1848

**On the Analogous Composition and on some Points of the
Organization of Echinoderms: A Translation of *Sub L'analogie de
Composition et sur Quelques Points de l'organisation des
Échinodermes***

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Recommended Citation

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*John Miller Lawrence
Paris, 1978*

INSTITUT NATIONAL DE FRANCE.

MÉMOIRE

SUR L'ANALOGIE DE COMPOSITION ET SUR QUELQUES POINTS

DE L'ORGANISATION

DES ÉCHINODERMES ;

PAR M. DUVERNOY.

Lu, pour la 1^{re} Partie, dans la séance du 17 janvier 1848.

(EXTRAIT DU TOME XX DES MÉMOIRES DE L'ACADÉMIE DES SCIENCES.)

PARIS,

TYPOGRAPHIE DE FIRMIN DIDOT FRÈRES,

IMPRIMEURS DE L'INSTITUT, RUE JACOB, 56.

—
1848.

NATIONAL INSTITUTE OF FRANCE

MEMOIR

ON THE ANALOGOUS COMPOSITION AND ON SOME
POINTS OF THE ORGANIZATION OF ECHINODERMS

DUVERNOY

Read, the 1st Part, in the meeting of 17 January, 1848
(EXTRACT FROM VOLUME XX OF THE MEMOIRS OF THE ACADEMY OF SCIENCE)

PARIS,
TYPOGRAPHIE FIRMIN, DIDOT FRÈRES
PRINTERS OF THE INSTITUTE, RUE JACOB, 56.

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Translation: John M. Lawrence

HERIZOS PRESS, TAMPA

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Georges Louis Duvernoy

Only Duvernoy's last name appears on the memoir. His full name was Georges Louis Duvernoy. He was born in Montbéliard 6 August 1777 and died 1 March 1855 in Paris. He received his medical degree in 1801 in Paris with a thesis on hysteria.

He had begun his medical practice at Montbéliard when his distant cousin, Georges Cuvier, made arrangements for a position in Paris. Duvernoy assisted Cuvier with the last two volumes of *Leçons d'anatomie comparée*. He returned to Montbéliard in 1805 after his marriage. In 1809 Cuvier asked him to take a post with the Faculty of Science in the College of France. Duvernoy did not accept the position but returned to Montbéliard where he practiced medicine for 25 years. In 1813 he became chief doctor at the medical hospital.

In 1827, Cuvier obtained a chair in natural history for Duvernoy in the Faculty of Sciences at the University of Strasbourg. Duvernoy taught comparative anatomy and zoology. He was an opponent of natural philosophy speculation, popular among French scientists at that time. He became dean in 1832. One of his students there was Armande de Quatrefages who wrote in 1854 in his book, *Souvenirs d'un naturaliste*, "I have given to this curious species the name of Duvernoy's synaptula (*Synapta Duvernaea*) in honor of the scholar who was my professor and always treated me as a friend." Unfortunately for Duvernoy, the name is a synonym of *Synapta inhaerens* (O.F. Müller)

Cuvier died in 1832. de Blainville succeeded to his chair in the Museum of Natural History. Duvernoy succeeded in 1837 to Cuvier's chair in the natural history of organisms in the College of France. In 1850 he succeeded to de Blainville's chair of comparative anatomy in the Museum of Natural History in the Jardin des Plantes and thus held both of Cuvier's former chairs simultaneously. He was elected to the Academy of Sciences in 1847. He was a member of the Institute and a knight of the Legion of Honor

Translator's note

Words and species names in the translation are italicized or not as done by Duvernoy. Duvernoy used *rayon* for both sea urchins and sea stars. I have translated it as *radius* for sea urchins and *ray* for sea stars unless radius is the obvious meaning. Duvernoy meant "bilateral symmetry" when he wrote "symmetry". "Skin" obviously refers to the epidermis in many places. I have translated "la boîte osseus" as test, despite what Duvernoy wrote at the beginning of his memoir. Duvernoy uses "vertebrae" for the ambulacral plates and "ribs" for the interambulacral plates. He did not consider them homologous to the vertebrae and ribs of vertebrates as previous workers had done. However, he said it would be more exact to call the region vertebral than ambulacral.

Species' names used by Duvernoy are not changed in the translation. Current species' names for those that have been changed are:

Duvernoy's names	Current names
<i>Asteracanthæon glacialis</i>	<i>Marthasterias glacialis</i>
<i>Asteracanthæon ruben</i>	<i>Asterias rubens</i>
<i>Asteriscus palmipes</i>	<i>Anseropoda placenta</i>
<i>Echinus neglectus</i>	<i>Strongylocentrotus droebachiensis</i>
<i>Echinus saxatilis</i>	<i>Paracentrotus lividus</i>
<i>Echinus spatangus</i>	<i>Echinocardium cordatum</i>
<i>Echinus brevispinosus</i>	<i>Sphaerechinus granulosus</i>

I have used "*embranchement*" instead of phylum, although both refer to the taxon below Animal Kingdom. The group Radiata was created by Georges Cuvier in 1812 as one of his four primary divisions (*embranchements*) of the animal kingdom (M.P. Windsor. 1976. Starfish, Jellyfish, and the Order of Life. Yale University Press, New Haven) According to Windsor, Cuvier called them "*zoophytes*" in preference to *radiates*," but used both in his Latin title: "*Animalia zoophyte s[ive] radiata*." She used the word *embranchement* without italics.

I thank Prof. Michel Jangoux, Université Libre de Bruxelles for assistance with several difficult passages. The error that remain are mine.

Pagination of the original text is indicated in the translation in bold, e.g. **12**.

MEMOIR

ON THE ANALOGOUS COMPOSITION AND ON SOME POINTS

OF THE ORGANIZATION
OF ECHINODERMS

DUVERNOY.

The first part read in the meeting of 17 January, 1848.

INTRODUCTION.

The sciences of observation, and those of organized bodies in particular, are composed:

- 1: Of observed facts;
2. Of their interpretation, which can be more or less subject to discussion;
3. Of their generalization, which should be the summarization of their existence, as to their number and the summary or the logical deduction of their interpretation.

The present memoir contains, if I am not mistaken, these three types of scientific ideas

I have written it because of the last letter of our colleague Agassiz, which I had the honor of communicating to the 4 Academy in the meeting 7 November last, and of the *Résumé d'un travail d'ensemble sur l'organisation, la classification et le développement progressif des Échinodermes dans la série des terrains*, that Agassiz himself made known to the Academy in the meeting of 10 August 1846.

Almost immediately after having become aware of this last communication in the *Compte rendu* of this meeting that I received at 100 kilometers from Paris, I sent our colleague some written observations.

1. *On the relations that he announced having discovered between the test of urchins and the body wall of sea stars;*

2. *On the tendency to bilateral composition that he believed to have recognized in a certain number of Echinoderms, and more particularly among urchins and sea cucumbers, while keeping their form or radial composition.*

My letter was dated 4 September 1846.

I had hoped he would make some mention of it in the subsequent publication of this *Résumé*, which appeared later in the *Annales des sciences naturelles* (numbers of November and December 1846).

The complete silence regarding this subject made me await the appropriate moment to reestablish, historically speaking, the succession of discovered facts, and some ideas that could have made some contribution to the progress of science in this direction. The letter of our colleague furnished the occasion. I have not been able to refrain from taking it.

My communication will not be only simply historical. It will contain some new studies that will serve perhaps to extend or better analyze already known facts.

First Part

Historical Summary

Until recently it was usual to consider the hard parts of *urchins* as an exterior envelope, as a *test*, comparable to that of crustaceans and known as a *shell*. If French naturalists still use the first name, German naturalists prefer to use the second.

Neither is correct.

The *test* properly is a hard production, exterior and superficial to the skin that can be detached by molting. The shell is likewise a production exterior to the skin. It is covered by a kind of epidermis.

The hard parts of *urchins* are, to the contrary, covered exteriorly by the skin and interiorly by a sort of peritoneum that lines the visceral cavity separated by the hard part.

My old friend, the celebrated *Tiedemann*, author of *Monographie anatomique* on the *holothuroids*, *asteroids* and *urchins*, that the Academy awarded a prize in 1812, clearly recognized these two membranes¹.

6 He saw, moreover, that *urchins* have twenty series of calcareous pieces bound by true sutures, that the number of these pieces, in series, increases with age, and that this increase in number, combined with the growth of the old pieces, explains the growth or development, in all senses, of which the urchins are capable with their spherical form.

But the illustrious correspondent of the Academy has not drawn from these anatomical facts, which need moreover a more complete analysis, the consequences that one can deduce from them on the analogy of the composition of the interior skeleton of *asteroids* and *urchins*.

de Blainville, already in 1825, in the article *Oursin* in the *Dictionnaire des sciences naturelles*², recognized, as had Tiedemann, that "the *external covering* that determines the form of an urchin is framed, for the greatest part of its extent, by *two membranes* one external and thicker and the other internal, so thin that the name pellicle is perfectly appropriate for it, and between them exists a very thick, solid, completely calcareous *test* composed 7 "of a very large number of small polygonal pieces, etc."

These two celebrated authors agree also on the cause of spine movement.

