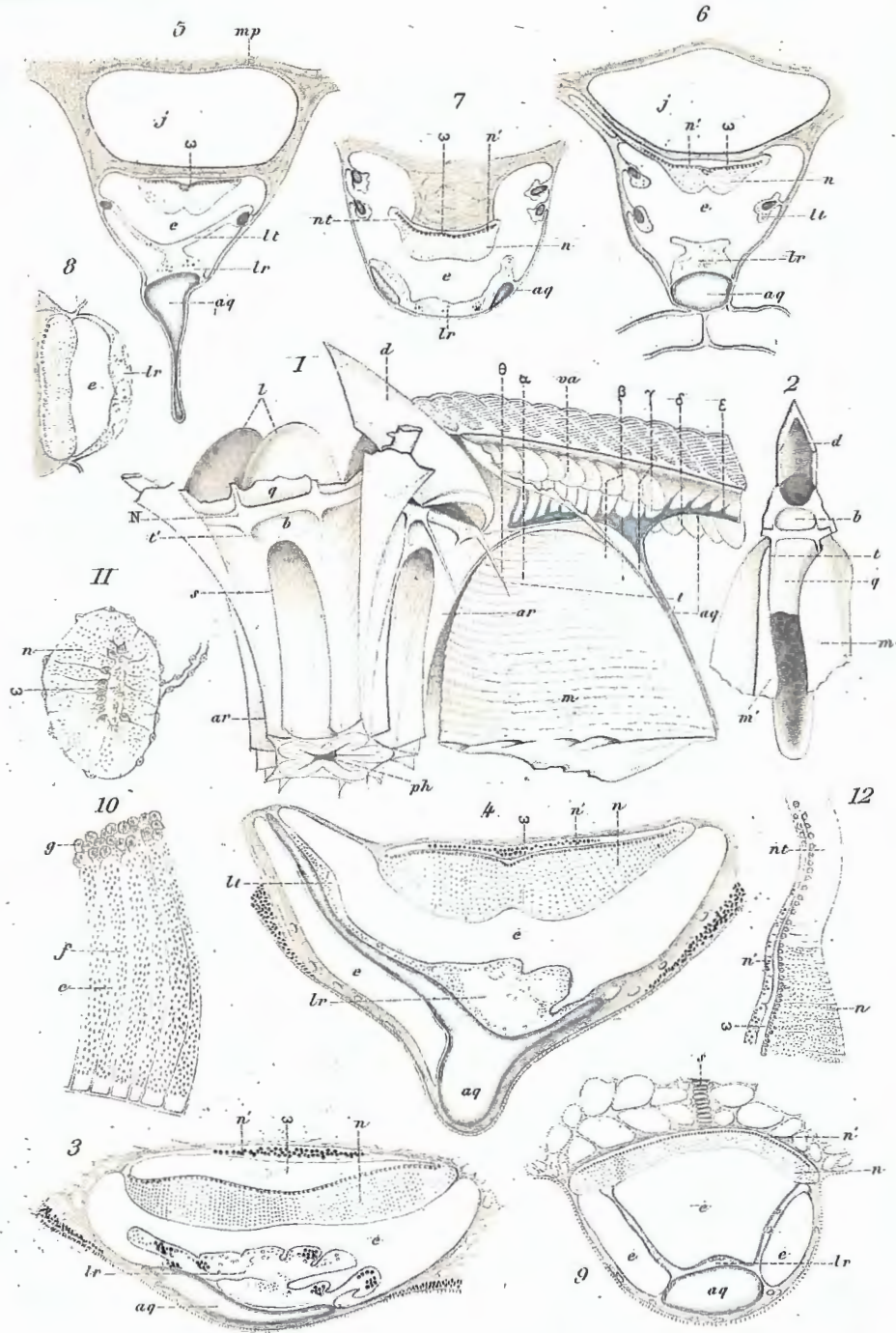
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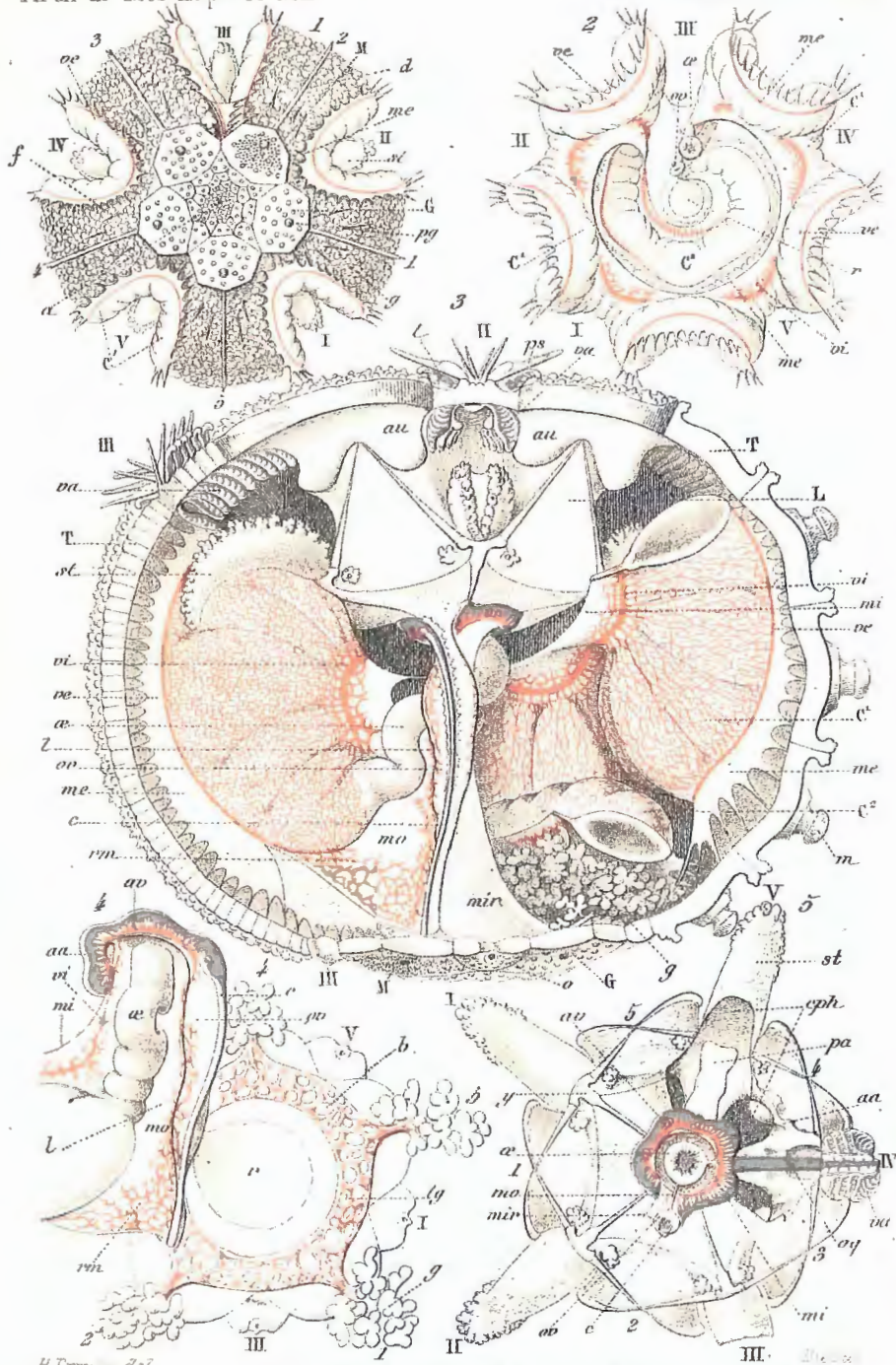
