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CONTRIBUTIONS

TO

THE STUDY OF THE DEVELOPMENT AND LARVAL FORMS OF ECHINODERMS

I—II

BY

TH. MORTENSEN

WITH PLATES I—VII

D. Kgl. Danske Vidensk. Selsk. Skrifter, naturvidensk. og mathem. Afd., 9. Række, IV. 1.

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1931

In my work "Studies of the Development and Larval Forms of Echinoderms", 1921, I have expressed the hope of being able to carry on those studies, towards a solution, particularly, of the interesting problem: the relation of the larval forms to the classification of the adults. For this purpose it is of the greatest importance to have our knowledge extended to as many forms as possible; every additional species the larval form of which is made known means a strengthening of the basis of our conclusions.

Since the publication of the work quoted I have had some opportunities of continuing my researches on the development and the larval forms of Echinoderms, particularly on two Expeditions to the tropical Seas, viz. the Danish Expedition to the Kei Islands, 1922, and my Java-S.Africa Expedition, 1929—30.

During the expedition to the Kei Islands I stayed about one month at Amboina in a small place, Gelala, a little outside the town of Amboina, in a country house situated close to the shore of the Bay. I had there quite a good temporary laboratory, and quite good opportunities of undertaking studies of the numerous species of Echinoderms found in this place so famous for its rich marine life. Fertilization was made of quite a number of Echinoderms which were found to have ripe sexual products at the time, viz. *Linckia lævigata* (Linn.), *Oreaster* sp.?, *Echinostrephus molaris* (Blainv.), *Prionocidaris baculosa* (Lamk.), *Coelopleurus maculatus* A. Agassiz & H. L. Clark — but all with very poor results. The fertilization was all right, and the cleavage proceeded normally until the blastula stage was reached; some did not go any further, while others developed to free-swimming gastrulæ and to the formation of the larval mouth and the first appearance of the skeletal spicules, but none beyond that stage, in spite of the repeated starting of new cultures. The reason for this failure of all my efforts — which gave as the only result that these species have pelagic larvæ — must be sought in the water of the Amboina Bay being unsuitable for the rearing of larvæ, probably because the P_H is too low. It was found, to begin with, that the water used for the cultures very soon became swarming with Flagellates; I then used filtered water, but with no better results. The fact that Amboina is a volcanic island is probably the main cause of the unfitness of the water for rearing larval cultures — in accordance with my previous experiences at Hilo, Hawaii (cf. "Studies of the Development and Larval Forms of

Echinoderms", p. 7). In the vicinity of coral reefs the water is much more fit for embryological experimental work, no doubt on account of higher alkalinity (P_H); this has been my experience on former occasions, particularly at Tobago, B. W. I., and now again. First, at the Kei Islands. I had no time here to undertake the rearing of Echinoderm larvæ, but only just to make a test for comparison with Amboina. It turned out as expected. An attempt was made with *Astropyga radiata* and proved a perfect success, the embryos developing rapidly and quite normally to the first larval stage; had there been time, it would no doubt have been quite easy to rear them to the final larval shape — but this there was, unfortunately, not.

In July 1926 I spent about three weeks on the Bermuda Islands, where Professor E. L. Mark kindly gave me an opportunity of working at his Biological Station at Hamilton. I could not do much in the way of rearing Echinoderm larvæ, succeeding only in rearing *Diadema antillarum* till about the beginning of its transformation into the second larval stage, and in rearing the young larva of *Ophiocoma echinata*.

Next, on my Java-S.Africa expedition in 1929, I had again an opportunity of carrying on researches on Echinoderm development at another coral island, the little island of Onrust in the Java Sea, a few miles outside Batavia. I worked here from April 19th to May 10th. A very good laboratory was arranged here on the open verandah of one of the buildings serving to house the numerous Mohammedan pilgrims, who return annually (June—July) from Mecca and are put up here in quarantine for a while. The director of the establishment, Mr. Steinfurth, and the quarantine doctor, Mrs. Steinfurth, met me here with the greatest kindness and hospitality and made my three weeks' stay here one of the most delightful experiences of my life. It was my friend, Dr. Jan Verwey, of the Biological Laboratory, Batavia, who called my attention to this place; to his ever ready help and his thorough knowledge of all the small coral islands in the region and their biological conditions is due, in first line, the success of my work here. The Echinoderms, of which I succeeded in rearing the larvæ, were *Diadema setosum* (Gray), *Archaster typicus* M. Tr., *Acanthaster Planci* (Linn.) and *Ophiactis Savignyi* (M. Tr.), those being the only species ripe specimens of which could be obtained. I was particularly disappointed in not finding *Echinothrix* ripe. But the rearing of the larvæ of the four said forms may well be regarded as a most satisfactory result of a three weeks' stay. It is rather interesting to notice that the water was not very pure here, the island being very close to the muddy, Mangrove-clad shore of Java. Very probably its alkalinity must be high. Anyhow, the difference between the results obtained here and those (not) obtained at Amboina is very suggestive.

The next place where I could do some work of this kind, was Mauritius. I had there a very good temporary laboratory at a place called Cannoniers Point, some miles to the North of Port Louis, close to the shore by a large lagoon and coral reef with a very rich fauna of Echinoderms. I worked there from September 17th to October 27th, and got good cultures of the larvæ of the following species:

Diadema Savignyi (Mich.), *Echinothrix diadema* (Linn.), *Stomopneustes variolaris* (Lamk.), *Toxopneustes pileolus* (Lamk.), *Lytechinus verruculatus* (Ltk.), *Tripneustes gratilla* (Linn.), *Echinometra Michelini* (Desm.), *Culcita Schmiedeliana* (Retz.), and *Heterocentrotus mamillatus* (Leske).

The cultures, here as well as on Onrust, were reared in the same way as done by me on former occasions, viz. the larvæ being transferred to fresh sea-water every day, or every few days — no culture of food organisms being available. This, of course, is a very laborious way of rearing the larvæ. On Onrust, where this was the main purpose of my stay, I had time to do the work myself. But at Mauritius, where I had to spend a good deal of the time in deep-sea dredging or making trips to other parts of the island, it would have been quite impossible to rear all these cultures without some assistance. I am therefore exceedingly indebted to the Director of the Bacteriological Institute of Mauritius, Dr. Barbeau, who very kindly let one of his assistants, Mr. L. Webb, be at my disposal during my stay at Cannoniers Point. He proved a very able man, who soon learned to manage the cultures and could do the work by himself during my absence.

The larvæ here, on the whole, developed somewhat more slowly than I have found it to be the case in other places. I suppose the explanation of this fact is to be sought in the temperature being rather unusually low during the time I was staying at Mauritius. As a consequence of this slow rate of growth the larvæ had not yet reached their full shape by the time I had to leave Cannoniers Point and move to Port Louis. But as a temporary laboratory could also be established there, I moved all the cultures along with me to Port Louis, and they stood the transport excellently. It was then arranged that water for the transferring of the cultures should be taken daily well outside the harbour. The first morning after having transferred the cultures to this water, Mr. Webb sent for me, saying that it seemed to him the cultures looked somewhat peculiar. They did. Everything was dead. The water evidently had not been taken far enough outside and thus was polluted by the harbour sewage, which, on account of the constant S. E. wind, is driven far out to sea. It became evident that one would have to go miles outside the harbour to get pure water (whereas at Cannoniers Point the water was always taken, perfectly safely, directly at the sandy beach). But the harm was done, and thus the work carried out so laboriously throughout some six weeks was for the greater part spoiled, whereas it would have been sure to be a complete success if the work could have been continued at Cannoniers Point. It was particularly a pity with the cultures of *Echinothrix*, *Stomopneustes*, and *Culcita*, the larvæ of these types being hitherto entirely unknown. — Another great disappointment here at Mauritius was this that *Eucidaris metularia* and *Echinoneus abnormalis*, which were found in fair numbers on the reef, were quite unripe during the whole of my stay. Thus these two highly important types still remain unknown as regards their larval development. Also *Stylocidaris badia*, found in considerable numbers in deep water off Port Louis, was found to be unripe.

During my stay in Cape Town in December—January 1929—30 I had an opportunity of making fertilization of the characteristic South African Echinoid, *Parechinus angulosus* (Leske), in the Marine Laboratory of St. James. Not having the time to attend to the cultures because of dredging trips and other research work I did not get these larvæ beyond the first stage; but as this larva was hitherto entirely unknown, even this is a result of no small importance.

Finally, during my stay at St. Helena in February 1930 I could undertake fertilization of *Pseudoboletia atlantica* H. L. Clark; but — as in the former experiments at Amboina — the embryos did not develop beyond the gastrula-stage; St. Helena, like Amboina, is a volcanic island, so the reason may well be the same as there. *Eucidaris clavata* Mrtsn. and *Tretocidaris spinosa* Mrtsn., which were found in great numbers at St. Helena, proved to be unripe during the time of my stay.

The larvæ reared at Onrust and Mauritius, with the one from the Cape and the two from Bermuda, will form the subject of the first part of the present paper. In the second part I shall record observations on some Scandinavian Echinoderm larvæ. These observations were made as long ago as 1918, during a stay at the Swedish Zoological Station at Kristineberg. The main results of the observations made on that occasion were published in my paper "Notes on the development and the larval forms of some Scandinavian Echinoderms" (Vid. Medd. Dansk Naturh. Foren. Bd. 71, 1920); but a good deal more, and particularly a number of coloured figures, drawn after living specimens of the larvæ, could not be included in this paper, for various reasons, among which this that I was expecting soon to get an opportunity of extending these observations. There has, however, been no such opportunity, and as I do not see any prospect of getting it in the near future, I am publishing these obervations and figures which, although more than 12 years old, have not been made superfluous in the meantime through publications from other hands.

I beg to express my cordial thanks to all who have assisted me in these researches: to my friend Dr. Jan Verwey, Batavia, and to Mrs. and Mr. Steinfurth on Onrust; to Dr. Barbeau and Mr. L. Webb, Mauritius, and no less to the Authorities of Mauritius and the Danish Consul in Port Louis, Mr. Arthur McIrvine, for helping me to the excellent laboratory at Cannoniers Point. My heartiest thanks are also due to Dr. C. von Bonde, Cape Town, Director of the St. James Laboratory, Professor E. L. Mark, Harvard College, Director of the Biological Station, Bermudas, and to the then Directors of the Swedish Zoological Station at Kristineberg, Professor Hj. Théel and Dr. Hj. Østergren. But above all I am indebted to the two grand Danish Scientific foundations, the Carlsberg Fund and the Rask-Ørsted Fund, for enabling me, through their liberal grants, to undertake the above mentioned expeditions, to the Kei Islands, in 1922, and to Java, Mauritius, and South Africa, in 1929—30, thus giving me an opportunity of studying the various important types of tropical Echinoderms.

In the "Studies" I gave a list of all the various Echinoderms, the development of which had been made known, more or less completely, up till then. In the course of the nine years passed since the publication of the "Studies" quite a good deal of work has been done, augmenting considerably our knowledge of the normal development and the larval forms of Echinoderms. It may be useful to give here a short review of the work thus accomplished — but it may not be superfluous to state that it is not the purpose to include in this brief review the experimental work done on Echinoderm development and larvæ; it is only the normal development and the normal larvæ that concern us here.

Echinoidea.

D. H. Tennent ("Early Development and larval forms of three Echinoids of the Torres Strait Region". Carnegie Inst. Washington. Publication No. 391, 1929) describes the larva of *Salmacis virgulata Alexandri* Bell, reared to nearly full size, though not to the beginning of metamorphosis. The posterior transverse rod had not yet appeared. Important information is also given of the I. larval stage of *Echinometra Mathæi*, and some remarks on the development of *Peronella Lesueuri.*

Sven Runnström ("Eine neue Spatangidlarve von der Westküste Norwegens". Bergens Museums Årbok, 1929) describes a Spatangoid larva which he refers, it seems with full right, to *Brisaster fragilis* (Düb. & Kor.). On account of the large size and yolky condition of the eggs of this species I had suggested ("Handbook of the Echinoderms of the British Isles", 1927, p. 326) that it would have direct development, without a pelagic larval stage. Runnström's discovery that it has, in spite of the said condition of the eggs, a true Echinopluteus of the typical Spatangoid form, though without postero-lateral arms, is, therefore, of unusual interest. In another paper, "Über die Larve von *Strongylocentrotus dröbachiensis* O. Fr. Müller" (Nyt Magaz. f. Naturvidenskab. Bd. 65, 1927, p. 307—319) Sv. Runnström gives information of this larva, of which he has reared only the youngest stage, the later stages, up to metamorphosis, being found in the plankton.

Goniocidaris umbraculum (Hutton) and *Tropholampas Loveni* (Studer) have been found to be brood-protecting, thus having no pelagic larval stage (cf. Th. Mortensen. Goniocidaris umbraculum, a brood-protecting species. New Zealand Journ. Sc. and Technology. VIII. 1926; H. L. Clark. The Echinoderm Fauna of South Africa. Ann. S. Afr. Museum. XIII. 1923, p. 396).

Asteroidea.

Sv. Hörstadius ("Ueber die Entwicklung von Astropecten aurantiacus L". Arkiv för Zoologi. Bd. 18. B. 1926) has studied the development of *Astropecten arancíacus*, through metamorphosis. The larva has no Brachiolaria stage.

H. Heath ("The early development of a Starfish, Pateria (Asterina) mineata". Journ. of Morphology. Vol. 29. 1917) and H. H. Newman ("An experimental analysis of asymmetry in the starfish Patiria miniata". Biol. Bulletin. Vol. XLIX. 1925) have shown this Asterinid to have a typical pelagic larva, with a Brachiolaria stage. H. L. Osterud ("Preliminary observations on the development of Leptasterias hexactis", Publ. Puget Sound Biol. Station. II. 1918) has shown this species to protect its brood, as do *Leptasterias Mülleri, Henricia sanguinolenta* etc., there being no free-swimming larva.

Ctenodiscus australis Ltk. and *Trophodiscus uber* Diakonov have been found to be brood-protecting, thus having direct development (cf. I. Lieberkind. Ctenodiscus australis, a brood-protecting asteroid. Vid. Medd. Dansk Naturh. Foren. Bd. 82. 1926; A. Diakonov. Zwei neue Seesterne aus dem Westlichen Nordpacific. Ann. Mus. Zool. Acad. Sc. de l'URSS. 1926).

Ophiuroidea.

D. M. Fedotov ("Einige Beobachtungen über die Biologie und Metamorphose von Gorgonocephalus". Zool. Anzeiger. Bd. LXI. 1924) has shown that the embryos of *Gorgonocephalus arcticus* (Leach) and *eucnemis* (M. & Tr.) live in the polyps of the Alcyonarian *Gersemia* (or *Nephthya*) *conglomerata*. My own observation that the eggs of *Gorgonocephalus caput-medusæ* (L.) are shed free in the water and pass through a regular cleavage process into a typical gastrula ("Observations on some Echinoderms from the Trondhjem Fjord". Kgl. Norske Vidensk. Selsk. Skrifter 1923. Nr. 3. p. 14) tend to show that the embryos pass through a free swimming stage before entering the coral polyps.

A few Ophiuroids have been found to be viviparous (besides those mentioned in my paper "On Hermaphroditism in viviparous Ophiurids". Acta Zoologica. I. 1920), viz. *Ophiomyxa brevirima* H. L. Clark, *Amphiura annulifera* Mrtsn., *Pectinura cylindrica* Hutton, *Pectinura gracilis* Mrtsn. (cf. Th. Mortensen. Echinoderms of New Zealand and the Auckland-Campbell Islands. II. Ophiuroidea. III—V. Asteroidea, Holo thuroidea and Crinoidea. Appendix, p. 391. Papers from Dr. Th. Mortensen's Pacific Expedition 1914—16. XX, XXIX. Vid. Medd. Dansk Naturh. Foren. Bd. 77. 1924, Bd. 79. 1925); further *Ophioconis vivipara* Mrtsn. (Th. Mortensen. Echinodermes du Maroc et de Mauretanie. Bull. Soc. Sc. Nat. Maroc. T. V. 1925, p. 186). Three of these are also hermaphroditic, the first has separate sexes, whereas the last, *Ophioconis vivipara*, is uncertain as to its sexual character. Likewise *Amphiura Stepanovii* Tschern. has been found to be viviparous and hermaphroditic (D. M. Fedotov. Zur Morphologie einiger typischen, vorzugsweise lebendiggebärenden, Ophiuren. Trav. Labor. Zool. et Station Biol. Sebastopol. Acad. Sc. Leningrad. Ser. II. Nr. 6. 1926).

Holothurioidea.

Sv. Runnström ("Leptosynapta inhærens, en Holothurie med förkortad utveckling". Bergens Mus. Aarbok, 1923—24; "Ueber die Entwicklung von Leptosynapta inhærens (O. Fr. Müller)". Bergens Mus. Aarbok. 1927) has shown this Synaptid to have direct development, without an Auricularia stage — in spite of the very small size of the eggs. This very important fact shows that small size of the eggs is, per se, no proof of a development through a pelagic larval stage — just as the same author's discovery of the *Brisaster fragilis* larva shows that large, yolky eggs are no proof of direct development, without a pelagic larval stage. From the facts hitherto known it must be concluded that, as a rule, small eggs give rise to a typical pelagic larva, whereas large, yolky eggs indicate a direct development. But *Leptosynapta inhærens* and *Brisaster fragilis* show that there are exceptions to the rule.

Densaburo Inaba ("Notes on the development of a Holothurian, Caudina chilensis". Science Reports Tôhoku Imp. Univ. Sendai IV. Ser. Biol. Vol. V. 1930) has studied the development of the Japanese *Caudina* (— referred, in my opinion erroneously, to *C. chilensis* —) through metamorphosis, and found it to have no typical Auricularia stage. This is the first Molpadid the development of which has been studied.

H. Ohshima (Notes of the development of the sea-cucumber *Thyone briareus*. Science. Vol. LXI. 1925. p. 420—422) has studied the development of this Dendrochirote Holothurian and found it to have no free-swimming stage at all; the embryo on escaping from the egg membrane has already five tentacles and the first pair of pedicels.

C. Vaney in an excellent paper, "L'incubation chez les Holothuries" (Travaux de la Station Zoologique de Vimereux. IX. 1925) has given a complete record of all cases of viviparity or brood-protection in Holothurians known till then. Three more cases are added in the same year by Sven Ekman in his report on the Holothurians of the Swedish Antarctic Expedition (Further Zoological Results of the Swedish Antarctic Expedition 1901—1903. Vol. I. No. 6. 1925. Holothurien), viz. the three new species of the genus *Psolus, Ps. incubans, Ps. figulus,* and *Ps. punctatus.*

I may still mention a paper by J. Barrois: "Développement des Echinodermes, accompagné de quelques remarques sur l'origine des Procordés" (Ann. Sc. Nat. Zoologie. X. Série. VII. 1924), illustrated by 18 plates containing a great number of coloured, diagrammatic figures, of such puerile character that it seems rather outrageous to claim that this should be regarded as science. The text seems to me of no greater value than the plates. I merely wish to protest against his distinguishing two types of larvæ, *Palæopluteus* and *Neopluteus,* which rests only on ignorance of the whole subject. Further I would say that his "stade à larvenrest" is nothing but the larva in the process of metamorphosis. There is not the slightest reason for having a special name for this constantly changing "stage". From a linguistic point of view we may well wonder how Barrois could make himself write such a barbarism as "stade à larvenrest", "stade larvenrestien". If he could not himself translate into French that truly difficult German word "Larvenrest", he might, I am sure, have found help with many of his colleagues. Still, this case may, perhaps, not offend those English writers on embryology who can condescend to use the word "anlage", even in the plural form "anlages". I confess that such barbarisms make me angry.

A second paper by J. Barrois: "Mémoire sur les enchainements du développement Echinodermien, et sur les perspectives résultant de ces enchainements." (Ann. Sc. Nat. Zoologie. X. Sér. X. 1927), a continuation of the one quoted above, does not directly concern the subject of the present paper, so I can spare myself any discussion of it.

Finally a few remarks may be made on H. E. Ziegler's paper "Beiträge zur Entwicklungsgeschichte der Echinodermen" (Zool. Jahrb. Abt. f. Anatomie. Bd. 46. 1924. p. 521). He has there something to say about the nomenclature of the various arms or processes of Echinoderm larvæ, as also of the designations of the various parts of the skeleton of the Ophiopluteus and Echinopluteus, which I introduced in my work "Die Echinodermenlarven der Plankton-Expedition", 1898, a nomenclature which, latinized, is now generally used by students of Echinoderm larvæ. Ziegler acknowledges that "es wird dadurch eine einheitliche und vollständige Benennung eingeführt"; but he finds this nomenclature "nicht anschaulich und darum schwer zu merken" and therefore adopts a different nomenclature, which seems by no means to have any advantage over the one generally used. Ziegler evidently argues from the first stage of the *Echinocardium cordatum* larva, which he has reared. But for judging of the homology of the arms in the Ophiopluteus and Echinopluteus a broader outlook is required; it is not enough to know one species of larvæ in its I. stage; particularly, we must compare the fully formed larvæ, in which all the arms have been formed. If Ziegler had done so, he would have seen that the postero-lateral arms of Ophiopluteus must be homologous with the postero-lateral arms of Echinopluteus (— not yet present in the I. stage of the Echinopluteus —), not with the postoral arms. And even though we cannot homologize in details the skeleton of the Ophiopluteus with that of the Echinopluteus, there is no reason to doubt the homology of the arms situated in a corresponding place in the various types of larvæ.

I.

The Development and Larval Forms of some Tropical Echinoderms.

The species dealt with here are: *Diadema setosum* (Gray), *D. Savignyi* Mich., *D. antillarum* Phil., *Echinothrix diadema* (Linn.), *Stomopneustes variolaris* (Lamk.), *Toxopneustes pileolus* (Lamk.), *Lytechinus verruculatus* (Ltk.), *Parechinus angulosus* (Leske), *Acanthaster Planci* (Linn.), *Archaster typicus* M. & Tr., *Culcita schmiedeliana* (Retz.), *Linckia lævigata* (Linn.), *Ophiocoma echinata* (Lamk.) and *Ophiactis Savignyi* (M. & Tr.).

As in my work "Studies of the Development and Larval Forms of Echinoderms" my object is mainly that of making known the characters of the larvæ, whereas the cleavage, gastrulation, and the formation of the mesoderm, hydrocoel and other embryological processes are only occasionally described. According to the sweeping statement of MacBride ("Nature" March 10th, 1923, p. 324), this is not embryology. That depends upon what definition is given of the term "embryology"; MacBride himself includes the larval forms in his "Textbook of Embryology", so it would seem that even he cannot avoid the larvæ in embryology. But otherwise my object is, very deliberately and unswervingly, this: to study the larval forms, not humbly to offer some contributions in the hope of having them accepted as rightly deserving to be incorporated within embryology as defined by MacBride. When I observe anything in the strictly embryological processes which I find worth mentioning, I do so; in the case of *Diadema setosum*, I have, because of the extraordinary larval form, thought it desirable to describe also the first embryological processes — which do not, however, offer any unusual features —. But my main interest attaches to the larval form itself, and also to the postembryonal development. As to this latter point I am sorry the observations recorded here do not give any contribution, the rearing of the larvæ through metamorphosis requiring, as a rule, a much longer stay at the given place than the time allotted would allow.

1. Diadema setosum Gray. (Pl. I; Pl. II. Figs. 1—3).

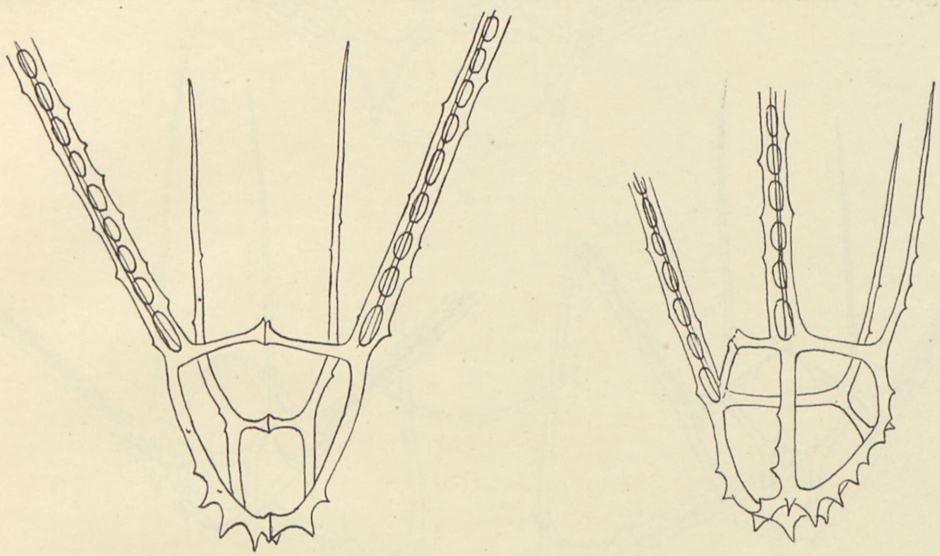
Whereas during my stay at Amboina in February 1922 not a single ripe specimen of *Diadema* could be found, although numerous specimens were opened, I found this species ripe during my stay at Onrust; not at once, though. On the first day of my stay, the 18th of April, I opened some fifty specimens, but only a pair of them had a trace of ripe eggs and sperma, not fit for fertilization, and I expected to be again disappointed in not being able to study the development of this important type. But on the 26th, when another lot of specimens were opened, several specimens were found to have excellent ripe sexual products, and artificial fertilization was made. Even later on, in the first days of May, when, after having found out how extraordinarily interesting this larva is, I thought it desirable to make a closer study also of the first developmental stages, I had no trouble in finding specimens with ripe sexual products so that new cultures could be started, — in marked contradistinction to my former experience, in April 1916, with *Diadema antillarum* (cf. Studies of the Development and Larval Forms of Echinoderms, p. 27).

The eggs are small, ca. 0.1 mm. or even a little less, clear, and the cleavage is perfectly regular, forming a very beautiful microscopical object. Immediately after fertilization the egg shows a distinct, clear outer layer — probably of lipoid nature — which remains distinct until the 8-cell stage (Pl. I. figs. 1—6). The blastula is formed in the course of ca. 5 hours, and in the course of ca. 7 hours the embryos have become free-swimming, showing already beginning formation of the mesenchyme (fig. 9). When about 16 hours old, the gastrulation begins and the first rudiments of the skeleton are formed (fig. 10), as also pigment begins to appear. In figs. 13—14, representing embryos 22 hours old, we may follow the further development of the two original spicules and ascertain the important fact that it is the lower edge of the gastrula which is being produced so as to form the first pair of larval arms, the postoral arms. In the stages represented in figs. 15—18 (25—32 hours old) the blastopore (or gastrula mouth) could no longer be distinctly seen; as a matter of fact it had the appearance of being closed; this would mean that the anal opening of the larva is not the direct continuation of the gastrula-mouth, but a new formation. This, however, would need to be verified on sections (for which I have no material).

In fig. 18, representing an embryo 32 hours old, the oral lobe has begun to appear, the body skeleton has assumed almost its full shape, and the antero-lateral rods have just begun to form; but there is still no mouth or anus. In the course of the second day the embryo has assumed the shape of the Echinopluteus in its first stage, in which it remains for about a week, increasing gradually in size, viz. mainly in the length of the postoral arms (Pl. I. fig. 19). The coloration consists of small irregular pink spots, distributed irregularly over the body; but there are a great number of these small pigment spots along the postoral ciliated band, a few in the middle of the postoral rod, and a very conspicuous accumulation of pigment at the end of each postoral arm.

The body skeleton of this first larval stage is a regular basket-structure (Text-figure 1). The body rods are rather coarsely thorny in the posterior part; the ventral transverse rods and the connecting rods between the recurrent rods are firmly united, distinctly widened at the end, where they join; they are perfectly smooth. The postoral rods are fenestrated in their whole length, moderately thorny.

The larva represented in Pl. I. fig. 19 is 8 days old. It shows some slight progress beyond the I. stage, in the postoral arms being somewhat widened in the middle, and also in the ciliated band being slightly produced, as if beginning to form vibratile lobes. (Also the very conspicuous suboral cavity should be pointed out.) In the skeleton two important changes are to be noticed, viz. that the body rods and the ventral transverse rods no longer join in the midline but are ending free (compare Pl. I. fig. 19 with textfigure 1. a). But there is no trace of new skeletal parts. Particularly one would expect the postero-dorsal rods to appear by this time; but nothing appeared, and watching the quite healthy looking larvæ the following



a. b.

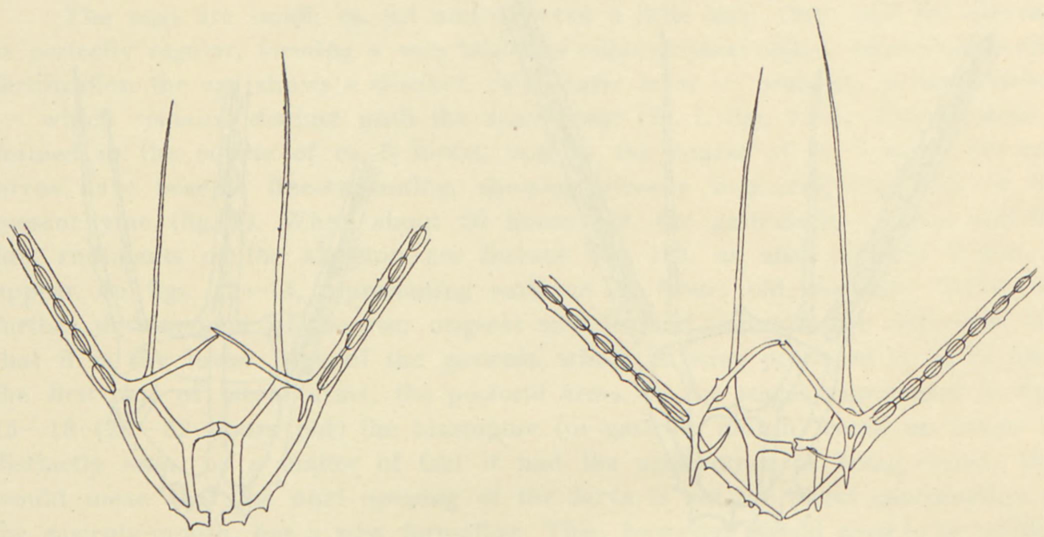
Fig. 1. Skeleton of the larva of *Diadema setosum*, in the I. stage. a. ventral aspect; b. side view. × 270.

days I was rather puzzled by this fact, until it became quite evident — the larvæ were then about 14 days old — that the larva was not to have any more arms, and that the Diadema-larva is identical with Echinopluteus transversus, that long known peculiar larva, with the enormous postoral arms, the parentage of which was till now a mystery.

The dissolution of the body skeleton (— in the stage represented in Pl. II. fig. 1 the union of the dorsal connecting rods has also been done away with —) results in the postoral arms, which were hitherto upwards directed, becoming more and more outward directed, until they are nearly horizontal. At the same time they grow conspicuously in length — in my farthest developed larvæ they had a length of ca. 2 mm.; they are very broad and flat as seen in Pl. II. fig. 3, which represents a larva seen from above. The antero-lateral arms do not grow in length — on the contrary, they gradually become reduced to short stumps, which fact tends to make the length of the postoral arms still more conspicuous.

The skeleton in this II. larval stage has assumed the structure so characteristic of *Echinopluteus transversus*, with the remarkable curved posterior transverse rod and the peculiar antler-like ventral — supplementary — transverse rods (textfig. 3. a—b). A small dorsal arch has also appeared, but postero-dorsal rods have not yet appeared; whether they will appear in later stages remains uncertain.

When I realized that the *Diadema* larva belongs to the type of *Echinopluteus transversus* it was too late to follow in all details the extraordinary transformation that must take place to change the typical basket-skeleton of the I. stage into the highly specialized skeleton of the fully formed larva. But fortunately some pre-



a. b.

Fig. 2. Skeleton of larva of *Diadema setosum* in transition from the I. to the II. stage. × 230.

served samples give important information of the way in which the change is produced. The first change that occurs is that seen in Pl. I. 19: the dissolution of the ends of the body rods and of the ventral transverse rods; only the dorsal connecting rods still remain joined together, but the body skeleton is now no longer a quite immovable basket as in the younger larva (Fig. 1). The next change is seen in fig. 2. a — it consists in the appearance of a small, posteriorly directed process from the base of the ventral transverse rods; this is the beginning of the ventral recurrent rods. In the next stage, fig. 2. b, more important changes have occurred: the ventral recurrent rods have grown considerably and have got a conspicuous, curved, medially directed branch, the supplementary ventral transverse rod; the ends of the body rods have dissolved so far that the connection with the (dorsal) recurrent rods is discontinued; also the joining of the connecting rods is about to be dissolved. The ventral transverse rods seem to have grown somewhat in length. In Pl. II. 1, the ventral transverse rods are evidently in incipient resorption, otherwise this larva must have been in a stage corresponding to that shown in fig. 2. b. I have no samples showing the transition to the stage shown in fig. 3. a, b. — where the supplementary ventral transverse rods have assumed the characteristic antler-shape, whereas the original ventral transverse rods have totally disappeared; the body rods and the dorsal recurrent rods are reduced to short thorns, one of the latter still showing the rest of the connecting rod.