¹ A whitish skin covers all the exterior part of the shell with the exception of the rounded articulating tubercles. It serves consequently to fasten the spines. This skin is irritable in the living state: the spines are erected when it contracts. They are inclined more or less towards the shell in its relaxed state. – Since there are no *particular muscles* that erect the spines or bind them, one can compare the irritable contractile skin that erects or lowers the spines and attaches them to the shell to the cutaneous muscles of mammals that erect the hairs. (Page 88 of this monograph.)

² T. 37, p. 61-64.

"These organs," says de Blainville, "articulated in a ball-and-socket joint on the mamelons of the test, are moved in all directions by *external tissues of the cutaneous covering*, attached to it at the circumference of the bourrelet at their base, and which appear to me stronger and more evidently muscular, to the spines of the base of the urchin. By dissection, it has been possible for me to perceive there distinct muscular fibers and sometimes even properly called muscles. It exists everywhere for the movement of the muscular apparatus."

One finds, on this subject, in Volume II of the *Mémoires* of Delle-Chiaje, *sur les Animaux sans vertèbres*, published in Naples in 1825, a perceptible progress in the terms

The pieces that compose the test of the urchins are called *ossicles*: this author calls the membrane that unites them and fills their intervals before their complete hardening the *periosteum*. He designates their ensemble under the name of bony box (*scatola ossea*).

All these expressions are repeated in his *Institutioni di anatomia e fisiologia comparata* (Vol. I) that appeared in 1832.

In the Prodrôme of a *Monographie des Radiaires ou des Échinoderms*³, read at the Société d'histoire naturelle de 8 Neuchâtel, 20 January 1834, Agassiz gave interesting details on the mode of growth of urchins and on the successive hardening of the test, from the buccal or anal pieces towards the greatest diameter of the animal.

He recognized, like Tiedemann, that the pieces of the test are less numerous in the young than in the old, in contrast to what Delle-Chiaje said. Around the anus, the membrane that unites all the plates and that is extended onto their surface in forming an articulating capsule around the base of the spines is softer, adds Agassiz, and more spongy than in the lower part where the plates are already joined, and the spines are raised at the center, a little like the manner in which horns of a deer are formed. They only become mobile after having reached a certain degree of development.

In this first memoir, Agassiz strongly insists on the tendency to bilateral form in *spatangoids*, reported long ago by de Blainville.

He then enters into the details of analogies that he finds between *urchins* and *asteroids*. But these analogies do not include the true determination of the hard parts and their distinction from the appropriately called skin. They obviously have the object of taking the rayed form of *asteroids*, considered in the complete plan of composition of these animals, to the cylindrical form in *holothuroids* or spherical in *urchins*, and leads then to the idea of bilateral parts that the author thinks to have found in certain *holothuroids* and in *spatangoids* among the *echinoids*.

9 However, Charles Desmoulins⁴ demonstrated, in a conscientious work on *echinoids*, that in all, even *spatangoids* that have only four ambulacra, the same composition of the (alleged) test could be verified.

The *Notice sur quelques points de l'organisation des Euryales*, that Agassiz communicated to the same Société de Neuchâtel, 18 January 1837, has not advanced the questions that I sought to resolve some days later before the Société d'histoire naturelle de Strasbourg.

On 1 February, 1837, I took the task of demonstrating and developing the ideas that appear here to this Society:

³ *Mémoires de la Société des sciences naturelles de Neuchâtel*, Vol. I. Neuchâtel, 1835.

⁴ *Études sur les Échinides*, by Charles Des Moulins; at Bordeaux, 1835-1837, in-8°.

“1° The skin of *urchins* covers not only the series of plates that make up their supposed test, but is extended (at least) onto the head of their baguettes or their spines.

2° These are articulated, like joints, with rounded projections of these plates and make a completely united articulating surface, completely analogous to that of bones (of limbs) of vertebrates.

3° Each articulation is attached by a ligamentous capsule, similar to the articulating capsules (of limbs) of vertebrates.

4° Between the skin and this ligamentous capsule are small muscles that are attached by one part to the base of **10** each spine and by the other to the plate that has its articulating tubercle.

5° The existence of these subcutaneous muscles of the skin that cover all parts of the hard parts; the serous nature of the membrane that lines the interior of the cavity formed by these same hard parts and which encloses the viscera, led me to the character of these hard parts and bones. I have compared them to the peripheral part of the skeleton of turtles.

The *urchins*, I added, will have thus an interior skeleton, but peripheral, that is to say, superficial. This skeleton will be composed of several regular series of vertebrae and ribs, articulated by sutures.

The *urchins* will be, under this relation, to *echinoderms*, as *turtles* are to other *reptiles*.

This character, I shall continue, of the hard parts of *urchins* establishes moreover a new, very important unification between these animals and *asteroids*. For a long time an internal skeleton has been recognized in the latter. In *asteroids*, which have five rays, there are clearly five vertebral columns. These different columns, whose number varies in different species and genera of this family, have thus rays more or less free towards their caudal end and joined at the buccal end.

Asteroids (with free rays) are thus the serpents of *echinoderms*, but serpents without a head, with several bodies and a single mouth.

Holothuroids, which have been combined with much reason by *G. Cuvier* with *urchins* and *asteroids*, have **11** only a rudiment of this internal skeleton, to which are attached five long flat muscles that line their skin, and on which are attached the tentacles that garnish exteriorly the opening of the buccal cavity.

As a consequence of these considerations, I said in closing, that *pedicellous echinoderms, which are true radiate animals, can be seen as composed of symmetrical animals, whose headless bodies are united their entire length (urchins, holothuroids) or free in a more or less long extension of their posterior part (asteroids)*⁵.”

These ideas on the actual character of the skin and skeleton of *urchins*, compared to the interior skeleton of *asteroids* and to the rudiment of the interior skeleton of *holothuroids* were the logical deduction from anatomical facts. They showed, with evidence, the analogous composition of the four orders of the class of *echinoderms* within the limits I have adopted for this class. They would analyze their radiate form, taking it to the multiple symmetrical form and seen in this higher class of *Zoophytes*, as was demonstrated for the higher class of the *molluscan* embranchement and for the higher classes of the *articulates*, traces of the plan of composition in the arrangement of hard parts of vertebrates relative to soft parts. But these are only traces, which do not decrease,

⁵ See the *Journal de l'Institut* de 1837, p. 208 and 209.

in our opinion, the great differences that **12** exist in the general plan of organization of each of the four great embranchements of the Animal Kingdom, differences universally recognized since the first revelation that science received about it, in 1812, from the genius of G. Cuvier.

On 6 November of the same year 1837, Agassiz wrote me from Neuchâtel: "I am personally obliged to you for your account of *echinoderms*. I have read it with all the greater pleasure as I am busy myself at this moment with a work on this class of animals. The research that you have dealt with there . . . is near the most perfect truth. *As for the principles that you give, I must tell you that I do not share them, no more than the conclusions you make from them.*"

Thus, in effect, our colleague, instead of analyzing, as I have done, the composition of *urchins* and *holothuroids* in order to find there the radiate form of *asteroids*, had sought in his *Prodrome*⁶, to take them to the spherical form of *Echinoids* or cylindrical form of *Holothuroids*.

In the comparison that he made of the plates of the supposed test of *urchins* with the body-wall parts of *asteroids*, it was not a question of distinguishing the skin and its appendages from parts belonging to the skeleton. Finally, far from seeing the symmetrical form in each ray of an *asteroid* **13** or in the corresponding parts of an *urchin* or a *holothuroid*, Agassiz sought to find traces of what he calls the form of *bilateral equality* in the whole or in the entire body of an *asteroid*, an *urchin* or a *holothuroid*.

It was not the same for all other naturalists. I find, among others, my ideas on the multiple symmetrical composition of *sea stars* adopted in an elementary work that was published by the teachers of the royal colleges in 1840⁷.

As for anatomical facts that have supported these theoretical deductions, they have been reproduced in all their details some years later by Valentin in his anatomical monograph on the genus *Echinus* that appeared in 1841⁸.

1° The author designates the skin of these animals under the name of *pigmented* membrane. (The translator has had to say *pigmented* or colored.)

It is found, he says, on the articulation of the spine and on the spine itself. It rests directly (these are always his expressions) on the surface of the muscles.

2° The muscles (*aculeate motor*) go from the articulating surface of a spine to the circumference of the corresponding tubercle.

14 3° The articulating capsule is a very strong articulating membrane.

4° A kind of *joint* is found between the spine and the head.

I have to be flattered, in reading this interesting monograph, of seeing confirmed there by such a very distinguished anatomist as Valentin, the principal facts I announced four years before.

Here is moreover, in a few lines, that which this author has added to our knowledge by giving, as was his practice, the microscopic structure of these parts.

1° He has seen that the muscular fibers of the small motor muscles of the spines have separated transverse lines and that one can perceive sometimes between them other transverse lines that recall the muscular fibers of vertebrates.

⁶ *Mémoires de la Société naturelles de Neuchâtel*, Vol. I. Neuchâtel, 1835.

⁷ *Leçons d'histoire naturelle*, etc., by L. Doyère, Professor of Natural History at the College Royal de Henri IV. Paris, 1840. pages 316 and 317.

⁸ *Monographies anatomiques*; I^{re} Monographie. Neuchâtel, 1841.

2° He has measured the diameter of the fibers of the articulating capsules and found it varies from 0.001 to 0.005 inches.

3° He has seen that the plates are composed of calcareous networks that have as their base an *organic skeleton of a fibrous tissue*: these are his statements⁹.

