

ON HERMAPHRODITISM IN VIVIPAROUS OPHIURIDS.

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With Plate I.

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I. INTRODUCTION.

In his "Studien über die Entwicklung von Echinodermen und Nemeriten" (1869)¹ METSCHNIKOFF announced the interesting discovery that *Amphiura squamata* — or *Amphipholis squamata*, as it must correctly be named — the well known and often studied viviparous Ophiurid, is hermaphroditic, the genital organs being arranged in this way that at each genital slit there is an ovary at the interradial side and a testis at the adradial side, the latter lying on the dorsal side of the arm². Another case of hermaphroditism in Ophiurids was announced by the present author in his "Echinodermenlarven d. deutschen Südpolar-Expedition" (1913)³, viz. *Ophiura nodosa* Lütken, which was found also to be viviparous. These were the only examples of hermaphroditic Ophiurids hitherto known.

¹ Mém. Acad. Imp. St. Petersbourg. 7. Sér. 14. 1869, p. 13.

² A detailed description of the arrangement of the genital organs in this Ophiurid was given by CUÉNOT in his "Études morphologiques sur les Échinodermes". (Arch. de Biologie. XI. 1891, p. 624.)

³ Deutsche Südpolar-Exped. Zoologie. Bd VI. 1913, p. 77.

It is true that DELAGE & HÉROUARD in their "Traité de Zoologie concrète" III. Les Échinodermes (1903, p. 136, text-note) state that "*Amphiura squamata* et *Ophioglypha* sont hermaphrodites. Cette dernière n'a que deux gonades à chaquebourse, une ♂ du coté radial, une ♀ du coté interradianal". With "*Ophioglypha*" is here evidently meant *Ophioglypha* (*Ophionotus*) *hexactis* E. A. Smith. This species has however, never been demonstrated to be hermaphroditic; on the contrary, STUDER in his paper "Ueber Geschlechtsdimorphismus bei Echinodermen"¹ describes specimens which he regards as male specimens. The description which DELAGE & HÉROUARD give of the genital organs of "*Ophioglypha*" ("cette dernière") is, evidently, meant to refer to *Amphipholis squamata*; as appears from the description of the genital organs of *Ophionotus hexactis* given below, it does not at all apply to that species.

In a paper "Ueber hermaphroditische Seesterne"¹ PAUL BUCHNER gives this statement: "Wenn wir von dem zum Teil hermaphroditischen Holothurien und den viviparen Ophiuren Abstand nehmen, ist der normale Hermaphroditismus bei Echinodermen etwas äusserst seltenes". This would imply as a known fact that viviparous Ophiurids, upon the whole are hermaphroditic. Since, however, the only viviparous Ophiurid, besides *Amphipholis squamata*, which had at that time been made the object of an investigation regarding the genital organs, viz. *Ophiomyxa vivipara* STUDER, was found to have separate sexes³, the explanation of this statement of BUCHNER must be this, that he has been thinking only of *Amphipholis squamata*.⁴

While studying the development of *Amphiura vivipara* H. L. Clark, a new viviparous Ophiurid discovered during the Carnegie Expedition to Tobago, B. W. I. in 1916⁵, I was naturally interested in ascertaining, whether this species would prove to be hermaphroditic like *Amphipholis squamata*.

¹ Zoolog. Anzeiger. 1880. N: r 67.

² Zoolog. Anzeiger. Bd 38. 1911, p. 315.

³ H. LUDWIG. Die Ophiuren der Sammlung Plate. Zool. Jahrbücher. Suppl. IV. 1898, p. 773.

⁴ Wishing, if possible, to have this confirmed by the author himself, I wrote to Professor BUCHNER, explaining him the matter. He kindly replied that he did not remember exactly the literary references used, but that he had made no special observations on viviparous Ophiurids himself. Perhaps it may be this statement by STUDER (Op. cit.) "Bei den viviparen Ophiuriden scheint zum Theil Zwitterbildung vorzukommen, so nach METSCHNIKOFF bei *Amphiura squamata*," which has caused BUCHNER to write as he did. In any case, the only hermaphroditic Ophiurid known when STUDER and BUCHNER wrote their papers, and DELAGE & HÉROUARD their "Traité de Zoologie concrète" was *Amphipholis squamata*. The suggestion of GIARD mentioned below, that also our common Ophiurids are hermaphroditic, may evidently be disregarded as source of information for the authors here quoted.

⁵ H. L. CLARK, Brittle-Stars, New and Old, Bull. Mus. Comp. Zool. Vol. LXII. 1918, p. 268.

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Finding this to be the case, the idea occurred to me that there might possibly be some connection between hermaphroditism and viviparity in the Ophiurids, and I resolved to investigate in this respect, so far as possible, all the Ophiurids known to be viviparous.

II. VIVIPAROUS OPHIURIDS.

In his paper on "Brutpflege bei Echinodermen"¹ LUDWIG records the following Ophiurids as being viviparous or otherwise protecting their offspring:

1. *Ophioglypha hexactis* E. A. Smith.
2. *Hemipholis cordifera* Lyman.
3. *Ophiactis Kröyeri* Lütken.
4. *Ophiactis asperula* (Philippi).
5. *Amphiura squamata* (Delle Chiaje).
6. *Amphiura magellanica* Ljungman.
7. *Amphiura patagonica* (Ljungman).
8. *Ophiacantha vivipara* Ljungman.
9. *Ophiacantha anomala* G. O. Sars.
10. *Ophiacantha marsupialis* Lyman.
11. *Ophiacantha imago* Lyman.
12. *Ophiomyxa vivipara* Studer.

