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**Investigations on the Echinoids of the Coasts of Provence: A
Translation of *Recherches sur les Echinides des Cotes de
Provence***

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John Lawrence

ANNALES
DU MUSÉE D'HISTOIRE NATURELLE DE MARSEILLE. — ZOOLOGIE
Tome I^{er}

MÉMOIRE N° 3

RECHERCHES
SUR LES
ECHINIDES DES COTES DE PROVENCE

PAR
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DU MUSÉE D'HISTOIRE NATURELLE DE MARSEILLE. — ZOOLOGIE

Volume 1

Memoir No. 3

INVESTIGATIONS
ON THE
ECHINOIDS OF THE COASTS OF PROVENCE

BY

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MARSEILLE
TYPOGRAPHIE ET LITHOGRAPHIE CAYER ET C^{ie}
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This translation is dedicated to my good friend and colleague for many years,

Professor Michel Jangoux

of the Université Libre de Bruxelles

John Lawrence, Michel Jangoux

Bruxelles, 1989

Réne Koehler

Jean Baptiste François René Kœhler was born 7 March 1860 in Saint-Dié and died 19 April 1931 in Lyon. He defended theses in both natural sciences and in medicine at Nancy in 1883. He entered the faculty of sciences at Nancy a *préparateur* in zoology and then at Lyon in 1889. He was named to the chair of zoology at Lyon in 1894. Koehler participated in excursions of the *Princesse Alice* with Prince Albert of Monaco. Koehler was a specialist in echinoderms but also worked with isopods. He was president of the Zoological Society of France in 1911. He became an Officer of the Legion of Honor in 1923. His extensive collection of echinoderms and his library are in the Collections de Zoologie, part of the Collections Patrimoniales Universitaires of the Université Claude Bernard (Lyon).

Much of the work for his thesis in natural sciences was done at the Station Endoume in Marseille. The station was still new, having been founded in 1869. Antoine-Fortuné Marion, director of the station, founded the *Annales du Musée d'Histoires Naturelles de Marseille* in 1883. Koehler's memoir appeared in the series that year.

The memoir is in three parts. The first part concerns the anatomy of echinoids and considers all the major systems. The second part concerns the echinoid species found on the coast of Provence, with a description of their anatomy, habitat and distribution. The third part is a short addendum with limited observations on early development of hybrids.

Translator's note:

I have been consistent with following Koehler's memoir, including whether or not a species name is italicized or diacritical marks are given or misspelled. I have retained the species names and authors used by Koehler. Because some of the names have changed, the present names of all species are given here. He still spelled his last name as Khler in 1883.

Species' names used by Koehler	Species' names at present
<i>Dorocidaris papillata</i> A. Ag.	<i>Cidaris cidaris</i> (Linnaeus)
<i>Arbacia pustulosa</i> Leske	<i>Arbacia lixula</i> (Linnaeus)
<i>Centrostephanus longispinus</i> Peters	<i>Centrostephanus longispinus</i> (Philippi)
<i>Echinus melo</i> Lam.	<i>Echinus melo</i> Lamarck
<i>Echinus acutus</i> Lam.	<i>Gracilechinus acutus</i> (Lamarck)
<i>Psammechinus microtuberculatus</i> Ag.	<i>Psammechinus microtuberculatus</i> (Blainville)
<i>Strongylocentrotus lividus</i> Brandt	<i>Paracentrotus lividus</i> (Lamarck)
<i>Sph��rechinus granularis</i> A. Ag.	<i>Sphaerechinus granularis</i> (Lamarck)
<i>Echinocyamus pusillus</i> Gray	<i>Echinocyamus pusillus</i> (O.F. M��ller)
<i>Spatangus purpureus</i> Muller	<i>Spatangus purpureus</i> O.F. M��ller
<i>Echinocardium flavescens</i>	<i>Echinocardium flavescens</i> (O.F. M��ller)
<i>Echinocardium cordatum</i> Gray	<i>Echinocardium cordatum</i> (Pennant)
<i>Echinocardium mediterraneum</i> Gray	<i>Echinocardium mediterraneum</i> (Forbes)
<i>Schizaster canaliferus</i> L. Ag. and Desor	<i>Ova canliferus</i> (Lamarck)
<i>Brissopsis lyrifera</i> Ag. and Desor	<i>Brissus lyrifera</i> (Forbes)
<i>Brissus unicolor</i> Klein	<i>Brissus unicolor</i> (Leske)

Pagination in the memoir is given in bold, e.g. **12**.

INVESTIGATIONS

ON THE

ECHINOIDS OF THE COASTS OF PROVENCE

INTRODUCTION AND HISTORY

The goal that I proposed to myself in beginning this work was to make as complete a study as possible of the different systems that constitute the internal anatomy of the irregular urchins living on the coast of Provence. The works published on this subject are, in fact, very few and the two most recent studies by Hoffmann and Teuscher address, moreover, only the single genus *Spatangus*. They also are contradictory regarding a large number of points, particularly on all that was reported about the circulatory system. For that reason it appeared necessary to return to this study anew. The internal anatomy of the regular urchins, which had been the object of more extensive and much more numerous works, seemed to me more advanced and known in a satisfactory fashion, especially after the research of Perrier on the circulatory system. Until then it was described in a very incomplete and vague fashion and often the subject of debate. After having finished the study of the spatangoids, I was led to occupy myself with the anatomy of regular urchins by the difficulty that I encountered in comparing the circulatory system of spatangoids with that of urchins. Moreover, the research of Teuscher published in 1876 did not agree in certain points with those of 6 Perrier. The histology of certain organs, the digestive tube and the tube feet, for example, required new investigations.

The coasts of Provence offered me in addition very rich material for study that I was fully able to take advantage of thanks to the generous hospitality I received at the Laboratory of Higher Studies of the Faculty of Sciences of Marseille. The regular urchins are, in fact, represented in the Gulf of Marseille by seven species, of which four are always found in very great abundance (*Echinus acutus*, *Strongylocentrotus lividus*, *Sphærechinus granularis* and *Psammechinus microtuberculatus*). The three other species (*Echinus melo*, *Dorocidaris papillata* and *Arbacia pustulosa*) are much rarer. The spatangoids are represented there by seven species belonging to the five genera *Spatangus*, *Echinocardium*, *Schizaster*, *Brissus* and *Brissopsis*. *Spatangus* and *Ech. flavescens* are very common; the other species are in contrast very rare. But, thanks to those specimens preserved in alcohol placed at my disposition by M. Marion, I have been able to study the anatomy of these latter three genera. As to the class of clypeasteroids, they are represented in the Gulf only

by *Echinocyamus pusillus*. The very small size of this species does not lend itself to anatomical investigations and I have completely set aside its study.

The most important knowledge we have on the anatomy of echinoids, especially on spatangoids, is not very old. Until 1870 there was still little information about this group although we had the old works of Monro, Tiedemann, Delle Chiaje, and the more recent works of Milne Edwards, Krohn, Valentin and J. Muller. The most important works on echinoids were particularly those of zoology and paleontological zoology. The paleontologists are presented, in fact, with fossil echinoids that abound in the earth and whose remains are in a quite remarkable state of preservation. The result of these investigations, accompanied most frequently with analogous observations on living animals, has been to make the external morphology of these beings known in a very detailed manner. One has a very complete knowledge of the studied types about the test, but in reality the internal anatomy of various echinoids still remains very obscure.

Nevertheless these investigations of paleontological zoology have given very important information on the path that this type has followed in its differentiation. They show us the ancient echinoids of the primitive earth (*Palaechini*) that by their obscure characters that approach the cystoids, acquire little by little the characters of echinoid types that begin with cidaroid forms. They differentiate then in a manner to offer a multiplicity of types unknown in the present. Several are very interesting because they fill the gaps that seem to exist if we examine only living forms. It is thus that we know all the intermediary types between the regulars and irregulars that are so different in our time. We can follow step by step the irregularity of the echinoid organism that began by this curious migration of the anus and which, in fossil genera, is shown in all its phases. It is possible to suppose that, according to the measure of irregularity attained, the various anatomical systems whose equilibrium was strongly disturbed have shown considerable modifications made necessary by the great changes related to the arrangement of the plates of the test. We can recognize traces of these in living spatangoids.

A comparative and very detailed study on the plates of the tests of living and fossil echinoids allowed Lovén¹ (1872-1874) to establish their morphology in a definitive fashion, to find numerous points of relation of the various plates between regulars and irregulars, and to show, in living urchins, evident traces, although transitory, of the relationship of echinoids with crinoids.

Important discoveries since Lovén's work resulted from dredges in the deep sea. They have allowed the study of certain interesting types, sometimes with a strange and supposedly extinct form. They were able to be used by Lovén, and thus complete the beautiful series of studies of the Swedish scholar.

We can thus say present knowledge of the test of echinoids studied in living animals and fossils is as complete as possible. This study, because of its scientific importance, is not the least interesting to us in echinoderms. It is a question that I must however lay aside because it is completely outside my subject. When I shall study the test in echinoids, I shall

¹LOVEN. *Etudes sur les Echinoïdes*. Kong. Svenska Vetenskaps-Akademiens Handlingar. Bd 11, n° 7. Stockholm.

occupy myself exclusively only with the external appendages. Their study has some interest from the anatomical and zoological points of view. I shall also lay aside all morphological discussion that, only addressing facts already known, will not find its place here.

I shall content myself with very rapidly reviewing the principal works published on the anatomy of echinoids. These works will be analyzed in the different chapters of this work. After that I shall occupy myself with these questions. This will allow me to consider them later rather than summarize them at this time.

8 As I just said, our knowledge of the anatomy of echinoids is very recent. The old works of Meckel² (1821-1823), Tiedemann³ (1816), Delle Chiaje⁴ (1823-1829) include however many interesting facts about the questions that concern us, principally on the anatomy of the ordinary urchin. A little later appeared the Règne animal of Cuvier the volume on Zoophytes that contains several plates on the anatomy of echinoderms by H. Milne-Edwards, and especially a plate on the anatomy of spatangoids. It shows the path and relations of the principal vessels as well as the communication of the vessels of the intestine with the peribuccal vascular ring, an arrangement of very great importance. The description of the circulatory system of spatangoids was given later by H. Milne Edwards in the third volume of the *Leçons d'Anatomie et de Physiologie comparées*.

In 1841 appeared the very important memoir of Krohn on the nervous system of echinoderms⁵, where the arrangements of this system in the different classes of the group are described with care. Krohn was the first to dissect the nervous system of echinoids and gave an excellent description accompanied by accurate figures. And although Tiedemann had glimpsed most of the arrangements described by Krohn, all the merit of their discovery belongs to the latter because the information Tiedemann gave us on this subject represented speculative views.

The important monograph on the genus *Echinus* by Valentin⁶ appeared the same year. It contains very accurate descriptions of the digestive tube, the nervous system, the gonads, and external organs. Unfortunately the research of Valentin concerning the circulatory system leaves much to be desired. The very difficult study of the circulatory system had scarcely been begun by his predecessors and, moreover, still remained for a long time —

²MEKEL *System der vergleichende Anatomie*. Halle

³TIDEMANN. *Anatomie der Rohren-Holothurie, des pommeranzfarbnen See-Sterns und des Stein-Seeigel*. Landshut 1816.

⁴DELLE CHIAJE. *Memorie sulla storia e notomia degli animali senza vertebre del regno di Napoli* (1823-1829).

⁵KROHN. *Über die Anordnung des Nervensystems der Echiniden und Holothurien im Allgemeinen*. Archiv für Anat. und Physiol. 1841.

⁶VALENTIN. *Anatomie au genre Echinus*. Neuchatel, 1841.

until 1875 — very obscure.

J. Müller, from 1848 to 1855, published a series of memoirs containing research on the entire group of echinoderms. Among them, his magnificent works on the embryology of these organisms is most important. The other 9 memoirs treating the anatomy of echinoderms, such as: *Anatomische studien über die Echinodermen* (1850), *Über die Semitæ der Spatangoïden* (1853) *Über den Bau der Echinodermen* (1853) give us important information on certain aspects of the anatomy of echinoids. But they add little to our knowledge of others, the circulatory system and the anatomy of *Spatangus*, for example.

Despite these works, there still remain many facts to discover, many obscure points to clarify. The histological study of the different groups was scarcely sketched; the circulatory system was little known. It is necessary for us to go up to 1871, the time of Hoffmann's⁷ research to find a work where the different anatomical systems as well as the appendages of the test of urchins and spatangoids were studied from the descriptive as well as the histological points of view. I very often shall have the occasion to cite the work of Hoffmann.

A memoir of Baudelot⁸ published in 1872 contains a very interesting and scholarly discussion of the opinions published until then on the nervous system of echinoderms, whose existence seemed doubtful to a certain number of observers. Baudelot compares and discusses all the known facts, and adds the results of his own research on the anatomy, physiology, and histology of the nerve trunks.

In 1874, Agassiz⁹ added to his *Revision of the Echini* a special volume summarizing the present state of the science on the modifications of the test and its appendages, and on the internal anatomy and embryology of regular and irregular urchins. This memoir, in addition to the presentation of facts already known, contains the research of Agassiz on various points of anatomy, the circulatory system of regular urchins for example, and embryology.

The following year appeared the important memoir of Perrier on the circulatory system of urchins¹⁰ where we find, in addition, a study of the relation of this system with the various functions of the animal and the explanation of the role, until then very obscure, of a peculiar canal annexed to the digestive tube, the intestinal siphon. The work of Perrier

⁷HOFFMANN. *Zur Anatomie der Echiniden und Spatangen*. Archiv für Zoologie. Bd I, 1871.

⁸BAUDELLOT. *Etudes générales sur le système nerveux*. Archives de zool. Exper. T. I, 1882.

⁹AGASSIZ. *Revision of the Echini*. Illust. Catalogue of the museum of Comparative Zoology at Harv. College. Vol. VII, 1872-1874.

¹⁰PERRIER. *Recherches sur l'appareil circulatoire des Oursins*. Archiv. Zool. Exper. Vol.. IV, 1875.

contains numerous new results on the structure and role of the so-called heart, on the distribution of intestinal vessels, **10** etc., that I shall often recall when I concern myself with the circulatory system.

This memoir was followed in 1876 by a work of Teuscher¹¹, who dealt with the anatomy of the various classes of echinoderms and included in particular his research on the anatomy of spatangoids and the ordinary urchin. Teuscher was particularly concerned with the circulatory system. The state of his specimens preserved in alcohol prevented, moreover, any histological research and permitted him only very rarely to make injections. He, by preference, studied the circulatory apparatus by the aid of successive sections.

In 1876 also appeared the research of Frédéricq¹² on the anatomy and physiology of the nervous system of the urchin, which completes our knowledge about this system. The physiological research undertaken by Frédéricq establishes the role of various portions of the nervous system and confirms the previous views given by Baudelot on this subject.

Some other work that have not had as the object of the research the internal anatomy concern special questions. Among these, I shall cite the memoirs of Perrier¹³ on the pedicellariae and the ambulacra of asteroids and urchins (1869), where a large number of these appendages are described and illustrated; Stewart¹⁴ on the structure of certain organs of cidaroids (pedicellariae, spines, spicules of the tissues) (1871) and on the peculiar appendages of the masticatory apparatus of *Dorocidaris* (1877); Geddes¹⁵ on the perivisceral fluid of urchins (1880); Sladen¹⁶ on the structure of the gemmiform pedicellariae of *Sphærechinus* (1881); of Fættinger¹⁷ on the same question (1881); of

¹¹TEUSCHER. *Beiträge zur Anatomie der Echinodermen*. Jenaische Zeitsch. Fur Naturwissen. Bd X, 1876.

¹²FREDERICQ. *Contributions à l'étude des Echinides*. Archiv. Zool. Exper. Vol. V, 1876.

¹³PERRIER. *Recherches sur les pédicellaires et les ambulacres des Asééries et des Oursins*. Ann. Sc. Nat. 5^e série, vol. XII et XIII, 1869-1870.

¹⁴STEWART. *On the minute structure of Cidaridæ*, Quart. Journal microsc. Sc. 1871. – *On certain organs of Cidaridæ*. Linnean Society of London. 1877.

¹⁵GEDDES. *Observations sur le fluide périviscéral des Oursins*. Arch. Zool. Exp. Vol. VIII. 1879-1880.

¹⁶SLADEN. *On a remarkable form of Pedicellariæ*. Ann. Mag. of nat. history, 1871.

¹⁷FÆTTINGER. *Structure des Pédicellaires gemmiformes*. Archiv. De Biologie. Vol. II. 1881.

Geddes and Beddart¹⁸ on the histology of the pedicellariae and the muscles of the urchin (1881).

Thus setting aside the comparative study of the calcareous plates of echinoids, I shall study first the exterior appendages of the test, spines, tube feet, **11** pedicellariae, etc., that have a certain importance in classification and whose histological structure often offers some interesting points. I shall occupy myself then successively with the anatomical study of the digestive tube, the nervous system, gonads, and finally the circulatory system, taking care to recall, in regard to each question, the different works that have reported and analyzed them or discuss them as rapidly as possible. I shall try to compare in a last paragraph the arrangement that certain anatomical systems in regulars and irregulars offer us, particularly the circulatory system, and look for information that the study of these systems can give us on the general physiology of the urchin.

In the second part, I shall give a list of the echinoids of the coast of Provence, recalling the general and specific characters of these different types and adding the characters taken from the internal anatomy. I shall indicate, after the description of each species, the places around Marseille where they are most commonly found. The nature of the bottom where they live, as well as the depth to which they descend will also be indicated.

I shall finish by the relating some trials of hybridization, during the month of April 1882, between different species of echinoids reproductive at this season, i.e., between the genera *Dorocidaris*, *Psammechinus*, *Strongylocentrotus*, *Spærechinus*, and *Spatangus*.

But before beginning the presentation of my research, I have a duty to fulfill. It was at the Laboratory of Higher Studies attached to the Faculty of Marseille and directed by Professor Marion that this work was done. It was there that I found, at the same time as the most sympathetic and cordial welcome, the numerous material for study for which I am extremely obligated to M. Marion. During the entire duration of my visit to his laboratory, he has aided in my research and has always shown the greatest kindness. Permit me to address to him my sincerest thanks and express to him my deep appreciation for all that he has done for me since the day he very willingly accepted me among his students. If this present work has merit, it is necessary to attribute all entirely to the master who has guided me in the way that I had taken.

Thanks to the specimens I prepared in Marseille, but thanks especially to the specimens that the laboratory has sent me, I continued these studies during the months that I was not able to pass on the coast at the Zoological Laboratory of the Faculty of Sciences of Nancy, directed by Professor Friant. I shall never forget the numerous marks of affection that M. Friant has always lavished on me since the time when he taught me the first **12** elements of zoology. I am happy to thank him for the excellent advice and encouragement that he has never ceased to give me until this day, and to publicly express all my deepest appreciation and the respectful affection that I feel for him.

I must likewise address all my thanks to Joseph Armand, the chief fisher of the Marseille laboratory, whose zeal and devotion are well known to all those who have

¹⁸GEDDES AND BEDDART. *Sur l'Histologie des Pédicellaires et des muscles de l'Oursin*. Arch. Zool. Exp. 1882 and Trans. of the Royal Society of Edinburgh. 1881.

worked there. Thanks to his great knowledge of the gulf and especially to the willingness with which he put himself at my disposal for undertaking sometimes laborious fishing, I have been able to have at all times in very large numbers fresh individuals in excellent condition.

TEST AND ITS APPENDAGES

The test of regular and irregular urchins is covered externally with a very thick connective tissue layer, lined with an epithelium with cilia. This layer is composed of thin fibrils of connective tissue, very loose in the superficial regions, denser and tighter in the deeper part, closely adhering to the test plates. In the middle of these fibers are cells of connective tissue, very numerous cells capable of ameboid movement, and especially a quantity of red or yellow pigmented masses, more or less considerable and deep according to the color of the test. This layer continues on most of the organs, spines, pedicellariae, clavules and fascioles that make up the exterior appendages of the test.

Interiorly the test plates are covered by a very thin connective tissue layer, rich in pigment granules and covered with a ciliated epithelium. This layer is continuous with all the organs enclosed in the general cavity to which it forms an external envelope.

One always encounters in *Spatangus* or *Echinocardium* masses of black pigment adhering to the inner surface of the test and in which are distinguished small transparent vesicles filled with a glassy liquid that contains small, white, opaque masses. These masses are made by the joining of a large quantity of cysts resembling psorospermy. These bodies have been described in *Echinocardium cordatum* at Wimereux by Giard who thought they were the spores of a chytridin fungus.

The internal surface of the test in spatangoids shows calcareous appendages that do not exist in regulars and that make a sort of internal skeleton. These calcareous plaques, fused to the plates of the test, project into the general cavity and serve as attachment sites for the solid mesenterial laminae that connect between them the different circumvolutions of the digestive tube. One finds, in fact, immediately to the left of the buccal opening, a large concave calcareous plate, **14** tapering to a point at its posterior end and whose long axis is parallel to the longitudinal axis of the test (Pl. I, fig 5, *P*). It has two insertions with the two ventral mesenterial lamellae whose relations will be described later. At the apical pole are attached two small thin calcareous plates, obliquely inserted onto the test in a fashion to converge towards each other and to form with the internal surface of the test a prismatic space in which is lodged the canal that extends from the excretory organ to the madreporite

plate. These plates (Pl. III, fig. 19, *PS*) give an insertion to the mesenterial lamellae that attach the rectum and the superior intestinal loop to the test.

The reticulated structure of the calcareous plates of urchins is well known, and a section made through a decalcified piece shows the connective tissue web that was infiltrated with calcium carbonate. This is composed of trabeculae forming a mesh and forms very large and irregular cavities filled in the living animal with an acellular connective tissue. Hoffman has sufficiently stressed the structure of the calcareous pieces of the echinoids. Their mesh is very dense at certain points, for example in the tubercles that serve for articulation with the very large spines. In contrast, the mesh is very large in the madreporite plate. I shall not dwell any longer on this point and continue with a description of the external appendages of the test, spines, tube feet, pedicellariae, fascioles and sphaeridia.

SPINES. — The spines have a constant form in the same species, and their characters are used in descriptive zoology. They articulate with mamelons of the test that have been named primary, secondary, and miliary tubercles. Their disposition and form also offer excellent characters for the description or the determination of genera and species. In some general certain radioles do not articulate on mamelons and are attached directly to the test (*Arbacia*, *Podocidaris*). But this is a very rare exception to the general rule. The two articulating surfaces of the spine and mamelon are sometimes bound by a very solid ligament (cidaroids). They are held in place by connective tissue and muscles that form a thick, circular envelope at the base. This envelope contains an external connective tissue layer rich in cells and pigments that is continuous with the membrane covering the test and extending to some extent onto the spine, a layer of circular fibers arranged in a circular zone and which insert onto the spine collar, and finally a dense and thick internal connective tissue layer composed of very compressed fibers. The muscular fibers are long and cylindrical. Their nucleus is very apparent and their content nearly homogeneous. One can observe sometimes, however, **15** a very faint longitudinal striation. These fibers often show cross striations that are more or less close to each other, but I have never been able to discover the cross striation that was described by Geddes and Beddart. Fibers treated with osmic acid, alcohol, or chromic acid solutions have always shown me the same homogeneous appearance. I have encountered, certainly, fibers showing cross striations that are very close to each other, But this series of striations, if they are close together, never produce in the fiber a succession of alternately light and dark parts that, alone make up the true cross striation of muscles. I have always found the same homogeneous appearance in the fibers that occur in other organs, the masticatory apparatus for example. In this regard, my observations agree completely with those of Hoffman.

The structure of the spines is identical in regulars and irregulars. Only the spines of cidaroids show a peculiar and very different structure from that seen in all other echinoids. In cross sections, their spines are made up of calcareous networks, and have a series of concentric lamellae bound together by more or less crowded trusses. They enclose a central space where more delicate calcareous deposits form an irregular tissue with a very small mesh. In cidaroids, this arrangement of concentric lamellae is not found, and the medullary cord is enclosed in a very thick zone made by radiating lamellae that are very close together

and bound by numerous thinner anastomoses.¹⁹

TUBE FEET. — The description of these organs has often been combined with that of the circulatory system because of the very close relation they have with the radial water canals. I prefer, however, their separate description and attach them to the study of the external appendages of the test, waiting to indicate their connection with the vessels when I consider the circulatory system.

The tube feet are thin and slender, capable of swelling and extension. They end, in regular urchins, in a slightly enlarged and concave extremity, sort of a sucker that adheres to nearby bodies, permitting thus the animal to move more or less rapidly. This is the reason the name tube feet (*Ambulacralfüssen*, *Saugfüssen*) is often given to them. They communicate with the interior of the test, or more exactly with the radial water canals, by means of single **16** or double pores. In addition, their number varies in different genera according to the ambulacral plates resulting in a more or less considerable number of pores. In cidaroids, for example, where each ambulacral plates has only a single pore, they are relatively less numerous than in *Sphærechinus* or *Strongylocentrotus* where the plates have at least four pairs of pores. Their soft tissues are filled with calcareous spicules often with a definite and characteristic form. Their terminal sucker likewise possesses a calcareous frame, sort of a rosette formed of reticulated tissue. The arrangement and different forms of these calcareous productions have been studied with much care by Perrier, who has described and illustrated a large number of them. He has shown the advantages that their study gives descriptive zoology. This is a question that I will lay aside completely in order to consider the external form of these appendages and especially the histological study of the elements that enter into their constitution.

The external form of the tube feet shows few modifications in the regular urchins. The tube feet that belong to the ambulacral plates are all alike. Those that are found on the buccal membrane and which, ten in number, surround the mouth inside the ophiocephalous pedicellariae, are shorter and a little smaller than the others. Instead of ending in a concave sucker, they end simply in a slightly enlarged, small head divided into two lobes by a slight median groove. They cannot attach to nearby bodies and consequently do not function in movement.

In spatangoids, in contrast, the tube feet show important modifications, but also undergo a considerable reduction in their number and development. Müller has already distinguished three forms of tube feet of *Spatangus*: 1° very developed tube feet grouped around the mouth in the peristomial area, ending in a tuft of small secondary branches enlarged at their free end. Müller called them *Tastfüssen*. 2° very short tube feet (*Ambulakralkiemen*) that are penniform and have a main trunk on which are inserted small appendages of a second order, always on the same side. They are part of the ambulacral petals. 3° very little developed tube feet that end in a cul-de-sac or in two or three short

¹⁹The structure of the spines was studied by Agassiz and, quite recently, by Mac'Intosh who has been able to classified regulars into several groups according to the structure of their spines.

digitations. They are found on the plates that belong neither to the peristomial zone nor the petals. Müller called them *einfache locomotive Füßchen*, but their rudimentary state does not permit them to have a function in locomotion.

Tube feet analogous to the peristomial tube feet, sometimes even longer and more developed, are found at the posterior end of the body on the ambulacral plates that are surrounded by the infra-anal fasciole. Their number **17** is always small: *Spatangus* has two pairs, *Brissopsis* and *Echinocardium* have three. They and the peristomial tube feet are the only tube feet capable of enlargement and movement. They can be seen principally in young spatangoids, stretched out in various directions, but they cannot attach to nearby bodies as in urchins. As far as the other tube feet, they are incapable of enlargement and seem to play no role at all. They seem to be simply organs transmitted by heredity from urchins to spatangoids. They no longer fill an active role in the latter as they fill in locomotion in the regulars. Locomotion, although greatly reduced in spatangoids, is effected only with the aid of the spines.

Cross sections of a tube foot of a regular urchin (pl. VII, fig. 48) shows, from the exterior to the interior) the following successive layers: a very developed external epithelium, a connective tissue layer, an elastic membrane, a muscular layer, and finally an internal epithelium. The external epithelial layer is filled with very small elongated, filiform cells with contours that are often poorly defined. They possess a large and finely granular nucleus. In the midst of these cells, usually at the base of the layer, the nuclei are often larger, strongly colored black by osmic acid. A thin envelope of cytoplasm can be recognized on their dissociation. The epithelial layer is bordered exteriorly by a thin cuticle that has cilia. The connective tissue layer shows an external foundation with circular fibers and an internal one with longitudinal fibers. In longitudinal sections, the latter shows strongly undulating fibers as seen in figure 48, *CL*, when the sections have been made on retracted fibers. Interiorly the longitudinal fibers are bounded by an elastic membrane usually showing numerous folds that are close together. They are produced during retraction of the tube foot. The muscular layer has only longitudinal fibers that insert onto the calcareous rosette of the sucker. The internal epithelium has a single foundation of small cells with cilia.

One usually finds in cross sections, in the midst of the connective tissue layer, a granular mass that is distinguished from the fibers of this layer by a yellow color. This is the section of the nerve that runs the length of the tube foot to end below the sucker in a slight swelling. The fine granulations correspond to the section of nerve fibers in the peripheral zone of the nerve.

At the level of the terminal sucker, the structure of the tube foot is **18** noticeably modified. A longitudinal section, containing both the tube foot and its swollen end analogous to that shown in fig. 48, allows the following arrangement to be recognized. The connective tissue layer continues up to the base of the sucker and expands into a hyaline circular zone. In the thickness of this zone are deposited the calcareous spicules which together form the rosette of the sucker. The rosette no longer exists in the preparation I have illustrated here under the action of decalcifying agents. The epithelium of the tube foot continues onto the lateral surface of the sucker up to the edge. But the concave surface of the sucker has a peculiar epithelium and an aspect different from the former although a

limit of demarcation does not exist between the two epithelia that pass insensibly from the one to the other. The cells there are in fact longer, their nuclei are united into groups, and they are bounded at the periphery by a cuticle that is thicker than on the stem. One sees, in addition, that the end of the cells shows very close to the cuticle a slight thickening that appears in the form of a dark point. Towards the interior, the epithelial layer is not clearly limited, but continues with a tissue formed of very fine fibers, intercrossed in all directions, containing numerous nuclei that seem embedded in a finely granular sparse fundamental substance. In some sections are encountered, moreover, in a certain point of this layer sub-adjacent to the epithelium, a fine granular yellow mass (*N*) enclosing some cells and presenting the same aspect as the section of nerves in other regions. It is not possible to consider this layer as being the continuation of the connective tissue layer of the tube foot because it is very distinct and does not have the same characters. It is just as difficult to admit that it belongs to the epithelium of the concave disc of the sucker. Although it continues without a line of demarcation with its cells, it has a completely different aspect. It is, moreover, covered by a true epithelium of the tube foot and it is not possible to admit that an epithelial layer could be covered by another epithelial layer. I believe rather that this sub-epithelial layer, which others have not yet mentioned, is nothing other than the expansion of the tube foot nerve that cannot be seen with the naked eye, beyond the base of the sucker. It contains, in fact, numerous nervous elements that cannot be distinguished in the sections but can be recognized very clearly in dissociations. Very good results are obtained in these tube feet treated with 1% osmic acid for 28 hours and then letting the pieces macerate in distilled water for the same time according to the method of Ranvier. The elements that are seen after dissociation of the head of the tube foot and after staining with picrocarmine are always in an excellent state of preservation. They are at first sight very long, filiform epithelial cells **19** swollen at the location of the nucleus and bounded on one side by a very thick cuticle under which is seen the deeper part of which I shall soon speak and on the other side by a thinned end often divided into two or three small filaments (pl. VI, fig. 47). Beside these characteristic epithelial elements, one encounters other larger cells with irregular boundaries and enveloped in a very thin membrane, containing a very finely granular, clear cytoplasm, and a large nucleus filled with large granules. Ordinarily these cells have a hyaline extension, but often also they have two. These extensions are sometimes very long and ramified at their free end. The characters of these cells are absolutely identical to those seen in the cells of the nerve trunks and it is permitted to consider them as being of nervous nature. One encounters, in addition, very fine, isolated fibers having a principal trunk from which leave secondary ramifications. They possess the same characters as the extensions of the nerve cells.

These fibers and nerve cells are doubtlessly connected with the nervous elements of the tube foot nerve. In longitudinal sections, it is impossible to fix the limits to the section of this nerve that is visibly continuous with the elements of the sub-epithelial layer. The swelling that one can see with the naked eye at the end of this nerve must be the center from which radiates the nerve fibers that come to form a nerve plexus containing numerous cells between the epithelial layer and the connective tissue layer. It seems reasonable to me to conclude that the fibers that arise from these cells communicate with the epithelial cells of the concave surface of the sucker. This explains why this layer does not have precise

limits on the internal surface. I was not able to obtain, either with osmic acid or gold chloride, preparations where I could recognize nerve fibers leading to the epithelial cells. This without doubt comes from the extreme fineness of these fibers as well as their fragility. They must, in fact, detach very easily from the cells at which they end.

The existence of a nerve plexus underneath the epithelial layer of the sucker is not surprising. One knows, in fact, that the suckers that end the tube feet are very sensitive organs and that it is sufficient to touch one, even very slightly, to see its tube and all the adjacent tubes retract immediately.

The tube feet of irregular urchins have a structure analogous to that we observe in the regulars. A longitudinal section of a peristomial tube foot of *Spatangus* (pl. V, fig. 32) shows the same succession of layers as in urchins. Only the elastic membrane is missing. The external epithelium **20** (*E*) contains very elongated cells with sometimes slightly accentuated boundaries. In their midst one finds large round cells (*CB*) with a very granulated protoplasm and nucleus that can be called *basal cells*. Semper gave this name to the analogous cells in holothuroids. They are perhaps glandular cells. It is probable that the much smaller cells that one encounters in the external epithelium of the tube feet of urchins have the same nature as these basal cells. The connective tissue layer is rich in pigment granules and in connective tissue cells that do not exist in urchins. It is also thinner and its tissue is looser than in the latter. It is crossed by the tube foot nerve that one recognizes in sections with its ordinary characters. The muscular layer contains only longitudinal fibers.

The tube feet of the other regions of the test have the same structure as the peristomial tube feet. The walls of the small stalks that make up their terminal crest resemble those of the tube that supports them. Their swollen end, in which continues the central cavity of the tube foot, shows only a thin layer of connective tissue (pl. V, fig. 33) supporting a well developed epithelial layer. The cells that make up the latter are analogous to those that we found in the sucker of the tube feet of regular urchins, i.e. they are very long, filiform, with only a slight enlargement at the level of the nucleus, but they possess only a very thin cuticle. It is probable that the nervous ramifications penetrate across the connective tissue layer up to the terminal tuft that, as in the tube foot of urchins, is highly sensitive.

PEDICELLARIAE. – The pedicellariae of echinoids have been the object of very extensive studies. The most important, that of Perrier²⁰, describes the numerous very varied forms in asteroids and echinoids he studied. There was very little interest in these singular organs before 1869, the date of publication of this memoir, and we have only some descriptions given by Delle-Chiaje, Valentin, and Sars on the most common regular urchins. Perrier was able to study the pedicellariae in most of the echinoid and asteroid genera in the collection of the Museum and showed their importance in descriptive zoological studies. Agassiz²¹ published in his *Revision of Echini* illustrations of a large number of **21** pedicellariae, most of which had been described or illustrated by Perrier. He also gave in

²⁰Loc. cit.

²¹Loc. cit.

the account of the trawls of the *Challenger* some plates showing the principal types of pedicellariae collected during the expedition. Finally, Sladen²² and after him Foettinger²³ described certain modified gemniform pedicellariae with true glands that are peculiar to some species of urchins. The histology of the soft parts was quite recently studied by Geddes and Beddart²⁴.

I shall recall only that the pedicellariae, whatever their form, always have jaws and a stem. The jaws, very variable in form, have three valves with a triangular base. Each has a more or less developed calcareous plate, the *apophysis*, on its concave surface. This serves for the insertion of adductor muscles of the valve. The stem, attached to the test, generally contains a small calcareous stalk articulated to a very small mamelon and soft parts joining its upper end to the bases of the valves of the jaws with which it sometimes directly articulates (cidaroids). The adductor muscles of the valves attach to this generally swollen end of the stem.

Four different forms of pedicellariae exist in echinoids: ophicephalus, tridactyl, gemmiform, and foliate. The first three were established by Valentin who recognized them in the ordinary urchin. The fourth, indicated with doubt by Valentin who considered it to represent developing pedicellariae, was established by Perrier. I have encountered pedicellariae with four extensions in *Schizaster canaliferus* that, to my knowledge at least, have never been reported. It is necessary to consider it a species with tetradactyl pedicellariae. (Pl VII, fig. 55). I have always found these pedicellariae, always in great abundance, in the various specimens of *Schizaster* that I have been able to examine. This is, moreover, the only genus in which I have observed this tetradactyl form that will be described later. I have observed also in most irregular urchins very small pedicellariae that do not correspond at all to the forms cited above. They approach foliaceous pedicellariae but are distinguished by triangular valves finely toothed on the edges.

I content myself with giving these indications of pedicellariae in urchins, having nothing to add to the excellent work of Perrier to which I return for everything concerning the descriptions of these organs. I have encountered in certain species of echinoids some forms of pedicellariae not yet described. I shall **22** concern myself with them in the part of this work that will treat more specially the fauna, where their description will be better. From the point of view of classification, these organs have, in fact, a certain importance on which Perrier correctly insists, the characters they present being constant for the same species and more often varying from one species to the other.

Morphologically, pedicellariae are only modified spines. Like them, they appear at the beginning in the form of small mamelons with a calcareous network that makes up the early test of the young echinoderm. At this moment, it is impossible to say if such a

²²Loc. cit.

²³Loc. cit.

²⁴Loc. cit.

mamelon will become a spine or a pedicellaria. Agassiz²⁵ followed the development of pedicellaria in asteroids. He saw (*Hippasteria*) that the mamelon that will become a pedicellaria shows first of all a slight groove that increases little by little to become deeper and thus divide the early mamelon into two halves. Each of these halves becomes mobile in separating from the test by a transverse groove. From this moment the perfectly recognizable pedicellaria grows rapidly. In *Luidia*, the early mamelon is divided into three parts by two grooves and thus become a small tridactyl pedicellaria.

What are the functions of these singular organs? Formerly it was thought that the pedicellariae serve to seize food particles and taken them to the mouth. We now know that they play no role in the capture of food. Agassiz assigned a much different function to pedicellariae. The material rejected by the anus fall on the periproct and are received by the pedicellariae that size them between their branches. They pass thus from one to the other until they reach the circumference of the test where they fall into the surrounding water: “*nothing is more curious and entertaining than to watch the neatness and accuracy with which this process is performed,*” adds Agassiz. This phenomenon is, in fact, easy to observe. But it is evident that this is the one of the least important of the functions that the pedicellariae must fulfill. Moreover, it is accomplished only by the tridactyl pedicellariae that are encountered both on the ventral and dorsal surfaces of the urchin. In spatangoids, which have the anus at the posterior end and where consequently transport of feces cannot take place, the tridactyl pedicellariae are however very numerous. In summary, in the present state of knowledge, it is impossible to assign any role at all to the pedicellariae.