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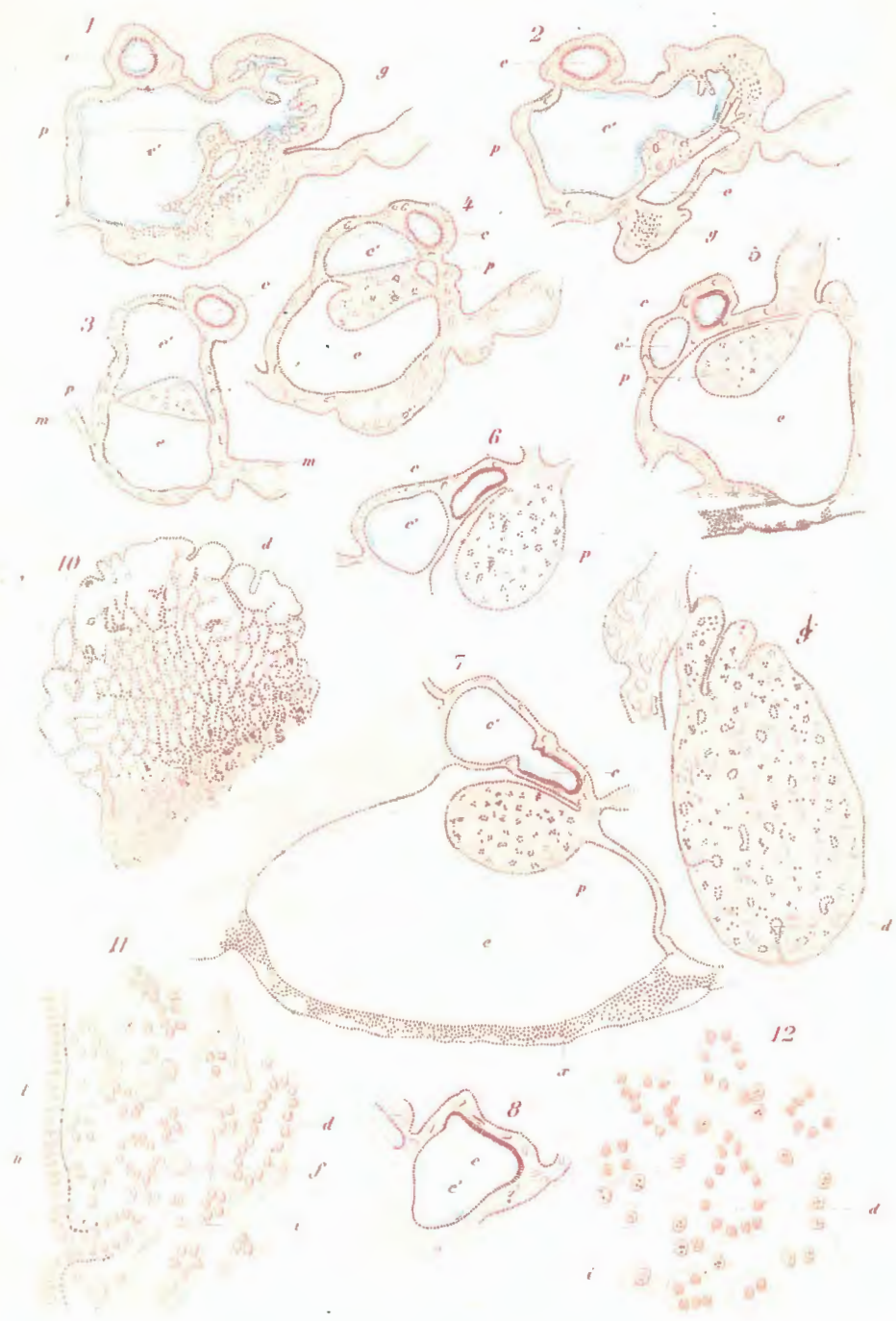