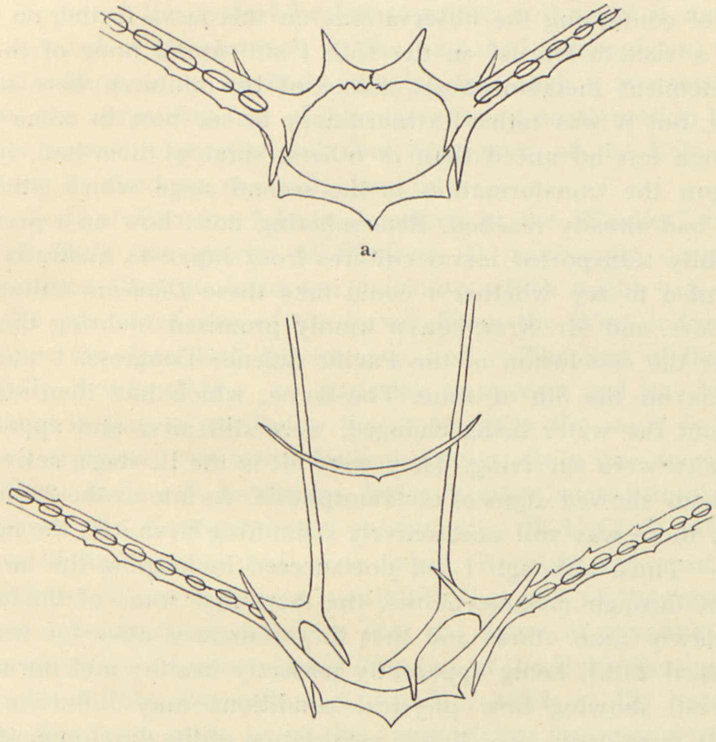


Fig. 3. Skeleton of the larva of *Diadema setosum* in the II. stage. a. from the ventral, b. from the dorsal side. × 270.

The remarkably well developed muscular system found in *Echinopluteus transversus,* led me ("Studies", p. 79) to the suggestion that this larva must swim actively by moving the long postoral arms — and the observation of the living larvæ gave the proof that it actually does so. The movements are rather quick, rhythmical, but generally only few, some 6—8 beats at a time; then the movements stop and the larva floats with its long arms stretched out horizontally. The swimming of this larva on the whole strikingly recalls that of some small Hydromedusæ of the *Obelia*-group. They are a very fascinating sight, these actively swimming larvæ — also a somewhat curious sight, the stiffness of the arms and the rapidness of the movements producing a peculiar automatical appearance, recalling the movements of puppets. — In the sea this swimming must, of course, be useful in keeping the larva floating; in the jars in which I had my cultures, with still-standing water, the larvæ, however, were lying at the bottom, and they could not raise themselves from the bottom by means of their swimming movements. (Lying at the bottom did not interfere with the health of the larvæ — as has been my experience also with other cultures of Echinoderm-larvæ).

As I had to leave Onrust already on the 10th of May there was, unfortunately, no possibility of continuing the observations on this larva further on through metamorphosis. At a visit to Onrust on the 15th I still found none of the larvæ showing signs of incipient metamorphosis. Some of the cultures were still in a fairly good condition, but it was rather extraordinary to see how in some of the jars the larvæ were much less advanced than in others; some of them had, indeed, by that time only begun the transformation to the second stage which others, of exactly the same age, had already reached. Remembering now, how on a previous occasion I had successfully transported larval cultures from Japan to Australia (cf. "Studies" p. 7—8) I wanted to try whether I could take these *Diadema* cultures along with me to Africa. Mrs. and Mr. STEINFURTH kindly promised to bring them onboard to me when, after the conclusion of the Pacific Science Congress, I was to leave Batavia. This was on the 8th of June. The larvæ, which had then stood for nearly a month without the water being changed, were still alive and apparently healthy, though not many were surviving. They were all in the II. stage, actively swimming, but none of them showed signs of metamorphosis. As late as the 22nd of June, halfway to Africa, there was still one, actively swimming larva left; the next day all had disappeared. — Thus, although I did not succeed in keeping the larvæ any longer, or getting them through metamorphosis, the facts that some of the larvæ developed much more slowly than others and that they remained alive for nearly 2 months (fertilization April 25th), being apparently perfectly healthy and normal, are of considerable interest, showing how physical conditions may influence the speed of development. It is evident, also, that a retardation of the development must increase the possibilities of the larvæ for transport by means of the currents, and thus be of importance to the geographical distribution of the adults of the species. (Cf. similar observations on the larva of *Tropiometra* in my "Studies in the Development of Crinoids." Publ. Carnegie Inst. No. 294, p. 14).

The larva of *Diadema setosum* shows considerable likeness to the species *f* of *Echinopluteus transversus*, described and figured in my "Studies on the Development and Larval Forms of Echinoderms" p. 91, Pl. XIII. 3—4, with which it agrees particularly in the very characteristic shape of the supplementary transverse rods. Perhaps it is even the same; the differences to be observed on comparing the skeletal structure of the two larvæ (cf. fig. 3 of the present paper with fig. 36, p. 91 of the "Studies") might well be accounted for through the different age of the two larvæ, the said species *f* of *Echinopluteus transversus* being in a far advanced stage of metamorphosis, whereas the larva figured and described in the present paper has not yet begun to show signs of metamorphosis. The locality where the "species *f*" was found, off Minicoi, Maldive Islands, would be in good accordance with the identity of the two larvæ, as *Diadema setosum* very probably occurs also at the Maldive Islands.

The riddle, to which Echinoid *Echinopluteus transversus* belongs, has thus finally been solved — and it was certainly a surprise to me that its parentage was to be found in *Diadema*. When, in 1916, I had found the body skeleton of the young *Diadema*-larva to be of the typical basket structure, I thought it therewith proved that *Diadema* was out of the question as the parent of *Echinopluteus transversus* (cf. "Studies", p. 92). How could anybody imagine that such a transformation was to take place? But the surprising fact of the marvellous transformation has been established. Remains now the question whether all larvæ of the *Echinopluteus transversus*-type belong to *Diadema* or to Diadematids.

From the Gulf of Panama I have described in the "Studies" two such larvæ species *b*. and *d*. Only one species of *Diadema*, *D. mexicanum*, occurs in the Gulf of Panama; but then there is *Astropyga pulvinata*, which might well come into consideration as the parent of one of the larvæ. From the West Indies three species of this larval type are described, species *a*, *c*, and *e*. The first of these has not yet the skeleton fully developed (— no posterior transverse rod has been formed as yet —), and there is thus a possibility that it is really the same as species *c*; but *c* and *e* at least represent two quite distinct species. Only one species of *Diadema* occurs in the West Indies, *D. antillarum*, but one other such littoral Diadematid is known from there, viz. *Centrostephanus rubricingulus* H. L. Clark. Although only a single specimen of this species has been found, it exists and must, no doubt, be plentiful somewhere. There is thus a possibility that one of the two *Echinopluteus transversus*-larvæ belongs to that species. But the figure of a young larva of *Eucidaris tribuloides* given by TENNENT in his "Studies of the Hybridization of Echinoids, Cidaris tribuloides" (Publ. Carnegie Inst. No. 312. 1922; p. 12) hardly leaves any doubt that also this larva must be of the *Echinopluteus transversus*-type. It is, therefore, quite possible that one of the larvæ of this type, which I have described from the West Indies, will prove to belong to *Eucidaris tribuloides*. It would be highly remarkable to find in two so widely different families as the Cidaridæ and the Diadematidæ the same highly specialized larval type. Appearances certainly point this way — but we may well leave the discussion of the case, until it has been definitely proved to be so.

2. Diadema antillarum Phil.

During my visit to Bermudas in July 1926 I had for the second time an opportunity of undertaking artificial fertilization of this species. I got the larvæ a little farther than on the former occasion (at Tobago, B. W. I. in April 1916; cf. "Studies", p. 25), so far that the shape of the body began altering, the postoral arms widening in the basal part, the postero-lateral corners of the ciliated band being somewhat downwards produced and the body widening at the level of these corners, then narrowing again towards the posterior end (fig. 4). But the body skeleton had not yet begun to dissolve, and this larva could, therefore, not yet give any suggestion of the transformation of this quite typical larva into the shape of *Echinopluteus transversus*. The larva has a very conspicuous accumulation of red pigment in the tip of the postoral arms and a few irregularly scattered spots of the same colour in the body and the widened part of the postoral arms.

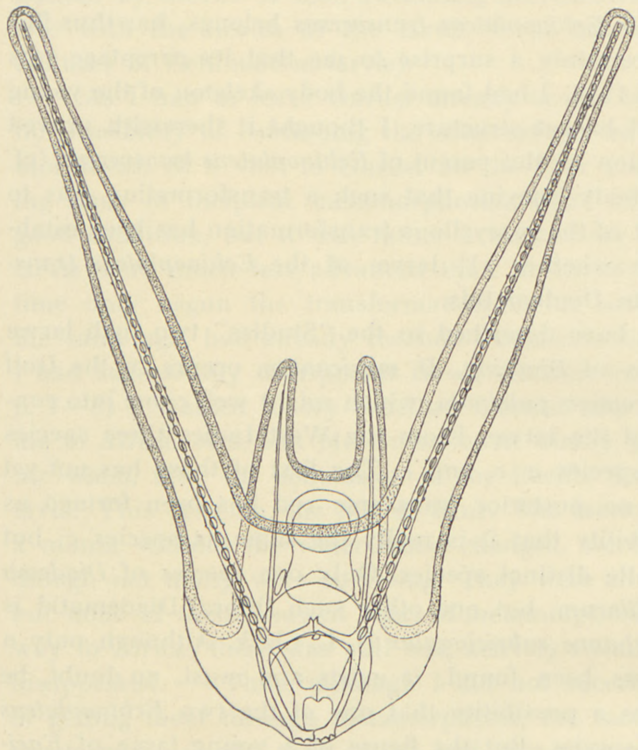


Fig. 4. Larva of *Diadema antillarum* I. stage. × 160.

3. **Diadema Savignyi** Michelin.

This species I found to be ripe during my stay at Cannoniers Point, Mauritius, and fertilization was undertaken on the 1st of October.

The eggs are very small, somewhat opaque. The 8-cell stage was reached after 2 hours. A clear outer layer is formed after fertilization as in *D. setosum*, remaining distinct until the blastula stage, which was reached in the course of five hours. 24 hours old the embryos were beautiful, free-swimming blastulæ, with fine mesenchyme, but still with hardly an indication of gastrula formation; at the age of 30 hours they were beautiful, typical gastrulæ, very clear and transparent. The first rudiments of the skeleton were found when the embryos were 2 days old; when 4 days old, the embryos were young plutei. These had from the beginning the postoral arms more diverging than in *D. setosum*, so that it had almost the appearance that the larvæ would pass directly into the *Echino-*

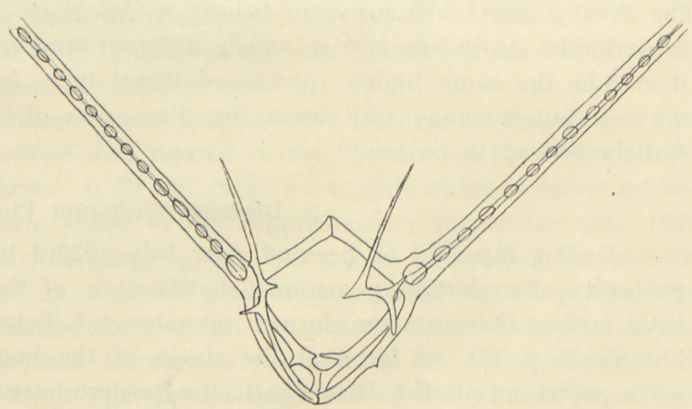
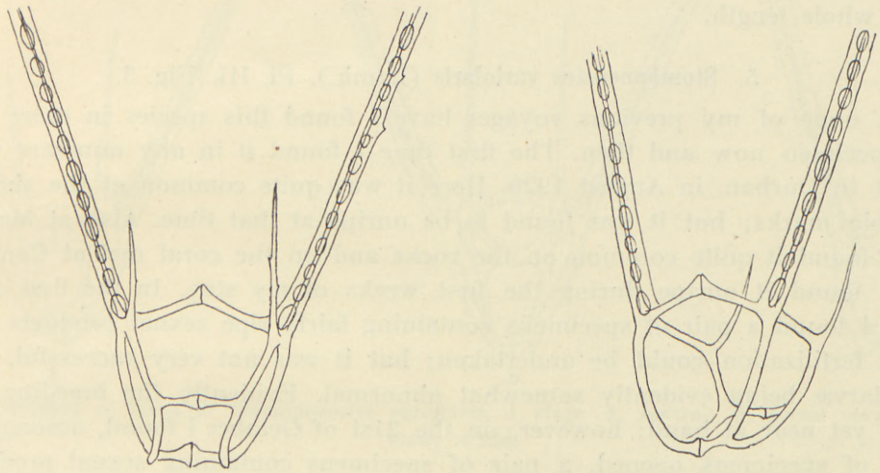


Fig. 5. Skeleton of larva of *Diadema Savignyi*. × 230.

pluteus transversus-shape. Also the body skeleton was more complicate than in the I. stage of the *D. setosum* larva. Although the larvæ went on growing apparently normally for nearly two weeks, they did not show any signs of further development. I am, therefore, inclined to believe that these larvæ were not quite normal and shall therefore confine myself to giving a figure of the skeleton of a two weeks old larva (fig. 5), leaving it to future researches to show whether it is normal or not — and to show how the fully formed larva differs from the larva of *D. setosum*.

4. Echinothrix diadema (Linn.). Pl. III. Fig. 1.

This species — or the other species of the genus, *E. calamaris* — I had never found ripe before, though numerous specimens were examined at Amboina in Febru-



a. b.

Fig. 6. Skeleton of larva of *Echinothrix diadema*, I. stage. a. from the dorsal side; b. in side view. × 230.

ary 1922, at Java in August 1922, and again at Java (Onrust) in April—May 1929. On my arrival at Cannoniers Point, Mauritius, it was also found unripe. It was not until the 19th of October that I succeeded in finding a few ripe specimens, which could be used for artificial fertilization.

The eggs are small, ca. 0.1 mm., not very clear. There is a clear outer layer to be observed on the eggs after fertilization and in the first cleavage stages, such as is found in *Diadema*, though somewhat less conspicuous. In general it is distinct only where it makes a bend between the cleavage cells, the space between it and the egg-membrane thus becoming larger (cf. the young cleavage-stages of *Diadema setosum*, Pl. I). The cleavage is beautifully regular; the 2-cell stage is found 1 hour, the 4-cell stage 2 hours after fertilization. 7 hours after fertilization the embryos were in the blastula stage, though as yet not rotating within the egg-membrane. At the age of 24 hours the embryos were gastrulæ, with beginning formation of the skeleton and of pigment. 2 days old they were plutei of typical I. stage form. They were evidently quite normal and healthy, but had not begun to show signs of transformation into the II. stage, when, on the 29th — thus 10 days old — they were transferred to Port Louis. The most unfortunate destruction of the larval cultures there, through polluted water, prevented the solving of the most important question whether the fully formed *Echinothrix*-larva is also of the *Echinopluteus transversus*-type, like the *Diadema*-larva, and I can thus only give information of the I. stage of this larva.

As seen from Pl. III. fig. 1 the young larva is of the usual form, showing no special features. It is only slightly pigmented, there being only an accumulation of reddish pigment in the tip of the postoral arms. The body skeleton (Fig. 6. a—b) is of the typical basket structure, very smooth. The postoral rods are fenestrated in their whole length.

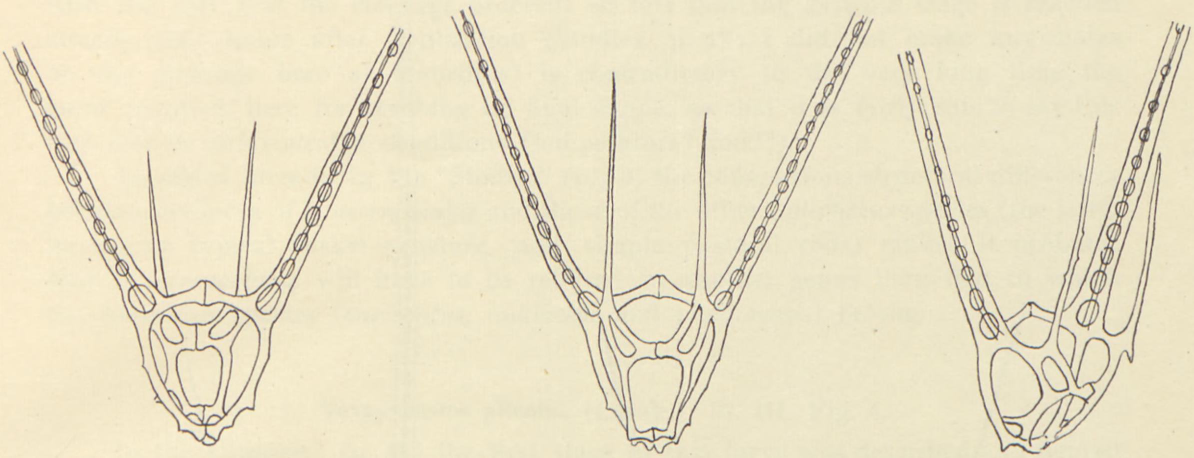
5. **Stomopneustes variolaris** (Lamk.). Pl. III. Fig. 3.

On none of my previous voyages have I found this species in more than a single specimen now and then. The first time I found it in any numbers was on my visit to Durban, in August 1929. Here it was quite common at the shore, between tide marks; but it was found to be unripe at that time. Also at Mauritius, where I found it quite common on the rocks and on the coral reef at Cannoniers Point, I found it unripe during the first weeks of my stay. In the first days of October I found a pair of specimens containing fairly ripe sexual products so that artificial fertilization could be undertaken; but it was not very successful, the resulting larvæ being evidently somewhat abnormal. Evidently the breeding season was not yet near at hand; however, on the 21st of October I found, among a great number of specimens opened, a pair of specimens containing sexual products in good condition, though they were not yet ripe enough for shedding sperma and eggs by themselves. The fertilization made from these specimens proved very good and gave rise to an excellent culture of the *Stomopneustes*-larva.

The eggs are very small, scarcely 0.1 mm., very opaque, whitish, the fertilization membrane standing very little off from the surface of the egg. The 2-cell stage was reached two hours after fertilization; after 7 hours the embryos were in the 32—64 cell stage. The cleavage is regular, but on account of the opaqueness of the eggs the details of the cleavage could not be seen distinctly on the living object. 30 hours after fertilization the embryos were free-swimming blastulæ, very intransparent, still without incipient gastrula formation. Two days old they were gastrulæ, with some peculiar large, yellow mesenchyme-cells, but still without skeletal rudiments, which did not appear until the third day. These observations are from the first culture. In the second culture the development proceeded much faster, the embryos reaching the gastrula stage in the course of one day, and being young plutei already on the second day.

Also the young plutei were very intransparent, so that it was rather difficult to see the skeleton distinctly, and no less difficult to make out the internal structure of the larva. As a matter of fact I thought at first that the larva would prove to be more or less rudimentary, somewhat like the larva of *Peronella Lesueuri* (cf. "Studies", p. 109); but gradually the oesophagus and mouth became distinct, and, as seen from Pl. III. fig. 3, the larva in the I. stage is of typical shape and structure, and as transparent as most other larvæ at a corresponding stage (the larva figured is 6 days old).

The culture was in excellent condition, containing numerous fine and normal



a. b. c.

Fig. 7. Skeleton of larva of *Stomopneustes variolaris*, I. stage. a. ventral; b. dorsal view; c. side view. × 230.

larvæ, when on the 28th it was, together with the other larval cultures, removed to Port Louis — to be destroyed by the polluted water. It would have been of the greatest interest to see what the fully formed larva of this isolated type of Echinoids looks like, but this must be left for future researches.

The first stage does not, in shape and general structure, offer anything of unusual interest (Pl. III. fig. 4). The skeleton (fig. 7. a—c) is of the Echinometrid type, the recurrent rod being double and there being two meshes on each side of the body. The posterior part of the body-rods is somewhat thorny. The postoral rods are fenestrated; in the distal part the holes become gradually smaller and more distant, and it is therefore probable that in the older larvæ these rods, on growing longer, will be unfenestrated in their distal part.

6. **Lytechinus verruculatus** (Ltk.) Pl. III. Fig. 2.

In the "Studies" (p. 42) I could only give the information about the larva of this species (reared at Hilo, Hawaii) that its body skeleton in the I. stage is of the typical basket-structure, no figures being given. During my stay at Cannoniers Point, Mauritius, I could again undertake artificial fertilization of this species and rear the larva to the beginning transition to the II. stage, the culture being then destroyed with all the other fine cultures after the transport to Port Louis. I can thus

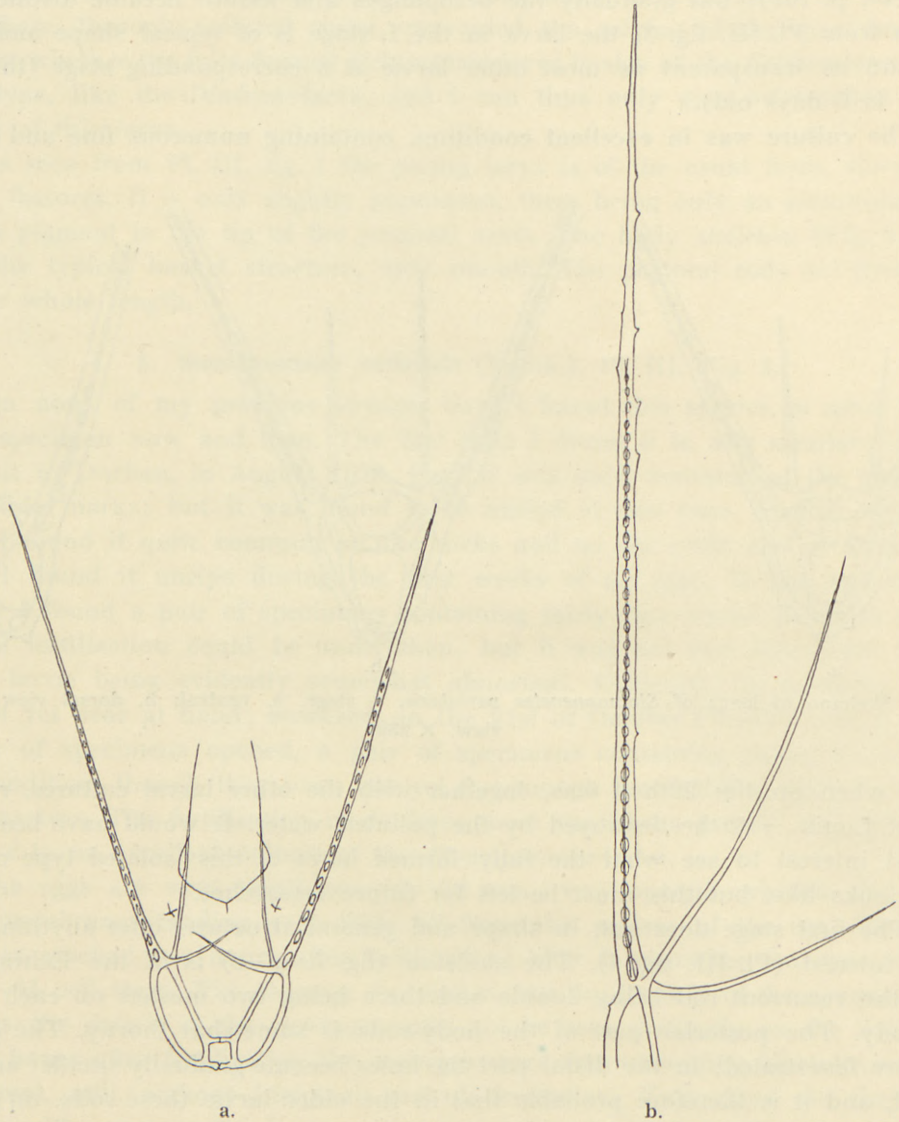


Fig. 8. Skeleton of the larva of *Lytechinus verruculatus*, I. stage. a. ventral view. × 125. b. the postoral rod, antero-lateral and ventral transverse rod. × 230.

as yet make known only the I. stage of this larva (Pl. III. 2). There is nothing especially noteworthy in the shape of the larva, which is of the form typical of the larvæ with basket-structure. The widening on the postoral arms indicates that it is about to transform into the second stage. There are only scattered pigment spots, no accumulation of pigment at the end of the arms.

The postoral rods are fenestrated, with very small holes, in the proximal two thirds, the distal third being a simple rod (fig. 8). In a larva, preserved when 28 days old, the dorsal arch and the postero-dorsal rods have begun to appear, the latter being apparently simple. The body skeleton has not yet begun to dissolve, and, accordingly, there is no trace of the posterior transverse rod as yet. Probably this larva has not normally so slow a rate of development (cf. the observations on the differences in the rate of development in the larva of *Diadema setosum*, p. 15). Also the fact that the cleavage proceeds so fast that the gastrula stage is reached already four hours after fertilization (Studies, p. 42; I did not make any notes on the cleavage here at Mauritius) is contradictory to the very long time the larva required here for reaching its final shape, so that it is fairly safe to say this was due to unfavourable conditions (temperature? food?).

As stated already in the "Studies" (p. 43) the conspicuous structural differences between the larva of *L. verruculatus* and those of the other *Lytechinus*-species (the latter having no typical basket-structure, and simple postoral rods) makes it probable that *L. verruculatus* will have to be referred to another genus than that to which the American species (*variegatus*, *anamesus* and *panamensis*) belong.

7. **Toxopneustes pileolus** (Lamk.). Pl. III. Fig. 4.

In the "Studies" (p. 43) the first stage of this larva was described and figured (Pl. VIII. 8). It was found that, at Misaki, larvæ nearly three weeks old had scarcely begun to change into the second stage. Here, at Cannoniers Point, Mauritius, a culture was started on September 25th, the larvæ living in good condition until October 29th, when they were killed by the polluted water from off Port Louis. Though thus nearly five weeks old they had not yet reached their full shape. The postero-dorsal arms had appeared, but evidently not yet reached anything like their normal length; also the preoral arms were about to appear, and the body about to assume the shape of the second stage, with its lobes and folds (Pl. III. Fig. 4). In a larva examined on the 19th of October, thus 24 days old, I noticed that the body skeleton had begun to dissolve, but that a posterior transverse rod had not yet been formed. In the specimen drawn from life, 27 days old, the body rods were still in connection at the posterior end. The postero-dorsal rods are simple.

It was, of course, a great disappointment to me that this fine culture of larvæ should be killed just before the final touch — the formation of the posterior transverse rod. — The fact that the larva proved to be so slow in its development, both in Japan and in Mauritius, need not mean that it is always so. Both these localities are at the limits of the distribution of this Echinoid. It is quite possible that in seas with a higher temperature (and a richer food supply) the development will proceed with greater speed.

8. **Tripneustes gratilla** (Linn.). (Pl. III. Fig. 5).

Fertilization of this species was undertaken at Cannoniers Point, Mauritius, on the first day of my stay there, the 17th of September. The culture, however, died off after the embryos had reached the gastrula stage, so a new culture was started on the 19th. The small eggs are fairly clear and transparent, but, on the whole, it is not a very good object for studying the cleavage. The fertilization membrane is very indistinct, lying close to the surface of the egg, which it follows at the first cleavage, so that it is difficult enough to see whether there is a membrane at all. The first cleavage occurred two hours after the fertilization, the 4- and 8-cell stages were found after about 5 hours. The gastrula stage was reached one day after fertilization, the gastrulæ being very clear, showing a beautiful arrangement of the mesenchyme cells. Three days after fertilization the embryos were beautiful plutei in the I. stage, as I had formerly found it on Hawaii, with basket-structure and fenestrated postoral rods ("Studies", p. 34). On the 13th of October I noticed that the larvæ, now 24 days old, did not yet show any sign of transformation into the II. stage, in regard to the skeletal structure, whereas the body was beginning to form folds, sign of the beginning of the II. larval stage. On the 19th — 30 days after fertilization — finally, the body skeleton had begun dissolving, the dorsal arch and the first rudiments of the postero-dorsal rods had just appeared. The larva represented in Pl. III, fig. 5 (after a sketch from life by Mr. Webb) is 32 days old; here neither dorsal arch nor postero-dorsal rods are found, this specimen thus not being among the very most advanced of the larvæ. On the 27th not one of the nearly 200 larvæ still left in the culture was found to have postero-dorsal rods or the dorsal arch — and then the culture perished with the others after being transferred to Port Louis.

The results regarding this larva are thus not very satisfactory, the final stage not having been reached, although the larvæ lived for more than 5 weeks. The larva represented in Pl. III. fig. 5 makes it probable that the fully formed larva will be found to resemble that of *Tripneustes esculentus* ("Studies", Pl. II). Whether the structure of the postoral rod is like that of the *Tr. esculentus*-larva (Studies, fig. 7; p. 34), the fenestration disappearing towards the end of the rod, I cannot say; the sketch by Mr. Webb is not sufficiently detailed to show this character, and — not remembering this character of the *Tr. esculentus*-larva, and not having brought my "Studies" along with me — I did not look out for it, and none of these larvæ were preserved. The fact that I had so much other work to do, must be my excuse for neglecting to look out properly for this character.

I can hardly doubt that the very slow development of this larva at Mauritius is abnormal, due, perhaps, to the temperature that year being rather unusually low and to the food supply of the cultures being too scarce — particularly to the latter cause, I suppose, as the species occurs numerously as far south as the Natal Coast (Durban), where the temperature must be somewhat lower than at Mauritius.

The cultures of *Echinometra mathæi* and *Heterocentrotus mamillatus* at Mauritius did not succeed so far as to give any results worth mentioning. Some sketches of the larvæ made by Mr. Webb are not detailed enough to give reliable information about the skeletal structures, and none of the larvæ were preserved. I think it better, therefore, to omit these larvæ from the present paper.

9. **Parechinus angulosus** (Leske).

Fertilization of this species was undertaken repeatedly at the marine laboratory in St. James, Cape Peninsula, in December 1929 and January 1930. As I had no time to attend to the cultures, it is no wonder that none of the larvæ survived the I. stage. This stage, however, is important enough, showing that this larva resembles those of the genera *Psammechinus* and *Echinus*, in accordance with what was to be expected from the conclusion reached in my "Studies", viz. that the larvæ of nearly related forms are essentially alike, so that the classification of the larvæ corresponds with that of the adult forms — if that classification be a natural one — expressing their true affinities.

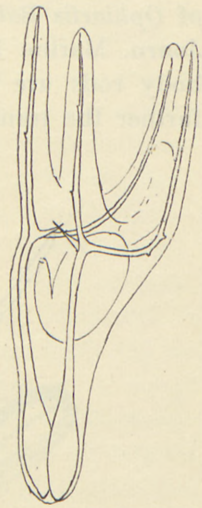


Fig. 9. Larva of *Parechinus angulosus*, I. stage. × 230.

The eggs are somewhat reddish; the fertilization membrane is very distinct. The first cleavage took place after $^1/_2$ hour; after 4 hours the blastula stage was reached, and ca. 30 hours after fertilization the embryos were small plutei.

The larva (fig. 9) has elongate, clubshaped, very smooth body rods, the body being correspondingly elongate. There is no trace of a recurrent rod. There are some scattered yellow pigment cells; some specimens have a slight accumulation of faintly purple pigment in the posterior end of the body. That the larva in the II. stage will conform with the *Echinus* and *Parechinus* larvæ, having epaulettes but no posterior transverse rod, I have no doubt — but it will be of great importance to have it actually confirmed.

10. **Ophiactis Savignyi** (Müller & Troschel).

During my stay on Onrust I found on the 19th of April some specimens of this species, living in a sponge; as they proved to have ripe sexual products, I set them aside in a dish, hoping that they might shed their eggs and sperm. And so it happened, though to a small extent only. The culture thus obtained was only a very small one, and not very successful; but a few of the eggs developed normally. Two days after fertilization the embryos, which were rather intransparent, yellowish-green, were beginning to form arms; on the third day they were normal small plutei. Only two of the larvæ survived till the 27th, thus being one week old. They were well formed Ophioplutei, of quite typical shape, with the arms moderately broad, and a faint yellow tinge in the tips of the postero-lateral arms and the posterior end of the body.

The skeleton (fig. 10) is of the type with double recurrent rod, as in the larva of *Ophiactis Balli* (cf. my paper "On the Development of some British Echinoderms". Journ. Marine Biol. Assoc. X. 1913, p. 12; fig. 13), only rather more robust; the body rods are somewhat thicker and more curved, and the end-rods are shorter; further the transverse rods are so short as to be almost non-existing.