Of these twelve species first *Ophiactis Kröyeri* and *asperula* must be omitted as not being viviparous. Regarding *Ophiactis Kröyeri* LUDWIG records² having found on some specimens of this species a number of quite young specimens (0,75 mm. diameter of disk) clinging to their disk and arms, and he thinks it justifiable to conclude from this fact that a sort of protection of the young is practised by this species, the young being carried for some time by the adult specimens. The suggestion that the species might also be viviparous was not confirmed, no young or developmental stages were found in the bursae; on the contrary, LUDWIG found the ovaries filled with a great mass of very small eggs, which "lässt es wahrscheinlicher erscheinen, dass die Eier abgelegt werden, aber keine freischwimmende, sondern kriechende Jugendformen entwickeln, die sich mit Vorliebe (oder nur gelegentlich?) den Körper der Mutter zum Aufenthaltsorte wählen".

My examination of this species entirely confirms LUDWIG'S statements that no embryos are found in the bursae, so that it is surely not viviparous.

¹ Zoologische Jahrbücher. Suppl. VII. 1904.

² H. LUDWIG. Die Ophiuren der Sammlung Plate. Zoolog. Jahrbücher. Suppl. IV. 1898, p. 759.

The sexes are separate. The eggs are very small, only ca. 0,05 mm. LUDWIG's suggestion that the young might be kleeping, not free swimming, I would not think probable. It is a general rule among Echinoderms that very small eggs give rise to pelagic larvae, larger eggs with much yolk-substance to larvae of worm-shape, provided only with ciliated rings (e. g. Comatulids, Dendrochirote Holothurians, *Solaster*, *Ophioderma brevispina*, *Ophionereis squamulosa*). Evidences are thus decidedly for the larvae of *Ophiactis Kröyeri* being typical pelagic larvae. But this again leads to the conclusion that the young found clinging to the adult specimens can only have assumed that place when sinking to the bottom after finishing their pelagic life; accordingly, it is exceedingly improbable that a young will ever find its mother to attach itself to. It must be supposed to cling to any grown specimen that happens to be at the place where the young sinks to the bottom, so that the protection of the brood practised by this species is only secondary and entirely passive from the part of the adult specimen. In case this supposition is correct — which can hardly be doubtful — it must be possible to find the young specimens clinging to both male and female adult specimens. I am sorry to be unable to test the correctness of my supposition in this way, for want of material.

The explanation set forth here is strongly supported by an observation on *Ophiothrix fragilis* made by the author. This species occurs in very great numbers in quite shallow water in a locality, Stensund, near Bergen, where a rich material was collected in June 1911. To the arms of these specimens quite usually are found clinging young specimens. Surely nobody would claim from this observation that *Ophiothrix fragilis*, which is known with certainty to have pelagic larvae, protects its young. There cannot be the slightest doubt that in this case the young quite accidentally cling to the arms of the adult.

With *Ophiactis asperula* the case appears to be exactly the same, the evidence for the alleged protection of the young in this species being only much more unsatisfactory, resting merely on the fact that LUDWIG¹ found in the same jar with a specimen from Puerto Bono, Smyth Channel, 10 tiny young specimens, 0,43—1,2 mm. diameter of disk, "die sich wahrscheinlich im Leben auf der Scheibe und den Armen der Mutter, ähnlich wie ich das bei *Ophiactis Kröyeri* (sic) beobachtete, festhalten". I find the eggs to be very small and numerous as in *Ophiactis Kröyeri*, so that evidence is decidedly for the species having pelagic larvae. The sexes are separate.

One more species is to be removed from the list quoted from LUDWIG, viz. *Hemipholis cordifera*, or as it should be named according to H. L. CLARK *Hemipholis elongata* (Say). This species was suspected by LYMAN ("Challenger" Ophiuroidea, p. 157) to be viviparous, because he found minute young

¹ Hamburger Magelhaensische Sammelreise. Ophiuroideen. 1899, p. 8.

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clinging to the arms and disk of the adult; he did not, however, find any direct proof of its viviparity, but states that the females were full of eggs (in January). LUDWIG (Op. cit., p. 693) suggests that the young are developing within the bursae, but gives no new facts to prove the viviparity of this species.

The specimens of this species preserved in the Copenhagen Museum being all very old and therefore not very suitable for anatomical study, I wrote to my friend Professor H. LYMAN CLARK at the Museum of Comp. Zoology at Harvard College, asking him to leave me some specimens for study. He very kindly did so, but it proved that also the material possessed by that Museum was of very old date. I then addressed the director of the Museum in Charleston S. C. (the harbour of Charleston being the type locality of the species, where it is found living gregariously) asking, whether he could possibly help me with some fresh material of the species. No reply was received, however — probably the letter was lost — and so I had to see what could be done with the old material.

I was at once surprised in finding that it has no bursae, a fact the more surprising, since LYMAN in his diagnosis of the genus *Hemipholis* expressly states: "Two genital openings beginning outside the mouth shields." What may have led to this statement is probably the fact that there is a shallow furrow along the arms with — at least in the males — a row of papillae along its outer edge, corresponding to the genital papillae occurring in some Ophiurids. The furrow thus evidently represents a rudimentary bursa. It is worth mentioning that in the very detailed figure of part of the ventral side of this species given by LYMAN ("Challenger" Ophiuroidea, Pl. XLIV. Fig. 13) there is no indication of bursal slits.