A special form, or rather a peculiar modification of pedicellariae was described quite recently by Sladen and by Føettinger. I want to speak of the glandular pedicellariae. In certain echinoids, the gemmiform pedicellariae are transformed into secretory organs, either they occur on the 23 stem of the glands themselves or the valves themselves support the glandular sacs. My observations agree in all points with those of Føettinger on the histology of the glandular pedicellariae of *Sphærechinus*. The characters that I have observed on the analogous pedicellariae of *Echinus acutus* and *melo* recall the arrangements that exist in *Sphærechinus*.

I shall examine first the glands of the stem.

In *Sph. granularis*, the gemmiform pedicellariae have three peculiar glands on their stem that show, to the naked eye, a more or less accentuated swelling. With a slight magnification, one sees three longitudinal grooves that divide them into three parts. The cross section of this swelling shows that it is composed of three very distinct sacs, each with its own muscular envelope of circular fibers. All three are surrounded by a common envelope of connective tissue, covered externally with epithelial cells belonging to the general envelope of the pedicellaria. The contents of the sac are a mucus that has the property of expanding greatly with contact with aqueous solutions. Also, most of the glands that are treated by such solutions do not delay in bursting and releasing their contents. It coagulates under the influence of fixatives. Under their influence, when examined at a slightly greater magnification, it often takes the aspect of a reticulated tissue with a very

²⁵AGASSIZ. *Revision of the Echini*. Vol. IV.

irregular mesh. This mucus results from a peculiar degeneration of the cells enclosed in the cavity of the sac. In fact, one finds in most of the preparations nuclei surrounded by protoplasm and debris of cell walls applied against the internal surface of the muscular layer. At the same time, one encounters entire and absolutely intact cells especially when it is a matter of a pedicellaria in which the glandular swelling is not large. One can therefore consider these sacs as being first filled with cells that deliquesce and are transformed into mucus at a given moment. The transformation first occurs in the central cells and then proceeds little by little to the peripheral cells. This process is confirmed by the appearance of the mucus coagulated by reagents being identical to that of the coagulated secretion of the diverticulum in spatangoids. This secretion is quite certainly a product of the degeneration of the epithelial cells lining the internal surface of the diverticulum.

Each sac has at its upper extremity a small opening by which the mucus escapes outside.

The valves of the head of the gemmiform pedicellariae also have, in *Sph. granularis* and *Echinus acutus* and *melo*, analogous glands to those just considered. The calcareous stalk of the stem of these pedicellariae articulates directly with the base of the valves. A very regular calcareous skeleton **24** is always present (pl. VII, fig. 58). The valves are composed of a calcareous piece with a basal part enlarged in the form of a triangle. This basal part is continuous with a slender stem ending in a sharp hook and supports voluminous glandular sac on its external surface. These sacs contain a mucus analogous with that of the glands of the stalk. It seems this mucus swells still more with contact with reagents than that of the stalk glands, particularly in *Echinus* where these sacs ordinarily burst with contact with alcohol or at least allow a large part of their contents to escape. The structure of these glandular sacs is identical to those of the stalk glands of *Sph. granularis*.

Towards the middle of the valve, the glandular sacs divide into two halves that remain separate up to the hook that ends the calcareous piece. They reunite at this level into a single very short canal that must end in a small opening. I say *must* because I have not been happier than Fœttinger who was unable to perceive this opening. Its existence, however, is very reasonable. In fact, when one treats these glandular pedicellariae with alcohol, a certain quantity of mucus always leaves and takes the appearance of a coagulated small, opaque, white mass that can be seen at the end of the valve. This phenomenon is particularly observed in the pedicellariae of the genus *Echinus*. Now, this mass is observed from the moment the pedicellaria is plunged into alcohol. This suggests that an opening really exists at this level because it is difficult to suppose that a rupture of the wall is always produced at the same place. Moreover, this rupture in *Echinus* most usually occurs only at the end of a certain time, and at a variable place towards the terminal end of the sac.

The glandular gemmiform pedicellariae of species of the genus *Echinus* differ from those of *Sphærechinus* only because the sacs are much more distinct and the pigmentation less developed, their walls lacking pigments are completely transparent.

Sladen described on the valves of these glandular pedicellariae some peculiar epithelial thickenings that he called *tactile cushions*. One encounters, in fact, in nearly all the sections of valves, towards the middle of the external surface, a swelling made up of certain epithelial cells that become longer and larger, and resemble very much epithelial cells of the stalk of the peristomial tube feet of *Spatangoids*. The cilia of these cells are very long, and it is possible these particular swellings play the role of tactile organs, but it is

impossible to find the relations between the cells that make them up and nervous elements.

I have encountered peculiar gemmiform pedicellariae in *Echinocardium flavescens*, analogous in some regards to the glandular pedicellariae of *Sphaerechinus*, **25** but differing in several characters (pl. VII, figs. 59 and 60). They are easily recognizable by the deep purple color due to a pigment soluble in alcohol and fresh water like the pigment found in such great abundance in spatangoids. These pedicellariae are observed only on the dorsal surface of the test of *Echinocardium*, distributed irregularly among the spines in a very variable number according to the specimens. Some have twenty, others three or four only. It is rare to find individuals with none at all. The three sacs supported by the calcareous stalk of the head of the pedicellariae resemble the glandular sacs of *Echinus*. However, their contents, instead of being a mucus that reagents coagulate, is composed only of small red spheres supported by fine connective trabeculae.

The movements of the gemmiform pedicellariae modified from *Sphaerechinus*, *Echinus*, and *Echinocardium* are characteristic. When they are detached from the test and placed in a cup of water, they immediately begin to open their valves and move in a peculiar fashion. This is a sort of oscillation of the head on the rounded end of the stalk. Instead of closing when irritated and inducing it in other pedicellariae, they always keep in contrast their valves open. When the valves of one of them close, it is often sufficient to touch it with the point of a needle in order to see it open immediately.

SPHAERIDIA. – Lovén recognized these peculiar organs in echinoids. He considered them sense organs and named them *Sphéridies*. They are found everywhere except in *Cidaris*. He has given in his work a complete description of them accompanied by numerous illustrations. I shall content myself to give here some information on the species of our coasts, having nothing to add to the observations of the Swedish scholar on the structure and arrangement of these organs.

Sphaeridia are very small globular bodies with a very short pedicel articulated with a mamelon of the test. The pedicel is formed of articulated calcareous tissue while the sphere is made in large part of a very hard, vitreous substance arranged in very thin concentric layers. The reticulated tissue of the pedicel generally continues into the interior of the vitreous globule and completely around its base. Externally the sphaeridium is covered with a very thin layer of connective tissue covered by a ciliated epithelium.

Sphaeridia are primarily grouped around the mouth and are only found in the ambulacral area. They occupy a constant position on the first peristomial plates. In many spatangoids, **26** one or two sphaeridia found on the peristomial ambulacral plates are joined in a small pit at the base of the tube feet (*Spatangus*, *Echinocardium*, *Brissopsis*). In *Brissus* and *Schizaster*, sphaeridia are grouped by two or three at the base of the tube feet on the plates of the trivium. They are generally more numerous in the bivium and in small pits, one behind the other.

In regular urchins, sphaeridia are more numerous and arranged alternately in the two rows of plates of the ambulacral areas, usually very close to the suture. *Arbacia* has only one sphaeridium placed in a small pit very close to the edge of the peristome.

Sphaeridia are exposed in regulars and most spatangoids. In some spatangoids (*Lovenia*), clypeasteroids and cassiduloids, they are covered with extensions of the test that

can even completely enclose them.

One sees thus that the structure of sphaeridia approaches very much that of spines and, like pedicellariae, are only modified spines. Lovèn, considering their situation constant next to the mouth and usually at the base of the peribuccal tube feet, thought that these small organs must be sense organs, probably functioning to perceive the nature of substances held in suspension in the surrounding water, and to thus guide the animal in the search for food.

FASCIOLAS. – Special bands are found on the test of spatangoids where spines are lacking and replaced by special bristles in the form of clubs, ciliated clavules according to Lovèn's expression. These clavules are made up of calcareous stalks, enlarged at the end, sometimes articulated, sometimes directly fixed to the test. They are covered by a connective tissue layer covered with ciliated epithelial cells. The cilia exist the entire length of the stalk, but they are very delicate and detach easily towards the enlarged end. The ensemble of these crowded stalks, each against the other, constitute these easily recognizable bands that were called *sémites* by Philippi and *fascioles* by Agassiz.

Fascioles occur in all existing spatangoids. They are lacking in the oldest types of this group (dysasteroids) and appear only with the cretaceous genera. Their arrangement stays very constant in a genus and their position served Lütken to establish a classification of spatangoids.

At first only one fasciole existed, bordering the subanal plastron and **27** including part of the unpaired interradius and posterior ambulacral zones. This is the *infra-anal* fasciole that exists in *Spatangus* and *Maretia*. A *peripetal* fasciole is added in the genera *Brissus*, *Brissopsis*, and *Metalia*. The genera *Schizaster*, *Moiria*, etc., have in addition to the peripetal fasciole, a *lateral* fasciole that leaves the peripetal fasciole and is directed towards the posterior end where it curves towards the ventral surface in order to pass under the periproct and rejoin the peripetal fasciole on the other side. In *Echinocardium*, which has an infra-anal fasciole, one finds in place of the peripetal fasciole, an *internal* fasciole that surrounds only the apical extremity of the test and includes only a part of the anterior unpaired ambulacrum and a very small portion of the petals. One could believe that the internal fasciole is only a very reduced peripetal fasciole if *Breynia* did not have both at the same time. Besides this usual arrangement, some arrangements exist peculiar to certain genera. Thus, in *Brissopsis*, one encounters sometimes two branches that leave from the infra-anal fasciole and climb onto each side of the anus. These branches are constant in *Echinocardium* where they make up a true anal fasciole.

It is presently impossible to indicate the origin of fascioles. Müller compared them to ciliated bands of larvae. But nothing proves that these so characteristic bands of larvae have any relation at all with the fascioles of adults. This relation is less probable as they develop on plates that have not yet appeared during the period the ciliated bands of larvae exist.

The function of fascioles is as obscure as their morphology. Müller has already remarked that the ciliated bristles that constitute them are very sensitive. Nevertheless, it is very difficult to consider them as sense organs. Agassiz thought that the use of these organs is evidently to protect the petal from foreign material. He said one always finds mud held in the midst of the bristles of the fasciole. I cannot share the opinion of Agassiz as it

seems that the very short bristles of fascioles are not strong enough to prevent foreign material from reaching the petals. Many genera do not have peripetal fascioles. If one considers that spatangoids live in general completely embedded in mud, it is difficult to understand what effective protection can be rendered by the bands as thin as the fascioles. Moreover, the petaloid ambulacra do not enclose, important organs and one cannot see the utility of the supposed protection. One always finds as much mud on the petals and in the midst of the dorsal spines of a spatangoid as in the midst of the clavules of the infra-anal fasciole.

DIGESTIVE SYSTEM

REGULAR URCHINS

The mouth in regular urchins opens on the ventral surface of the buccal membrane. This latter, sometimes naked, sometimes covered with imbricated scales, closes the peristomial opening that is more or less large according to genus. This membrane has outside the mouth, bordered by the five points of the pyramids, a circle of ten tube feet whose form is a little different than those that belong to the calcareous plates of the test, then a crown of very crowded ophicephalus pedicellariae, and finally towards the periphery ten branchial vesicles that communicate with the general cavity. The buccal membrane is entirely composed of a very dense connective tissue layer covered on its internal surface by the peritoneal epithelium and on its external surface by the membrane covering the test.

The anal opening, diametrically opposite the mouth, opens to the environment from the periproct, i.e., the space bordered by the genital and ocular plates, and is filled with small plates of different sizes (except in *Arbacia* which has only four plates arranged in a cross). Lovén showed that in very young urchins this space is filled with only a single plate: this is the central disc homologous to the centrodorsal piece of crinoids. From a very early time, the substance of this disc is slowly resorbed towards the point where the anus will later penetrate. At the same time that the central space enlarges, small plates come to develop between the slightly indented edge of the central disc and the corresponding genital pieces. The number of these plates increases little by little. Their dimensions become much larger, and finally all the space surrounded by the genital plates is filled by a more or less considerable number of plates, where it will be difficult to distinguish the single original piece and in the midst of which opens the anus.

I can pass rapidly over all that concerns the pathway of the digestive tube of regular urchins, which has been studied for a long time by numerous **30** observers (Tiedemann, Delle Chiaje, Valentin, Hoffmann) and there is not a single zoologist who has not verified

that which has been said on this subject. It is the same for the masticatory apparatus complex, particularly studied by Meyer. It would have been good for me to say something about the some peculiarities shown by the genera *Dorocidaris* and *Arbacia*, but this description will be better in the part of this work more especially devoted to the fauna and description of the species. As to the very complicated structure of the calcareous pieces that are a part of the masticatory apparatus, it was first studied by Hoffmann, then by Giesbrecht, who showed that these organs have a different structure than that of the calcareous plates of the test. I shall content myself to referring to the descriptions and figures given by these two scholars, because it would be difficult to summarize here their results and that have moreover only a relative value.

Several distinct regions can be distinguished in the digestive tube of urchins. These are the pharynx, esophagus, the first or inferior curve, the second or superior curve, and finally the rectum. The pharynx extends from the buccal opening up to the upper plane of the lantern where the vascular rings occur. The pharynx is pentagonal in its lower part and becomes circular as it approaches the esophagus. The five ridges are marked by five pairs of ligamental bundles that run the length of the pharynx, inserted on the walls opposite the vascular rings. Below, the two bundles that make up each pair join in a single mass that inserts on the lower extremity of the jaws. The esophagus, which follows the pharynx, has differences in its length that correspond to the more or less pronounced flattening of the test, according to the genus. It extends vertically in general towards the madreporite, which it does not reach, then curves in the direction of the anterior radius (radius I according to Lovén's system) and comes to open into the beginning of the inferior intestinal curve. In *Dorocidaris*, its trajectory is slightly rectilinear and it extends directly from the lantern to the inferior intestinal curve. This itself, being against the internal surface of the test to which it is attached moreover by numerous, fine mesentery tracts, describes a complete circle in order to return very close to the point of departure in interradius 5. Here it abruptly reflects and takes an inverse direction in order to continue with the second, superior curve. This latter ends in the rectum which is extended all along radius I.

At the level of the point where the esophagus connects to the inferior curve a sacciform dilation ordinarily occurs, a kind of diverticulum, more **31** or less developed according to species. This is homologous to the organ of the same name in spatangoids. Although the diverticulum attains considerable development in the latter and is modified in structure to fulfill special functions, the diverticulum of regular urchins is only the beginning of the first curve and its structure differs in no way from that of the intestine.

The inflections of the intestinal curves, each showing a series of concave and convex parts, are too well known for me to talk about them here. The genus *Dorocidaris* alone shows some peculiarities in this regard that will be mentioned when I consider the fauna.

It is known that the two curves of the digestive tube of urchins show notable differences in their color. The first curve is always darker, generally brown, while the second curve is lighter and yellow. These differences in color correspond to the differences in the distribution of the vessels that ramify on inferior curve only and in the structure of the two regions that evidently have different functions from the point of view of the urchin's nutrition.

A peculiar organ already seen by Delle Chiaje is attached to the digestive tube. Its

relations and functions were discovered by Perrier, who proposed naming it the *intestinal siphon*. It is an open canal from the last portion of the esophagus to the end of the inferior intestinal curve. It is applied throughout its trajectory against the internal border of the digestive tube, between it and the internal marginal vessel. Its caliber, approximately one or two millimeters according to the size of the specimen, is a little larger at its origin.

The walls of the digestive tube, always very thin except for the entire length of the esophagus, show in their structure the following layers from the exterior to the interior (Pl. VI, fig. 37): external epithelial layer, muscular layer, internal connective tissue layer, and finally an epithelial layer. This latter is very developed. It is at least 10 or fifteen times greater than all the other layers combined.

The external epithelium (*E*) contains a single layer of small, ciliated cells with a granular protoplasm. These are the same cells that cover the mesenteric lamellae and the membrane that lines the internal surface of the test.

The connective layer is very thin and formed of very fine fibers of connective tissue.

The muscular layer (*M*) always contains cross fibers that are very apparent in cross sections. Some longitudinal fibers occur **32** nevertheless, but they are not very abundant and do not make up a continuous layer as in *Spatangus* where they are especially located in the walls of the esophagus. They generally cannot be seen in the cross sections, but longitudinal sections and dissections show their existence clearly.

The internal connective tissue layer (*Tc*) is a little thicker than the external layer, but it is nevertheless very thin except in the esophagus where it acquires a certain development. In the entire length of the first curve, it is filled nearly completely with intestinal capillaries. The coagulated blood there forms a series of very concentrated yellow, granular islets. The connective layer forms in the esophagus a series of longitudinal projections corresponding to the folds that can be seen with the naked eye on the internal surface of this organ. It is constituted especially of fine connective fibrils sometimes containing cells and sometimes pigment granules. It is certain from the sections of the esophagus that it contains two different layers: an ill-defined outer layer which circular fibers and an internal layer with irregular fibers intercrossing in all directions.

The very large and very developed internal epithelial layer (*E*) is formed by several layers of elongated cells. The cells are small and crowded in the basilar region but become very long towards the periphery. It is lined interiorly by a fine cuticle with cilia. The aspect of the epithelial layer differs somewhat in the different intestinal regions. The epithelium of the esophagus contains long, thin cells with a slightly granulated protoplasm and an inconspicuous translucent nucleus at the periphery. At the base of the layer are found very clearly limited round spaces inclosing numerous granules. These can be considered a specific modification of the epithelial cells with a secretory function. In the inferior curve, the peripheral cells are very long and enlarged at their free end. They have a protoplasm filled with numerous large granulations, particularly in *Strongylocentrotus*. In the superior curve, the granulations become less large, much less abundant, and finally disappear in the last portion of the intestine. It is probable that this granular epithelium must play the role of a glandular organ, and fill the functions of secretion for the digestion of food.

I have not encountered in the digestive tube of urchins the numerous mucus cells and the special glands of the intestine of spatangoids. At the most, one can consider as

rudimentary glands the granular masses that occur at the base of epithelial cells of the esophagus.

33 The structure of the siphon is similar to that of the intestine. The walls are, however, much less thick and the epithelial layer is much less developed.

The different layers encountered in the structure of the digestive tube of urchins are identical to those of the digestive tube of spatangoids. I have not spoken of the histological characteristics of the different elements that make them up. We will return to them, in fact, in spatangoids where their study is easier because of the considerably greater development of the intestinal walls. That which I shall say about the muscular and connective elements in spatangoids is just as applicable to those of urchins.

If one compares the description that I just gave of the structure of the digestive tube in urchins with that made by Hoffmann, one will see that it differs in some respects. Hoffmann describes, in fact, an external connective tissue layer lined by an epithelium, a longitudinal muscular layer, a circular muscular layer, and finally an internal connective tissue layer. We stop at the characters that he has given to the latter. It contains, he says, an external, peculiar connective tissue layer covered with an epithelium, a longitudinal muscular layer, a circular muscular layer and finally an internal primarily cellular layer that he calls *Drussenschicht*. It is in the thickness of the first, rich in fibers, that the capillaries of the intestine ramify. The glandular layer in the pharynx and esophagus is composed of connective networks containing finely granular cells with pigmented nuclei. Throughout the rest of the intestine it is made up only of round, reddish brown cells, with or without nuclei that have a granular content. It seems from this description that Hoffmann has given the name *Drusenschicht* to the epithelial layer. He never speaks, in fact, of an epithelial layer except in a single phrase where he says an internal ciliated epithelium does not exist. Now, the characters that he gave to this glandular layer do not refer to those of the epithelium as I have described above. Still it is not possible to refer this glandular layer, which follows the connective tissue layer, to any other thing than the epithelium. I believe that Hoffmann's error results from the mode of preparation to which he submitted his pieces for histological analysis. He used, in fact, only chromic acid or potassium bichromate, which cannot preserve elements as delicate as those of the intestinal epithelium of urchins. I have made sections on portions of the digestive tube treated only by chromic solutions and the aspect that they show recall, in fact, the description of Hoffmann. The pieces destined for histological study in animals with tissue as easily changed as the urchins, require absolutely a preliminary treatment with osmic acid which is the only one that results in **34** suitable preparations. The epithelial cells there are then very distinct and in a good state of preservation. According to Hoffmann, the innermost layer of the intestinal wall is a glandular connective tissue layer. This would certainly be the first example of a digestive tube lacking an internal epithelium.

The various portions of the digestive tube are attached to the test by thin mesenterial tracts, but the circumrevolutions are not interconnected by solid mesenterial lamellae as in spatangoids. Their existence there is made necessary by the special food of these animals, solid material that is always very heavy. Urchins have only a single, very thin fibrous lamella that extends from the recurved part of the esophagus to the diverticulum of the inferior curve and inserts on the corresponding portion of the test near the apical pole. This

mesenterial lamella contains glandular elements already described by Perrier. They consist of cells lacking an enveloping membrane with an irregular cytoplasm and a very voluminous nucleus more or less filled with pigment granulations. By these cells are found numerous pigmented masses assembled in a more or less voluminous piles.

SPATANGOIDS

The eccentric position of the mouth and anus characterize the irregular urchins and distinguishes them immediately from the regulars. The peristomial opening of spatangoids is brought forward in the direction of the medial line, i.e. the anterior radius. It has an ovoid form and is filled with a membrane in which are developed small calcareous plates. The ensemble forms a sort of upper lip. The buccal opening is bordered in front by this upper lip and behind and below by the first piece of the posterior interradiar area which becomes preeminent and thus forms thus a lower lip. This overlaps a little above the upper lip so to cover its extreme free end when one looks at a spatangoid by the ventral surface. The calcareous quadrangular or pentagonal calcareous plates of the upper lip are slightly moveable among each other and larger anteriorly. They become smaller and more mobile at the same time they lose their solidity as they approach the posterior border. The lower lip is, in contrast, perfectly fixed.

35 This situation of the mouth carried back to the posterior border of the buccal membrane, very different from that its location at the exact center of this membrane in urchins, does not exist in very young animals where the rest of the body form is much less irregular. Lovén, in studying a young spatangoid only several millimeters long, has noted in fact that the peristome has the form of a nearly equilateral pentagon with the mouth at the center surrounded by small buccal plates. Little by little, as the animal grows and these plates increase in size, the mouth moves backwards in the direction of the posterior interradius until it finally is located at the posterior border of the buccal membrane. It is thus transformed thus into an upper lip and the first piece of the interradius that becomes protuberant forms a lower lip.

The anus, carried back in present types to the extreme posterior of the body in the unpaired interradius, opens at the center of an oval periproct bordered by three or four pairs of pieces of this interradiar area. It is composed of small calcareous pieces larger at the periphery than at the center.

The path of the digestive tube was described with care by Hoffmann who distinguished several regions to which he gave the names of pharynx, esophagus, stomach, small intestine, large intestine, and terminal intestine or rectum. Obviously these terms can be very broad in the body of a description, but they do not correspond to the anatomical regions defined. They have the inconvenience of relating regions known under the same names in higher animals certain portions of the digestive system which are however quite distinct from both the anatomical as well as physiological point of view. Although Hoffmann made the remark that he used these terms only to facilitate the descriptions, the reasons that I just gave prevent me from preserving them except for esophagus and rectum that correspond to these distinct and clearly defined regions. Hoffmann describes also in

the intestine of spatangoids, four different curves: the first extends from the mouth up to the level of the opening of the diverticulum; the second part from this point in order to describe a nearly complete circle and returns near its point of departure; the third, which is directed in the inverse direction, follows the internal surface of the test above the preceding and ends at the level of the madreporite plate; the fourth finally contains the terminal intestine.

As concerns the names of the various regions of the digestive system, I take the opinion of Teuscher who sees in the intestine of spatangoids, as in urchins, only two curves, superior and inferior. There is no more reason, in fact, to describe four curves in the latter as in urchins where the esophagus could just as well be considered **36** the first curve and the rectum as the fourth²⁶ Only Teuscher calls the esophagus the complete region between the mouth and opening of the diverticulum. Now, it seems more rational to me to recognize that the esophagus is much shorter and give this name only to the first part of the digestive tube, against which is applied the stone canal. The following portion contains numerous glands and especially receives vessels, which permits assigning it a role not assumed in general by the esophagus in digestion and absorption.

The path of the digestive tube is nearly the same in the various genera of irregular urchins that I have been able to examine. I shall study first that of *Spatangus* and indicate then some of the peculiarities that I have observed in other types.

When one opens a spatangoid by the ventral surface, one sees only the esophagus and the inferior intestinal curve (Pl. I, fig. 1). The esophagus (*Æ*) that follows the mouth is fixed to the edge of the two lips that border the buccal opening, which is always smaller than the diameter of the esophagus. Moreover, the two small mesenterial lamellae that join the esophagus on one hand to the supporting plate and to the stone canal on the other also insert to the two angles of the buccal opening. At the same time they attach to the upper semicircle of the esophagus. They continue to the upper lip in the form of a thin membrane that reaches to the vascular rings. Thus a kind of narrow sinus is set off at the level of the upper lip between the internal membrane of the test intimately applied against the calcareous pieces of the upper lip and the membrane that is the continuation of the mesenterial lamellae annexed to the esophagus.

There is no muscle in connection with the upper lip that permits it to open or close voluntarily. The slight movements, moreover, that it can accomplish, as well as the entry of material into the digestive tube, seem to be made in a completely mechanical fashion.

The esophagus is the narrowest portion of the digestive tube. It is generally flat and, if its cavity is not completely filled with stone, its form is always slightly irregular. It extends in a straight line towards the posterior end in the direction of the unpaired interradius and keeps the same dimensions up to the point where it is continuous with the beginning of the inferior curve. **37** The inferior curve has a much larger caliber than the esophagus and goes

²⁶I shall thus use only the terms esophagus, first or inferior curve, second or superior curve, and rectum. If in different notes addressed to the Academy of Sciences, I use Hoffmann's names, it is only to avoid a discussion of terms that would not have been appropriate in these communications.

in a different direction. The stone canal (*C* and *c'*) that accompanies it from the mouth passes to this level above the esophagus in order to place itself on the large ventral mesenterial plate (*MV*) that connects the different regions of the inferior curve. The inferior curve (*CI*) describes more than a complete circumference. It climbs first up to the anterior radius where it receives a large sacciform dilation, the diverticulum, that one cannot perceive in looking at the animal from the ventral side. It then circles the test in order to end near the anterior radius in the interradius that precedes it (interadius 5 of Lovén). It keeps a uniform caliber throughout its path and shows, approximately two centimeters past its origin, a slight transverse swelling (50) indicating the trace of the siphon that opens here. From there, up to the level of the orifice of the diverticulum, its external surface shows a series of clear circular lines (Fig. 5b) that correspond to the path of vessels of this region. Past the orifice of the diverticulum up to its end, it shows nothing special.

If one opens the spatangoid by the dorsal surface (pl. 1, figs. 2 and 3), one sees the superior curve (*CS*) that goes in the inverse direction of the preceding. It describes a little more than a half circle the length of the internal surface of the test and continues opposite the madreporite plate with the rectum (*R*). The rectum extends the length of the posterior interradiar zone and ends at the periproct on calcareous pieces to which it is solidly fixed by mesenterial tracts. The highest region of the test is occupied by a voluminous organ (*D*), enlarged in its median portion and narrowing at its two ends. This is the diverticulum that extends from the inferior curve to the madreporite plate. It is deep brown in color and its irregularly embossed surface has numerous transverse folds. It opens into the inferior curve at a point situated in the anterior radial zone by a narrow elliptical orifice that can be seen by opening and exposing the walls of the intestine (pl. II, fig. 7, *OD*).

The digestive tube is fixed to the test by numerous fibrous bands (*TM*), and the different circumvolutions are attached to each other by strong mesenterial lamellae that Hoffmann described under the name dorsal and ventral mesenterial lamellae. They are four in number. The two ventral mesenterial lamellae take their point of attachment at the internal supporting apparatus *PS*. The small lamella (*mv*) attaches to the length of the esophagus. The large lamella (*MV*) attaches to the entire length of the internal border of the inferior curve. At the dorsal surface, a first lamina (*md*) is attached to the length of the rectum and is fixed to the corresponding portion of the test. Another lamina (*MD*) binds the diverticulum to the superior curve and is attached to the test at the level of two small calcareous plates that protect the end of the stone canal (pl. III, fig. 19, *PS*). It sends a **38** small extension onto the rectum that parallels the preceding lamina and is fixed, like it, to the internal surface of the test. These two laminae continue up to the end of the rectum where they are developed to form a complete circle that is attached on one hand to the circumference of the rectum, and on the other to the peripheral calcareous plates of the periproct (fig. 20).

No more than in the regular urchins, no special muscles occur in spatangoids to facilitate the passage of feces across the opening bounded by the periproctal plates. Defecation results from contraction of longitudinal and circular muscles belonging completely to the walls of the rectum.

A canal is annexed to the intestine that Hoffmann, thinking himself the first to discover its relations with the digestive tube, called *convoluted organ* (gewundene Organ), which is

homologous to the siphon of urchins. This canal (*S*) leaves from the commencement of the inferior curve in *OS*, directs itself transversely towards the esophagus under which it passes and comes to cross the internal marginal vessel at *a*, fig. 1. At this moment, it changes direction, applies itself closely against the internal border of the digestive tube and accompanies it for a while in order to open again at (*S'O'*), i.e. at a point located nearly opposite its origin and three or four centimeters distant from the end of the inferior curve. The siphon thus shows two different directions, according to whether it is free or attached to the digestive tube. Its aspect changes also at the same time that it changes direction. It is slightly flat and its diameter is considerably greater (approximately 3 millimeters) in the portion between its point of origin and the internal marginal vessel. In the following portion, in contrast, it becomes cylindrical and has less thick walls and a much smaller caliber. To these external differences correspond likewise important differences in its histological structure. Its second orifice (*S'O'*) in the digestive tube has nothing special. The siphon ends there in a simple circular opening. At the other end (*SP*), its upper surface continues into the thickness of the intestinal wall. This gives birth to the slight transverse swelling that one sees at the beginning of the inferior curve. In opening the digestive tube at this level, one sees that this prolongation of the siphon appears to form a slight groove (pl. II, fig. 7, *S'O'*), accompanied with a series of small mamelons (fig. 7, *M*) that do not appear to have any special function.

This organ had already been illustrated by Milne-Edwards who considered it a vessel. Hoffmann was not the first to indicate its relation with the digestive tube, for although he says that “den meisten Beobachtern entgangen zu sein wird, da weder von J. Müller noch von Delle Chiaje das Organ erwähnt wird” Delle Chiaje has perfectly described and illustrated it. In plate XXV, 39 fig. 12 of his book “Sulla storia degli animali senza vertebre” is represented by letter *h*, a channel that opens on both ends into the digestive tube and which is nothing else than the siphon. Here is the rest that Delle Chiaje said about the digestive tube of *Spatangus*. “Andamento alquanto diverso rimarcasi nel tubo intestinale dell’*Echinus spatagus*, il cui œsofago è senza denti, un poco allargato nel principio, assottigliato è dritto in seguito; ove nasce il duodeno che gli passa per sopra, ed un canale abbastanza ristretto e trasversalmente diretto verso l’incominciamento del digiuno, ove si apre.” Delle Chiaje also illustrated the siphon of *Echinus edulis* and described it in a very clear fashion: “Giacchè nel margine interno libero è costeggiato da un canale rotondo avento longitudinali e poco profonde rughe, che incomincia dal termine dell’œsofago e finisce al principio dell’intestino tenue; stabilendosi in tal modo una comunicazione diretta tra questo budello e l’œsofago.” There is thus no reason to keep the name Hoffmann’s Organ that Teuscher attributed to him. It seems preferable to me to use the name intestinal siphon that Perrier gave the identical organ in urchins, considering the important functions it must have.

The two intestinal curves keep nearly the same dimensions their entire length. They are cylindrical and completely filled with stone, small shells, foraminiferans, and food debris of all kinds. These are never found in the siphon whose lumen always appears empty, nor in the diverticulum that is filled with a deep brown liquid. The violet color of the walls is uniform the entire length of the intestine. One cannot see the differences in color observed in urchins as well as in other spatangoids. But, in opening the digestive tube, one finds that

certain regions show a special aspect and color. Thus, in most of the intestinal length, the internal epithelium is a deep yellow to clear brown color. In contrast, certain portions of the inferior curve, particularly the dorsal surface, the epithelium has a very deep brown color. Now, these parts having a dark epithelium are precisely those that receive vessels. These differences in exterior appearance of the corresponding epithelial cells also correspond to modifications in their form and histological characters.

In other spatangoid genera, the path of the digestive tube recalls that of *Spatangus*. In certain genera (*Echinocardium*, *Brissopsis*, *Schizaster*), the very marked difference in color between the inferior curve, which is gray, and the superior curve, which is yellow or brown, is similar to that in regular urchins. One also observes sometimes (*Echinocardium* and especially *Schizaster*) a very notable difference in volume between the 40 inferior curve and the superior curve that is much greater than it and extends above it. Everywhere one observes these differences in coloration of the internal surface of the digestive tube, the epithelium is always darker in the regions with vessels. The rectum has at its origin in *Echinocardium flavesceus* (Pl. III, fig. 10) a small diverticulum that appears to function only as a reservoir for feces as one always finds there material analogous to that which fills the rectum and its structure is the same. *Schizaster* has an analogous diverticulum but relatively much smaller and situated lower.

The path and length of the siphon varies greatly according to genus. In *Echinocardium* (fig. 15, s), it shows as in *Spatangus* a first portion with a thick wall up to the point where it crosses the internal marginal vessel. From there it goes forward, climbs parallel to the esophagus up to the level of the mouth, then recurves to descend again in the opposite direction. It is applied against the internal border of the inferior curve that it accompanies up to its extremity where it terminates. In *Schizaster*, the siphon is very short. It has a thick wall at the beginning, crosses the internal marginal vessels and is applied immediately against the digestive tube into which it quickly opens (Pl. III, fig. 14). In *Brissopsis*, it is not longer than in *Schizaster*, but instead of having a thick wall at the beginning, it enlarges in contrast between the esophagus and the inferior curve in a kind of very vast pouch with an irregular form whose walls are very thin (Pl. II, fig. 11). In *Brissus*, the path of the siphon recalls that of *Spatangus* and *Echinocardium*. It is a tube with very thick walls and transverse wrinkles that reascends in passing under the esophagus up to the mouth, then abruptly recurves, crosses the internal marginal vessels and is applied against the inferior curve that accompanies it up to the adjacent point of its anterior extremity (Pl. II, fig. 10).

An interesting anatomical fact to verify in *Schizaster*, *Brissus* and *Brissopsis* is the existence of a second canal comparable to the siphon that opens on both ends into the digestive tube at two points, variable according to genus, with the inferior curve (fig. 10, 11, 14, *S A*, *g* and *h*). One can consider this canal as a second siphon, a kind of accessory siphon. It is very short in *Schizaster*. In this genus as well as in *Brissus*, it is joined to the digestive tube, while in *Brissopsis* it runs a certain distance from the intestine, always staying parallel to it. This accessory siphon exists neither in *Spatangus* nor in *Echinocardium*.

The diverticulum does not have in these various genera the same appearance as 41 in *Spatangus*. It is a simple, flat cul-de-sac, more-or-less long according to whether the apical pole is more-or-less elongated at the anterior end. It has clear, smooth walls without

transverse folds.

The differences that exist between the digestive tube of regular urchins and those of spatangoids come in part from the displacement of the mouth and the anus. This necessarily entrains certain modifications in the path of this canal. The digestive tube, all things equal otherwise, is longer in the irregulars than in the regulars. The first portion of the intestine, instead of directing itself vertically in order to recurve then towards the anterior ambulacral area, is extended in the direction of the posterior interradius. Morphologically, one should consider it the portion of the digestive tube in spatangoids that corresponds to the esophagus of urchins, as comprising all the region situated between the mouth and the anterior radius, i.e., between the mouth and the point of insertion of the diverticulum. This is in fact only a special adaptation with a physiological goal of the cul-de-sac that the first curve of the urchin has at the entrance of the esophagus. However, from the physiological point of view, one cannot give the name of esophagus to all the portion of the intestine situated this side of the orifice of the diverticulum. I have already said above that it seems preferable to me to reserve the name esophagus to the portion situated in the posterior interradius and to consider as belonging to the properly called intestine, i.e. to the region in which digestion occurs, the following portion that is modified and plays a certain role in absorption of nutritive material since it possesses vessels. The first curve of the intestine ends at the same point in the urchin and *Spatangus*: in the interradius that has the madreporite plate (interradius 5). The rectum is simply elongated in spatangoids. Situated in the regulars in the anterior radial area, it has continued its road in a straight line the length of the unpaired radius in order to open at the posterior end of the body, taking thus the place occupied at first in the urchin by one of the five gonads.

It is also necessary to note that the digestive tube no longer has in spatangoids characters of constant uniformity that occur in the regulars, thus verifying the differences reported above in the paths of the siphon and the existence in certain genera of an accessory siphon or of a diverticulum annexed to the rectum.

Other modifications brought into the intestinal structure have been introduced by the change in life and are only due to exterior circumstances. The digestive tube of the urchin would not have sufficed for an animal that eats only solid material, stone or shell debris. Also we see in spatangoids that it has acquired much thicker walls and is attached to the internal surface **42** of the test by strong mesenterial strings that maintain in position the circumvolutions of the intestine that is always filled with very heavy material.

Finally, an important improvement that characterizes the digestive tube of spatangoids is the differentiation of special glandular organs, such as the diverticulum and certain glands developed in the very thickness of its walls, organs that do not yet exist in the regular urchins.

STRUCTURE OF THE WALLS OF THE DIGESTIVE TUBE – The walls of the digestive tube have an identical structure in all the spatangoids that I have studied. This structure moreover approaches much that we have found in the regulars. In a cross section of the intestine (pl. IV, fig. 21, 22, 23) one encounters, from the exterior to the interior, an external epithelium, a connective tissue layer, a muscular layer, a second connective tissue layer, an elastic membrane, and finally an internal epithelium. Some of these layers have the same

character the entire length of the intestine. Others, the connective tissue layer and the internal epithelium for example, have different characters according to the region to which they belong, differences related to the presence or absence of vessels in these regions.

The epithelial and external connective tissue layers have the same characters as in the urchins: epithelial cells are small and granular with cilia; the underlying connective layer is always very thin and the fibrils that make it up are loose and not abundant.