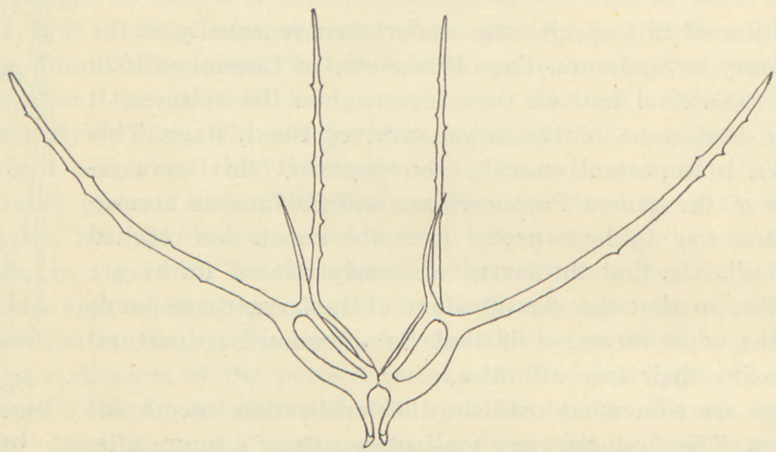


Fig. 10. Skeleton of larva of *Ophiactis Savignyi*. × 270.

It is very satisfactory that it has thus been proved that at least two of the species of the great genus *Ophiactis* have the same type of larvæ, a fact which lends support to the view set forth in my "Studies" (p. 213—214) that also in Ophiurids the larvæ have an important bearing on classification.

11. **Ophiocoma echinata** (Lamk.).

During my stay at Bermuda in 1926 I found on the 9th of July some specimens of *Ophiocoma echinata* in very ripe condition. When put into a dish they shed their eggs and sperm, and fertilization followed directly. As it was late in the evening I could not follow the cleavage process, only noticed that the egg-membrane seemed to be strongly spiny; this is in accordance with the observation by CASWELL GRAVE ("Embryology of Ophiocoma echinata, Agassiz." John Hopkins University Circulars. No. 137. 1898; cf. "Studies", p. 131) who found that the fertilized eggs "threw about themselves a tough, prickly egg membrane". The suggestion that this membrane serves as a floating apparatus (Op. cit.) thus still lacks verification through actual observation.

At the age of 2½ days the embryos were young plutei, showing the skeletal structure typical of the *Ophiocoma*-larva (Fig. 11). At the age of 6 days they had reached the shape shown in fig. 57 of my "Studies", from a sketch by CASWELL

Grave of a larva $11^1/_2$ days old; only the arms were found more broadly rounded at the ends than shown in the figure quoted. (Fig. 11. b, to be compared with fig. 57 of the "Studies", p. 131). The ciliated band was of a faint yellowish colour, somewhat stronger in the arm tips.

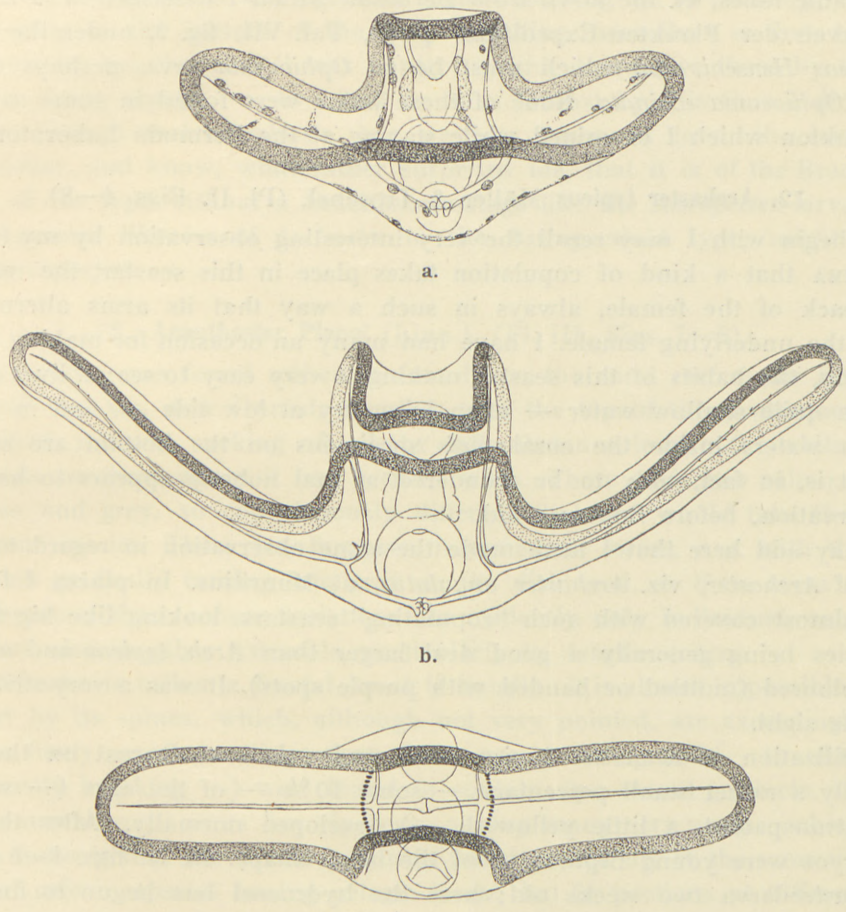


Fig. 11. Larva of *Ophiocoma echinata*. a. $2^1/_2$ days old; b. 6 days old; c. larva 3 days old, seen directly from above, showing the two nerve bands. × 150.

On examining the larva directly from above — which is easy enough, this remarkably broad larva usually floating in a vertical position directly under the surface (— in the quiet water of the dish; in nature it will, of course, rarely be able to assume that position —) — one sees the nervous system very distinctly, in the shape of a series of nuclei on each side of the stomach (Fig. 11. c). This is in perfect accordance with the observations on the nervous system in Ophiurid larvæ which I have published elsewhere (cf. my paper "Notes on the Development and the Larval Forms of some Scandinavian Echinoderms". Vidensk. Medd. Dansk Naturhist. Forening. Bd. 71. 1920. p. 158—160).

As the larvæ did not live for more than 7 days, they did not nearly reach their full shape, which must be of great beauty, the *Ophiocoma*-larva being provided with vibratile lobes, cf. the larva from Bermuda which I described in "Die Echinodermenlarven der Plankton-Expedition" p. 62, Taf. VII, fig. 2, under the name of *Ophiopluteus Henseni*, and which must be an *Ophiocoma*-larva, perhaps even the larva of *Ophiocoma echinata*. None of these larvæ were found in some samples of fresh plankton which I examined while staying at the Bermuda Laboratory.

12. **Archaster typicus** Müller & Troschel. (Pl. II. Figs. 4—8).

To begin with I may recall the very interesting observation by my friend Dr. H. Boschma that a kind of copulation takes place in this seastar, the male lying on the back of the female, always in such a way that its arms alternate with those of the underlying female. I have had many an occasion for making the same observation, the habits of this seastar making it very easy to see: it lives on sandy bottom in quite shallow water — often lying dry at low tide —, and in the clear and calm waters inside the coral reefs specimens on the bottom are seen very clearly; it is, in fact, only to be wondered at that nobody appears to have made this observation, before Boschma did.

I may add here that I have made the same observation in regard to another species of *Archaster*, viz. *Archaster angulatus*, at Mauritius. In places I found the bottom almost covered with such "copulating" seastars, looking like big Solasters, this species being generally a good deal larger than *Arch. typicus* and also more highly coloured (mottled or banded with purple spots). It was a very striking, unforgettable sight.

Fertilization of *Archaster typicus* was undertaken at Onrust on the 21st of April; only a rather small percentage — some 10 % — of the eggs (— which are rather intransparent, a little yellowish —) developed normally. After three days the embryos were young Bipinnariæ of the usual shape. Pl. II. figs. 4—5 represent the *Archaster*-larva two weeks old; here the hydrocoel has begun to form lobes, the larva thus being nearly fully formed. It is a very ordinary type of larva, with very short arms. The frontal area is rather broad; there are no preoral arms. The ventral median lobe is somewhat longer and broader than the dorsal. Antero-dorsal arms (or lobes) are fairly distinct, the postero-dorsal ones less so. The postero-lateral lobes are quite short, though distinct, whereas postoral lobes are not indicated. In the middle of the ventral median lobe papillæ are beginning to appear, one larger in the middle, two smaller a little below and one in the middle above it — showing that the Archaster-larva has a Brachiolaria-stage. The first indication of these papillæ was, however, seen already in some larvæ only 8 days old. Pl. II. figs. 6—7 represent another larva, also two weeks old, but in a more advanced stage, having reached its full shape, and finally Pl. II. fig. 8 represents a larva in beginning metamorphosis, 24 days old. The papillæ are now developed into distinct suckers, whereas the larval arms are scarcely longer than in the larva of two weeks; there are, however, now also small preoral arms. The larva is quite transparent, without any pigment.

Some of the larvæ at this age had begun resorbing the larval body; they were found clinging to the bottom of the dish, attaching themselves so fast, by means of their sucking papillæ, that it was hardly possible to remove them by the water jet from a strong pipette. — As I had to leave Onrust by this time I did not see the larvæ through metamorphosis, but we now know, at least, the larval form of this seastar, and know, what rather surprised me, that it is of the Brachiolaria-type, not of the type without a Brachiolaria-stage like the *Astropecten*-larvæ, which from the general likeness of *Archaster* to the Astropectinid type, might perhaps have been expected.

13. **Acanthaster Planci** (Linn.). (Pl. III. Figs. 7—8).

This species was found rather commonly on the coral reef at the little island Haarlem off Batavia, near Onrust, crawling over the top of the madreporarian corals on which it feeds, sucking off all the soft substance, leaving the white skeleton of the corals to show where it has been at work. There were two colour varieties, purple-blue and grey, so conspicuously different that one would take them to be two different species. There are, however, intermediate forms, e. g. with the purple of the arms gradually turning into grey on the disk, and, as there seem to be no other differences, these colour variations are evidently only individual, such as we know occur also in other Asteroids, particularly in *Asterias rubens*.

Acanthaster is rather a fearful beast to handle; it is almost impossible to avoid being hurt by its spines, which, although not very pointed, are exceedingly sharp, with three finely serrate, cutting edges. Some specimens opened (— the skin is very delicate, easily breaking —) were found to contain ripe sexual products, though in a rather unusual way: some few ripe eggs among many very unripe, which would appear to indicate that the sexual products are not shed all at the same time, as is the general rule in species having pelagic larvæ, but in portions at different times. The sperm was immovable in ordinary sea-water, but a little potassium added to the water to increase the alkalinity made it very active. Fertilization was undertaken on the evening of April 30th.

The eggs are small, 0.1 mm., of a faint yellowish tint, but otherwise fairly clear. After 14 hours a few swimming gastrulæ were found, but most of the embryos were still lying within the egg-membrane as folded blastulæ. The formation of the gastrula begins before the embryo leaves the egg-membrane, so that it emerges as an incipient gastrula, with an invaginated, still solid plug of cells.

The young Bipinnaria (Pl. III, fig. 7; six days old) is characteristic through its elongate, broad ventral median lobe; the dorsal median lobe is about equally long and broad; the other lobes only indicated. At the age of 16 days the larvæ had begun to form papillæ in the ventral median lobe, this larva thus also having a Brachiolaria-stage (Pl. III. fig. 8). The papillæ are still of simple form; whether they would assume a more complicate shape is uncertain, the larva not yet having begun metamorphosing; but it seems probable that they will remain quite simple suckers, as in the larva of *Archaster typicus*. The lobes are fairly well developed, but of the short, non-movable type, as in the *Archaster*-larva. Some small brownish pigment spots are found along the vibratile band and in the posterior part of the body. The larva, at this stage, was a very active swimmer.

As I had to leave Onrust at this time, I could not rear the larva beyond this stage; the rather few larvæ still surviving I left in the laboratory, eventually to be brought onboard to me by the STEINFURTHS, when I should have to leave Java. There was, however, nothing to be discovered in what was brought me. It would have been particularly interesting to see what the newly metamorphosed seastar would be like; but already the fact now disclosed that the *Acanthaster*-larva passes through a Brachiolaria-stage is of considerable interest.

14. **Culcita schmiedeliana** Gray. (Pl. III. Fig. 6).

This species was not rare in the lagoon inside the reef at Cannoniers Point, Mauritius. As I had formerly found to be the case with *Culcita novæ-guineæ* in the Malay Archipelago, particularly at Banda (cf. my paper "The Danish Expedition to the Kei Islands 1922". Vid. Medd. Dansk Naturhist. Foren. Bd. 76. 1923. p. 75), this species was found to be the host of a *Fierasfer*, the fish lying in the body-cavity of the seastar. In every specimen opened the fish was found, mostly two or three specimens, rarely only one. These new observations do not, any more than those from the Malay Archipelago, give the definite clue to the very puzzling problem, how the fish enters the seastar. I can only repeat the suggestion which I gave loc. cit., viz. that it must enter through the mouth of the seastar, going into its stomach, and then biting a hole in the stomach wall and through this entering the body cavity (which is rather large, so as to give the fish sufficient space). It may also be suggested that it feeds on the genital organs of the seastar, which would form a very rich food supply for it. For the sake of breeding the fish, no doubt, must leave its host, the same way it entered. It would be an easy matter to make direct observations of this extraordinary case of parasitism if a good aquarium were available, which was not the case either at Banda or Mauritius.

The *Culcita* was found to have ripe sexual products during the time of my stay at Mauritius, and fertilization was undertaken on September 22nd — in the evening. There was then no possibility for observing the cleavage; it was only noticed that the fertilization membrane was very distinct, being formed almost instantaneously on the adding of the sperm to the eggs. The blastula, still lying within the membrane, is strongly folded.

The culture proved to be only partly good, several of the young embryos being abnormal; still about a hundred of them were normal and went on developing normally. I was surprised to find the number of the apparently quite normal larvæ rapidly diminishing, till I found that when being shifted from one dish into another with fresh sea-water they would adhere to the bottom of the dish and be destroyed. It was mainly owing to this fact that only half a dozen larvæ were left at the time, when, at the end of October, the cultures were transferred to Port Louis — to be killed there by the polluted water.

The larva (Pl. III. fig. 6) is a Bipinnaria of the simple type, with the arms indicated only as short, rounded lobes. The ventral median lobe is conspicuously broader than the dorsal; they are of equal length. The larva is unusually flat; there is no pigment. On examining the larvæ (Oct. 28th) before transferring them to Port Louis, I found that a pair of small papillæ, laterally directed, had developed at the base of the ventral median lobe. This very probably means that also this larva is a Brachiolaria, when fully formed. I noticed, however, that there was as yet no indication of a sucking disk. There is thus no definite proof that there is a Brachiolaria stage, but I do not see what else the appearance of the two small papillæ might mean. Unfortunately there was no time for making more than a quite rough sketch of the larva in this stage — and the death of the cultures soon after made an end of the observations.

The fact now disclosed that the larvæ of *Archaster* and *Acanthaster*, and most probably also that of *Culcita*, pass through a Brachiolaria stage, has a bearing on the very interesting question, whether the simple Bipinnaria, as found in *Astropecten*, or the Brachiolaria represents the original type of the Asteroid larva. In my "Studies", p. 220, I have maintained that the simple Astropectinid Bipinnaria is the primitive type, the Brachiolaria a later, more specialized type. We know now the Brachiolaria to be the more generally occurring type, the true Bipinnaria being known to occur only in *Astropecten* and *Luidia*, whereas the Brachiolaria is known to occur in *Archaster*, *Acanthaster*, *Asterina*, *Porania*, *Asterias*, as also the *Solaster* larva must be regarded as a reduced Brachiolaria. This fact might perhaps speak for the Brachiolaria being the original type, as is the opinion of MacBride. Still, the fact that all the larvæ pass through a typical Bipinnaria stage, before reaching the Brachiolaria stage, is decidedly in favour of regarding the more simple Bipinnaria as the primitive type; so too is the fact that the simple Bipinnaria is peculiar to the Astropectinids, which are generally regarded as the more primitive type of Asteroids — in spite of MacBride's sweeping statement that "all admit the Spinulosa to be the more primitive type of Asteroids" (cf. the discussion in "Nature" December 22. 1921, p. 530). The same conclusion, that the Bipinnaria is the primitive, the Brachiolaria the more specialized type of larva, is reached by Hörstadius on purely embryological grounds (S. Hörstadius. Über die Entwicklung von Astropecten aurantiacus L. Arkiv. f. Zool. Bd. 18. B. 1926, No. 7. p. 4—5). As pointed out in my "Studies", p. 220, this view of the two Asteroid larval types is opposed to regarding the Brachiolarian sucker as homologous with the Pelmatozoan stalk.

15. **Linckia lævigata** (Linn.).

Fertilization of this species was undertaken at the laboratory in Batavia on July 21st 1922, and proved fairly successful. The blastula still lying within the egg-membrane is much folded. On the third day the embryos were small Bipinnariæ of typical form. The observations could be continued only until July 31st, and by that time the 10 days old larvæ were still of the typical Bipinnaria shape, only the preoral part being somewhat shorter and thicker than usual. — There is thus no proof whether or not this larva has a Brachiolaria stage, and my observations on this species, in the absence of figures after the living larvæ or of preserved material from which figures could be made, do not come to much more than the proof that this seastar has a typical pelagic larva.

II.

Observations on some Scandinavian Echinoderm Larvæ.

In my paper "Notes on the Development and Larval Forms of some Scandinavian Echinoderms" (Vidensk. Medd. Dansk Naturh. Foren. Bd. 71. 1920) I published some observations on this subject from a stay at the Swedish Zoological Station, Kristineberg, Fiskebäckskil, in August—September 1918, dealing with the (supposed) larva of *Ophiura affinis*, the breeding habits and the larva of *Amphiura filiformis*, the larva of *Brissopsis lyrifera*, the supposed larva of *Stichaster roseus* (in reality the larva of *Astropecten irregularis*), and the development of *Antedon petasus*. Finally some observations on the larval nervous system in various Ophiurid larvæ and in the larva of *Echinocyamus pusillus*.

During the same stay I made, however, quite a good deal of other observations on some Echinoderm larvæ which have been unpublished till now, and I also made careful colour drawings of various larvæ from life, which may well deserve publication, no such figures existing in literature. Conditions for such work were at that time particularly favourable at Kristineberg. With strong north-westerly winds water from the Skagerrak is pressed into the Gullmar Fjord, teeming with pelagic organisms in fine condition — such as *Amphioxus*-larvæ, *Polygordius*-larvæ, *Tonaria*, and, particularly, numerous Echinoderm larvæ. The laboratory standing close to the water, one can stand at the pier towing for the pelagic organisms and thus take them fresh from the sea directly into the laboratory. The larvæ are thus available in any number in the finest condition, undamaged and, as they have been reared in nature, one is sure that no laboratory conditions can have influenced their shape; we have them here in their full, normal shape and perfect beauty.

The larvæ thus studied are the following:

1. **Ophiura albida** Forbes (**Ophiopluteus paradoxus**). Pl. IV. Fig. 3.

This larva is very characteristic through its broad, full arms, the skin standing widely off from the skeletal rods. The tips of the arms, particularly the posterolateral arms and the right, longer, antero-dorsal arm are of a conspicuous crimson colour. A fainter patch of this colour is also found in the posterior end of the body. The stomach is greenish; the body otherwise uncoloured, beautifully transparent, the larva being, on the whole, a strikingly beautiful microscopical object.

2. **Ophiura texturata** Lamk. Pl. IV. Fig. 4.

Although so closely related to *Ophiura albida*, the larva of this species is so different from the larva of *O. albida* that it is very hard to imagine how they could belong to two nearly related species; one would rather think them to belong to different families! This is, indeed, one of the mysteries of the Echinoderm larvæ. For the present we have got to accept the surprising fact offered by the great difference between two so closely related larval forms.

The *O. texturata* larva is by no means so elegant a form as the *O. albida* larva; nothing very graceful about it! The arms are all short and thin, ending at the same level (excepting the postero-dorsal arms); the fact that the larva, when kept in a dish, usually stands quite close under the surface film of the water has some connection with the ends of the arms being at the same level. On account of this habit it is easy to examine the larvæ directly from above with the microscope, a very convenient position for studying their nervous system (cf. "Notes on the Development and Larval Forms of some Scand. Echinoderms", p. 158—159).

The larva is not very transparent, particularly on account of its large, green stomach. The yellowish-red pigment is in the main distributed along the skeleton, particularly the basal part of the posterolateral rods, so strikingly different from all other Ophiurid larvæ known till now in being fenestrated. There is a slight indication of yellowish-red colour in the ends of the arms and along the posterior end of the body, which is broad, straight, not elegantly rounded as in most other Ophioplutei.

3. **Amphiura filiformis** (O. Fr. Müller). (Pl. IV, Fig. 5).

That this larva, originally described (Echinodermenlarven. Nordisches Plankton) under the name of *Ophiopluteus mancus* Mrtsn., belongs to *Amphiura filiformis* was proved by direct rearing from the egg (cf. "Notes on the Development and Larval Forms Scand. Echinod.", p. 138). Also its metamorphosis was studied to some extent (see below, p. 37).

This is a very striking larva, differing from all other known Ophioplutei, excepting *Ophiopluteus dubius* Mrtsn., in having no postero-dorsal arms. The antero-lateral arms are long and slender, the right one considerably longer than the left. The postero-lateral arms have a large spot of crimson at the end, which makes the larva very conspicuous and at once recognizable. Otherwise there are only some very small spots of the same colour on the basal part of the postero-lateral rods and on the body skeleton. The stomach is yellowish-green.

4. **Ophiocomina nigra** (Abildgaard). (Pl. IV, Fig. 1).

Among the Ophiurid larvæ of Scandinavian seas this larva is conspicuous through the ciliated band forming a pair of ciliated lobes at the base of each postero-lateral arm; (there is, however, an indication of such lobes also in the *Ophiura albida*-larva (Pl. IV, fig. 3)). The shape of these lobes is better seen on the sketch of the larva seen from above, given in my "Notes on the Development and Larval Forms of Scand. Echinod.", p. 159.

The arms are moderately broad, flat; the antero-lateral arms are of equal length. Also this larva has the habit of standing directly below the surface film of the water, when kept in a dish, thus lending itself for examination from above. The stomach is of a conspicuous yellowish-red colour. There is a trace of the same colour in the ends of the arms, otherwise the larva is colourless, beautifully transparent.

In view of the fact that the relationship of this species — formerly referred to the genus *Ophiocoma* — to the family of the Ophiocomidæ is debatable (H. L. CLARK, in his "Catalogue of Recent Ophiurans" refers it to the family of the Ophiacanthidæ, nay, even to the genus *Ophiacantha*), it is important that the larva is very

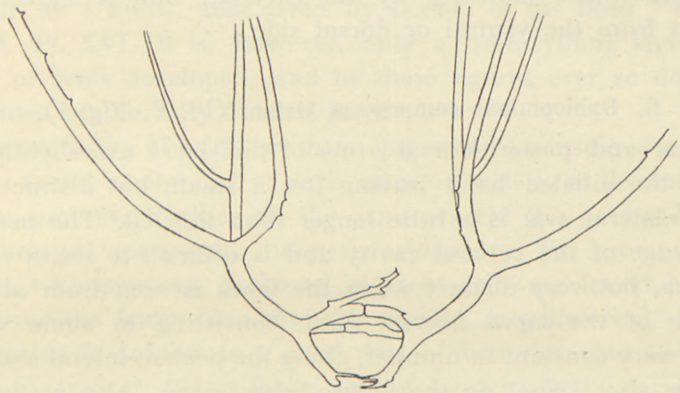


Fig. 12. Skeleton of larva of *Ophiocomina nigra*. × 215.

different from the true *Ophiocoma*-larvæ. It is true that it has vibratile lobes, somewhat recalling those of the *Ophiocoma*-larvæ (— we know, however, the vibratile lobes of the *Ophiocoma*-larvæ only from preserved specimens, no fully formed *Ophiocoma*-larva having ever been drawn from life, or, at least, no such figure has been published —); but as there is an indication of such vibratile lobes also in the *Ophiura albida*-larva, this character cannot afford any proof of relationship between the larva of *Ophiocomina nigra* and the *Ophiocoma*-larva. But then, on the other hand, the skeleton of the *Ophiocomina nigra*-larva (fig. 12) is very conspicuously different from that of the *Ophiocoma*-larvæ (cf. above, fig. 11, and "Studies", p. 133, fig. 58). This fact then is rather against *Ophicomina* belonging to the family Ophiocomidæ. But so long as we know nothing of the larvæ of any other genus of Ophiocomidæ, and, on the whole, the value of Ophiurid larvæ for classification is still somewhat uncertain (cf. the larvæ of *Ophiura albida* and *texturata*!), we cannot see in the characters of the larvæ any definite proof against the relationship of *Ophiocomina* with the Ophiocomids.

5. **Ophiothrix fragilis** (Abildgaard). (Pl. VII, Fig. 1).

This larva, so well known already from JOH. MÜLLER's investigations, is particularly characterized through its very long postero-lateral arms, banded with two or three very conspicuous bands of dark colour. As seen in the microscope the colour of these bands is not really black, but a dark brownish. A spot of the same colour is found at the posterior end of the body, between the end rods. There is a slight accumulation of the same colour at the base of the antero-lateral arms, finally there is a fine tint of brownish colour along the body rods and the basal part of the postero-lateral rods, as also along the rods of the three pairs of shorter arms, whereas the ends of these arms are uncoloured. The stomach is yellowish, not green as is so often the case in Ophiurid larvæ.

The nervous system of this larva is situated rather far out on the postero-lateral arms, at the place indicated by the asterisks, and is scarcely visible when the larva is seen from the ventral or dorsal side.

6. **Ophiopluteus compressus** Mrtsn. (Pl. V, Fig. 1).

The postoral and postero-dorsal arms of this larva are slightly broader than the other arms, the ciliated band leaving free a small, but distinct median space. The right antero-lateral arm is a little longer than the left. The nervous system is situated in the edge of the suboral cavity and is difficult to see in ventral or dorsal view of the larva, but very distinct when the larva is seen from above.

The colour of the larva is very faint, consisting in some small purplish-black spots, not very constant in number, along the postero-lateral and postero-dorsal arms, sometimes also a spot on the antero-lateral arms. Also at the posterior end of the body and on the transverse rods there is a trace of the same colour. The stomach is a faint yellowish-green.

It is quite uncertain to which Ophiurid this larva belongs. The fact that it was found to be quite common at Kristineberg only shows that it must belong to one of the species common in the Scandinavian seas, and as we know the larvæ of several of these there are not so many left for guessing. I have suggested (Handbook Echinod. British Isles, p. 238) that it may be the larva of *Ophiura Sarsi,* but it is merely a suggestion; *Ophiura robusta* or *Ophiocten sericeum* might equally well come into consideration.

7. **Echinocyamus pusillus** (O. Fr. Müller). (Pl. IV, Fig. 2).

When fully formed, this larva has a pair of well developed vibratile lobes at the base of the postoral arms; also on the sides of the body the vibratile band forms a fairly conspicuous lobe between the base of the postoral and the postero-dorsal arms, and a somewhat smaller lobe is formed on the dorsal side at the base of the postero-dorsal arms — cf. fig. 5, p. 157 in my "Notes on the development and larval forms of Scand. Echinoderms." In this figure is shown also the remarkable semicircular nervous band, to be observed when the larva is seen directly from above, which is very easy on account of the habit of this larva of keeping quite close under the surface film of the water.

The colour of the larva is very inconspicuous. A few small yellowish pigment spots may occur irregularly scattered in the body and in the ciliated band, particularly the preoral band, and there is a very faint yellowish tint in the ends of the arms. Also the stomach is of a very faint yellowish colour.

8. **Echinocardium cordatum** (Pennant). (Pl. V, Fig. 2).

In its general characters this larva, of course, is very well known, but the extraordinary beauty of the fully formed larva does not come out in any of the figures hitherto published. The only attempt at showing the natural colour of the larva is, as far as I know, that given by Gosse, in his book "Tenby, a sea-side holiday", 1856, Pl. XVI. It is, however, only a quite young larva, with only the first two pairs of arms developed, and be these figures ever so delicate, they give, of course, no idea of the fully formed larva.

There is a profusion of bright crimson pigment; a conspicuous accumulation of this pigment is found at the end of each arm, as well as at the end and at the base of the posterior process. Further all the arms, except the postero-lateral ones, are, in perfectly developed specimens, distinctly widened in the proximal half and here richly provided with pigment. Scattered pigment cells are found in the rest of the arms and all over the body. The stomach, finally, is yellowish.

The coloration is subject to a good deal of variation, but that here described I must regard as typical, being found in the most perfectly developed specimens, as also the swelling of the proximal part of the arms is distinct only in such specimens. When thus developed this larva is certainly among the most beautiful of Echinoderm larvæ and a most strikingly beautiful microscopical object.

9. **On different Types of Metamorphosis in Ophiurids.**

In MacBride's Textbook of Embryology the *Ophiothrix* metamorphosis is taken as the type of metamorphosis in Ophiurids with a typical pelagic larva — very naturally, since this is the only such form the metamorphosis of which has been studied in detail. This type is characterized by the postero-lateral arms remaining unchanged to serve as a floating apparatus for the young Ophiurid, until it is ready to assume the life of the adult on the bottom, when the long larval arms are simply thrown off and perish. In my "Studies" I have shown this same type to occur at any rate also in the larva which I have designated as *Ophiopluteus opulentus*, where, however, it appears that a new larval body can regenerate from the thrown off postero-lateral arms (cf. "Studies" p. 124, Pl. XX, figs. 3—5).

It is, however, by no means all Ophioplutei in which these larval arms remain intact, to be thrown off ultimately. In other larvæ all the arms, also the postero-lateral ones, are gradually resorbed during the metamorphosis, nothing being thrown off. This type has been made known already by Joh. Müller in his very first memoir on the Echinoderm larvæ (1848) viz. his *Pluteus paradoxus* =

the larva of *Ophiura albida*. In the said memoir a series of figures are given on Taf. I—II which show very clearly (particularly Taf. II. figs. 1—3) how the skeleton and all the arms are gradually resorbed.

The figures given in the present paper give proof that this same type of metamorphosis obtains also in the larva of *Amphiura filiformis*, cf. particularly Pl. VI. fig. 4. It is seen there that the postero-lateral arms gradually shorten, the skeletal rod breaking up, but remaining in the flesh of the arm to be gradually resorbed. The ciliated band has taken a new course, going now directly across the body so as to continue from one arm to the other.

Also as regards the fate of the other larval arms, there is a remarkable variation, as seen by a comparison of Pl. VI. 3 of *Amphiura filiformis*, with the corresponding stage of the *Ophiura albida* larva, Pl. VII. 3; it is here particularly the postoral arms which undergo a different fate: in *Amphiura filiformis* they are simply resorbed, so to speak in place, whereas in *Ophiura albida* the right postoral arm is thrown over towards the left side lying broadly across the ventral side. These two figures also show the gradual dissolution of the ciliated band; in Pl. VI. fig. 3 the band of the postero-lateral arms is seen in the course of growth across the larval body.

It is a curious fact that the right antero-lateral arm in several larval forms takes a special development, reaching a much greater length than the left and, like the postero-lateral arms, evidently playing an important part as locomotor organ for the metamorphosing larva. This is the case in the *Ophiura albida* larva, as well as in *Ophiopluteus undulatus, Ophiopl. pusillus*, and *Ophiopl. formosus* (cf. "Studies" Pl. XXIV. 3; Pl. XXIX. 3; Pl. XXX. 2). In the *Amphiura filiformis* larva it is something similar, but not quite the same; here (Pl. VI. 3) the right antero-lateral arm is also considerably longer than the left — but the vibratile band has disappeared. — The facts here pointed out may suffice to show what a great variation is found in the metamorphosis of the Ophioplutei in regard to their outer form. But also in regard to their inner transformation there are some remarkable differences.

If we compare Pl. VI, fig. 2 with Pl. VII, fig. 2, we see a striking difference in the hydrocoel. In the former, the *Amphiura filiformis* larva, the hydrocoel, in forming the hydrocoel ring, grows upwards, to bend over to the other side a b o v e the larval oesophagus; in the latter, the *Ophiura albida* larva, the hydrocoel is turning in the opposite direction, b e l o w the larval oesophagus. Although the result is the same, it cannot be but that this growing in the opposite direction of the hydrocoel must have some noteworthy influence on the process of metamorphosis in the two forms.

In my "Studies" (p. 158) I have called attention to the remarkable thickenings in the bottom wall of the suboral cavity, thickenings which will, evidently, play an important part in the metamorphosis of the larva. The same peculiar structure is found in *Ophiopluteus bimaculatus*, figured and described at some length by Joh. Müller in his V. Memoir on the Echinoderm larvæ. In other larvæ nothing nearly like it is found. Here we have thus again a very noteworthy difference in the metamorphosis of Ophiurid larvæ.