The sexes are separate. The eggs appear to be small and very numerous. These facts: the absence of the bursae and the great number and small size of the eggs, would seem to preclude the idea of this species being viviparous. The undeniable fact that young specimens may be found clinging to the disk and arms of the adult specimens must then evidently be explained in the same way as in the case of *Ophiactis Kröyeri*, viz. that the newly metamorphosed young (probably from a pelagic larvae), when sinking to the bottom in places where the adult specimens abound, actively clings to the latter for some time. The protection of the young would thus also in this case be of a secondary character, merely passive on the side of the adult specimen, which will, in most cases, not at all be the parent of the young clinging to it. — The case affords quite an interesting problem, and it is to be hoped that somebody, who has access to living material of the species, will undertake a careful study of it.

I must suppose that the same explanation should be applied to the

protection of the young stated by BERNARD¹ to occur in *Arbacia Dufresnii* — in case the young specimen that was found on the buccal membrane of an adult specimen had not got there quite accidentally during the capture in the dredge. I may mention that also in *Notechinus magellanicus* I have once found a quite young specimen attached to an adult; but I have hardly any doubt that it had got there quite accidentally during the capture.

Of the twelve species of Ophiurids mentioned by LUDWIG as protecting their young, thus only the nine are really viviparous. Some other species, however, have more recently been recorded to be viviparous, viz. *Amphiura capensis* (by DJAKONOW)² *Stegophiura vivipara* and *Amphipholis japonica* (by MATSUMOTO)³ *Amphiura vivipara* (by H. L. CLARK)⁴, *Stegophiura nodosa* and *Ophiotjalfa vivipara* (by the present author)⁵. Further the following new cases are recorded in the present paper: *Amphiura borealis* (according to an observation, hitherto unpublished, by the late Miss ELISABET PETERSSON), *Amphiura constricta* LYMAN, *Amphipholis tenuispina* LJUNGMAN, *Amphipholis sobrina* MATSUMOTO and *Ophiomitrella clavigera* (LJUNGMAN). Two more statements of viviparous Ophiurids must be mentioned on this occasion.

FEDOTOV in his paper "On the anatomy of *Gorgonocephalus eucnemis* M. & Tr."⁶ records having found a specimen "with a young individual in the depth of the bursae". As, however, it was found only in one specimen out of several hundreds, this cannot be accepted as a proof that this species is viviparous, and FEDOTOV himself also adds that "this question is not yet solved". The fact that the ovaries are present in very great numbers, arranged in several rows on the bursal wall, is decidedly against assuming this species to be viviparous, and the single young specimen found in a bursa doubtless must have come there accidentally.

¹ F. BERNARD. Échinides recueillis par l'Expédition du Cap Horn (1882—1883). Bull. Mus. d'hist. nat. 1895. N: r 7.

TH. MORTENSEN. The Echinoidea of the Swedish South Polar Expedition. Wiss. Ergebn. d. Schwed. Südp. Exp. 1901—03. Bd VI. 4. 1910, p. 32.

² A. DJAKONOW. Über Viviparität und Wachstumserscheinungen bei *Amphiura capensis* Ljungman. Zool. Jahrbücher. Abt. f. Syst. Bd 36. 1914, p. 291.

³ H. MATSUMOTO. A new Classification of the Ophiuroidea; with descriptions of new Genera and Species. Proc. Acad. Nat. Sc. Philadelphia. 1915, pp. 71, 79.

⁴ H. L. CLARK. Brittle-Stars, New and Old. Bull. Mus. Comp. Zool. Vol. LXII. 1918, p. 268.

⁵ TH. MORTENSEN. Echinodermlarven d. deutschen Südpolar-Expedition. Deutsche Südp. Exped. Bd XIV. 1913, p. 77. Some new Echinoderms from Greenland. Vid. Medd. Dansk Naturh. Foren. Köbenhavn. Bd 66. 1913, p. 40.

Possibly some statements may have been overlooked, no Zoological Record having appeared for the years after 1914.

⁶ FEDOTOV. On the Anatomy of *Gorgonocephalus eucnemis* M. & Tr. Travaux Soc. Nat. Petrograd. Bd 46. 1915.

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A very startling statement is made by A. GIARD¹, viz. that all the Ophiurids of our seas are viviparous and probably also hermaphroditic. It will be necessary to quote at some length from GIARD's paper, the more so as it has apparently been quite overlooked (it is true, that it is quoted by CUÉNOT in his "Études morphologiques sur les Échinodermes", but only in the bibliographical list, no reference being made in the text to the remarkable statements contained in it).

In the paper quoted GIARD says, after having enumerated the viviparous Ophiurids known to him from literature: "Presque toutes les Ophiures que j'ai observées dans la Manche, sont également vivipares. Je citerai entre autres l'*Ophiothrix fragilis* et l'*Ophiocoma neglecta* que j'ai plus particulièrement étudiées au point de vue de la reproduction."

"Il est, dans la reproduction des Ophiures, un fait bien curieux, sur lequel j'ai vainement cherché des renseignements chez tous les microtomistes ci-dessus nommés (viz. TEUSCHER, SIMROTH and LANGE, these "microtomists" being treated rather contemptuously in a previous paragraph). A un certain moment de l'année, on trouve des embryons dans toutes les Ophiures que l'on ouvre indistinctement (excepté chez celles qui sont infestées par les *Orthonectida*). Y aurait-il hermaphroditisme chez ces animaux? J'incline à le penser. Si l'on renverse sur le dos un *Ophiothrix fragilis* ou une *Ophiocoma neglecta*, on arrive très facilement à détacher, avec une aiguille, tout le disque ventral et les bras qui y adhèrent. Il reste alors ce que j'appellerai la cupule dorsale; au points des bords de cette cupule, où s'inséraient les bras, on trouve de petites pièces calcaires formant un V. Chacune des jambes de ce V porte en son milieu une vésicule dans laquelle on perçoit parfois un mouvement très vif d'apparence vibratile. J'avais d'abord considéré ces vésicules comme organes de sens, des sortes d'otocystes. Mais, je m'aperçus bientôt que chez beaucoup d'individus ces vésicules étaient vides et renfermaient seulement un contenu granuleux assez analogue à des éléments testiculaires. Ces vésicules seraient-elles des glandes mâles?"