MUSCULAR LAYER. – Under the connective tissue layer one finds circular muscles, then longitudinal fibers with nearly the same thickness. The transverse layer is however a little more developed. These fibers are especially very numerous in the walls of the esophagus and rectum. They have the same development in the first and in the second curve, and I have never been able to confirm the differences indicated by Hoffmann relative to the thickness of the muscular regions in certain regions. The fibers are generally very long, thin, and possess a clearly bounded nucleus. In preparations fixed with osmic acid and then treated with alcohol or chromic acid, they do not always have the ordinary characters of muscle fibers, but appear most often in the form of stiff fibers with strongly accentuated contours and are difficult to stain with picocarmine. They recall, in a word, the elastic fibers and so much more that the nucleus cannot be seen. But in treating pieces of the digestive tube with a solution of chromic acid at 4/1000 in sea water **43** for twenty four hours, then with the same solution in fresh water for the same time, and finally with alcohol, and then staining with carmine of Grenacher (carmine with borax), one obtains preparations where the characters of the muscular fibers are then very clear, and that one can dissociate after a short stay in 33% alcohol. One then finds, if the stain has not been pushed too far, nuclei strongly stained red that stand out clearly on the fibers that remain paler (fig. 25). The fibers no longer have contours so strongly indicated that they would have in preparations treated with osmic acid. These contours are less regular, more sinuous. The fibers, swollen at certain points and narrow at others, have at last all the characters of true muscle fibers. Moreover, this difference in aspect that affects the muscle fiber following its fixation in extension or contraction is not special to urchins, but has already been observed in various invertebrates.

INTERNAL CONNECTIVE TISSUE LAYER. – It generally constitutes the thickest layer of the intestine, and it is in this thickness that the numerous capillaries of the digestive tube ramify. Also it is preferable to study it first in the regions that do not receive the vessels, the superior curve for example, as it is in these regions that it is less developed. It is made up of two distinct layers. One finds, in fact, in cross sections, an external layer overlying longitudinal muscles that appears in most preparations as a thin, homogeneous, very refringent zone, having the aspect of a brilliant, uniform band. But in pieces that have been submitted to alcohol, one recognizes that it is formed of connective fibrils that are slightly undulating, very fine, and packed (fig. 22 and 23, *C e*). This layer includes neither connective fiber cells nor granulations that one recognizes in the rest of the layer. It is observed the entire length of the digestive tube, except in the esophagus where connective fibers with a circular direction do not exist. The internal layer (*F*), much thicker than the preceding, is constituted of thin fibrils intersecting in all directions forming a loose layer

that includes numerous cells of connective tissue, masses of red or yellow pigment, and some protoplasmic masses (*G*) with irregular contours that look like ameboid cells. The pigment granules are principally abundant in the connective tissue of the esophagus and the superior curve, but one encounters them likewise the entire length of the digestive tube. This loose connective tissue layer is particularly developed in the portions lacking vessels. In the vascular region (dorsal surface of the inferior curve for example) it contains capillaries so numerous that it almost completely disappears and no longer appears **44** in the sections, as in the very narrow interstices that separate them. The vessels never penetrate into the external zone with circular fibers (fig. 23). The lumen of the capillaries is obstructed by coagulated blood, i.e. by a grayish or brown, fine granulated mass that is not stained by reagents, containing blood corpuscles in more or less large quantities. The walls of these capillaries are formed by a layer of the connective tissue layer itself, but they possess an endothelial covering that permits considering them as true capillaries and not as simple holes hollowed into the connective tissue layer. As I remarked when I studied the structure of the vessels, it often happens that the blood corpuscles imprisoned in the clot are preferentially fixed against the wall of the capillary. One could be tempted to consider these cells as forming the true endothelium, if a more in depth examination did not allow easy recognition of the real nature.

Outside the connective tissue layer is found a very thin elastic membrane that supports the epithelium and that does not show special characters (*El*).

EPITHELIAL LAYER. – The epithelium that covers the internal surface of the digestive tube is very developed especially in the regions that receive the vessels. One recognizes in the sections (figs. 21, 22, 23 *E*) that it is formed by several rows of cells, very small at the base and becoming longer and thicker as they approach the free surface of the epithelial layer. The superficial cells can attain considerable length (fig. 26). They always possess a large, very granular nucleus. Their protoplasm is nearly homogeneous, very finely granular, and one never encounters the very marked granulations that exist in regular urchins. It is on the dorsal surface of the inferior curve in *Spatangus*, and in a general fashion in all the vascularized regions, that the epithelium attains its maximum development and that the cells have the largest size. In the other regions, the layer preserves the same appearance but its thickness decreases notably and the cells there are always smaller. The epithelium that lines the esophagus and the rectum is little developed. There is thus a constant relation between the form and the development of epithelial cells and the presence of vessels in the walls of the digestive tube. It is also in the regions that receive the vessels that the cells can undergo a special modification to be transformed into mucus cells that will soon be considered.

For the entire length of the intestine, the internal surface of the epithelial layer has a cuticle lacking cilia.

45 STRUCTURE OF THE DIVERTICULUM. – The walls of the diverticulum has a structure very different from that of the intestine. The muscular layers there are very little developed. The connective tissue is formed of anastomosing fibrils containing cells and pigment granules. One encounters there sections of numerous capillaries. The epithelium is formed,

as in the intestine, by several layers of cells. But the superficial cells are not limited clearly towards the interior. One sees, in fact, in the sections (pl. VI, fig. 38) that they are continuous and are mixed into a mass constituted sometimes by a granular mixture, sometimes by fine reticulum in the middle of which one distinguishes nuclei, protoplasmic masses, debris of cell membranes, in a word, remains of dead and degenerating cells. This mixture, which forms a more or less thick layer, is nothing else than a part of the brown secretion that fills the diverticulum, left attached and fixed by the reagents against the internal surface of its wall. It is easy to be certain, in studying the epithelial layer, since the base where the cells are very distinct up to the point where one finds only granular debris, that the superficial cells degenerate and fall into deliquescence and that it is at their cost that the liquid of the diverticulum is formed, which is emptied into the intestine and which must play an important role in digestion, if one can judge on the development of the organ that secretes it.

GLANDS OF THE INTESTINE. — The diverticulum is not the only secretory organ possessed by the digestive tube of irregular urchins. One finds, in fact, in the thickness of the intestinal walls, and that in all genera, two sorts of special glands. There exists first of all in all parts of the inferior curve that receives vessels, numerous mucus cells situated in the midst of the epithelial cells, appearing in the form of clear spaces, never stained by picrocarmine and that, seen at a very high magnification, show an enveloping membrane and a transparent, very finely granular hyaline content. The characters and the situation of these elements must make them considered as epithelial cells that are transformed into mucus cells and that open ultimately into the intestine. Moreover, the existence of similar elements in the digestive tube is a very frequent fact in different animals.

Other much more perfect glandular organs are encountered at the commencement of the inferior curve, in the region between the end of the esophagus and the first opening of the siphon. These are true glands composed in the form of pears or bottles situated in the thickness of the connective tissue underneath the epithelium. Although they occupy only a relatively restricted space, **46** they are very numerous because they are dense and often superposed. They have a properly called glandular part. This is spherical and contains long cells with a very apparent nucleus and a finely granular protoplasm that radiate from the center to the periphery, and an elongated neck lined with small cells that open at the surface of the epithelial layer. When the glands have been divided by the razor exactly according to their axis, which is not the most usual case, one can distinguish there a central cavity that is continuous with the lumen of the neck and containing slightly granular material that is nothing else than the secretion of the gland coagulated by the reagents (fig. 21, *G l*).

These glands exist in no other part of the intestine. I have sectioned the entire length of it without ever encountering them elsewhere. They are observed in the same region and have the same characters in *Echinocardium*, *Brissus*, *Schizaster*, and *Brissopsis*, at least as far as I have been able to judge in the three latter types by samples preserved in alcohol that I had at my disposal. They evidently do not correspond to the glands that Hoffmann illustrates pl. VII, fig. 52 and that he found near the opening of the diverticulum (in the latter third of the stomach). I have sought these glands in this region with more care than anywhere else. I have encountered only the mucus cells of which I spoke above. I cannot

explain the nature of the elements that the author represented in this figure. At least it is not a matter of a mass of nuclei belonging to the epithelial cells united into a more or less compact mass as I have encountered in different parts of the digestive tube that have been submitted to the action of chromic acid. Moreover, I can repeat here the remarks that I made regarding the digestive tube of urchins, on the results that Hoffmann attained in his histological research. In *Spatangus*, as in the urchins, he has taken the epithelium for a connective tissue layer rich in cells and poor in fibers. He has described as “eine Drüsenschicht fast ganz ohne Fasern, zum größten Theil nur aus Zellen gebildet, welche in einer sehr sparsamen hyalinen Grundsubstanz liegen.” The glandular cells that he found there are nothing other than the nuclei of epithelial cells whose contours have disappeared, altered as they were by a reagent insufficient to preserve them. This explains why he has seen neither the cells with mucus in the intestine, nor the modifications that the epithelial cells of the diverticulum undergo. He says, in fact, in speaking of the diverticulum, “Die Drüsenschicht ist gelblich gefärbt und besteht aus denselben zelligen Elementen, wie sie im Anfangstheil des Dickdarmes auch vorkommen.”

STRUCTURE OF THE SIPHON. — The siphon has a structure that differs according **47** to whether one studies its free portion or its portion attached to the inferior curve. In this last part, the cylindrical siphon has a thin wall with an exterior ciliated epithelium, a little-developed connective tissue layer, a circular muscle layer (without longitudinal fibers), a connective tissue layer with an outer layer with circular fibers and an internal layer with longitudinal fibers containing numerous pigment granules, and finally an internal epithelium containing elongated cells with large nuclei. Hoffmann denied the existence of muscular fibers in the siphon walls. However, I have constantly found a muscular layer, little developed to be sure, but however quite recognizable. In the free portion, the siphon has a very thick wall and the form of an isosceles triangle in cross section. Its lumen also has a triangular form. The thickness of the wall is not the same for all three faces. The face turned towards the beginning of the inferior curve and which forms the base of the triangle has in fact only a layer of ordinary connective tissue lined on its two surfaces with epithelial cells. The two upper and lower faces are re-enforced with a thick layer of gelatinous tissue interposed between the connective tissue layer and the internal epithelium. These layers become thinner as they approach the base of the triangle to give the aspect shown by Hoffmann in his Pl. VII, fig. 54, *b*. This gelatinous connective tissue has (Pl. IV, fig. 27) a fundamental homogeneous mass in which are embedded numerous connective tissue cells, sending very fine and anastomosing extensions in all directions. The external connective tissue layer is very thin. The internal epithelium has the same characters as in the adjoining region of the digestive tube.

These modifications in the structure of the siphon walls are very curious and it is difficult to explain them. Hoffmann noted that the digestive tube, being filled with stone, could easily compress the walls of the siphon and completely close the lumen if its walls did not have sufficient resistance. In the region adjoining the inferior curve, this compression cannot take place as the gelatinous tissue is not found there. But if one keeps in mind that the circumvolutions of the digestive tube are kept fixed with the aid of very resistant mesenterial laminae, it is difficult to understand how they could compress the

siphon. Moreover, even supposing that the weight of the stone that they contain could change their position, the pressure that they could exert on the siphon certainly would not be very great as it is necessary to take into account the liquid of the body cavity and the decrease of relative weight that it would cause. Moreover, the walls of the first portion of the **48** siphon are not very thick in *Brissus* and they are very thin in *Brissopsis*.

I shall add still some words on the structure of the mesenterial laminae. They are made of a layer of connective tissue formed of very dense and very tight fibers, lined on both surfaces by small ciliated cells. The laminae are continuous with the external connective tissue layer of the digestive tube and, at the level of attachment points, with the internal membrane of the test. They show this in particular at the point of insertion on the digestive tube. Their two surfaces are re-enforced by muscle fibers parallel to the axis of the intestine. We see the same thing in regard to the vessels.

NERVOUS SYSTEM

The nervous system of echinoids has been known with certainty only for a short time, and its existence was even controversial for the past years. The opinions of different anatomists who considered the question were summarized and discussed by Baudelot who added to the descriptions of his predecessors some anatomical facts and very precise structural details. One knows that Tiedemann was the first to indicate the existence of a pentagonal ring surrounding the buccal opening of regular urchins that sent branches into the ambulacral zones. But Tiedemann's descriptions were based only on theoretical ideas and not on anatomical observations. His hypothetical views were confirmed by Van Beneden and particularly by Krohn who, in a work published in 1841, determined the exact disposition of the nervous system and gave excellent figures to which his successors found little to add.

Shortly after the publication of Krohn's memoir, Agassiz expresses doubts on the importance that should be given to the threads previously described as nervous, especially based on the difference in relation the nerve band had with the ambulacral calcareous pieces in urchins and asteroids. This objection was opposed by Duvernoy²⁷ first and then by Müller²⁸. Then, in 1866, Vulpian²⁹ was led by his physiological experiments to acknowledge the existence of the nervous system in asteroids, but he thought nevertheless that "the very fact of the existence of a nervous system, such as has been described by previous authors, could be doubted.

50 Baudelot confirms all points of Krohn's research on echinoids, as he easily verified by allowing the test of urchins to macerate in dilute nitric acid. He demonstrated that there are principally in the external region of the nerve band, numerous apolar, unipolar, and bipolar cells and returned to Agassiz' question: Are the organs described as belonging to the nervous system really representative of the system? The anatomical disposition that had been described as the subject of this system and which Baudelot had verified exactly, are certainly in agreement, he said, with what one would expect of a nervous system of a rayed animal, but one cannot *a priori*, being given a cell or fiber belonging to a part

²⁷DUVERNOY. *Mémoire sur quelques points de l'organisation des Echinodermes*. – Mém. Ac. Sc. Paris 1849.

²⁸MÜLLER. *Anatomische Studien über die Echinodermen*. – Archiv. F. Anat. und Phys. 1850.

²⁹VULPIAN. *Leçons sur la physiologie du système nerveux*. – Paris 1866.

considered as nervous, say that it is really a nerve element. The physiological experiments done by Baudelot certainly support the existence of a nervous system, but do not permit him to say with certitude that the peribuccal pentagon and the branches that leave it correspond really to the nervous system. He thinks this question is far from settled and that it is necessary to have new investigations.

The study of the nervous system was resumed in 1876 by Frédéricq who described with more care than his predecessors the pathway and termination of the nerves and undertook a series of experiments on the physiology of the system. The result of his research, more complete than that which had been done by Baudelot, allowed him to conclude that the system described by Krohn is really the nervous system. As a special nervous center does not exist in urchins, the different portions of the nervous system can function separately and the pentagonal nerve allows simply the coordination of movement. I shall have little to add to the memoir of Frédéricq.

One knows that the nervous system of regular urchins is made of a pentagonal ring immediately applied against the internal surface of the buccal membrane, surrounding the beginning of the pharynx, and sending into the ambulacral zones five nerves that end at the level of the ocular plates. The nerve ring that is very difficult to see in fresh animals because of its adherence to the pieces of the masticatory apparatus. It lets itself be isolated most easily in animals that have been macerated in 20% nitric acid, following the method indicated by Baudelot. The five ambulacral nerve trunks are surrounded by a connective tissue sheath covered with epithelial cells whose relation to the circulatory system will be a question. I cannot consider it as a true vessel. This envelope is not continuous on the nerve beyond the peristomial ring. If one can make an injection into this perineural space one sees the material always escapes at the point where the nerve passes under the auricles and expands into the general cavity.

51 From each angle of the peribuccal pentagon arise ambulacral nerves whose caliber is nearly the same as that of the pentagon and increases as soon as they cross the auricles. They keep the same thickness until the middle of the ambulacral zone, then gradually decrease in thickness and disappear at the ocular pore without sending out trunks that cross this pore in order to spread out on the external surface of the test. The internal surface of this band is, like the upper surface of the peribuccal ring, divided into two halves by a shallow longitudinal groove. The internal border of this ring produces, at the level of each angle, two small threads that extend the length of the pharynx with the five pairs of ligamental sheaths that accompany this canal. These nerves were described for the first time by Frédéricq. This dissection is very difficult because of their fineness but is made much easier by using nitric acid. It is probable they go to the muscles of the lantern.

At the level where the radial water canals send their branches to the corresponding ampullae, the nerve band sends a branch that follows the external border of the ampulla and reaches the tube foot by the tube foot pore that is nearest the mid-line, as shown by Frédéricq. This nerve penetrates into the wall of the tube foot which it follows throughout its length and ends immediately below the sucker in a small enlargement. It is easy to verify the path and the termination of the nerve by observing in a species that is not very pigmented, such as *Echinus acutus*, either a living tube foot where the nerve has a brownish color or a tube foot fixed in extension and stained with picrocarmine where the nerve

appears in the form of a ribbon slightly more stained than the tissue of the tube foot. In cross sections, the section of the nerve is seen equally in the form of a mass of very fine granules with a certain number of nerve cells on its surface.

In cross section of the ambulacral nerve, one sees that the nerve band has two distinct regions: an internal part nearly exclusively composed of fibers, and an external cellular part. The internal region has a considerable number of tightly packed small dots. These are the sections of the nerve fibers. Rare nerve cells occur in the midst of these fibers. The external region, in contact with the internal surface of the test, contains a large number of small cells with conspicuous nuclei. These are very dense towards the periphery and become more and more spread out towards the central part. There is thus no absolute edge separating the fibrous and cellular regions.

The characteristics of the nerve fibers cannot be defined in the sections. **52** It is necessary to resort to dissociation to study them. A very advantageous procedure consists of treating the nerve with a solution of chromic acid (4/1000) in sea water for several hours, then a solution of chromic acid in distilled water, finally with alcohol and staining with Grenacher's carmine. The elements are easily dissociated and the nerve cells show the following characteristics. The large nucleus is very granular and deep red in color. The colorless cellular protoplasm is filled with fine granules. The enveloping membrane is very thin (Pl. VI, fig. 45). Most of the cells have one, two, or sometimes three extensions. It is rare to find cells that lack them. I have never observed that nerve cells were completely bipolar with extensions disposed in as regular a fashion as shown by Frédéricq. The nerve fibers resemble those of other invertebrates. They are very fine, very pale, and with little variation. They are difficult to stain with ordinary reagents.

The structure of the nervous system is identical in the ambulacral nerves and in the peribuccal pentagon. In the nerve strands that extend to the tube feet, we still find the same distinction between a fibrous portion and a cellular portion. Only here the cells are grouped around the fibrous portion.

The swelling at the end of the ambulacral nerve has numerous nerve cells. It is quite probable that the numerous strands leaving these cells and making, under the epithelial layer of the sucker, a nerve plexus very rich in cells. It is certain that these nerves, from the moment that they cross the test, give off a certain number of branches, and these themselves ramify within the connective tissue layer that lines the external surface of the test. Until now, I have not been as fortunate as Frédéricq and it has been impossible for me to see this nervous network. The preparations made either with osmic acid, chromic acid or gold chloride have not given any satisfactory result at all. However, a network analogous to that Lovén showed in spatangoids should exist in urchins. We know, in fact, that fragments of the test of an urchin can live for a long time and that the spines and especially the pedicellariae continue to show active sensibility when they have been detached from the test. The spines can still move, weakly it is true, while the internal organs are already in a state of very advanced putrefaction and the liquid of the general cavity emits a repulsive odor. These facts can be explained only by the existence of a nervous plexus made up by fibers and cells occupying all of the superficial connective tissue layer.

53 Frédéricq relates a certain number of physiological experiments that he has done on urchins and that I have repeated several times. These experiments show that a central

nervous region does not exist in these creatures, and that the ambulacral nerves can function separately as distinct centers. It is easy to cut the ambulacral nerves close to their exit from the peribuccal pentagon with incisions on the buccal membrane. After this operation, the tube feet and spines move as rapidly as before, but the urchin has lost the faculty of coordinating its movements. The tube feet move in all directions, but the animals always stays in the same position. If it is turned onto its back, it cannot regain its normal position.

It is useless to dwell on the different experiments that one can make on this subject (sectioning nerves at different levels, galvanic excitation, etc.) that are reported in Frédéricq's memoir. They show, in every case, that these organs considered since Krohn as a nervous system actually belong to this system, a result that, moreover, was already known.

There is little to say on sense organs in urchins. The most developed sense in these animals is that of touch. The tube feet that serve for location must be, in fact, very perfect tactile organs seeing their richness in fibers and nerve cells. The sphaeridia equally can be considered as sense organs, whose nature is difficult to determine. Lovén thinks that they are taste organs. As for the pigmented layer that Valentin had found on the ocular plate and that he considered as an organ of vision, we have known for a long time that it does not exist and that there is no question now of a sense of vision in urchins.

SPATANGOIDS. – The details that I just gave on the nervous system of urchins permit me to describe rapidly the nervous system of spatangoids. The nerve pentagon that surrounds the mouth is directly applied against the test and has the same form as the peribuccal ring. In spatangoids, its two lateral sides are smaller than the anterior side and the slightly convex posterior side. In the species with a large peristome, the nerve pentagon tends to take a more regular form, the two lateral sides becoming nearly as long as the anterior sides. Research on this ring is much easier than in urchins. It is sufficient to remove the membrane that covers the upper lip in order to see very distinct adjacent vessels in the form of a thin brown cord. From the five angles of **54** the pentagon leave nerves that go to the ambulacral zones. As in urchins, they are enclosed in a space opening into the general cavity and send from time to time oblique branches that leave by the ambulacral pores to go to the tube feet. Instead of having a groove in the middle of their internal surface, these nerve bands are, to the contrary, swollen in their median portion and thin at the borders (Pl. V, fig. 35 N).

The nerves that go to the interior of the tube feet do not have a swelling at their ends. One can follow them in sections only a certain distance. Near the end of the tube foot, the nerve divides into a large number of branches. These go into the terminal crest of these tube feet up to the expanded ends. Very probably they are connected with the special epithelial cells that form these swellings.

The structure of the nervous elements in spatangoids is the same as in urchins.

Lovén has illustrated the superficial nerve plexus in *Brissopsis lyrifera*. I have never been able, no more than in urchins, to confirm the existence of such a plexus. Moreover, the same facts that explain the existence of this plexus in urchins are also seen in spatangoids where portions of the isolated test and detached pedicellariae continue to show

great sensitivity for a long time.

I have made sections of the ambulacral nerves of spatangoids, but the experiments did not lead to any conclusive results, the functions of locomotion being extremely reduced in these animals because they generally stay immobile.

The sense organs are no more developed in spatangoids than in urchins. The tube feet can be considered as tactile organs. It is the sole function they have because they do not function in locomotion. It is easy to see in young spatangoids, whose movements are more active than those of adults, placed in glass bowls extend their peribuccal tube feet in all directions and apply them to the walls of the vase. One sees also *Echinocardium* extend the long tube feet that surround the infra-anal fasciole, which seems to help it recognize the nature of adjacent bodies. As in the regulars, Lovén considered the sphaeridia of spatangoids to be special sense organs.

GONADS

The gonads are found in the interambulacral areas of urchins and are nearly the same form and size in an individual. However, one observes that the gonad in interradius 5, according to Lovèn's notation, is always a little less developed than the four others. They generally extend nearly the entire length of the ambulacral zone. Such is the case in *Dorocidaris*, *Arbacia*, *Strongylocentrotus* and *Sphærechinus*. In *Psammechinus*, the gonads are reflected toward the apical pole, so that one usually does not see them in an animal opened by the ventral surface unless the digestive tube is raised. They show moreover this peculiarity, that all five are joined in a very thick ring that surrounds the end of the rectum and which is open only on the side of radius 1, from which the rectum extends. Their interambulacral portions, strictly speaking, are not very extended and one could even say correctly that they are simply conical expansions that the perianal ring sends into the interambulacral zones. The gonads attain the minimum of their development in *Sphærechinus*. They are reduced to simple linear bands, not very large even in the season of sexual maturity. Outside this season, they are indicated in each zone by a small brownish track. One can see with a microscope the withered and atrophied glandular culs-de-sac. In *Dorocidaris*, *Arbacia* and *Strongylocentrotus* they are always very large, even outside the season of reproduction. They have the form of a triangular prism with its convex surface molded to the concavity of the test and the others connected to the curves of the digestive tube. In *Echinus*, they are connected to the upper part of the test and generally do not pass the middle of the interradiar zone. In contrast, they are very large and globular.

The gonads of urchins are clusters of gonias, made up of distinct cul-de-sacs that join in canals of the second order **56** which form a common excretory canal that opens to the exterior by the genital pore. The genital elements, eggs or sperm, develop along the entire length of these cul-de-sacs at the cost of the epithelial cells that line them.

One knows that no external differences exist that permit distinguishing males from females. Only examination of the products permit this. Outside the season of reproduction it is impossible to distinguish the sex. In *Strongylocentrotus*, the testes are generally pink, while the ovaries are yellow. In *Psammechinus*, the male glands are smaller and more strongly colored brown than the ovaries which have the same color as in *Strongylocentrotus*. In the other species, the color of the gonads do not differ.

One knows that the gonads of urchins are active at seasons fixed for a determined species, but generally variable in different genera. However, I have found most species in Marseille in full sexual activity in the months of March and April. *Strongylocentrotus* is already apt to reproduce from the month of September, the season in which they become edible, until the month of April. But it is not unusual to encounter in any season of the year

individuals whose gonads are filled with eggs and sperm.

In spatangoids, the number of gonads never exceeds four; the posterior gonad, that which belongs to interradius 3, has disappeared and its place is occupied by the rectum. In the types that have four gonads, one always sees that the anterior pair is the less developed and that, of these two anterior gonads, that which occupies interradius 5 is always very small. This is what happens in *Spatangus*, *Echinocardium*, and *Brissopsis*. In *Brissus*, it has completely disappeared. Finally, in *Schizaster*, the two posterior gonads alone are preserved. There is no longer a trace of the anterior pair (Pl. II, fig. 12).

The form of the gonads in irregular urchins is globular. They are, as in regulars, gonad clusters with very distinct acini and a tissue much firmer than in urchins. If the distinction of the sexes is up to a certain point possible in the latter, it is no longer the same in the irregulars, where the color of the testes and the ovaries is the same. This color, of a deep red purple in *Spatangus*, yellow in *Echinocardium*, is due to the considerable development of red or yellow pigment in their walls. This pigment is not developed in the gonads of *Schizaster*, which are completely colorless. The season of reproduction in *Spatangus* does not occur until spring, during the month of 57 March or April. It is at this moment alone that it is possible to distinguish the male and female gonads, whether the liquid that escapes is white, opaque like milk or resembling a transparent jelly containing eggs.

The structure of the gonads is the same in urchins and spatangoids. In the former, the walls of these organs are only thinner and more delicate than in spatangoids, but the same tissues exist in the two types and show the same characteristics. A cross section of an ovary of *Spatangus* (Pl. VI, fig. 43) shows, going from the exterior to the interior, the following layers: an epithelial layer analogous to that found on the external surface of all organs contained in the general cavity: a connective tissue, a muscular layer, and an internal epithelium. The connective tissue layer has outer transverse fibers (*c*, *t*) and longitudinal inner fibers (*c*, *l*). They contain numerous pigment granules and corpuscles of connective tissue. The muscular layer (*MI*) has only circular fibers. It is always very developed. The internal epithelial layer is the most important. It is at the expense of the cells that constitute it that the eggs are formed. Their development is very simple. The cells that, outside the season of reproduction form a layer without any special characters, multiply actively when this moment arrives. They increase rapidly in volume, detach from the wall of the ovary and fall into the cavity of the tube. They are large cells with a very granular protoplasm, offering a very clear germinal vesicle and a dark germinal spot. Once the egg is completely mature, the granules of the protoplasm become much more abundant at the same time that the vesicle and germinal spot completely disappear. The eggs develop in the same way in all echinoids.

The testes have the same layers in their walls as the ovaries. They differ only in the destiny of their epithelial cells that give rise to the spermatozoa. When one observes, in a fresh state, the contents of the testes tube of an urchin, or a spatangoid at the season of reproduction, one can very easily account for the modifications of these cells and the mode of development of the spermatozoa. One finds first (Pl. VI, fig. 46) a great number of very finely granulated cells, whose nucleus cannot be seen or rather whose nucleus occupies the entire cell (*a*). These cells must not correspond to the epithelial cells of the tubes, but probably result from a division prior to the latter. I have, in fact, encountered, very rarely

it is true, these smaller cells joined in **58** regular groups of 4 or 8 having the aspect of groups of cells that had just divided. This makes it possible to suppose that echinoids have a first generation analogous to that which was discovered quite recently by Sabatier in annelids. These spermatospores are not slow in becoming morula (*b*, *c*, *d*) containing a considerable number of small nuclei, each of which becomes a spermatozoa and that thus make up the second generation. The transformation of spermatozoa in the morula stage does not take place according to a regular division, but is the result of an endogenous production from the interior of the mother cell from nuclei that develop at the expense of the protoplasm itself. This, at first indistinct and poorly delimited (*b*), differentiates little by little and acquires very clear contours(*c*, *d*). I have never observed tails of spermatozoa to develop at this moment. Once the nuclei of the morula are completely developed, they separate and are seen sometimes isolated, sometimes joined in groups of four or five (*d*, *e*). They are not slow in acquiring much greater dimensions while preserving their spherical form. This is when the tail of the spermatozoa appears as a simple elongation of the protoplasm of the nucleus. At the same time that the tail develops, a small brilliant and very refringent nucleus (*g*) differentiates at its base. The development of the spermatozoa is from that time nearly finished. It still grows a little, the tail elongates and the head takes the characteristic form (*h*) of an ovoid ending in a point. The brilliant spot that marks the point of insertion of the tail persists and is found in completely developed spermatozoa.

Such is the mode of development of spermatozoa in *Spatangus purpureus* that I have studied during the month of April. After that I observed at the same season and to the month of August in *Sphæchinus granularis* the same phenomena that come about in a manner identical to regular urchins.

CIRCULATORY SYSTEM

REGULAR URCHINS

Circulation in regular urchins has been the object of a large number of investigations by several scholars. But until 1875, the date that Perrier published his work on the circulatory system of urchins, we had only very vague results and many points of inaccurate views on this difficult question.

One knows the theory that Valentin has given for the circulation of the urchin, a theory established with difficulty and sometimes not in accord with the facts that had been observed. There exists, according to him, two vascular rings around the esophagus on the upper surface of the lantern and two vascular rings around the anus. One of these would be in communication with one of the periesophageal rings by a vertical canal to which is attached the heart. The other periesophageal ring produces the intestinal artery that runs along the border of the intestine and opens at the second perianal ring. Each vascular circle of the anus produces five radial water canals, and the blood that arrived by the internal intestinal vessel passes into one of these radial water canals to respire in the ampullae and the tube feet, and empties into the second vascular anal ring by the second radial water canal. It is this latter that produces the intestinal vein or external vessel that send numerous branches to the test. From these esophageal rings also leave two vascular systems, arteries and veins that ramify in lantern muscles.

One sees that the circulation in the urchin, according to the ideas of Valentin, is very difficult to understand. The connections that he supposes exist between the four rings that surround the two extremities of the digestive system are not clearly established. After having spoken first of only *one* anal ring, he supposes a second to complete his theory. There is no reason to discuss or refute Valentin's theory that at several points is in complete disagreement with the facts.

60 Valentin recognized two distinct intestinal and ambulacral circulatory systems that communicate with each other. According to him, other observers, Siebold and Gegenbaur, expressed at the same time some doubts on the exactness of the facts observed by Valentin, thinking there was reason to distinguish the properly named circulatory or intestinal system and the ambulacral system.

Gegenbaur³⁰ says of the circulatory system: The water system contains the five radial water canals that join in an esophageal ring, to which are annexed the Polian vesicles, and

³⁰GEGENBAUR. *Manuel d'Anatomie comparée. Edition français*. Page 309.

which communicate with the madreporite plate by the stone canal. The circulatory system strictly speaking is represented by an esophageal ring distinct from the preceding, but in communication with it by a tubular heart with an anal ring. The two rings emit radiating ramifications. "There can be no question of a distinction between an arterial and venous path. All arrangements of the ensemble seem designed especially to transport liquid nourished by the intestine into the rest of the body, to distribute it there where it encounters at the same time conditions necessary for gas exchange.... If previously one thought that the two systems were clearly distinct from each other, one presently has good reasons to support the contrary opinion. Communication of the two systems seems to be always the most probable."

Communication of the two systems was established definitively by Hoffmann in the regulars and especially in *Spatangus* where it had already been discovered by H. Milne-Edwards. Hoffmann is occupied principally with circulation in *Spatangus* where its study does not present the same difficulties as in urchins, and gives few details on the subject of regulars. For him, there is only one periesophageal vascular ring, to which end the stone canal and the two vessels of the intestine. There is no anal vascular ring, nor vessels that go into the walls of the test. As for the structure and probable function of the heart, Hoffmann had very little to say.

The existence of the vascular anal ring denied by Hoffmann is acknowledged again by A. Agassiz³¹. It receives, according to him, the intestinal vein. Moreover, the anal ring sends a parallel vessel to the stone canal, which swells at a certain point of its path in an ovoid, hollow dilation that is the heart and ends at the periesophageal vascular ring from which goes the intestinal artery (internal vessel). The intestinal vein gives at the same time branches to the digestive tube and test. How does the intestinal artery end and what is the origin of the intestinal vein? **61** Agassiz does not say. The vessel that goes to the anal ring and to the esophageal ring is distinct from the stone canal. But how does the stone canal end? Agassiz says, "The stone canal, starting from the madreporic body runs along the heart to the circular ring." Is this circular ring the same as the vascular ring that he just questioned, or instead a second ring superimposed on the first? Agassiz has not responded to this question.

The arrangement described by Agassiz is, one sees, still very obscure and it is not possible according to his work to have a clear idea of circulation in urchins.

Perrier (1875) took up the study of the circulation of urchins and obtained very important results about the distribution of this system. After having demonstrated that the anal vascular ring does not exist, he studied the organ thought to be heart and its relation with the stone canal. He shows that this organ is nothing other than a gland independent of the stone canal and opens by a distinct canal under the madreporite plate. He remarks that the gland in question is completely closed below and produces on a vessel parallel to the stone canal. Cross sections show well that the stone canal is completely independent of the gland. It is connected to it for its entire length but has no other relation with it. The five radial water canals that end in a cul-de-sac at the apical end, open into a single esophageal

³¹AGASSIZ. *Revision of the Echini*. 1874.

circle to which detaches the stone canal from one side and the internal marginal vessel from the other. The two systems, water and intestinal, are thus in direct contact. The internal marginal vessel runs the length of the esophagus and sends branches only at the first curve of the digestive tube. The external marginal vessel, which also furnishes branches only at the first curve of the digestive tube, has no communication with the circle of the lantern and receives blood by numerous anastomoses with the internal marginal vessel. The second curve of the intestine does not receive vessels. As for the branches described by Agassiz as going to the walls of the test, they do not exist. Finally, the external vessel is in connection with a special vessel discovered by Perrier, *the collateral vessel*, which does not send branches to the digestive tube and seems to be, he says, a sort of reservoir where the excess contents of the circulatory system could be diverted.

The results Perrier reached are, we repeat, very important. They reveal several new arrangements of great interest and establish definitively the most controversial points of the circulatory system, the true nature of the heart of the old anatomists, the absence of the vascular ring around the anus, and the exact arrangement of the vessels on the digestive tube. However, **62** a memoir of Teuscher appeared the following year, where the work of the French scientist is not mentioned and where we find described arrangements very different from those that had been discovered by Perrier. The work of Teuscher, being little known in France, makes me dwell on them for a moment.

According to Teuscher, urchins have, as in all echinoderms, two circulatory systems: the vascular strictly speaking; the other, water. Both have a true esophageal ring. The first contains two distinct parts, one belonging to the visceral system, the other to the nervous system.

We shall first consider the water system. It consists of five ambulacral water vessels that, at the level of the lantern, run the length of the pyramids to empty into the periesophageal water ring. This is the ring to which belong the five Polian vesicles and from which leaves the stone canal, which runs the length of the esophagus along the heart and ends at the madreporite plate. As in asteroids and spatangoids, the heart is of no utility at all in the adult animal and must be an embryonic development or even an ancestral organ passed on by heredity.

The vascular system belonging to the viscera is comprised of a ventral vessel and a dorsal vessel that follow the borders of the intestine. The first, more developed, runs along the internal border of the digestive tube up to the rectum. The second, of smaller caliber, follows the external border and divides in two at a certain part of its path along the first curve.

Teuscher has not been able to recognize the anal vascular ring, but he did not doubt its existence. It is made nearly evident by the fact that the ventral vessel preserves, he says, the same caliber up to the beginning of the rectum, and it is hardly probable that it would end abruptly in a cul-de-sac. It must, on the contrary, continue its path and empty into the perianal ring.

The ventral vessel continues the length of the esophagus to empty into the periesophageal ring. It seems likewise to Teuscher that the dorsal vessel, despite its small caliber at the level of the esophagus, must empty into this ring.

In addition to the five ambulacral water vessels, each ambulacral zone has, as in

spatangoids, a vessel that surrounds the nerve band. This is the perineural vessel. Only, contrary to that which Teuscher observed in other echinoderms, particularly in spatangoids, a vascular ring does not exist around the nerve pentagon in communication with the perineural vessel of the ambulacral zones. At the level of the opening of the auricles, the ambulacral and perineural vessels, as well as the nerve band, all three tightly united up to there, separate. The nerves continue their path in a straight line and converge towards the neural pentagon. The perineural vessels cease to surround the neural system in order to rejoin the 63 pharynx, climbing the length of this canal and emptying into the periesophageal vascular ring. The water vessels are applied against the external surface of the lantern and climb the length of the pyramids in order to end in the periesophageal ring. Teuscher has not injected these five vessels that run the length of the pharynx, in the very interior of the lantern, but he has recognized the following arrangement in his cross sections. The pharynx has five pairs of ligamental sheaths that accompany it for its entire length. In the furrow that separates the two sheaths of each pair is an opening that corresponds to a vessel. Now, these five vessels can open only into the periesophageal vascular ring.

As for the communication of the two water and vascular systems, Teuscher says nothing of it in his memoir. He says only, in the summary that ends his work, that this communication appears uncertain to him in urchins.