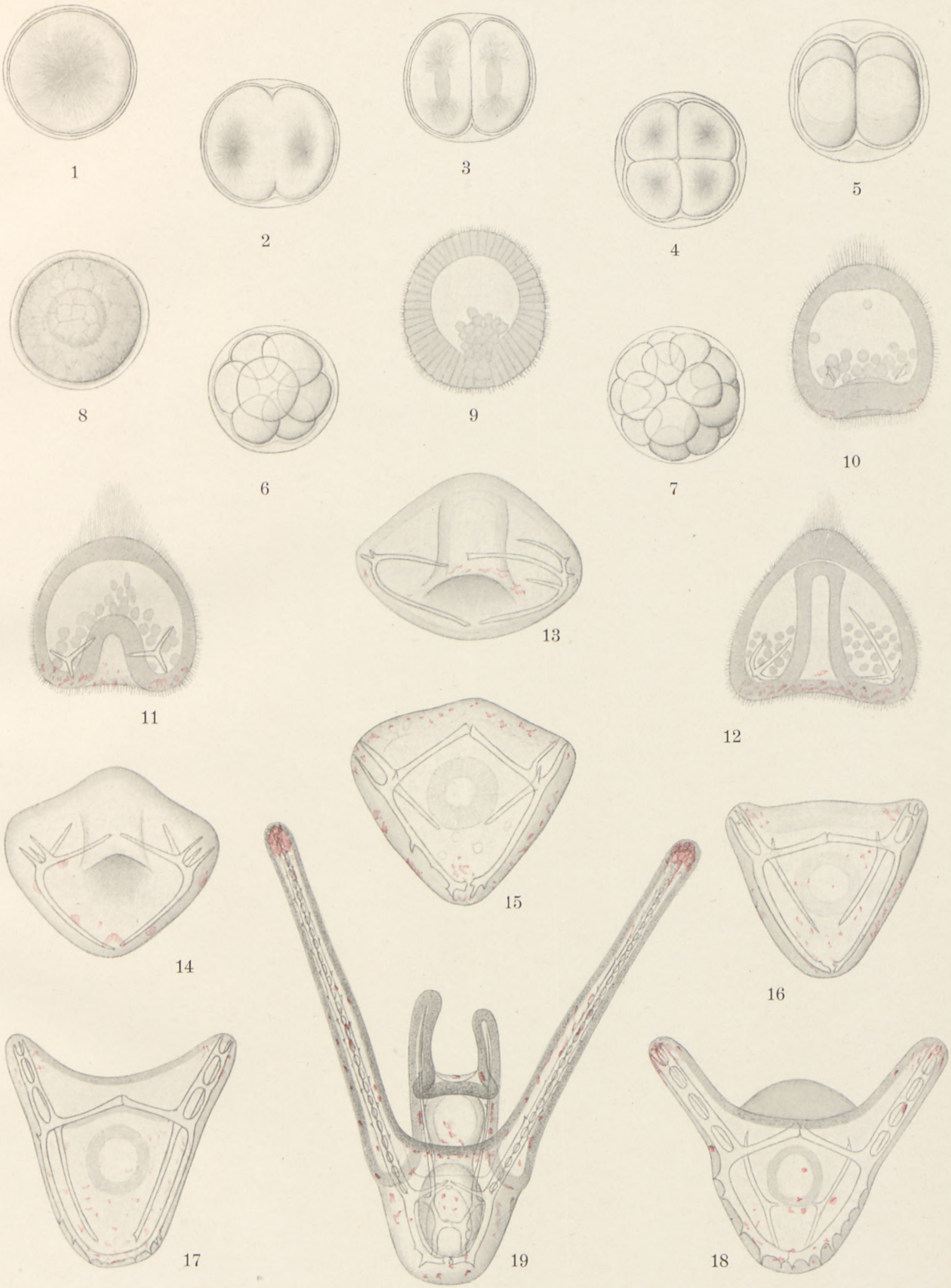
Such differences as pointed out here must necessarily to a considerable degree influence the process of metamorphosis and show that there is more to learn about the metamorphosis of Ophiurids than can be gathered from the study of the metamorphosis of *Ophiothrix fragilis.* A comparative study of the metamorphosis of these various types of Ophiurid larvæ must be fascinating work. I regret that I must here content myself with pointing out the problems.

Plate I.

All figures of *Diadema setosum*.

Fig. 1. Egg, immediately after fertilization.
- 2. Beginning cleavage, 20 minutes after fertilization.
- 3. First cleavage, nuclei in mitosis; 35 minutes after fertilization.
- 4. Four cell stage; 50 minutes after fertilization.
- 5. Another four cell stage, seen in oblique view.
- 6. Eight cell stage; 2 hours after fertilization.
- 7. Sixteen cell stage; 3 hours after fertilization.
- 8. Blastula stage; 5 hours after fertilization.
- 9. Free swimming embryo; $7^1/_2$ hours after fertilization. Mesenchyme cells wandering into the blastocoel cavity. Optical section.
- 10. Incipient gastrula formation, and the first rudiments of the skeleton. The embryo is 16 hours old. Optical section. Pigment has begun to form.
- 11. Slightly more advanced embryo, 18 hours old. Optical section.
- 12. More advanced gastrula, 22 hours old. Optical section.
- 13—14. Embryos 22 hours old, showing a further development of the skeleton, with the beginning formation of the postoral rods which are distending the basal corners of the gastrula to form the postoral arms. The blastopore or gastrula mouth showing beginning reduction in fig. 14.
- 15—16. Embryos 25 hours old, showing further development of skeleton.
- 17—18. Embryos 32 hours old, having already assumed the shape of a young Pluteus. In fig. 18 the oral lobe is beginning to protrude.
- 19. Echinopluteus in full shape of the first stage, 8 days old.

Figs. 1—18 all × 250; fig. 19 × 120.
All figures drawn from life.



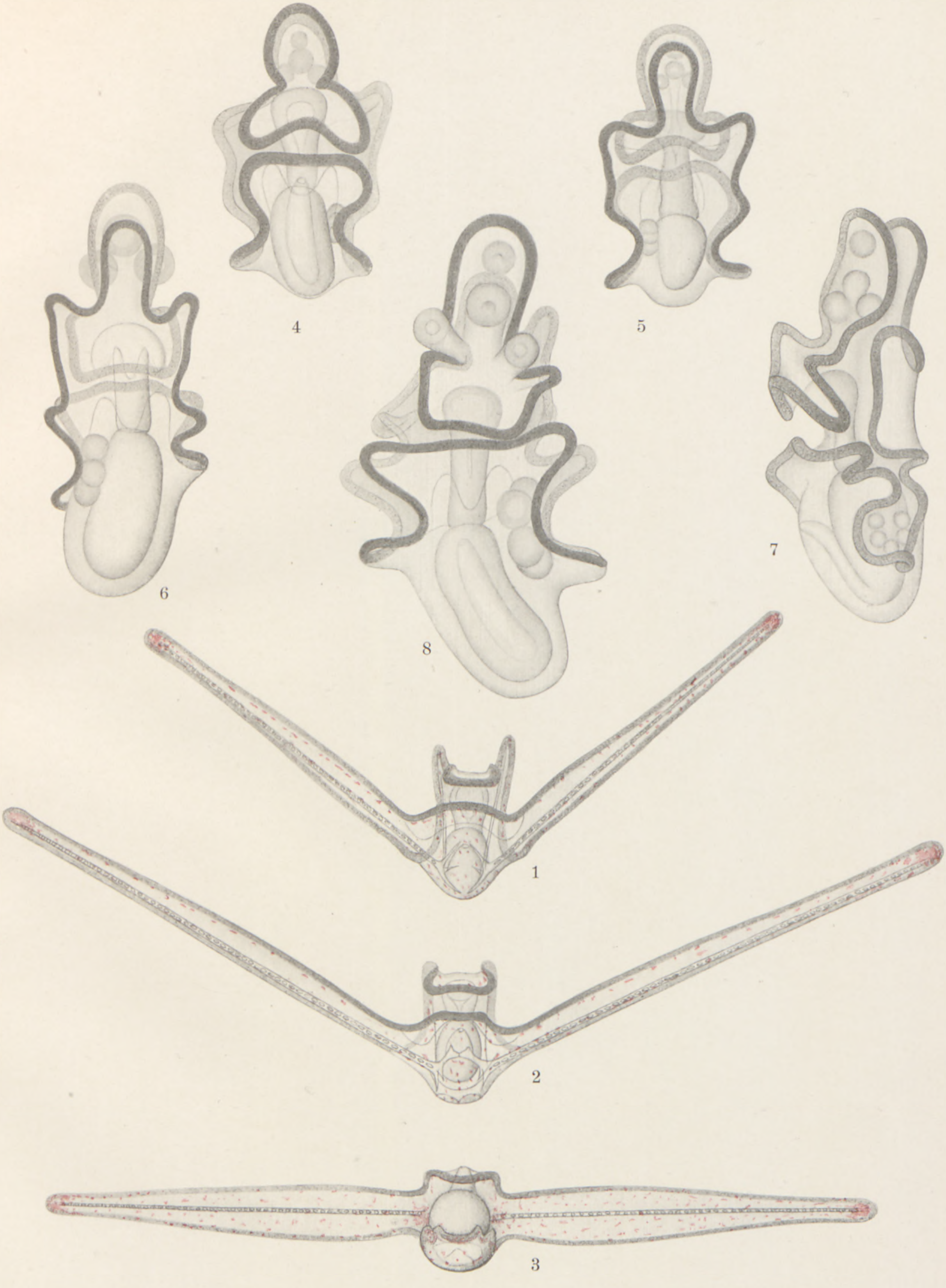
Th. M. del.

E.H.P.

Plate II.

Diadema setosum (figs. 1—3) × 85, and *Archaster typicus* (figs. 4—8) × 120.

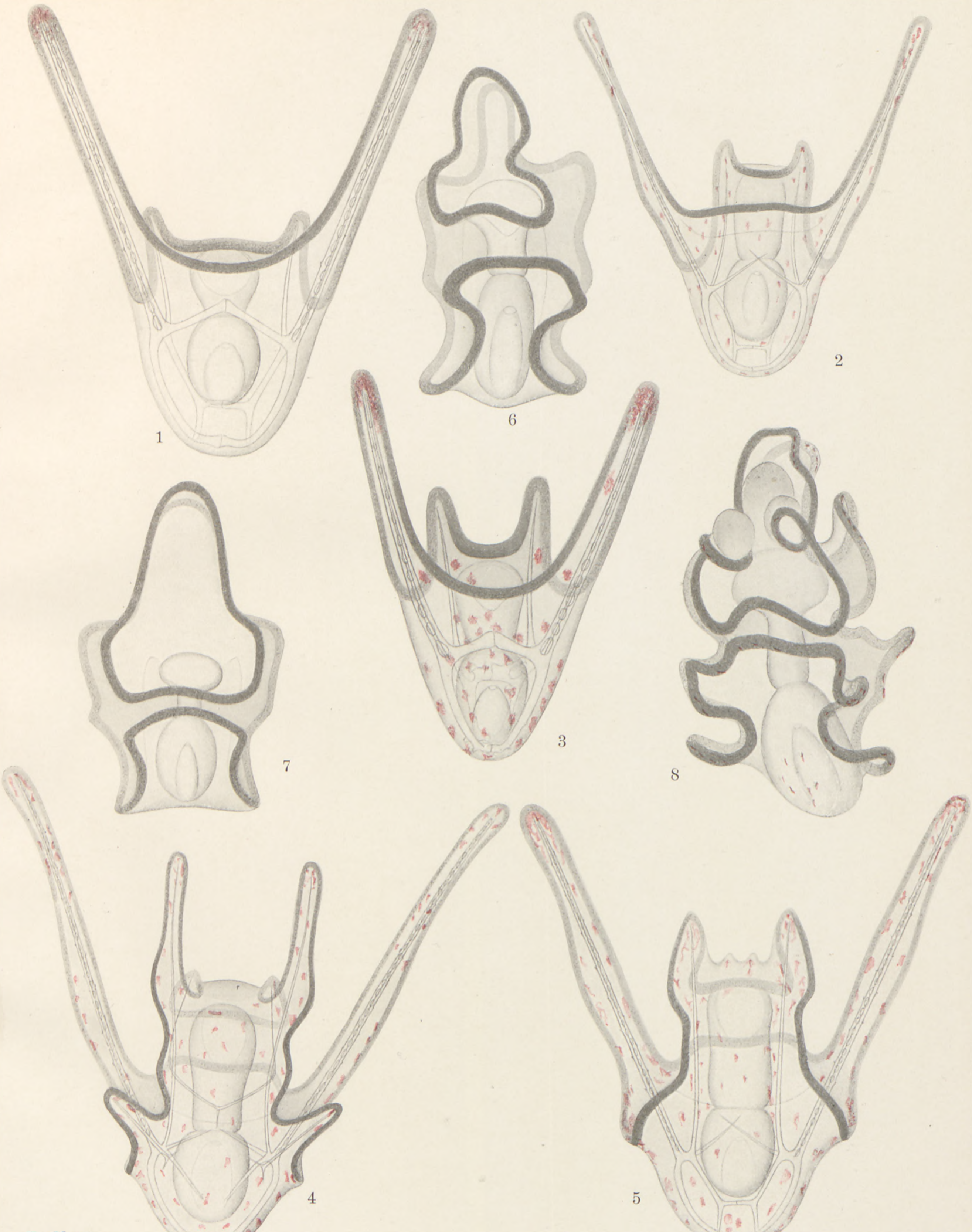
Fig. 1. Larva, 9 days old, in transition from the I. to the II. stage.
- 2. Larva in the II. stage. 11 days old.
- 3. Larva in the II. stage, seen directly from above. 13 days old.
- 4. Young Bipinnaria of *Archaster typicus*, seen from the ventral side. Two weeks old.
- 5. Larva in the same stage, from the dorsal side.
- 6. Fully formed larva, in the Brachiolaria-stage, seen from the dorsal side. Two weeks old.
- 7. Larva in the same stage, in side view.
- 8. Larva in beginning metamorphosis, from the ventral side. 24 days old. The young skeletal plates omitted. The rectum not distinctly discernible in the preserved specimen, from which the figure was drawn; it has been introduced in the figure on free hand.



Th. M. del. E.H.P.

Plate III.

Fig. 1. Larva of *Echinothrix diadema*, I. stage. 3 days old. × 180.
- 2. — - *Lytechinus verruculatus*, I. stage. 20 days old. × 85.
- 3. — - *Stomopneustes variolaris*, I. stage. 6 days old. × 180.
- 4. — - *Toxopneustes pileolus*; nearly fully formed; dorsal view; 27 days old. × 85.
- 5. — - *Tripneustes gratilla*; between I. and II. stage; dorsal view; 32 days old. × 85.
- 6. Young Bipinnaria of *Culcita schmiedeliana*. 27 days old. × 95.
- 7. — — - *Acanthaster Planci*. 6 days old. × 85.
- 8. Nearly fully formed larva of *Acanthaster Planci*. 16 days old. × 120.

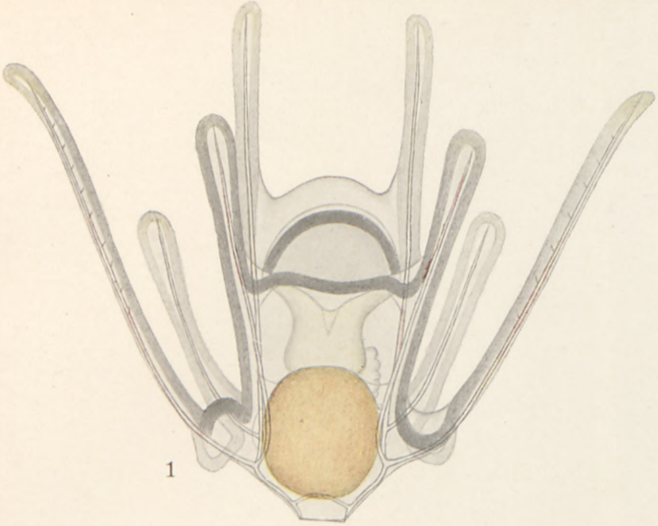


Th. M. del.

E.H.P.

Plate IV.

Fig. 1. Ophiopluteus of *Ophiocomina nigra*. × 100.
- 2. Echinopluteus of *Echinocyamus pusillus*. × 100.
- 3. Ophiopluteus of *Ophiura albida* (*Ophiopluteus paradoxus*). × 100.
- 4. — - *Ophiura texturata*. (Postoral band not always so strongly sinuate). × 100.
- 5. Ophiopluteus of *Amphiura filiformis*. × 100. Note the thick wall at the bottom of the suboral cavity.



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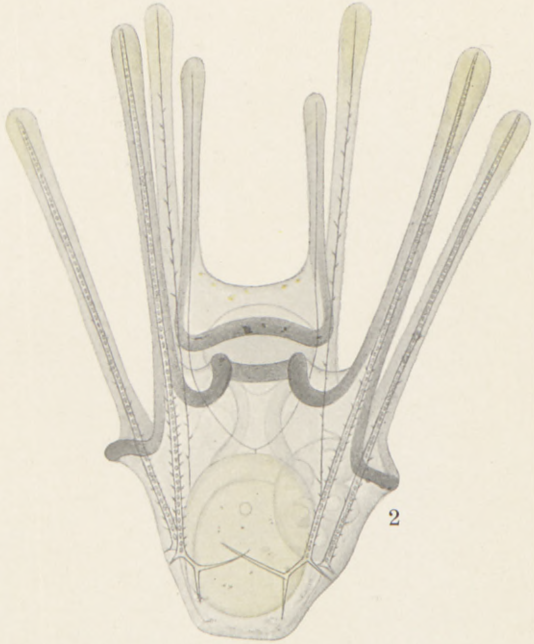

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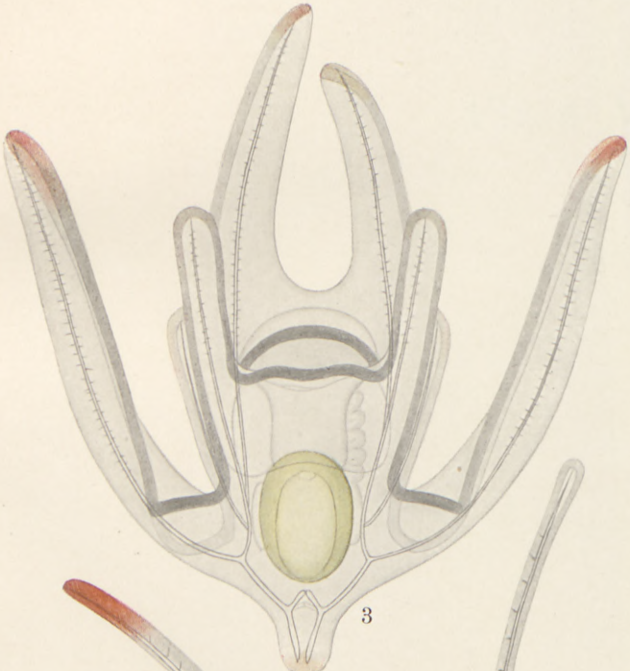

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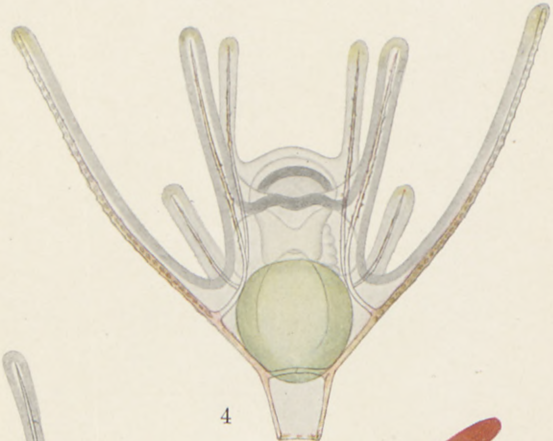

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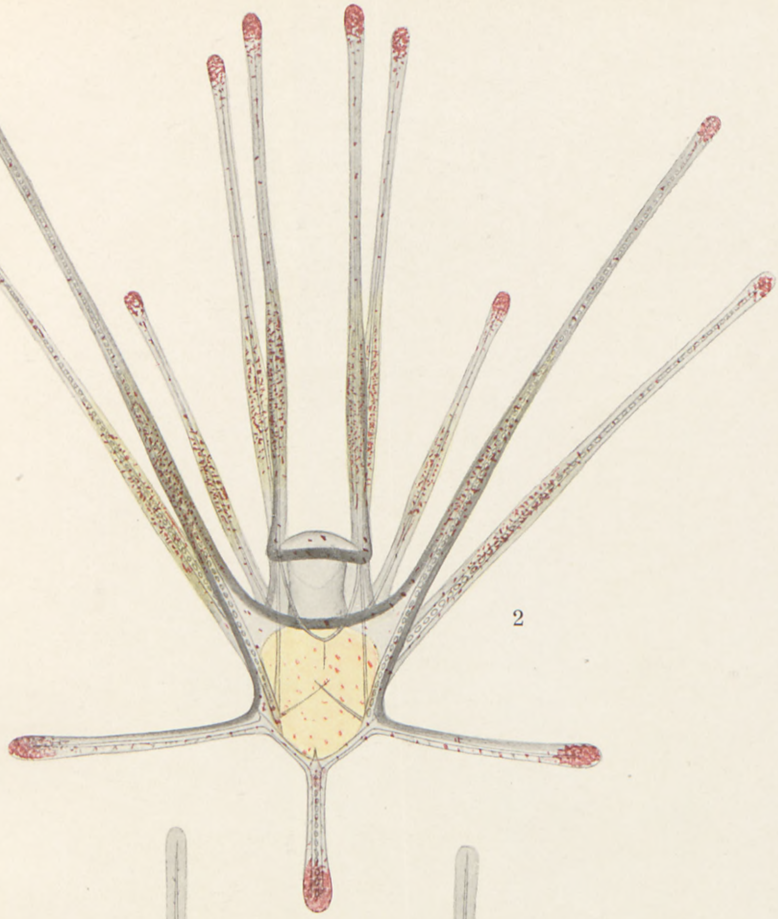
Th. M. del. E.H.P.

Plate V.

Fig. 1. *Ophiopluteus compressus.* × 100.
- 2. Echinopluteus of *Echinocardium cordatum.* × 70.



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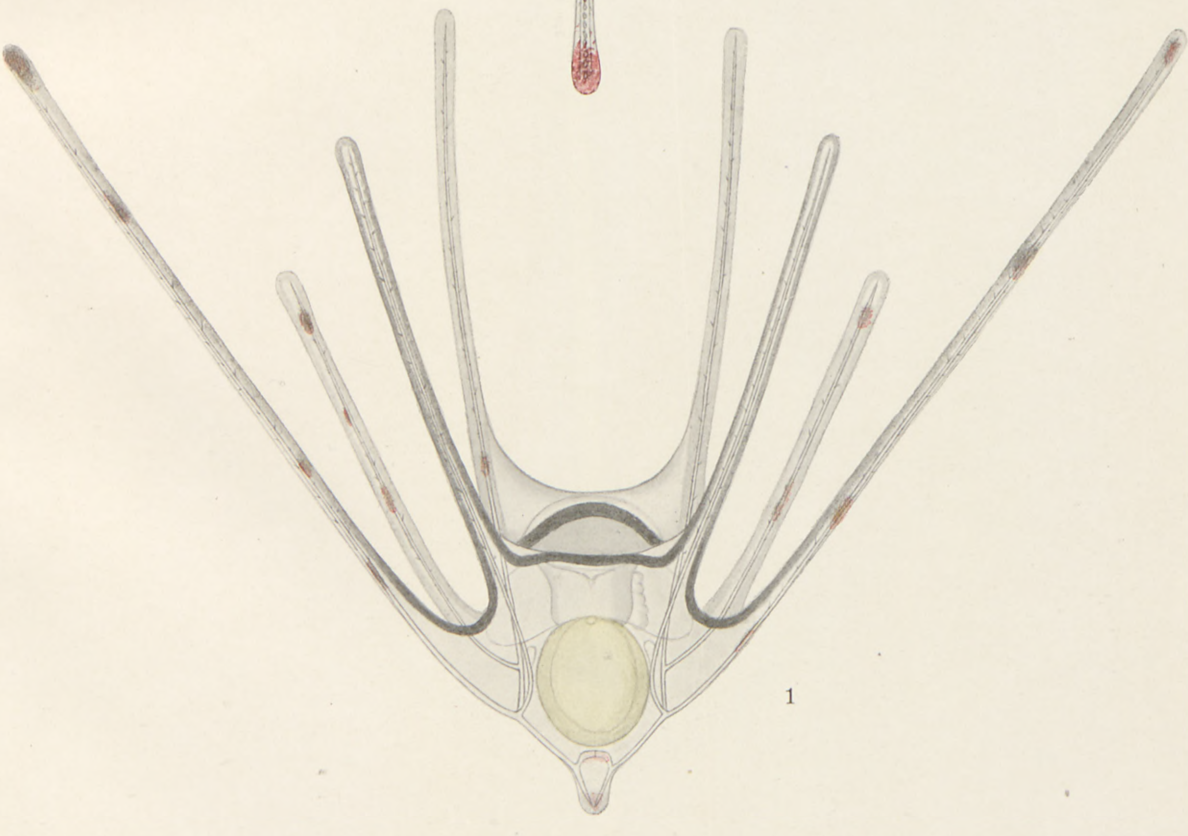

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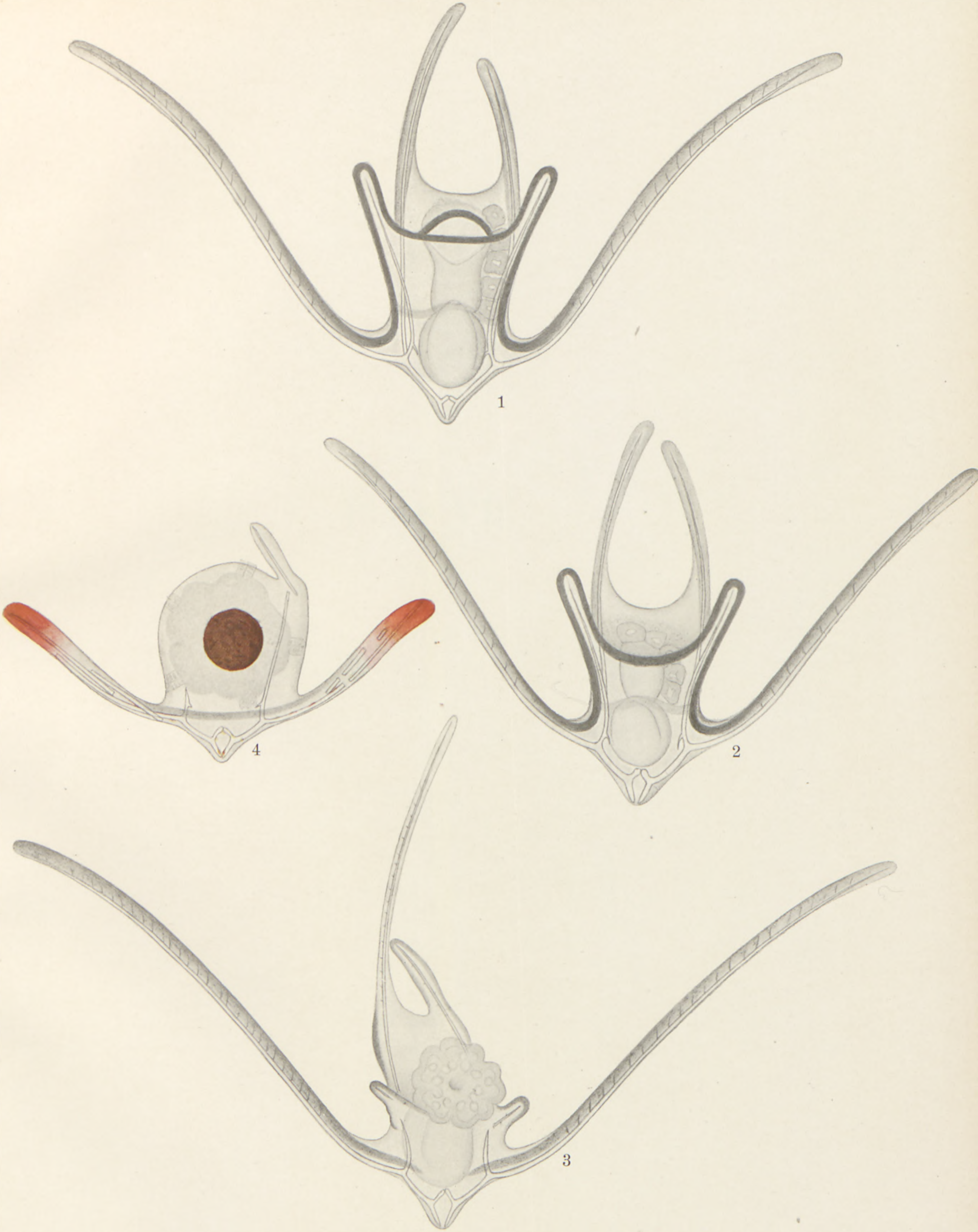
Th. M. del. E.H.P.

Plate VI.

Figs. 1—4. Ophiopluteus of *Amphiura filiformis*, in various stages of metamorphosis: Figs. 1—2 show the hydrocoel growing upwards, above the oesophagus, to form the hydrocoel ring. Fig. 3 shows a stage in which the hydrocoel ring is complete; the larval arms are in beginning resorption, the vibratile band has nearly disappeared, except on the postero-lateral arms, where it is still strongly developed and is about to continue across the body from one postero-lateral arm to the other. Fig. 4 shows the metamorphosis nearly completed, the larval arms having been almost completely resorbed. All × 100.



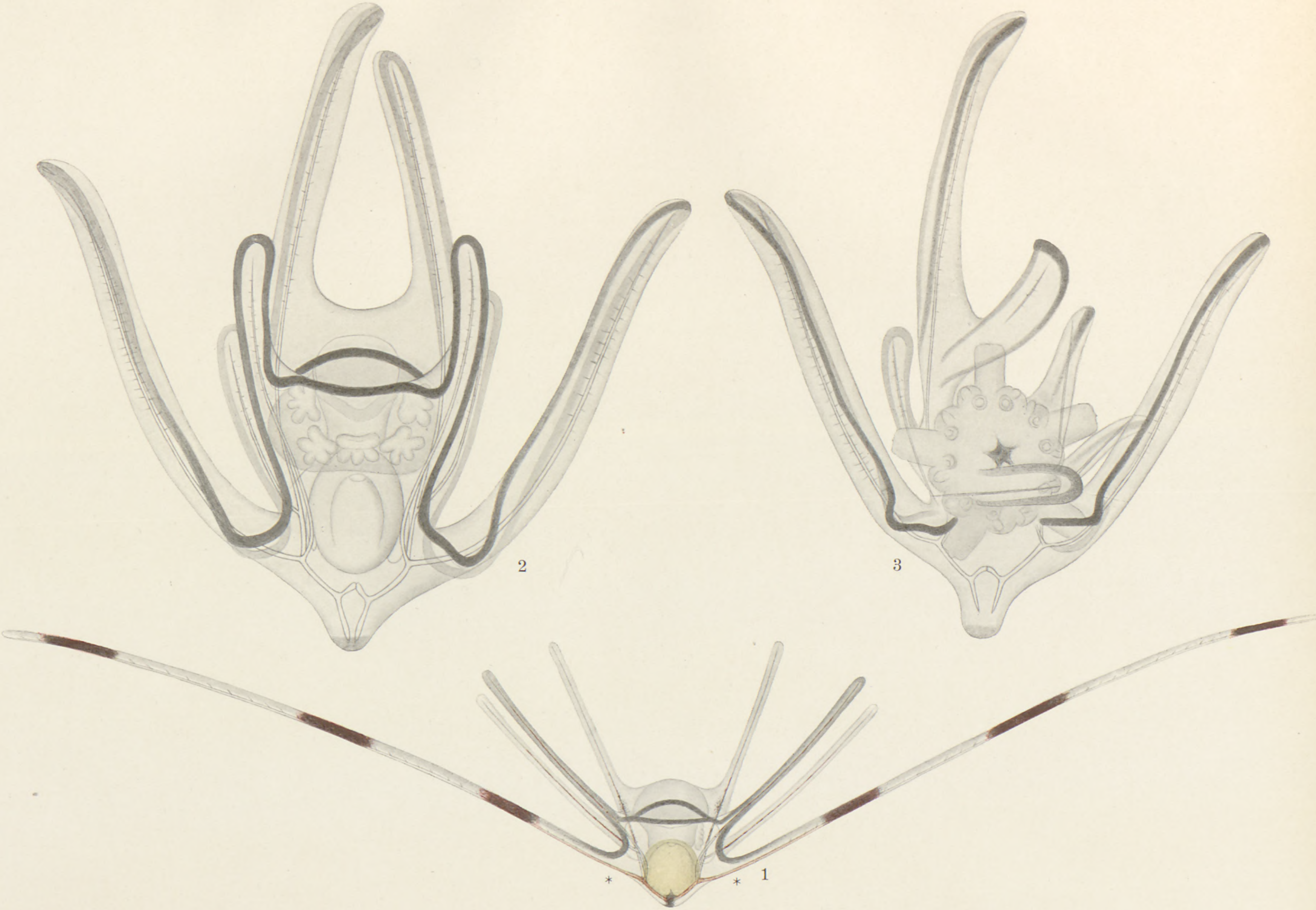
Th. M. del.

E.H.P.

Plate VII.

Fig. 1. Ophiopluteus of *Ophiothrix fragilis*. × 65.

- 2—3. Ophiopluteus of *Ophiura albida* in two different stages of metamorphosis. Fig. 2 shows the hydrocoel growing round the base of the oesophagus; in fig. 3, where the young Ophiurid has been formed, the more or less translocated arms are in the course of resorption.