"Il est bien étrange qu'un fait aussi remarquable que l'existence de l'hermaphroditisme chez tout un groupe d'Échinodermes n'ait pas plus fortement attiré l'attention des zoologistes allemands."

It is very unfortunate that GIARD does not state at which time of the year he has observed these Ophiurids to contain, embryos, but only says "à un certain moment de l'année". I have not had the opportunity of examining them, at all times of the year, but at least during the summertime they are not viviparous. *Ophiura albida*, *texturata*, *affinis* and *Amphiura filiformis* I have examined in the beginning of November. They had their genital organs

¹ A. GIARD. Particularités de reproduction de certains Échinodermes en rapport avec l'éthologie de ces animaux. Bull. Scientif. du Dep. du Nord de France. IX. 1878, p. 296. Reprinted in A. GIARD. Oeuvres diverses. I, p. 509.

normally developed and there was no trace of viviparity. From the middle of January I have had specimens for examination of *Ophiura texturata*, *albida*, *Amphiura filiformis* and *Chiajei*, sent to me from the Zoological Station, Kristineberg; the result was the same. The gonads are only less developed containing no ripe sexual products, except in *Amphiura Chiajei*, which has its breeding season in the winter, and — of course — there are no young in the bursae. It seems quite inconceivable how GIARD has come to this statement; in spite of the fact that I have not had the opportunity of examining these Ophiurids at all times of the year, I cannot have the slightest doubt that this alleged viviparity of all our Ophiurids at certain times of the year, while at other times they have pelagic larvae, is purely phantastic.

Also the statement of the hermaphroditism in these the common Ophiurids of our coasts is entirely mistaken. It is hard to say what it really is that GIARD has seen, but it is certain that they have all separate sexes. — Upon the whole these statements of GIARD are so phantastic and must be due to such imperfect methods of research that it is hard to realize.

I may mention here that GIARD has also maintained *Echinocardium cordatum* to be hermaphroditic¹: "Des recherches que j'ai poursuivies à Viméreux . . . il résulte que cet oursin présente une sexualité successive avec protandrie, les œufs commençant à paraître vers la mi-juillet dans les glandes génitales jusque-là manifestement mâles et bourrées de spermatozoides." — I think I can explain how this statement has been brought about. The gonads of Echinoids when unripe — or emptied — generally contain a white, milky fluid, which has a considerable likeness to ripe sperma. A microscopical examination, however, at once shows that it is not sperma; it consists of small globular bodies which move more or less vividly; but they are quite different in shape from spermatozoa and no tail is to be seen. They are either a fatty degeneration product of the cells of the gonads or parasitic organisms (Flagellates?); their movements would appear to point towards their being Flagellates, but I do not wish to state anything definitely about this question. But, in any case, they are not spermatozoa. In this fluid one may often find eggs, either degenerating or young eggs. I have not the slightest doubt that GIARD has taken this fluid for the sperm and thus, on finding eggs in it, has been led to the conclusion that *Echinocardium cordatum* should be a proterandric hermaphrodite. Another no less remarkable statement by GIARD in regard to the larval development of the Ophiurids of our seas (the occurrence of different larval forms in the same species — Poikilogony, he names this remarkable diversity of development —) will be dealt with in a memoir on Echinoderm larvae under preparation.

After this critical review of the statements of viviparity in Ophiurids

¹ A. GIARD. A propos de la Parthénogénèse artificielle des œufs d'Echinodermes. C. R. de la Soc. de Biologie. 4. Août 1900. (Œuvres diverses. I. 1911, p. 370.)

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found in literature we know at present in all 20 species of viviparous Ophiurids, of which, however, three, namely *Amphipholis japonica*, *sobrina* and *tenuispina* are so closely related to *Amphipholis squamata* that it may well be doubted, whether they can be regarded as distinct species.

There can hardly be any doubt that many other species of Ophiurids will be found to be viviparous, especially within the families of the Ophiacanthidae, Amphiuridae and Ophiolepidae. At present however, viviparity is definitely known to occur only in the following species.

1. *Ophiomyxa vivipara* Studer.
2. *Ophiacantha vivipara* Ljungman.
3. *Ophiacantha imago* Lyman.
4. *Ophiacantha marsupialis* Lyman.
5. *Ophiacantha anomala* G. O. Sars.
6. *Ophiomitrella clavigera* (Ljungman).
7. *Amphiura magellanica* Ljungman.
8. *Amphiura capensis* Ljungman.
9. *Amphiura constricta* Lyman.
10. *Amphiura borealis* (G. O. Sars).
11. *Amphiura vivipara* H. L. Clark.
12. *Amphipholis squamata* (Delle Chiaje).
13. *Amphipholis tenuispina* Ljungman.
14. *Amphipholis japonica* Matsumoto.
15. *Amphipholis sobrina* Matsumoto.
16. *Amphipholis patagonica* Ljungman.
17. *Ophiotjalfa vivipara* Mortensen.
18. *Stegophiura nodosa* (Lütken).
19. *Stegophiura vivipara* Matsumoto.
20. *Ophionotus hexactis* (E. A. Smith).