Such are, in summary, the principal results of the work of Teuscher on the urchin (*Echinus esculentus*). A first reproach to address to the German naturalist has to do with the incomplete knowledge of the previous published work on the question. He seems, in fact, not to have known the memoir of Perrier that had appeared in advance of his, and whose principal results had been communicated to the Academy of Sciences in November 1874. Otherwise his attention would have been drawn to certain arrangements that the eminent professor of the Museum had made perfectly clear and on which he correctly insists. Among them is the certain, easily verifiable absence of the vascular anal circle, the path of the ventral vessel that does not reach the rectum but stops at the beginning of the second intestinal curve, and the structure and the role of the so-called heart as Teuscher continues to call it, recognizing that nothing in the structure permits it to be considered as such. It is true that Teuscher had at his disposal only animals preserved in alcohol and most of his observations have been made on sections done at different levels in the regions with the vessels. The process of successive sections and different orientations constitute an excellent means of control, but are not sufficient to reach a complete and certain knowledge and can, moreover, very often result in error when it is not accompanied by a dissection made on injected specimens. The vessels that Teuscher reports and illustrates along the pharynx and which do not exist in reality, proves it in a very clear manner. This is moreover a point to which I shall return, as to many other facts indicated in his memoir.

Whatever defects of the procedures Teuscher used, his work merits serious consideration. Although the research of Perrier did on living animals with all the desirable care appears to have definitively fixed the circulation of urchins, the conclusions of the two scientists 64 differ on a great number of points so that it appears necessary to take up again this interesting but very difficult question. I was led likewise more willing as it was difficult to reconcile the results that I had obtained earlier in studying the circulatory system of

Spatangus with that which was known about urchins. In particular, the existence of two peribuccal rings, the fact that the stone canal, divided in the esophageal region into two distinct canals, one of which opened into the peribuccal ring, far from remaining distinct from the organ of excretion, acquires the most intimate relations with it, do not correspond with what Perrier described in regular urchins.

When at the beginning of my studies, not yet occupying myself with the circulatory system of urchins, I studied the structure of the ovoid gland in order to compare it with that of the homologous organ of spatangoids, one thing struck me. In making sections of this organ fixed in osmic acid and then fixing in absolute alcohol, I saw the stone canal perfectly distinct from the excretory organ as Perrier had illustrated. But I perceived here and there, especially in the peripheral part and principally in the sections from the inferior end of the gland, irregularly arranged islets filled with a grayish, finely granular coagulum. These reminded me in all ways of the vascular spaces filled with coagulated blood that are found in so great abundance in the walls of the digestive tube. Evidently, the liquid blood, if the lacunae in question really contain coagulated blood, did not reach the ovoid gland by the stone canal which is independent of it. Perhaps then the stone canal is not a simple canal as most of the naturalists have described but is formed of two joined canals as is the case for the stone canal in Spatangus, at least for a certain part of its path. The question must be examined attentively, and I directed my research to this aspect from the beginning.

Before giving the facts that I have been able to observe, I must say that, for all that regards the study of the circulatory system, I have addressed myself preferentially to *Sphærechinus granularis*, of which I was able to obtain large specimens easily and in abundance at the laboratory in Marseille. Because of its size *Sphærechinus* is the best type. *Echinus melo* and *acutus* reach, it is true, often larger dimensions, but they are rarer, the first especially, than *Sphærechinus* and live in places too far from the coast for me to obtain them regularly. Lastly, I had *Strongylocentrotus lividus* and *Psammechinus microtuberculatus* in abundance.

I preferred to use for injections soluble Prussian blue or ammonium carmine precipitated or not by acetic acid. ⁶⁵ Lead chromate obtained by precipitation also constituted a good mass with granular injection but had the inconvenience of being too large. The very large particles that form the precipitate often plug up the end pierced from the canal and stop injection. The parts injected with Prussian blue have, moreover, the advantage of fixing by the alcohol which permits preserving it and even sectioning it later.

Injections made by the radial water canals, when they reach the stone canal, really penetrate well only into a single canal that always remains distinct from the ovoid gland and preserves the same caliber up to the madreporite plate. I then tried with specimens injected in this manner, with a syringe filled with a solution of a different color from that which I had used in the first experiment, to the middle of the tissue of the gland in order to make an interstitial injection. My first tries were fruitless, or rather did not lead me at all to the result that I had hoped to obtain. The injection filled the excretory canal of the gland and went up to the madreporite plate to the outside or sometimes into the general cavity of the urchin. I had made several injections that always gave me the same results. When I tried, instead of embedding the syringe into the middle of tissue of the gland, to inject it as near as possible to the inferior end, at the place where it ends insensibly into a point. It

seemed to me, in fact, that the gland, from this point, was not as clearly limited as Perrier had illustrated. This time, the injection passed into a canal distinct from the stone canal and the two conduits, filled with liquids of different colors, were very easy to distinguish. Moreover the injection, to the degree that it filled this new canal, penetrated into a system of very fine vessels that branched onto the ovoid gland. From this moment I would succeed nearly always in all my injections. In regarding, in fact, with attention the surface of the non-injected gland, it is very easy to see two branches larger than the others that go on each side of the organ in the form of two small vessels. It is possible to introduce the syringe into one of these vessels and inject it. The injection succeeds equally well if, in injecting the tissue of the gland, one is careful to place the syringe up to the inferior limit of the organ, staying as close as possible to its surface. It often happens that the point of the syringe perforates the injected tissue. Other times one is happier as the syringe penetrates one of the small numerous capillaries that are very numerous at this level, and the injection is easily done.

There is, thus, at the side of the stone canal, a second canal, to which it is attached from the ovoid gland to the upper plane of the lantern, or, if one prefers, the **66** stone canal is double. This arrangement is similar to that in *Spatangus*.

For better simplicity in the descriptions, I shall continue to call the stone canal the vessel (*c*, fig. 13) independent of the ovoid gland that has always been designated by this name. I shall call the *glandular canal* (*CG*) the second canal that communicates with the gland, a name that justifies the close relation with the latter.

It is not even necessary to have recourse to injections in order to recognize these two canals. With an attentive examination with the microscope of the stone canal and the excretory organ of an urchin, one can distinguish two vessels. One is very fine, white and transparent. The other is a little larger, browning and with some dark granules here and there. The first is the stone canal that has been described in the literature. It runs the length of the ovoid gland and has no relation with it. The second remains distinct up to the point of the gland with which it seems to be continuous.

It sometimes happens in specimens preserved in alcohol that the blood coagulated in the interior of the vessels takes a very marked yellowish tint and produces thus a natural injection as apparent as injections made with the aid of a colored solution. Now, I have sometimes found in the excretory organs injected in this fashion, and in which the glandular canal and its branches on the gland were filled with this yellow coagulum. This demonstrates very well that the arrangements that I have just described are not artifacts or due to ruptures.

When injections made by the glandular canal are very successful, the injected material passes into a periesophageal ring, fills the Polian vesicles, and penetrates into the internal marginal vessel that runs along the esophagus. The injected Polian vesicles have the form of small vascular branches that extend into and branch two or three times in a way to reproduce the appearance that has been illustrated by Perrier. But the stone canal is not injected. Sometimes however, in pushing the injection with a certain force, one sees the Polian vesicles fill completely – they can even burst under the pressure of the penetrating material – and the stone canal is injected. But this rarely happens. Most often the injection, after having filled the periesophageal circle, penetrates only the internal marginal vessel.

It is the same thing for the radial water canals that are injected only when the stone canal is injected also.

If, after having made an injection of the glandular canal (with soluble Prussian blue, **67** for example), taking care not to push too strongly for fear of bursting the Polian vesicles, one introduces in the same piece a syringe filled with carmine or lead chromate into one of the radial water canals, one will see the injection penetrate into the vesicles that run the length of the pyramids, reach the esophagus, and empty into a second periesophageal ring (AI) very distinct from that which was injected in blue, pass into the Polian vesicles and empty into the stone canal. This shows us that besides the esophageal ring into which penetrates the glandular canal and from which leaves the internal marginal vessel, is found a second ring into which empties the radial water canals and the stone canal. In the pieces injected in the manner indicated above, these arrangements are easy to confirm as long as the injection is not pushed too strongly. In fact, when the two canals are completely filled and swollen by the injection, as they are superimposed, the upper ring covers the lower ring. In order to see the latter, it is then necessary to dissect the region very carefully and raise all the pieces of the lantern, a delicate and always difficult operation as the vessels are attached to these calcareous pieces by a very resistant connective tissue. It is very nearly impossible to make this dissection without more or less tearing up the vessels that one would like to isolate. When, in contrast, the upper ring is slightly injected and is not entirely filled, the arrangements are very much easily exposed. In injecting one of the systems with Prussian blue and the other with ammonium carmine, precipitated by acetic acid, and then leaving the piece for some hours in alcohol, one obtains a preparation whose dissection is a little less difficult, the alcohol having fixed the Prussian blue and agglutinated the fine particles of carmine.

Just as the injection made by the glandular canal does not penetrate into the stone canal, an injection made by the radial water canals passes only rarely into the internal marginal vessel. It is a fact that Teuscher has made already. When this vessel is injected, one still finds that the Polian vesicles are completely filled with the material.

The two esophageal rings and the systems of vessels that are attached to each of them communicate only at the level of the Polian vesicles. Still this communication is not made by a complete canal as the Polian vesicles are not hollow sacs but are made up of a dense tissue whose structure I studied a little further and that is interposed between the two systems.

The mode of termination of the stone canal and the excretory canal of the ovoid gland, which is basically only the continuation of the glandular canal at the level of the madreporite plate, has already been described by Perrier. These canals do not empty directly into the exterior. In fact, the madreporite plate is **68** covered by a very thin lamella of connective tissue that is continuous with the same mesenterial layer, extended from the esophagus to the rectum. The very narrow space, thus limited, is comprised in part by a brownish spongy tissue into which empties side by side the two canals in question (Pl. III, fig. 13), and it is not rare to see the injection made into one of the canals penetrate into the other at the same time it escapes outside across the pores of the madreporite plate or even, sometimes, into the general cavity. This question of communication at this level with the fluid of the general cavity will be discussed later.

A longitudinal section made at the level where the esophagus starts contains the peribuccal ring and confirms, first of all, that there are two distinct canals and not just one. One sees that the superior canal (consequently the one that communicates with the internal marginal vessel) has a caliber a little smaller than the superior ring. The structure of these rings is very simple: a connective tissue layer covered with epithelial cells. Numerous pigment granules are contained in the midst of these fibers. No muscular elements are encountered.

The structure of the intestinal vessels is identical to those that I shall study further in *Spatangus* where the preparations are made more easily, in view of the much considerably larger dimensions.

RADIAL WATER CANALS. – Teuscher acknowledges the existence in each ambulacral zone of two vessels, one of which surrounded the nerve band. It is the perineural vessel. The other, in contrast, is independent of it and completely superficial. This is the water vessel. This is the arrangement that I have never been able to confirm, and I cannot acknowledge the existence of a perineural vessel. There actually exist two vessels in each ambulacral zone. But both, although closely connected to the nerve, are however quite distinct.

First of all, in a fresh piece, it seems there is only a single vessel in each ambulacral zone. When one introduces the needle of a syringe to inject, one sees the material pass into the vessels that goes the length of the pyramids. These are very simple vessels. The fact is easy to confirm. However, in the pieces belonging to specimens of larger size, one recognizes easily the existence of two vessels. One is superficial and narrow. The other is situated immediately below and is a little larger. Each of them produces transverse branches to the ampullae. The two branches that go to each ampulla are very distinct, although attached. This disposition is seen in a very evident fashion when one allows the test of the urchin to macerate for several days in picric acid. They are very clear **69** in the preparation I have shown in Pl. V, fig. 36. It is possible to inject the two vessels with different colored solutions and to show thus that each ampulla receives two branches, one belonging to the superficial vessel (*Vs*), the other to the deep vessel (*Vp*) that remain distinct up to their entrance into the ampulla where they both open. A careful dissection shows that the deep or external ambulacral vessel (*Vp*) is independent of the sub-adjacent nerve band.

The schematic section of an urchin ambulacrum illustrated by Teuscher (Pl. XX, fig. 7) is not very exact in my opinion. The sections made at different levels of the ambulacral show a superficial vessel and a deep, larger vessel tightly applied against the nerve. Although very thin, the external wall of this vessel is easy to distinguish. Teuscher has not seen this external wall of the ambulacral vessel and this is what he thought surrounded the nerve band. The sections that I have obtained of the ambulacra in the urchin are identical with those that I have illustrated in *Spatangus*, Pl. 5, fig. 35. The only difference is that the nerve, instead of being attenuated at each end is to the contrary swollen in the urchin and narrower in the center. The nerve band is not directly applied against the test, but is separated from it by a narrow interval. One sees in Fig. 35 that it is enclosed in a space limited by connective tissue walls. Now, this space is not a vessel but really a portion of the general cavity. It sometimes happens, in fact, when an injection is made by the radial

water canals, that the needle, instead of penetrating into one of the vessels *Ve* or *Vp* lodges in the space *Cg*. In this case, the material goes the length of the ambulacral zone and spreads into the general cavity at the level of the auricles, i.e. at the level of the point of origin of the vessels that run the length of the pyramids. An analogous fact is observed in *Spatangus* where, under the same conditions, the material injected comes to fill the space left free between the upper lip and the membrane that covers it. According to the figure of Teuscher, this fact cannot be explained because, for him, this interval *Cg* corresponds to the perineural vessel and is not part of the general cavity.

The injection never fills the ampullae immediately, but follows the external border of each ampulla and fills it little by little by penetrating into the small alveoli limited by numerous partitions that divide the cavity. Teuscher and Frédéricq have already spoken of this arrangement that is seen in cross sections of these organs, particularly, as I indicated before, in the vesicles treated with 1/5 nitric acid. After the action of this reagent, the walls become firm and cannot attach to one another so that the two surfaces remain distinct.

The wall of the ampullae show, on the inside of an external connective tissue **70** layer, a well developed muscular layer and formed everywhere of circular fibers.

A question that is connected with the study of the circulatory system is to know how the ampullae communicate with the tube feet. Baudelot and Frédéricq have shown that each ampulla corresponds to a tube foot, and that communication is made with the aid of two small, very fine canals that cross the test through the pores of the poriferous zones and open into the cavity of the tube foot. This arrangement is easily verified in *Sphaerechinus*, *Echinus*, *Strongylocentrotus*, by macerating test fragments in nitric acid. In *Dorocidaris*, where the ambulacral pores are not geminate as in the previous genera, but are simple, to each ampulla corresponds well a tube foot. Only the communication is established with the aid of a single canal that crosses the test pore. I have never seen that the tube foot was double for the greatest part of its length, that it showed in cross sections two tubes joined as the barrels of a double-barreled rifle as Baudelot said. It is formed by a single cylindrical canal through its entire length.

Once they reach the level of the border of the peristome, the radial water canals, double as they were, become single and form then the five branches that climb the external surface of the lantern and come to open into the inferior periesophageal ring. At the same time that the vessels of each ambulacra fuse into a single canal, the wall is slightly modified in structure. It is filled with pigment, brown granules, analogous to those found in other vessels and that are not found in the ambulacral trunks.

Branches from the radial water canals directed towards the lantern do not exist other than these five vessels. Teuscher described, as I said above, five other vessels that run the length of the pharynx and open into the superior periesophageal ring. These vessels would be the continuation of the perineural vessels, while the ambulacral water vessels would open only into the inferior esophageal ring. Now, Teuscher has not injected these pharyngeal vessels, and has never followed them. It is from studying sections of the pharynx that he believed he recognized them between the five pairs of ligamentous fascia. Moreover, injections were never made suggesting their existence. I do not see how Teuscher explains how the vessels that surround the nerve band in the ambulacra quit it abruptly to go the end of the pharynx. It would be necessary then to admit that the nerve,

enclosed in the interior of the perineural vessel, perforates immediately the wall of the **71** vessel in order to reach the neural pentagon, an arrangement that would be very strange. The fact that, in urchins, the neural pentagon is not situated in the interior of a vessel, as it was in the ambulacral zones and as it is, according to Teuscher, in all echinoderms, seems astonishing to him. I do not know if the nervous system is surrounded by a vessel in the other echinoderms. But I affirm that, in echinoids, such an arrangement does not exist. The connective tissue sheath containing the nerve is continuous with the internal membrane of the test to the level of the auricles and is not a vessel. It does not go up to the pharynx which is simply re-enforced with ligamentous fascia, but possesses no vessels.

One will be able to believe, first of all, when looking at an urchin injected without removing the pieces of the lantern that these five pharyngeal vessels exist. In fact, the radial water canals are not completely finished in giving off the vessels that run the length of the pyramids, but continue still a little towards the mouth in the form of small thin branches applied closely against the internal surface of the buccal membrane. It is easy to be assured, by raising the pieces of the lantern, that these vessels whose path was described and illustrated by Perrier are destined to the ten tube feet that surround the opening of the buccal membrane and that they disappear before reaching the pharynx.

The vessels of the ambulacral zone end in a cul-de-sac at the level of the apical pole. However, I am not absolutely certain if both these vessels end there in a cecum or if they join at their end. All my observations tend to make me suppose that they both end in a cul-de-sac without communicating with each other. This is, moreover, a question of a secondary interest to know if they communicate or not at the apical extremity, because they are placed in communication the entire length by branches they each send to the radial water canals and are joined in a single vessel when they reach the lantern.

The path of the intestinal vessels has been described with care by Perrier. My research has reached the same results as the scholarly professor of Paris. It would no longer be a question now of a vascular ring around the anus, the marginal vessels not passing the beginning of the upper intestinal curve. However Teuscher declares that they continue up to the rectum and even finds, in the existence on the rectum of a marginal vessel that has there, he asserts, the same diameter as on the first curve, an argument in favor of the existence of the anal vascular ring. The error of the German naturalist is easily explained. If one examines the internal border of the upper curve of any urchin, one sees that it is accompanied by a very narrow mesenterial lamella having, very near **72** the very edge of the intestine, a dark band that resembles a vessel. This band continues up to the rectum. It is nothing other than an accumulation of pigmented granules and special cells, reproducing a little the appearance of the mesenterial lamella described by Perrier, and extending from the esophagus to the anus. One understands that this dark line can be taken for a vessel and that Teuscher, having at his disposition only animals preserved in alcohol and studying them principally with the aid of histological sections, was able to suppose that the internal marginal vessel continues up to the rectum and empties into a perianal ring.

After the preceding, the circulatory system of regular urchins can be understood in the following fashion. Two superposed vascular rings surround the esophagus on the upper surface of the lantern. From the upper ring leaves the internal marginal vessel that runs along the esophagus and the internal border of the inferior intestinal curve to which it

furnishes numerous branches all along its length. It does not pass the beginning of the second curve. The branches of the internal marginal vessel are also the branches of origin of the external marginal vessel, also limited to the first curve, and which turn back gradually to the esophagus without reaching the periesophageal ring. A third vessel, discovered by Perrier, who named it the collateral vessel, makes the circuit of the test parallel to the inferior intestinal curve. This is a dependence of the external marginal vessel to which it is attached by a dozen anastomosing branches. They communicate neither with the periesophageal ring nor with the internal marginal vessel. This collateral vessel seems also to have been seen by Teuscher who speaks of a doubling of the dorsal vessel forming "ein zweites, frei in die Leibeshöhle herabhängendes Rückengefäß aus, mit dem eigentlichen durch zahlreichen Anastomosen communicirend und etwas weiter als dasselbe. Neither of the two marginal vessels continues onto the second curve, a fact that is sufficient already to show that he did not know of the existence of the vascular ring around the anus.

The stone canal, considered ordinarily as a simple canal of very small diameter, is formed by the joining of two connected canals, of which one comes to empty into the upper periesophageal ring, the other into the lower ring. The half that opens into the upper circle, or glandular canal (*Cg*, fig. 13) communicates with the ovoid gland and permits it to receive blood in very great quantity. The other half (*C*), which leaves from the lower ring and which corresponds to that which until now has always been called the stone canal, remains distinct from the ovoid gland and reaches to the madreporite place with the excretory canal of the latter or, if preferred, with the end of the glandular canal.

The lower periesophageal ring leaves the five ambulacral **73** vessels that remain single while they leave the lantern and which double from the point where they reach the ambulacral zones of the test into two superposed vessels. Each sends a branch to the radial water canals. These vessels are distinct from the nerve band which is connected to them. A perineural vessel does not exist, but only a perineural space. The radial water canals are not in direct communication with the upper periesophageal vessel because there does not exist in the interior of the lantern along the pharynx a vessel establishing such a communication. Finally, from each of the two esophageal rings leave branches that go to the Polian vesicles and ramify. Blood of one of the rings therefore cannot pass into the other without having traversed the glandular tissue of these vessels.

In order to end the study of the circulatory system of the urchins, it remains to me to speak of the structure of the excretory organ or ovoid gland, as well as the structure of the Polian vesicles, the glandular canal, and the properly so-called stone canal. The excretory organ has, in fact, too close relations with the circulatory system for it to be possible to study them separately. On the other hand, the Polian vesicles have a composition identical with that of this organ, and the glandular canal, which continues insensibly with it, has a structure comparable in all details to that of the ovoid gland. These reasons have determined me to combine in the same paragraph the study of these organs that, however, can pass for being very different.

OVOID GLAND. – The form of the ovoid gland differs according to the species and seems proportionally most elongated in the tallest test. In *Echinus melo* and *acutus*, it is a fusiform

organ, very long, terminated in a point at its two ends. In *Strongylocentrotus lividus* and *Sphærechinus granularis*, it is much less elongated, relatively, than in *Echinus*, more rounded and a little irregular in its contours. It is the same in *Psammechinus*, where it is nearly globular. It is everywhere a dark color, from yellowish to clear brown, and its surface is speckled with numerous brown granules. It is connected to the esophagus by a thin mesenterial lamella and extends, as we know, from the esophagus to the rectum, extending towards the madreporite place in the form of an excretory canal that ends with the stone canal. The surface that is opposite the esophagus is creased with a longitudinal groove in which is lodged the stone canal. When, after having raised this, one separates the two lips that limit this groove, one sees a canal larger than the stone canal, extending the entire length of the organ and receiving a considerable number of small canals, very distinct at the place where they empty into the principal canal but that are not slow to anastomose and to **74** lose themselves in the parenchyma of the gland. This canal is the excretory conduit of the ovoid gland (Pl. III, fig. 18).

This organ has always been considered a heart until the day when Perrier refuted this erroneous opinion. Most naturalists who have described this heart have based their opinion on no certain fact. The structure of this singular organ, that no one had been able to recognize, was, in fact, very embarrassing and did not fit well from the little that was known of it, with the idea that one could make a heart of it. The existence of muscle fibers was, moreover, very controversial. Hoffmann considered it as “a spongy organ with a large central cavity in its interior appearing to be continuous with the vessel that leaves from the inferior part. In sections, one sees that this central cavity is surrounded by networks of trusses forming a mesh. At the periphery, the tissue becomes more compact.” The nature of these fibers remains doubtful for Hoffmann. He thinks, as Leydig, that they are, in part, muscle fibers, circular for the most part, but he has never been able to dissociate them in a satisfactory fashion. In the midst of these fibers are encountered a considerable quantity of pigmented masses and small colorless spherules. Teuscher describes it as an organ “constituted of a slightly transparent tissue containing some fibers that become more numerous at the extremity and of whose histology he could say nothing. Between the fibers are numerous pigmented granules and isolated cells that rather resemble nuclei, all contained in a fundamentally granular substance. Irregular gaps are found here and there but no large internal cavity.”

One sees here that the descriptions that Hoffmann and Teuscher have given of this organ are not of a nature to inform about its structure, still less about its functions. The former calls it a heart, without nevertheless indicating its role. Teuscher thinks that it is the remains of an embryonic or ancestral organ that has no function in the adult. Perrier gave a definitive solution to this problem in showing that this organ, absolutely deprived of muscle fibers, possessed all the characters of a true gland, constituted by acini particularly clear in *Psammechinus* and including glandular cells. “These cells, he says in fact, are arranged in columns, as occurs in compact glands, the liver of mammals for example. They are about 24 μ and are filled with refringent spherical granules that are colorless in certain cells and more or less brown in color in others. This is the explanation of the existence of these cross-barred masses of brown granules that we have already reported. Each small mass represents the contents of a glandular cell. Each **75** column of cells represents a

glandular acinus and the columns are themselves grouped in a manner to give the appearance of divergent digitations from a common trunk. The columns of the cells leave between them more or less great intervals in which filters the secretory product as in all compact glands of this nature. Certain of these intervals, larger than the others, are secondary cavities of the heart described so minutely by Valentin and that we have shown in the section that we give of the ovoid gland of *Echinus sphœra*.”

The organ called heart by the old anatomists is thus only a gland annexed to the stone canal and expelling outside, across the pores of the madreporite plate, excretory products. This explanation puts a decisive end to discussions that the structure of this enigmatic organ had previously raised, in view of the difficulty that one had in finding the ordinary characters of a heart, i.e. of an organ with essentially muscular structure capable by contracting of circulating blood.

In studying this organ in various genera that I have had at my disposal by sections and dissections always made on pieces fixed with osmic acid, I obtained results a little different from those of Perrier, not on the very nature of the organ which is quite evidently glandular, but on its fine structure. According to my observations, the structure of this gland approaches, in fact, much that I observed in *Spatangus*. In pieces of the gland fixed by osmic acid and treated then with alcohol, then dissociated, the most numerous elements encountered, other than brown pigment granules that the osmic acid turned completely black, are cells with an irregular protoplasm emitting fine extensions, lacking enveloping membranes and a granular nucleus. The nucleus appears finely granular in some cells while in others it is completely filled with large granules. From the nucleus with fine granules up to those which have, so to speak, only an accumulation of pigmented masses, are all the intermediaries. The protoplasm is itself finely granulated and more or less abundant. The cells of which the nucleus is very granular have only a thin protoplasmic envelope. Here and there are found cells with clearer and freer boundaries with a smaller nucleus and a very finely granular protoplasm.

The sections through the body of the ovoid gland shows that it is made up of a very regular network of connective tissue with trabeculae limiting the spaces nearly all the same size and form in the peripheral region, becoming smaller and anastomosing to form a dense, more irregular mesh towards the 76 center (Pl. VI, fig. 41). The alveoli thus limited contain the cells described above in varying number, but generally not great, one to four per alveolus (*Cr*). Here and there, in the peripheral region are found alveoli filled only with small brown nuclei. My first idea, in studying sections of this gland, was that I was quite in the presence of a cellular tissue as described by Perrier. The remarkable regularity of the boundaries led me to believe in cells arranged side by side, enclosing a granular nucleus surrounded by a zone of irregular protoplasm and connected to the membrane by some extensions, as could often be seen. However, in encountering here and there cells having two or three nuclei each surrounded by a distinct protoplasmic layer, I wondered if it were really a cellular tissue or if really that which I had considered first as a cellular membrane were rather a reticulum of connective tissue, the more so as the central part of the organ had a network of very distinct connective tissue fibers supporting small cells with a ramified protoplasm. It seemed difficult to accept that the same organ was made up in its peripheral region by cells and in the central part by connective fibers as there was not a

distinct line of demarcation between the fibers and the cells and the one continued visibly with the other. In other preparations where the arrangements were clearer, analogous to those that I have illustrated Pl. VI, fig. 41, and where most of the alveoli contain two or three nuclei surrounded by protoplasm, proved to me in a certain way that it was actually a matter of connective fibers and not of cellular membranes, and that the substratum of the gland connected of connective tissue trusses arranged very regularly to the periphery of the organ with an appearance easily resembling a cellular tissue, and becoming more numerous but also more characteristic towards the central part. It is in the cells supported by this connective tissue substratum that are arranged the pigmented granules that become more and more numerous. They end by completely filling the alveoli, producing a considerable accumulation of dark granules that is preferentially found in the peripheral portion of the gland. This structure is in all points comparable to the homologous organ of *Spatangus*, and which can still confirm my opinion, with this sole difference however, that in the latter the trusses of connective tissue are much less regular, larger, and better characterized in urchins, which makes the interpretation of their arrangement easier.

As for the lacunae that have been described in the interior of the gland, they correspond to the section of small canals that empty into the excretory canal. One knows, in fact, that these lacunae are arranged irregularly and do not have ⁷⁷ the same form or dimension in all sections. Their number and their aspect depend on the way the blade has gone through a more or less number of canals. But all the lacunae do not correspond to excretory conduits. There are, in fact, especially towards the periphery and in the lower part of the gland, those filled with a granular coagulum and that is nothing other than the section of numerous vessels that we have seen ramify to the surface of the ovoid gland.

The same arrangement is seen in the genera *Echinus*, *Sphærechinus*, *Strongylocentrotus*, and *Psammechinus*.

POLIAN VESICLES. – A structure analogous to that of the ovoid gland is found in the Polian vesicles. One knows that these organs have been considered to be diverticula of the periesophageal water ring serving as a blood reservoir, or even as contractile expansions destined for blood circulation (Gegenbaur). Such an opinion can no longer be supported. It has long been known that their walls do not have muscular fibers. Tiedemann, and Valentin after him, have not been able to find them. Hoffmann passes rapidly on the structure and the role of Polian vesicles. According to him they are made up of two epithelial layers, one external and the other internal supported by a thin connective membrane rich in small nucleated cells. Teuscher says that their very thick walls are made up of a tissue analogous to that of the heart, by fibers, nuclei and masses of pigment enclosing in one fundamental, finely granulated substance. Because of the smallness of their cavity and the slight elasticity of their walls, these organs cannot serve as a blood reservoir, but it is, nevertheless, difficult to indicate their functions.

The Polian vesicles in most urchins (*Strongylocentrotus*, *Psammechinus*, *Sphærechinus*) look like very thin organs fixed to the upper part of the lantern, in the doubling of the membrane that covers it between the muscles of the compass and the vascular rings. Their borders are not clearly defined. With the microscope, one distinguishes in the interior slight trails of brown granules that become more numerous and

more apparent towards to the periphery. In the species of the genus *Echinus* they are a little thicker than in the other types and their surface appears lobed or irregularly nipped.

Injected material, when it penetrates into the Polian vesicles, does not fill them completely, but is diverted into some secondary branches that ramify in their interior, and follows these small trails of brown granules. The appearance is the same whether the injection is made by the **78** upper or lower esophageal ring. Their structure is a little more complication than believed and resembles that of an excretory organ. These organs show, in fact, a cavernous texture. They are made up of a substratum of connective tissue, arranged in the form of large bays and anastomosed to be united and connected in a manner to resemble alveoli of unequal size filled with cellular elements. We encounter here cells lacking membranes, with an irregular protoplasm surround a nucleus more or less filled with granules that we have encountered in the ovoid gland. Here and there, granules are grouped in a voluminous mass and have replaced the cells in the cavities of the alveoli. This is the ensemble of cells and granules that give to these vesicles this characteristic appearance of brown stripes (Pl. V, fig. 31).

The structure of the Polian vesicles is thus in its essential elements analogous to that of the ovoid gland and makes it necessary to consider it a glandular organ probably functioning in excretion.

STONE CANAL AND GLANDULAR CANAL. – We find finally analogous relations in the wall of the glandular canal. Imagine a section of this canal made at a point equidistant from the ovoid gland and the upper surface of the lantern. We obtain at the same time a section of the stone canal. This is the preparation I have drawn Pl. VI, fig. 40 which shows three distinct canals with very different characters. One of these canals (*CS*) is the stone canal that one recognizes with its internal epithelium formed of small, elongated, and very regular cells. Its wall is made up only of connective tissue containing some rare pigmented granules and these calcareous spicules in the form of crescents or circular arcs that are found so abundantly in all the tissues of urchins. The second canal (*L*) has a connective tissue wall lined on both sides with small epithelial cells and has no importance. Sometimes when trying to inject the glandular canal by the lower end of the ovoid gland, the injection flows into a small space that one could take for a vessel. Only this canal does not reach up to the lantern and it diminishes away from the ovoid gland. The existence of this interstice is easily explained. The connective tissue wall that covers the ovoid gland in fact continues onto the stone canal and the glandular canal. Because these are not absolutely connected at the level of the lower level of the gland, there results a small empty space in which the needle can sometimes be lodged. This is nothing other than the median canal *L* that can be seen in the section. The third canal (*CG*) is the most important. This is the glandular canal. It is a little larger **79** than the stone canal and has a very different structure. The external epithelium and the connective tissue layer have nothing special in their arrangement and their elements. Only this latter sends by the internal surface several partitions that divide the cavity into a certain number of secondary spaces. Some of these are covered by small ordinary endothelial cells and others, to the contrary, are crossed by trabeculae of the third order that anastomose to form small irregular networks with fine mesh, supporting elements analogous to those of the ovoid gland, i.e. oval cells with irregular contours and

fine granular protoplasm, and cells with a clear protoplasm surrounding an irregular zone with a granular nucleus. Here and there are pigment granulations. Between the ordinary endothelial cells and the other elements identical to those of the ovoid gland, one can find transition forms that can be considered modified endothelial cells. In sections closer to the peribuccal ring, these conjunctive tissue bays become less abundant. Although if sections are continued towards the ovoid gland, the caliber of the canal increases little by little and its walls are continued insensibly, without an abrupt transition, with the tissue of the gland. The trabeculae become more numerous and more regular. The elements that they support become more abundant. The lacunae lined with a simple endothelium also become more numerous and make up vessels that ramify into capillaries at the surface of the gland and that can be seen at the edge of the section. As for the first canal, i.e. the stone canal, it keeps the same characters throughout its length and always remains perfectly distinct from the ovoid gland. To the degree they approach the upper end of the gland, the sections become smaller and smaller and one passes to the excretory canal with very thick walls and a structure analogous to that of the gland itself.

The study, with the aid of successive sections, of vessels running from the periesophageal ring to the madreporite plate, thus confirm the results which we obtained by injections and show that beside the properly called stone canal exists a second canal that can be considered as an extension of the ovoid gland up to the upper periesophageal ring. In other words, the periesophageal ring communicates with the exterior on one hand by the intermediary of a simple canal, the stone canal and, on the other hand, by the intermediary of a complex canal, having glandular elements its entire length that agglomerate at a certain point to form a true gland.

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SPATANGOIDS.

The bibliography of the circulatory system of spatangoids is less developed than that of urchins, and I shall consider only the two memoirs of Hoffman and of Teuscher. According to Hoffman, the circulatory apparatus of spatangoids is made up in the following way: a ventral vessel (internal marginal) and a dorsal vessel (external marginal) accompanying the digestive tube and sending numerous branches to it. The ventral vessel, which at first follows the entire length of the diverticulum, passes under the digestive tube at the level of the orifice of this diverticulum, runs on the large ventral mesenterial lamellae, and comes to attach opposite the siphon. It continues its path up to the level of the second orifice of the vessels into the digestive tube. Throughout its path it regularly sends vessels to the digestive tube. The dorsal or external vessel, which arises likewise from the diverticulum, follows the external border of the digestive tube and furnishes it, like the ventral vessel, with numerous vessels.

The dorsal vessel and the ventral vessel cannot be followed up to the end of the inferior

curve (second curve of Hoffmann). As a consequence, they cannot give branches either to the esophagus or to the stomach (first region of the inferior curve) or to the superior intestinal curve. The distribution of blood is made in a special way. At the level at the point where the ventral vessel crosses the siphon, it gives off a branch that is attached to this latter and follows it up to the point where it opens into the stomach. This is the vessel that, because of its distribution, Hoffman calls *intestinal vessel*. It must in fact, furnish blood to the esophagus at the beginning of the inferior curve and to all the superior curve including the rectum. A little after its origin, this intestinal vessel produces a small vessel that runs the length of the esophagus in order to empty into the peribuccal water ring. Hoffmann calls it the *branch of communication* (*Verbindungszweig*). From the peribuccal ring leave the five radial water canals and the stone canal. This latter, whose complicated trajectory Hoffman describes with care, ends at the *water heart*, the head process of the head process located at the end of this diverticulum. This organ has a very complex structure and resembles a gland as well as a heart. Hoffmann calls it sometimes *Wassergefäßherz* sometimes *Wassergefäßsdrüse*. Its functions are unknown to him, and he does not know of the homologous organ in urchins or holothuroids. After its exit from the heart, the stone canal comes to terminate at the madreporite place, passing under two small calcareous plates that constitute a protective apparatus for it.

81 Such is, in summary, the information that Hoffman gives us on the circulatory system of spatangoids. Without speaking of certain inaccuracies and several gaps to which I shall return further, I shall make here only a grave reproach to Hoffmann. His figures are not always in agreement with his text. He speaks in his text of an intestinal vessel charged with distributing blood to the stomach, the esophagus, and to the superior intestinal curve. But why does he pass over so rapidly the path of this curious vessel that would be very interesting to know, being given the different organs to which it has to be distributed. If he does not describe it in his text, he illustrates it still less in his plates, and his figure 42 does not accord with that which he said of the intestinal vessel: “ein Ast, das Magengefäß, welcher..... sich ungefähr bis gegenüber der Stelle wo das gewundene Organ in Magen ausmündet verfolgen lässt, um sich dann in Magen, Dünndarm und Esophagus zu verzweigen” (page 69). Now, in this figure 42, he shows in *t* this intestinal vessel as a branch that runs along the siphon, whose caliber diminishes insensibly, and which disappears before reaching the digestive tube. This exists in reality. The intestinal vessel does not at all merit this name, because after having given the branch of communication, it very quickly becomes thinner and disappears. It is very difficult to understand why Hoffmann describes this vessel as being in charge of carrying blood to different regions of the intestine while in his figure he makes it stop before even having reached the digestive tube. I believe that the few words that he says about it and the disagreement between his plates and his text, to this regard, shows that it is necessary to keep some doubts about the path and ramifications of this vessel.

Teuscher had at his disposition for the study of the circulatory system of *Spatangus* only specimens preserved in alcohol. He confirms some of the results of Hoffmann, describes some new arrangements, but disagrees with him on several points. His memoir, unfortunately, lacks clarity and it is often difficult to follow his descriptions that he did not make with much order. I am going to try to summarize his work as clearly as possible. As

in urchins, the circulatory system is made up of two distinct parts: a water system and a vascular circulatory system. Each system has a vascular ring around the mouth. The vascular system has five perineural vessels that empty into the peribuccal ring which encloses the neural pentagon in its interior. The ambulacral water vessels, situated more superficially in the ambulacral zones, empty into the water ring, distinct from the former and from which leaves the stone canal that goes to end at the madreporite plate. In its path it meets the heart placed at the end of the diverticulum. But, contrary to what **82** Hoffman says, it acquires no other relation with it than a relation of contiguity. It is attached to it more tightly than in the urchin, but does not communicate with it. It is always separated by a distinct wall. If, in introducing the needle into the heart and pushing strongly, the injection passes into the canal, this is because the very thin partition that separates them is ruptured. There is thus no difference between the heart of urchins and that of spatangoids. Nothing, moreover, indicates the heart is a gland. Its physiological significance is the same as in the urchin. It is an embryonic or ancestral organ that has no use in the adult.