4° He has assured himself that the spines are formed of two calcareous substances. One is *simple* (I think that he meant to say compact, homogeneous), the other reticulated.

5° One does not see, no more than in the plates, the internal structure that characterizes bones of vertebrates.

15 They differ also in regard to their chemical composition by the absence of phosphoric salts¹⁰.

6° Finally, Valentin has seen the skin (that his translator always calls the *pigmented membrane*) covers all parts of the test; and he has not been able to see on its surface, no more than Forbes, the ciliated epithelium reported by Ehrenberg¹¹.

I have without doubt been affected by the reception of the letter of our colleague, Agassiz, dated 6 November 1837, of not having his agreement to my manner of envisaging the general plan of organization of echinoderms. But I believe my reasoning is correct, and no personal authority, respectable as it is, can alone shake and change my convictions. I have no less 16 persisted in teaching, in all my courses, that doctrine that I have adopted on this subject¹².

Also I was very agreeably surprised in the perusal of the *Résumé* already cited of reading there the present doctrines of the author (page 180 of volume XXIII of the *Compte rendus*) on the identity of the composition of asteroids and urchins, and (page 201) on their obvious radial form, whose mouth is the center around which all the organs are disposed.

In the letter I addressed to our colleague, as soon as I was aware of this *Résumé*, after having told him how happy I was to see him approach my doctrines, that I believed it necessary to remind him I sought to explain them to him, among others, expressed in this way in the fourth paragraph:

"It seems to me that it was necessary, in order not to be perplexed in determining the body plan of echinoids, of distinguishing, as I had done¹³ in my courses, the different

⁹ *Mongr. Anat.*, p. 18, and pl. II, figs. 18 and 19.

¹⁰ Here is the chemical analysis of fresh plates done by Brunner:

Calcium carbonate	86.81
Calcium sulfate	1.38
Magnesium carbonate	0.84
Other salts and loss	1.14
Organic matter	<u>9.83</u>
Total	100.00

The spines differ only in a greater proportion of calcium carbonate 89.40

And by the smaller quantity of organic matter 7.59

¹¹ One finds in fact the following phrase of this well-known author in the Archives of Müller in 1834, p. 578: "All the spines of *Echinus saxatilis* are covered with an epithelium (*Haut*) with cilia.

¹² See among others the extract of my course given at the Collège de France in 1846. *Revue zoologique* of the month of February 1846.

¹³ *Revue zoologique*, February 1846

principal systems of their peculiar organization, either those of relation or sensitivity and movement, or those of reproduction, or those of nutrition.”

I added in the fifth paragraph:

“5° This analysis of the organ systems, which are all three rayed in *stellerides* (despite, in my 17 opinion, the anal opening), which lose this form in the alimentary tract in *crinoids* and *echinoids*; which show only traces in the *holothuroids* in the nervous system, the longitudinal muscles of the body, the rudiment of the skeleton and the buccal tentacles. This analysis, I said, facilitates moreover the more precise expression of your system or of your ingenious ideas on the passage of the radial form to the symmetrical or bilateral form.”

These observations, still without response, have however continued to change the ideas of our colleague, if I can judge by the following paragraph of his last letter to de Humboldt:

“I believe I have demonstrated today that the solid pieces of *asteroids* are identical to those of *urchins*, as much by their arrangement as by their relation with the soft parts From which I conclude that there is morphological and physiological identity in the skeleton of *asteroids* and that of *urchins*.”

I must be flattered in reading these lines, written 30 September 1847, as taking recognition of those printed in the minutes of 10 August 1846, of the agreement they have with my publication of February 1837.

They show that, for the essential relations that I have learned over more than ten years between the hard parts of the four orders that compose the class of *echinoderms*, the scholarly, multiple, thorough studies of our colleague, have made him abandon the negativeness of his letter of 6 November 1837, in order to adopt my point of seeing, at least in the essential parts, the existence of an 18 internal skeleton in *urchins*, analogous to that of *asteroids*.

We thus are in perfect agreement on these facts, since the *Recherches anatomiques* of Valentin, undertaken at the request of Agassiz, and even for their interpretation¹⁴. It is necessary to say that, if this interpretation varies according to the observer, it is that they are often entrained by preconceived ideas or by those that prevail momentarily in the science they cultivate.

It is thus, in order not to leave my subject that Sars, to whom one owes important discoveries on lower marine animals, believed to see the bilateral form in four transitory attachment appendages that appear at a certain time in the development of a species of *asteroid*¹⁵.

The larval body of this species, in its successive metamorphoses, changes from spherical to slightly oblong. It forms, in succession at one of its extremities with the greatest diameter, four attachment appendages by means of which this larva attaches itself to the wall of the brood chamber of its mother.

The body of the small *asteroid* develops independently of these appendages. It flattens like a target in taking on a more regular circular form. Then it raises a central part, remaining circular, while forming 19 five rounded lobes that are going to separate

¹⁴ There remains only some disagreement on the subject of their generalization that time will make disappear.

¹⁵ The same that MM J. Müller and Troschel have dedicated to him later under the name of *Echinaster Sarsi*.

more and more with growth of the small asteroid in order to form the rays. When it has become pentagonal from the circle it was, the four suckers join in pairs at the time of their greatest development, still attached at the edge of the star in the angle of two lobes or two rudimentary rays. These transitory organs are not slow in atrophying and disappear successively in the same way they were developed¹⁶.

Their appearance, as accessory organs, and their momentary existence have changed nothing in the natural process of development of the body of the asteroid that is shown from the beginning with the spherical or rounded and flattened form, and consequently with the elements of the radial form. In order to infer from the disposition connected with these transitory appendages the bilateral form of the asteroid, it is necessary to forget the circumstance that predominated in this observation in order to see only its accessory role.

The very recent observations of Dufossé¹⁷ and Derbes¹⁸ on this development of *urchins*, joined to these here on *asteroids* seem to me on the contrary to confirm the idea that, from the beginning of its development, each animal has the characteristics of the *embranchement* to which it belongs.

20 "Each animal," as G. Cuvier has very well said, "is itself from the embryo, and its characteristics of class (this word is taken here for higher class, that is to say *embranchement*) shows almost from the first instant when it appears to the eye. One sees the vertebrae from the first days of incubation a vertebrate, etc."¹⁹.

¹⁶ *Fauna littoralis Norwegiæ*, by Sars. *Erser Heft. Christiania*, 1846, p. 47 and following; and pl. VIII, figs. 1-43.

¹⁷ *Annales des sciences naturelles*, 3rd series, 1847.

¹⁸ *Ibid.*, same year.

¹⁹ *Leçons d'Anatomie comparée*, 2nd edition, vol. I, p. 35.

SECOND PART²⁰COMPARATIVE DETERMINATION OF THE DIFFERENT PARTS OF THE
SKELETON OF ECHINOIDS AND ASTEROIDS

§ I.

The skeleton of *echinoids* and that of *asteroids* are absolutely comparable as I wrote in February 1837. But for this comparison to be exact, it is necessary to begin by recognizing the different radii that make up the test, whatever be its form, which constitutes the surrounding skeleton of *echinoids*.

These radii are easily recognized in *cidaroids* or regular urchins, where they are arranged like meridians **22** and are regularly joined to each other from the pole where the mouth is located to the pole where the anus and genital pores are found.

Each of these five radii is symmetrical and is composed in the middle by a double series of bony pieces that one must regard like vertebrae. In the lateral parts are another series of bony pieces that one must regard like ribs.

These are joined with the corresponding part of the neighboring radius and together make up the region called *interambulacrum*. The region called *ambulacrum* is the *vertebral* part of the same radius.

The various *vertebral* pieces or *ribs*, in the terminology we have adopted, are the same form in each series. They differ only in the proportions, decreasing from the equator of the test to one or the other pole.

The radial composition is absolutely the same in all the other *echinoids* included in the families of *clypeasteroids*, *cassiduloids*, and *spatangoids*, as Agassiz has recognized and characterized.

We shall take, for demonstration, a species of this latter family, *heart urchins*, that is generally regarded as much removed from the radial form and approaches more the symmetrical form.

Its skeleton is composed of five radii, like those of the *edible urchin*. These radii have the same buccal opening for their point of departure. But as this opening is transverse and a little behind the edge of the test, one can distinguish in the inferior face an unpaired radius and **23** two paired radii. The first is perpendicular to the lip nearest the edge of the test.

The pair that comes immediately after this radius leaves from this same lip, on the sides and goes to the periphery, arcing a little from the side of the unpaired radius.

The two other radii leave from each corner of the mouth and go, separating very little from each other, towards the farthest edge of this opening where the anus is found.

²⁰ This second part was read to the Academy of Sciences in the meeting of 28 February 1848. See the accounts of this meeting, p. 266 and following. Parts II, III, and IV comprise new studies on the facts indicated in the title of this memoir. These new studies, having become much more extensive than I had foreseen, forced me to change the simple title of *Note* that I had first given to this work to that of *Memoir*, or which the third and fourth parts will be the subject of the next lecture.

These five radii are very unequal in length on the inferior face of the test because of the position of the mouth which is very eccentric. They converge regularly on the upper side towards the center of the vault that forms the test and where the four openings of the gonads and the genital pole are found.

They are composed of the same series of vertebral and costal pieces that we have recognized in the *regular urchins*.