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BYGNINGEN AF SNUDEN OG ANSIGTSMUSKULATUREN HOS NOGLE PINNIPEDIER

MED SÆRLIGT HENSYN TIL OPPUSTNINGSSÆKKEN HOS KLAPMYDSEN

AF

H. V. BRØNDSTED

MED 12 TAVLER

MIT EINEM DEUTSCHEN RÉSUMÉ

D. KGL. DANSKE VIDENSK. SELSK. SKRIFTER, NATURVIDENSK. OG MATHEM. AFD., 9. RÆKKE, IV. 2

KØBENHAVN

HOVEDKOMMISSIONÆR: ANDR. FRED. HØST & SØN, KGL. HOF-BOGHANDEL

BIANCO LUNOS BOGTRYKKERI A/S

1931

De foreliggende Undersøgelser er for ca. 12 Aar siden foretaget paa den Kgl. Veterinær- og Landbohøjskoles Zoologiske Laboratorium. Den daværende Bestyrer, Prof., Dr. phil. J. E. V. Boas, paa hvis Initiativ jeg tog fat paa Arbejdet, skylder jeg oprigtig Tak for den store Liberalitet, hvormed han stillede Laboratoriets Materiale til min Raadighed; jeg gik heller aldrig forgæves, naar jeg bad Professor Boas om Raad og Vejledning. Naar Undersøgelserne først publiceres nu, skyldes det forskellige ydre Aarsager.

Med Hensyn til Materiale og Methode kan jeg fatte mig i største Korthed. Materialet var i de fleste Tilfælde spirituskonserveret, enkelte Stykker til at begynde med friske. Methoden var simpel Dissektion, oftest under Lupe. Tegningerne er foretaget med Prisme. Fig. 12 og 16 er tegnet af Fru Bodil Strubberg, de øvrige af mig selv.

Hvad Terminologien angaar slutter jeg mig til den af Boas og Pauli [2] angivne. Læseren henvises i det Hele til dette fortrinlige Værk hvad Pattedyrenes Facialmuskulatur angaar. — I Arbejdet i sin nu foreliggende Form gaar jeg kun i ringe Grad ind paa principielle Spørgsmaal angaaende Facialmuskulaturens Genese; kun hvor det foreliggende Materiale har frembudt Lejlighed til at diskutere Detailspørgsmaal denne Sag vedrørende har jeg fundet det værd at knytte nogle Bemærkninger af teoretisk Interesse til de fundne Fakta. Jeg skal derfor ikke her indlade mig paa en Diskussion om de divergerende Anskuelser, der kommer for Dagen angaaende Facialmuskulaturens Genese hos Boas og Pauli [2] paa den ene Side og Huber [9—12] paa den anden.

Om Bygningen af Pattedyrenes Snudebrusk og den dertil knyttede Terminologi henvises til Freund [7] og Kormann [13].

I Beskrivelsen gaar jeg ud fra en Sammenligning med Hunden, hvis Forhold er nøje studerede af andre, og som danner et naturligt Udgangspunkt for Behandlingen af de beslægtede Sæler.

Zalophus californianus.

Snudebygningen.

Snuden er hos Zalophus ret smal, ligesom hele Hovedets Form jo er slankere end Phocidernes. Næseborene fremtræder som smalle Spalter, svagt skraatstillede, idet den øvre Ende er noget udadbøjet; de adskilles af Næseskillevæggen, der er ret smal, Næseborene altsaa temmelig tæt ved hinanden; Forfladen sort pigmenteret, haarløs, forsynet med smaa Fordybninger, der minder om Haarsække; dyb, skarp philtrum. Næseføjene haarklædte, Behaaringen fortsætter sig ca. 4 mm ind i Næseboret; dette er sort pigmenteret helt ind paa Slimhindefolderne. Paa foreliggende Spirituspræparat (formolinjiceret) er Næseborene omtrent lukkede, saaledes at der lades en Spalte paa ca. 1 mm aaben; men som vi senere under Phoca skal se, har jeg Grund til at antage, at dette er Hvilestillingen. Udvendig ses intet Spor til Hundens sulcus ventralis alaris, thi Næseboret er selve sulcus, noget, der vil blive nærmere paavist under Phoca.

Snudebrusken. Fig. 1. Trods store Afvigelser erkender man dog let de samme Grundtræk i Bygningen af Næsebrusken hos Zalophus og Hund. Forsvunden er dog cart. acces., samt cart. lateral. anter. Fra øverste Rand af septum cartil. (*s*) udgaar i hele dets Længde vandret ud til Siderne proc. lateral. dors. (*pld*), hvorved et Næsetag dannes, der bagtil er ca. 1 cm bredt men fortil jævnt afsmalnende; herefter bøjer proc. lateral. dorsal. nedad og indad i en Bue, ganske som den tilsvarende hos Canis; men der er dog den Forskel, at den her naar saa langt ind, at Randen næsten naar septum; paa denne Maade dannes et Rør, der fortil bliver snævrere. Saa bøjer proc. lat. dors. nedad parallelt med septum og ganske tæt op til dette; den er fortil skraat afskaaret, idet den dorsalt naar meget længere frem end ventralt. Indgangen til Næsehulen er altsaa en ganske smal Spalte. I Sammenhæng med det nederste Parti af proc. lateral. dorsal. er cartilago navicularis (*cn*), der bagtil har omtrent samme Udseende og Lejringsforhold som hos Hunden, men fortil er Forholdet væsentlig anderledes; i Stedet for som hos Hunden, hvor der hele Vejen ud til den distale Ende blot er en Fure mellem cartil. navicul. og proc. lateral. dorsal., saa er her cartil. navicul. i hele sin forreste Del fri; endvidere er cartil. navicul. her mærkelig ved, at den rager frit fremad som en lang smal Bruskstrimmel, rendeformig paa den mediale Side; Spidsen er paa en ejendommelig Maade dorso-caudalt krogformigt ombøjet. Proc. later. ventral. er kun svagt udviklet og indskrænket til den caudale Del af Snudebrusken; dens forreste Begrænsning ligger ret langt tilbage, ud for det Sted, hvor den frie Del af cartil. navicul. begynder, den lægger sig tæt op til Mellemkæben og gaar over i cartil. navicul., der bagtil ligger langt ned, dens ventrale Rand kun lidt højere end Underkanten af septum; hele den forreste store Del af septum har altsaa en fri ventral Rand, der rager et ret betydeligt Stykke ud over Mellemkæben.

Snudemuskulaturen.

Søløvens (Otaria jubata) Ansigtsmuskulatur er undersøgt af Murie [17] 1872, men der er en Del Fejl og Misforstaaelser i hans Opfattelse af disse Musklers Forhold, hvilket aabenbart skyldes, at man dengang var under Trykket af at finde den størst mulige Ensartethed i Bygningstrækkene hos en større Dyregruppe; Resultatet er da ogsaa i dette Tilfælde blevet, at Otarias Ansigtsmuskulatur i for høj Grad fremstilles som lignende den almindelige generelle Pattedyrtypes, som den opfattedes dengang. Navnlig er m. nasalis' Komplikation ikke erkendt, ligesom m. naso-labialis ikke har faaet det, der tilkommer den. Muries' levator labii super. alaque nasi er en Del af m. naso-labialis; hans levator lab. super. proprius er ogsaa en Del heraf, hvilket man kan se deraf, at dens Udspring beskrives som øvre Del af Maxillen og Orbicularis-Omkredsen. Derimod er det vanskeligere at identificere hans m. levator anguli oris; den beskrives som bredest oventil gaaende fra øvre Del af Præmaxillen til Hjørnetandsgruben, dækket af Nerver og depressor nasi (= m. maxillo-labialis); maaske den er en Del af m. nasalis; herpaa tyder, at m. compressor naris beskrives som værende i Sammenhæng med den; men efter Beliggenheden svarer den snarere til pars supralabialis m. buccin. En Del af m. nasalis, nemlig den, der gaar op over Snudebrusken, er rigtig erkendt som m. compressor naris, Udspringet fra Præmaxillen har Murie iagttaget. Derimod er m. maxillo-labialis opfattet galt: baade m. dilator naris (= port. super.) og m. depressor alæ nasi (= port. infer.) beskrives som naaende Næseborenes Omgivelser og forreste Del af Snuden, medens deres Bundter i Virkeligheden standser forinden og breder sig mellem Sinushaarene. Pars rimana m. buccin. beskrives her under sit gamle Navn, m. orbicularis oris. Næseborenes Aabning skyldes efter Murie m. dilator naris (= Port. super. m. maxill.-labial.), idet saaledes m. recti nasi ganske er overset. Vi gaar nu over til en Beskrivelse af Snudemuskulaturen efter egne Undersøgelser (fig. 2—6).

Platysma (fig. 2, 3 *pl*, *pld*) har en ganske ejendommelig Bygning hos Zalophus, idet den paa en meget særegen Maade er delt paa tværs, ganske svarende til hvad Ruge [20—21] forstaar ved »Kontinuitätstrennung«. Hovedmassen har sit Udspring fra den dorsale Midtlinie af Halsens forreste Del (se fig. 2, *pld*); hvor langt bag til paa Halsen Muskelbundter udspringer kunde ikke konstateres, fordi det Snit, der har skilt foreliggende Hoved fra Kroppen har truffet platysma, saa at en Del heraf sidder paa Kroppen, som jeg ikke har haft til Disposition.

Muskelbundterne gaar fra den nævnte Linie nedad og bøjer saa lidt fremad, indtil de naar en Linie, der gaar fra Øret bagud og lidt nedad (fig. 2); her afbrydes de alle som én; og det er denne Brydnings- eller Delingslinie, som er saa karakteristisk[1]). Kun ved ganske tynde Senebaand er disse dorsale Muskelbundter forbundne med dem i den ventrale Platysmadel; denne strækker sig fra den omtalte Linie som en meget flad Muskel under Øret og fremad (fig. 3, *pl*); dens ventrale Muskelbundter udspringer et Sted paa Halsen (Stedet bortskaaret) uden med Senebaand at være forbundet med den dorsale Del af platysma. Fortil naar platysma til hen under bageste Del af Øjet og til Mundvigen med ganske faa ventrale Bundter. Den distale Ende af flere af platysmas Muskelbundter er indflettet i og gennemkrydses af Bundter fra m. orbicul. oculi og port. oris sphinct. prof., idet de dog aldrig gaar parallelt, der er altsaa ikke nogen Forbindelse at paavise.

Navnlig den dorsale Del af platysma er overordentlig vel udviklet.

Sphincter profundus (fig. 2—3, *sp*). Denne Muskel er her saa vel udviklet, at man kunde fristes til at kalde den fuldstændig; man kan nemlig kun teoretisk skelne mellem dens fire Dele, idet den fremtræder som en sammenhængende Muskelplade, hvis Udstrækning ventralt bagtil jeg dog ikke har kunnet konstatere. I den ventrale Midtlinie krydser Muskelbundterne over hinanden med et Par cm (fig. 3, *spo*). Denne Krydsning er interessant, thi de korte overkrydsende Ender af Bundterne har ganske samme Retning, nemlig skraat bagud og opad, som en sphincter superficialis vilde have; hvis derfor nogle af disse Bundter fra hver Side i Stedet for at fortsætte sig i sphinc. prof. indgik Forbindelse med hinanden, et Fænomen som meget ofte finder Sted paa andre Steder af facialis-Muskelgruppen, og noget der, saa vidt jeg kan se, virkelig har fundet Sted hos Cystophora (se senere), saa vilde vi have en veritabel sphinct. superficialis. — At denne Muskel virkelig kan være opstaaet paa denne Maade formoder da også Boas og Pauli. Fra Midtlinien strækker Musklen sig dorso-nasalt; med den bageste Del naar den Øret, saaledes dannende en port auricularis (fig. 3, *pa*), der virker som depressor-retractor auric.; mellemste Del, portio intermedium (*pi*), naar til Strækningen mellem Øret og Øje; tredje Del, port. palpebralis (*pp*), fortsætter sig med nogle Bundter direkte i m. orbicularis oculi, hvilket er en Kendsgerning af betydelig Interesse; og med andre hefter den sig til bageste Øjekrog; og endelig omgiver forreste Del, port. oris (*po*), bageste Del af Mundaabningen som en »m. orbicularis oris«; denne Del er iøvrigt interessant ved sin Differentiation i den ventrale Del; her er den nemlig spaltet i tre Lag, en overfladisk, en mellemste og en dybeste, der dog alle tre er forbundne med hinanden ved flere aberrerende Bundter, saa at Billedet er noget udvidsket, og idet Hele taget kun kan iagttages ved meget omhyggelig Dissektion. Spaltningen begynder noget ovenfor Mundvigen; den dybeste Del er simpelthen Fortsættelsen af sph. prof.; den mellemste Dels Bundter gaar over sph. prof., men under platysma, under hvis forreste Del nogle standser, medens Hovedmassen, der er temmelig kraftig udviklet, fortsætter sig nedad til den ventrale Midtlinie, idet de bageste bøjer lidt bagud, de forreste fremad, alle løber de ud i Huden; endelig er der den overfladiske Dels Bund-

[1]) Hos Ursus malayanus har jeg fundet den samme Deling af Platysma; men her skyder Muskelbundterne af de to Afsnit sig over hinanden, hvilket ikke er Tilfældet hos Zalophus.

ter, der træder ud fortil mellem platysma-Bundterne for at fortsætte sig nedad og bagud til lidt nedenfor platysma, hvor ogsaa de taber sig i Huden. Fortil over Munden gaar port. oris omtrent til en Linie fra forreste Øjekrog til de bageste Sinushaar paa Snuden; den bageste Halvdel af Mundspaltens øvre Rand begrænses af port. oris.

M. orbicularis oculi (fig. 2, 3, 4, *oo*), er her interessant ved, at den fuldstændig omgiver Øjet, dog ikke kontinuerligt, men Afbrydelsen finder Sted ved bageste Øjekrog, ikke ved forreste, som ellers er det almindelige, og ved at den direkte hænger sammen med port. palpebr. sph. prof., og endelig ved, at den inderligt slutter sig til m. naso-labialis. Forløbet af Bundterne er angivet i den skematiserede fig. 4[1]). En meget stor Del af m. orb. oc. er faktisk dannet af Muskelbundter fra sph. prof.: fra port. palpebralis fortsætter Muskelbundterne sig over Øjet dannende Midterdelen af orb. oc.; flere af dem fortsætter sig helt rundt om Øjet, og gaar bag bageste Øjekrog opad og bagud, idet de noget vifteformigt udbreder sig i Huden. Fra hvad man kunde kalde aller forreste Del af port. palpebral. gaar der Bundter op foran Øjet, de bøjer bagtil ovenover og igen nedad bag Øjet, hvor de rettes skraat fremad, idet nogle ikke er langt fra at krydse sig selv igen under Øjet, medens andre ikke naar saa langt; de danner yderste Del af orb. oc. Endelig udgaar fra en lille Senestribe ved bageste Øjekrog Muskeltraade fremad over Øjet omkring dette fortil og under dette bagud, hvor nogle ender ved Udgangspunktet (den fuldstændige Ring, der altsaa kun afbrydes af den omtalte Senestribe), medens andre fortsætter horizontalt bagud ganske fremtrædende som en *m. horizontalis* (Boas og Pauli); de sidder nøjagtigt paa samme Sted som m. horiz. hos Hunden, og Sammenligningen styrkes yderligere ved, at enkelte af Bundterne har løsrevet sig og standser ved, eller rettere begynder ved bageste Øjekrog ganske som hos Hunden; jeg mener herefter, at der ikke kan være Tvivl om Homologien af disse horizontale Muskelbundter hos Zalophus og m. horizontalis hos Hunden; og da m. horizontalis her ganske klart er en Del af m. orbic. oc., om end smaat paa Vejen til at spalte sig fra, saa anser jeg det for sikkert, at m. horizontalis hos Hunden er afspaltet fra m. orbic. oc., hvilket ogsaa Boas og Pauli antyder.

Bagved m. orbicularis oc. ligger Bundter, der paa deres midterste Del er koncentriske med m. orb. oc., men opad og nedadtil løber vifteformet ud i Bindevævet under denne; de er temmelig korte, naar kun i Højde med henholdsvis øverste og nederste Rand af m. orb. oc. Ganske lignende Bundter ligger foran Øjet, dog gaar de her jævnt over i m. naso-labial., forbinder altsaa m. naso-lab. med m. orb. oc., eller rettere sagt med port. palpebral. sph. prof. Jeg betragter det som utvivlsomt, at vi her har at gøre med henholdsvis *m. post- og præorbicularis;* thi ved deres Beliggenhed og Afledning svarer de nøje til, hvad der af Boas og Pauli er fundet hos en hel Række Pattedyr. Man kunde fristes til ogsaa at kalde den Muskelvifte, der skraat bagud og opad søger bort fra Øjet for en m. postorbicularis, men dens Dannelsessted

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[1]) I fig. 4 er det væsentligste, interessanteste, af Muskelbundternes Forløb skematisk angivet. Det maa straks bemærkes, at Muskelbundter, der kun vilde gøre Figuren uklar uden tillige at være nødvendige for Forstaaelsen, selvfølgelig er udeladte (f. Eks. de frie Bundter af forreste Del af port. palpebral., der ligger over nogle af de dybere, der fortsætter sig i m. orbicul. oc. (se forøvrigt fig. 2)).

og -maade viser, at det er uberettiget, idet vi med B. & P. ved m. postorbicular. vil forstaa en Muskel, der ligger bagved m. orb., og bestaaende af fra denne afspaltede oprindelig koncentriske Bundter. Det vil være unyttigt at give den omtalte Muskelvifte, der kunde forveksles med en m. postorb., et særligt Navn. Ansigtsmusklerne er saa tilbøjelige til Udspaltning og individuel Fortsættelse af Bundter, at man aldrig kunde blive færdig med at give Navne til alle Variationer; kun til de Variationer, der optræder konstant hos et større Antal Pattedyr er det formaalstjenligt at give Navne.

De Slutninger, jeg her er kommet til, skal jeg atter summere: m. orbicularis oculi dannes hos Zalophus for en meget væsentlig Del af sphinct. prof.; M. horizontalis dannes af m. orbicul. ocul.; M. post- og præorbicul. af m. orbicul. ocul. eller sphinct. prof. Med andre Ord, m. orbicularis-Komplekset synes hos Zalophus at være udgaaet fra sphinct. prof., og ikke som hos saa mange andre Pattedyr fra platysma. Man kommer her uvilkaarlig til at tænke paa Forholdet hos homo, hvor m. orbicul. ocul. efter FUTAMURA [8] embryonalt først dannes af sphinct. prof., derefter af platysma, idet der er Mulighed for, at det samme fandt Sted hos andre Pattedyr; man kunde da tænke sig, at Zalophus er blevet staaende ved Dannelsen af m. orb. oc. fra sphinct. prof.

M. naso-labialis (fig. 2, *nl*). Denne Muskel er overmaade kraftigt udviklet; den fremtræder med to Lag, som er ret vel adskilte; det overfladiske udspringer fra Midtlinien af Pandehuden, eller rettere fra det subcutane Bindevæv mellem Øjnene og omtrent ned til det Sted, hvor Snudebrusken bliver fri af Næsebenene; herfra strækker Bundterne sig naso-ventralt ned til Vibrissæ, mellem de øverste af hvilke de insererer sig; denne overfladiske Del er i direkte Sammenhæng med m. præorbicul.; den overlejres til Dels af frit i Huden endende Bundter af port. oris. sphinct. prof. Det dybere Lag udspringer fra Kraniet lige foran Øjehulen, samt fra en distinkt Senestribe lidt foran og under forreste Øjekrog; (det bemærkes, at til den øverste Side af Senestriben, der ligger parallelt med Øjespalten, hefter sig m. orbicul. oculi-Bundter; det ser altsaa ud, som om m. orbicul. ocul.-Bundter kom dorsalt omkring Øjet og dannede en Del af m. naso-labial., blot afbrudt ved denne Senestribe; Kontinuitätstrennung?). Derfra gaar det parallelt med den øvre Del over port. super. m. maxill.-labial. ind under port. infer. maxill.-labial., og ind mellem Bundter af pars rimana m. buccin. til Overlæben.

M. maxillo-labialis. Ligesom hos Hunden finder vi her to vel adskilte Dele. Udspringet er fra Overkæben lidt under og bag foramen infraorbitale; Retningen er nasal parallel med Mundranden; ganske kort efter Udspringet viger de to Dele, port. infer. og port. super., ud fra hinanden adskilt af m. naso-labialis, der kiler sig ind mellem dem.

Portio inferior, som efter sit Lejringsforhold snarere skulde kaldes port. superficialis, da de to Afsnit mere fremtræder som et ydre og et indre Lag end som et øvre og nedre, strækker sig fremad under port. oris sphinct. prof. hen til bageste Del af det Parti af Snuden, hvor Sinushaarene sidder og ind mellem disse, hvor de ret hurtigt taber sig; deres Forløb er ret vanskeligt at udrede paa Grund af de enorme sinus vibrissarum (de kan være over 1 cm lange og 0,4 cm brede). Musklens Form er smalt vifteformig, idet den ved sit Udspring er mere rundagtig og smallere end i sin distale Del, hvor den er bred og flad.

Portio superior ligger som nævnt dybere, breder sig ikke distalt, men beholder omtrent samme Gennemsnitstykkelse i hele sit Forløb; den distale Ende ligger i Højde med Overkanten af Sinushaarenes Omraade, den inserer sig mellem nasalis-Bundter, og standser inden Næsefløjene er naaet.

M. buccinatorius (fig. 5—6) er vel udviklet. Den minder i sin Bygning meget om Hundens. Der er ogsaa her en mere overfladisk Del med dorso-ventrale Bundter, der bøjer ud i Over- og Underlæbe som en pars rimana, og en dybere Del, med longitudinale Bundter.

En Slimhindefold, der findes hos Hunden, er ogsaa til Stede her, omend ikke saa dyb.

Den overfladiske Del har sin største Bredde dorso-caudalt for Mundvigen; de bageste og mest overfladiske Bundter gaar ikke omkring Mundvigen, men tager deres Udspring i Bindevævet bag denne (sammenlign de tilsvarende hos Hunden), gaar derfra dorso-nasalt, bøjer omkring den dorsale Kant af Slimhindefolden og insererer sig paa Maxilla over de bageste Præmolarer; de forreste Bundter gaar bueformigt omkring Mundvigen, jo dybere beliggende de er, desto længere naar de frem i Underlæben; i Overlæben forholder de sig paa samme Maade, idet ogsaa her de dybere naar langt frem, dannende en ret kraftig *pars rimana* (sphincter oris partim, Autt.) (fig. 5, *rb*); de mere overfladiske standser ud for p2 eller er rettet noget opad; og her gentager sig da det samme som man finder hos Hunden, blot mere udpræget: der dannes en *pars supralabialis* (fig. 5, *slb*); dette Muskelafsnit fremtræder nemlig hos Zalophus som en selvstændig Muskel, hvis Bundter er rettet ventro-dorsalt; Udspringet er vævet ind mellem Bundterne af pars rimana, enkelte Bundter synes (ligesom hos Hunden) at være i direkte Fortsættelse af de omtalte opadbøjede rimana-Bundter; Musklen breder sig lidt vifteformigt og insererer sig paa Maxilla. Pars rimana fortsætter sig videre ud paa Overlæben liggende tæt op til Slimhinden, og naar helt ud til Snudespidsen under septum nasi, hvor den mødes med de symmetriske Bundter; men her er det meget vigtigt at bemærke, at Musklen i dette sit distale Afsnit skifter Karakter; fra at være en flad og ikke særlig kødet Muskel svulmer den nu op, og fremtræder ganske som en Del af m. nasalis, men som en Del, der ikke paa nogen Maade naturligt lader sig sondre fra denne Muskel, den er altsaa en integrerende Del af m. nasalis. Dette Forhold spiller, som vi straks skal se, en afgørende Rolle med Hensyn til Forstaaelsen af m. nasalis' Genese.

Ventralt bøjer buccin.-Bundterne omkring Mundvigen og ender vifteformigt under første Tredjedel af Underlæben, idet nogle af Bundterne gaar langs Læberanden, andre derimod er rettet skraat nedad og fremad; af disse sidste har de dybeste et nogenlunde ret Forløb, idet de ikke bøjer omkring Mundvigen, men standser udfor og bagved denne.

Den *dybere Del* af m. buccin. hefter sig bagtil til tuber maxillare, og har herfra Retning mod Mundvinklen, hefter sig lige bag denne paa Kindens Slimhinde; den er smallere og mere dorsalt beliggende end hos Hunden.

M. nasalis (fig. 5, 6, *n*). Som allerede nævnt hænger denne paa det nøjeste sammen med m. buccin. Den har her som hos de andre af mig undersøgte Pinnipedier opnaaet en enorm Udvikling. Udspringet er fra en udstrakt Basis: for det første fra hele Mellemkæben ligesom m. nasalis hos de terrestre Rovdyr, men herfra udbreder den sig til Partiet foran Mellemkæben under Snudebrusken, hvor Bundterne dels hefter sig med smaa senede Partier paa nederste frie Rand af septum cartil. nasi og dels mødes med de symmetriske; bagtil griber Udspringet lidt over paa Overkæben, nemlig ud for Hjørnetanden; Bundternes Forløb fra denne Basis er meget kompliceret, navnlig fortil: fra forreste Del af Mellemkæben og fra septum samt fra Partiet under dettes frie Del udstraaler Bundterne radiært som i en Halvkugle, saaledes at de inderste Bundter ligger tæt op til Snudebrusken og Næseslimhinden og Mellemkæben, medens de øvrige gaar ud til Huden nogenlunde vinkelret paa denne, idet Snudepartiet jo her er stærkt hvælvet; saaledes løber Bundter ud mellem og parallelt med Sinushaarene, andre op over Næseryggen og mødes saa vidt jeg kan se her med de symmetriske, og nogle løber tilbage direkte over i pars rimana m. buccin., konstituerende største Delen af denne. Fra Mellemkæben og forreste Del af Overkæben gaar m. nasalis-Bundterne dorsalt lidt caudalt; de inderste ligger tæt op til Snudebruskens Sidedele samt det benede Parti lige bag Snudebrusken, idet de naar op paa Næseryggen insererende sig i Huden ovenpaa denne; de mere yderligt beliggende kiler sig ind mellem m. naso-lab.-Bundterne, idet de straaler ud omtrent vinkelret paa Huden, ud mellem Sinushaarene og m. maxillo-labial.-Bundter.

Som tidligere nævnt formoder allerede Boas og Pauli at m. nasalis stammer fra m. buccin.; og Forholdet hos de terrestre Rovdyr, som jeg har undersøgt, sandsynliggør denne Opfattelse. Her hos Zalophus (og som vi skal se ogsaa hos andre Pinnipedier) synes Beviset for Opfattelsens Rigtighed at foreligge. Denne Opfattelse gaar da nærmere ud paa følgende: analogt med Dannelsen af pars supralabialis m. buccin. er Dannelsen af pars nasalis m. buccin. foregaaet: fra Insertionsstedet af m. buccin.-Bundter er andre Bundter, tildels ved »Kontinuitätstrennung«, opstaaet, Bundter som formeres i Antal og derfor maa have bredere Udspringsbasis, hvilket for m. nasalis' Vedkommende resulterer i, at de griber over paa Mellemkæben; og endvidere forandres Retningen eftersom nye Opgaver overtages af de nye Bundter. Tilsidst bliver Bundterne frie, dannende en særlig vel afsondret Muskel uden paaviselig Sammenhæng med Modermusklen.

Min Opfattelse af m. nasalis' Genese er altsaa denne: Pars rimana-Bundter m. buccin. har som en Del af »orbicularis oris« strakt sig helt fortil til Næseborenes Sidevæg og til nedre Del af Næseskillevæggen. Nogle af disse Bundter er degenererede i deres proksimale Del, saaledes at kun den distale Del, der hefter sig i Næseregionen, er bevaret, og den frie Ende heraf kommer saaledes til at ligge i det omgivende Bindevæv, overfladiske Bundter kan endog naa Huden; andre saadanne Bundter har da udviklet sig; deres fixe Punkt maa da for at faa Plads rykkes ind paa Overkæben og Mellemkæben, og deres frie Ender straaler mere og mere lodret ud mod Huden, ja nogle af dem, de øverste, bøjer endda opad mod Næseryggens Hud, viser et Forløb altsaa, der er meget divergerende fra de oprindelige Bundters Retning.

M. mentalis (fig. 3, *m*) er ligeledes kraftig udviklet; den udspringer fra den dorsale Rand af Underkæben samt fra ca. tre fjerdedele af forreste Halvdel af dennes laterale Flade, uden Afbrydelse gaaende over i den symmetriske. Den fremtræder snarere som et Antal mere eller mindre isolerede Bundter end som en sammenhængende sluttet Muskel; dette Forhold skyldes det, at Bundternes Retning ikke er den samme overalt, men som det ses paa Billedet snart mere nedad langs Underkæbens Flade, snart mere udefter, vinkelret paa Huden; snart mere caudo-ventralt, snart mere ventralt eller endog lidt antero-ventralt rettede. Nogle er kortere, nemlig de, der er mere vinkelret paa Huden, andre længere, nemlig de, der ligger op ad Underkæben; fælles for alle Bundterne er det, at de alle naar Huden, samt deres ventrale Retning. De kraftigste Bundter findes dorsalt, Udspringet tæt ved Alveolærranden af p1—p2.

Det ejendommelige ved denne Udformning af m. mentalis i Modsætning til Hundens vel afgrænsede Muskel er altsaa denne Individualisering af Bundterne; dette Forhold er interessant; thi det oplyser Forholdet mellem m. mentalis og m. recti labii inferioris; mange af disse m. mentalis-Bundter kunde nemlig udmærket godt fortjene Navnet m. recti lab. infer., hvis Beliggenhed og Anordning er identisk dermed. Naar jeg alligevel giver hele Komplekset Navnet m. mentalis, ligger det i, at der ikke kan etableres nogen Forskel mellem én Gruppe Bundter i Modsætning til en anden, idet der er alle Overgange mellem typiske m. mentalis-Bundter og typiske m. recti-Bundter. Heraf tør man vel slutte, at m. recti labii inferioris sandsynligvis kan afledes fra m. mentalis. — Derimod er det desværre ikke lykkedes mig her hos Zalophus at paavise nogen Forbindelse mellem m. buccin. og m. mentalis, der kunde benyttes som Basis for den sidstes Afledning fra den første.

M. recti labii inferioris fremtræder altsaa ikke som en Muskelgruppe for sig.

M. recti nasi (fig. 6, *rn*) har her en smuk og sammenhængende Udvikling, den præsenterer sig virkelig som en afsluttet Muskel, hvis Udspring gaar fra Grænsen mellem cart. navicul. og proc. lateral. dorsal. samt fra Slimhinden, der forbinder disse Bruske længere fremme, hvor de ellers er fri af hinanden, helt hen til øverste Del af Næseborets laterale Væg. Den strækker sig i omtrent hele Snudebruskens Længde, saaledes at kun den allerforreste og allerbageste Del heraf er fri. Fibrenes Retning er skraat opad vinkelret paa Huden. De frie Ender kiler sig ind mellem m. nasalis-Bundter og de forreste m. naso-labialis-Bundter; her kan man se dem stikke frem, naar Huden er bortdissekeret, dog naar jo som ovenfor nævnt ogsaa m. nasalis-Bundter til Huden i denne Egn, saa det er umuligt uden videre at afgøre, til hvilke af disse to Muskler de frie Ender hører, førend man har fulgt deres Forløb nøje.

Nervus facialis

(fig. 7).

Nerven træder som sædvanlig frem bag Masseterranden caudo-ventralt for Øret; Grunddelen, inden den deler sig, er omgivet af gl. parotis, dog frigør den sig fra denne Kirtel hurtigere end hos Hunden. Allerede under Parotis afgives *r. postauricularis* (= n. occipitalis posterior, Ruge [20]), der straks deler sig i to Grene. Fra Stykket mellem Afgivelsen af denne og Delingen i de tre Hovedstammer, der finder Sted i selve Kanten af gl. parotis, udgaar to spinkle Grene til platysma, af disse kommuniserer den forreste med en lille Gren fra r. temporalis. Saa afgives r. mandibularis og umiddelbart herpaa deler n. facialis sig i r. maxillaris og r. temporalis, denne sidste spalter sig imidlertid øjeblikkelig ud i flere Grene saa at Facialisdelingen her nærmest fremtræder som en Deling ikke i to, men i flere Grene.

R. maxillaris (*rm*) løber nu fremefter lidt under Overkanten af platysma, uden paa Masseters Overflade, den deler sig allerede omtrent midt paa denne Muskel i to lige kraftige Grene, der viger lidt ud fra hinanden, ca. 1 cm, for atter ud for Mundvigen at løbe sammen igen, idet de dog undervejs har anastomoseret; den dorsale af de to anastomoserer livligt med et Par af Grenene fra r. temporalis udfor forreste Masseterrand; kort foran det derved dannede Pleksus afgives en kraftig Gren til m. naso-labialis i stærk Modsætning til Forholdet hos Hunden, hvor samme Muskel innerveres fra r. temporalis. Straks efter afgives Grene til m. maxillo-labialis. Den ventrale af de to r. maxillaris-Grene modtager *r. communicans*, der kort inden Samlingsstedet afgiver en lille Gren til sph. prof.; endvidere innerverer den m. buccin.s bageste Parti; som en kraftig Nerve løber den nu sammen med den dorsale Gren; den atter samlede r. maxillaris afgiver et Par Smaagrene til pars rimana m. buccin.; inden den deler sig i flere kraftige Grene løber den mellem Sinushaarene ned til n. infraorbitalis, til hvilken den lægger sig tæt op, uden dog saa vidt jeg kan se, at anastomosere med denne; de distale Grene ligger ret dybt; de fleste af de Muskler, de innerverer, ligger jo ogsaa ret dybt: port. super. m. maxillo-labial., m. nasalis, m. buccin., m. recti nasi.