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DOROCIDARIS PAPILLATA



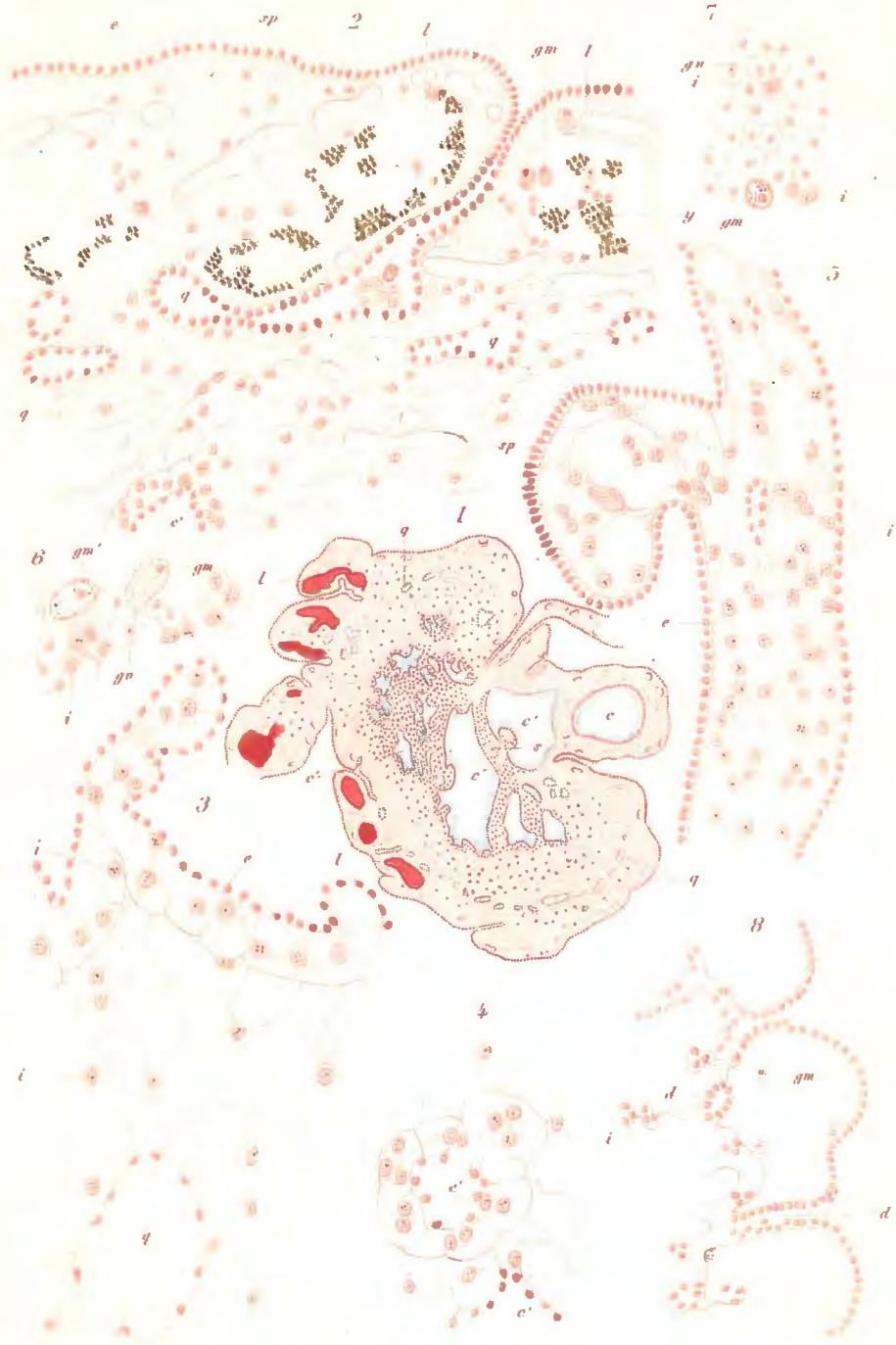