The *vertebral* pieces differ little between themselves in form and even in dimensions, at least on the inferior face. On the superior face, they decrease according to their nearness to the genital pole.

But the costal pieces that fill the intervals of the radii and join these radii to each other are so much larger as these radii separate from each other. Joined on the inferior face, without doubt to solidify movements, they are not numerous. But they correspond again to vertebrae by their number on the superior face of the test.

The test of *spatangoids* presents thus an **24** identical situation with that of *cidaroids*. One sees there the same five radii that go from the mouth to the upper or genital pole. Each radius is composed likewise of two series of vertebrae that form the middle part and two series of costals that are joined by suture of their two sides.

The vertebral pieces across which the external tube feet of each species, either tactile, respiratory, or locomotory, communicate with the corresponding internal organs have, because of these connections, more constancy in their form and number than the costals that do not have this function.

But the eccentric position of the mouth has brought about an inequality in the length of the radii, differences more or less great in extent of the intervals that separate them, and in the dimensions of the pieces that fill these intervals. The result is these radii are no longer symmetrical and that this asymmetry is notable only in the ribs of each radius.

The displacement of the anus, which is separated from the genital pole to be positioned between the ribs of two radii, has hardly any influence on the form and proportional dimensions of these radii and the pieces that compose them. Also it can open at the extreme edge, or even be separated more or less from it to occupy the inferior or superior face. This does not form an important distinguishing character. Systematic zoologists have recognized it in each case.

What has just been said shows that it is otherwise for the position of the mouth, from which leave the five **25** radii that always make up the test of *echinoids* to converge towards the genital pole.

When one looks only at the difference in the general form of *spatangoids*, and especially in the position of the mouth and the anus without recognizing their radial composition is also formed of five radii, one stops, in my opinion, at the surface without seeing that this comparison of regular *urchins* and *spatangoids* and consequently of all *echinoids* shows most important relatively to the *uniformity of its radial composition*.

§ II.

After these preliminaries on the general composition of the skeleton of *echinoids*, we can undertake to compare *asteroids* with them without fearing to be misunderstood.

In order to give the details in which we are going to go easier to understand, we have had drawn²¹ the cross section of a free ray of *Astérie glaciale*²² (*Asteracanthion glacialis*, M. and T.) from near the base, that of one of the five rays **26** of *Asteriscus palmipes* M. and T., (1) and that of the section of a radius of the *edible urchin* (2), indicating by the same letters comparable and exactly corresponding parts.

The section of the *urchin* represents that of a radius that is composed of the area called *ambulacral* in its middle and half of the two *inter-ambulacrals* areas on the sides. These latter are the ribs and the middle part is the vertebral column of this symmetrical radius.

One recognizes easily that the middle pieces (*a* and *b*) in the two species of *asteroids* and in the *urchin*²³ forming that which one has regarded for a long time in *asteroids*²⁴ as the body of the vertebra. The lateral piece (*c*) is a kind of rib, very short in *asteroids*, very long in the *urchin*. At the exterior of this last piece are seen in the *urchin* several series of small pieces (*d*) that support the spines. These same pieces, close together in the *urchin*, are more or less separated in the *asteroid* and each of them is likewise connected to a spine and supports it.

In a ray separated from an *asteroid* the skeleton is also on the surface in all its parts as that of the *urchin*, **27** equally covered by the skin and covered inside by the peritoneum into which the visceral cavity extends.

Only in certain species (*Astérie glaciale*) is the actual vertebral part the most exterior, while the rib parts are separated from the skin by enlargements of the fibro-cellular tissue and are embedded in a connective tissue coating.

I do not understand, after this, no more than Agassiz, how one is able to regard the actual vertebrae of a ray as forming an internal skeleton and the lateral parts that connects to them on the sides as constituting an external skeleton. This difference does not exist. The ensemble of all these pieces, in *asteroids*, composes an internal skeleton as I just said, but superficial, or peripheral, as in *urchins*²⁵.

In an *asteroid* with free rays, the two internal edges of **28** the ribs of the ray are connected in order to divide the visceral cavity that makes up each ray.

In the *urchin*, they are joined to the corresponding parts of the skeleton that form the two adjacent radii in a manner that the five radii form only a single common visceral cavity.

Something analogous takes place in the *asteroid* with fused rays, except that the visceral cavity is limited to the central part of the pentagon and the cavity of the rays is

²¹ It is Focillon, Licentiate in Natural Sciences, and my assistant at the Collège de France, who drew these figures with all the intelligence and exactness desired.

²² Pl. I, fig. 1.

²³ They are crossed by one or two canals established by the connection between the tube feet (p. p.) and the corresponding internal vesicles (v.)

²⁴ See, in the work cited of the celebrated Tiedemann, the explanation of fig. 1 of pl. IX.

²⁵ See the comments of J. Müller.

"Asteroids are star-shaped or polygonal echinoderms, more generally of polygonal form that, in addition to a cutaneous skeleton, have an interior skeleton that is lacking in all others.

"This skeleton consists as much as a series of articles joined by articulations in the arms, and always leaves from the ventral side of the common covering and particularly from the mouth.

"In asteroids, these series of articles form the floor of the ventral groove. ?? The skeleton of the skin is applied to both sides of the groove on these vertebrae in such a way to form a visceral cavity into which are extended the stomach caecum and part of the gonads, etc."

divided by bony columns that extend from one surface to the other and that abut isolated pieces of the peripheral skeleton. The analogues of these support the spines in *asteroids* with free rays.

This disposition recalls the bony partitions that divide the visceral cavity of flat urchins, such as those of the family of *clypeasteroids*.

In the *urchin*, all the skeletal parts are so articulated by sutures that their ensemble forms a true test, allowing only an empty space with two poles for the accessory pieces belonging to the mouth or gonads. In others, they retain a certain mobility either between themselves or relative to the rest of the skeleton.

In a ray of the *asteroid*, to the contrary, ossification is incomplete. The ensemble is still only membranous. It is a general periosteum in which other capsules of the same nature are formed. It has distinct parts, remaining cartilaginous or more or less ossified.

29 Most of the hard pieces are only cartilaginous. Instead of touching each other, they are dispersed throughout the membranous skeleton.

The aspect of the median pieces in the cavity of the ray is striking in its resemblance to the vertebral column of a vertebrate, considered within the visceral cavity in general or within the thoracic or abdominal cavity of those that have separated them.

This incontestable comparison, by correct intuition, obliges considering the *urchin* as showing in all parts only its dorsal surface and the *asteroid* as having its dorsal surface precisely on the side that one has designated till now as the abdominal surface.

The position of the principal nerve cord of each ray of the *asteroid*, the length of the median line of the groove between the rows of feet under the skin and at the dorsal side of the vertebrae seems to corroborate the conclusion we just indicated.

This relative position is, in fact, that of the vertebral canal that is lacking here.

But in *urchins*, it is necessary to recognize, the same relations are changed. The principal nerve cord of each radius is within the skeleton, in the visceral cavity, where it is joined to the vascular trunk that runs from the branches to the double series of respiratory vesicles in conformity with the tube feet.

This relative position, if different, that seems to transform the spinal cords of *asteroids* in terms of sympathetic cords in *sea urchins*, shows that in this case only the layout and general connections are 30 changed, and not the special distributions and functional uses.

We conclude that there are, in the organic arrangements in which we seek to appreciate the similarities, of very evident and very many analogies, rather than a full identity.

§ III

Spines in Echinoids

In *echinoids*, the spines are always articulated with a round tubercle, more or less protruding, belonging to one of the vertebral or ribs, like an epiphysis belonging to its bone in vertebrates. The articulating facet of the spine is more or less concave in order to

move itself on the convexity of the tubercle. One can detach very easily the spine from the plate to which it belongs.

In the *heart urchins*²⁶ the articulating part of each spine is composed of a large surface (*a*), unequally conical, crowned with a crest (*b*) to which the articulating muscles (*i*) are attached. Its summit is a spherical tubercle (*c*) forming properly the articulating facet. In the middle of this tubercle is a small hole for attaching a ligament (*d*), similar to that which fixes the head of the femur 31 in man and mammals at the bottom of the corresponding articulating cavity of the pelvis.

It is around this tubercle that the articulating capsule (*k*) is attached. It is fixed from the other part of the corona from small tubercles (*f*) that surround the base of the articulating mamelon (*g*) of the plate. One sees likewise, at the pole of this mamelon, a small hole (*h*) to attach it to the other extremity of the round ligament.

There do not exist in vertebrates articulations more perfect for the freedom of movement in all directions, and better armed with muscles to produce them, if not with a strong force, at least in all directions since small muscles completely surround this articulation and can flex it from all sides.

The distance between their attachment to the spine and the fulcrum of this lever facilitates again their action.

In the genus *Echinus*²⁷ the part of the spine surrounded by small muscles (*i*) is more regular. It is crowned with a circle of tubercles (*b*) to which about the striations of the spine and which provide attachment to the small muscles that envelop also all parts of this articulation. The articulating projection (*a*) of the spine has at its top a more marked articulating cavity (*l*) into which penetrates the tubercle (*d*) of the corresponding plate of the skeleton. This cavity does not have a hole to attach a round ligament. Our species show no more of them in the tubercles of the plates. If some appear 32 to have them, it is by accident when hardening is not complete in the axis of the tubercle as at its circumference. Moreover, no ligament is attached there.