Ramus temporalis (*rt*) er i endnu højere Grad end r. maxillaris pleksusdannende og udspaltet. Som ovenfor bemærket spalter den sig lige fra Grunden i flere Grene, nemlig i seks; af disse maa vel den dorsale tildeles Navnet r. tempor., eftersom dens Forløb svarer ret nøje til r. tempor.s' Forløb hos de terrestre Carnivorer, ligesom den ogsaa er den kraftigste. Vi begynder imidlertid ventralt med de andre Grene; den første ligger nærmest r. maxillaris; den skiller sig helt ud fra Resten, hæver sig op over sph. prof. og innerverer platysmas' forreste Del. De andre fem anastomoserer livligt, danner i Grunden tilsammen ét kraftigt Pleksus; den ventrale af disse fem løber sammen med r. maxillaris omtrent ud for forreste Masseterrand; fra dette Sted afgiver den en Gren til port. palpebralis sph. prof. og m. orbicular. ocul. Den næste Gren innerverer de samme to Muskler; den tredje ligeledes, navnlig pars horizontalis m. orb. ocul.; den fjerde og femte, som altsaa er den egentlige r. tempor., danner et særligt udarbejdet Pleksus; de innerverer med deres distale Forgreninger bageste og øverste Del af m. orbic. ocul.; iøvrigt bemærkes følgende om r. tempor.: den afgiver en lille Gren til platysma lige under Øret, en lille Gren, der som før nævnt anastomoserer med en lignende kommende fra selve facialis-Stammen; derefter afgiver den tre r. auriculares anteriores i Stedet for én som hos Hunden; og fra dens midterste Parti udgaar Grene til m. scutularis. Det bemærkes altsaa, at r. temporalis ikke innerverer m. naso-labialis, men standser i m. orbicul. ocul.

R. mandibularis (*rd*) er ogsaa rigere udspaltet end hos de terrestre Carnivorer. Kort efter sit Udspring er den forbundet med r. maxillaris ved en ret kraftig Gren; derefter udsendes ventralt Grene til sph. prof. og platysma; saa afgives r. communicans, hvorefter den deler sig i to omtrent lige kraftige Grene, dorsalt den egentlige r. mandibul., ventralt en Gren, der udspaltes til Innervation af ventrale Partier af sph. prof. Den dorsale, altsaa r. mandibul., innerverer nu under Pleksusdannelse Dele af sph. prof. samt af m. buccin.; hidtil har den løbet paa Masseter lidt over dennes Underkant, men nu ligger den tæt op til Underkæben, i sin distale Del innerverende Underlæbemuskulaturen.

Diskussionen om Funktionen af det nu omhandlede Kompleks, vil vi for at undgaa Gentagelse gemme til Omtalen af Phoca, idet Forholdet i det væsentlige er ens hos de to Grupper af Pinnipedier.

Phoca vitulina.

Snudebygningen.

Snudepartiet (fig. 8 forestiller Halichoerus grypus, men Phoca er ganske lignende) hos Phoca er bredt og fladt, uden nogen fremspringende Snude; dette hænger sammen med, at Snudebrusken ikke rager frem over Mellemkæben. Næseborene har Form af to lateralt konkave, skraatstillede Buer, skraatstillede baade i Forhold til Hovedets Midtplan, idet deres dorsale Ende viger længere ud til Siderne end den ventrale, samt i Forhold til Hovedets Længdeakse, idet deres dorsale Ende ligger længere bagud end den ventrale. Næseborene fremtræder paa de af mig undersøgte Eksemplarer (Spirituspræparater) som to ganske lidt aabne Spalter. Septum narium (Partiet mellem Næseborene) er smalt lidt under Midten, bredende sig saavel dorsalt som ventralt, derved bestemmende Næseborenes Form; det er haarløst paa det største midterste Stykke, sort pigmenteret og forsynet med ganske fine Gruber, ikke feltet som hos Hunden; Overlæbens Philtrum fortsætter sig op paa den. Naar bortses fra det nævnte haarløse Parti er Næseborene helt omgivne af Haarklædning, der endog paa den laterale Side strækker sig lidt ind i den ligeledes sort pigmenterede vestibulum nasi.

Plica alaris, den forreste Fortsættelse af Maxilloturbinale, har nu Plads paa Næsehulens laterale Væg; den slaar sig, idet den gaar fremad mod Næseboret, opad over Næsehulens Loft og videre over paa Næsehulens mediale Væg, hvor den taber sig inden Næseboret er naaet, saaledes at den altsaa ikke ses udvendig i dettes Aabning. Det bliver sulcus, der her danner største Delen af Næseaabningen, ja man kunde sige, at sulcus *er* Næseboret hos Pinnipedierne. Beviset for denne Opfattelses Rigtighed maa først og fremmest søges i plica alaris' Forhold; den distale Ende heraf ligger jo hos Hunden medialt for sulcus, lateralt for det egentlige Næsebor; plica alaris ligger medialt for en smal Slidse, som derfor maa være sulcus, selve Næseboret er forsvundet fordi dets laterale Begrænsning, plica alaris, er faldet bort.

Snudebrusken (fig. 9) slutter sig som venteligt nær til Zalophus, dog er der visse betydningsfulde Afvigelser.

Septum cartilagineum nasi (*s*) naar ikke udenfor Mellemkæben, hvilket som ovenfor nævnt betinger Snudepartiets Afstumpethed; det fremtræder som en forholdsvis tykkere Bruskplade end hos Hunden, besidder altsaa større Stivhed; fra Dorsalranden udspringer processus lateralis dorsalis (*pld*); dens vandrette Del er bredest bagtil, jævnt tilsmalnende fortil; set ovenfra bliver »tectum nasi's« Form derfor en aflang ligebenet Trekant med Apex fortil; den bøjer saa nedad med en stor lateral Flade, der ligeledes har Form som en Trekant, og som ventralt bøjer ganske jævnt indad mod septum, ikke skarpt som hos Otaria; ogsaa denne Flade er bredest bagtil, idet Underkanten som en skraa Linie løber naso-dorsalt, længst oppe og fremme løbende ud i en Spids paa Siden af septum; denne skraa Underkant og septum danner Indgangen til Næsehulen, der saaledes bliver en skraatstillet Spalte omtrent vinkelret paa den skraatstillede Spalte som Næseborene betegner. Fra proc. lateral.s bageste nederste Hjørne udspringer cartil. navicul. (*cn*), ligesom hos Zalophus en dorso-nasalt rettet Bruskstrimmel, kun ved en smal Bruskstilk forbundet med proc. lateral. dorsal.; den er halvrendeformet, Konkaviteten medialt, og ligger omtrent parallelt med processus lateralis' Skraakant, Længden godt to Tredjedele af denne.

Processus lateralis ventralis er noget bedre udviklet end hos Zalophus, lægger sig tæt op til Mellemkæbens Inderside, smallest fortil, bredest bagtil, hvor den standser omtrent ud for process. later. dorsal.s bredeste Parti, den er uden Forbindelse med denne eller cartil. navicul. I Modsætning derimod til Zalophus findes her en vel udviklet *processus lateralis anterior*, der som et lille trekantet Fremspring udgaar fra septums forreste Kant.

Snudemuskulaturen.

Facialis-Muskulaturen hos Phoca vitulina er beskrevet af Miller [16]; men denne Beskrivelse lider af væsentlig de samme Mangler som Muries for Otarias Vedkommende. Saaledes opfatter Miller de forskellige Lag af m. naso-labialis som tre særskilte Muskler; saaledes benævnes det midterste Lag levator labii superioris proprius; den Funktion, der er udtrykt i Navnet, har Musklen virkelig, saa for saa vidt er Navnet meget betegnende; men her har vi netop et af de Tilfælde, hvor Navngivning af en Muskel efter dens Funktion viser sig at være forfejlet; thi m. levator labii superioris proprius hos f. Eks. Hunden er jo en Del af m. maxillo-labialis; det fælles Navn givet paa Grund af samme Funktion faar jo nemlig én til at tro, at det drejer sig om homologe Muskler; for at undgaa dette er det derfor nødvendigt med den voksende Erkendelse at indføre neutrale Navne. M. naso-labialis' øvre

Lag bliver som sædvanlig kaldt m. levator labii superioris et alæ nasi, medens de dybeste Lag, der her hos Phoca opnaar en vis Selvstændighed, kaldes m. levator angula oris. M. maxillo-labialis' to Afsnit er rigtigt erkendt, men ogsaa her, ligesom hos Otaria, beskrives de som gaaende helt frem til Næseborenes Omgivelser, medens de dog standser forinden mellem Sinushaarene. M. constrictor nasi (= compressor nasi) er den Del af m. nasalis, der fra Mellemkæben gaar omkring Snudebrusken, medens den øvrige komplicerede Del af samme Muskel ikke er erkendt. MILLERS m. orbicularis oris er antagelig den overfladiske transversale Del tilligemed pars rimana af m. buccin.; hans m. buccin. er lig den longitudinale Del af samme Muskel.

Platysma (fig. 10, *pl*)[1]) strækker sig hen over Siden af Hovedet; hvor langt tilbage de ventrale Bundter udspringer kan jeg ikke afgøre, da kun selve Hovedet (afskaaret i Nakkeleddet) stod til min Disposition. De nederste Bundter forløber ret, parallelt med Hovedets Længdeakse; de ender tæt bag og nedenfor Mundvigen i Huden og i det subcutane Bindevæv; derimod er de dorsale Bundter bueformede, des mere jo mere dorsalt de ligger, idet deres Udspring ligger højere oppe i Forhold til deres Endepunkt; og ca. øverste Halvdel af platysmas Bundter har deres Udspring fra Nakkens og Hovedets dorsale Midtlinie (herfra undtages dog de aller forreste eller om man vil aller øverste Bundter, hvis Udspring er noget fjernet fra Midtlinien); Bundternes Retning er først transversal, dernæst jævnt bueformet fremad, efterhaanden antagende et Forløb omtrent parallelt med de ventrale Bundter; Insertionspunkterne (i Bindevævet) ligger i en Linie, der fra et Punkt lidt bag og dorsalt for Mundvigen svagt bueformet, Konkaviteten fremad, naar tæt op foran og under Øreaabningen; paa dette Sted findes ligesom indbalsamerede i Spæk nogle svage korte Muskelbundter, som vel maa regnes for degenererede platysma-Bundter. Nogle ligeledes meget diskrete Bundter ligger ogsaa ovenpaa de nys beskrevne, paa et mindre Parti lidt bag Øret, Udspring dels fra Nakkens dorsale Midtlinie ligesom de andre, dels fra Bindevævet lidt til Siden herfor, og atter endende i Bindevæv efter et Par cm.s Forløb; ogsaa disse gør et noget degenereret Indtryk.

Sphincter profundus (*sp*) er ogsaa her en veludviklet Muskel, der som en sammenhængende Plade strækker sig hen over Undersiden og Siden af Hovedet. Bundterne i de to symmetriske Halvdele krydser ganske kort over hinanden paa samme Maade som hos Zalophus; jeg har ikke med Sikkerhed kunnet konstatere, om nogle af Bundterne løber direkte over i hinanden, saa at vi vilde faa et sammenhængende Muskelbaand fra højre til venstre Halvdel af Hovedet uden Afbrydelse; med Hensyn til Virkningen vil dette ogsaa være ligegyldigt, idet de overkrydsende Ender er indfiltrede i og fastheftede til hinanden med Bindevæv. — Man kan ogsaa her skelne mellem en port. auric., port. intermed. og port. palpebralis.

Port. auricul.-Bundternes (*pa*) Forløb er noget skraat i Forhold til Hovedets Længdeakse; regnes den ventrale Tilheftning for Udspringet er Retningen dorsonasal; de naar dels til Øret, og dels taber de sig i det under platysma liggende Binde-

[1]) Den hos Zalophus forefundne Deling af Platysmas dorsale Afsnit synes mærkelig nok ikke at forekomme her.

væv; de bageste Bundters Udspring kunde ikke konstateres, da Muskulaturen her var overskaaren.

Port. intermed.-Bundternes (*pi*) dorsale Endepunkter er ligeledes i Bindevævet under Platysma; en Linie gennem alle Endepunkterne er omtrent ret og gaar fra Partiet under Øret ventro-oralt til et Punkt lidt bag Mundvigen; her støder de først sammen med *port. palpebralis* (*pp*), der saaledes dorsalt er adskilt fra port. intermed., og derfor faar en selvstændigere Udvikling, mere Udseende af en særskilt Muskel; denne strækker sig som et ca. 1 cm bredt Baand dorsalt, inserer sig mellem nederste Bundter af m. orbicularis oculi eller fortsætter sig med en Bøjning fremad og opad parallelt med denne Muskel, hvis forreste ventrale Del den saaledes udgør. En *port. oris* mangler; i alt Fald er der kun Antydning til en Fremadbøjning af de forreste ventrale Bundter af sph. prof., men de naar ikke ind i Underlæben, taber sig i Bindevævet paa Undersiden af Underkæben.

M. orbicularis oculi (*oo*). Øjet er stort og fremstaaende, derved faar m. orbic. ocul. en ejendommelig Form; den bliver omtrent en Del af en Kegleflade med Apex udefter i Øjets Akse. Den er vel afgrænset; der findes ingen post- eller præorbicularis, i alt Fald kun svage Antydninger af den første som nogle ganske smaa diskrete isolerede Bundter bag Øjet i det tykke Lag fedtfyldte Bindevæv, der ligger i Fordybningen mellem Øje og Øre. Heller ikke findes Spor af en m. horizontalis. De fleste Bundter standser ved forreste Øjekrog, medens enkelte fortsætter sig helt rundt, og som saaledes bliver virkelige »sphincter«-Bundter. Som ovenfor nævnt udgøres den forreste ventrale Del af Musklen af Bundter fra port. palpebral. af sphincter profundus. Øjensynligt er dette det samme Forhold, som gør sig gældende for Zalophus Vedkommende i langt større Stil, saaledes at ogsaa Phoca afgiver Støtte for min Anskuelse, at m. orbicul. ocul. kan dannes af sph. prof.

M. naso-labialis (*nl*) er en kraftig Muskel med stort Tværsnit i sin distale Del. Retningen er ventro-oral, alle Bundterne paralelle. De bageste Bundter udspringer fra Øjekrogen under m. orbicul. ocul., de følgende fra Bindevævet paa Pandens og Næseryggens Midtlinje fra helt bag Øjnene og til lidt bag Næseborene. Musklen tiltager i Tykkelse distalt. Et overfladisk Lag inserer sig i Huden mellem de dorsale Rækker af Vibrissæ og længere bagtil lægger det sig hen over Overkanten af m. maxillo-labialis. Hovedparten kiler sig ind mellem m. maxillo-labialis' to Dele, samt ind mellem de dorsale Bundter af disse to Muskelafsnit. De dybest beliggende Bundter strækker sig ind paa Inderfladen af m. maxillo-labialis port. super. Endelig fremtræder nogle af de dybeste Bundter distalt som et selvstændigt Muskelafsnit, der naar til Overlæben, lidt foran dennes Midte, lige over Mundranden, insererende sig i Slimhinden. Fortil gør hele Musklen et noget reduceret Indtryk og dens Bundter naar ikke ind i Overlæbens Vulst, idet de ligesom fortrænges af m. nasalis.

Mellem orbicul. ocul. og m. naso-labial. er der ikke den intime Sammenhæng som hos Zalophus; de to Muskler optræder vel afgrænset fra hinanden, om end deres Samhørighed er umiskendelig.

M. maxillo-labialis (*ml*) er ogsaa her delt i en port. super. og en port. infer., der begge viser den samme Ejendommelighed som hos Zalophus: de standser længe forinden Næsefløjene er naaet.

Udspringet for de to Dele af Musklen er fælles; det ligger mærkeligt langt tilbage og har stor Udstrækning, det ligger paa en Linie fra et Punkt lige under foramen infra-orbitale til midt paa Kindbuens laterale Flade, hvor denne rager længst ud til Siden. Fra bageste Halvdel af dette Omraade udspringer Bundter, der forsyner baade port. infer. og port. super., medens forreste Halvdel kun giver Udspring for Bundter til port. super. Adskillelsen af disse to Afsnit finder Sted lidt bag Mundvigen.

Port. infer. er som sædvanlig overfladisk beliggende; den breder sig fortil smalt vifteformigt, idet dens Bundter kiler sig ind mellem de bageste Sinushaar tabende sig i Bindevævet mellem disse. Adskilt fra port. infer. ved r. maxillaris n. facialis, samt ved n. infraorbitalis, der efter sin Udbreden fra Foramen infraorb. fra Ventralsiden skyder sig ind mellem de to Afsnit, og endelig ved Bundter af m. naso-labialis, ligger *port. super.*, dækket i hele sit Forløb, undtagen lige akkurat i sin forreste Del af Udspringet, af andre Muskler; dens Retning er lidt dorsal, den naar ikke længere frem end port. infer., idet ogsaa den standser i den bageste Del af Overlæbens tykke Vulst; dens fleste Bundter ligger under Sinushaarene, og indkiler sig for største Delen mellem m. naso-labial.-Bundter.

Vi har altsaa her samme Forhold som hos Zalophus, at m. nasalis ligesom har fortrængt m. maxillo-labial. Naar man lægger et Snit parallelt med denne Muskel mellem to Længderækker af Sinushaar og fører det transversalt igennem til Benet, saa vil man meget smukt se, hvorledes nogle m. maxillo-labialis-Bundter lægger sig omkring de bageste Sinushaar, medens andre bøjer skraat udad mod Huden, og de dybest liggende standser udfor de øverste, medens m. nasalis-Bundter i store smukke Buer breder sig vifteformigt mellem Sinushaarene for omtrent vinkelret at naa Huden. (Paa et saadant Snit ses ogsaa smukt n. infraorbitalis ganske regelmæssigt vifteformigt spalte sig, idet den afgiver en Gren til hvert Sinushaar).

M. buccinatorius er ret svag. Den dybere longitudinale Del bag Mundvigen er ganske smal og af ringe Tykkelse. Udspringet fra Kindens Slimhinde omtrent i Højde med bageste Øjekrog, Retningen oral, Insertionen lige bag Mundvigen paa dennes Slimhinde og mellem Bundterne af den overfladiske Del af m. buccin.; denne kan her kun ret uegentlig kaldes den transversale Del, idet den som et smalt Baand bøjer skarpt om Mundvigen for som en pars rimana at danne en »orbicularis oris«; *pars rimana* i Overlæben standser godt halvvejs ude i denne, omtrent hvor det ovenfor omtalte selvstændige Afsnit af m. naso-labialis insererer sig; *pars rimana* i Underlæben er noget kraftigere, breder sig vifteformigt ud over Underkæben; de dorsale Bundter langs og parallelt med Underlæberanden naar omtrent helt ud til Underkæbesymfysen. Der findes intet Spor til nogen m. supralabialis. Mærkelig er denne ringe Udvikling af m. buccin. i Modsætning til Zalophus store komplette Udformning af samme Muskel; vi har her et af de mange Eksempler paa Phocidernes større Afvigelse fra Carnivortypen end Otaridernes.

M. nasalis har altsaa her slet ingen Forbindelse med m. buccin., saa hvis man ikke kendte Forholdet hos Zalophus og de terrestre Rovdyr, vilde man paa Grundlag af Forholdet her intet kunde udsige med Hensyn til m. nasalis' Genese. Ogsaa her er dens Udvikling stor, snarest endnu større end hos Zalophus paa Grund af Snudepartiets større Bredde fortil. Udformningen og Lejringsforholdene er ellers de samme: Udspring fra Mellemkæben, fra process. lateral. anter. og Partiet under Snudebruskens forreste Del; Bundternes Retning herfra vifteformigt til alle Sider: de fra Mellemkæben og process. lateral. anter. særlig op omkring Snudebrusken, hvis dorsale Midtlinie naas; de fra Partiet under Snudebrusken ud i Overlæbevulsten hen under og derpaa bueformigt op mellem Vibrissæ omtrent vinkelret paa Huden, dog naaes kun de midterste, store Vibrissæ; som ovenfor bemærket ses dette Forhold særlig smukt paa et Snit parallelt med Vibrissæ-Rækkerne ned mellem disse.

M. recti nasi har her naaet deres mest komplicerede og kraftigste Udvikling. Af de ret simple Forhold hos Zalophus, som atter utvungent afledes fra de terrestre Rovdyrs, er Forholdet her en videre Uddannelse.

Der findes først de sædvanlige recti-Bundter, der udspringer fra Grænsen mellem processus dorsal. lateral. og cartil. navicul.; de begynder helt inde fra Stedet, hvor de to Bruske hænger sammen endnu, Retningen er opad og lidt bagud, Insertionen i Huden noget til Siden for Næseryggens Midtlinie, indkilende sig mellem de dorsale Bundt-Ender af m. nasalis; de findes helt ud til Næseborets dorsale Kant. Andre recti-Bundter begynder ogsaa ved Grunden af cart. navicul., men deres Forløb er nogenlunde parallelt med denne Brusks Overkant, dog hæver de sig distalt, saa at Huden naas ovenfor og foran Bruskens Spids. Atter andre recti-Bundter udspringer fra forreste Del af cart. navicul.s laterale Flade og navnlig fra Underkanten med Retning dorso-nasalt, Insertion ligeledes i Huden; lignende Bundter har Udspring paa den bløde Næseslimhinde foran cartil. navicul. med Retning mere og mere udefter, vinkelret paa Huden; de vil svare til de forreste af m. recti hos Zalophus.

— Jeg har hos *Halichoerus* fundet ganske fine Muskeltraade fra Forkanten af septum cartil. til Næseborenes mediale Kanter og Huden derimellem, Muskulatur, der altsaa ligger i Partiet mellem Næseborene, og vel nærmest kunde regnes med til m. recti nasi-Komplekset.

Nervus facialis.

(fig. 11).

Ogsaa hos Phoca kan n. facialis føres tilbage til det sædvanlige Skema. **R. maxillaris** (*rm*) er saa langt den kraftigste; bortset fra den stærkt forgrenede *r. postauricularis* afgives meget kort efter Nervens Udtræden fra Kraniet en *r. mandibularis;* derefter, lige foran den bruskede Øregang en *r. temporalis;* efter et kortere bueformigt opefter rettet Forløb afgiver Nerven, der nu kaldes r. maxillaris, en ret spinkel Gren til m. orbicul. ocul., port. interm. sph. prof., samt platysma; r. maxillaris gaar nu ret fremefter; udfor Øjet afgives en lille Gren til port. palpebral. sph. prof., og umiddelbart herefter optages *r. communicans;* derefter innerveres m. maxillo-labialis, m. naso-labialis samt m. nasalis og m. recti nasi.

R. temporalis søger opad mellem Øret og Øjet i den dybe fedtfyldte rendeformige Fordybning, der findes her; paa Vejen afgives en ret kraftig Gren til Øremuskulaturen samt en noget spinklere, men livligt forgrenet Gren til m. orbicul. ocul., hvorefter Hovedgrenen innerverer m. scutularis og dorsale Del af m. orbicul. ocul.; den naar ikke fremad til m. nasolabialis, der som nævnt her innerveres fra r. maxill.

R. mandibularis fremtræder med en rig Forgrening og kraftig Pleksusdannelse. Ret kort efter Udspringet fra r. maxillaris deler den sig i to omtrent lige kraftige Grene, af hvilke den dorsale repræsenterer Hovedgrenens Fortsættelse, medens den ventrale spalter sig ud innerverende sph. prof. samt platysma. Hovedgrenen afgiver snart efter *r. communicans*, derefter under livlig Pleksusdannelse Grene til platysma og sph. prof., samt en kraftig Forbindelse til r. communicans lige inden denne sænker sig ind i r. maxill.; fremdeles innerverer r. mandib. i sin distale Del Underlæbens Muskulatur.

R. communicans er omtrent lige saa svær som r. mandibular; den naar r. maxill. ud for Øjet lidt bag port. palpebral. sph. prof., men lige forinden afgives en kort og kraftig Gren, der naar til r. maxill. lidt længere fremme; fra denne korte Gren innerveres M. buccin., samt en Del af m. maxillo-labialis.

Funktionen.

Vi kommer nu til hele dette Kompleks' Funktion; først og fremmest til Spørgsmaalet om Næseborenes Aabning og Lukning. Den gængse Opfattelse desangaaende er vistnok den, der kommer til Orde i Weber's »Säugetiere« [25] p. 545: »Die äusseren Nasenöffnungen sind durch die Elastizität ihrer Wände geschlossen und verhinderen damit das Eindringen von Wasser beim Tauchem. Durch willkürliche Muskeln werden sie beim Atemholen geöffnet.« Andre Forfattere deler denne Anskuelse, f. Eks. Boas i sin Lærebog [1] p. 657: » — Næseborene spalteformede, lukkes af sig selv ved Væggens Elasticitet, aabnes ved Muskelvirkning.« I andre Angivelser er det umuligt at se, om Forfatteren anser Lukningen iværksat af Elasticitet eller Muskelvirkning eller paa anden Maade. I Brehm's »Tierleben« [3] p. 580 finder man saaledes følgende, saa vidt jeg kan se paa Selvsyn bygget, Angivelse om hvilende Sæler: »— — nur die regelmässig sich öffnenden und schliessenden Nasenlöcher geben Kunde von ihrem Leben«; og et andet Sted p. 603; »Die Nasenlöcher werden beim jedem Atemzuge geöffnet, hierauf sofort wieder geschlossen und bleiben auch wenn das Tier auf dem Lande ruht, bis zum nächsten Luftwechsel zusammengekniffen«. Eller for at tage et Citat fra Lütkens [14] Lærebog: »Næseborene kunne spiles meget vidt op, naar Sælen trækker sit Vejr over Vandet, men lukkes ganske tæt til naar den dykker«.

Skarpt imod Antagelsen af Næseborenes Lukning paa Grund af Væggens Elasticitet hos i alt Fald Hvalrossen staar Murie [18] p. 435—436: »In the living Walrus, which I had many opportunities of watching, it was curious to observe the manner of closure and dilatation of the nares. In coming out of the Water, or under other circumstances, where a full inspiration takes place, the dilatatores narium act sharpely and drag the alar fibro-cartilages with a jerk outwards, producing a wide oval orifice to each nasal opening. Then, as respiration becomes easier, the nares assume the appearance delineated in fig. 5, Pl. LII (— man ser her en spalteformet Aabning svarende til den der ses paa min Figur 8). After a time, or when reentering the water, a quick sudden closure of the nostrils is effected by muscular action, when the alar fibro-cartilages and their appendices are thrown inwards and outwards, affectually obliterating the outer nasal openings, which are reduced, as depicted in fig. 4, *an*, Pl. LII, to two obtuse angular slits. Whilst the above is the more pronounced mode of action, yet, under quieter conditions, these steps of dilatatation and closure occur more gradually, though the process is similar to what has been described.«

Man kunde maaske vente at finde nogle Fingerpeg i Retning af Spørgsmaalets Løsning ved en Betragtning af Billeder i Litteraturen. Men her bliver man skuffet. Fotografier maa, for overhovedet at være brugelige i denne Sammenhæng, være Momentoptagelser, og disse kan ligesaa godt gengive den ene som den anden Stilling af Næseborene; man ser saaledes i Brehm [3] p. 595 to Fotografier, det ene af Phoca vitulina med halvaabne Næsebor, det andet af Halichoerus grypus med stærkt tilknebne dito. Fotografier af levende Dyr kan altsaa ingen Oplysninger give os, ligesaa lidt som Tegninger af levende Dyr, idet her Tegneren efter sin Opfattelse af det karakteristiske ved Dyret vil gengive Næseboret aabent eller lukket. De eneste Tegninger, der kunde give os Oplysninger er i Virkeligheden saadanne af Lig, saa underligt det end lyder; thi naar Musklerne er bløde, efter at Dødsstivheden har forladt dem, vil Næseborenes Vægge stille sig i absolut Hvilestilling; hvis det nu er Elasticitet i disse Vægge, der bevirker den tætte Tillukning, der finder Sted, naar Dyrene dykker, saa vil vi paa døde Dyr finde Næseborene tæt tillukkede; og vi skal ret straks komme tilbage hertil. Hvis nu Tegninger af Lig viser Næseborene tæt tilknebne, saa er der Sandsynlighed for, at der er Elasticitet med i Spillet. Nu har jeg i Litteraturen imidlertid kun fundet ét saadant Billede, som direkte er angivet tegnet efter et Lig. Det er i Challenger reports [4], Pl. I, forestillende en ♀ af Macrorhinus leoninus, og det fremstiller Næseboret temmelig vidt aabent. Men nu skal det villigt indrømmes, at det ikke er tilladeligt heraf at drage den Slutning, at Næseborets Hvilestilling er den aabne, thi det tegnede Eksemplar har været nedsaltet, og det er ikke godt at vide, om der ikke under Nedsaltningen af Dyret er øvet Vold paa Næseboret, f. Eks. ved Indpropning af Salt el. lign., eller om man har aabnet Næseboret for at give Dyret et mere levende Udtryk. — Nu har jeg imidlertid selv, inden jeg overhovedet havde skænket hele dette Spørgsmaal en Tanke, tegnet Snudepartiet af en Halichoerus grypus set forfra (fig. 8). Eksemplaret (et Hoved) blev forsigtigt taget op af den Spiritus, hvori det var konserveret, forsigtig skyllet af, stillet op og tegnet med Prisme. Man ser her Næseborene som to svagt aabnede Spalter. Jeg har senere undersøgt et Par andre konserverede Eksemplarer af Phoca vitulina og Halichoerus grypus og fundet det samme: Næseborene fremtræder som to svagt aabnede Spalter paa døde Dyr; disse Fund støtter altsaa ikke Antagelsen om Næseborenes Sammenknibning under Dykning paa Grund af Elasticitet i deres Vægge.

Vi vil nu se paa hvorledes det forholder sig med Elasticiteten; dette kan ikke afgøres paa konserveret Materiale; her har Hærdningen vel bevirket en Fixering af Næseborenes Hvilestilling, men tillige at Vævene er blevet stive og derfor ikke giver noget korrekt Billede af de friske Vævs Forhold. Jeg var imidlertid saa heldig at kunne undersøge en Halichoerus død i Københavns Zoologiske Have i frisk Tilstand, d. v. s. Dagen efter dens Død. Næseaabningerne viste netop den svage spalteformige Aabning, jeg nylig har talt om; trak man deres Ydervægge til Siden ydedes ingen følelig Modstand, og naar man derefter gav Slip, antog Næseborene kun langsomt den tidligere Form; der var altsaa ikke Tale om Elasticitet af anden Art end den, der altid giver sig til Kende, naar man forandrer bløde, døde Vævs naturlige Form, f. Eks. Muskler, hvoraf netop det omhandlede Partis Hovedmasse bestaar; og den beklædende Hud besidder heller ingen Elasticitet, derom overbeviste jeg mig ved den efterfølgende Dissektion paa det friske Materiale. — Noget anderledes forholder det sig med Zalophus. Her synes der at gøre sig en vis Stramhed gældende i Bygningen af Huden i Næsefløjene (Næseborenes laterale Væg); om virkelig Elasticitet kan der dog heller ikke her være Tale; men Hvilestillingen synes dog at være en tættere Tillukning af Næseborene end hos Phociderne; men selv her frembyder det ikke nævneværdig Modstand paa konserveret Materiale at aabne Næseborene[1]).

Vi kommer saaledes til det Resultat, at en ren automatisk Tillukning af Pinnipediernes Næsebor under Dykning ikke er fyldestgørende til at forhindre Vandets Indtrængning i disse (herimod kunde maaske gøres gældende, at Vandet i Stedet for at trænge ind i maaske snarere ved Tryk paa Omgivelserne vil lukke Næseborene).

Min bestemte Opfattelse er denne: Den faste Tillukning besørges af m. nasalis. Som vi har set lægger denne Muskel sig op omkring Snudebrusken; idet den trækker sig sammen, bliver den kortere, og da den i slap Tilstand beskriver en Bue med Konkaviteten indefter, vil den nu afflades, hvorved cartil. navicul. samt Slimhinde og proc. lateral. dorsal. føres ind mod septum, samtidig med de bløde Dele distalt for disse Bruske; og aller yderst omkring Næseaabningen, hvor m. nasalis ikke kan antages at have nogen direkte Sphincter-Virkning (ialt Fald har jeg ikke kunnet paavise m. nasalis-Bundter her, der kunde antages at have den Virkning), vil Huden følge med de umiddelbart indenfor af m. nasalis paavirkede Dele, og trykkes indad mod Næseborets mediale Væg; vi faar saaledes netop den hurtige pludselige Lukning af den sidste spalteformige Aabning, som Murie har iagttaget hos Hvalros; hans Opfattelse af Forholdet hos Hvalros kan jeg altsaa for mit Vedkommende føre over paa De øvrige Pinnipedier ogsaa.