The system of vessels of the intestine agrees with the description given by Hoffman. In some places of the intestine that one makes a cross section, one always finds a dorsal vessel and a ventral vessel. Teuscher acknowledges thus the existence of two marginal vessels continuous the entire length of the intestine. As for the anal vascular ring, which Hoffman does not mention, Teuscher cannot confirm its existence in a precise fashion, but he thinks it exists as in urchins. "Sah ich doch", he says in fact, "wie beim Echinus, aus der ammittelbaren Hage des Afters ein zartes Gefäss mit dem Steincanal zum Herzen hinabsteigen, welches sich auch nach dem Austritt aus demselben wiederer kennen liess, und am Mastdam sehe ich zwischen den zwei Blättern des ventralen Mesenteriums ein nich unbedeutendes Gefäss, dicht an jene Gegend herantreten; also ist auch sein Vorhandensein wahrscheinlich (page 535)." I have cited textually the passage of Teuscher because it is impossible for me to understand what he means by this vessel that leaves from the area of the anus and goes towards the heart with the stone canal.

How can a communication now be made between the two circulatory systems. Here the descriptions of Teuscher are very obscure. There is first the branch of communication of Hoffman that connects the peribuccal water ring with the ventral vessel. But the stone canal is also in relation with the intestinal vessel. This communication is made with the marginal vessel of the upper intestinal curve at the level of the point where the stone canal abruptly recurves in order to pass the dorsal surface to the ventral surface. It remains to find the relations of the peribuccal vascular ring, as the stone canal and the branch of communication empty into the peribuccal water ring. Here is all Teuscher says on this subject: in making a section of the stone canal at the level of the esophagus, he finds beside it a vessel of nearly equal caliber and that also runs the length of the esophagus without decreasing in size. It is very likely that this vessel must communicate with the vascular ring.

The upper lip is covered on its internal surface with a fine, acellular membrane **83** that Hoffmann considers as the internal membrane of the test that is detached at this point. If one carefully makes a small hole from the exterior into one of the calcareous pieces of the upper lip and introduces into this opening the point of a conical needle, it is easy to inject this cavity and its extension on the edge of the lower lip. The injection penetrates into the

radial water canals.

I have not followed in this presentation the order of the memoir of Teuscher. One sees that, on most of the points, the information that he gives is very obscure. For him, urchins have two marginal vessels the entire length of the intestine, and he thinks there is an anal vascular ring. This arrangement is so important that the existence of this ring must be, in order to be definitively acknowledged, be based on actual observations and not on simple suppositions. Teuscher disagrees with Hoffmann on several points. E.g., he describes two peribuccal rings, two distinct vessels in each ambulacral zone, a heart independent of the stone canal, results that are contrary to those of Hoffmann. Regarding the relation of the vascular and water systems, he speaks of a vessel that accompanies the stone canal and has to empty into the peribuccal vascular ring. But where does this vessel come from? We certainly see that it ends at the level of the mouth, but we do not know its origin. Finally, according to Teuscher, the membrane that covers the upper lip would be a dilation, a vast sinus formed by the peribuccal vascular ring. In addition to this arrangement not being very clearly explained and seeming very bizarre, it is still in contradiction to the observations of Hoffmann.

On these points, the greatest divergences thus exist between Teuscher and Hoffmann. I wanted to summarize these memoirs as completely as possible and to show the points on which one can from the beginning and before all anatomical observation conceive serious doubts, because they are the points that I particularly applied myself to clarify. My results differ notably from those of the two scholars whose observations I have related.

The five genera of irregular urchins whose anatomy I have been able to study (*Spatangus*, *Echinocardium*, *Brissopsis*, *Brissus*, *Schizaster*) show in the arrangement of the vessels some constant differences regarding to the path of the stone canal, the path and the distribution of the vessels of the digestive tube, and principally of the internal marginal vessel. The genus that serves as my type in this description is *Spatangus*, which I have studied mainly the circulation because of its size and especially the ease with which I have been able to have a large quantity at Marseille. *Ech. flavescens* was very easy to obtain, but is usually too small to make injections easily. As for **84** the other genera, all that I dissected were preserved in alcohol. I described thus the circulatory system of *Spatangus*, reporting when they occurred, differences and specializations that I observed in the other types.

When one opens a *Spatangus* from the ventral surface, one sees very easily on the large ventral mesenterial lamella, a vessel with a very large caliber (*V.M.I.*, pl. I, fig. 1, 2, 3). This is the ventral vessel of Teuscher and Hoffmann. As in urchins, I shall call this the internal marginal vessel in contrast to the external (dorsal) marginal vessel. These terms, used by Perrier, specify better the position of the two vessels than those of ventral and dorsal, which can give only a false idea of their position. The internal marginal vessel, which emerges above the inferior intestinal curve, describes first a very pronounced curve with the convexity turned towards the exterior. It is then very distant from the digestive tube. Then it approaches it gradually, crosses the siphon, and comes to be attached to the internal border of the latter that it accompanies up to the level of the its second opening in the digestive tube, keeping always the same caliber (*b*). From the opening of the siphon, the diameter of the internal marginal vessel abruptly decreases. It continues up to the end of the lower curve, in the form of a small, very thin vessel, which disappears rapidly in

giving some small branches to the digestive tube and without reaching the upper curve.

If we follow the internal marginal vessel in the opposite direction, we see it pass under the digestive tube (in *c*, fig. 1) to the level of the opening of the diverticulum, reach the diverticulum, and accompany it to its end, decreased progressively in diameter and giving it numerous branches that ramify within the thickness of its walls.

Hoffmann describes and illustrates the internal vessel as regularly giving branches its entire length to the digestive tube. This is incorrect. The distribution of these branches is far from being regular everywhere, and varies according to whether it is a matter of the dorsal or ventral surface of the intestine. In the recurved portion, i.e., in the portion not attached to the siphon, it gives seven or eight branches to the left which, taking a right angle, reach the digestive tube and ramify immediately to form a very tight and very rich plexus. These vessels extend equally to the dorsal and ventral surfaces of the lower curve. These are the only ones, other than the small, very thin branches of the thin end of the internal marginal vessel, that ramify on the ventral surface of the lower curve. Nearly all of the blood that circulates in the internal vessel is destined for the dorsal surface of this curve, and it arrives there in a peculiar fashion. To perceive this arrangement, it is necessary, after having injecting the vessels, to open the animal by its dorsal surface and detach the upper curve. ⁸⁵ This preparation is represented in Pl. I, fig. 2. One sees then the internal marginal vessel abruptly divides at the level of the end of the siphon into five or six large trunks that run the length of the dorsal surface of the intestine in the opposite direction of the vessel from which they originated. They then anastomose by dividing rapidly to form a network of very abundant and very dense capillaries. This vascular plexus is not developed on the entire dorsal surface of the lower curve, but in approximately half. The vessels gradually decrease in size and end by disappearing without anastomosing with those of the plexus that are found a little higher and are developed at the expense of the branches that leave the recurved region of the internal marginal vessel.

The internal marginal vessel thus does not give off branches the length of its path and the arrangement of capillaries is very different on the upper and lower surface of the intestinal curve. Hoffmann shows on the two surfaces of this portion of the intestine regular branches from the internal vessel that ramify on the largest part of the lower curve. It is difficult for me to explain his error in this regard. The slightest injection shows the arrangement that I show and it is sufficient to look at the digestive tube from the upper surface to see the particular termination of the internal marginal vessel at the level of the siphon.

The distribution of the external marginal vessel is simpler and more regular (*VME*, Pl. I, figs. 1, 2, 3). It follows the diverticulum its entire length, passes from there over the external border of the lower curve which it accompanies for a while keeping the same caliber up to the level of the second opening of the siphon, the point of departure from which it gradually decreases in size to completely disappear towards the end of the lower curve, like the internal marginal vessel. It gives to the diverticulum numerous branches that anastomose with the analogous branches coming from the internal marginal vessel, then, over its entire length, regularly spaced branches to the digestive tube up to the point where it is going to disappear. These branches, which are distributed on the two surfaces of the intestine, anastomose with the branches of the marginal vessel at the points where they

form the capillary network.

The result of this arrangement is that the dorsal surface of the lower curve receives much more blood than the ventral surface. I shall recall to this subject the differences that I have reported in the structure of the two surfaces of this curve. In the vascularized region, the epithelial layer, of a dark color, is much thicker, shows larger and more numerous cells, and a considerable number of mucus cells, characteristics that are no longer found in the regions lacking vessels.

The result is that the external marginal vessel does not communicate with the **86** internal marginal vessel except by the intermediary of the capillaries developed on the wall of the digestive tube. It has no relation with the peribuccal rings, an analogous fact exists in urchins. But the capillaries that join the two vessels are so numerous that the connection can be established easily. An injection passes very rapidly from the internal vessel into the external vessel. It is not uncommon to make an injection into the internal vessel in one direction and see it return by the other end and in the opposite direction. The path is easy to follow. The injection, I suppose, is distributed by the branches of the internal marginal vessel to the level of the opening of the siphon on the dorsal surface of the digestive tube, passes into the capillaries that communicate with the divisions of the external vessel, follows this vessel up to the opening of the diverticulum, near from which a new anastomosis with the capillaries of the internal marginal vessels permits it to reappear in the latter. At the level of the point where it crosses the siphon (*a*, fig. 1), the internal marginal vessel produces a very big branch that continues parallel to the siphon and gives off very close to its origin a vessel that runs the length of the esophagus and empties into the peribuccal rings (*Bc*, fig. 1, 4, 5). Hoffmann gives this vessel, already described and figured by H. Millne-Edwards, the name *branch of communication* because it connects the properly so-called vascular system, i.e. of the digestive system, with the water system. Although this separation between the two systems does not actually exist, it is convenient to keep the name that Hoffmann applied to the vessel. The branch that it produces has been called by the same scholar, intestinal vessel. This vessel, which has been considered above, gives off, according to him, blood to the regions of the digestive tube that do not receive blood from the marginal vessels. Actually, this supposed stomach vessel ends quickly after having given off the branch of communication without even reaching the digestive tube. I have made this the subject of very careful investigation, but I have seen in no instance the colored material penetrate more than a centimeter from the origin of the branch of communication. To the contrary, the caliber of the vessel decreases progressively, and often at the point where it appears to end, the injected material penetrates some into the neighboring mesenterial lamella. Nothing has ever led me to suppose that the vessel continues towards the intestine. At the beginning, I was very embarrassed, and after the affirmations of Hoffman, I could not understand why I did not obtain by injection the system of which he spoke. I thought that, for some reason that I could not guess, my injections were not successful. I then employed more penetrating material, such as colored turpentine. In large specimens of *Spatangus*, I introduced a copper needle into the intestinal vessel to be able to make a ligature and made the injection with strong pressure. **87** The results were always the same. There remained to me finally a last means to verify if this vessel is continuous or not up to the digestive tube. This was to make successive cross

sections the entire length of the vessel starting with its origin. In making thus a series of sections, it was easy to recognize that this vessel, very recognizable with yellowish coagulated material that filled its cavity, decreased rapidly in size after having given off the branch of communication, and did not reach at all to the intestine. In the last sections, there are in fact, no longer any trace of vessels. There thus does not exist an intestinal vessel, and still less, in consequence, branches that leave it in order to go to the digestive tube. It is based on a pure and simple supposition that Hoffmann was able to say that it furnishes blood to the esophagus, stomach, and the upper curve.

As in urchins, the vessels in *Spatangus* ramifies only on the lower intestinal curve. The upper intestinal curve completely lacks them and to the first alone seems to have the devolved the function of absorption, facilitated by the special structure and the numerous glands that can be observed in this region.

In examining with the microscope portions of the injected digestive tube, one is struck by the richness of the capillary network of its walls. In fact, nearly the entire extent of the wall is filled with anastomosed vessels and in some places even they are so dense that it is impossible to distinguish the capillaries one from another. In the diverticulum, the secondary branches are always parallel and are divided into branches of the third or fourth order that also remain parallel and end by anastomosing in a plexus as rich as in the intestine.

The path of the two marginal vessels of the intestine in the other types of spatangoids, is analogous to that which we just saw in *Spatangus*. Both are limited to the upper intestinal curve. The distribution of the internal marginal vessel has however very important modifications that merit reporting. In all the genera that I have studied, it always has this constant character of giving the most important secondary branches to the digestive tube only at its termination point at the level of the secondary opening of the siphon. In *Ech. flavescens*, where the siphon opens at the point the lower curve joins with the upper curve, the internal marginal vessel runs a longer pathway than in any other type. It ends as in *Spatangus*, and at the same time as the siphon (Pl. III, fig. 1, 5, 6), i.e., that it divides into a fascia of five or six large secondary branches that ramify in numerous capillaries on the dorsal surface of the lower curve and anastomose with the branches coming from the external marginal vessel. Some 88 small vessels spread to the ventral surface, but they are very little developed. At its opposite end, i.e. in the recurved region not attached to the intestine, the vessels are less numerous and less developed than in *Spatangus*. In the other species, the internal marginal vessel no longer gives any branches that leave from the second opening of the siphon. In *Brissus unicolor* (Pl. II, fig. 10), these branches branch only the upper surface and have an arrangement analogous to that of *Spatangus*. In *Brissopsis lyrifera* (Pl. II, fig. 11) and *Schizaster canaliferus* (Pl. III, fig. 14), it furnishes near the opening of the siphon numerous branches to the two surfaces of the digestive tube. This continues up to the end of the lower curve in the form of a canal that gradually decreases in size and gives off numerous branches its entire length to the dorsal surface and ventral surface of the last part of the lower curve.

The distribution of the external marginal vessel and vessels of the diverticulum is identical in all the genera to that which was described in *Spatangus*. These two vessels never continue onto the upper curve which is absolutely depauperate in vessels as the

rectum and esophagus.

The branch of communication that connects the internal marginal vessel to the peribuccal rings is easily found in the different genera. It goes directly from the intestinal vessel to the buccal opening. It no longer produces, as in *Spatangus*, a branch analogous to that which Hoffmann called stomach vessel. In *Brissus* (*BC*, fig. 10), it is detached from the internal marginal vessel, nearly opposite the mouth, descends towards the posterior region of the animal in order to turn back abruptly and go up the length of the esophagus to the mouth. It describes thus a nearly completed curve. In fact, the ventral mesenterial lamina is doubled at its point of insertion on the esophagus in a superficial lamina and a deep lamina. It is on the deep lamina that runs the portion of the vessel that appears to cross the other lamina on which is applied the second part of the branch of communication.

In order to end the description of the vessels of the digestive tube, I have only to speak of the special system of vessels destined for the first portion of the lower curve, included between the first opening of the siphon and the opening of the diverticulum. This system does not appear to have been seen until now by any observer. At the level of the opening of the diverticulum, the internal and external marginal vessels form a very tight plexus, limited to the periphery of this diverticulum, and that cannot be seen from the outside. In order to see it, it is necessary to cut the walls from the interior and expose them. One then obtains the aspect of preparation shown (Pl. II, fig. 7). From this plexus leaves two vessels that descend from each **89** side in following the borders of the lower curve towards the first opening of the siphon. They form two marginal vessels analogous to the vessels of the other parts of the intestine. These two vessels (*v* and *v'*, fig. 1, 2, 7) are joined by a series of transverse rings (*t*, *t*, fig. 7) from place to place up to the point of termination where they are a little thinner. The transverse branches exist on the dorsal surface as well as the ventral surface. They remain simple their entire path and never divide into capillaries as the other vessels of the digestive tube. This system is rarely injected, probably because of the difficulty experienced by the injected material to pass across the network formed of very fine capillaries that surround the opening of the diverticulum. The external marginal vessel *V* gives, in addition, some small branches that ramify on the nearby mesenterial lamella and continues onto the lamella that reunites the diverticulum to the two intestinal curves. Among these ramifications, one notes a very distinct vessel, although of very small caliber (*v*, fig. 1, 2, 3), to which all the capillaries finally come to join and which goes between the marginal vessel of the diverticulum and the stone canal. It continues up to the end of the diverticulum and gives off, to the right and left, small anastomoses to this marginal vessel and the stone canal, establishing thus a communication between the latter and the vessel of the intestine.

This system of special vessels very probably exists in all spatangoids, but I have encountered it for certain only in *Brissus*. In the only specimen of *Schizaster* that I could inject, I saw, in injecting the internal marginal vessel, the material penetrate further from the opening of the diverticulum into two small transverse vessels that undoubtedly belong to this system. As the injection did not penetrate further, it was not possible for me to continue to follow them.

Teuscher speaks in his work of a communication of the stone canal at the point of reflection on the ventral mesenterial lamella with the intestinal vessel. This communication

is not the one of which I just spoke. He says, in fact: “An dieser Stelle (wo die untere Darmwindung sich in die obere umbiegt) tritt der Steincanal in Verbindung mit dem Ventralblutgefäß der oberen Darmwindung, so dass alle von mir in das Herz gemachten Injectionen mehr oder weniger weit, meist einen bis zwei Zoll in dieses Gefäß eindringen, während ich eine Fortsetzung der Injectionen in das entsprechende Gefäß der untern Darmwindung niemals beobachtete” (pages 532 et 533). Now, no marginal vessel exists on the upper intestinal curve. This is a fact that injections and sections give certain evidence. In consequence, such a communication could not exist. It **90** is impossible for me to understand that which Teuscher means by this communication of the stone canal with the ventral vessel of the upper curve, especially as the figure that he gives of the circulatory system of *Spatangus* leaves other things to be desired and where he represents in OC (pl. XXI, fig. 16) this “obere communication der Waser-und Blutgefäße” give no information at all in this regard.. It shows us an extension of the stone canal that continues on the upper curve and ends after a short path. But, as Teuscher has not figured this marginal vessel of the upper curve, it is not possible to have an idea of the disposition that he describes.

Whatever the case, the stone canal actually does communicate with the vascular system of the intestine. But this communication which really must be of little importance, given the small caliber of the branches that it produces, exists at the level of the diverticulum and not at the level of the upper intestinal curve.

The internal marginal vessel is the only contractile part of the circulatory system ensemble. One can often, in specimens of *Spatangus* that are opened alive, observe, especially in the region not attached to the siphon, contractions that have no rhythmic character at all. The walls of the internal marginal vessel are stronger than those of the external marginal vessel, whose caliber is often irregular and seems to depend more or less great quantity of blood found there. It seems to be only a sort of reservoir for the blood of the internal marginal vessel. One finds in the walls of this latter numerous muscular fibers, while the external vessel does not possess any. Figure 44, pl. VI, represents a cross section of a part of the internal marginal vessel and the adjacent mesenterial lamella. The wall of the vessel is made of a layer filled with connective tissue and an internal layer of very developed circular muscle fibers whose characters are those of ordinary muscle fibers. Their nuclei are easily seen in the dissociations. There are also some very rare longitudinal fibers. One generally does not find them in cross sections. However they are easily seen in longitudinal sections and in dissociations. They are sparse in the midst of the circular fibers and do not constitute a distinct layer. The lumen of the vessel is ordinarily filled with a greyish, finely granular coagulum that does not stain with picrocarmine. In it are encountered some pigment granules and several contorted blood corpuscles in the form of cells with boundaries and very clear nuclei. These cells are especially numerous in the portion of the coagulum next to the wall of the vessel and remains attached, often in a very regular fashion, **91** against the internal surface of this wall. One can even believe that one is in the presence of a special endothelium with very voluminous cells if one did not encounter these same elements in the midst of the mass of the coagulum, and if a slight impression on the cover slip was not sufficient to detach them. The endothelium is, moreover, easy to recognize, without the aide of sections, the cells that constitute it being

of too small dimensions, but in studying the internal surface of the vessel carefully stripped of coagulum and stained with picrocarmine. Impregnations with silver nitrate on living tissues give equal evidence, but they are not always successful and the precipitate of silver chloride that is formed is very difficult to observe. These endothelial cells are small, with very regular boundaries and a very apparent nucleus.

The mesenterial lamellae on which runs the vessels come to mix with the connective tissue itself. Now, and we have already observed an analogous fact regarding the digestive tube, at the moment that this lamella touches the vessel, it is reenforced on the two surfaces of the muscle parallel to the axis of the vessel. These fibers are continuous even on the vessel wall from which they leave to the area of the lamella. They enclose simultaneously muscle fibers on the two surfaced of the connective tissue layer, one circular and the other longitudinal. The latter cannot be considered as part of the vessel but of the mesentery. They exist, moreover, only on a very limited portion of the vessel circumference.

The internal marginal vessel has the same structure in its region attached to the siphon. As for the external marginal vessel and the two marginal vessels of the diverticulum, they lack muscle fibers.

STONE CANAL. – The stone canal (*C* and *C'*, fig. 1, 2, 3, 4, 5, 8) extends from the mouth to the madreporite plate. It accompanies the entire length of the esophagus to which it is attached by a very thin mesenterial lamella. It quits the esophagus at the level of the point where the esophagus becomes the lower intestinal curve and comes to be placed on the ventral mesenterial sheath, the length of which it runs parallel to the lower curve. Towards the point where this is continuous with the upper curve, it abruptly changes direction and, instead of being ventral becomes dorsal. It is recurved on the mesenterial sheath which extends from the marginal vessel of the diverticulum, up to the organ that was called the heart by the old anatomists but which is really, as in the homologous organ of the urchins, an excretory organ. I shall study further the relations of the stone canal with this organ and its mode of termination towards the madreporite plate.

The path of the stone canal is the same in *Echinocardium*, *Brissus*, and **92** *Brissopsis*. In *Schizaster*, its path is much shorter than all the others. The ventral mesenterial lamella does not extend beyond the second opening of the siphon (pl. III, fig. 14, *MV*). The stone canal changes its direction at this level, reflected onto the free edge of this lamella, plunges into the depth towards the apical pole, and thus reaches directly to the end of the diverticulum. It thus changes direction only once in *Schizaster*, while in the other types, it changes direction at the level of the esophagus and at the level of the lower curve.

Hoffmann considered the stone canal as a simple canal. Teuscher recognized in cross sections that it is accompanied the length of the esophagus by a second vessel that goes like it to the vascular peribuccal rings, but he gives no information at all on the origin of this vessel. It is easy to verify that the stone canal is double the entire length of the esophagus and to show it is made of two connected canals (pl. I, fig. 1, 4, 5, *C* and *C'* pl. V, fig. 34). One of these canals (*C'*), which is not applied directly against the esophagus, has a deep color and appears strongly pigmented. Its caliber is not the same its entire path, and it has small sinuosities that make it a little irregular. The second canal (*C*), to the contrary, directly applied against the esophagus, has a perfectly rectilinear path and non-

pigmented walls. At the point where the esophagus terminates, the sinuous canal decreases little by little and ceases to be distinct. It joins the second canal that remains from then single and continues its path up to the end of the inferior curve and from there up to the excretory organ. A cross section of the stone canal (fig. 34) gives a good account of the existence and the reciprocal arrangement of these two canals.

RADIAL WATER CANALS. — When one injects the internal marginal vessel, the material passes easily into the branch of communication and goes to fill a vascular ring that surrounds the mouth in the form of a pentagon with irregular sides, corresponding close to the periphery of the peristome. It then penetrates into the stone canal and into the radial water canals. The peribuccal vascular ring always appears as a simple canal, as Hoffmann has illustrated. However, a fact astonished me at first. Most usually the material penetrates into the two halves of the stone canal. Other times it penetrates only into one, sometimes into the external half, sometimes into the internal half. Moreover, it seems that, in certain injected pieces, the peribuccal ring was larger than in others. In examining with a microscope a piece injected where the ring appears very thin and in which a single half of the stone canal was filled by the material, I have been able to distinguish, right beside the injected ring, **93** a second ring whose existence had not been suggested by anything. In injecting a substance of a different color than the first, the liquid fills this second ring, passes into the half of the non-injected stone canal and penetrates into the ambulacral zones in filling vessels different from those that had been injected first. It was easy to be assured that the two rings were perfectly distinct and that, moreover, the neural pentagon appears in the form of a perfectly independent small band situated a little outside these vessels (pl. I, fig. 4 and 5). In making the inverse experiment, i.e., injecting with the differently colored material the two vessels whose joining constitutes the stone canal at the level of the esophagus produces the identical result.

The study of pieces injected like that permits the following conclusions to be made. There exists around the mouth of spatangoids two distinct vascular rings (fig. 4, 5, *AE*, *AD*), as in the urchins, independent of the nervous system but each in communication with one of the halves of the stone canal and both furnishing vessels to the ambulacral zones. The branch of communication is in connection with the two rings. Single nearly its entire length, it bifurcates at its end. Each of the two branches empties into one of the peribuccal rings. Teuscher thus is perfectly correct in saying that beside the stone canal is found another canal that has to communicate with the vascular ring. Only, an error is induced by the fact that he has misinterpreted, in my opinion. He has considered this vascular ring as forming a vast dilation at the level of the upper lip, a large sinus limited by this membrane that Hoffmann has taken for the internal membrane of the test detached at this level. It is easy to repeat the experiment of Teuscher and to be assured that it is correct. In introducing a strongly conical copper needle into an opening made on one of the pieces of the upper lip, the material will fill the sinus in question and penetrate into the ambulacral zones. Now, we shall see immediately that the space injected into these latter cannot be considered a vessel. As for the sinus of the upper lip, it always remains distinct from the peribuccal ring with which it does not communicate. One can inject these rings after having injected the sinus to be assured that they always keep the same caliber and are perfectly regular. The

nature of this supposed sinus remains to be determined.

The two vessels that are produced in each ambulacral zone are, as the peribuccal rings, distinct and independent of the nerve. A cross section of an ambulacra of *Spatangus* (pl. III, fig. 35) shows the same arrangement as in the urchin. A vessel of small diameter, superficial or internal (*Vs*), a second larger vessel situated outside (*Vp*), and finally the nerve **94** placed between this latter and the internal wall of the test (*N*). The ambulacral nerve is not immediately applied against the test. It is situated in the midst of an enclosed space (*Cg*) limited on the inside by the external vessel and on the outside by the test. Now, this is the space (*Cg*) that Teuscher considered as a vessel and that he calls perineural vessel. No more than in urchins, this interval is not a vessel and it has no relation to the peribuccal rings. It is in precisely this space that the colored fluid enters when the sinus of the upper lip is injected. One can rest assured that the true and only vessels of the ambulacra of the injected pieces are those whose section is shown by *Vs* and *Vp*, fig. 35. Moreover, it is possible to inject the peribuccal rings by the radial water canals, and according to whether the needle will be placed into the internal vessel or into the external vessel, one will fill the internal ring or the external ring. If, on the contrary, the needle comes to be lodged in the interval *Cg*, the material will fill the space included between the upper lip and the membrane that covers it interiorly. One thus cannot consider this space, or the sinus of the upper lip, as belonging to the circulatory system, but simply as a portion of the general cavity, more or less perfectly closed, into which is placed the nervous system as in urchins.

The two radial water canals give off branches to the ampullae. Each ampulla corresponding to a tube foot, one should expect to find them very numerous in the peristomial region and in the petaloid ambulacra. It is there, in fact, that they are the most developed. In the peristomial zone they have the form of small rounded, pyriform vesicles with smooth, transparent walls, completely swollen by the blood liquid and proportionally more separated from each other as one goes from the peristome. The ampullae of the petaloid ambulacra resemble, on the contrary, those of urchins. They are elongated, flat, and close to each other. Their cavity is separated into numerous secondary chambers by small membranes running from one surface to the other. The structure of their thin walls is the same as in urchins: an external epithelium, a connective tissue layer, a muscular layer, and finally an internal epithelial lining. The connective tissue is formed of fibers oriented principally according to the axis of the ampulla. The muscle fibers form a discontinuous layer, less developed in the ampullae of the petaloid ambulacra. In the peristomial ampullae, this muscle layer has a characteristic appearance, shown in pl. VI, fig. 39. The muscle fibers are arranged in parallel groups, whose contractile zones are nearly equal, and reach nearly the same height in forming thus more or less waves of contracted muscle fibers. The direction of these fibers is perpendicular to the axis of the ampulla.

95 The two vessels that go to the ampulla are joined to the ambulacral nerve and remain distinct up to their entry into the ampulla. The peristomial ampullae, like those that are not part of the petaloid ambulacra (except in *Schizaster*, in the anterior ambulacral groove where the pores are double in each plate), communicate with their tube foot by a single canal passing through the single pore that corresponds to its base. The ampullae of the petals communicate, to the contrary, with their tube foot by two extensions that pass through the two pores of each plate.

In the posterior ventral ambulacral zones, the regular order of the secondary vessels that leave from a common trunk alternatively to the right and to the left, is disrupted at the level of the infra-anal fasciole. One knows that this encloses in its area two (*Spatangus*) or three (*Echinocardium*, *Brissopsis*, etc.) pairs of well developed tube feet, often even longer than those of the peristomial area, and which by consequence are found separated from the ambulacral trunks. Also the vessels that leave them are longer and produced on the same side of the principal vessels to be directed towards the midline.

STRUCTURE OF THE EXCRETORY ORGAN AND THE STONE CANAL. — It remains now for me to study, in spatangoids, the organ homologous to the ovoid gland of urchins, its relations with the madreporite plate, and to say some words on the structure of the stone canal. This organ, up to now called heart, is nothing other than a gland having all the characters of an excretory organ, like the ovoid gland of urchins. This organ, because of its form, cannot be designated ovoid. I shall call it madreporic gland because of its relations with the plate of this name.

The gland placed on the path of the stone canal, at the end of the diverticulum to which it is joined by a narrow mesenterial sheath and attached to the internal surface of the test by a mesenterial lamella that is continuous with that which is extended the entire length of the rectum, is dark in color and very voluminous. The mesenterial sheath that maintains it in a fixed position is doubled to provide a thick and resistant envelope. The details given by Hoffmann and Teuscher on its structure are very incomplete. Hoffmann has found “a very delicate stroma whose mesh is filled with cells. The stroma is made up of very fine fibers, the cells are small and more or less pigmented.” Teuscher found “A granular connective tissue mass containing nuclei, cells, and fibers. There is no reason to consider these fibers muscular. Moreover, because they are little developed and have an irregular arrangement, they cannot be agents of contraction of **96** the heart. However, there is a large central cavity with accessory cavities that are lacking in urchins. This large cavity is divided into secondary chambers by membranes and thin trabeculae.” These descriptions are insufficient. They tell us only that the organ is made up of fibers and cells, and not how the elements are arranged, what value one should give them, or what importance it is necessary to attribute to this organ. Hoffmann calls the organ sometimes *Wassergefäßsherz*, sometimes *Wassergefäßsdrüse*. Teuscher calls it *heart*, adding that it must be an ancestral or embryonic remnant, useless in an adult, and that nothing in its structure permits attributing to it the role of a gland or justifies the expression *Wassergefäßsdrüse*. It is probable that the difficulty encountered by these two scholars in recognizing the structure of this organ resulted from the method of preparation and the state of preservation of the specimens they had, as Hoffmann studied pieces treated in chromic solutions and Teuscher studied animals preserved a long time in alcohol. Now, it is not possible to obtain suitable preparations if one does not employ fresh pieces and above all treated with osmic acid. A cross section (Pl. V, fig. 28 and 29) made on a piece first fixed by this reagent and then hardened in alcohol, shows first of all that there is no central cavity, and permits after staining recognition of the following arrangements. The peripheral portion is made up of a thick layer of connective tissue with distinct fibers, covered with small epithelial cells. It is not part of the gland itself and is nothing but its mesenterial envelope. The spongy

parenchyma is formed of trabeculae of transparent, glassy connective tissue that is looser and more spaced towards the periphery, and thinner and denser in the central portion (*FC*). At the periphery, these passages seem to be grouped according to a certain order to form small distinct acini. However, towards the center, the acini lose their individuality. The trabeculae cross in every direction to form a tissue with an irregular mesh and thus forming alveoli of different dimensions, very small in the central part and filled with special cellular elements identical to those of the homologous organ of the urchin but smaller. These are cells (*Cr*) with very large and granular nuclei surrounded by a zone of clear protoplasm and lacking the membrane envelope. They have small extensions that can anastomose with either other and thus form sometimes in the interior of the alveoli a very fine reticulum formed only of protoplasm. These very numerous cells are applied against the wall of the alveoli or fill their cavities. Some have a finely granular nucleus while the others have larger granules. In others, finally, the nucleus is only a mass of red or yellow granules **97** surrounded by a thin protoplasmic envelope. Other cells, much less numerous, appear as masses of finely granular protoplasm with a distinct outline and a small, more or less granular nucleus. Finally, one encounters numerous masses of red or yellow pigment (*G*) analogous to those found in the general cavity. These are sometimes small spheres, sometimes large splotches of pigment. They are especially abundant in the peripheral region of the gland and evidently are formed from the cells lodged in the alveoli. These masses of pigments are not equally developed in all individuals. In some, they are not abundant relative to cellular elements. This was the case in the two preparations that are illustrated here. In others, they are very numerous and constitute in large part the contents of the peripheral alveoli. The essential characteristics of this gland are thus identical to the ovoid gland of urchins: a connective tissue reticulum supporting cellular elements undergoing a special degeneration that results in the formation of numerous pigmented masses.

It is important to study the exact relations of this gland with the stone canal and to investigate if it can or cannot receive blood, the more so as Hoffmann and Teuscher have reached absolutely different results regarding this relation. The first considers it a dilation of the stone canal while the second states that it is distinct and that this canal itself is simply attached. Sections made the entire length of the stone canal that show both the structure of its walls are in this regard very interesting. At the level of the esophagus (Pl. V, fig. 34), the stone canal is double and the two canals that constitute it, with walls formed by connective tissue, differ from each other only by the fact that the canal nearest the esophagus (*C*) is lined with ordinary epithelial cells while in canal *C'* they are replaced by larger cells with a strongly granulated voluminous nucleus and with pigment masses. From the end of the esophagus, canal *C'* having disappeared, sections show only a single canal lined with small endothelial cells whose characteristics are not modified although they remain applied to the ventral mesenterial lamella. But as soon as it comes to the dorsal surface and reaches the diverticulum, its lumen is divided into two or three secondary cavities by longitudinal membranes (Pl. IV, fig. 24, *C*) and the characters of the endothelial cells begin to be modified. They are now larger cells with a granular nucleus, an irregular protoplasmic zone which, instead of forming a simple covering on the internal surface of the walls, is multiplied and fills in part the secondary cavities of the canal. To the degree

that the sections become closer to the gland, the compartments become more numerous and the cellular elements are grouped in a way to take **98** the appearance that they show in the gland itself, to the tissue of which one passes by insensible gradation. The stone canal is thus clearly in communication with the latter and even in perfect continuity with its tissue. This is so true that it is impossible to say exactly where one ends and the other begins. Never, in the sections of the gland, are found traces of a canal that could be attached to it as Teuscher says. But continue with the sections towards the apical end of the gland. As it is approached and the glandular parenchyme becomes less developed, one sees differentiated little by little two particular canals (Pl. V, fig. 30). The central one (*CM*) appears first at the thin extremity of the gland with a cavity divided by numerous partitions lined with cells identical to those of the latter and reproduces its structure. The other peripheral one, seen only in the subsequent sections (*CV*), is lined interiorly with a regular cellular covering. Usually, the lacunae limited by the membranes of canal *CM* are filled with a grayish, finely granular coagulum, often containing numerous cells detached from the wall by the action of the blade. This is nothing other than the coagulated secretion of the excretory organ. Finally, the tissue of the gland disappears and the two canals remain only. They run parallel to each other towards the apical pole.

When an injection is made in the stone canal in the direction of the gland, the material easily fills its spongy tissue and appears at its surface in the form of small, greatly ramified vascular branches (pl. II, fig 6 *Ca*). Cross sections made on a piece thus injected (pl. II, fig. 9), shows that the organ is penetrated completely by the material that comes to occupy all the empty spaces of the interior and fill the alveoli, a result, moreover, that had been anticipated from the study of sequential sections. After having filled the excretory organ, the colored material penetrates into one or two superficial canals (*Vc*) that runs on the mesenterial sheath extended from the extremity of the gland to the internal surface of the test. This mesenterial lamella is continuous on the two small calcareous plates annexed to the internal surface of the test at the level of the madreporite plate and becomes lost in the end of the genital ducts, merging with their walls (pl. II, fig. 6, *Cg*). Now, the injection that penetrated the canals *Vc* (sometimes two canals exist, sometimes one) is lost within this mesenterial sheath and forms a network with a large and irregular mesh (*RV*). It seems that the material penetrates into the interstices of the connective tissue of this lamella rather than a system of defined vessels with distinct walls. Often it even crosses it and appears in the general cavity. It is precisely this canal *Vc* whose cross section is shown in *CV*, pl. V, fig. 30.

At the same time that the colored material loses itself in the midst of the connective tissue **99** of this mesenterial lamella, it leaves by the madreporite plate to the outside. In fact, dissection of the gland (pl. III, fig. 19) makes it possible to recognize in the midst of the bays that form the spongy tissue, small canals that go towards its end and are joined into larger canals that converge into a single canal (*CM*). This leaves the gland to go towards the madreporic plate underneath canal *Vc* of fig. 6. This is the canal we saw in section in *CM*, fig. 30 and that we can call the madreporic canal. Always covered by mesenterial sheath of which it was always a question, it goes into the triangular space formed by the union of two small plates *P* and *P'* which have been pulled aside in figure 19. The space left free between this canal and the walls of the plates that form a kind of

protective apparatus is in part filled by a brownish spongy tissue simply formed of connective tissue fibers and pigment granules. This canal does not empty directly into the exterior across the pores of the madreporic plate. Its end loses itself in the midst of the spongy tissue that surrounds it. The injected material that has entered it can just as well escape outside across the pores of this plate where it spreads out into the mesh of the spongy tissue and enters into the general cavity. In some individuals, the madreporic canal remains distinct up to the madreporic plate. This is the case for the piece shown in fig. 19. Other times, it loses its individuality much earlier and merges with the spongy tissue before it enters into the triangular space limited by the two plates.

Two different canals thus leave the madreporic gland in spatangoids. One, because of its structure, seems to be an extension and represents its excretory canal. It continues towards the madreporic plate and allows the liquid secreted by the gland to go to the exterior. The other, on the contrary, does not empty outside and is quickly lost in the midst of the interstices of the connective tissue.

The considerations that can be deduced from this arrangement will be given and discussed in the following paragraph where I shall try to compare the circulatory system in regular urchins and spatangoids, and to indicate some notions that can give us anatomical results on the role of the circulatory system and its relation with the general nutrition of the urchin.

In the preceding descriptions I have not made a distinction between the water system and the strictly defined vascular system. However, most authors who have described the circulatory apparatus of urchins have always indicated two distinct systems in these animals, one fulfilling more specially the functions **100** of nutrition, which is the system to which belong the vessels of the intestine, and the other serving more specially locomotion and respiration and communicating with the exterior by the stone canal and the madreporic plate. We have thus to examine if this distinction really exists and if it is found to the same degree in urchins and spatangoids.