In the *edible urchin* and, according to all appearances, in all species of this genus, the circular ligaments of articulation are missing. This results in the spines being much frailer than in *spatangoids*. After death the true *urchins* often lose them to a great extent after death while *spatangoids* have conserved theirs.

The result again is, as we shall show in the following paragraph, the spines are the principal organs of movement in *spatangoids* while in true *urchins* this function seems shared equally with the tube feet.

The cross section of a spine of *Echinus esculentus* shows a colorless axillary part. Around this axis is a first row of thin lamella, equally colorless, that form like rays separated by empty intervals and rejoined at the border by a circular lamella. Beyond this axis, they continue to thicken and show two colors that seem to indicate again two other stages of growth.

These extensions of the first series of lamina lack small spines, which have only this first series and the colorless axis that they surround.

The articulating tubercle of the plate on which each spine moves, supplements it and develops with it, appears like an epiphysis on each plate, which is easily detached.

²⁶ Pl. III, fig. G – 1, 2, and 3.

²⁷ Pl. III, fig. H-4.

§ IV.

Spines in Asteroids

Asterias glaciale (*Asteracanthion glacialis*, J. M. and T.) has large spines²⁸, either on its dorsal surface or its ventral surface, between which are found smaller ones²⁹. All make up the skeleton. They always rest on one of the tubercles belonging to this skeleton³⁰.

Like these tubercles, they are developed in a capsule comparable to the periosteum and analogous in nature.

One should say even that it is continuous with that of the tubercle, to leave free a part of its base, forming a slightly concave articulating cavity that moves freely on the corresponding summit of the tubercle on which the spine is placed.

These same spines are covered by the skin that is contractile, and it seems to me to be the sole means of moving them.

There is thus a very great analogy between the spines of *asteroids* and those of *urchins*, and the differences come from those that exist between the skeleton, more completely ossified in the latter, much less ossified in the former.

The result is that the spines in one (*urchins*) are part of the organs of movement while, in the 34 other (*asteroids*) they are more defensive structures.

In this regard, we have discovered a peculiar and very unusual arrangement in *Asteriscus palmipes* M. and T.

One sees on each side of the double series of vascular feet, four rows of spines joined by pairs. Each pair is articulated on the same tubercle and seems to have to come together at the point in contractions of the skin³¹.

The series nearest the tube feet is much longer than the feet. The external series is even longer. These two series of pinchers are evidently defensive structures, arranged to protect the tube feet against marine animals that would make them their prey.

This explanation will become more evident when we shall have shown in the *Third part* of this memoir, the use of *pedicellariae* that are lacking in this species of asteroid but that exist in other species of some genera of this family.

²⁸ Fig. I, *e e, e' e'*.

²⁹ Fig. I. *Ie'', e''*.

³⁰ Fig. I, *d*.

Vol. XX.

³¹ Pl. I, fig. 2, *e' and e''*, and fig. 2 following which represents these pairs of large spines.

THIRD PART.

PEDICELLARIAE

§. V.

Pedicellariae in General

Pedicellariae found on the surface of the body of *urchins* and some species of *asteroids* have been the second subject of my studies.

They are small bodies, several millimeters in length, most often composed of a stalk and a head in the form of pincers with three or two branches attached to the integument of these animals.

Their use is still problematic, although the opinion that they are organs belonging to the integument prevails at this moment and can be demonstrated.

It was O. F. Müller, the celebrated author of the *Zoologie du Danemark*, among others, who is credited with discovering them. He named and described them in this work as animals of a singular aspect that he had found between the spines of *Echinus saxatilis*. He distinguished them and illustrated three types: these are *pedicellaria globifera*, *tridens* and *triphylia*. (Pl. XVI, fig. 1-9)

36 In the first edition of *Animaux sans vertèbres*, which appeared in 1801, Lamarck classified the genus *Pédicellaire* with the *Corynes* and the *Hydres*, among the *Polypes nus*, and cited, for example, the *Pedicellaria globifera* of Müller that he regarded as the type of this genus.

G. Cuvier assigned the same importance to the *Pédicellaires* in the first edition of his *Règne animal*, preserving the genus *Pedicellaria* of O. F. Müller and of Lamarck. He likewise classed it among the *Polypes nus*, with the *Hydres*, the *Corynes*, etc., however warning that *various authors regarded them as organs of urchins*.

In 1825 de Blainville believed it necessary to consign, for the history of science, in the *Dictionnaire des sciences naturelles* (Vol. 37) to the word *Pédicellaire*, the characters of this genus and three species described by O. F. Müller that this author and Lamarck recognized. He even added a fourth species, *Pedicellaria rotifer*, described by Lamarck. But he was careful to express his doubts on the animal individuality of the three first species and the confidence that he had acquired, according to his own observations that the fourth species had been made from the tentacular cirrus around the mouth of urchins on which Lamarck had believed to discovered this alleged species.

In the same year (1825) Delle-Chiaje gave the opinion that the pedicellariae are, without any doubt, organs of the urchins. According to this author, the supposed polyps make an integral part of the body of the urchins and serve to attach to surrounding objects and seize small animals for nourishment.

They have a bony pedicel, 37 articulated with a condyle, as the spines. Their free end is composed of a group of fibers distributed to three bony, long, slender, pointed and articulated pieces.

Those of *Echinus spatangus* are smaller than the pedicellariae of *Echinus edulis*. In *Echinus neglectus*, they resemble the fruit of the spindle-tree.

Valentin, in his *Monographie anatomique du genre Echinus*, already cited, distinguishes three forms of *pedicellariae*, analogous to the three species that O. F. Müller had named. These are *gemniform*, *ophiocephalous* and *tridactyl pedicellariae*.

These last are seen, according to this observer, around spines of the interambulacral area. Their average length is 0.0044 m and that of the head from 0.0005 to 0.001 m. Valentin rejects the idea that these diverse forms belong to different degrees of development of one and the same organ as he had not found intermediate forms.

In a note of this Monograph, added by Agassiz, this scholar gave the hypothesis that the pedicellariae of *urchins* are a first developmental stage.

One year later, in 1842, Professor Erdl published in the *Archives di'histoire naturelle* of H. F. Erichson, some detailed observations on the structure and the vital phenomena of *pedicellariae*, that have led to the same conclusions as Delle-Chiaje and Valentin.

The skin of the *urchin* continues onto the stalk, the head, and the branches of these integumentary organs and appears likewise 38 spotted with colored patches.

The first form corresponds to the *Pedicellaria globifera* of O. F. Müller and the *Pedicellaria gemniformis* of Valentin.

The head is composed of three valves, forming a nearly spherical button when they are closed and showing when they are open, at the center of the end of the stalk that supports them, a cavity having a triangular vent.

The skin that covers them has vibratile cilia on the inside.

These three valves have continuous movement when the animal is still full of life by means of which the organ opens and closes alternatively. The stalk likewise flexes and straightens. Erdl has seen movements of the valves persist for some minutes after having detached the organ from the body of the urchin.

He distinguishes this first form as his first kind of *organ with valves*. His second sort is, according to him, a transitory form from the first to the third. He calls this organ *with foliated valves*. The three mobile valves of the head are in the form of leaves edged with sawlike teeth.

The stalk is more rounded than in the first type, although covered likewise with a colored skin and provided with vibratile cilia. It is bent into a spiral. The valves move with less vivacity than in the first type and their movements cease as soon as the organ is separated from the body of the urchin. This type of organ with *foliaceous valves* corresponds to the *Pedicellaria triphylla* of O. F. Müller and to the *Pedicellaria ophicephala* of Valentin. The valves touch their entire length when they are closed and their teeth mesh.

39 The third type of organ distinguished by Erdl is his pedicellaria with jawed pincers. This is the largest of the three. It is colored through its length. Each of its three branches, which are narrow, elongated and recurved in a point at their end, has three ridges of which the second laterals are sawtoothed. Closed, only their ends touch. Their movements are quick and energetic.

The author has observed these organs over all the surface of the urchin, between the spines and between the tube feet or its suckers. He has found those of the first type more numerous in the buccal or inferior hemisphere and less numerous in the anal hemisphere where those of the third type are more numerous. The least numerous were those of the intermediate form, foliaceous.

Erdl has regarded them as prehensile organs, seizing a prey suitable to their volume and transmitting it nearer and nearer down to the mouth, at least for those that are far from this orifice and so to speak at the pole opposite from the body. He has seen *nereids* several inches long seized in this way by these organs that detach from the body rather than release their prey when he tried to free them.

The observations of Delle-Chiaje and Valentin, after those of Erdl, have greatly advanced knowledge of pedicellariae relative to their structure and their nature as organs of echinoids.

There is lacking however a complete comparative work done on a large number of species of the order of *echinoids* to determine if their existence is general **40** or if they are characteristic of certain genera or only some species of other genera as J. Müller and Troschel have seen for *asteroids*.

Is it necessary to ascertain if their form and their proportions vary according to age and sex? If certain forms can be seen in the same individual, do they occupy preferentially certain parts of the body? Does their presence, as to their number relative to their form, have some constancy in all individuals of the same species and in different parts of the surface of their body where they are attached?

While waiting for this complete work to be done by a skilled hand, having at his disposition a large collection of these animals, I ask permission to present, for the profit of science, my modest contribution of observations and the conclusions that I believe can be drawn from them.

§ V.