Il Vostro del

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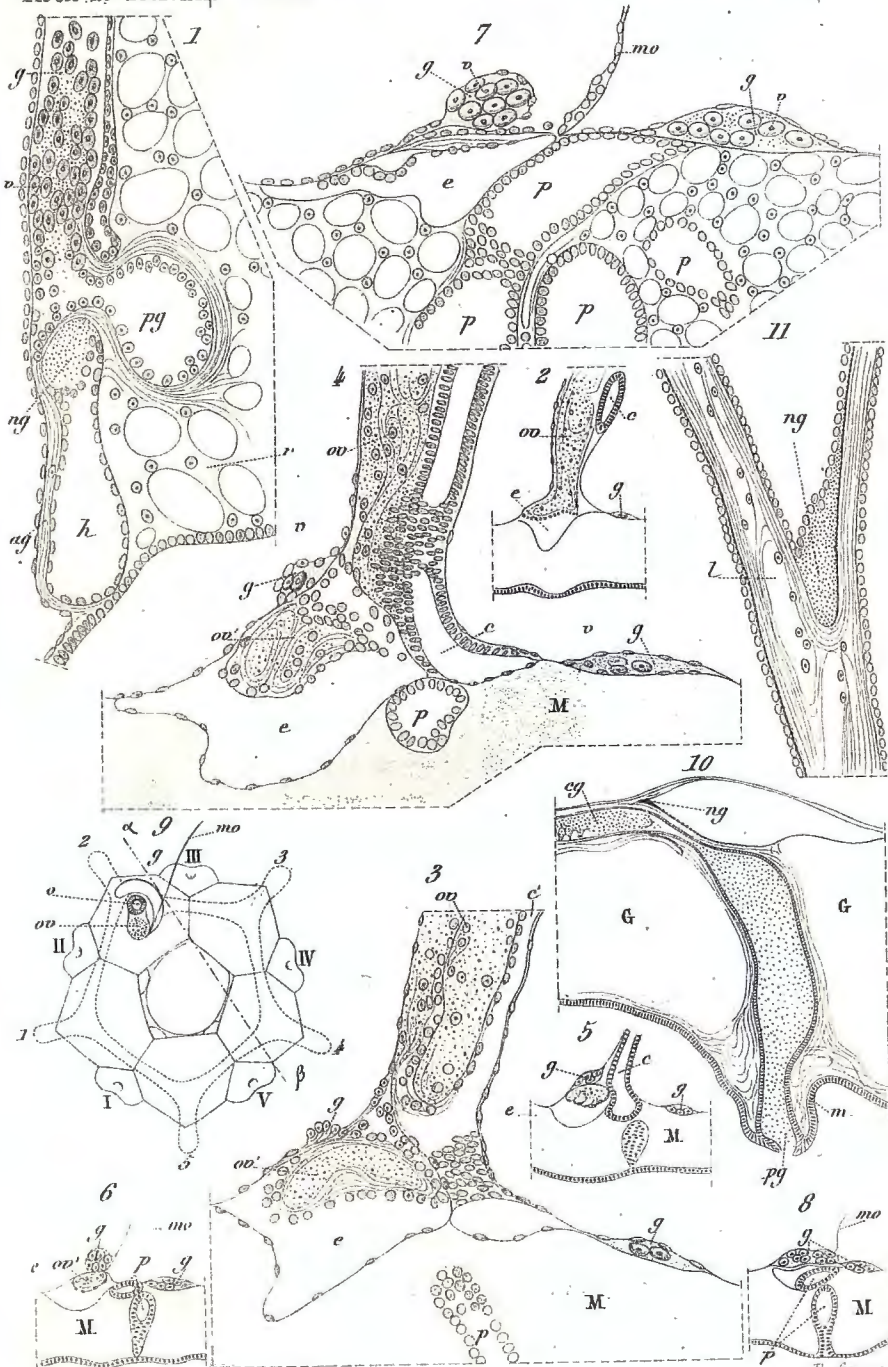