III. THE SEXUAL CHARACTER OF VIVIPAROUS OPHIURIDS.

In the following a detailed report of the authors researches into the sexual character of the different viviparous Ophiurids is given. With the sole exception of *Ophiacantha marsupialis*, known as yet only in the two specimens (now dried) dredged by the "Hassler" off Juan Fernandez, I have had the opportunity of examining all the viviparous Ophiurids known. Of most of these material is found in the collections of the Copenhagen Museum, in some cases, however, I have had to ask for material from colleagues in other countries. I beg to tender herewith my sincere thanks to these colleagues and their institutions, namely Professors A. BRINKMANN (Bergen), H. L. CLARK (Cambridge, Mass.), R. HARTMEYER (Berlin), L. JÄGERSKJÖLD

(Gothenburg), R. KOEHLER (Lyon), TH. ODHNER (Stockholm) and Dr. R. KIRKPATRICK (British Museum, London).

Ophiomyxa vivipara Studer.

As stated above LUDWIG has found this species to have separate sexes. My results (— four specimens examined, none of them in a very good condition —) are in perfect agreement with those of LUDWIG. That it is not a case of proterandric hermaphroditism is evident from the fact that the males are not found exclusively among the young specimens and the females not exclusively among the larger. LUDWIG records a male specimen of 17 mm. diameter of disk; the specimens at my disposal are one male of 14 mm., three females of respectively 11, 14 and ca. 20 mm. diameter of disk.

The ovaries are placed in a close row along the outer, interrarial border of the bursal slit, ca. 8 in number, and 1—3 along the adradial side. The eggs are large, ca. 0,5 mm. rich in yolk. The testes are large and somewhat lobed; there are ca. 5 of them at the interrarial, 2 at the adradial side of the bursae.

Ophiacantha vivipara Ljungman.

A young specimen, 10 mm. diameter of disk, has male gonads on the adradial side, while those on the interrarial side of the bursae are female or hermaphroditic. (A pair of large young were found in the bursae.) A somewhat larger specimen, 12 mm. diameter of disk, has the adradial gonads hermaphroditic, while the interrarial ones appear to be purely female. In larger specimens there may be a small quantity of sperma in some of the adradial gonads, but upon the whole the larger specimens are purely females. Exceptionally a specimen of 14 mm. diameter of disk was found to be purely male. Judging from the material available (which is mostly old and in no good histological preservation) this species is a protandric hermaphrodite, probably purely male in the young stages, then first the interrarial gonads turn female, later on also the adradial ones; the latter may, however, partly retain their male character even in adult specimens. There are two adradial, two to four interrarial gonads. The eggs are large, ca. 0,5 mm. and yolk-laden.

The statement of WYVILLE THOMSON ("The Atlantic" II. 1877, p. 243) that the eggs and embryos of this species are found lying free in the body cavity in the interbrachial spaces is, evidently, due to the fact that the bursae of Ophiurids were unknown at that time. It is true, STUDER had stated (1876) in his description of *Ophiomyxa vivipara*¹ that "die Entwicklung der

¹ TH. STUDER. Ueber Echinodermen a. d. antarktischen Meere. Monatsberichte d. Akad. d. Wiss. Berlin. 1876, p. 462.

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Jungen geschieht in eigenen Bruttaschen von ovaler Form in welche die grossen Genitalschlitze direkt münden". But, of course, WYV. THOMSON could hardly have any knowledge of this, when he wrote his book "The Atlantic". That the young are really lying in the bursae, as should be expected, is easy enough to see.

In his "Revision de la Collection des Ophiures du Museum d'hist. naturelle de Paris" KOEHLER¹ has suggested that in this species there should be a remarkable sexual dimorphism, the males having only five, the females more than five arms, because he had never found any of the five-armed specimens to carry young. More recently² KOEHLER has himself corrected this suggestion.

Ophiacantha imago Lyman.

This species has separate sexes. Of the three specimens examined one, 5 mm. diameter, was purely male, the two others, 6 and 8 mm. diameter of disk, purely female. The male had three adradial and four interradial gonads, the females one adradial and two interradial gonads. The eggs are large, ca. 0,4 mm. Numerous young of the same size in each bursa.

In the specimen of 6 mm. was found a large, sac-shaped parasite with a pair of long filaments, probably related to that found in *Ophiomitrella clavigera*. It does not castrate its host.

I am indebted to the authorities of the British Museum for placing these specimens (from the "Challenger" Collections) at my disposal for study.

Ophiacantha anomala G. O. Sars.

This species is hermaphroditic. The testes are arranged in a series along the interradial side of the bursal slits, while the ovaries are placed along the adradial side. There are generally five testes, but only three ovaries to each bursa. The eggs are large, ca. 0,5 mm., yolk-laden.

Ophiomitrella clavigera (Ljungman).³ (Fig. 1.)

In a small specimen, 2,5 mm. diameter of disk, there is only a single, small, globular testis at the middle of the interradial side of each bursa; one of these testes has an indication of small eggs in it. A specimen of 3,5 mm. diameter of disk has two testes along the interradial side of the bursae; they show distinctly eggs lying in the sperma mass. (Fig. 1.) A specimen of 6 mm. diameter of disk has two large ovaries at the interradial side, the outer of them the larger; in one radius there is moreover a small testis

¹ Bull. Scientif. de la France et de la Belgique. XLI. 1907, p. 322—23.