Pedicellariae of Echinoids

I have observed pedicellariae of two species of the genus *Echinus*, *Echinus esculentus* and *miliaris*³² and one species of *spatangoid*, the *heart urchin*³³.

41 The pedicellariae of the *edible urchin* are of three kinds:

1° The most numerous, but at the same time the smallest, have a very long stalk proportional to the head, which is oval and formed of three vales that look very much like a tulip.

The stalk is composed of a slender, cylindrical bony part, a little enlarged at its base, by which it articulates to a small tubercle of the skeleton and, at the opposite end, beyond which this stalk is no more than a double transparent membranous tube. The tube exterior

³² Encyc., pl. 133, fig. 1 and 2.

³³ My specimens of *E. esculentus* come from Brest. They are 0.080 m from one pole to the other, and 0.110 m in diameter at the equator. The spines are clear green, the largest are violet at the end. The skin still shows traces of carmine red after several years in alcohol.

is formed by the continuation of the skin. The interior essentially belongs to the organ and is the contractile part.

We believe it is possible to consider the first development of this form that which is shown in our plate II (fig. I, *a*) and its complete development that shown as (*a'*). Here one sees in the middle of the three main valves three other smaller valves.

Other pedicellariae, much less numerous, have divisions of the knob, or the head, enlarged and elongated in form of leaves as Erdl showed them (Pl. II, fig. 5 and 6).

We consider them a transitory form, as a stage of development of the definitive form that is shown in figure (*c*). One also sees, in this first stage of development, the form designated by Valentin under the name *ophiocephalus*. We note the skin is extended still over the entire organ, even around the valves and that the membranous tube and muscles that covers it is distinguished by its spiral form (fig. I, *b*). This form 42 recalls the contractions, in this sense, that the tube exerts in the living state.

In the final form, shown in (*c*), the three branches of the head are very elongated and slender except at the base that is very enlarged without any indentations. When they come together, they touch only for about the last third of their length. The feet show us nothing in particular. The membranous tube has its integumentary part much larger than that formed by the muscular-membranous wall of the pedicellaria. This continues with the body pedicel that is long, slender, and enlarged at its two ends.

These pedicellariae with pincers are the largest. We have found them having 0.006 m length, composing the head, which measures 0.0025 m. The entire surface of the urchin, principally at the base of the spines of the ambulacral areas or interambulacral areas of those near the feet, is armed. When the pedicellaria is connected by its foot to a bony tubercle, it is attached by its skin.

In the second species of *Echinus*, *Echinus miliaris*, of which the examples were very much smaller than those of the first, we have found the various forms shown in Figure II, *a*, *b*, *c*, *d*, *e*. These diverse forms seemed to us to evidently indicate different degrees of development, from the first (*a*), which is simplest, up to form (*e*), which is the definitive form in this species.

One sees how the proportion of the head increases in the various degrees of development. In the pedicellaria *c* of Figure IIc, we have found pieces 43 of membranes that seem to have enveloped the branches of the still undeveloped pincer. Figure II*d* is the last transition before passing to the definitive form, to which this form evidently leads. In it, the branches of the pincer are hollowed out like a spoon and toothed at their edge. They touch along the greatest part of their length when they come together.

The forms of pedicellariae that we have observed in the *heart urchin* have given us analogous differences. They are shown exactly in Figure III, *a*, *b*, *c*, *d* in our Plate II.

It is impossible, it seems to us, of not going to the idea that the three first are only degrees of development of the fourth, which seems to us to be the definitive form. This is distinguished by the branches of the pincer, which are slender for the greatest part of their length, very enlarged at their base, and spatula like at the extremity by which they touch. Figure *b'* represents one of these pedicellariae taken between the pincers of its neighbor. One encounters this very often and thus has the appearance of one devouring the other.

If one compares the three definitive forms that we just described and which are shown in our plate with the analogous forms of the pedicellariae of *Echinus saxatilis* described by Erdl (Pl. II, fig. 8 and 9) to those of *Echinus brevispinosus* Risso, of the memoir of

Valentin (Pl. IV, figs. 45-50), one cannot help thinking that the different species of the same genus *Echinus* each have forms of pedicellariae that are their own.

§ VI.

Pedicellariae of Asteroids.

In *Astérie glaciale*, *Asteracanthion glacialis* M. and T, (Encycl. Pl. 119, fig. 1), one finds pedicellariae on both surfaces of the body.

On the dorsal surface, there are two kinds: the larger one is arranged very regularly between each lateral series and the middle series of the spiny tubercles. There are consequently two regular series of them. Each pedicellaria is very distinct from the preceding and the following so that their number is scarcely, for each series, more than ten or twelve. They have moreover an identical form and volume and do not show all the differences that we have seen in the pedicellariae of urchins.

Each pedicellaria is composed of two thick valves of calcareous nature³⁴, flattened inside and rounded outside, a little elongated, and touching their entire length when closed. These two valves rest and move on a tubercle of the same nature (*k*) by a hinged articulation. Two external muscles, one on each side, serve as abductors³⁵, and two internals, adductors, for each of these valves³⁶.

45 This organ is supported by a short pedicel that is membranous and non-calcareous but very resistant because it supports the weight of that which we call the head of the pedicellaria. The foot is continuous with the skin of the asteroid.

Much smaller pedicellariae, extremely numerous, cover the tubercles from the middle of which emerge the spines. They are grouped irregularly on these tubercles (as can be seen in Fig. IV, *b*). They are attached there directly, without the intermediary of a pedicel.

Can these rudimentary pedicellariae, which appear to be only granulations to the naked eye have any use?

Developed pedicellariae, analogous to those of the dorsal surface, are seen on the inferior surface between the outer series of spines and the lateral tubercles. They are few in number. The most numerous are between the feet and spines. We have counted more than sixty of them per series.

These pedicellariae are larger than those of the dorsal surface. Their branches are paddle-shaped. They also move on a common tubercle that is sheathed by a membranous foot. The latter is very ample, sac-like, for a great part of its length and narrows rapidly before ending at the skin³⁷.

³⁴ Fig. IV, *a*. This figure shows a pedicellaria holding sand grains between the valves.

³⁵ Fig. IV, *a*, 1-1.

³⁶ Fig. IV, *a*, 2-2.

³⁷ Our Fig. V, *b'*, represents one of these pedicellariae seen from the side; *b''* one of the branches seen from the front, *b'''*, the branches or the valves and the tubercle on which they move, detached from the membranes that envelope it; *a'* is a smaller pedicellaria of the same species but not being completely developed.

46 We have also encountered on this inferior surface some pedicellariae of a similar form but smaller. They seem to be the same kind to us but developing.

In *Astérie rouge* (*Asteracanthion rubens*), the pedicellariae have a singular disposition. The only ones that are a little developed are grouped irregularly around and near the end of the spines that border the groove where the feet are found. These pedicellariae are also sessile, that is to say, without feet as those rudimentary ones of the tubercles of *Astérie glaciale*. Their form is more compressed, a little more elongated, more pincer-like³⁸. The other parts of the body of this species do not have any of them.

The principal difference between the pedicellariae of *asteroids* and those of *urchins*, as observed by J. Müller, consists in the number of branches of their head. There are only two in the pedicellariae of *asteroids* while those of *urchins* have three.

Another remarkable difference consists of the absence of hard parts in the foot that is uniquely membranous and muscular and with no bony stalk as those of pedicellariae of *urchins*.

But one cannot ignore the analogies that exist between them. They are always very small 47 organs, appropriate to seize objects proportional to their volume. These organs are so far from the mouth that one cannot give them the function, as proposed by Erdl, of serving as organs of grasping food material and of transferring it from one pedicellaria to another from those furthest from the mouth to those that are closest.

Here is the hypothesis that I believe I must conclude on their usage.

The pedicellariae in *urchins* as in *asteroids* are closer to tube feet and the respiratory tentacles in *asteroids*.

These delicate membranous organs that the animal cannot withdraw into the visceral cavity must be protected against the innumerable small animals that are abundant in the sea.

It seems to me that one can regard pedicellariae as defensive arms, by means of which *urchins* and *asteroids* repulse the aggressions of these small, voracious animals of all species, by seizing them between their pincers.

Also *urchins*, which have the greatest need of these defensive arms because of their small capacity for location and stiffness or immobility of the parts of their skeleton, are more abundantly provided. *Asteroids*, more mobile, have much fewer species that are armed and a large number lack them.

In the present state of science, it is no longer possible to consider pedicellariae, with O.F. Müller, as 48 parasitic animals; no more than as *urchins* or *asteroids* developing on the surface of their parents, following the hypothesis advanced by Agassiz in 1844 that he seems to have completely abandoned at this time.

Pedicellariae do not exist only in the class of echinoderms. A genus of the order of *Polypes cellulaires* or *ascidiens*, the genus *Acamarchis* Lamouroux, has a species well known since Ellis (*A. avicularisi*), that has, near the entrance of each cell, an *appendage in form of a bird's head*, whose inferior mandible approaches or extends from the superior by continual alternative movements, according to observers. These appendages

³⁸ See our Fig. VI.

that one has never understood up to the present, to my knowledge, either usage or analogies, are the pedicellariae of these animals³⁹.

³⁹ See pl. 69, 2, of the illustrated edition of the *Régne animal* of Cuvier (Zoophytes); and, in the first place, Jean Ellis, in his *Essai sur l'histoire naturelle des Corallines*, pl. XXXVIII, fig. 7, G, H, I, K, L., et pl. XX, 2, A; and the *Fauna pontica* of Nordmann, pl. 3.