If we consider the ensemble of the circulatory system of a regular such as was described above, we find that in fact there seems to exist two quite distinct systems. The first system is composed of single or double radial water canals according to the portion of their path considered and emptying into a peribuccal ring from which leaves a canal that ends directly at the madreporic plate. A second system is comprised of the vessels of the intestine that is reduced, in last analysis, to numerous capillaries developed on the wall of the digestive tube and uniting in an internal marginal vessel that empties into a second periesophageal ring. From this leaves a canal that ends at the madreporic plate, but in the trajectory of which is found interposed an excretory organ. Now, these two systems communicate only at two points. Still these communications are not direct and one of them can be only of little importance. It is at the level of the madreporic plate and by the intermediary of the Polian vesicles that the two external and internal rings receive blood that the two systems are connected. We know in fact that the excretory canal of the ovoid gland, which is after all only the continuation of the glandular canal coming from the internal esophageal ring, ends with the stone canal coming from the external ring in a common space limited by the

madreporic plate and a very fine membrane that is a continuation of the mesenterial lamella that extends from the esophagus to the rectum. Perrier has already remarked that an injection made by the excretory canal of the ovoid gland fills this space and penetrates into the stone canal. It is thus possible to have communication between the two systems at this level. We remark here, as at the level of the Polian vesicles, the communication of the two systems is not made by a complete canal: the blood that is found in the upper ring can pass into the lower ring, but with the condition that it crosses the tissue of the Polian glands or the ovoid gland. It seems that the two systems maintain their independence in urchins.

Now, these two systems that are distinct in urchins are no longer distinct in *Spatangus*. There are two vascular rings around the mouth, but each sends branches into the ambulacral zones. The two vessels that constitute the stone canal at the level of the esophagus and each of which is in communication with one of the peribuccal rings, are not slow to fuse into a single canal that ends in the gland placed at the end of the diverticulum. **101** Finally, the internal vessel, or that which is the same thing, the branch of communication, bifurcates at its extremity and communicates simultaneously with the two rings.

The arrangements that exist in regular urchins being primitive, because these animals are more ancient than spatangoids, one can acknowledge in principle that the circulatory system in echinoids is constituted typically by two distinct systems that maintain their independence in regulars, where one functions in absorption of nutritive material and the other in locomotion, but that they merge in spatangoids while keeping however traces of their original separation. Now, we know that the system of the water vessels (radial water canals and stone canal) originates from the water system of the larva. It is destined to put in the pluteus the general cavity in communication with the exterior system. The system appears very early and must, in consequence, be very ancient. The vascular system developed on the walls of the digestive tube appear only very much later when the young urchin is already formed on the pluteus. Although the first systems of larval origin maintain in echinoids and in all echinoderms nearly the same characters, it seems, to the contrary, that the ensemble of vessels that constitute this newer system has been susceptible in echinoids to vary in very wide limits from the moment where the path of the intestine is modified because of the change in the relative position of the mouth and the anus. The different arrangements that it takes in present spatangoids show, in fact, that it does not possess in its distribution the constant characters that are always maintained in regular urchins. We have seen the internal marginal vessel terminates at two points of the lower curve and have very different arrangements according to genus. There is nothing astonishing in this that this recent system that maintains its primitive independence in the regulars and is put only very indirectly in relation with the water system can, at the same time that it submits to profound modifications, be subordinated in spatangoids to the water system and tends to be merged with it.

Moreover, the anatomical modifications that, in spatangoids, have involved certain organs belonging to the circulatory system or are in more or less direct relation with it, have had to have an immediately influence on its development and have been able to contribute to some degree to the fusion of the two systems. We know, in fact, that the tube feet that in urchins serve for locomotion and are developed on the entire surface of the body in a variable, but generally very considerable number on each ambulacral plate, always

form **102** a very important system. In spatangoids, to the contrary, their ensemble loses much of this importance. Each ambulacral plate has only one tube foot. Moreover, a certain number of them are atrophied and the others are localized in limited and not extensive regions. Finally, they are incapable of playing any role whatsoever in locomotion. This remarkable reduction is constant in the entire class of spatangoids and constitutes in consequence a structural characteristic trait of these beings. We know also that the Polian vesicles, tightly bound in the regulars to two vascular rings of the upper surface of the lantern, no longer exist in spatangoids. The disappearance of these vesicles and the reduction of the tube feet, particularly to which it is convenient to add the disappearance of the masticatory apparatus and the displacement of the digestive organs, have had to lead to correlative changes in certain vessels that have followed different directions than those they had primitively, to come closer or to merge. It is thus that the periesophageal rings, primitively separated from the test, have come to attach there after the disappearance of the masticatory apparatus. These same changes perhaps have determined also the vessels of the ambulacral zones to come closer to the peristome, where precisely are found the most developed tube feet and to open separately into the vascular rings. As for the stone canal which is at first a straight line from the periesophageal rings to the apical pole, the appearance of solid mesenterial lamellae have provoked certain modifications in its path and has forced it to take a convoluted path to reach the madreporic plate.

However, these profound unexpected changes in the circulatory system of spatangoids appear to have a more considerable importance from the anatomical point of view than the physiological one because the same liquid circulates in the vessels of the digestive tube and in those of the ambulacra (at least a liquid having the same properties and containing elements that appear identical). Spatangoids and urchins have moreover, in the arrangement of the circulatory system, a large number of points in common. Thus, the existence of two vascular rings around the esophagus, the interposition at a certain point of the path of the vessels of a glandular organ destined without doubt to remove useless products from the blood and to let them escape across the madreporic plate to the outside, the existence of two vessels in each ambulacral zone each sending branches into the ampullae, an arrangement eminently favorable for the circulation of blood, are the specific things that are found in all representatives of the two orders.

The most striking fact in the distribution of the vessels on the walls of **103** the digestive tube is the considerable development of capillaries on the inferior curve while the upper curve lacks them completely. This is a constant fact, recognized in urchins by Perrier and one that I have verified in spatangoids. Even in the latter, the localization of the capillaries is accentuated still more, as the vessels are distributed only in certain special regions of the lower curve, the dorsal surface for example whose structure is different from those that do not receive any. It is also interesting to note that the path of the internal marginal vessel is linked to that of the siphon, and that modifications that these can have seem to have corresponding modifications entrained in the path of the vessel. Only, in this regard, different genera of spatangoids have different arrangements. Whereas in *Spatangus*, *Echinocardium*, and *Brissus*, the internal marginal vessel only gives branches to the region situated this side of the second opening of the siphon, carried back towards the end of the inferior curve, in *Schizaster* and *Brissopsis*, to the contrary, the capillaries exist only in the

region situated beyond the opening of the siphon that occurs in these two genera at a point further from the end of the lower curve. However, in spite of these different arrangements, it is no less evident that the first curve has the most important role in digestion and absorption in the two orders. It is there that the intestinal capillaries draw the nutritive principles to then transport them to the circulatory system. Still it is probable that the second curve is not completely irrelevant to the general nutrition of the organism, and it is possible that all the nutritive products produced in the first curve will not be absorbed by the intestinal capillaries and that the part not absorbed by these capillaries pass into the second curve and penetrate then by endo-osmosis across the walls of the intestine into the liquid of the general cavity.

The capillaries of the digestive tube are united finally into the internal marginal vessel that ends at one of the rings or to the two vascular rings from which leave all the vessels of the urchin or of *Spatangus*. The vessels of the intestine have to be considered as the origins of the circulatory system, but it is not possible to indicate the direction of circulation. Is there even a defined, constant current establishing a circulation in the physiological sense of the word, or only a simple oscillation of the liquid produced by irregular currents that is effected in diverse directions and produced by the contraction of the internal marginal vessel in *Spatangus*, of the internal marginal vessel and collateral vessel in the urchin? This last hypothesis is the most probable. It is even the only possible. Because it is impossible, in considering the ensemble of the circulatory apparatus, to establish in which direction circulation could be made. **104** The problem is complicated more by the fact that the connections of the intestinal vessels with the rest of the circulatory system are different in urchins and in spatangoids, and because there exist on the path of the vessels glandular organs having excretory functions. One of these, restricted to urchins, has only a connection with the circulatory system. These are the Polian vesicles, the others are interposed between the vessels and the exterior, namely the ovoid gland of urchins, and the gland placed at the end of the diverticulum in spatangoids. It thus seems in echinoids, there is not a defined direction for circulation. Pushed by the contraction of the intestinal vessels, the blood can ebb and flow to go in one direction or the other, and there is always mixed the liquid coming from the intestine and the liquid coming from the radial water canals that has penetrated into the tube feet and can be respired there. It is quite probable also that there is a mixing of the blood with the liquid of the general cavity. This is a question that I shall examine soon. But as the blood can penetrate into the general cavity only after having crossed the glandular organs in communicating with the madreporic plate, it is necessary first to study the exact relations of these organs and compare them in urchins and in spatangoids.

The histological structure of these glands permits us to consider them as excretory organs. The cells that fill them undergo in fact a peculiar degeneration whose final phase is the transformation of the cell into a mass of pigmented granules. Now, a cell that is full of pigments is in process of destruction. When it is completely transformed into a mass of pigment, it seems that it has fulfilled its role, that it must die. It also tends to be eliminated. Whether it belongs to an excretory organ or to the liquid of the general cavity, a mass of pigment is never only a residue, an organic waste. It can perhaps play a certain role in respiration, serving to fix oxygen, as Geddès seems to think, but it will not do this at least

in the final phase of the life of a cell. I thus believe that one can consider the madreporic gland as filling an excretory function. It probably produces there something other than pigment, but this is the only form under which is manifested to us the result of the physiological work of this organ.

If we compare the anatomical arrangements shown at the level of the madreporic plate in urchins and in spatangoids, we find again in the presence of very different structures. We know, in fact, that there exists in urchins, at the level of the madreporic plate, a sort of infundibular space, using the expression of M. Perrier, limited towards the interior by the madreporic plate. This is where open, side by side, the stone canal and the glandular canal **105** or, if one prefers, the excretory canal and the ovoid gland that is only an extension. As a result of this arrangement, there can be at the level of the madreporic plate a mixture of a part of pure blood with blood more or less modified by its passage across the excretory organ. Once this madreporic space fills, does all the liquid empty into the environmental water or better, does some go instead across the thin membrane that separates the general cavity in order to mix with the liquid that fills the latter? Both are possible. And even the direct return into the general cavity is shown possible by injections that often penetrate this cavity. It is true that the fact could be done from a rupture, but still it is always permitted to admit the possibility of osmotic phenomena permitting blood to cross the thin membrane that separates it from the liquid of the general cavity.

The conditions are quite different in spatangoids. Here the two vessels that make in the area central rings that one can call the stone canal. They do not remain, as in urchins, distinct up to the madreporic plate. They are merged into a single canal that crosses the excretory organ. Now, two canals leave the gland. One is rapidly lost into the interstices of the connective tissue. The other reaches up to the madreporic plate, but does not open to the exterior with a full canal to cross the pores of this plate. Its end is lost in the midst of spongy tissue that fills the small space left free between its walls and the two calcareous plates that over it. This is so true that injected material, at the same time that it leaves across the pores of the madreporic plate, penetrates into the mesh of this spongy tissue and can thus reenter into the general cavity. It seems thus that in spatangoids communication of the circulatory system with the liquid of the general cavity can be done easily in a fashion more direct than in the urchin. And it is permitted to admit that in echinoids, the blood that crosses the excretory organs can at the same time empty to the exterior or better penetrate directly or by endo-osmosis into the general cavity.

This communication of the circulatory system with the general cavity has formerly been accepted as a necessary fact, although one has never been able to prove it. It was quite rational to suppose that the liquid of the general cavity must take into the circulatory system the elements that permit it not only to live, but also and especially to nourish the organs that do not receive vessels. The identity of these corpuscles that one encounters in the blood and in the perivisceral liquid confirm moreover this point of view. As for the resemblance of the globules of the two liquids, there is nothing there that should astonish us. They do not prove *a priori* that the two systems communicate. **106** We know, in fact, that the vessels are formed at the expense of the general cavity. In the larva, at the same time that the caeca of the digestive system develop and grow in order to become the general cavity of the urchin, we see them detach and differentiate certain parts that organize in an independent

fashion and give rise to the aquifer system. Later, when the young urchin is already formed, the new vessels have no other origin. The cells that form the walls of the vessels and those that line the general cavity are thus of the same nature. They are mesodermal cells. They fall into the general cavity where in the lumen of the vessel, they develop always in the same way and become corpuscles that one finds in the adult in one or the other of these systems. It is thus very natural that we encounter the same forms of figured elements in the blood and in the liquid of the general cavity (1).³²

Whatever it is, the liquid that circulates in the vessels can, in spatangoids, communicate with the liquid of the general cavity. It is very reasonable also that such a communication, although it cannot be confirmed anatomically, is found in urchins by endo-osmosis across the thin membrane that lines the interior of the madreporic space. Should one see in this arrangement an essential fact and one of real physiological utility? The rudimentary state of our knowledge on the physiology of lower animals and all invertebrates in general does not permit us to give an answer to this question. It is, in fact, impossible to know if the blood that crossed this excretory organ mixes with the liquid of the general cavity in very large proportions, and if it furnishes it with elements for the nutrition of the organs it bathes. It **107** is completely impossible to acquire experimental or theoretical results on the nature of phenomena that occur in the madreporic gland of echinoids and to investigate the significance of an organ evidently fulfilling an excretory function, whose products, more or less mixed with blood, can at the same time be expelled to the exterior or pass into the liquid of the general cavity. But this liquid should move by endo-osmosis across the walls of the intestine the principal nutrients that it needs. It should, in fact, nourish not only all the organs contained in the general cavity, but also the external organs that do not receive vessels, and the test itself. If we compare the volume of perivisceral liquid to the volume of the liquid that circulates in the vessels, we shall in fact be able to attribute to the first a much greater importance and to relegate to the second the circulatory system, for that which

³²I have not spoken here of the characters of the corpuscles that one finds in the blood and in the liquid of the general cavity. These corpuscles are, in fact, analogous, in spatangoids, to those that have been described very recently with much care by M. Geddès in the perivisceral fluid of urchins.

A chemical analysis of the liquid in the general cavity of spatangoids, for which I am obliged to Dr. Garnier de Nancy, has given the following results:

Density 1.030

Residue per 100 cc, 4 g 448;

Thus: ashes, 3 g 478, containing 2.20 of sodium chloride, sulfuric acid, traces of phosphoric acid, lime (little), magnesium (much), traces of potassium.

Ether extract per 100 g solid residue.....0.1122

Alcohol extract42.8030

Water extract.....57.0848

The liquid does not contain albumin. The coagulum that is produced in the liquid sometimes after opening the body of the urchin seems formed by mucine as well as by fibrine.

regards nutrition. It is in urchins, as in many lower animals in which the circulatory system, a more or less perfectly separated part of the general cavity, has only a secondary importance compared to the liquid of this cavity. In certain worms, we see this system sometimes exist, sometimes completely lacking in species of the same genus (Polynoë), which indicates that its functions are still poorly defined.

In echinoids, the different functions of absorption, nutrition, excretion, and I shall add also respiration, which are devolved to the circulatory system, appear to function in a very obscure fashion and are very mixed so that it is possible to be part of each of them, and to acquire some notions of the exact importance of this system. For myself, I think that a large part of the nutrients produced in the intestine pass by endo-osmosis across its walls into the liquid of the general cavity, and that a much smaller part of these nutrients, absorbed by the capillaries of the digestive tube serves the nutrition of the tube feet as well as into the liquid of the general cavity. But I do not believe it is possible, in the present state of our knowledge, to indicate the nature of changes that the blood must undergo in the excretory gland before entering into this liquid, nor the importance that must be attributed to the communication of this gland with the exterior.

A function closely tied to circulation in echinoids is respiration. As has been said for a long time, the blood that is forced into the tube feet by the contraction of the ampullae, at the same time that it causes the extension of the tube feet, must also respire across their thin wall that permits gas exchange. One has to consider also the ten external gills as **108** organs across whose walls the liquid of the general cavity can respire. Evidently, there should be, across the walls of the tube feet and those of the external gills, respiratory exchange between the gas of the surrounding water and that of the liquid contained in these organs. However, I do not believe that these exchanges are very active. In fact, the surface of the external gills is not very extended and the quantity of liquid that penetrates them is very small relatively to the liquid of the general cavity. As for the tube feet, respiration cannot occur in a continuous fashion and it is completely dependent on locomotion. Moreover, these conditions do not occur in spatangoids, where the external gills do not exist and where the system of the very reduced tube feet offers only a very slight respiratory surface. This again makes us believe that respiratory exchange that is effected across the walls of the tube feet or the gills have only a secondary importance because the spatangoids must, without doubt, respire as actively as urchins. The best respiratory organ is the digestive tube, and this function of the intestine has been shown recently by Perrier who demonstrated that gas exchange must occur more actively and easily than elsewhere between the seawater constantly swallowed by the urchin and the liquid of the general cavity, and this especially at the level of the upper intestinal loop. He demonstrated, in fact, that in regular urchins, seawater swallowed by the animal passes preferentially by the siphon and arrives directly and completely pure in the upper loop while only a small part goes into the lower loop. The experiment that he did to demonstrate this phenomenon is easy to repeat. It consists of placing an urchin in water colored with fuchsin that allows recovering in the very walls of the siphon and the intestine traces of movement of the seawater. It is very reasonable that the siphon should fulfill the same role in spatangoids as in urchins. It does not serve in fact for passage of food particles and its lumen is always perfectly free. However, I have repeated the experiment of Perrier with spatangoids without

ever being able to demonstrate this passage of water by the siphon. Marion has also attempted it other times with the same species without obtaining results. It remains meanwhile no less evident that urchins or spatangoids swallow water constantly with their food. Whether this water passes directly into the upper intestinal curve by the siphon or by the digestive tube is not important. The exchanges are made no less actively across the wall of the intestine between this water and the liquid of the general cavity. It is very probable also that respiration can occur by the capillaries of the first loop, this latter always containing a certain quantity of water that permits gas exchange.

109 A phenomenon that, in echinoids, is connected directly to locomotion and consequently to circulation, is the entrance or the exit of sea water by the madreporic plate. One had thought previously that sea water was indispensable to the life of the urchin, and should penetrate into its body in a very great quantity. It seems rather that one should consider this function as secondary. It is done in a completely passive fashion, and I place myself completely in the point of view of Perrier. He thinks that water reaches the madreporic plate only in a very small quantity and when it is there it is impelled by the decrease in pressure in the liquid of the body of the urchin. When the tube feet are retracted, the ampullae are swollen by blood that produces an increase in pressure in the entire circulatory system or in the liquid of the general cavity. The equilibrium can be established only by the expulsion of a certain quantity of blood from the stone canal across the pores of the madreporic plate. Inversely, when the erection of the tube feet provokes a decrease in pressure in the circulatory system, there would be a movement of a certain quantity of water that would come to reestablish the equilibrium. It is not only the stone canal that communicates with the exterior. The liquid of the general cavity can also escape outside across the madreporic plate, or reciprocally the surrounding water can penetrate into the general cavity. Whatever it be, these exchanges should not be done in a continuous fashion, but only when they are determined by the changes of pressure that can be provoked by the extension of the tube feet or by the projection below of the masticatory apparatus that lifts up the buccal membrane, and increases proportionally the volume of the general cavity. If these changes of pressure are not produced, there is no reason for the surrounding water to penetrate into the cavity of the urchin, which itself is a body filled with a liquid of density nearly equal to that of sea water. It thus does not seem that sea urchin is necessary to the nutrition of the urchin. This seems all the more probable that, if in the urchin, it penetrates into the interior of the body in a very great quantity. In spatangoids, this quantity is very small and nearly none. In fact, the peristomial tube feet have nearly alone the faculty of swelling and extending. Their extension or retraction should not produce very noticeable changes of pressure in the circulatory system. From this it follows that only an inappreciable quantity of water penetrates into the body of spatangoids. Because, not only in urchins, it can only penetrate in response to the decrease in interior pressure.

In summary, in urchins, the ensemble of tube feet being well developed and fulfilling the important function of locomotion, their abrupt extension and successive retraction must produce rapid changes in the interior pressure that necessitates the entry or exit of a certain quantity of **110** liquid, blood or sea water. In spatangoids, to the contrary, where some tube feet associated with the peristome or the infra-anal fasciole, are alone able to expand or move, the movement of sea water will be nearly null. Perhaps one can see in this fact an

explanation of the cause that leads to the changes in the canals that communicate with the periesophageal rings with the madreporic plate. In fact, in regular urchins, the water that must penetrate into the radial water canals will not pass by the glandular canal because it will encounter in the tissue of the ovoid gland a considerable resistance that will slow its speed proportionally. It passes by the stone canal that offers it an easy way to penetrate into the lower esophageal ring and from there into the radial water canals that leave from it. In spatangoids, the introduction of seawater into the circulatory system no longer taking place, or occurring in a very rudimentary fashion, the canal that permits this introduction in the urchin no longer has any utility and has disappeared. The portion that remains, limited to the esophagus only, shows however that in a prior state this canal must have existed perfectly developed. This would produce a mechanical cause to add to the anatomical causes considered above, and that have contributed to determine the important modifications that we have encountered in the circulatory system of spatangoids.

There results from this fact the consequence that, in spatangoids, the stone canal is not homologous with the stone canal of urchins, but indeed with the glandular gland of these animals. This hypothesis is made probable by this fact that the stone canal, which has a glandular structure in spatangoids on part of its path, has in others the same relation with the excretory organ that the glandular canal has in urchins with the ovoid gland.

It is time to terminate this already too long discussion of the considerations that are attached to the study of the circulatory system in echinoids. I have thought it would be useful to expose all the consequences that one could pull from the study of this system; and since it is impossible to resolve presently the question of nutrition and circulation in echinoids, to investigate at least how one can comprehend from the physiological point of view the different systems that make up the anatomical constitution of these beings, whose functions are still so diffuse and closely associated with each other.

It is in fact impossible to separate the functions of absorption, nutrition, excretion, locomotion and respiration that are all attached to the circulatory system. One should not think that these biological acts in urchins as corresponding to distinct anatomical and physiological states, nor to specific and definite functions being brought about independently **111** of one another. The words by which one ordinarily designates them, and which recall these functions that one is used to seeing brought about separately in higher animals, do not correspond in urchins to independent acts. All is mixed in the circulatory system: That which should dominate in the life of these animals is the ease and rapidity of osmotic changes across the walls of the tissues that go into their organization.

These osmotic changes should make very simple the physiological relations of the vascular system, a system of absorption with the liquid of the general cavity, nourishing system, although these relations appear very obscure from the anatomical point of view. The perivisceral liquid should be considered as the reservoir where the nutritive materials of the organism are accumulated. It receives these from the circulatory system, or rather takes them up directly by endo-osmosis in the digestive tube. It is likewise by endo-osmosis that it nourishes all the organs that it bathes.

The important changes reported in the study of this study of the circulatory system between the spatangoids and the urchins are necessitated and explained even by anatomical and mechanical modifications that have accompanied the passage from regulars to the

irregulars. They show equally with what ease the still very plastic organism can adapt to new conditions and how the differences that exist between the relations of vessels contribute little to the accomplishment of the functions, probably because of the mixing of these diverse functions.

ECHINODERM FAUNA

OF THE COASTS OF PROVENCE

G. DOROCIDARIS. A. AG.

The genus *Dorocidaris* differs from the genus *Cidaris* from which it was recently separated by the ambulacral areas narrowed in the middle and the small number of primary tubercles in the interambulacral areas. The naked median part of the interambulacral zones forms a more or less deep groove. The scrobicular areas are very deep, the scrobicular circles formed by dense granules.

DOROCIDARIS PAPILLATA. AG.

Cidiaris affinis, Philippi, Sars, Heller, Thompson.

“ *hystrix*, Lamk., Riss., Blainv., Grube, Philip., Aradas, Sars, Heller, Lovén.

“ *papillata*, Leske, Flem., Desm., Forbes, Philip., Ag. Et Des., Gray, Sars, Thompson.

Cidarites hystrix, Lamk., Desm.

Leiocidaris affinis, Duj. et Huppé.

“ *hystrix*, Duj. et Hup.

“ *papillata*, Duj. et Hup.

- “ Stokesii, Duj. et Hup.
 Orthocidaris affinis, A. Ag.
 “ hystrix, A. Ag.
 “ papillata, A. Ag.
 Phyllacanthus hystrix, Brandt.

Test nearly spherical, slightly depressed horizontally. Interambulacral grooves furrowed the length of their median line. Scorbicular areas deep, elliptical. Poriferous zones separated by a broad zone of secondary and miliary tubercles, the first being arranged in irregular radial rows separated by slight grooves. Periproct pentagonal, formed of more or less pointed plates, extended between the genital plates up to the ocular plates. **114** Genital plates rectangular with truncated borders; broad genital openings. Ocular plates cordiform. Genital and ocular plates covered in their central parts by miliary tubercles with borders marked by a line of small tubercles. The long spines, striated longitudinally, often reach a length three times the diameter of the test. They are frequently found in old individuals taken in certain stations. Some varieties and even true species have been proposed for the variations observed in the dimensions, number, coloration, and the degree of integrity of these spines (*D. Stokesii*, *D. affinis*, etc.).

The pedicellariae of *D. papillata* show all the characters common to cidaroids and indicated by Perrier, with the calcareous rod of the stem articulating directly with the base of the head, without being separated from it by a more or less considerable interval formed only by soft parts. The head does not articulate with the properly so-called stem, but with a small calcareous rod, the *tigelle* of Perrier, which attaches on the end of the stem and is continuous with its tissue. At the point where the rod inserts on the stem, the calcareous rods that constitute the latter are not at all unified, which gives it the appearance of a kind of small collar formed of pointed calcareous rods surrounding the lower end of the rod. It is to this small collar and the length of the rod that the adductor muscles of the valves insert.

D. papillata has three kinds of pedicellariae of which two are found only in the interambulacral area; the third, which is very abundant, is observed on the entire surface of the test as well as on the buccal membrane. On finds, in fact: 1° tridactyl pedicellariae (pl. VII, fig. 51) with three long valves, very wide at the base and narrow abruptly into very elongated, concave baskets covered the entire length of their edges with very fine and very close teeth. 2° Very large, bulging pedicellariae (fig. 49) that are much smaller at the lower part, narrow at their extremity. Their valves, strongly concave, have their borders covered with numerous fine teeth that become stronger and sharper as well as less numerous in the upper region of the valve that ends in a small hook. 3° Pedicellariae smaller than the preceding, relatively much less wide at the base and with a more regular profile. The valves in the form of concave baskets are covered with fine teeth becoming a little longer at the upper part. The concavity of the valve is separated into two unequal chambers by a calcareous bar that crosses the valve three-fourths in going from one border to the other and limits thus a small upper triangular cavity (pl. VII, fig. 50). A division into two analogous cavities exists already in the pedicellariae of the preceding type, but the disposition there is much less clearly indicated than in the form **115** considered now. This form of pedicellaria is more widespread. One finds them in large number on the buccal

membrane in the midst of the scales that cover it. One could think these pedicellariae are perhaps very young pedicellariae of the second type. But their very different form, the existence of the transverse bar and the teeth that maintain nearly the same form the entire length of the edge of the valves, and finally the fact that they are found in certain regions of the test where one encounters them to the exclusion of the two other types makes them considered as representing a type really distinct and well defined.

The pieces of the lantern of *D. papillata* show certain peculiarities that merit being reported. The two branches of the five jaws are united nearly the entire length of their borders. The free space that limits the separate portions is thus smaller than in other species. It is only a simple notch that scarcely merits the name of fenestra because it is not closed above but is simply limited by two small points belonging to the jaws that advance towards each other without touching. Between the two branches of each jaw one sees across the transparent membrane that covers the masticatory apparatus a short endognath that reaches right up to the upper plane of the lantern. Its calcareous tissue softens towards its upper end, but does not constitute a true dental plume. The non-bifurcated compass is terminated only by a small bilobed head.

The membrane enveloping the lantern has five peculiar appendices that are very curious. They expand in the direction of the ambulacral zones (pl. III, fig. 16, *Ap*). These appendices arise at the level of the enlarged end of the compass. They are hollow and have a conical form. Their upper surface is smooth and their lower surface, irregularly slashed, shows a double row of small, round, brown, unequal protuberances that become smaller towards the free end of the appendix. Injection of these small diverticula fills all the empty space left between the lantern and the membrane that covers it. This is stronger and more resistant than in any other species. The walls of these appendices are formed of a connective tissue lamina filled with calcareous spicules like the membrane of the lantern and that which lines the internal surface of the test. The lamina is covered with a ciliated epithelium on both surfaces. The brown color of the protuberances on the lower surface is due to the deposition of pigmented granulations of the same color.

Stewart³³, in 1878, first described the diverticula of the lantern of **116** *D. papillata*. But it seems to me that the illustrator of preparations of Stewart has made the appendices much too large relatively to the dimensions of the specimen. At least I have never seen them reach this size in the animals I have dissected. Moreover, certain details of the structure of the upper surface of the lantern are incorrect, and the auricles are shown as being united at the base. In 1880, H. Ludwig, ignorant of the work of Stewart, reported again these parts that he described as a new organ in cidaroids³⁴. I have thought it necessary to give a new figure of those of *Dorocidaris papillata*.

The digestive tube of *D. papillata* differs in certain regards from that of other regular urchins. The esophagus is rectilinear (pl. III, fig. 17). The lower curve shows a series of

³³STEWART. *On certain organs of Cidaridæ*. Trans. Linn. Soc. London, 1877.

³⁴H. LUDWIG. *Ein neues Organ bei den Cidariden*. Zeitsch. f. w. Zoologie. B. XXXIV, n. I, p. 82, pl. III. 1880.

strongly accentuated concavities and convexities. The convex parts are molded onto the gonads that they envelop in part. The volume of these latter being very considerable, it follows that the curves of the digestive tube are more marked than everywhere else. The internal border of the lower curve is regular and edged by the internal marginal vessel and the intestinal siphon. The upper curve shows a more regular path. It is simply sinuous on its external border. The internal border of the two intestinal curves is accompanied by a large mesenterial band.

The voluminous gonads extend the entire length of the interradian zones, and occupy the space left free between the test and the intestine. It is covered in large part by the circumvolutions of the lower curve.

The different organs that constitute the internal anatomy of *Dorocidaris* (digestive tube, vessels, ambulacral vesicles, ovoid gland) show the common characteristic of being filled with very numerous and very packed calcareous spicules. The calcareous spicules, ordinarily with three branches, that are found in ovaries have been illustrated by Stewart.

HABITAT. — *D. papillata* has not abandoned the great depths. The individuals taken nearest the coast, at Marseille come from muddy depths of the north-west region of the gulf at 80 m. This species is encountered principally to the south of Planier in muddy stones. At first associated with *Echinus acutus*, it is soon replaces it and descends up to 250 m of depth at the edge of the Peyssonel cliff. Towards Toulon and up to Nice, it is encountered always in analogous stations, sometimes in mud, sometimes in muddy stone or even in the deep coralligenous bottoms, as below Cape Sicié from 90 to 100 m. It **117** is, moreover, capable of descending deeper in the abyss. The expedition of the *Travailleur* collected it in the Gulf of Gascogne at very great depths (1,190 m, 1,200 m, 1,350 m).

G. ARBACIA. GRAY.

Test thick, circular, flattened. Narrow ambulacral areas. Tubercles imperforate disposed in two irregular vertical lines in the ambulacral areas and at least in four lines in the two interambulacral areas. These lines sometimes reach the number 12 in the interradian areas, but none reach the top of the test. Poriferous zones constituted by a simple vertical pair of pores. But the pores become much more numerous, and the zones take a petaloid appearance in the area of the peristome. This is very large, limited by the prominent ambulacral borders that lack deep slits. Periproct constituted by four plates arranged in a cross. Buccal membrane naked. Auricles not united. Spines strong with a structure analogous to those of cidaroids.

ARBACIA PUSTULOSA, LESKE.

Agarites loculatus. Ag. Et Des.

Cidaris pustulosa. Klein, Leske.

Echinocidaris æquituberculata. Desm., Ag., Aradas, Troschel, Muller, Sars, Bronn,

Duj. et Hup.
 Echinocidaris grandinosa. Ag., Perrier.
 Echinocidaris oculata. Ag., Duj. et Hup., Perrier, Desm.
 Echinocidaris pustulosa. Ag., Duj. et Hup., Perrier, Desm.
 Echinocidaris æquituberculatus. Blainv.
 Echinus oculatus. Blainv.
 Echinus pustulosus. Gmel., Lam., Blainv., M. Edw.
 Echinus Neapolitanus. Delle Chiaje.
 Tetrapyrgus æquituberculatus. Ag.
 Tetrapyrgus grandinosus. Ag.
 Tetrapyrgus pustulatus. Ag.

118 Peristome very large. Periproct surrounded by the very small genital plates. Coronal plates narrow, completely covered with tubercles disposed parallel to the sutures. The disposition of the tubercles in vertical rows is apparent only in young individuals. The rows of tubercles of the ambulacral plates are connected and separated by some miliary tubercles. The interambulacral plates of the periphery of the test carry four, five, or six primary tubercles occupying a large part of the plate and separated by miliary tubercles arranged in a circle.

The number of tubercles of the plates is susceptible to vary within limits, which has previously brought about the creation of several species (*Echinocidaris oculata*, *pustulosa*, *æquituberculata*, etc.)

The pedicellariae belong to two different types. One, with a large head, forms a very dense crown around the buccal opening, and is encountered also on the entire surface of the test. These are the ophicephalous pedicellariae whose very strong valves are slightly narrowed in the middle and have borders covered with very marked teeth. The apophysial area of the internal median branches recall the arrangement illustrated by Perrier in *Arbacia punctulata*. The figure I give makes it unnecessary for me to describe it (pl. VII, fig. 52). The stem is separated from the head only by a narrow space. For nearly the entire length, the calcareous rod shows a fibrous aspect that could make one suppose it was made of connective tissue if carbonic acid did not result in a rapid dissolution. It is enlarged at its end with an elongated button where one finds the ordinarily reticulated structure of calcareous deposits in echinoderms. Adductor muscles of the valves leave from this enlargement. The head and the stem of the pedicellariae are covered with a thick connective tissue membrane filled with black granulations (which is, moreover, very widespread on the entire external surface of the test). This often makes observations very difficult. The pedicellariae of the second type recall by the form of their head tridactyl pedicellariae. The concave valves at their lower part are filled with semi-circular arcs less developed than in the preceding form. The calcareous rod of the stem shows equally a fibrous aspect nearly its entire length, and terminates in an enlargement composed of reticulated calcite that is always separated from the head of the pedicellaria by a large space occupied by soft parts (muscle and connective envelope).

The pieces that make up the Aristotle's lantern show the following arrangement. As in *Dorocidaris*, the jaws are not united above by transverse arcs. The opening called the

fenestra is thus incomplete and is limited above only by two small extensions that come from **119** the end of the jaws that approach each other without touching. As a result, the endognath is visible from the exterior its entire length as its insertion on the jaw up to the end of the dentary plume. The compass, terminated at the peripheral end by a simple enlargement, does not lie directly on the rotula, but is always far away. They are strongly curved according to their length.

The lantern is relatively small. Because of the separation of the compass and the rotula, its upper face is strongly concave in the center. Because of the slight development of the lantern and of the size of the peristomial opening, the muscles that extend from the auricles to the compass are strongly oblique instead of being vertical as in other species.

HABITAT. — This species is absolutely coastal where it is found associated with *Strongylocentrotus lividus*. But while it is quite common in the littoral of Algeria, it becomes rare on the northern shores of the Mediterranean. It lives ordinarily in tropical seas and Marseille is its northern limit. It has been collected only occasionally at Marseille, on the northern coast of the gulf at Méjean, Niolon, Morgilet, and on the coast of Cassis. It is more frequent at Nice.

GEOGRAPHICAL DISTRIBUTION. — Coasts of Sicily, Naples, Adriatic Sea, western coasts of Africa, Liberia, Madeira, Cape Verde Islands, Canary Islands, Brazil (Rio de Janeiro).

CENTROSTEPHANUS LONGISPINUS, PETERS.

(*Diadema longispinosa*)

I can only cite this species as I have not been able to make an anatomical study. It was captured at Nice quite recently. This station is the northernmost for this beautiful echinoid, reported previously at Naples, on the coasts of Sicily, to the Canaries and at Madiera, but rare everywhere.

G. ECHINUS. RONDELET.

Swollen test more or less globular. Tubercles relatively small, imperforated, as large on the ambulacral areas as on the interambulacral areas, arranged in each zone in two principal rows with other rows **120** of smaller tubercles. Spines moderately long, striated longitudinally. Ambulacra lacking trigeminate pores. Peristome small, with shallow slits. Buccal membrane naked. Jaws and auricles small.

ECHINUS MELO. LAM.

Echinus ventriculosus. D. Chiaje.

Test nearly globular, with a color always approaching green. The coronal plates are elongated, the primary tubercles are small, and the rest of the plate is covered with numerous secondary tubercles. The genital plates are pointed and covered on the anal side with six or seven secondary tubercles. Genital openings a little separated from the external angle of the plate. Ocular plates pentagonal. The periproct is surrounded only by the genital plates. The primary spines are short, small, slender, clearly striated with a red-brown color at the base and green the rest of the length of the spine. The peristome is smaller and the auricles thinner than in *E. acutus*.

E. melo has four types of pedicellariae. 1° Very numerous glandular gemmiform pedicellariae, whose stems articulate directly with the heads. Each valve of the head, with a reduced calcareous skeleton, has a bifurcated glandular sac at its upper end. The wall of these sacs, which contains a mucus material, has a muscular layer, a connective tissue layer, and an external epithelium whose cells in certain ways has a peculiar structure and form kinds of small buds that are probably sensory. 2° Large and strong tridactyl pedicellariae with straight elongated, thin valves, finely toothed on the edges. 3° Ophiocephalous pedicellariae forming a dense crown around the mouth. 4° Trifoliate pedicellariae, very abundant on the entire surface of the test and whose characters were described by Perrier.

The anatomical characters of *E. melo* are of a completely secondary order. The very globulus gonads do not extend half the interambulacral zone. The diverticulum formed by the lower intestinal curve at the entrance of the esophagus is better defined than in other types. The ovoid gland is very elongated. The pigmentation of the tissue is generally little developed.

HABITAT. — *E. melo* lives on muddy bottoms of the N.O. at seventy and eighty meters. It is always very rare in the gulf. In contrast, it is very common at Nice.

121 GEOGRAPHICAL RANGE. — Mediterranean (Naples, west coast of Italy, Algiers, Oran); coasts of Portugal and Spain; Cape Verde Islands, Canary Islands; west coast of Africa.

ECHINUS ACUTUS. LAM.

Echinus Flemingii. Ag. Et Des., Forbes, Sars, Duj. et Hup., Fischer, Thompson.