² R. KOEHLER. Échinodermes. Deuxième Exped. antarctic Française. 1908—10, p. 141.

³ This species was hitherto wrongly referred to the genus *Ophiolebes*.

near the proximal end of the genital slit. Further this specimen has at the adradial side of the genital slit a small ovary, containing very young eggs. One of the adradial gonads has close to it another small, hermaphroditic gonad. It is evident from these facts that this species is a protandric hermaphrodite.

The eggs are very large, 0,9 mm., and rich in yolk substance. No more than two young were found in the same bursa, generally only one. — In some specimens was found a very remarkable parasitic Crustacean (Copepod, with four egg-sacs), which has the effect of castrating its host.

Amphiura magellanica Ljungman.

Some specimens of this species were collected by the author in December 1914 at the Auckland Islands. The examination of this material has given the result that this species is hermaphroditic. The arrangement of the gonads is quite different from that known to occur in *Amphipholis squamata*. There is generally 3—4, sometimes only two gonads at the interrarial side and one, sometimes two, at the adradial side of the bursa. Any of those on the interrarial side may be a testis, mostly only one, but sometimes even three; often, however, all of them are ovaries. Those at the adradial side are generally ovaries, but sometimes also a testis is found here. Not two bursae in the same specimen show the same disposition and number of the gonads. Sometimes a few young eggs were found in a testis among the spermatogonia; the single gonad thus may have a more or less hermaphroditic character. The eggs are not very large, ca. 0,2 mm., but full of yolk.

Amphiura capensis (Ljungman). (Fig. 2.)

This species is hermaphroditic. There is a single, large, sausage-shaped testis at the adradial side, and one ovary at the interrarial side of the genital slit. The eggs are not very large, ca. 0,2—0,3 mm.

DJAKONOW, in describing the viviparity of this species (Op. cit.) thinks that normally the young are liberated through the rupture of the skin in the interrarii. He has observed one young with an arm protruding through the bursal slit, but leaves it undecided "ob das nur ein Zufall ist, dass die junge Ophiure bei ihrer Bewegung innerhalb der Bruttasche mit einem Arm in die Bursalspalte geraten ist, oder ob daraus geschlossen werden kann, dass die Jungen auch bei dieser Art gelegentlich durch die Genitalöffnungen auskriechen". Since the young are lying within the bursae, it is certainly to be expected that they are normally leaving the parent specimen through the natural opening, the bursal slit. The fact that ruptures may occur in the interrarii is easily accounted for by damage done accidentally by the collecting, as everybody, who has collected *Amphiuras* with naked or slightly

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scaled skin on the ventral side of the disk, knows is exceedingly liable to occur. Direct observations on the living specimens are necessary for settling the question. — I am indebted to Professor HARTMEYER at the Zoological Museum of Berlin for material of this species.

Amphiura constricta Lyman. (Fig. 3.)

This species is hermaphroditic. It shows the unusual feature of having no gonads at the adradial side of the genital slit (only in one case I have found a single ovary at the adradial side of one of the genital slits); at the interradian side there is an ovary at the middle of the slit and a testis at its proximal end.

The specimens examined, which were collected by the author in 1914 off the coast of N. S. Wales in a depth of 30—50 fathoms, differ from the type in having only 5 armspines (there are 6 in the type). Since, however, there are no other noteworthy differences I see no reason to doubt that is really this species.

Amphiura borealis (G. O. Sars).

During a stay at the Swedish Biological Station, Kristineberg, in the summer of 1918, I met Miss ELISABET PETERSSON from the Gothenburg Museum, who told me, she had found a viviparous Amphiurid on a dredging trip in the Trondhjem Fjord, and asked me which species it could be; it was not *Amphipholis squamata*, she was quite sure. I could only state that she had then discovered a new case of viviparity in Ophiurids and promised to identify the species for her. On my return to Copenhagen I received the specimen and found it to be *Amphiura borealis* (G. O. Sars). I suggested to Miss PETERSSON to publish a notice about her interesting discovery, which she consented to do. Soon after, however, she fell sick and died after an operation. The director of the Gothenburg Museum, my friend Professor L. JÄGERSKJÖLD, then asked me to publish her discovery, Miss PETERSSON not having left any manuscript notes about it, only a pair of photographs of the specimen. I am then including the note on the viviparity of *Amphiura borealis* in this paper, the credit for the discovery of which belongs to the late Miss PETERSSON.

The single specimen dredged by Miss PETERSSON is 3 mm. in diameter of disk, and has a pair of arms of a young protruding through a bursal slit. On opening the specimen very carefully so as to avoid destroying it I could find only a single ovary at the interradian side of the genital slit, while there was no trace of gonads at the adradial side. Wishing to get a more definite result as regards the sexual character of this species, I applied to the director of the Bergen Museum, Professor BRINKMANN, who kindly sent me the few specimens that could be spared, the species being evidently

not very common in the Scandinavian Seas. (The material in the Copenhagen Museum consisted only in a few specimens from Prof. Sars and a single more recent, dried specimen.) Unfortunately the specimens from the Bergen Museum were in a poor state of preservation, having partly been dried, so that no definite information was to be gained therefrom. Fortunately I then found among some unidentified material of Ophiurids in the Copenhagen Museum a few specimens of this species in a fairly good state of preservation. It was found to be a constant feature that there is only a single interradiation gonad, none along the adradial side of the bursa. All the larger specimens were only females; a single specimen, somewhat smaller, proved to be a male, the testes being found in the same place as the ovaries. A closer microscopical examination of the testes disclosed the fact that small eggs were seen among the spermatogonia, and thus the fact was established that this species is a protandric hermaphrodite. — The eggs are large, ca. 0,5 mm.