FOURTH PART.

Locomotory, respiratory and tactile tube feet that occur on the vertebral pieces of the radii in echinoids

One of the most singular, most exceptional organ systems that distinguishes most *echinoderms* (the *echinoderms with tube feet*) is, without contradiction, that of the more or less retractile and protractile cylindrical or conical vesicles that appear in certain parts of the surface of the family of *holothuroids* and that occur on and border, on each side, the ambulacral areas or the *vertebral series* of the radii in *echinoids* and *asteroids*.

Tiedemann and Delle-Chiaje have described and drawn it in detail, and after them, Volkmann⁴⁰. — I have recognized it in volume VI of *Leçons d'anatomie comparée* (2nd edition) that appeared in 1839 under the name of *cutaneous vascular locomotory system*.

The differences that occur in this system in its different 50 parts have need of being studied again in a certain number of species of diverse natural families. Those offered to me in the *edible urchin* (*Echinus esculentus*) and *heart urchin* (*Spatangus purpureus*) persuaded me.

§ VII.

In the *ture urchins* and in all the family of *cidaroids*, this sub-vertebral vascular system appears to have only locomotory appendages. These appendages, known under the name of *tube feet*, are arranged in regular rows that go, like the meridians, from the edge of the opening of the skeleton that is the buccal pole up to that of the anal pole.

Their muscular-membranous structure, the sucker at their end, their cylindrical form that is a little enlarged at the base, their numerous muscular fibers arranged circularly that constitutes their middle membrane between the skin that covers them and their internal membrane are well known.

In *Echinus esculentus*, where we have studied them, each of these feet communicates with a corresponding vesicle attached to the same part of the skeleton by two oblique tubes that are the continuation of their internal membrane and the walls of the vesicle into which they open. These tubes run through two canals of the same dimension pierced through one of the vertebral pieces⁴¹ in a way that their 51 external openings are closer and their internal openings more separated.

All the tube feet of each radius have the same structure and the same use.

These are the feet or prehensile and locomotory organs that extend considerably by contraction of their circular fibers and manage thus to extend beyond the spines and from

⁴⁰ Wiegmanns archive. 1838.

⁴¹ Pl. III, fig. D.

which the animal applies the sucker to surrounding bodies. It moves towards these bodies by the shortening of these same feet produced by contraction of the longitudinal muscular tissue that these feet contain and that is attached from one part of the corresponding vertebral piece to the sucker.

The internal vesicle (*vr*) that belongs to this foot does not seem to me to be able to contribute to extending it by the impulsion that a strong contraction of the walls of this bladder would give to the liquid that it contains. The idea that it extends it by forcing this liquid there, an idea repeated in all works, seems still more erroneous to me.

I have not been able to discover in the walls of this vesicle any very evident muscular fibers. The tissue of its walls, seen with low magnification, has shown me only granules and non-fibrous cells.

Each of these internal vesicles (fig. D *vr*) is an organ of respiration, flat and triangular in form, into the extent of which ramify blood canals. Their principal trunks communicate to the outside, by two conduits that cross the skeleton, with a tube foot and inside with a vascular branch (fig. D *br*) that belongs to the trunk that runs the entire length of the median line 52 of a radius to open into a central vascular ring situated around the origin of the alimentary canal. This arrangement is well known.

There is in the structure of these vesicles much analogy with those of the branchial gills of crabs.

The nourishing fluid that fills this system of vessels, respiratory vesicles and feet, is moved by contractions and dilations of these latter appendages. They are, in regard to this system, like so many hearts, giving movement to the liquid that they contain, but not receiving any from it.

There are in *urchins*, and in the species in particular that we just studied, two other types of appendages located at the buccal pole but which take no part in the locomotory and respiratory vascular system.

One type is prehensile appendages and without doubt tactile. They are retractile and protractile membranous tubes, ten in number, noticeably close together in pairs. They do not communicate with the visceral cavity but are attached to as many round calcareous plates projecting from the internal side.

The distal free end of these appendages is a bulb and can clearly serve principally to hold to the mouth the prey that the animal is busy devouring.

The other kind of appendage, which is not connected directly with the cutaneous vascular system that we just described, is seen, as we just said, at the same buccal pole as the preceding, but further from the buccal opening in the border of the skin that fills the rosette-shaped space that leaves from this side of the test.

53 These appendages likewise number ten, brought together in pairs between the two angles of the buccal membrane that corresponds to the interambulacral spaces or to two costal series belonging to two radii while the five pairs of the first sort, or prehensile tentacles, correspond to the vertebral series of each radius.

The latter appendages are forked tubes in their free part, having the ends of these branches open and opening by their trunk around the lantern or bony arcs that make part of the skeleton and the complicated mechanism of mastication. One regards them generally as organs that expels the respiratory liquid and empties it into the visceral cavity.

They belong, in this case, to the system of respiratory vascular and motor organs that we have described in the first place, but without having an immediate connection with this system.

Thus the true *urchins* and, to all appearances, all genera of the family of *Cidarides* Agassiz and those of *Galérides*, that we shall propose at the end of this work to separate from *Cassidulides*, will have in the vertebral part of their radii, from one pole to the other, only motor appendages (the tube feet) of the same structure in immediate contact with the internal respiratory bladders and the sub-vertebral vascular system.

We shall propose to unite these urchins in a first section of Échinides under the name *Homopodes*. This section contains the families of *Cidarides* and *Galérides*.

54]

§ VIII.

Before examining in more detail in this report the four families that Agassiz and Desor just recognized in this ORDER OF ÉCHINIDES, I must describe the same system of sub-vertebral vascular and respiratory organs and the different external appendages in the *heart urchin*.

Here the new points of view under which we have studied this system have led us, if we are not mistaken, to a more exact knowledge of the different structures, their relations and functions, as well as important conclusions on the natural families of this *Order*.

There are in the *heart urchin*, belonging to the same vascular system and attached by the principal branches of this system: 1° tube feet or locomotory appendages; 2° prehensile and tactile appendages that surround the mouth to a great distance; 3° internal and external branchial or respiratory vesicles.

The vascular system is here very easy to recognize by its black color. It is composed of a central part in the form of a ring that follows the contours of the mouth or pharynx and five trunks that leave this ring to follow the median ling of the five series of vertebral pieces and consequently of the five radii.

From the five vascular trunks arise, alternatively to right and left, transverse branches that go to the double series of internal vesicles and [55] external tube appendages that are attached inside and out of the vertebral part of the radii.

1° *Tube feet* of the *heart urchin* are not numerous in the four radii that have external branches. I have counted twelve to fourteen or more per radius in the longer pair and only ten in the shorter pair.

The feet of the radius that lacks internal gills are much more numerous; there are thirty four of them.

Their form is cylindrical and elongated. The sucker at the distal end is disk-shaped and separated from the properly called foot by a constriction.

One observes, across the very thin and transparent skin that covers them, a layer of muscular fibers or rather muscular bundles that circle them like rings and make them elongate by contracting⁴².

Each of these feet has only a single canal communicating with a small internal bladder applied against the visceral wall of the same vertebral piece of the skeleton. This

⁴² Pl. III, fig. B and B'p.

same canal continues in a vascular branch that goes immediately into the common trunk that runs from the buccal ring up to the genital pole, the length of the median line of each radius.

This single canal, while there are two of them in the tube feet of *echinoids* that we call *Homopodes*, is not the only difference that this apparatus shows in the *urchins* and the *spatangoids*. The vesicles are smaller and their walls are evidently muscular. The fibers of this [56] nature are disposed there in different directions for contractions in all directions.

2° *Tactile appendages*. Very numerous appendages of another nature occur on each radius at its origin around the mouth. There are eight of them in the locomotory radius, eleven or twelve in the anterior pair and six or seven in the posterior pair of the respiratory radii.

These tactile appendages or tentacles are cylindrical or slightly conical and end in a disc with many papillae. These papillae are in greatest number around the circumference and in smaller numbers on it, which gives the free end the aspect of a tuft (fig. C t.). Each of these papillae is conical and attached to the top of the cone. It is supported by a small, cylindrical calcareous rod.

The base of the tentacle is attached to a protuberance (*tb*, fig. C) of the corresponding vertebral piece. It is composed of the continuation of the skin, with very slightly pronounced circular fibers and longitudinal fibers that go from the tubercles that we just indicated to the terminal disc.

This tentacle has, like the tube feet, a single canal of communication with an internal bladder (*vt*), more voluminous but of the same structure as those of these feet and in the same connection by a transverse vascular branch (*br*) with the vascular vertebral-radial trunk.

We shall note here a very great difference between the palps of the *edible urchin* and those of the *heart urchin*. In the former, they have no connection at all with the complicated vascular apparatus that we describe while in the latter they make an essential part.

[57] 3° *Respiratory appendages*. The third type of appendage that we have to describe in the *spatangoid* is that which belongs to this part of the four dorsal petal-shaped radii.

These appendages are external gills⁴³, triangular in form and circumscribed by two principal canals that go round them and that communicate with each by a certain number of transverse branches more or less divided in ramifications.

Each of these external gills are continued by two membranous canals that cross obliquely two bony canals of the corresponding vertebral piece (*pv*) with a very much larger internal gill of the same structure. This has its transverse vascular branch that empties into the common radial trunk⁴⁴.