“ *Pseudomelo*. J. Müller.

“ *Sardicus*. Cailliaud.

“ *melo*. Gauthier, Marion.

The form of the test is more or less conical and the ventral surface flat. The interambulacral spaces are slightly concave in the middle. Also the contour of the test appears sub-pentagonal from above. Two principal rows of primary tubercles in each interambulacral zone. At the periphery of the test are two other vertical rows, but these do not reach the

top. Genital plates pointed with a row of three to four secondary tubercles on the anal border. Genital openings very close to the external border of the plate. The general color of the test is pink or red, but it is not uniform. The ventral surface is nearly white, slightly pinkish, while the dorsal surface has a series of alternately white and red bands. The white bands correspond to the lines of sutures of the plates and disappear as they approach the uniformly red top. This alternation of colors is especially marked in large specimens. The primary spines are longer, strongly, less clearly striated than in *E. melo*. Their color is purple-red at the base, then green, then white and again red at the top.

E. acutus is very common at Marseille. But it was considered at the laboratory as corresponding to *E. melo* up to the day when Marion had from Nice and even Marseille the true *E. melo* whose differential characters could be clearly recognized. The frankly conical form of the test with alternating pink and white bands, the color and dimension of the spines distinguishes, in fact, *E. acutus* from *E. melo*, whose test is spherical and of a generally green color. The other characters (secondary tubercles less numerous on the coronal plates and on the genital plates, larger peristome, stronger auricles, genital openings closer to the external border of the genital plate), although less apparent, again justify the separation of *E. acutus* from *E. melo*.

The pedicellariae of *E. acutus* are identical to those of *E. melo*, and the internal anatomy of the two species does not differ.

122 HABITAT. — *E. acutus* is abundant on widespread corraline bottoms and on muddy bottoms of the [N.-O.] from 40 to 80, 100 and 200 meters depth. Some individuals of small size have been found exceptionally in the basins of Cape Pinède. This species is much less frequent at Nice, where *E. melo* is by contrast very abundant.

GEOGRAPHIC RANGE — Western coast of Norway, Shetland Islands, Mediterranean (Port-Vendres, Toulon, Naples, Algiers, Oran), Ascension Island, Halifax, near New York.

G. PSAMMECHINUS. AG.

Test more or less flattened. Tubercles imperforate, smooth. Ambulacral plates with trigeminate pores. Peristome lacking deep slits. Spines thin, pointed, very finely striated longitudinally.

The *G. Psammechinus* was combined by A. Agassiz in his *Revision of the Echini* with *G. Echinus*. I believe however that one can consider *Psammechinus* as forming a separate genus, obviously very close to *Echinus*, or even as a subgenus. It differs, in fact, from all the species of the genus *Echinus* by the arrangement of the buccal membrane.

PSAMMECHINUS MICROTUBERCULATUS, A. AG.

Echinus microtuberculatus, Blainv., Heller, Ag.

“ *miliaris*, Risso, Aradas, Grube.

- “ parvituberculatus, Blainv., Desm.
 - “ decoratus, L. Ag.
 - “ pulchellus, Müller.
- Psammechinus pavituberculatus, Duj. et Hup.
- “ pulchelus. Bronn., Duj. et Hup.

The primary tubercles are arranged in two principal rows in each ambulacral and interambulacral zone. The rest of the coronal plaques are covered with irregularly arranged secondary tubercles separated by numerous miliary tubercles. The abactinal system is projecting. The ocular and genital plates are covered likewise with small secondary tubercles. The genital openings are large. The periproct, surrounded only by genital plates, is formed of small regular plates covered with fine tubercles. The peristome is large and the buccal membrane is covered with very crowded irregular scales, **123** imbricated as the tiles of a roof. The spines are thin, pointed, green or gray, yellowish at the point.

The pedicellariae are of three types: gemmiform, ophiocephalus and tridactyle. They were described and illustrated by Perrier.

The gonads of *P. microtuberculatus* show this characteristic fact, that they are not independent of each other. All five converge towards the apical pole, and are united to form a large circular band that surrounds the rectum and is interrupted only on the radial side *I*. It would be even more exact to say that the genital apparatus of Psammechinus consists of a glandular ring surrounding the rectum, and having short conical extensions in the interambulacral zone.

HABITAT. — *P. microtuberculatus* is abundant on muddy or stoney spaces situated in the midst of zostera meadows. It is generally associated with *Sphærechinus granularis*, but always much more abundant than it. It does not approach as near the shore as *Str. lividus*.

GEOGRAPHICAL RANGE. — Mediterranean (Marseille, Nice, Genoa, Naples, Messina, Trieste, Venice, Oran, Algiers); coasts of Portugal and Spain, Cape Verde Islands, Canary Islands, west coast of Africa.

G. STRONGYLOCENTROTUS, BRANDT

Test circular, globular, more or less flattened. Tubercles small, imperforate, unequal, forming vertical rows. Five or six pairs at least of pores on each ambulacral plate. Peristome decagonal, with shallow notches. Buccal membrane not covered with large plates. Spines long, of medium size, striated longitudinally.

STRONGYLOCENTROTUS LIVIDUS, BRANDT

Echinus lividus, Lam., Blainv., L. Ag., Desm., Forbes, Krohn, Val, Grube, Duj. et Hup.,
Heller, Metschnikoff, Ludwig.

“ saxatilis, Tiedemann, Grube, D. Chiaje.

“ purpureus, Risso, Gray.

“ vulgaris, Blainv., L. Ag.

Euryechius lividus, Verrille

Toxopneustes lividus, Sars, Lutken, Heller, Fischer, Perrier, Hoffmann, Fredericq, Stossich.

124 Two principal rows of primary tubercles on each ambulacral or interambulacral plates. In the interambulacral zones, each principal row is accompanied by two rows of secondary tubercles that decrease little by little in size at disappear near the apical pole. The middle of the ambulacral zone is occupied by a row of small tubercles forming a zigzag line. All the principal tubercles forming the vertical lines in the ambulacral and interambulacral zones are surrounded by a circle of miliary tubercles. The poriferous zone generally contains five pairs of pores arranged in an arc around the primary tubercle. The apical system is projecting. Only the very large genital plates surround the periproct. The small ocular plates, lodged in the angle of the genital plates, touch the periproct only in young individuals. The genital plates have three to five tubercles on the anal border. The genital openings occur near the external border of the plate. The peristome is small, and the buccal membrane is covered with very small plates. The medium sized auricles, with a large opening, are united by a projecting edge. The long, thin and pointed spines vary in color from olive green to deep violet.

Strongylocentrotus lividus was once united with the genus *Toxopneustes*. This genus, such as it is established now, is distinguished from it by its deep peristomial slits and its buccal membrane completely covered with large imbricated plates.

HABITAT. — *St. lividus* is the most abundant species of the Gulf of Marseille, where it is fished each year and delivered for consumption in very considerable quantities from the month of September up to the month of April.

The edible urchin of the Gulf of Marseille lives, as in the ocean, on rocky shores, and it is not uncommon to find it along some islands numerous individuals lodged in cavities in the manner of *St. lividus* of Brittany whose holes have been noted for a long time. It is in the shallow-water meadows of *Zostera* (*Posidonia Caulini*) that *St. lividus* is primarily abundant. It goes deeper, up to thirty or thirty-five meters, to reach the lower limits of the meadows of the monocotyledons, but it no longer reaches the size of coastal individuals.

St. lividus resists to some degree impure water and it penetrates into the outer harbor and the first dock of the National Port under Cape Pinède. Marion made a very interesting observation on the subject of the relative hardiness of this species. After the digging of the maritime canal connected the lagoons of Caronte and Berre with the Gulf of **125** Fos, the waters of the lagoons in the neighborhood of Martigues became in 1875 much saltier than before. The plutei of *St. lividus* established around Port-de-Bouc in the open sea were always entrained by entering currents towards Martigue, but they reached it without producing anything while the salty water did not enter as abundantly. Little by little, small urchins were discovered in Carone. They became established up to Martigues, then later up to Jaï along the southern coast of the Méde. In Caronte, these small urchins have become

very abundant, and one can state that, despite their small size scarcely a fourth the maximum, the reproductive organs were in perfect state.

This dwarf race, born under the influence of the brackish water of the lagoons, was not established permanently in this locality. The exceptionally rigorous cold of the year 1880 caused such a great mortality in the population of the frozen lagoons of Caronte and Berre that these small *St. lividus* were exterminated so that one can no longer find a single living individual.

GEOGRAPHICAL RANGE. — Western coast of France, Mediterranean (Marseille, Cette, Nice, coast of Algeria, Messina, Trieste, etc.). Southern coast of England, Azores, Brasil.

G. SPHÆRECHINUS. DESOR.

Thick test nearly spherical, numerous imperforated tubercles of equal size in the two areas. Peristome decagonal, provided with deep slits. Four pairs of pores on each ambulacral plate. Buccal membrane thin, showing some projecting plates.

SPHÆRECHINUS GRANULARIS. A. AG.

Echinus albidus, L. Ag.

“ *brevispinosus*, Risso, L. Ag., Val., Müller, Heller.

“ *dubiuis*, Desm.

“ *esculentus*, Lamk., D. Chiaje, Blainv., Grube, Hoffmann.

“ *granularis*, Lamk.

“ *æquituberculatus* Blainv., Desm., L. Ag.

“ *ovarius*, Rond.

“ *subglobiformis*, Blainv., Desm.

Sphærechinus brispinosus, Desor. **126**

Toxopneustes albidus, Ag. et Desor., Duj. et Hup.

“ *brevispinosus*, Ag. et Desor., Müller, Krohn, Sars, Duj. et Hup., Heller, Thompson, Dohrn, Strossich.

“ *granularis*, Ag. et Desor., Duj. et Hup.

The test on the ventral surface is flat, slightly depressed, sometimes conical, other times nearly spherical. The pores of the poriferous zones are arranged in a straight line or in arcs with four pairs on each plates and more in large specimens. The primary tubercles are arranged in two or four vertical rows in the interambulacral zones. They form likewise horizontal lines and are separated by numerous secondary tubercles. The genital plates and oculars carry several tubercles on the side of the periproct. This, slightly oval, is formed of irregular plates, large at the periphery, smaller at the center. It is surrounded by the genital plates and the ocular plates. The genital openings are situated at the center of the plates.

The auricles are solid and have large openings. The spines are short, blunt, very dense, of equal length. Their color varies from violet to white, to brown, to yellow. Sometimes they are entirely violet, sometimes colored at the base and white at the end, or better still completely white.

I have nothing to report on the internal anatomy of *Sphærechinus*. It is with *St. lividus* the species that served as my type for all that touches the history of regular urchins. I have already remarked that the gonads of *Sphærechinus* are always not large and often form only a simple linear band running the length of the interambulacral zone. I shall recall likewise that the gemmiform pedicellariae of *Sp. Granularis* are of glandular nature. I have sufficiently spoken of it in the first part of this work not to be obliged to return there. The other forms of pedicellariae have been described by Perrier.

HABITAT. — *Sp. granularis* (urchin *racasso* of the Provençaux) has its center of habitat on the muddy stones of the periphery of zostera meadows at twenty to thirty meters depth. It penetrates moreover into these meadows as is associated, although very fewer in number, with *St. lividus*.

GEOGRAPHICAL RANGE. — Mediterranean (Marseille, Nice, Genoa, Naples, west coast of Italy, Sicily, northern coast of Africa); coasts of the Adriatic Sea, **127** western coasts of France, Spain, and Madeira; Cape Verde Islands, western coast of Africa.

ECHINOCYAMUS PUSILLUS. GRAY.

(Fibularia Tarentina)

Inhabits coralline bottoms and muddy stones from twenty-five meters up to sixty meters. Associated sometimes with *Sp. granularis* and with *Ps. microtuberculatus*, sometimes with *Spatangus*, or with *E. acutus*. Its remains are encountered in great abundance in the intestine of *Spatangus*. It is always of very small size.

G. SPATANGUS. KLEIN.

Test moderately swollen, heart-shaped. Petals large. Anterior groove wide, more or less deep. Infra-anal fasciole protruding, undulating. No lateral or peripetal fascioles. Tubercles on the five interambulacral areas large and perforated.

SPATANGUS PURPUREUS. MULLER.

Echinus purpureus, Gmel., Pennant.

Spatangus meridionalis, Risso, Blainv., Philip., Ag., Gray, Sars, Duj. et Hup., Perrier, Teuscher.

“ Reginæ, Gray.
 “ spinosissimus, Ag. Gray.

The cordiform test, truncated obliquely at the posterior end, shows a regular contour. The ventral surface is flat. The wide anterior groove reaches its greatest depth at the level of the test circumference. The apical pole is carried a little forward. The anterior petals are a little longer, and form together an angle more obtuse than the posterior petals that are a little narrower and closer. The periproct is broad, elongated transversely. The infra-anal fasciole is strongly concave on the side of the anus. The mouth is broad and the lower lip slightly protruding. The elongated, triangular plastron shows a slightly marked enlargement at its center. The ventral, posterior ambulacral areas are broad, and the lateral areas are triangular. The pores of the peristomial tube feet are surrounded by a deep circle. It is in the interradial areas of the dorsal surface that the tubercles attain the greatest **128** dimensions. These tubercles are arranged near the apical border of the plates and are united in more or less numerous groups having the form of a V or a triangle. These large tubercles do not reach the periphery of the test. The border of the anterior groove has several rows of smaller tubercles that become less numerous towards the periphery of the test where they are continuous with the tubercles of the ventral surface. All the rest of the dorsal surface is covered with miliary tubercles. The tubercles of the ventral surface, smaller than the large tubercles of the dorsal surface, are more reduced towards the periphery of the test and pass insensibly to the miliary tubercles of the dorsal surface. The tubercles of the ventral plastron become smaller and smaller the more they approach the median line. The spines of the large tubercles of the dorsal surface are very long and pointed. The spines of the ventral surface are much smaller. They are striated longitudinally and transversely, and never enlarged into a club or a spatula. Their color, generally violet-purple, passes sometimes to yellow.

The pedicellariae belong to three different types. The large tridactyl pedicellariae and the ophiocephalous pedicellariae have been described by Perrier. One encounters moreover, in great abundance, on the entire surface of the test, small pedicellariae with a long stem, very short, triangular valves that have fine teeth on their edges. This form exists in most of the spatangoids, a pedicellaria analogous apparently to *Echinocardium flavescens* is shown in pl. VII.

HABITAT. — *Sp. purpureus* is very common in the Gulf of Marseille where it lives in very firm stone or stoney-mud bottoms. In some sites, as southeast of Château-d'If, it scarcely reaches 15 or 18 m depth. It goes down to 30 to 40 m in the corraline bottoms of the Ile de Riou and Podestat. It is generally associated with *Sph. granularis*, *Ps. microtuberculatus*, *Ech. flavescens*, etc.

GEOGRAPHICAL RANGE. — West coasts of Norway, Lofoden Island, Shetland, North Sea, western coasts of France (La Rochelle), Cherbourg, Marseille, Nice, Naples, west coast of Italy, Malta, Trieste, Suez, Bermuda, Azores.

G. ECHINOCARDIUM. GRAY

Test cordiform, petaloid ambulacra more or less triangular. Anterior ambulacra forming a more or less distinct groove. Posterior end truncated vertically. An internal fasciole surrounds the anterior ambulacra **129** and a part of the petals. An infra-anal fasciole has branches ascending each side of the periproct. The portion of the petals, limited by the internal fasciole, has only small, simple more-or-less obliterated pores.

ECHINOCARDIUM FLAVESCENS

Amphidetus ovatus, Düben och Koren, Ag. et Desor, Sars, Perrier, Thompson.

“ *roseus*, Forbes, Möbius.

Echinocardium ovatum, Gray, Duj. et Hup., Lutken, Ag.

Sptangus flavescens, Muller.

“ *ovatus*, Fleming, Blainv., Desm.

Test oval, regularly arched. It is truncated posteriorly and has a more regular profile than in the other species. The posterior interradiar protrusion of the dorsal surface is less accentuated than in *Ech. cordatum*. The ambulacral zones are not deep and the anterior groove little marked. Often, the anterior ambulacra is level with the test. The internal fasciole is large. The infra-anal fasciole is terminated below in a slightly marked point. The mouth is small, and the posterior lip narrow. The periproct is broad, slightly elongated, transverse. The ventral ambulacral zones are slightly wider than in *Ech. cordatum*. The spines are very long and very strong, spatula-like on the ventral plastron. The color is gray or dirty white.

The pedicellariae are of four kinds. 1° Large gemmiform pedicellariae with a short stem, valves slightly narrowed in the middle, toothed at the end. 2° Tridactyl pedicellariae with wide, [rapproches], very elongated valves with a short stem. 3° Pedicellariae with a small head, triangular valves finely toothed on the borders and whose calcareous rod of the stem is separated from the head by a very long membranous portion (pl. VII, fig. 57). 4° Finally, larger pedicellariae with fleshy valves of a very deep purple color and irregularly distributed on the dorsal surface of the test only. Some specimens have twenty of them, others only five or six. Some seem completely devoid of them. The three valves are united at the base by a clear, white, transparent membrane sprinkled with small red dots made up of the fibers of the adductor muscles of the valves (figs. 59 and 60). These pedicellariae resemble in their form and composition of their calcareous skeleton the glandular gemmiform pedicellariae of *Sphærechinus* or *Echinus*, i.e. that the calcareous rod of the stem articulates directly with the valves of the head, and that the calcareous skeleton of each valves contains an enlarged basal part and a very narrow terminal part. These calcareous rods **130** each support a small sac whose wall is formed by a very thin membrane of connective tissue and a thick layer of muscular fibers and which contain only red or yellow pigment granules, but never a mucus substances as in the genera cited above.

When one puts a drop of alcohol on these pedicellariae, one sees the red pigment dissolve rapidly and the sac is not slow to shrink and wither. It must be noted that the red pigment exists only in these pedicellariae. All other parts of the test of *Ech. flavescens* contain only the yellow pigment.

HABITAT. — This species has been found at Marseille by Marion in 1869. It was reported by Gauthier in 1874 from individuals collected at the laboratory of Marseille, and it has been found since at Capri (Ludwig, Echinodermen des Mittelmeeres). These are the only two stations where one knows it in the Mediterranean. The first individuals collected at the laboratory came from stone and coralline gravel of the gulf on the edge of the Ile de Pomègue at 40 and 60 m. Then, *Ech. flavescens* was discovered in a habitat to the southeast of Château-d'If in a small area of mud situated in the middle of zostera meadows. The individuals of this habitat are, in general, of very large size (about 3 cm long). Quite recently, fishermen have found, between the port of Frioul and Château-d'If in another muddy band, some specimens of a truly remarkable size. They reach, and in fact pass even four and a half centimeters in length.

Ech. flavescens is, in general associated with *Spatangus* and *Schizaster canaliferus*.

GEOGRAPHICAL RANGE. — Coasts of Norway, North Sea, Shetland, Dublin, Belfast, Cape of Good Hope, Florida, Gulf stream.

ECHINOCARDIUM CORDATUM. GRAY.

Amphidetus cordatus, Forbes, Ag. et Desor, Duben och Koren, Müller, Sars, Fischer, Mobius, Perier.

“ kurtzii, Girard.

“ pusilluls, L. Ag.

Echinus cordatus, Pennant.

Echinospatagus cordiformis, Breyin.

Spatangus arenarius, Lamk., Blainv. Dem.

“ cordatus, Fleming.

“ pusillus, Leske

The test is thin, cordiform. The posterior interradius enlarged in a very marked protuberance. **131** The anterior ambulacral groove is very much deeper than the lateral ambulacra, and the test slightly protrudes on each side of this groove. The very deep petals are triangular. The infra-anal fasciole is elliptical and ends in a lower point. The periproct is elongated vertically. The ambulacral spaces that surround the mouth decrease rapidly in size as they advance towards the edge of the test. The pores of the anterior ambulacrum are very numerous and very dense. The ventral plastron is oval. The spines of the dorsal surface are very thin and silky. They are longer on the ventral surface and spatula-like on the actinal plastron, but always less strong and less long than in the preceding species.

The test is flattened horizontally and its contour, seen from above, is always less regular than in *Ech. flavescens*. According to Agassiz, the American specimens have the posterior

interradial protrusion more accentuated, the periproct more circular, made up of more numerous plates, than the specimens of Europe where the plates are less numerous and larger.

Marion possessed in his collection some specimens of *Ech. cordatum* dredged from the road of Syra and which deviated quite notably from the normal type. Their study has, in this regard, a certain interest. These specimens, of different sizes, are a little more elongated than the Atlantic individuals, the anterior groove and the petaloid ambulacra are less deep, the spines longer and stronger than in the normal type. The spatula-like form of the spines of the ventral plastron is also more accentuated than ordinary. The youngest of these specimens has a normal periproct, elongated longitudinally. The medium examples have it rounded. It becomes transversely elongated in the two largest individuals. In one of the latter, the contour of the test is nearly regular and in fact resembles, when looked at from above, *Ech. flavescens*. Seen from the side, it resembles *Ech. cordatum* because of the flattening of the dorsal surface. The anterior groove and the petals are still less deep than in the four other specimens.

These individuals are certainly *Ech. cordatum*. But the characters of this species tend to disappear and to be replaced by those of *Ech. flavescens* with increase in age (transverse elongation of the periproct, disappearance of the anterior groove, regularity in the contour of the test, development of the spines). They evidently form a type of transition between these two species that is interesting to verify.

HABITAT. — *Ech. cordatum* is rare in the gulf of Marseille. Some individuals have been taken in the gulf of Madrague and that of Prado at 2-4 meters of depth in stone. The species becomes more abundant towards **132** the stoney beaches of the mouths of the Rhone, and appears very commonly at Fos. All individuals from Provence are always of small size.

GEOGRAPHICAL RANGE. — Coasts of Norway, Mediterranean, North Sea, Shetland, Great Britain, Brest (Crozon), west coast of France, Naples, east coast of North America, Florida, Brazil.

ECHINOCARDIUM MEDITERRANEUM. GRAY.

Amphidetus gibbosus, Ag. et Des., Fischer.

“ *Mediterraneus*, Forbes, Ag. et Des., Sars, Heller.

Echinocardium gibbosum, Gray, Duj. et Hup.

The test is elevated, flattened above. The anterior end is vertical and the posterior end truncated obliquely. The contour of the test, when one looks at the animal from the ventral surface, shows two lateral angles at the level of the mouth, and a posterior angle on the ventral plastron. The posterior interradian swelling is very pronounced. The anterior ambulacral groove is shallow. The petals are less triangular than in the other species. The periproct is elongated vertically. The internal fasciole is near the anterior end and the infra-anal fasciole ends in a point below. The ventral surface is flat, the ventral ambulacral zones and especially the posterior zones are very wide.

HABITAT. — *Ech. Mediterraneum*, very rare at Marseille is, in contrast, very abundant on the beaches of the mouths of the Rhone, around Fos up to Aiguesmortes (Grau du Roi). Waves very often throw tests up on the beach that are nearly always broken, and it is very difficult to obtain this species by dredging in the stone where it is buried.

GEOGRAPHICAL RANGE. — Marseille, Cette, Nice, Genoa, Naples, coasts of Sicily, Trieste, Ionian Sea, coasts of Algeria.

I have had at my disposal only dry specimens of *Ech. cordatum* and *mediterraneum*, of which I have not been able to study, as a consequence, either the pedicellariae or the internal anatomy. The anatomy of *Echinocardium flavescens* is little different from that of *Spatangus*. The lower intestinal curve is a gray color, the upper of a clear brown color. The rectum has at its origin an appendix in the form of a diverticulum, sort of a waste reservoir, filled with mud as the rest of the digestive tube, and whose walls show nothing peculiar¹³³ in structure. The diverticulum has no transverse folds. The siphon, which describes a very pronounced curve on the ventral mesenteric sheet, opens into the digestive tube only at the end of the lower curve. The internal marginal vessel gives in advance some vessels to the digestive tube and continues up to the second orifice of the opening, at the level of which it divides into several branches that ramify in very great part on the dorsal surface of the lower curve.

GENUS SCHIZASTER. AG.

Test oval, elongated, swollen, apical pole posterior. Anterior ambulacrum marked by a very wide and very deep groove. Ambulacral petaloides very unequal, anterior petals long, slightly flexuous, deep, nearly parallel to the anterior groove. An angular peripetal fasciole closely surrounding the petals and a lateral fasciole leaving from the end of the anterior petals. Posterior lip very prominent. Two to three genital openings.

SCHIZASTER CANALIFERUS. L. AG. et DESOR.

Echinus lacunosus, Lin., Gmel.

Micraster canaliferus, L. Ag., Philip.

Nina canallifera, Gray

Ova canaliferus, Gray

Schizaster cordatus, Brohn.

Spatanugs canliferus, Lamk., Blainv. Desm., Krohn.

“ *lacunosus*, Leske.

The test is slightly cordiform. Seen from the side, it appears thin in front and rapidly becomes wide as it approaches the posterior end where it attains its greatest width. The

posterior interradius is swollen in a rounded protuberance. The posterior end is truncated vertically. The lower surface is convex. The anterior petals are flexuous, deep, a little larger at the end. The posterior petals are small and rounded. The apical end of the petals is narrow, terminated in a point and the pores there are very small. The anterior groove forms a very large and very deep rectangular depression with vertical edges that decrease in depth from the point where passes the peripetal fasciole. It becomes round and attenuates little by little towards the mouth. The very numerous pores are located in the angle formed by the lower plane and the vertical edges of the groove. The pores of the posterior petals are smaller **134** than those of the anterior petals. The ventral ambulacral zones are narrow. The tubercles of the dorsal surface are small and equal, except on the edge of the anterior groove where they are larger. The tubercles of the ventral surface are large and of similar size. Those of the ventral plastron are smaller, arranged in series and decrease in size as they approach the posterior end. The short, thin spines on the dorsal surface completely cover the petals and anterior groove. They are longer and spatula-like on the ventral surface where they are united in tufts that leave from the same point, two lateral tufts and a posterior tuft. The color is a grayish-white.

The pedicellariae of *Schiz. canliferus* are very characteristics and of four different forms. 1° Pedicellariae with four branches, constant and very numerous. Their valves, wide at the base, rapidly become very narrow at keep the same dimensions up to their end which is slightly recurved. The edges do not have teeth in the strict sense, but simply have small pointed tubercles and spaced closer together towards the end of the valves (Pl. VII, fig. 55). The calcareous rod of the stem is slightly elongated from the head of the pedicellaria. 2° Pedicellariae recalling the ordinary type of tridactyl pedicellariae. The valves are wide at the base, narrow in the first fourth, and enlarged again in concave spoons with borders armed with large teeth. 3° Large, thick pedicellariae, very numerous especially in the area of the periproct, but exist also on other parts of the test. Their valves, very wide at the base, narrow to their end which has a very strong curve and are covered with a connective tissue envelope. Their edges lack teeth, but the upper end of each valve is, in contrast, provided with five or six pointed, very strong teeth. The apophyseal apparatus of the valves is very developed. The calcareous rod of the stem articulates directly with the lower surface of the head of the pedicellaria and it has, at a certain distance from its end, a very pronounced enlargement. It is on this enlargement and the length of the subjacent portion of the rod that are inserted the adductor muscles of the valves. The three valves of the pedicellaria are surrounded by a common membrane that envelop them two thirds of their length (Pl. VII, fig. 56). 4° Finally, small pedicellariae with three triangular valves finely tooth on the edges, whose stem has a short calcareous stem and a very long membranous portion.

The esophagus is very short. It goes very obliquely to the left and becomes very narrow in its posterior portion before opening into the lower curve. The latter, gray in color, is much narrower than the upper curve that is three times larger and brown in color. The rectum has near its middle a diverticulum analogous to that of *Echinocardium*, **135** but relatively smaller. The siphon has at its origin a portion with a thick wall as in *Spatangus*. Its path is very short. Outside this siphon exists an accessory siphon analogous to that of *Brissopsis* and *Brissus*, but that comprises only a very small extend of the lower intestinal curve against which it is closely applied (Pl. III, fig. 14, SA). The diverticulum is very long

because the apical pole is very far from the anterior border. It does not have transverse folds. The big mesenterial lamella is not extended up to the end of the lower curve as is the ordinary case, but stops a little after the second orifice of the siphon. The internal marginal vessel, which furnishes no branch to the intestine from the diverticulum up to the orifice of the siphon produces at this point (*b*) numerous vessels that ramify on the dorsal surface and the ventral surface of the latter portion of the lower curve. The stone canal follows a very direct way to reach the excretory organ. It runs along the border of the esophagus, crosses the lower curve and along the free border of the ventral mesenterial lamella to plunge into the depth and is directed towards the madreporic plate (*c*). The anterior gonad does not exist. The two posterior gonads are, in contrast, very voluminous (Pl. II, fig. 12).

HABITAT. — *Schizaster canaliferus* is very rare in the gulf of Marseille. It has been found in muddy bottoms southeast of Château-d'If and east of Pomègue where it lives associated with *Spatangux* and *Ech. flavescens* at 20 to 40 m depth. Most specimens arrive dead and lacking spines. It was reported by Gauthier around Cape Couronne.

GEOGRAPHICAL RANGE. — This species has been reported only in the Mediterranean: Marseille, Nice, western coasts of Italy, Naples; Trieste.

G. BRISSOPSIS. KLEIN.

Ovoid test swollen. Apical pole near center. Anterior ambulacra marked by a shallow groove. Petaloid ambulacra unequal. Two entire peripetal and infra-anal fascioles.

BRISSOPSIS LYRIFERA. AG. et DES.

Brissus lyrifer, Forbes, Duben och Koren, Mobius.

“ pulvinatus, Philip.

Schizaster incertus, Aradas.

136 The test is thin, oval, moderately swollen, slightly depressed. The petaloid ambulacra are always the same depth and the posterior less extended than the anterior. The pores form longitudinal lines equally separated from each other. The peripetal fasciole, slightly sinuous, crosses the posterior petals. The infra-anal fasciole is slightly concave beside the anus. The periproct is nearly circular, slightly elongated vertically. The plates that constitute it are wider at the periphery, especially beside the infra-anal fasciole, small and irregular at the center. The ventral posterior ambulacral zones are wide, which makes the actinal plastron narrow and elongated. The ventral surface is covered with large tubercles that nearly reach the mouth with their great size. The dorsal surface is covered with smaller, less numerous tubercles on the extension of the petaloid ambulacra and in the posterior interradiial zone. The spines of the ventral plastron are generally arranged in two groups on each side of the median line. The spines, short on the dorsal surface, are longer

on the ventral surface. They are never enlarged nor flattened spatula-like. Four genital openings.

Sometimes the infra-anal fasciole extends on each side of the anus two climbing branches that constitute thus an incomplete anal fasciole. Agassiz reported this character as peculiar to American individuals in which this anal fasciole is very clearly defined, while it is scarcely marked in European specimens. I have, in fact, never seen it in the specimens that I have had at my disposition some that came from the coasts of Provence and others from the coasts of Sweden.

The pedicellariae of *Br. lyrifera* are of three kinds and show some striking characteristics that permit making a special description. The gemmiform pedicellariae are generally small, and the calcareous rod of the stem is lightly separated from the head. The tridactyl pedicellariae are large. Their valves, supported by a short stem, have strong, separated teeth and in their lower half, finer and closer together in their upper half. Finally, the third kind contains the small long pedicellariae with triangular valves identical to those in *Spatangus*.

The anatomical characters of *Brissopsis lyrifera* are the following. The two curves of the digestive tube are very wide relatively to the dimensions of the animal. Also the mesenterial lamellae, in addition to being very thin, are themselves very close together in joining the different portions and principally the large dorsal mesenterial lamella on which runs the stone canal. The two nearby regions of the interior curve, which are very separated in the other types, nearly touch in *Brissopsis* (Pl. II, fig. 11). The upper curve is a yellow-brown color that contrasts with the gray color of the lower curve. **137** The rectum is very short and, because of the width of the intestine and the elevated position of the anus, is completely covered by the lower curve when one looks at the animal from the ventral surface. The siphon, instead of having thick walls at its origin, shows to the contrary a considerable dilation and very thin walls. It opens, after a short path, on a point of the lower curve situated near the posterior interradius (*SO*). There exists, moreover, an accessory siphon much narrower than the principal siphon that opens on both sides in the inferior curve (*SA*). This second siphon runs a certain distance on the ventral mesenterial plate from the digestive tube, to which it remains parallel throughout its path.

The internal marginal vessel (*VMI*) gives no branch at all to the digestive tube from the diverticulum up to the level of the second orifice of the siphon. From this point, it furnishes numerous branches that ramify on the dorsal and ventral surfaces of the end of the lower curve. The path of the stone canal is analogous to that of *Spatangus*. There are four gonads. The anterior gonads are less developed than the posteriors. They are positioned very forward and their afferent canals are very long.

HABITAT. — This species does not abandon deep regions. It has been captured by the nets of the “beef” boats that drag their engines off the mouths of the Rhone at 100 and 120 meters depth. It is found off Port-de-Bouc in bottoms of mud and stoney mud. It also appears to exist before Fos (Gautier).

G. BRISSUS. KLEIN.

Ovoid test more or less elongated. Apical pole positioned forward. Petaloid ambulacra narrow, very deep. The anterior petals are both nearly on the extension. The posterior petals, very close together, together form a narrow angle. Anterior ambulacra level with the test or marked by **138** a slight groove. Two fascioles, infra-anal and peripetal, the latter very sinuous. Four genital pores.

BRISSUS UNICOLOR. KLEIN.

Brissus carinatus, Risso, Aradas.

“ *colombaris*, Gray, L. Ag., Lamk., Lütken., Perrier.

“ *dimidatus*, Ag. et Des., Gray.

“ *placenta*, Philip.

“ *scillœ*, A. Ag., Gray, Brohn, Lovèn, Duj. et Hup., Perrier.

Echinus ovatus, Gmel.

“ *unicolor*, Gmel.

Spatangus columbaris, Lamk., Blainv.

“ *ovatus*, Gmel. Desm.

“ *unicolor*, Gmel.

The elliptical test is broadly enlarged posteriorly. The posterior extremity is truncated vertically. There is no enlargement on the posterior interradius. The petals are always the same length and the same depth. The peripetal fasciole shows only a single re-entrant angle in the interradiial areas. The infra-anal fasciole is slightly concave beside the anus. The anterior ambulacrum is even with the test and marked by a band of small dense tubercles between the poriferous zones. The periproct is wide, elongated vertically. The peristome is large, the lower lip slight protruding. The ventral surface is slightly concave. The actinal plastron is wide and elliptical. The posterior ambulacral areas are narrow. The dorsal surface of the test has primary tubercles of the same dimension before the anterior petals. The rest of the dorsal surface is covered with very small tubercles. The tubercles of the ventral surface become smaller towards the posterior end. The spines are short on the dorsal surface and slightly longer on the ventral surface. They widen spatulate-like towards the posterior end of the actinal plastron.

Br. unicolor differs from *Br. carinatus*, which is very close to it, by the single re-entrant angle present in the anterior interradius and the vertical truncation of the posterior extremity of the test, which is oblique in *Br. carinatus*.

The pedicellariae are of three types. 1° Pedicellariae with short, narrow valves, enlarged at the base. Their borders lack teeth on nearly their entire length. The end alone has some. The calcareous rod of the stem is separated from the head by a long interval filled by soft parts (Pl. VII, fig. 54). 2° Tridactyl pedicellariae that have teeth only on their upper half. The lower half has an **139** irregular jagged border (Pl. VII, fig. 53). 3° Short, bulging pedicellariae with valves covered in an enveloping membrane and terminated at the end by some strong teeth. The head articulates directly on the calcareous rod of the stem. They are

analogous to those that I have reported above in *Schizaster* and differ only in the smaller size.

The digestive tube of *Br. unicolor* has nearly the same path as that of *Spatangus*. The siphon, which keeps nearly the same caliber its entire path, describes on the ventral mesenterial plate a very pronounced curve before joining the lower curve that accompanies it up to a point near its end (Pl. II, fig. 10, *SO*). There exists, as in *Brissopsis* and *Schizaster*, an accessory siphon of small caliber, closely applied against the inferior curve, in which it opens at its two ends (*SA*, *g*, and *h*). The internal marginal vessel furnishes branches to the digestive tube only at the level of the second orifice of the siphon, *b*, and most of the branches ramify on the dorsal surface of the inferior curve as in *Spatangus*. The communicating branch (*BR*) has a direct path and reaches the peribuccal ring after describing a very pronounced curve. There are only three gonads. It is the right anterior gland (interradius 5) that has disappeared.

HABITAT. — *Br. unicolor* is rare at Marseille. It has been taken sometimes in the muddy stones around Château-d'If and in the National harbor. It lives in general at a depth of 10 to 20 meters.

GEOGRAPHICAL DISTRIBUTION. — Western coast of Italy, Sicily, Palermo, Cape Verde Islands, Canary Islands, Gulf-Stream, Guadeloupe, Bermuda, Jamaica, Cuba, Haiti, west coast of India.

I am obliged to Professor Greeff of Marburg for sending some specimens of *Brissus unicolor*.

HYBRID FERTILIZATIONS.

During the months of March and April, the season in which most of the echinoids of the coasts of Provence are in the state of sexual activity, I attempted a series of trials of hybridization between some species of regular urchins as well as between *Spatangus* and these same species. I made these experiments on the advice of Marion who had already

made some trials of this type between *Strongylocentrotus* and *Sphærechinus* and had been able to obtain hybrid plutei.¹ It was interesting to see if the same results could be obtained by crossing other types of urchins, and especially to know if the results that would be obtained by fertilizing eggs of *Spatangus* with the sperm of regular urchins, or reciprocally the eggs of these latter species by the sperm of *Spatangus*, to investigate, in a word, in what limits hybridization is possible between these types that show such great differences in their internal organization.

It would have been very interesting also to undertake the same experiments on irregular urchins. Unfortunately, I did not encounter *Ech. flavescens*, the sole species with *Spatangus* that I could obtain alive, in the state of sexual activity either in spring or fall.