Amphiura vivipara H. L. Clark. (Fig. 4.)

This species is hermaphroditic. There is one ovary at the middle of the interradiation side, one testis at the adradial side of the bursal slit. The eggs are large, 0,5 mm., yolk-laden. The cleavage is superficial. (Numerous specimens collected by the author at Tobago, B. W. I., April 1916.) This species is of special interest in being the first truly tropical Ophiurid found to be viviparous, all the other viviparous Ophiurids belonging mainly to the cold regions.

Amphipholis tenuispina Ljungman, *japonica* Matsumoto and *sobrina* Matsumoto. (Fig. 5.)

These three species agree very closely with *Amph. squamata* in regard to their sexual character, having a single small ovary at the interradiation side and a single small testis at the adradial side of the bursa. The eggs are very small, and it can hardly be doubted that the development goes on as in *Amph. squamata*, to which species those named above are so closely related, that their specific rank may be regarded as doubtful. It should, however, be mentioned that embryos found in the bursae of the two Japanese species show the rudimentary larval skeleton developed into a close meshwork in the posterior end, differing rather conspicuously from that generally found in the embryos of *Amph. squamata*.

There is every reason to expect that also *Amphipholis australiana* H. L. Clark and *laevidisca* H. L. Clark, which belong to the *Amph. squamata*-group, will prove to agree with *Amph. squamata* in regard to their sexual character. I have had no material of these two species at my disposal.

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Amphipholis patagonica Ljungman.

Also this species agrees with *Amph. squamata* in regard to its sexual characters, being hermaphroditic, with one small testis on the adradial side and one ovary at the interradian side of the bursa. The eggs are very small, the development may then be supposed to be in accordance with that of *Amph. squamata*. (Material examined: two small specimens from Puerto Madryn, Patagonia, received from Prof. TH. ODHNER, Stockholm.)

Ophiotjalfa vivipara Mortensen.

Of the two specimens known of this species the smaller 4 mm. diameter of disk, is a purely male specimen. There are three testes at the interradial side, one, sometimes two, at the adradial side of the bursa. The larger specimen, 5 mm. diameter of disk, has been dried, so that, unfortunately, it is impossible to obtain full certainty with regard to its sexual character, the more so as it ought to be kept as intact as possible, being the type of the species. So far as can be ascertained under these circumstances, the specimen appears to be purely female. Evidences are thus decidedly for this species having separate sexes. In case it were a proterandric hermaphrodite it should be expected that there would be indication of eggs in the gonads of the smaller specimen, the difference in the size of the two specimens being so small; but there is decidedly no trace of eggs in the gonads of this specimen. Still it would be very desirable to have the matter reexamined on fresh material. — The eggs appear to be rather large and yolk-laden.

Stegophiura nodosa (Lütken).

As stated already previously (1913) this species is hermaphroditic. Both male and female gonads are placed along the interradial side of the bursal slit, generally in this order: proximally two testes, then one, large, ovary at the distal end of the slit. Often, however, there are two ovaries and then only one testis at the proximal end, and sometimes the latter is totally wanting. Generally there is a testis at the adradial side, near the outer end of the bursa. The eggs are large, 0,5—0,6 mm. rich in yolk. In spite of this fact the cleavage is total and regular. About a dozen eggs and embryos may be found in each bursa, all in the same stage of development. They may lie so closely that they are quite irregularly compressed; the space for the young stars is then so limited that it is almost inconceivable how they can assume their regular shape.

A detailed study of the development of this species in comparison with that of *Amphiura vivipara*, with superficial cleavage, would be of the greatest interest. This is, however, not the place for such study, which, by the way, meets with a special difficulty, the fact that all embryos in the same

specimen are in the same stage of development necessitating an exceedingly rich material for securing all the different stages of the development.

Stegophiura vivipara Matsumoto. (Fig. 6.)

This species is also hermaphroditic, but the arrangement of the gonads differs somewhat from that found in *S. nodosa*. There is a single, rather large male gonad about at the middle of the interradial side of the bursal slit and a female gonad near its outer end. Along the adradial side of the bursa there are two ovaries, sometimes only one. The eggs are large, 0,3—0,4 mm., yolk-laden.

(Material: three specimens collected by the author in the Sagami Sea, June 1914.)

Ophionotus hexactis (E. A. Smith)¹.

This species was held by STUDER (in the paper quoted) to have separate sexes and even to be among the very few Echinoderms, in which sexual dimorphism can be observed. "Bei einer grossen Menge von *Ophioglypha hexactis*, welche ich Gelegenheit hatte zu untersuchen, fand ich Individuen, welche keine Jungen enthielten, sich durch flachere Form der Scheibe und durch stärkere Hervortreten der Kalkplatten auszeichneten. Ich halte diese für männliche Thiere."