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Pierre sc.

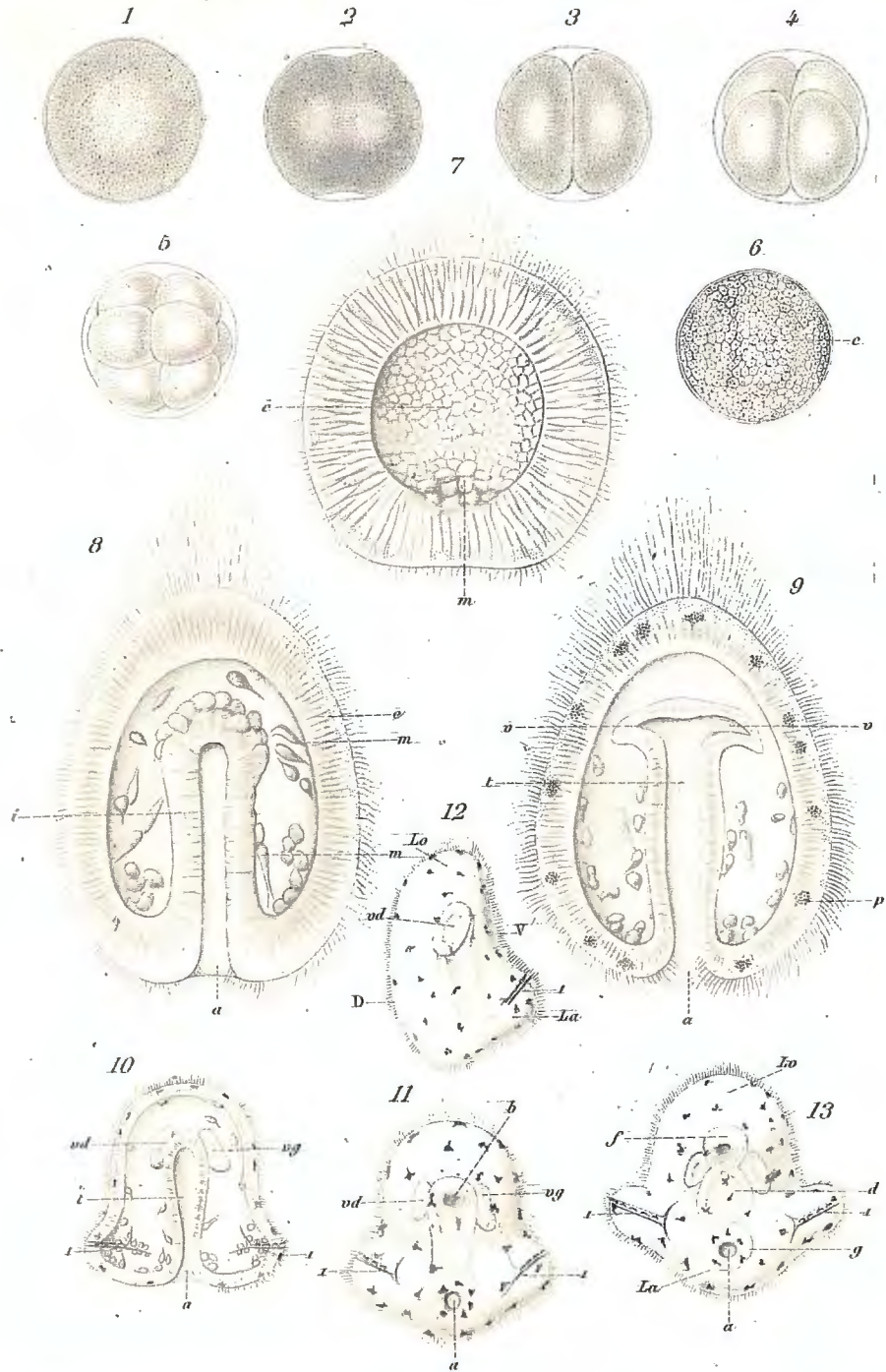
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