I have obtained in all the experiments normal segmentation, then morula and blastula, and usually the gastrula and pluteus. One knows that the embryos obtained by artificial fertilization in general do not live more than a dozen days. Whatever care one takes for their preservation there arrives a certain stage of development in which they remain stationary or become monsters and are not slow to perish. There is a kind of critical embryonic period that cannot be passed. It has been the same of course for the plutei that I have been able to obtain by cross fertilization. This arrest in development that opposes important embryonic development that the pluteus has to undergo later is very regrettable because it would have been very interesting **142** to know what later became of these hybrid plutei. I am far from claiming that the phenomena of development are necessarily continued in them up to the appearance of the young echinoderm. But it is possible that if these hybrid plutei encountered in aquaria under the conditions necessary for ordinary development of normal plutei, they can, like the latter, continue to increase and would offer without doubt a very interesting subject of study. Still, it is not possible to perceive how they would develop and one still has not encountered in nature urchins having characters indicating hybrid individuals. But it is correct to remark on this subject that many species of echinoids live in different habitats and at different depths and that often also in species found together in the same localities, gametes are not developed at the same season of the year. It is possible, however, that *Ech. cordatum* found at Syra, and whose characters I have described above, are intermediary between those of the *Ech. cordatum* type and *Ech. flavescens* as the result of a cross between these two species. Agassiz, in reporting the possibility of obtaining bipinnaria hybrids between female *Asteracanthion Berylinus* and male *Ast. pallidus* adds "it is not surprising, if fertilization between related species is possible, that hybrids are found among the numerous species of a genus, which contributes much to the already considerable difficulty in distinguishing the species of a genus." (Arch. Zool. Exp., 1874)

I do not want to investigate the scientific value of the existence of a hybrid of spatangoids and urchins, nor the possibility of development of such a pluteus up to the critical period that cannot be passed with artificial fertilizations. I shall state only the following conclusions that can be made immediately from the experiments that I shall relate further on.

¹MARION. — *Fécondations hybrides d'Echinodermes*. Comptes-Rendus, 1873.

I. In all the experiments that I had both types, I was able to obtain embryos that reached the stage of blastula, gastrula or pluteus. Cross fertilizations are thus possible, and in very broad limits, between certain species of echinoids. The embryos resulting from these fertilizations develop rapidly and, in most cases, reach the pluteus stage. These continue to live as long as those coming from legitimate fertilization.

II. If one compares development of a embryo hybrid of the two species of regular urchins to the development of embryos from self fertilization, one sees that the embryonic processes correspond in the two cases. I.e., that after the same lapse of time, one observes the same modifications, very nearly the same in these diverse embryos. When, to the contrary, it is a matter of **143** *Spatangus* and a regular, the phenomena of development operate in a slower fashion than in the case of direct fertilization.

III. Hybrid embryos take the form of the species that functions as the female in the experiment, or at least a very close form. Plutei obtained by fertilization of eggs of *Strongylocentrotus* or *Spatangus* by *Psammechinus* resemble the pluteus of these two first types and not that of *Psammechinus*.

IV. Plutei obtained by the cross between regular urchins have some slight differences in shape with legitimate plutei of the species from which the eggs were obtained. Plutei obtained by the cross of a female *Spatangus* and a regular urchin does not produce, to the contrary, the form typical of legitimate plutei of *Spatangus*. In fact, the differences are observed already in the gastrula which is much less rich in pigment in the first case than in the second. These differences are increased in the pluteus whose arms stay shorter, the form thicker than in the legitimate pluteus. Especially, one does not observe in them this calcareous rod that is raised on the point of plutei and characterizes those of *Spatangus*. Although these hybrid plutei live for some days, they never acquire this characteristic form.

V. Although the eggs of one species can be fertilized by the sperm of another and produce a perfect pluteus, it does not follow that the reciprocal is true, and that the embryos obtained in reversing the experiment must necessarily develop to the pluteus stage. The eggs of *Spatangus* fertilized by *Psammechinus* become plutei. The eggs of *Psammechinus* fertilized by *Spatangus* do not pass the blastula stage.

VI. As far as I can judge from the results I have obtained, if one combines all the diverse experiments where hybridization was done between regulars, and those where it was done between a *Spatangus* and a regular, one will find, in a general fashion, the embryo will reach a much more advanced stage in the first case than in the second. In a word, development is easier when the two parents are closer. — We know that it is also more rapid.

I restrict myself to draw these few conclusions from my experiments. Going further and attributing to them an importance that they cannot have would be, in fact, to leave the

domain of observed facts to advance hypotheses. As incomplete as these experiments are, — and they are necessarily so because of the particular conditions **144** that plutei require in order to live and develop, conditions that it is impossible to realize artificially, — I have thought they have perhaps some interest, and this is what has led me to report them. They prove at least one thing, eggs coming from any echinoid genus can be fertilized by sperm of a very distant genus and produce embryos that reach a fairly advanced stage of development. *A priori*, the distance that separated Psammechinus, i.e. a regular type, from Spatangus constructed on an anatomical type completely different and belonging to a different order, seems to exclude all possibility of fertilization between these two genera.

One could verify the conclusions I have stated above in looking over the list I give here of four observations that summarize the different phases of development of hybrid embryos obtained by crossing the genera Sphærechinus, Strongylocentrotus, Psammechinus, Dorocidaris, and Spatangus fulfilling successively the role of male and female towards each other. As the same experiments were repeated several times, and as in some of them the embryos reached a stage not attained in others, I have chosen those in which I have encountered the most advanced stage and that are naturally the most conclusive.

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OBSERVATION I.

STRONGYLOCENTROTUS LIVIDUS FEMALE.
SPHÆRECHINUS GRANULARIS MALE.

The fertilization was done 14 April at 4 hours in the afternoon.

14 April, 7 h. $\frac{1}{2}$ evening. — All the eggs are regularly segmented, most into four, some into eight spheres.

15 April, 9 h. morning. — The larvae are in a very mobile blastula stage, some have a few mesodermal vesicles detaching from their dense pole.

7 h. evening. — All the larvae have a very deep gastric invagination reaching nearly to the center of the gastrula. Calcareous spicules with three branches have developed on each side of the blastopore. Numerous mesodermal vesicles surround the gastric cavity. Numerous deposits of red pigment can already be encountered.

16 April, 10 h. morning. — I encounter still some gastrulae whose complete gastric invagination reaches the pole opposite the blastopore and in which one observes the constriction that will separate the vaso-peritoneal vesicles from the primitive intestine. Most of the larvae are in the pluteus stage having two pairs of very elongated arms and a median unpaired arm. The calcareous rods extend from the tip of the pluteus up to the end of the arms. The digestive tube is still little differentiated, but the vaso-peritoneal vesicles are completely detached.

6 h. evening. — The characters of the pluteus are accentuated. The arms are elongated. The digestive tube is differentiated into an esophagus, a stomach and a terminal intestine. The unpaired lobe is always wide and simple.

17 April, 8 h. morning. — The unpaired lobe has a more or less accentuated opening. This opening becomes much deeper at 6 h. in the evening.

18 April, 7 h. evening. — All the plutei have four distinct arms supported by calcareous rods on which commence to develop small secondary rods. After this day, the form of the pluteus does not change. The arms still elongate a little on the 19th day, then remain stationary. They continue to live up to 23 April.

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OBSERVATION II.

STRONGYLOCENTROTUS LIVIDUS FEMALE.
PSAMMECHINUS MILIARIS MALE.

Fertilization was done 5 April at 4 in the afternoon.

5 April, 7 h. $\frac{1}{2}$ evening. — All the eggs are regularly segmented into 2 and 4, some into 8.

6 April, 9 h. morning. — Most of the larvae are in the mobile blastula stage having at their dense pole some mesodermal vesicles. Still some morulae.

2 h. afternoon. — All larvae are in the blastula stage. The mesodermal vesicles have become more numerous. In some larvae, one already observes a slight depression, first trace of the gastric invagination, and small calcareous spicules with three branches.

7 April, 9 h. morning. — Nearly all the larvae are already very advanced plutei having two very long paired arms and one unpaired lobe supported by completely formed calcareous rods. Numerous pigmented cells. Still some gastrulae.

3 h. afternoon. — The plutei are more developed. Small secondary branches appear on the calcareous skeleton of the arms. The digestive tube is completely differentiated.

8 April, 9 h. morning. — The unpaired arm has a slight marked opening that accentuates during the day and the middle of its height in the evening.

9 April, 9 h. morning. — The four arms are perfectly distinct. The pluteus become still a little larger and the arms continue to elongate up to the 10th. From this day, the larvae have no more modifications and remain alive until the 15th.

OBSERVATION III.

STRONGYLOCENTROTUS LIVIDUS FEMALE. SPATANGUS PURPUREUS MALE.

Fertilization done 14 April at 4 in the afternoon.

14 April, 7 h. $\frac{1}{2}$ afternoon. — A certain number of eggs are intact, the others are segmented into 4 or into 8. Most of the non-segmented eggs are however completely mature because one can no longer perceive the vesicle or the germinal spot.

147 15 April, 8 h. morning. — Still a large number of non-segmented eggs. Those that were fertilized are for the most part in the very early blastula stage. Still several morulae.

7 h. evening. — The larvae, still very few relatively to the non-fertilized eggs, are at the blastula stage having several mesodermal vesicles.

16 April, 9 h. morning. — A certain number of larvae alive the evening before are dead. Here and there, I encounter some of them still living. They have numerous mesodermal vesicles and are beginning gastric invagination.

The larvae did not pass this very early gastrula stage. By evening, not a single one remained alive.

OBSERVATION IV.

STRONGYLOCENTROTUS LIVIDUS FEMALE.

DOROCIDARIS PAPILLATA MALE.

Fertilization done 13 April at 5 hours in the evening.

The only two *Dorocidaris* found during my visit at Marseille in the month of April had already been collected for a long time before they were brought to the laboratory. Both were males. Although they were not in perfect condition, as I still found mobile sperm in examining the contents of the gonads, I tried fertilization without hoping nevertheless to obtain results.

13 April, 8 h. evening. — A certain number of eggs are regularly segmented, into 4 for the most part. The others remain intact.

14 April, 8 h. morning. — I find still a certain number of non-segmented eggs, but blastulae in large quantity. These, very mobile, have no mesodermal vesicles. The same evening, at 7 hours, all the larvae were dead.

Eggs of *Psam. microtuberculatus* exposed to sperm of *Dorocidaris* show no signs at all of development.

OBSERVATION V.

SPHÆRECHINUS GRANULARIS FEMALE. STRONGYLOCENTROTUS LIVIDUS MALE.

The attempts of hybridization that I undertook between female *Sphærechinus* and male *Strongylocentrotus* in the month of April have generally given only **148** negative results. It is with difficulty, in one or two happier experiments, some larvae reached the blastula stage. Marion, in his experiments done in 1873, at close to the same season of the year, had not been able to obtain larvae at a more advanced period of development. This difficulty in success of the experiments comes without doubt from the imperfect state of maturity of the female elements of *Sphærechinus* at this season. In fact, in the months of March or April, the gonads of *Sphærechinus*, that anyway never reach a considerable size at any season of the year, are always very little developed and often one is obliged to open ten or fifteen specimens in order to find a single one whose glands contain some perfectly ripe eggs.

I repeated the same experiment in the month of August, season in which I found several specimens whose ovaries were more developed and with nearly all eggs at maturity. I obtained then, and in all the experiments, larvae that developed completely.

I report here one of these experiments in which fertilization was done 17 August, at 6 hours in the afternoon.

18 August, 9 h. morning. — All the larvae are in the very early blastula stage. I no longer encountered a single morula.

2 h. afternoon. — The blastulae move rapidly and, in some of them, some mesodermal vesicles are already developed and fall into the central cavity of the larva. Some very rare larvae have begun gastric invagination, with numerous mesodermal cells and calcareous spicules with three branches.

6 h. evening. — All the larvae have a very deep gastric invagination and calcareous spicules with three branches. There is still no deposit of red pigment in the mesodermal cells.

19 August, 9 h. morning. — I encounter still more gastrulae whose gastric invagination is complete. The other larvae are plutei with a thick form, short but very distinct arms, with a completely developed calcareous skeleton. The red pigmented masses are very numerous. The vaso-peritoneal vesicles are separated from the intestine.

6 h. evening. — There are no more gastrula. The pluteus form is little modified.

20 August, 9 h. morning. — The arms of the pluteus are elongated, the digestive tube is completely developed and has three distinct regions.

21 August, 9 h. morning. — The unpaired arm is elongated. The plutei have become a little larger.

22 August, 10 h. morning. — The plutei have continued to grow. The unpaired arm is well developed and commences to indent.

149 *24 August, 10 h. morning.* — The bifurcation of the unpaired arm is achieved and the plutei, having since then four distinct arms, live still for several days without showing important modifications.

OBSERVATION VI.

SPHÆRECHINUS GRANULARIS FEMALE. PSAMMECHINUS MICROTUBERCULATUS MALE.

Fertilization done 14 April at 5 hours in the evening.

14 April, 9 h. morning. — A large number of intact eggs of which most have the vesicle and germinal spot. Some morulae. Several very early blastulae.

7 h ½ evening. — The fertilized eggs have all become blastulae that have some mesodermal vesicles detaching for the dense pole.

15 April, 8 h. morning. The mesodermal cells have become more numerous. There is still no trace of gastric invagination. A certain number of the larvae are already dead. On 16 April, in the morning, there was no longer a single larva.

I recall that all the Sphærechinus females that I opened in the month of April and which I used in this experiment, as well as in the following, had very little developed gonads. They contained scarcely any mature eggs.

OBSERVATION VII.

SPHÆRECHINUS GRANULARIS FEMALE.
SPATANGUS PURPUREUS MALE.

Fertilization done 14 April at 4 hours in the evening.

14 April, 7 h. ½ evening. — No segmentation at all has yet occurred.

15 April, 8 h morning. — Many intact eggs. Some have been fertilized and show different stages of development. I found some segmentation into 16 and more. Several morulae and some blastulae. Finally, some irregular segmentations have given morula whose cells on one hemisphere are much larger than those of the other.

7 h. evening. — The blastulae are a little more numerous than in the morning, but they are very early and have no mesodermal vesicles.

16 April. — All the larvae are dead.

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OBSERVATION VIII.

PSAMMECHINUS MICROTUBERCULATUS FEMALE.
SPHÆRECHINUS GRANULARIS MALE.

Fertilization done 5 April, at 6 hours in the evening.

6 April, 8 h. morning. — A certain number of intact eggs. Those that have been fertilized are at the morula stage, some at the blastula stage.

7 h. evening. — The blastulae have at their dense pole numerous mesodermal cells. Some already have begun gastric invagination.

7 April, 8 h. morning. — Scarcely any gastrula remain living. The gastric invagination has become a little deeper, but most of the larvae still have no calcareous spicules.

OBSERVATION IX.

PSAMMECHINUS MICROTUBERCULATUS FEMALE.
STRONGYLOCENTROTUS LIVIDUS MALE.

Fertilization done 25 March, at 10 hours in the morning.

25 March, 3 h. afternoon. — All the eggs of regularly segmented into 8 or 16. I no longer found any divided into 2 or 4.

7 h. evening. — Segmentation is completely finished, all the eggs have become morulae.

26 March, 10 h. morning. The very mobile blastulae have their pole very filled with numerous mesodermal cells.

5 h. evening. — Still some blastulae having mesodermal cells more numerous than in the morning. Most of the larvae are gastrulae with a slight invagination having neither calcareous spicules nor pigment granulations. The mesodermal cells have filled all the space between the ectoderm and the gastric depression.

27 March, 9 h. morning. — The gastrulae are completely developed and the gastric cavity reaches the pole of the larvae opposite the blastopore. The calcareous spicules are developed, but there is still no deposit of pigment in the mesodermal cells. Most of the gastrulae have the transverse depression that separates the primitive intestine from the vaso-peritoneal vesicles.

7 h. evening. — Many very early plutei with the arm still little developed and very short. The three branches of each spicule have developed small **151** calcareous bumps that extend from one part into the arm and from the other to the top of the pluteus, or they still do not exist. The pluteus does not end in a point at its upper part.

28 March, 8 h. morning. — The plutei in the form of a truncated pyramid are little modified in their shape. The arms are elongated. The unpaired arm has become very large. The cells with a red pigment begin to appear. The three regions of the digestive tube have become distinct, and the completely detached vaso-peritoneal vesicles appear beside the digestive tube.

2 h. evening. — The plutei whose top ends in a point have become a little larger, and small secondary branches begin to appear on the principal rods.

29 March, 9 h. morning. — The secondary calcareous rods have been stronger. The unpaired arm is strongly notched.

30 March, 8 h. morning. — The division of the unpaired lob is nearly completely finished. The arms have become longer.

1st April, 9 h. morning. — All the plutei have four arms of equal size. From this moment, they remain stationary and continue to live until 3 April.

OBSERVATION X.

PSAMMECHINUS MICROTUBERCULATUS FEMALE. SPATANGUS PURPUREUS MALE.

Fertilization done 14 April, at 4 hours in the afternoon.

14 April, 7 h. evening. — The eggs are not segmented.

15 April, 8 h. morning. — Most of the eggs have not been fertilized. I found however some morulae and some very rare blastulae. A certain number of the morulae are monstrous.

7 h. evening. — Some blastulae, a little more advanced than in the morning, alone remain alive. They have some mesodermal cells at a slightly dense pole.

16 April. — All the larvae are dead.

OBSERVATION XI.

SPATANGUS PURPUREUS FEMALE. SPHÆRECHINUS GRANULARIS MALE.

Fertilization done 11 April, a 4 hours in the afternoon.

152 11 April, 7 h. $\frac{1}{2}$ evening. — Nearly all the eggs are segmented into 2 or 4. A certain number eggs, although mature, have not been fertilized.

12 April, 8 h. morning. — The larvae have passed the morula stage and are in the very early blastula stage. Always a certain number of non-segmented eggs. Some irregular segmentations into 5 or more unequal spheres.

7 h. evening. — The very mobile blastulae have some mesodermal cells.

13 April, 9 h. morning. — Still some blastulae having mesodermal cells, more numerous than the previous evening. The other larvae are gastrulae that have begun gastric invagination.

6 h. evening. — The gastric invagination is slightly accentuated. Most of the larvae have calcareous spicules and rare granulations of red pigment.

14 April, 8 h. morning. — All the larvae are dead.

OBSERVATION XII.

SPATANGUS PURPUREUS FEMALE. STRONGYLOCENTROTUS LIVIDUS MALE.

Fertilization done 14 April, at 4 h in the afternoon.

14 April, 7 h. $\frac{1}{2}$ evening. — Most of the eggs are regularly segmented into 2 and 4 spheres.

15 April, 8 h. morning. — Still some morulae. Nearly all the larvae are in the slightly advanced blastula stage.

7 h. evening. — The blastulae are very numerous and very mobile. Some have a certain number of mesodermal cells.

16 April, 8 h. morning. — I still encounter some blastulae with numerous mesodermal cells. A certain number of larvae have become gastrulae with very slightly accentuated gastric invagination.

7 h. evening. — The gastric depression is slightly accentuated. Some pigmented cells begin to appear. I still encounter some blastulae.

17 April, 8 h. morning. — The gastrulae are more advanced than the evening before. The gastric cavity has passed the center of the larva. The red pigment has become more abundant, and calcareous spicules are developed on each side of the blastopore. There are no more blastulae. Some gastrulae are still more advanced. They have a very deep gastric invagination and the transverse constriction that will separate the vaso-peritoneal vesicles. The larvae have not passed the stage of perfect gastrulae.

153 OBSERVATION XIII.

SPATANGUS PURPUREUS FEMALE. PSAMMECHINUS MICROTUBERCULATUS MALE.

Fertilization done 25 March at 10 h. in the morning.

25 March, 2 h. evening. — Most of the eggs are regularly segmented into 4, some only into 2, others, less numerous, into 8. The non-segmented eggs all show their vesicle and germinal spot.

7 h. evening. — Segmentation is completely terminated and the eggs are in the morula stage.

26 March, 9 h. morning. — All the morulae have become very mobile blastulae, some of which have several mesodermal cells detaching from their dense pole.

5 h. evening. — The larvae are close to the same stage as in the morning. The thickening of the pole and the formation of mesodermal cells exists in most of the blastulae.

27 March, 9 h. morning. — The mesodermal cells have become more numerous. One observes a very slight gastric depression.

4 h. evening. — The gastrulae are not more advanced than in the morning.

28 March, 8 h. morning. — Still gastrulae whose gastric depression still has not reached the center of the sphere. All the larvae have calcareous spicules with three branches and some granulations of red pigment. The mesodermal cells have multiplied.

7 ½ h. evening. — The gastric cavity has become deeper and has passed the center of the larvae. The calcareous spicules are more developed and the median branches that go to meet each other have jointed. The mesodermal cells fill all the cavity of the gastrula. The cells with pigment are equally numerous. However, the pigment is much less abundant than in the legitimate gastrula of *Spatangus*. The gastrula starts to become deformed.

29 March, 9 h. morning. — The larvae, still in the gastrula stage, resemble an irregular pyramid. Some of them already have the first rudiments of extensions that will become the arms. The calcareous rods of the spicules elongate equally. The gastric depression is very deep and one can observe the transverse constriction that will separate the vaso-peritoneal vesicles.

6 h. evening. — Few changes since the morning. The arm rudiments have become a little longer.

154 30 March, 10 h. morning. — The pluteus form is accentuated and the three arms

have become distinct. The calcareous skeleton, nearly completely developed, takes this reticulated appearance that one observes in all the larvae of *Spatangus*. Still a certain number of gastrulae.

1st April. 4 h. evening. — There still exist some rare gastrulae. The form of the pluteus is a little modified. The calcareous skeleton continues with its development. The arms have become longer. It still however remains relatively thick. The vaso-peritoneal vesicles have detached from the digestive tube that is completely developed. Besides these ordinary forms, I have found in all the experiments other less numerous forms whose aspect differs in certain regards from the ordinary pluteus. Thus, in certain individuals, the two arm pairs become must longer than the unpaired lobe. Others have in the calcareous skeleton certain irregularities, unimportant surely, but however easy to demonstrate. Certain larvae are compact and nearly globular.

After the 1st of April, the plutei are stationary. In most cases, I have obtained results analogous to those that are recorded in this observation. Other times, the phenomena of development are stopped before the larvae reach the pluteus stage. They do not pass the gastrula stage.

Whatever it be, the plutei obtained in these experiments are never identical to larvae obtained by direct fertilization, which take consecutively a characteristic form due to the extreme elongation of the arms and the formation of a long rod that leaves the top of the pluteus. The plutei obtained by hybridization remain always smaller and more compact, their arms are shorted, sometimes unequal, and pigmentation is always larier and less abundant than in legitimate plutei.

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EXPLANATION OF PLATES.

PLATE I.

FIG. 1. *Spatangus* opened from the ventral surface. The esophagus has been cut at the level of the mouth and the supporting plate detached from the internal surface of the test. Digestive tube and circularly system. Natural size.

Æ. Esophagus.

CI. Lower intestinal curve.

CS. Upper intestinal curve.

R. Rectum.

S. Siphon.

MV. Large ventral mesenterial lamella inserting on one hand from the supporting plate *P*, and on the other to the entire length of the internal border of the lower curve.

mv. Small ventral mesenterial lamella inserting on the border of the esophagus.

TM. Mesenterial tract running from the digestive tube to the internal surface of the test.

VMI. Internal marginal vessel; *a*, point where it crosses the siphon and gives rise to the transverse vessel from which it produces the branch of communication *BC*; *b*, its point of termination ; *c*, point where it passes under the inferior curve in order to continue the length of the diverticulum.

VME. External marginal vessel; *d*, point where it leaves the lower curve in order to reach the diverticulum.

V, V'. Marginal vessels from the beginning of the lower curve. *E*, point where vessel *V* forms at the expense of the capillary network that surrounds the opening of the diverticulum.

v. Small branch formed by the small capillaries that arise from the external vessel *V* and continue the length of the diverticulum between the internal marginal vessel and the stone canal.

FIG. 2. *Spatangus* opened from the dorsal surface. The two small plates *PS* that cover the madreporite canal have been detached from the test, and the two dorsal mesenterial sheets *MD* and *md* have been cut.

D. Diverticulum.

MD. Large dorsal mesenterial lamella that extends from the diverticulum to the upper curve and inserts on the supporting apparatus *PS*. It sends a sheath *M'D'* that runs the length of the rectum and fixes it to the internal surface of the test.

md. Small dorsal mesenteric lamella

C. Stone canal.

CM. Stone canal at the exit of the excretory organ or madreporic canal.

GG. Gonads.

162 *Oe.* Excretory organ or madreporic gland.

The other letters as in figure 1.

FIG. 3. *Spatangus* opened from the dorsal surface. The diverticulum has been moved outside. The upper curve and the rectum have been removed.

A. Transverse branch parallel to the siphon that gives rise to the internal marginal vessel and that disappears after having produced the branch of communication.

The other letters as in the preceding figures.

FIG. 4. Vascular and peribuccal nerve rings. The esophagus, whose borders are indicated by a dotted line, has been removed as well as the upper lip.

Natural size.

LS. Upper lip.

C and *c'*. The two canals that constitute the stone canal at the level of the esophagus.

BC. Branch of communication.

AI. Internal vascular ring. *AE.* External vascular ring.

AN. Nerve ring.

VE. Ampullae.

VA. Radial water canals. *va.* Branches they send to the ampullae.

P. Supporting plate.

FIG. 5. Esophagus and beginning of the lower curve. The esophagus and the peristomial zone have been turned up and inverted outside in order to show the insertion of the mesenterial lamella *MV*, the upper lip *LS*, and the small clear transverse bands, *b, b, b*, that indicate the path of the vessels in this region. *Spat. purpureus*. Natural size.

T. Bundle of stretched conjunctive tissue fibers from the supporting structure to the siphon.

The other letters as in the preceding figures.

PLATE II.

FIG. 6. Posterior end of the diverticulum with the excretory organ *Oe* injected by the stone canal *C*. *Spatangus purpureus*.

Ca. Small capillaries that leave the excretory organ.

Vc. Superficial canals that leave the excretory organ and form a network of irregular mesh on the connective membrane that lines the supporting structure. *CG.* Duct of the gonad on which this membrane merges.

FIG. 7. Esophagus and first portion of the lower inferior curve cut open its entire length and spread out to show the vascular network surrounding the orifice of the diverticulum *OD*. The two marginal vessels *VMI* and *VME*, and the two vessels *V* and *V'* that arise from this network and accompanies the lower curve up to the first opening of the siphon. *Spatangus purpureus*. Natural size.

t. Transverse anastomoses uniting these two vessels.

s'o'. First opening of the siphon into the digestive tube. *M.* row of small tubercles that leave this opening.

FIG. 8. Scheme of the circulatory apparatus of spatangoids.

Same letters as in the preceding figures.

FIG. 9. Transverse section of the madreporic gland of *Spatangus* injected by the stone canal.

Injection with Prussian blue; fixed in absolute alcohol. Magnification 35/1.

v represents the section of vessel *v* of fig. 8.

FIG. 10. *Brissus unicolor* opened by the dorsal surface. The esophagus is cut at the level of the mouth. Digestive tube and circulatory system. Natural size.

163 SA. Accessory siphon. *g* and *h* its two openings into the lower curve.

BC and *B'C'*. The two portions of the branch of communication.

PM. Fold formed by the large ventral mesenterial lamella.

The other letters as in figure 1.

FIG. 11. *Brissopsis lyrifera* opened from the ventral surface. Digestive tube and circulatory system. Natural size.

DS. Dilation in form of a pocket that has the siphon at its origin.

Same letters as in the preceding figures.

FIG. 12. *Schizaster canliferus*. Dorsal region of the test, internal surface, magnified two times.

GG. Gonads.

AR, *AL*, *AP*. Anterior, lateral, and posterior ambulacral zones.

PLATE III.

FIG. 13. *Sphaerechinus granularis*. Ventral surface of the test and masticatory apparatus.

The dorsal surface has been removed, except the apical end that has been placed outside in order to show the relations of the principal vessels. Magnification: 2/1.

AS. Upper or inner periesophageal ring.

AI. Lower or external ring.

VP. Polian vesicles.

C. Stone canal.

CG. Glandular canal parallel to the preceding that is continuous with the ovoid gland.

Oe. Excretory organ or ovoid gland. The surface is covered with vascular ramifications.

Pm. Madreporite plate.

Re. Projecting edge that surrounds the internal surface of the test of the abactinal zone.

VMI. Internal marginal vessel.

Vs. Superficial or internal ambulacral vessels.

Vp. Deep or external ambulacral vessels.

FIG. 14. *Schizaster canliferus*, opened by the ventral surface. Digestive tube and circulatory apparatus. Magnified approximately 4 times.

Letters as in figure 10.

FIG. 15. *Echinocardium flavescens*, opened from the ventral surface. Digestive tube and circulatory apparatus. Magnified approximately 6 times.

Letters as in the preceding figure.

FIG. 16. *Dorocidaris papillata*. Ventral surface of the test and masticatory apparatus. Natural size.

VP. Polian vesicles.

MI. The membrane that covers the lantern.

Ap. Its peculiar appendages.

OE. Esophagus, and *C*, cut stone canal.

FIG. 17. *Dorocidaris papillata*, opened by the ventral surface. Two gonads have been moved slightly outside. Natural size.

OE. Esophagus.

CI. Lower intestinal curve.

CS. Upper curve.

S. Intestinal siphon.

C. Stone canal.

GG. Gonads.

lm. Mesenterial lamella that accompanies the lower curve.

l'm'. Mesenterial lamella that accompanies the upper curve.

FIG. 18. *Sphaerechinus granularis*. Ovoid gland. The stone canal has been removed, and the two borders of its groove slightly opened to show the excretory canal *E* and its afferent branches, *e*, *e*. Magnification 10/1.

FIG. 19. *Spatangus purpureus*. Madreporite gland dissected to show the madreporite canal. The two small plates that cover this at the level of the madreporite plate have been detached and placed outside. Magnification 10/1.

Oe. Spongy tissue of the excretory organ.

CM. Madreporite plate. *R*, its afferent branches.

PS. Calcareous plates that cover the end of the madreporite canal.

ts. Spongy tissue that fills the space between the madreporite canal and the two small calcareous plates.

FIG. 20. *Echinocardium flavescens*. Last portion of the digestive tube.

Cs. Upper curve.

R. Rectum.

Zp. Periproct. *an*, anus.

PLATE IV.

FIG. 21-23. Sections of the digestive tube, *Sp. purpureus*. Magnification 350/1.

FIG. 21. Longitudinal section of the glandular region between the end of the esophagus and the first opening of the siphon.

FIG. 22. Transverse section of the lower curve, ventral surface.

FIG. 23. Transverse section of the lower curve, dorsal surface.

E. Internal epithelium.

El. Elastic membrane.

TC. Internal connective layer with irregularly intersecting fibers, enclosing numerous

- granulations *G*.
- ML* and *MT*. Longitudinal and transverse muscles.
- Ce*. External connective layer.
- Ee*. External epithelium.
- F*. Layer of fine and dense connective fibers appearing ordinarily on sections in the form of a refringent band.
- Gm*. Mucus glands of the epithelium.
- Gl*. Pear-shaped glands of the intestine. *S*, secretion coagulated in the cavity of the gland and in its excretory canal.
- LV*. Section of intestinal capillaries filled with coagulated blood.
- Fig. 24. Transverse section of the diverticulum and stone canal. *Sp. purpureus*. Magnification 40/1.
- C*. Stone canal divided into several secondary cavities.
- D*. Wall of the diverticulum. *LV*. Sections of the capillaries that ramify from it.
- VMI*. Internal marginal vessel.
- V*. Small vessel that runs the length of the diverticulum between the stone canal and the internal marginal vessel.
- MD*. Large dorsal mesenterial lamella.
- FIG. 25. Dissociated muscular fibers of the intestine. *S. purpureus*. Magnification 570/1. *n*, nucleus of these fibers.
- FIG. 26. Dissociated epithelial cells of the lower intestinal curve, dorsal surface. *Spatangus purpureus*. Magnification 550/1.
- FIG. 27. Gelatinous tissue of the siphon. *Sp. purpureus*. Magnification 300/1.
- Cc*. Cells of the connective tissue with ramifying and anastomosing extensions.

PLATE V.

- FIG. 28. Section of the madreporite gland, peripheral region. *Sp. purpureus*. Magnification 120/1.
- Ee*. External epithelium
- TC*. Connective tissue forming the envelope of the organ.
- FC*. Trabeculae of connective tissue lining the irregular alveoli filled with cells with protoplasm having extensions, *Cr*, and granulations *G*, of red or yellow pigment.
- FIG. 29. Section of the central region of the madreporite gland. *Sp. purpureus*. Magnification 160/1.
- Same letters as in the preceding figure.
- FIG. 30. Transverse section of the canals found between the madreporite gland and the madreporite plate. *Sp. purpureus*. Magnification 85/1.
- CM*. Madreporite canal (see fig. 19, *CM*).
- CV*. Superficial canal going from the excretory organ to the lamella of the connective tissue covering the two small plates that protect the end of the canal *CM* (see fig. 6).

Oe. Section of the last portion of the excretory organ.

LC. Lamella of connective tissue covering the canal *CM* that is part of the large dorsal mesenterial lamella and is continuous on the supporting apparatus attached to the apical pole.

FIG. 31. Polian vesicles. Fragments obtained by dissociation. *Sphaerechinus granularis*. Magnification 230/1.

FC. Bundle of connective tissue that limits the alveoli filled with cells *a*, provided with extensions *C* and pigmented granulations *G*.

FIG. 32. Longitudinal section of a peristomial tube foot. *Spatangus purpureus*. Magnification 440/1.

E. External epithelial cells.

Cb. Basal cells.

CT. Connective layer with transverse fibers.

CL. Connective layer with longitudinal fibers.

G. Granulations of the connective tissue.

ML. Longitudinal muscles.

Ec. External epithelium.

FIG. 33. Section of a terminal swelling belonging to the tufts of the peristomial tube feet. *Sp. purpureus*. Magnification 370/1.

CC. Central cavity.

TC. Layer of connective tissue lined inside with small cells whose nuclei only can be seen.

n. Nuclei of these epithelial cells.

FIG. 34. Transverse section of two vessels that make up the stone canal at the level of the esophagus. *Sp. purpureus*. Magnification 105/1.

C. Canal nearest to the esophagus, lined with small ordinary endothelial cells.

C'. Canal parallel to the preceding, lined with numerous very granulated nuclei and by pigment granules.

lm. Lamella joining the canal *C* to the esophagus.

FIG. 35. Transverse section of the ambulacral vessels and nerve. *Sp. purpureus*. Magnification 120/1.

Vs. Superficial or internal ambulacral vessel.

Vi. Deep or external ambulacral vessel.

Cg. Perineural space, belonging to the general cavity.

N. Ambulacral nerve. *l*, one of its lateral branches.

RC. Calcareous network of the test.

FIG. 36. Radial water canal and ampullae of a regular urchin. *Echinus acutus*. Magnification 4 times.

Vs. Superficial radial water canal. *Vs.* Vessel it sends to the vesicles.

Vp. Deep canal. *Vp.* Its lateral branches.

Ve. Ampullae.

PLATE VI.

FIG. 37. Transverse section of the digestive tube towards the middle of the lower curve. *Strongylocentrotus lividus*. Magnification 490/1.

E. Internal epithelial layers having large and very granular cells in the internal half of the layer, then and lacking granules, containing many nuclei in the external half.

TC. Very thin internal connective layer containing numerous islands of coagulated blood.

M. Muscle fibers.

Ec. External epithelial layer.

FIG. 38. Section of the wall of the diverticulum to which is remains attached a certain quantity of liquid it secretes. One sees distinct epithelial cells at the base of the layer, insensibly continuous with a reticulated tissue enclose some nuclei, membranous debris, and some protoplasmic masses. It is the aspect most usually shown by the secretion of the diverticulum. *Sp. purpureus*. Magnification 245/1.

Same letters as in the preceding figure.

FIG. 39. Peristomial ampulla seen by the internal surface. *Sp. purpureus*. Magnification 390/1.

FIG. 40. Section of the stone canal and glandular canal. *Sph. granularis*. Magnification 130/1.

Cs. Stone canal.

CG. Glandular canal whose internal surface sends into the interior numerous connective trusses *Tc*, some of which form a very fine reticulum supporting cells with ramified protoplasm.

L. Interval that separates the two canals for the greatest part of the length.

FIG. 41. Transverse section of the ovoid gland. *Sph. granularis*. Magnification 380/1.

TC. Connective trabeculae limiting the alveoli some of which contain pigment granulations *G*, others cells with ramified protoplasm *Cr*. Towards the left part of the section, corresponding to the central part of the gland, the trabeculae become finer and irregular.

FIG. 42. Section of the madreporite canal larger than in fig. 30. *Sp. purpureus*. Magnification 185/1.

TC Trabeculae of connective tissue that divide its cavity into numerous chambers containing cells *Cr* analogous to those of the excretory organ, and filled for the most part by a very finely granular mass that is nothing else than the excretory fluid coagulated by the reagents.

FIG. 43. Transverse section of a female gonad. *Sp. purpureus*. Magnification 350/1.

Ee. External epithelium

Ct. Connective layer with transverse fibers. *Cl*. Layer with longitudinal fibers.

Mt. Circular muscles.

Ee'. Internal, very granular epithelial cells gradually become very large eggs.

FIG. 44. Transverse section of the internal marginal vessel, in its recurved, free portion with the adjacent mesenterial lamella. *Sp. purpureus*. Magnification 300/1.

Mt. Circular muscles..

TC. Connective tissue of the vessel that is continuous with the later of the same nature belonging to the mesenterial lamella.

ML. Muscles that cover the two surfaces of this lamella and that are continuous on the external surface of the vessel.

CS. Corpuscles of blood applied against the internal surface of the vessel that together give the appearance of a cellular layer.

FIG. 45. Nerve cells of an ambulacral nerve with one or two extensions. *Sp. purpureus*. Magnification 1200/1.

FIG. 46. Development of sperm. *S. purpureus*. Magnification 1200/1.

FIG. 47. Dissociated epithelial cells from the sucker of a tube foot. *Strongylocentrotus lividus*. Magnification 600/1.

PLATE VII.

FIG. 48. Longitudinal section of an ambulacral section. *Strongyl. lividus*. Magnification 220/1.

E. External epithelium.

PN. Nerve plexus underneath the epithelium of a sucker.

n. Nuclei of epithelial cells of the sucker, joined in numerous groups.

N. Section of the tentacular nerve.

Ct. Layer of connective tissue with transverse fibers.

Cl. Layer of connective tissue with longitudinal fibers.]

Ce. Elastic layer.

ML. Longitudinal muscles.

FIG. 49, 50, and 51. Three pedicellariae of *Dorocidaris papillata*.

FIG. 52. Valve of a ophiocephalus pedicellaria of *Arbacia* seen by the internal surface.

FIG. 53 and 54. Two pedicellariae of *Brissus unicolor*.

FIG. 55 and 56. Two pedicellariae of *Schizaster canaliferus*.

FIG. 57. Small pedicellaria of *Echinocardium flavescens*.

FIG. 58. Glandular gemmiform pedicellaria of *Echinus acutus*.

FIG. 59 and 60. Gemmiform pedicellaria of the dorsal surface of *Echinocardium flavescens*.

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