This statement may perhaps be due to STUDER having taken large, senile specimens, which have finished breeding (— I have seen a specimen in that condition —) to be the males. In any case it is wrong. This species is hermaphroditic. The male gonads are situated at the adradial side, the female gonads at the interradial side of the bursa. In young specimens just beginning their sexual activity — ca. 12—15 mm. diameter of disk — there is only one testis developed; in somewhat larger specimens another testis has appeared proximally to the first, and later still one more appears proximally to the second; even in the largest specimens

¹ The discovery of the viviparity of this species is due to STUDER. In his paper "Über Geschlechtsdimorphismus bei Echinodermen" (Zool. Anz. 1880. No. 67—68), it is true, STUDER ascribes the discovery to WYVILLE THOMSON. This however, is a mistake. WYV. THOMSON ("The Atlantic" II, p. 241) describes a viviparous Ophiurid under the name of *Ophiocoma* (?) *vivipara*, which he supposes — quite correctly — to be identical with LJUNGMAN'S *Ophiacantha vivipara*; he then further states that "we had previously got either the same or a very closely allied form in great abundance in the Fjords of Kerguelen. The Kerguelen variety has been noticed by Mr. Edgar Smith, under the name of *Ophioglypha hexactis*." This is evidently a slip of memory on the part of WYV. THOMSON, due to the fact that both *Ophiacantha vivipara* and *Ophioglypha hexactis* are found at Kerguelen. The form mentioned by WYV. THOMSON is *Ophiacantha vivipara*, not *Oph. hexactis*, and the credit of having discovered the viviparity of the latter species therefore is due to STUDER.

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examined (39 mm. diameter of disk) no more than three testes were found at each bursa. The number of the ovaries is rather inconstant; generally there are only 3—5, but I have observed as many as 8 of them at one bursa. The outer one of them is situated at the outer corner of the bursa, just below the articulation between the radial shield and the genital plate, and this is the first to contain ripe eggs. Sometimes there is also a gonad situated adradially to the latter, at the outer end of the bursa, and this gonad is sometimes male, sometimes female.

The development of this species shows some features of exceptional interest. It is intraovarial, and the embryo assumes the scape of a true, well formed larva. A detailed report of this remarkable case of intraovarial development, almost unique among Echinoderms¹ will be given in a larger work on Echinoderm larvae under preparation.

IV. CONCLUSION.

While *Amphipholis squamata* was the only case of hermaphroditism hitherto known among Ophiurids, it has now been proved through these researches that hermaphroditism is of general occurrence among the viviparous Ophiurids, no less than 16 out of the 20 species known to be viviparous having been shown to be hermaphroditic, one, *Ophiacantha marsupialis* remaining unknown as regards its sexual character. Three species alone, *Ophiomyxa vivipara*, *Ophiacantha imago* and *Ophiotjalfa vivipara* have separate sexes.

Hermaphroditism being otherwise totally unknown among the non-viviparous Ophiurids, it is evident that there is some direct relation between viviparity and hermaphroditism in Ophiurids. How this interrelation is to be explained seems rather enigmatical. The fact that in some cases (*Ophiacantha vivipara*, *Ophiomitrella clavigera*, and *Amphiura borealis*) it is a protandric hermaphroditism does not seem to make the explanation easier.

The suggestion that the hermaphroditism might serve to make fertilization more certain is directly disproved by these cases of protandric hermaphroditism — as also, upon the whole, selffertilization is not generally the object aimed at in nature — on the contrary! That selffertilization is possible in most of these cases seems, however, beyond doubt, judging from the appearance of the gonads in the preserved specimens.

¹ Intraovarial development is known to occur only in one other Echinoderm, *Chirodota contorta* Ludwig. (LUDWIG. Holothurien d. Hamburger Magelh. Sammelreise. 1898, p. 77—81.)

The fact the *Ophiomyxa vivipara* is among the most primitive Ophiurids might possibly be thought to have some bearing on the question of the origin of hermaphroditism in viviparous Ophiurids. Since, however, *Ophiotjalfa vivipara*, belonging to the most specialized Ophiurids, has also separate sexes (— so far as can be ascertained on the scanty material available —), that way to an explanation is closed. Also the fact that of the three viviparous *Ophiacantha* species one has separate sexes, the other is a protandric hermaphrodite, while the third is a true hermaphrodite, seems rather inexplicable. Upon the whole, I would regard the problem as insolvable at present. Most probably many more Ophiurids will be found to be viviparous; detailed researches on the sexual characters of these, together with researches on the sexual characters of Ophiurids in general may be necessary for discovering the reason, why hermaphroditism should be combined with viviparity especially in this class of Echinoderms.

January 31st 1920.

EXPLANATION OF THE PLATE I.

Fig. 1. Genital pieces and gonads of *Ophiomitrella clavigera*, from a specimen 3,5 mm. diameter of disk. The gonads are hermaphroditic, being essentially male, but with some few, young eggs. 85/1.

Fig. 2. Genital pieces and gonads of *Amphiura capensis*, showing the large, sausage-shaped testis at the adradial side, the ovary at the interradiial side. 30/1.

Fig. 3. Genital pieces and gonads of *Amphiura constricta*; the gonads are placed at the interradiial side only, proximally a testis, at the middle an ovary. 85/1.

Fig. 4. Genital pieces and gonads of *Amphiura vivipara*; showing one ovary, containing a very large egg, at the proximal end of the interradiial side and one testis at the adradial side. 60/1.

Fig. 5. Genital pieces and gonads of *Amphipholis japonica*, showing one small ovary at the interradiial and one small testis at the adradial side. 60/1.

Fig. 6. Proximal part of an arm of *Stegophiura vivipara*; the disk, stomach and bursae removed, so as to show the genital pieces and the gonads in their natural position: one testis at the proximal end and one ovary at the middle of the interradiial side, one or two ovaries at the adradial side of the genital slit. 30/1.

In all the figures the larger of the genital pieces represents the genital plate, with its condyles; the smaller the genital scale. The knob marked * serves as point of attachment for the adductor muscle.