⁴³ Pl. III, fig. A. This figure shows the two gills, or internal (*vr*) and corresponding external (*vr'*) respiratory bladders, and their relation.

⁴⁴ Fig. E gives a clear idea of this ensemble of internal gills belong to the four radii. One sees that they are not developed equally and that their length is proportional to the space they can occupy from the communicating holes up to the median line of the radius. They disappear earlier toward the genital pole, from the anterior side of each radius, than in the opposite row. I have counted twenty one in the anterior row and four or five more in the other.

These vesicles, while vessels of the same system, contain a black blood composed of numerous, lentil-shaped globules⁴⁵, each having a considerable nucleus that [58] seems to contain more particularly the colored material. These globules resemble closely those observed by de Quatrefages in *Duvernoy's synaptid*. Their diameter is 0.008 mm.

Thus, the three types of appendages that we just described in the *spatangoid* belong to the same vascular system, containing a blood with black globules.

These appendages are modified for three different functions, locomotion, tactile and respiration.

CONCLUSIONS

If I am not mistaken, here are the improvements in ideas and consequently in the terminology, in classification of *echinoids* and in their physiology that the anatomical observations that are the subject of this memoir can introduce to science.

1° Each radius of the *urchin* or *echinoid* is composed in the middle part of two series of bony vertebral pieces carrying tube feet, or external gills. It will be more exact to name this region *vertebral* than to call it *ambulacral*.

2° The region called *interambulacral* will be the *rib region*, composed of two series of ribs belonging to two neighboring radii. This region, in *echinoids* has spines only and has no tube feet.

[59] 3° The order of *echinoids*, in the method I propose, will be divided into two sections: that of *homopode echinoids*, whose vertebral region is uniform in each radius and has, from one pole to the other, only tube feet.

And that of *exobranche echinoids*, which have a rosette with four or five more or less pronounced petals on the dorsal surface and the vertebral part of their radii, and external gills instead of tube feet in this part.

In *echinoids* of this latter section, there is a double series of holes in the vertebral pieces which form the contours of the petals, while in the rest of the vertebral part of the radii, which have the tube feet or tactile appendages, each appendage has only a single hole going through a single vertebral piece.

4° The first section contains two families: that of *cidaroids* that Agassiz and Desor have described and that of *galerides* that I propose to be separated from the *cassiduloids* of these authors. It is composed of *echinoids* of this family that Agassiz and Desor say have *simple ambulacra*, that is to say, they lack the dorsal rosette and consequently, according to us, external gills.

Desor has already presented, in his monograph of the genus *Galérîte*, the relation that exists between this genus and *cidaroids*. The anatomy, which has made me appreciate the important character indicated by the presence of this rosette, has led me to the physiological and organic understanding of this relation and to better classify this group of *cassiduloids*.

⁴⁵ Fig. J.

5° Our second section of echinoids contains:

A. The family of *cassiduloids*, that no longer contains [60] genera with a dorsal rosette, that is to say, with external gills,

B. The family of *clypeasteroids*,

C. And that of *spatanagoids*, that Agassiz and Desor described and characterized.

6° The growth of the spines seems to me to take occur by stages and layers that are covered later by a subcutaneous periosteum. (see part 2, page 608).

7° The *homopode echinoids* having a great number of tube feet, that correspond to as many internal gills, that should be the principal organs of movement.

Tiedemann has seen *Echinus saxatilis* climb by means of these feet the vertical walls of vessels in which he maintained them.

8° In *exobrach echinoids*, the number of tube feet is small, the spines are more numerous, their articulation better made. These spines appear to me to be for the echinoids of this section the principal motor organs.

9° Their external gills, which exist simultaneously with the internal gills, contribute without doubt to a more complete oxygenation of their blood and give more strength to the muscles of the spines.

10° Their blood is black and composed of numerous globules varying a little in their diameter, having a large nucleus in the middle, which contains more particularly their colored substances, as in the higher animals.

11° The tube feet and the corresponding gills in the *homopode echinoids* form, with the vascular branches [61] and the median canal of the radii to which these branches unite, and the circumpharyngeal vascular ring into which the five radial canals open, a moving and respiratory blood system in which the blood must have a back and forth motion which results from contractions and dilations of the tube feet.

The respiratory vesicles do not appear to me to contribute to this although erection of the tube feet has been attributed to them up till now.

12° The external and internal organs of respiration of *exobrach echinoids* belong to the same vascular system but do not contribute to the movement of blood in this system.

The tube feet, to the contrary, as well as being tactile appendages, are part of this same vascular system. Thus the internal vesicles corresponding to each of these appendages with evident muscular fibers are here the organs moving the life-giving fluid.

13° The pedicellariae are organs of defense of *echinoids* and *asteroids* as foreseen.

They defend the tube feet and other membranous appendages of these animals against attacks of myriad voracious animals that abound in the sea.

These organs appear to have different forms in each species.

They have general distinctive characters in *echinoids*, in which their pincer always has three branches, and in *asteroids* where they have no more than two as Müller and Troschel have already said.

[62] Their pedicel is moreover a calcareous stalk in echinoids that is missing in asteroids.

The pedicel can be completely lacking in the latter.

The different forms of *pedicellariae* that one observes in the same individual are more often different stages of development of these organs.

14° The organs in the form of a bird's head of certain *cellular polypes* are the pedicellariae of these animals. (see page 624.)

Figure Legends

Plate I.

Fig. 1. Transverse section of a ray of *Asteracanthion glacialis*, J.M. and T.

Fig. 2. Same section of *Asteriscus palmipes*, J.M. and T.

Fig. 2 *a'*. One of the pair of spines (*e''*), enlarged.

Fig. 3. Same section of *Echinus esculentus*, L.

In the three principal figures:

a and *b* are the vertebral pieces.

c, a rib piece.

d, series of pieces that will support the spines; they are dense in the *urchin* and separated in *asteroids*.

[63] *e*, *e'*, *e''* are spines.

p, *p*, the tube feet.

v, *v*, the internal vesicles that correspond with these feet.

e' and *e''*, fig. 2, are the two series of spines arranged and articulated by pairs on the same tubercle, outside the series of tube feet of the same side and forming the pincer to protect these feet in place of the *pedicellariae* that are lacking in this species.

Plate II.

Pedicellariae of *urchins* and *asteroids*

Fig. 1. *a*, *a'*, *b*, *c*, Pedicellariae of the *edible urchin* (*Echinus esculentus*, L.)

Fig. II. *a*, *b*, *c*, *d*, *e*, Pedicellariae of *Echinus miliaris*.

Fig. III. *a*, *b*, *b'*, *c*, *d*, Pedicellariae of *Spatangus purpureus*.

Fig. IV. *A*, *b*, Pedicellariae of *Asteracanthion glacialis*, dorsal surface.

Fig. V. *a*, *b'*, *b''*, *b'''*, Pedicellariae of the same species, ventral surface.

Fig. VI. Pedicellariae of *Asteracanthion rubens*, ventral surface, near the tube feet.

Plate III.

Fig. G., 1, 2, 3. Details of the articulation of a spine of the *heart urchin*.

Fig. H. 4. Same details for *Echinus esculentus*. (See p. 606-608)

Fig. A, B, B', C, E, F. Relative to the tube feet, tactile appendages, respiratory appendages and gills of the *heart urchin* and the *edible urchin*.

In all these figures, (*vr*) indicates a respiratory vesicle or an internal gill; (*vr'*), an external gill; (*pv*), the vertebral piece pierced by one or two pores that go from an internal

respiratory or non-respiratory vesicle with an external gill, a tactile appendage or a [64] tube foot; (*br*) is a vascular branch that goes from an internal vesicle to the median vessel of each radius, whose opening is marked.

In figure B, one sees a tube foot (*p*) that communicates with an internal vesicle (*vp*) by a single canal, pierced across the vertebral piece (*pv*). Figure B' is one of the feet of the abdomen, as that of figure B, but less contracted; (*d*) is its fixed end and (*e*) its free end. This figure must be in a vertical position.

Figure C represents a tactile appendage, such that one sees around the mouth of the *heart urchin*: (*t*) is this appendage; (*tb*) is the tubercle of the vertebral piece (*pv*) to which it is attached; (*vt*) is the internal vesicle that connects with this appendage by a single pore.

Figure E shows the upper internal wall, and F, the lower internal surface of the test of the *heart urchin*: numbers 1-21 mark the internal gills of the four radii that correspond to the external gills. These internal gills have been drawn with much care in the relative proportions.

The vesicles of the feet of the median radius number 17 on each side, of which the first two are seen at the floor of the test (fig. F) and the others at the top of this same box (fig. E).

The posterior radii have five of them on one side at this same floor and two at the vault, indicated by numbers 1-7.

These vesicles and the tube feet that correspond to them are still fewer in number than in the anterior pair of radii.

In the five radii, the vesicles nearest the mouth appear to be tactile appendages (fig. C.). They number nine in the unpaired anterior radius, eleven in each radius of the anterior pair, and seven in each radius of the posterior pair, indicated by these numbers (fig. F).

A. J. Fortin delinavit.

Berville sculp.

Pièces correspondantes du Squelette des ASTÉRIES et des OURSINS.

PÉDICELLAIRES des OURSINS.

PEDICELLAIRES des ASTÉRIES

Borrone & Co.