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[1]) Efter at dette var skrevet modtog vi paa Zoologisk Laboratorium i Sommeren 1920 en selvdød Zalophus fra Zoologisk Have. Den viste det samme Forhold som ovennævnte Halichoerus: De spalteformige Næsebor var 2—3 mm vide, altsaa ikke tæt tillukkede; og der var ikke tale om Elasticitet i deres Vægge, omend disse var noget mere stive end hos Halichoerus.

Man kunde heller ikke godt tænke sig Tillukningen besørget alene af den forholdsvis svage Kraft, som Elasticitet altid vilde have, hvis Næseboret skal kunne aabnes med nogenlunde Lethed, naar man tænker paa den voldsomme Byttefangst under Vandet, hvor sikkert alle Facialmusklerne kommer i Bevægelse, hvorved f. Eks. ved Sammentrækning af m. maxillo-labial. Næseboret let kunde tænkes aabnet.

Hvorledes iværksættes nu den modsatte Bevægelse: den ved Indaandingen regelmæssige Aabning af Næseborene? — Efter de ældre Forfattere, Murie for Otarias Vedkommende [17], Miller for Phoca vitulinas Vedkommende [16] iværksættes den ved Kontraktion af m. dilator naris (= port. super. m. maxillo-labial.). Efter de tidligere anførte anatomiske Data vil enhver imidlertid let se, at det vilde være et altfor stort Apparat at sætte i Gang for at faa Næseborene aabnede; hele den kolossale Overlæbe med Sinushaarene og m. nasalis maatte altsaa flyttes for hver Gang; og tilmed vilde dette ikke engang være tilstrækkeligt, thi kun den ydre Del af Næseaabningen med Næsefløjene vilde blive paavirkede, medens dog ogsaa den længere tilbage liggende cartil. navicul. og proc. later. dorsal. med den forbindende Slimhinde maa føres udad for at skaffe vid Adgang for Luften til det ofte stærkt lufttrængende Dyr. (At imidlertid en kraftig Kontraktion af M. maxillo-labial. bevirker, at Næseaabningens laterale Væg trækkes til Side, er en Selvfølge, idet jo hele Overlæbevulsten med Vibrissæ danner en ret fast Enhed paa Grund af det faste Bindevæv mellem Vibrissæ og den overliggende Hud; et Træk i Vulsten bagud vil derfor forplante sig til dens forreste Ende, altsaa til Næseaabningen; og dette vil let kunne ske under Byttefangsten i Vandet; her vilde der opstaa en Fare for, at Vandet kunde trænge ind i Næsehulen, hvis denne ikke lukkedes ved Muskelvirkning.)

Opgaven er da ogsaa løst paa en meget snildere Maade: den Udvidelse af forreste Del af Næsehulen ved Hjælp af m. recti nasi-Bundter, man finder Begyndelsen til hos Fissipedierne, har her naaet sin fulde Udvikling. *M. recti*-Bundter opstaar praktisk talt paa hele Lateralvæggen af forreste Del af Næsehulen; nøjere Lejringsforhold er omtalt; da Huden, de insererer sig i, er forholdsvis fast, (den bliver det navnlig naar de to symmetriske m. recti-Grupper kontraheres samtidig, thi saa strammes Huden over Næseryggen) vil en Kontraktion bevirke en kraftig Udvidelse af hele den Kanal, som det paagældende Omraade danner; Luften faar let og uhindret Adgang. Det siger sig selv, at det er af stor Betydning, at Aabningen og Lukningen er henlagt til Muskler i Næseborenes umiddelbare Nærhed; herved kan de Muskler, der ellers hos andre Rovdyr bevirker Udvidelsen, anvendes til andre Formaal; af hvilken Beskaffenhed disse er skal vi nu straks undersøge.

Som tidligere nævnt findes der hos Halichoerus, og formodentlig ogsaa hos Phoca, nogle fine Muskelbundter fra septums Forkant til Næseborenes mediale Kanter; en Kontraktion af disse vil yderligere bidrage til at aabne Næseboret, idet dets mediale Rand derved trækkes indad mod Midten; man ser da ogsaa baade paa levende Dyr under stærk Indaanding og paa Fotografier af Dyr under denne Proces, at Næseborenes mediale Rand viser en kraftig Konkavitet, kraftigere end naar Næseborene er i Hvile.

— Naar man betragter de store Sinushaar i Overlæben, er man klar over, at de for at kunne opfylde deres Formaal som Sanseredskaber fuldt ud, maa kunne bevæges. Flere Forfatteres Iagttagelser gaar da ogsaa ud paa, at Vibrissæ kan bevæges baade en masse og enkeltvis, det sidste i alt Fald for nogle Formers Vedkommende. Navnlig er her et Arbejde af Schmidtsdorff [22] lærerigt. Det omhandler Hvalrossens Overlæbe, særlig Sinushaarene; (Spørgsmaalet om deres eventuelle Funktion som Siapparat skal vi her ikke komme ind paa). Det viser sig, at Sinushaarene sidder ligesom i en lille Sæk (ikke at forveksle med selve Blodsinus'en), en Indkrængning af Huden, men en Sæk, der kan krænges ud; og da Sækkens Bund er fastheftet til Sinussækkens Overkant vil Udkrængningen bevirke, at ogsaa Sinushaaret skydes frem, nemlig dobbelt saa langt som Sækkens Dybde. Efter Schmidtsdorff findes der paa Sinussækken hos Hvalros to ringformige Opsvulmninger; til den øverste af disse hefter der sig Muskler, der gaar saavel skraat opad som skraat nedad: »Sie bewirken meiner Ansicht nach das Ausstülpen und Einziehen der Borsten.« Da jeg ikke selv har undersøgt Trichechus, skal jeg ikke videre udtale mig om dette Forhold. Men hos de af mig undersøgte Pinnipedier har jeg ikke kunnet eftervise noget saadant; derimod har jeg i alt Fald hos Zalophus kunnet paavise en Muskelvifte med Basis af Sinushaaret som Insertionssted og herfra straalende bagud tabende sig i Bindevævet. Antagelig tjener disse smaa Muskler til at føre Spidsen af Sinushaaret fremad, idet dets Basis trækkes tilbage. Men Spørgsmaalet bliver da: hvorledes »krænges« Sinushaarene ud af de Sække, som nemlig ogsaa er til Stede hos Zalophus, Phoca og Cystophora? Her bragte et nylig i Zoologisk Have i København dødt Eksemplar af Halichoerus Klarhed: Naar man trak i Sinushaarene, krængede man Sækken ud, saaledes at dens Bund kom til at staa frem som en lille Høj over den omgivende Hud; og ved et Tryk paa Hudens Overflade vinkelret indad, kunde man faa samme Udkrængning i Stand; særlig smukt viste Fænomenet sig, da Huden var bortdissekeret: ved det vinkelrette Tryk paa Overlæben indefter kunde man faa Sinushaarene til at springe frem som Trolde af Æsker; og da jeg ikke havde kunnet paavise særlige Smaamuskler til Sinushaarene, der kunde trække dem udefter, sluttede jeg, at Hudens Overflade maatte føres indad for at faa Udkrængningen i Stand, (det, der skete ved de ovenfor omtalte Trykforsøg, var jo det, at Trykket i Overlæbevulsten indenfor Huden steg, hvorfor det eneste eftergivelige Parti, nemlig den lille Sæk, hvori Sinushaarene sidder, maatte give efter og derfor udkrænges). Og den eneste Muskel, der er i Stand til at føre Huden mellem Sinushaarene indefter er jo m. nasalis; thi dennes Anordning er jo netop den, at store Dele af dens Bundter straaler vinkelret ud paa Huden, ud mellem Sinushaarene; i Stedet for et kunstigt Tryk udefra indefter kommer saaledes et Træk indefra. Saaledes bliver da m. nasalis' Funktion en dobbelt. — Til at »rejse« Sinushaarene, det er føre dem fremefter, tjener aabenbart — foruden de hos Zalophus paaviste Smaamuskler — sikkert ogsaa m. maxillolabialis, idet en Kontraktion vil udøve Træk paa det faste Bindevæv mellem Sinushaarene, saaledes at Sinus tvinges til at indtage en mere lodret Stilling vinkelret paa Huden: Vibrissæ rejses.

— Ogsaa Murie [18] har iagttaget Vibrissæs Spil hos Hvalros. »The bristles are characteristically affected by all motor changes of the muzzle.« Han siger endvidere, at hver »bristle individually possesses a certain amount of special motor power by reason of a pencil of muscular fibres at its roof«, hvilket ganske svarer til, hvad jeg har fundet hos Zalophus.

Cystophora cristata ♀.

Snudebygningen.

(fig. 12).

Formen af Snuden slutter sig nær til de andre Phociders; den er bred og kraftig, forholdsvis kort; Næseborenes Form ligeledes som hos Phociderne i Almindelighed: to lateralt-konkavt buede Skraaspalter. Til Forskel fra Phoca er septum narium overalt haarklædt; Haarklædningen fortsætter sig et Par mm ind i Næseaabningen paa Lateralvæggen og Medialvæggen. Det subcutane Bindevæv midt paa Oversiden af Snuden har en ejendommelig svampet Beskaffenhed, paa det Sted nemlig, der ligger over den Slimhindefold, der hos ♂ opnaar en saa enorm Udvikling; Partiet staar frem som en Pude, fortil og bagtil begrænset af en svag Fure. Det bemærkes dog, at Haarklædningen her ikke afviger fra de omgivende Partiers, saaledes som hos ♂. Trods den stærke Udvikling af Overlæbevulsten er Sinushaarene ikke paafaldende udviklet; flere af dem er ganske vist ret tykke, men alle er de korte, til Dels maaske som Følge af Slid. Paa de fleste af de til Raadighed staaende Eksemplarer var Næseborene til Dels deformerede, men hvor de ikke var det (to Eksemplarer), viste de samme Forhold som Phoca: de var ikke helt tillukkede.

Snudebrusken (fig. 13). Under Dissektionen er det til at begynde med ret vanskeligt at komme til Klarhed over, hvordan Snudebrusken her skal afledes fra Phoca (fig. 9); man ser imidlertid snart, at Forskellen kun er tilsyneladende, væsentlig begrundet i proc. lateral. dorsal. og cartil. navicul.s Reduktion i Længden; Udformningen staar naturligvis ogsaa i Relation til Hovedskallens ejendommeligt udformede Ansigtsparti; Næseaabningerne er som bekendt meget store og rykkede langt tilbage, idet Nasalia er meget korte, Præmaxillæ lange, Ethmoidet højt.

Septum cartil. nasi (*s*) er en høj, kraftig, lodret Plade, der ikke naar ud til Mellemkæbens Spids, den forreste Ende derfor ikke forskydelig, ligesom desuden Underkanten er fastheftet til Vomer. Snudens Bevægelighed til Siderne er saaledes umuliggjort; Septums forreste Ende er omtrent lodret afskaaret.

Processus lateralis dorsalis (*pld*) udgaar fra Septums Overkant i omtrent hele dennes Længde, men kun bagtil naar den en anselig Udvikling; den hæver sig opad og udad som en smal Vinge paa Septum, ganske smal fortil bredende sig ud bagtil, hvor den er vandret; her bøjer den skarpt om med ventral Retning og Form omtrent som en trekantet lodret Plade, hvis Forkant tilnærmelsesvis er lodret, hvis Underkant er skraat opstigende forfra bagtil; paa Ombøjningsstedet findes et Indsnit i Brusken forfra, saaledes at den nys beskrevne lodrette Del af proc. lateral. dorsal. har ca. to

Tredjedele af sin Dorsalrand fri; kun en Slimhindefold forbinder saaledes paa dette Sted den vandrette og lodrette Del af proc. lateral. dorsal. Fra den omtalte trekantede Bruskplades skraa Underkant udspringer *cartil. navicular.* (*cn*); trods dens noget reducerede Udseende har den dog i Hovedsagen bevaret sin karakteristiske Form med en paa den mediale Side konkav Rende; den løber fortil ud i en Spids, der rager lidt længere frem end den Plade, hvorfra den udgaar; midt fra dens Ventralkant udgaar nedad et lille smalt brusket Fremspring; for øvrigt er dens Ventralkant ved Slimhinde forbundet med Overkanten af Mellemkæben paa dennes tilsvarende Stykke. Den trekantede lodrette Del af proc. lateral. dorsal. med cartil. navicul. danner saaledes et Kompleks, der kun foroven bagtil er i Sammenhæng med den øvrige Brusk, derfor ret bevægelig; føres det udad udvides Indgangen til selve Næsehulen, altsaa væsentlig samme Forhold som hos Fissipedierne; dog maa det bemærkes, at Slimhindefolden, der forbinder de to Afsnit af proc. later. dors. ikke er særlig eftergivelig, saa Bevægelsen kan ikke blive videre stor; vi skal senere se, hvordan dette udformes videre hos Hannen.

Proc. lateral. ventralis er kun svagt udviklet, udgaaende fra bageste Del af septums Ventralrand.

Fra septums forreste Rand udgaar ventralt en kraftig *proc. lateral. anterior*, der ligger tæt op til Mellemkæben.

— — Det er blevet sagt, at der hos Cystophora ♀ ikke findes nogen Antydning til Sæk; det viser sig imidlertid, at man kan eftervise Spor af denne ogsaa hos Hunnen, thi den Slimhinde, der dækker det før omtalte Indsnit i proc. later. dors., er ikke stramt siddende, men hvælver sig poseformigt opad og bagud, omend kun i ringe Udstrækning (Størrelsen af denne lille Sæk kunde maaske lettest karakteriseres derved, at ca. 1—2 cm af den stumpe Ende af en Blyant kan optages deri); den ligger under bageste Del af den før omtalte Pude af svampet subcutant Bindevæv, der paa Snudens Overside hæver Huden lidt i Vejret; jeg mener bestemt, at Forholdet kun kan opfattes som et Rudiment af Sækken hos Hannen.

Snudemuskulaturen.

(fig. 14).

Denne Muskulatur kan her gennemgaas med forholdsvis Korthed, da den ikke afviger synderligt fra Phociderne.

Platysma (*pl*) er afbrudt bag Øret langs en Linje fra dette ventro-caudalt; de dorsale Bundter (*pld*) skyder sig noget henover de ventrale, der saaledes har Udseende af at være puttet ind under de dorsale; Retningen er ikke den samme, thi selv om de øverste af de ventrale Bundter er noget dorsalt rettede med deres bageste Ender, saa danner de dog en stump Vinkel med de dorsale, hvis Retning er ventral lidt nasal; Musklens to Afsnit har altsaa her større Selvstændighed. Det ventrale Afsnit strækker sig med væsentlig longitudinale Bundter hen til Mundvigen; de dorsale naar lidt ud i Overlæben, de ventrale standser noget bag og under Mundvigen i Huden;

den ventrale Begrænsning af Musklen er ved et Mellemrum paa 7—8 cm bagtil og 2—3 cm fortil adskilt fra det tilsvarende paa Hovedets anden Side.

Sphincter profundus præsenterer sig som en sammenhængende Muskelplade fra noget bag Øret til noget bag Mundvigen; ventralt overkrydser Bundterne hinanden med 1—2 cm. *Port. auric.* (*pa*) naar ikke Øret; *port. interm.* (*pi*) er smal paa Grund af Øjets og Ørets Nærhed ved hinanden. Disse to Afsnit har i deres dorsale Del en omtrent transversal Retning. *Port. palpebral.* (*pp*) er kraftig, gaar med sine forreste Bundter direkte over i m. orbic. ocul.; ligesom hos Phoca er den ret selvstændig, idet den allerede under Platysma har skilt sig ud fra port. interm. saaledes, at den paa et Overfladebillede fremtræder som en særlig Muskel. En port. oris kan jeg ikke eftervise.

M. orbicularis oculi (*oo*) er stor og bred, naar bagtil næsten hen til Øret; fortil er de inderste Bundter afbrudt af en Senestribe. De bageste Bundter følger ikke Øjet rundt, men breder sig dorsalt i Subcutis paa Panden, ventralt i Subcutis foran Øret; i Subcutis paa Panden breder sig ogsaa de forreste Bundter. Den nøje Forbindelse med port. palpebral. er omtalt. Nogle aberrerende Bundter fra m. orbicul. ocul. og fra m. naso-labialis ligger tværs over Panden og Næseryggen.

M. naso-labialis (*nl*) er forholdsvis mindre end hos Phoca, idet den ikke naar saa langt ud paa Snuden. Den fremtræder ogsaa her som en direkte Fortsættelse af M. orbic. ocul.; en Del af de bageste Bundter tager deres Udspring fra et senet Parti foran Øjekrogen samt fra selve Pandebenet; andre begynder i Subcutis paa Panden og bageste Del af Næseryggen; herfra strækker Musklen sig naso-ventralt; nogle af de bageste Bundter lægger sig som en særlig lille Muskel ovenpaa bageste Del af m. maxillo-labialis; andre overfladiske Bundter lægger sig hen over Overkanten af samme Muskel i dens videre Forløb; men Hovedmassen kiler sig ind mellem de to Afsnit af m. maxillo-labial.; en Del Bundter naar ned til Overlæben ud for p1—p2; Bundterne sammenflettes til Dels med Enderne af pars rimana m. buccin.

M. maxillo-labialis (*ml*) naar ligesaa lidt som hos andre Pinnipedier til Næseføjene; ogsaa her har vi de to sædvanlige Afsnit, der her har fælles Udspring omkring foramen infraorbitale. *Port. super.* er ikke videre kraftig, den søger skraat opad, standses omtrent ud for bageste Vibrissæ af m. nasalis; *port. infer.* er kraftig, den breder sig vifteformigt i bageste Del af Overlæbevulsten, kiler sig ind mellem bageste Sinushaar og de her beliggende m. nasalis-Bundter; de to Afsnit adskilles i deres distale Del som nævnt af m. naso-labial.

M. buccinatorius opnaar kun en ret ringe Udvikling. Den dybere Del kort og ret svag, forsynet med meget fedtholdigt Bindevæv mellem Bundterne. Den overfladiske Del fortsætter sig omkring Mundvigen i *pars rimana*, der i Overlæben er kort og svag, kun naar halvvejs ud, idet den standser der, hvor m. naso-labialis insererer sig, og indkiler sig mellem dennes Bundter; i Underlæben er rimana derimod kraftig, straaler vifteformigt fremad og nedad, standser dog halvvejs ude i Læben.

M. nasalis er endnu kraftigere og mere kompliceret formet end hos Phoca, hvilket naturligvis hænger nøje sammen med det øvrige Snudepartis Afvigelser;

navnlig er det Mellemkæbens Form, der betinger Forandringen; Mellemkæben er lang, fordi Kraniets ydre Næsebor er rykket langt tilbage; og der udspringer m. nasalis-Bundter fra næsten hele dens dorsale Rand, undtagen fra det allerbageste Stykke. Langt den største Masse af Bundter udspringer fra Mellemkæben ud for septums Forrand, samt fra den fra denne Rand udgaaende proc. lateral. anter.; Bundtretningen er for inderste Lags Vedkommende, som lægger sig op omkring Næseindgangen, nasal, naso-dorsal, og dorsal, naturligvis med alle Mellemretninger; for de ydre Lags Vedkommende er det som hos de tidligere beskrevne Pinnipedier, at Bundterne straaler vifteformigt ud i Overlæben; fra det bagved liggende Parti af Mellemkæben udspringer som før nævnt ogsaa m. nasalis-Bundter, disses Retning er dorsal, langs Slimhinden af Næsehulen, endende i Huden paa Næseryggen; nogle af dem gaar endog helt op omkring denne. Endelig findes der fortil i Overlæben under septum en hel Del mere eller mindre tydelig udprægede Muskelbundter, hvis Retning hovedsagelig er parallel med Mundranden; deres Lejringsforhold er kontinuerlige med de andre m. nasalis-Bundter; de udspringer fra Midtlinien eller Forfladen af Mellemkæben, og danner en Del af Overlæbens Masse udfor Fortænderne; man kan med Rette regne disse Bundter med til m. nasalis, men man kan sikkert med lige saa stor Ret regne i alt Fald de ventrale af dem for de distale Ender af m. buccin., som har mistet Forbindelsen med den øvrige rimana-Del.

M. recti nasi. Det har ikke været mig muligt med tilstrækkelig stor Nøjagtighed at fremstille disse Muskelbundter paa Præparater, saa at jeg kunde foretage en nøjagtig Sammenligning med Forholdet hos Phoca. Der findes Bundter i ikke alt for stort Antal fra hele Næsehulens Sidevæg foran Snudebrusken samt fra denne, det vil sige fra proc. lateral. dorsal. og cartil. navicul., herfra er Bundternes Retning dorsolateral insererende sig i Huden.

M. recti labii inferioris (*ri*) er faa og ubetydelige, findes i forreste Tredjedel af Underlæben.

M. mentalis[1]) er kraftig; dens Udspring er tæt ved Underkæbesymfysen, herfra rettet bagud og nedad; Bundterne insererer sig mellem pars rimana-Bundternes distale Ende, som de overkrydser under en meget stump Vinkel. Nogen Parallelitet eller endog Sammenhæng mellem pars rimana og m. mentalis kan ikke paavises.

Nervus facialis.

(fig. 15).

Man erkender klart det samme Grundtræk som hos de øvrige Pinnipedier; saaledes er f. Eks. r. maxillaris' Overvægt over r. mandibul. og r. tempor. iøjnefaldende.

Lige efter sin Udtræden af Kraniet afgiver Nerven en r. postauricularis, der hurtigt spalter sig i to Grene; umiddelbart derefter afspaltes en lille Gren til platysmas dorsale Del. 1—2 cm foran denne Gren sker den sædvanlige Tredeling i r. maxillaris,

[1]) som jeg ikke har fundet hos andre af de af mig undersøgte Pinnipedier.

r. temporalis og r. mandibularis, idet de to sidste udgaar fra den første fra noget nær samme Sted.

R. maxillaris (*rm*) er til at begynde med at se til som en kraftig Nerve af den sædvanlige cylindriske Form, men snart begynder de enkelte Nervebundter at skille sig lidt ud fra hinanden, saaledes at r. maxill. nu ikke fremtræder som en enkelt Nerve, men som et Knippe af parallelt løbende Nerver kun sammenholdt af lidt løst Bindevæv; det er klart, at der fra denne Tilstand ikke er noget stort Spring til en fuldstændig Afspaltning med divergerende Retning af Bundterne; hvis denne Afspaltning finder Sted, og hvis den finder Sted noget før eller senere, har det da selv sagt ikke nogen principiel Betydning, selv om det i de to Tilfælde kunde se ud som om det var forskellige Nerver. Vi følger nu atter r. maxill. Fra det udspaltede Stykke udgaar en Gren til m. orbic. ocul., øjensynlig den samme som findes hos Phoca; lige efter denne naar en lille Gren til port. interm., maaske svarende til en lignende hos Phoca, hvor den dog paa et længere Stykke er forenet med den nys nævnte Gren til m. orbic. ocul. Under og udfor port. palpebral. kommer r. maxill. i Højde med platysmas Overkant, ellers har den som sædvanlig løbet under denne Muskel (og under sph. prof.); den modtager her den svære *r. communicans;* forstærket af denne fortsætter den med Retning mod Næseboret atter som en cylindrisk, samlet Nerve, der derefter livligt afgiver Grene til m. maxillo-lab. og til m. naso-labial. (jeg har her kun kunnet følge Grenen i den distale Del af Musklen; og længst fremme innerverer den under voldsom Udspaltning m. nasalis.

R. temporalis (*rt*) er forbavsende spinkel; den udgaar i en næsten ret Vinkel fra n. facialis, anastomoserer kort efter med den ovenfor nævnte lille Gren til platysma, fortsætter parallelt med den bruskede Øregang; som sædvanlig afgiver den foran denne et Par Grene til de smaa Øremuskler, og omtrent udfor Øreaabningen afgives en Gren til m. orbicul. ocul. ligesom hos de øvrige Pinnipedier; derefter gaar den videre liggende i Indsænkningen bag ved m. orbic. ocul., mellem denne og m. scutularis, for at ende med en mindre men livlig Forgrening i m. orbicul. ocul. og i de aberrerende Muskelbundter i Pandens Subcutis.

R. mandibularis (*rd*), der udspringer fra n. facialis under en temmelig spids Vinkel er tilsyneladende meget kraftig i sin Begyndelse; men det ligger i, at den her i Virkeligheden hovedsagelig udgøres af de Nervetraade, der bliver til **r. communicans** (*rc*); denne selv, der ganske fremtræder som den egentlige Fortsættelse af r. mandibul. (hvilket den altsaa ogsaa med en vis Ret kan siges at være) er kort og svær, og støder til r. maxill. paa det under denne omtalte Sted. Fra Midten af r. communicans udspringer en Gren til m. buccin. *R. mandibularis* afgiver kort efter sit Udspring en Gren til platysma og sphincter profundus, en Gren der udspalter sig ret livligt, og som anastomoserer med r. mandibul. længere fremme. Denne sidste er som sagt meget uanselig; saa snart den har afgivet r. communicans, innerverer den under sit Forløb forreste Del af platysma samt port. palpebral.s ventrale Del, videre fremme pars rimana m. buccin. i Underlæben samt m. mentalis under livlig Forgrening.

Funktionen af Snudepartiet er i det væsentlige den samme som hos Phoca, medens det ejendommelige for Cystophora vil blive diskuteret under C.-Hannen.

Cystophora cristata ♂.

Allerede Hans Egede [5] omtaler Sækken hos Cystophora cristata: »— (foruden Klap-Myssen, saa kaldet, fordi hand har ligesom en Hette paa, hvilken hand kand skyde over Øynene, naar man vil slaa ham paa Hovedet,) —«. Hans Egede har endog et Billede af Cystophora, hvor man, omend meget ufuldkomment, ser en stor Bule paa Dyrets Hoved; den begynder lidt bag Snuden. (Dyret kaldes paa dette Sted Klapmüts). Imidlertid har Hans Egede aabenbart ikke betragtet Dyret paa nært Hold, i alt Fald ikke naar det har pustet sin Sæk op. Overhovedet hviler de ældre Forfatteres Angivelser neppe paa Selvsyn, men paa de Indfødtes og Rejsendes Beretninger, eller de er Omskrivninger af tidligere Forfatteres Angivelser[1]).

Herfra maa maaske undtages Otto Fabricius [6]. Han skriver om »Phoca leonina«: »Phoca capite antice cristato. Caput antice tuberculo in vesicam inflabili frontem tegente, medietate carinata; foeminae tamen pullique tuberculum non habent, licet carinam, ut rudimentum illius. Praeter nares veras mares etiam habent spurias in tuberculo, iam 1, iam 2, pro aetate[2]); — —«; som man ser en adskillig rigtigere Opfattelse af Sækkens Forhold end Hans Egedes. Men en kontrollabel, paa Selvsyn bygget Fremstilling finder jeg først hos Merriam [15]. Han gjorde det eneste rigtige, man bør gøre, naar man da kan faa Lejlighed dertil, han tog op og undersøgte de levende Dyr. Han siger om det første Møde med en gammel Han: »— — and discovered that the male — — instead of having a crest, or fold of skin, on the top of his head, was provided with a great proboscis, suggesting that of the sea-elephant of the antarctic (fig. 3)«. Ogsaa Funktionsmaaden har han Lejlighed til at iagttage, idet Dyret lykkeligvis bliver vred: »He at first showed his displeasure by frowning and wrinkling the skin on his long snout. The tip of the proboscis was then inflated and emptied several times in rapid succession, after which the entire 'hood' was partially inflated. In addition to its numerous and ever-changing contractions, there was one rather constant constriction about opposite the nostrils, incompletely dividing it transversely into two portions, the anterior of which, though dark in colour, much resembles a bladder, and explains the vulgar epithet, 'bladder-nose', often applied to this species. A curious fact observed was during the alternate filling and emptying of the sac, a noice was produced which closely resembles that of bubbles of air rushing into a bottle from which a liquid is being poured. It was a loud gurgling sound, audible at a distance of twenty-five metres or upward. On approaching nearer, the animal

[1]) Merriam [15] citerer saaledes efter Griffith's »Cuvier«, »that the hooded seal has the power of bringing a fold of skin placed on the forehead foreward, so as to cover the eyes, which it does when threatened, or about to be struck —«, som man ser en Omskrivning af Hans Egedes Ord.

[2]) Hvad disse »falske Næsebor« er, forstaar jeg ikke, maaske Beskadigelser.

became furious. He inflated his hood to such an extent that all traces of constriction were obliterated, and, by a series of ugly tosses of the head, kept it swinging from side to side«. MERRIAM maalte Sækken hos en stor Han (10 Fod lang): »The uninflated proboscis extended two hundred and twenty-five millimetres (nearly nine inches) in front of the upper lip. The height of the proboscis midway between the nostrils and the tip, was two hundred and thirty millimetres; height at mouth, three hundred and twenty millimetres«. MERRIAM mener, at Sækken begynder at vise sig i 3. Leveaar, og vokser vedblivende i 10—12 Aar. Videre skriver han: »This curious development is purely a sexual character, no trace of it existing in the female.« Dette er ikke ganske rigtigt; som vi saa hos Hunnen, besidder denne en Antydning til Sækken. Med Hensyn til Bygningen er MERRIAM klar over Hovedsagen, nemlig at Sækken er den forreste Del af Næsehulerne, selvom han ikke direkte siger dette; men hans Figur viser, at hans Opfattelse er den rette. Om Lukningen af Næseborene siger han: »The nostrils (fig. 4) are capable of closure by the contraction of muscular fibres, which are so arranged as to act as sphincters«, hvilket ogsaa i Hovedsagen træffer det rette. Endvidere giver han et meget godt skematisk Længdesnit af den oppustede Sæk siddende paa Kraniet. Man ser her bl. a. Snudebrusken, hvis Form er ganske godt gengivet, blot er Stillingen af cartil. navicul. urigtig, idet han har tegnet dem parallelt med septum, medens deres Stilling, naar Sækken er oppustet, er vinkelret derpaa. Paa en nøjere anatomisk Undersøgelse har MERRIAM imidlertid ikke indladt sig. — En Førstehaandsundersøgelse af Sækkens Forhold har jeg ikke fundet senere. Der eksisterer en hel Del nyere Litteratur om Cystophora cristata, særlig i amerikanske Tidsskrifter og Magaziner, men den omhandler væsentlig Dyrets Fangst, Størrelse, Udbredelse, Udbytte o. s. v.

Snudepartiet.

(fig. 16).

Udover det i den historiske Indledning om Sækken meddelte, skal her bemærkes følgende.

Snudepartiet bredt og, bortset fra Sækken, fladt, som hos Hunnen; det rager temmelig langt frem over Underkæben, bærer Næseborene paa Spidsen. Disse er meget store, har i Hvilestillingen den sædvanlige Facon: opad stærkt divergerende, udad konkave Buer, septum narium bliver følgelig meget bredt oventil. Overlæbevulsten enorm, atter her som hos Hunnen mere paa Grund af m. nasalis' kolossale Udvikling end paa Grund af Sinushaar; disse er nok anselige, men dog ikke relativt saa store som hos Zalophus f. Eks., hertil svarer, at Sinushaarenes Længde er ringe (paa foreliggende Præparat ikke mere end ca. 4 cm), hvilket maaske tildels skyldes Slid. Septum narium er overalt haarklædt, men Haarklædningen standser her paa Randen af Næseindgangen, kun forneden strækker den sig nogle faa mm ind i denne; derimod fortsætter Haarklædningen sig fra Overlæben indtil ca. 20 mm ind paa den laterale Væg af Næsegangen.

Sækken hos Cystophora ♂ er i Virkeligheden blot det stærkt udvidede forreste

Afsnit af Næsehulerne: udvidet opad, idet Huden ligesom er løftet i Vejret af de store Rum, og udvidet bagtil, idet Snudebruskene er blevet en Del forkortede, og tillige idet der sker en Indposning af Næseslimhinden ovenover Næsebruskens Tag, altsaa mellem proc. lateral. dorsal. (»tectum nasi«) og den ovenover liggende Hud; der opstaar altsaa paa denne Maade to korte Blindsække (truffet paa Snittet, fig. 19). Sækkens mediale Væg, altsaa den bløde Fortsættelse af septum cartilag. nasi er tynd, noget elastisk og forsynet med Muskelbundter kommende fra Snudebrusken (se senere under m. recti nasi). Desværre har Materialet ikke tilladt en mikroskopisk Undersøgelse af Epithelet; det vilde ellers være interessant at faa godtgjort, hvor langt det flerlagede Pladeepithel, der slaar sig ind fra den ydre Hud over Næseborenes Rande, fortsætter sig ind i Næsehulen; idet vi paa den Maade vilde faa oplyst, hvor langt Forgaarden, Vestibulum nasi, strækker sig bagud, altsaa hvor stor Andel i Sækken den har. Sækkens laterale Væg er tykkest forneden, bliver jævnt tyndere opad; i den forreste Halvdel af den laterale Væg findes en Del cavernøst Væv.

Snudebrusken (fig. 17) viser i det væsentlige samme Forhold som hos Hunnen, dog er den noget mere afvigende fra de øvrige Pinnipedier.