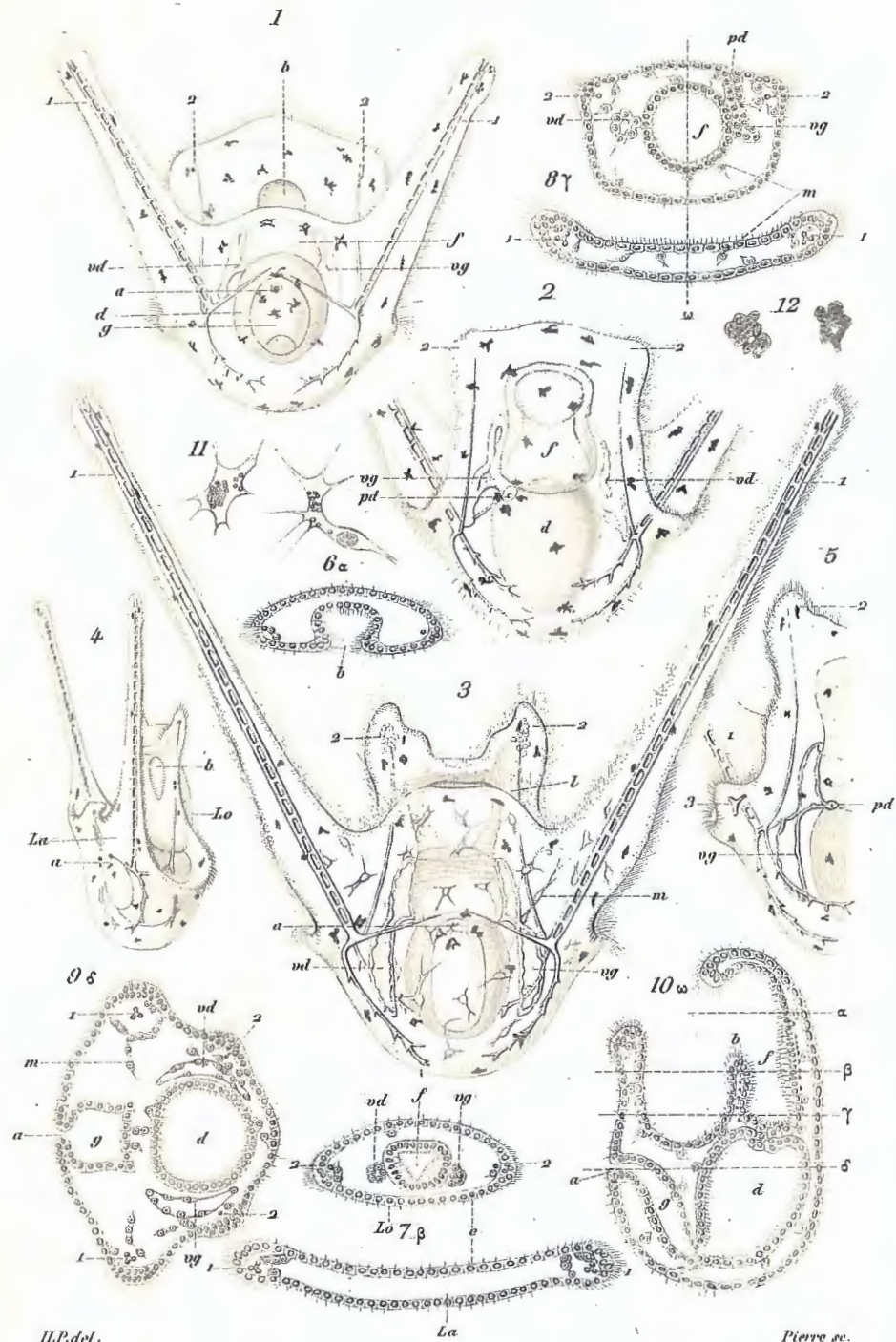
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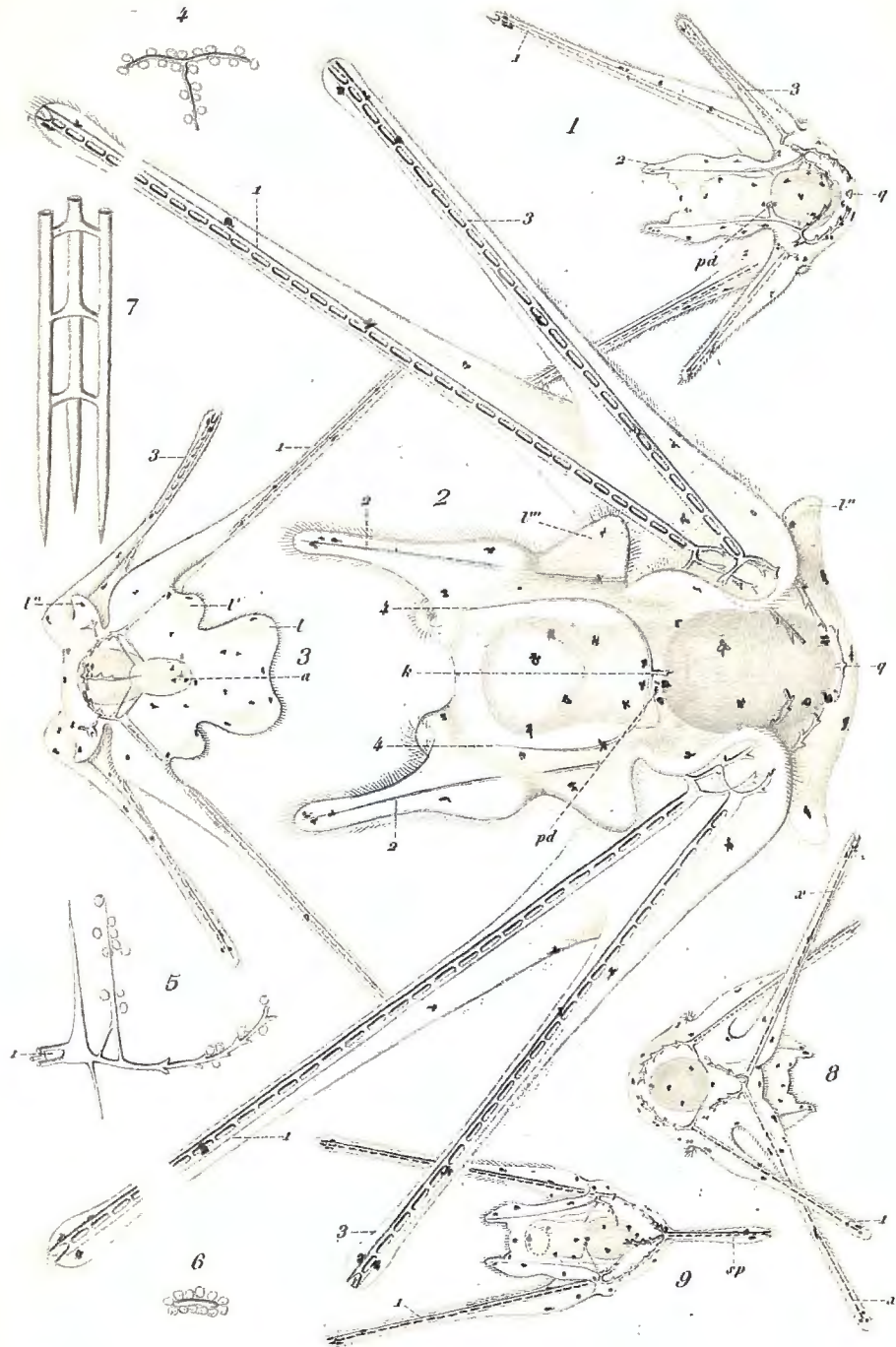
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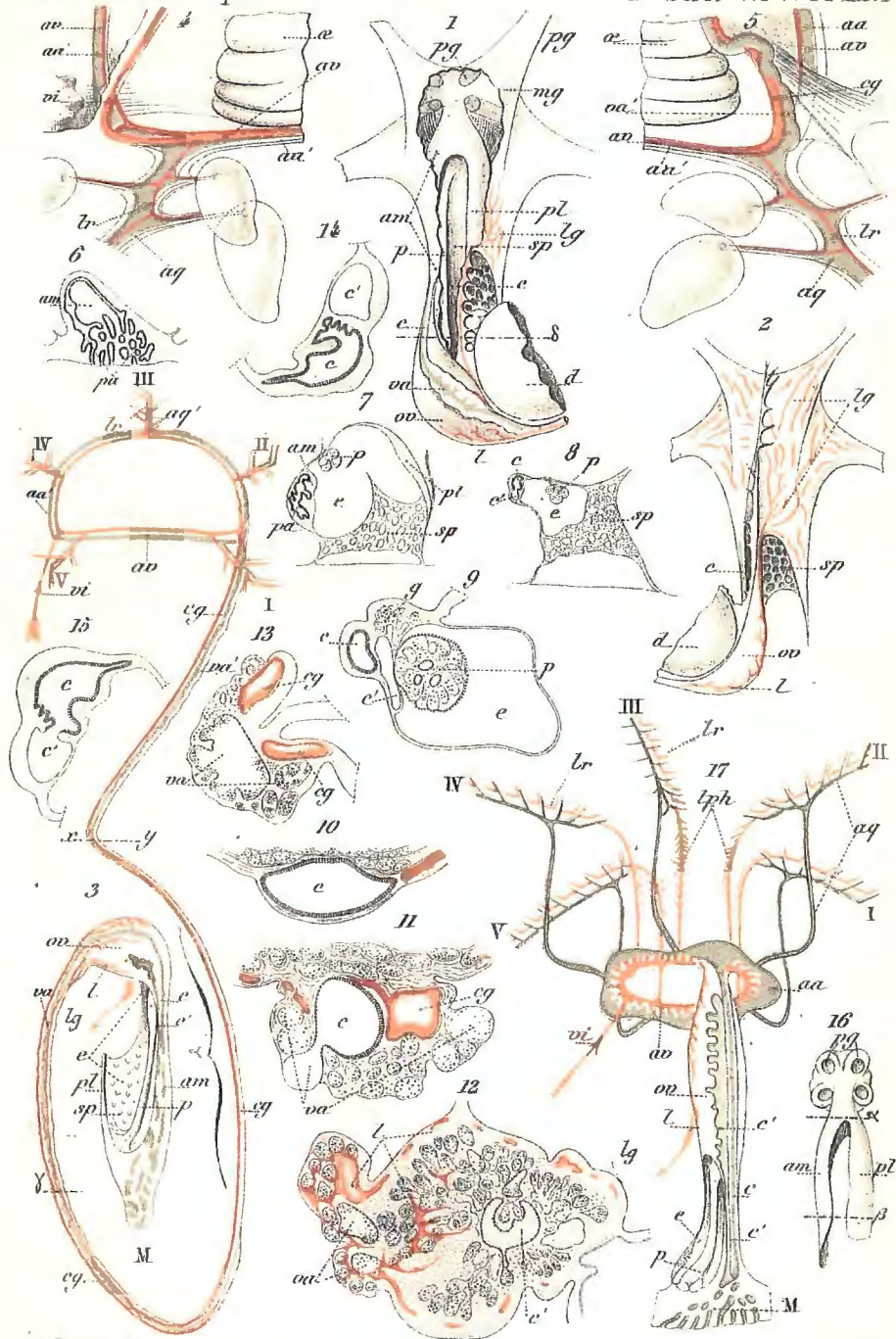
DOROCIDARIS PÄPILLATA



H.P. del.

Pierre sc.

DOROCIDARIS PAPILLATA



SPATANGUS PURPUREUS

Dufour sc.