Septum cartilagineum (*s*) er meget højt, ret kort, naar ikke ud til Mellemkæbens Spids, men det er ogsaa afkortet bagtil, idet det forbenede Mesethmoid staar temmelig langt frem; septum er solidt fæstnet til sit Underlag med stramt Bindevæv, saaledes at det ikke kan skydes til Siden; det er højest fortil, falder saa i en Bue hurtigt ned, herved dannende Forranden, der hælder noget skraat indefter.

Fra hele Dorsalranden af septum udgaar *proc. lateral. dorsalis* (*pld*), der fortil søger skraat opad (fig. 20), bagtil omtrent vandret udad; den tiltager jævnt i Bredde bagtil, hvor den er ca. 2 cm bred paa foreliggende Eksemplar (voksen Han); kun bagtil er en nedadgaaende lodret Del udviklet, men denne har saa til Gengæld faaet en meget ejendommelig Uddannelse. Som vi saa hos Hunnen, var den nævnte Del her let at erkende som det homologe Bruskstykke til den lodrette Del af Phocidernes proc. lateral. dorsal.; den var blevet meget kort og der var dannet et Indsnit mellem den vandrette Del og lodrette Del af proc. later. dors. (et Indsnit som forresten allerede er antydet hos Phociderne); men Overkanten af det lodrette Bruskstykke var endnu i Højde med Kanten af den vandrette Del (se fig. 13). Her hos Hannen har imidlertid det omtalte lodrette Bruskstykke opnaaet en ganske anderledes Selvstændighed; det er bagtil, hvor det udgaar fra det vandrette Stykke, ikke i direkte Forbindelse med dette, men adskilt ved en Stribe smalt Bindevæv; herved faar det lodrette Bruskstykke en fuldstændig fri Bevægelighed; naar det staar i en Stilling svarende til sin Oprindelse, altsaa med sin Flade omtrent parallelt med septum, ses det, at Overkanten aldeles ikke er parallel med proc. lateral. dorsal.s Kant, men forreste Hjørne rager højt op; men det kan ogsaa klappes til Siden til en Stilling, der illustreres ved fig. 22; man ser hvorledes Brusken ligger med Dorsalranden lateralt i Stedet for nasalt rettet; Næsehulen kan derfor paa dette Sted blive meget vid. Formen paa Brusken er paa det nærmeste en ligesidet Trekant. Fra dens bageste Hjørne udspringer *cartil. navicul.* (fig. 17, *cn*), der i det væsentlige har samme Udseende som hos Hunnen; en kort udefter stærkt konkav baadformet Brusk, fortil noget afsmalnet, udsender fra sin Midte nedefter en Udvækst nogle mm lang. Nogen selvstændig Betydning har cart. navic. næppe, den deltager i Sidebruskens Bevægelser, til hvilken den er heftet med Bindevæv, hvori der er indlejret nogle Smaabruske.

Proc. lateral. ventral. ligger tæt op til Indersiden af Mellemkæben paa dennes midterste Del, smallest fortil, saaledes dannende Gulvet i et Stykke af Næsehulen; dens Udvikling er ringe.

Fra nederste Del af septums Forrand, paa det Sted, hvor dets For- og Underkant støder sammen, udgaar en *proc. lateral. anterior* (*pla*), som er meget kraftig; den ligger lige under Sækkens Bund.

Snudemuskulaturen.

(fig. 18).

Platysma (*pl*). Hvor langt denne Muskel strækker sig tilbage, ved jeg ikke, da Halsen ikke staar til min Disposition. Den er en anselig Muskel, der dækker hele Siden af Hovedet under Øret. Med sin øvre Del udgaar den fra Hovedets Overside lidt under Midtlinien, strækker sig nedad, idet den først gaar paa tværs af Hovedets Længdeakse, men saa bøjer den omtrent ud for Øret i en Bue fremad, beskriver altsaa den sædvanlige Kurve. Fortil naar den i Højde med Mundvigen, de øverste dorsale Bundter dog knapt saa langt. Mellemste Del af platysma strækker sig omtrent ret fremad til Mundvigens nederste Del; de ventrale Bundter er ogsaa fremadrettet, de bøjer, især de mest ventrale, kraftigt nedad, dog naar kun enkelte, saa vidt jeg kan se, Halsens ventrale Midtlinie; de fleste standser et Par cm derfra og blander sig med de overkrydsende Bundter af sph. prof. (se senere), og det paa en saadan Maade, at det kan være ret vanskeligt at afgøre, hvilke Bundter der hører til platysma og hvilke til sph. prof. En særlig Omtale fortjener dog endnu den øvre bageste Del af platysma: Paa en Linie ud for Øret og bagtil er de fleste af Bundterne afbrudt, men saaledes, at den øverste Dels Bundter skyder sig tagformet ned over de øvre Ender af nederste Dels Bundter; dog er Forholdet ikke helt simpelt, som hos ♀, da der her finder en ret udstrakt Sammenfletning Sted; Forholdet er altsaa ikke som hos Zalophus en simpel »Kontinuitätstrennung«, men minder om det hos Phoca.

Sphincter profundus er ligesom platysma udmærket godt udviklet og viser ligesom de andre Pinnipedier temmelig primitive Forhold. Vi inddeler den som sædvanlig i fire Dele; dog er Inddelingen ogsaa her for saa vidt kunstig, som de fire Afsnit gaar fuldstændig jævnt over i hinanden, dannende en sammenhængende Muskelplade. *Port. auricul.*s bageste Begrænsning er temmelig skarp, den ligger ud for Ørets Bagrand; selv naar den ikke Øret, men standser ca. 2 cm nedenfor. *Port. interm.* (*pi*) er paa Grund af Ørets ringe Afstand fra Øjet smal; den naar til en nedefter konveks Buelinje fra Øre til Øje. *Port. palpebralis* (*pp*) er langt det største Afsnit af sph. prof.; bageste Bundter indkiler sig i m. orbicul. ocul., mellemste naar ligeledes denne Muskel, enkelte lægger sig endog op over den; forreste lægger sig parallelt med Forranden af m. orbic. oc., hvorved man faar samme Indtryk som hos Zalophus, nemlig at der er en nøje Forbindelse mellem de to Muskler, dog er Sammenhængen ikke saa inderlig her som der. *Port. oris* (*po*) naar kun ringe Udvikling; en øvre Del er egentlig blot repræsenteret af nogle faa Bundter af port. palpebral., der bøjer sig fremad ud over den store Vulst som Overlæben danner, parallelt med de mere overfladiske Bundter af m. maxillo-labialis; en dybere Del, den egentlige port. oris, bestaar af faa Bundter, der bøjer skarpt om Mundvigen og slutter sig nøje til pars rimana m. bucc.

Som en sammenhængende Muskel gaar saa sph. prof. ned over Siden af Hovedet, skraat bagud; kun Bundterne af port. oris bøjer ventralt fremad, men disse naar ikke den ventrale Midtlinie, hvilket derimod de bagved liggende Bundter gør, og de naar endda længere, idet deres dorsale Ender slaar sig om paa den modsatte Side af Hovedet og, navnlig bagtil, overdækker platysma med flere cm, altsaa samme Forhold som hos Zalophus, hvor ogsaa Forholdets teoretiske Interesse er diskuteret; og her synes endda nogle af Bundterne ventralt at have afspaltet sig, saa at de ligger som korte tværgaaende Muskelstrænge, altsaa fremtrædende som korte Bundter af en Sphincter superficialis.

M. orbicularis oculi (*oo*). I nær genetisk Forbindelse med sph. prof. staar altsaa efter min Mening m. orbic. ocul. Den er hos Cystophora ♂ i Forhold til Øjet af en meget anselig Størrelse. Dens Form er oval. Ovalens Længdeakse faldende sammen med Øjespaltens Retning. Af Figuren faar man ikke et helt rigtigt Indtryk af Formen, fordi Hovedet jo ses lige fra Siden, medens m. orbic. oc., da den nærmest ligger paa Oversiden af Hovedet, hvor dette krummer, ses i Forkortning. Der findes ikke Spor af Antydning til en m. horizontalis. Saa vidt jeg kan se, løber ingen af Bundterne helt omkring Øjet, saadan som Tilfældet var hos Zalophus, men de standser alle udfor forreste Øjekrog, dog hefter de sig ikke, som det synes, til en Senestribe. M. orbic. oc. udfylder hele Rummet mellem Øje og Øre.

M. naso-labialis (*nl*). I direkte Sammenhæng med m. orbic. oc. er m. naso-labialis, som det jo ogsaa var at vente, naar Hensyn tages til de tidligere beskrevne Former. Den er smal, men i alt Fald distalt en kraftig Muskel; den er paa Grund af Sækken og dermed m. nasalis' Udvikling trukket noget tilbage; den gaar fra Snudens øverste Del skraat fremad og nedad til Overlæben, det vil sige til Sinushaarene; den overlejres til Dels af de overfladiske Bundter af m. maxillo-labial.; dens Mægtighed er stor, men dens Fladeudbredelse ret beskeden, idet den ikke breder sig ud over den egentlige Sæk. Dorsalt blandes dens Bundter med m. nasalis, der fra Dybden træder frem til Overfladen; her er den altsaa vanskelig at følge, men den naar dog, saa vidt jeg kan se, Næseryggen eller snarere Panden, nemlig Partiet mellem Øjnene; en stor Del af dens Overflade er vinkelret gennemsat af Muskelbundter, der vinkelret insererer sig i Huden (de mørke Punkter paa Figuren); det er dels m. recti nasi-Bundter, nemlig de dorsale, dels m. nasalis-Bundter, de mere ventrale. Ventralt tiltager den i Mægtighed, naar sin kraftigste Udvikling over og udfor port. super. m. maxillo-labialis; derpaa smalner den til, idet den kiler sig ind mellem de to Afsnit af m. maxillo-labial.; største Delen af Bundterne taber sig mellem og under og caudalt for bageste Sinushaar, andre naar ned til m. buccin., insererer sig i Overlæbens Slimhinde.

M. maxillo-labialis har den sædvanlige Udvikling, delt i en port. superioris og en port. inferioris. Disse udspringer i Fællesskab paa Overkæben under og bag foramen infraorbitale, men snart viger de to Portioner ud fra hinanden, adskilt af m. naso-labial.; begge søger udad; port. infer. naar hurtigst Overfladen, nemlig lige bagved bageste Vibrissæ, mellem hvilke dens Bundter insererer sig; den ligger tæt over Mundranden i Overlæben. Port. super. naar ikke frem til Overfladen, men er adskilt fra denne ved M. naso-labial.; den er adskilt fra Kæben først ved n. infraorbitalis, længere ude ved m. nasalis; ogsaa den naar kun et Stykke ind under og mellem Sinushaarene, mellem hvilke den altsaa taber sig.

M. buccinatorius ligger meget dybt nedsænket, hvilket skyldes Over- og Underlæbens store Tykkelse; den er vel udviklet i sin proksimale Del, men pars rimana er kun svag og kort.

Den overfladiske Del er kraftigst bag Mundvigen; den hænger nøje sammen med port. oris sph. prof.; *pars rimana* bøjer saa om i Overlæben som en, i alt Fald i Forhold til de øvrige Snudemuskler, svag Muskel, Bundterne taber sig efterhaanden, naar ikke ud til Snudespidsen. Paa Grund af Overlæbens Tykkelse er pars rimanas Bredde blevet stor, men Højden er til Gengæld ringe, og Musklen er ikke kompakt, men rigelig gennemsat med fedtfyldt Bindevæv, rigeligere jo længere distalt man kommer. Der er ingen port. supralabialis. *Pars rimana infralabialis* er langt kraftigere; den strækker sig vifteformigt ud paa Underkæben naaende Midtlinien; de dorsale af Bundterne løber parallelt med Underlæberanden, men et Stykke under denne. Ogsaa pars rimanas Bundter er tæt sammenhængende med sph. prof., saa at de tilsammen danner en »m. orbicularis oris«.

M. nasalis (*n*) har hos Cystophora ♂ opnaaet en aldeles kolossal Udvikling, hvilket ligger i, at den er blevet den store Sæks fornemste Muskel; men Anordningen er i Princippet den samme som hos de øvrige Pinnipedier. Udspringet er fra proc. lateral. anter. og den i forreste Del af septums Underkant eventuelt forekommende Forbening, samt fra Mellemkæben og endog tilgrænsende Dele af Overkæben. Mellemkæben er lang, afgiver derfor stor Flade for Udspringet af de talrige m. nasalis-Bundter, hvilket ogsaa er nødvendigt, for at Sækken kan faa den Muskelforsyning, den maa have; paa øverste Del af Sækken ser man m. nasalis-Bundter træde frem i stort Antal. Bundterne fra proc. lateral. anter. gaar skraat fremad over den bløde laterale Væg af Næsehulens forreste Del, fremad fordi Snudepartiet med Næseaabningerne rager et godt Stykke frem over Mellemkæbens Forkant, hvorover proc. lateral. anter. ligger; Bundterne har et bueformigt Forløb med Konveksiteten udefter; dette bueformige Forløb fremkommer derved, at proc. lateral. anter., hvorfra de udspringer, ligger inde under Næsehulens Gulv, og Insertionsstedet ligger i Huden og Bindevævet i den dorsale Midtlinje over Næsehulerne. Iøvrigt har vi den sædvanlige vifteformige Udstraaling mellem Sinushaarene vinkelret paa Hudens Overflade.

M. recti nasi (fig. 19—20) hefter sig i stort Antal paa proc. later. dorsal., samt i Slimhinden dorsalt herfor, endvidere i ret stor Mængde paa den laterale Væg af Næsehulen foran Sidebruskene; Retningen er overalt vinkelret paa Huden; Længden af de ventrale Bundter er stor, idet den Væg de har at gennemløbe, har en betydelig Tykkelse, især paa Grund af m. naso-labial. og længere fremme af m. nasalis.

Fra forreste Rand af septum, samt fra de frie Rande af de horizontale Partier af proc. lateral. dorsal. udgaar en Del kraftige Muskelbundter beliggende i den bløde Næseskillevæg mellem de to Sække; de gaar vinkelret ud paa Huden. Jeg antager, at det er de samme Bundter, som vi fandt paa samme Sted hos Halichoerus, blot i kraftigere Udvikling, fordi de bløde Dele her har langt større Mægtighed end der.

M. mentalis er mindre kraftig end hos Hunnen, men har ellers samme Lejringsforhold.

M. recti labii inferioris er faa og spinkle.

For yderligere at søge Klarhed over Snudemuskulaturens indbyrdes Anordning, hidsætter jeg her en noget udførlig Beskrivelse af et Par Tværsnit lagt gennem den paagældende Region. Tværsnittene er lagt parallelt med Næseborene, og da disse viser skraat nedad og bagud, er Snittene altsaa ogsaa rettet skraat paa Hovedets Længdeakse: dorsonasalt-ventrooralt; Tykkelsen er 2—3 cm. Snittene er tegnet set fra Bagfladen, det er altsaa højre Sides Muskulatur, der er fremstillet. Jeg har paa Tegningerne bibeholdt de tilfældige Foldninger i Næsehulen, hellere end at fremstille Konturerne udjævnede, thi det vilde have medført, at jeg enten maatte have tegnet Sækken i udspilet Tilstand, hvilket vilde tage for megen Plads, eller jeg maatte have konstrueret Folderne, som de maa antages at være, naar Sækken er sammenfaldet, og det lader sig næppe gøre efter Spirituseksemplarer med nogenlunde Nøjagtighed, vilde derfor ingen synderlig Interesse have.

Fig. 19 forestiller det bageste af de fremstillede Snit; det har ramt bag Mundvigen samt i selve Næsehulens forreste Del, man ser Hulningen hvori forreste Del af Maxillo-turbinale har ligget (*mtu*). Næseskillevæggen (*ethm*) er i sin største Del forbenet; bageste Del af septum nasi cartilag. (*s*) er dog truffet; man ser proc. lateral. dorsal. (*pld*), baade den vandrette og den lodrette Del, og man ser den nedenfor denne liggende cartil. navicul. (*cn*) med de smaa forbindende Bruskstykker. Af Muskler bemærker vi *Platysma* (*pl*), hvoraf kun de allerforreste Ender af Bundterne bag Mundvigen er ramt; dernæst *port. oris sph. prof.* (*po*); *m. naso-labialis*' ventrale Del (*nl*) ses at være en særdeles kraftig Muskelmasse, der allerede her er begyndt at indkile sig mellem de to Afdelinger af m. maxillo-labialis; denne Muskel har sit Udspring umiddelbart bag foreliggende Snit, som endog har ramt allerforreste Del af port. super.s (*mls*) Udspring fra Overkæben (i denne ses Længdesnit af m_1); allerede saa tæt foran Udspringet ses port. super. at være adskilt fra port. infer. (*mli*). Da Snittet ligger bag Mundvigen er den transversale Del af m. bucc. (*b*) ramt; den ses inderst tæt op til Mundhulen; pars rimana (*rb*) ses i Overlæben som en flad Muskel, der naar helt ind til Overkæben; den ligger langt inde og har ikke den sædvanlige Form som et Baand, der viser Fladen udad, men som et Baand, hvis Flade viser opad og nedad, den er temmelig svag. I Underkæben ligger ventrale rimana-Bundter (*rb*). Alle Muskelbaandene fra Sidebrusken og Næsehulens bløde Væg, der søger vinkelret ud mod Overfladen er m. recti nasi (*rn*); udfor disse ses dorsalt Længdesnit af svage Muskelbundter, det er Udløbere fra m. nasalis (*n*).

Om Tværsnittet kan endvidere bemærkes, at Sækken er truffet i den Del, der har krænget sig hen dorsalt over Snudebrusken (man ser lidt af den parrede til venstre paa Tegningen). Mellem port. super. af m. maxillo-labialis og Overkæben ligger Grene af n. infraorbitalis og ramus maxillaris. Foruden det tykke Spæklag er der mellem Musklerne og mellem disse og Knoglerne og Næsehulen udviklet betydelige Bindevævsmasser. De sorte Pletter med hvid Rand er Kar.

Fig. 20 forestiller det Snit, der ligger lige foran det nys beskrevne. Det særlig bemærkelsesværdige er, at m. nasalis (*n*) allerede her fuldstændig har taget Têten. Det ovale Muskeltværsnit forneden til højre er port. infer. m. maxillo-labial. (*mli*), det lille trekantede Muskelafsnit er den ydre dorsale Del af samme; port. super. ligger ovenfor (*mls*), nu fuldstændig adskilt fra port. infer. ved den ventrale Del af m. naso-labialis (*nl*). Pars rimana (*rb*) er allerede langt svagere. Fra Mellemkæben, som Snittet nu har ramt tilligemed Overkæben, udgaar m. nasalis; et dorsalt Afsnit søger fortrinsvis fremad, et mellemste er rettet opad, nogenledes parallelt med Snittet, saa at man ser, hvorledes m. nasalis-Bundter omgiver Sækken dorsalt direkte fortsættende sig i de symmetriske; et nederste Afsnit endelig sender sine Bundter mere udad og noget bagud; de to sidste Afsnit er gennemsat med Bundter fra forreste Del af m. nasalis-Bundter, der er rettet caudo-lateralt udad mod Overfladen. M. recti-Bundter (*rn*) findes nu alene paa Sækkens bløde Væg. Septum nasi cartilag. (*s*) har her fuldstændig erstattet den benede Næseskillevæg; vi er nu foran det dorso-caudalt udkrængede Parti af Næsehulen. Ved Indersiden af port. infer. m. maxillo-labial. ses r. maxillaris n. facialis, og ovenover denne ligger n. infraorbitalis, begge indlejrede i betydelige Mængder Bindevæv. Tanden i Længdesnit er p4.

Nervus facialis.

(fig. 21).

Paa Grund af m. nasalis' enorme Udvikling er ogsaa n. facialis særdeles kraftig, idet den jo maa indeholde Nervetraade i tilstrækkeligt Antal til Innervation af denne Muskel. Iøvrigt er Bygningen i Hovedtrækkene naturligvis den samme som hos Hunnen. Af mindre Afvigelser kan bemærkes følgende: *Ramus mandibularis* (*rd*) udgaar under en mindre spids Vinkel fra r. maxillaris og fjerner sig ventralt mere fra denne, hvilket aabenbart hænger sammen med, at Hannens Hoved er højere end Hunnens; Innerveringsforholdene af platysma og sph. prof. fra r. mandibul. er lidt anderledes end hos Hunnen: umiddelbart efter r. mandibul.s Udspring fra r. maxillaris udgaar en kraftig Gren til de to nævnte Muskler, og den anastomoserer ikke med r. mandibularis længere fremme. Og selve r. mandibul. er efter at have afgivet r. communicans spinklere end hos ♀, Underlæbemuskulaturen er jo heller ikke saa kraftig her som der. Den distale Udspaltning af *r. maxillaris* (*rm*) finder Sted noget længere tilbage end hos ♀, fordi m. nasalis indtager en forholdsvis større Plads af Snudepartiet.

Funktionen.

Som vi saa hos Phoca var det ved Hjælp af to Muskler, m. nasalis og m. recti nasi., at Næseborene og forreste Del af Næsehulerne hos Pinnipedierne lukkedes og aabnedes. Trods det nye Apparat, som er kommet til hos Cystophora ♂, Sækken, er det dog stadig de samme to Muskler, der behersker dennes Bevægelser.

Sækken er oppustelig: Luften fra Lungerne fylder og udspiler den, og som vi i den historiske Indledning har set, kan den udspiles enormt; Trykket i den bliver altsaa stort; Næseboret maa derfor kunne lukkes med Kraft. Om Elasticitet er her saa lidt som hos andre Pinnipedier Tale; om det erektile Væv i forreste Del af Sækkens laterale Væg ved stærk Blodfyldning kan bidrage til Lukning er vel nok muligt, men det kan i alt Fald kun have en ganske sekundær Betydning. Den effektive Lukning besørges her som hos de andre Pinnipedier af Muskelvirkning. Dette har Merriam [15] rigtig set; men en klar Opfattelse af hvad det er for en Muskel, samt dens nøjere Lejringsforhold, synes han ikke at have.

Som vi saa, gaar der fra proc. lateral. anter., der ligger under Sækkens Bund, kraftige m. nasalis-Bundter skraat fremad og opad bueformet uden omkring Næsehulens forreste ventrale Væg, insererende sig i Huden lige over den bløde Næseskillevæg lidt bag Næseborenes Omraade; hver Næseindgang bliver saaledes omgivet af en Halvring af Muskelbundter, der mødes med hinanden dorsalt; tilsammen vil de derfor ved deres Kontraktion virke som en Klemhane, hvorved de laterale Vægge trykkes indad mod Medianvæggen, og en Berøring og fast Tillukning finder saa meget lettere Sted, som Væggene her paa Grund af rigeligt Bindevæv hvælver sig noget indad mod Lumen. At denne Tillukning af Sækken er effektiv, anser jeg for ganske sikkert; jeg har ogsaa overbevist mig derom ved en Vandprøve foretaget paa følgende Maade: jeg hældte paa et Spirituseksemplar af et afskaaret Hoved Vand bagfra ind i Sækken, idet Hovedet holdtes lodret med Næseborene nedad; Vandet løb da frit gennem disse; men ved et Tryk paa Sækkens Sider 2—3 cm bag selve Næseboret, nemlig der hvor Hovedmassen af de nys omtalte m. nasalis-Bundter ligger, kunde jeg standse Vandstrømmen momentant; og her maa man jo ovenikøbet huske paa, at Vævene var hærdnede i Spiritus; hvor langt mere fuldkomment maa saa ikke de levende bløde Væv føje sig til hinanden.

I selve Næseborets Rande har jeg ikke kunnet paavise Muskulatur, som kunde antages at bevirke en tæt Tillukning af disse Rande; men det viser sig altsaa, at Tillukningen (som forresten sandsynligvis vil trække de distalt for dette Omraade beliggende Væv, altsaa selve Næseborenes Rande, med sig ind mod septum narium), at Tillukningen bag ved Næseborene er tilstrækkelig til at holde Luften tilbage i Sækken, og naturligvis ogsaa til at holde Vandet ude under Dykning.

Naar Hensyn tages til denne kraftige Tillukning under Opblæsning af Sækken, kunde der være Fare for en Sprængning af denne ved for stærk Luftudspiling; men ogsaa denne Fare undgaas ved Hjælp af m. nasalis, idet, som vi har set, kraftige Bundter af denne Muskel fra Mellemkæben og tilgrænsende Partier af Overkæben strækker sig opad overalt i Sækken, helt opad til den dorsale Midtlinie; Sækken (eller retter de to Sække) bliver saaledes omgivet af et Muskellag, der kun tillader en begrænset Udspiling; og ved dette Lags kraftige Kontraktion kan Luften atter presses ud og Sækken føres tilbage til sin normale Slaphedstilstand; hertil bidrager ogsaa de Muskelbundter, der ligger i den bløde Skillevæg mellem de to Afdelinger af Sækken.

Foruden Luften, der fra Lungerne pustes ud i Sækken, bidrager ogsaa m. recti nasi til at forstørre Rummet, idet de ligesom hos de øvrige Pinnipedier trækker den frie Del af proc. lateral. dorsal., cartil. navicul. og den foran liggende Slimhinde udad; og her er det interessant at se den særlige Udvikling, som den frie trekantede Del af proc. lateral. dors. har faaet (fig. 22, I, II): Naar Sækken er i Ro, ikke oppustet, er dens Lumen ogsaa bagtil forholdsvis ringe, fordi den nævnte Brusk da indtager sin oprindelige Stilling, nemlig fremad rettet med Fladen parallelt med septum; naar Sækken derimod fyldes med Luft, gælder det om at faa Rummet saa stort som muligt; Brusken bliver da ved Kontraktion af de m. recti-Bundter, der hefter sig paa den, svinget ud til Siden, og denne Svingning kan naa et Maximum af 90°, saa at Brusken nu staar vinkelret paa sit forrige Plan, altsaa transversalt paa Hovedets Længdeakse; herved bliver da Sækkens bageste Del gjort betydelig videre. Iøvrigt er m. recti nasi's Funktion her den samme som hos de andre Pinnipedier, nemlig den at udvide forreste Del af Næsehulen ved Indaanding.

Det vilde have haft stor Interesse at undersøge Søelefanten, Macrorhinus, med Henblik paa de her omhandlede Forhold, idet der mig bekendt ikke er foretaget nogen anatomisk Undersøgelse desangaaende. Townsend [24] synes at have undersøgt »Snabelen« bedst. Jeg skal her citere hans Beskrivelse af »the proboscis«: »The proboscis is broad and fleshy to the tip where the nostrils are placed, the nasal openings being wide apart and directed somewhat downward and outward. The length of the proboscis forward from the canines is about equal to the distance between the canine and eye. It is exceedingly thick and heavy and its width is about equal to the space between the eyes. In one of our specimens, not the largest, it was about nine inches long, but the proboscis of the dead animal can be streched out somewhat longer. When the animal is crawling the proboscis is relaxed and pendant; when sleeping, it rests upon the sand in a shapeless mass. When persistently annoyed the old male slowly raises his head, and retracting the proboscis opens the mouth very wide. He does not bellow loudly but there is much blowing out of the breath through the nostrils with a gurgling sound, the whole proboscis vibrating heavily with the effort.

Sometimes when the head is turned up, the proboscis relaxes until it hangs into the open mouth. The animal may continue to turn his head over backwards until the half-relaxed proboscis actually overhangs to the rear. We did not at any time see the trunk thrown into a rounded or tubular form. In fighting it is closely retracted and the seal is apparently succesful in keeping it out of harm's way, as many of the animals with badly damaged necks, had trunks showing no injury whatever.

When the proboscis is fully retracted it exhibits three bulging transverse folds on top separated by deep grooves. The upper groove remains distinguishable when the proboscis is relaxed, while about it the upper fold remains as a fleshy hump. We did not observe any actual inflation of the trunk, which, as, examined during the skinning operations, is fibrous and fleshy throughout. There was no special expansion of the nasal passages observable, and while the photographs appear to indicate an inflation, such is not the case; the heavy folds of the retracted proboscis must be produced by purely muscular action. It cannot be capable of inflation in the sense that the trunk of the male hooded-seal (*Cystophora*) is inflated. The massing of the heavy fleshy appendage into compact folds on the top of the head, is really the opposite of inflation.« Som man ser, mener TOWNSEND, at Snabelens Bevægelser er af ren muskulær Oprindelse, hvorpaa hans Billeder ogsaa tyder; paa intet af dem ser man noget i Retning af den stærkt oppustede Sæk hos Cystophora. Et noget andet Indtryk faar man af RING's [19] Meddelelse, p. 432: »— — The beachmasters were found to measure from about 18—21 feet in length; and had always a well-developed proboscis, which is an enlargement of the snout nearly resembling that of the tapir than the trunk of an elephant; whence, however, is derived the name »Sea-Elephant«. As long as a bull is undisturbed this »proboscis« hangs flabby and lump to one side of the jaw; but when excited, or roused to anger, it becomes rapidly inflated with air and enormously enlarged, the process of inflation being accompanied by short snorts. The bulls, when fighting each other, are very careful to prevent the trunk from being seized, contracting and raising them, as far as possible out of harm's way. The dams are entirely devoid of this enlargement of the nose, which is a sign of sexual maturity in the males, and is most pronounced during the rutting period; while it is perceptible in the pups when only seven to eight weeks old. — —«

Efter dette Citat at dømme, synes Søelefantens Snude at fungere efter nogenledes samme Princip som Blæresælens. Imidlertid er det ikke muligt at fælde nogen endelig Dom herom før efter en nøjere anatomisk Undersøgelse.

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RÉSUMÉ.

Die vorliegende Untersuchung wurde vor ca. 12 Jahren im zoologischen Laboratorium der kgl. tierärztlichen und landwirtschaftlichen Hochschule angestellt, das damals unter der Leitung von Professor Dr. J. E. V. Boas stand. Für das reichliche Material, das zu meiner Verfügung stand, sowie für Rat und Anleitung bringe ich hiermit Herrn Professor Boas meinen aufrichtigen Dank. Das Material war in Alkohol konserviert, in einzelnen Fällen frisch. Fig. 12 und 16 sind von Frau Bodil Strubberg gezeichnet, die andern von mir. In der Terminologie halte ich mich an die von Boas und Paulli [2] angewandte, und was den Schnauzenknorpel betrifft, an die von Freund [7] und Kormann [13]. Die Arbeit beschäftigt sich in der Hauptsache nur mit den gefundenen Facta.

Zalophus californianus.

Die Ruhestellung der Nasenspalte ist wahrscheinlich die spaltförmige, mit ca. 1 mm. Oeffnung. Am Schnauzenknorpel (Fig. 1) fehlen die cartil. access. und die cartil. lateral. anter. Der Eingang in die Nasenhöhle wird dadurch spaltförmig, dass der proc. lat. dors. sich dicht an das septum anlegt, dessen ventraler Rand ein gutes Stück über den Zwischenkiefer hinausragt.

Platysma (Fig. 2—3 *pl*, *pld*) ist hinter dem Ohr querüber geteilt, Ruges [20—21] »Kontinuitätstrennung«; das distale Ende von mehreren der Bündel kreuzt Bündel des sph. prof. Dieser letzte Muskel (*sp*) ist besonders gut entwickelt; die ventralen Enden der Bündel kreuzen sich und weisen darauf hin, dass ein sphincter superficialis wahrscheinlich durch Abspaltung solcher verlängerter profundus-Bündel entstanden ist. — Uebrigens ist der sph. prof. gut entwickelt mit einer port. auricularis (*pa*), einer port. intermedia (*pi*), einer port. palpebralis (*pp*), die sich mit einigen Bündeln direkt in den m. orbicularis oculi fortsetzt, sowie schliesslich einer port. oris (*po*), die teils als ein m. orbicularis oris fungiert, teils sich unter dem Mundwinkel fortsetzt, in drei Schichten von verschiedener Tiefenlage zerspaltet.

M. orbicularis oculi (oo, Fig. 4) schliesst sich eng an den m. naso-labialis und die port. palpebralis sph. prof. Er ist u. a. interessant dadurch, dass er zeigt, wie man sich den m. horizontalis des Hundes entstanden denken kann, nämlich durch Abspaltung von orbic. oc-Bündeln; sowie auch, wie der m. post- und präorbicularis entstanden sein müssen: ebenfalls durch Abspaltung von orbic. oc. Es ist beachtenswert, dass der m. orbicularis oc. -Komplex bei Zalophus zweifellos vom sph. prof. und nicht wie bei so vielen anderen Säugetieren vom Platysma gebildet ist.

M. naso-labialis ist in eine oberflächliche Schichte (Fig. 2 *nl*), von dem subcutanen Bindegewebe des Nasenrückens bis zur Haut zwischenVibrissae reichend und in eine tiefere Schichte geteilt, die vom Schädel dicht vor der Augenhöhle entspringt, und sich in die Oberlippe zwischen Bündeln der pars rimana m. buccin. inseriert.

M. maxillo-labialis ist durch den naso-labialis in eine port. infer. und eine port. super. gesondert. Die distalen Bündel der port. infer. heften sich fächerförmig zwischen den Sinushaaren (Vibrissae) an. Port. super. inseriert sich in die Oberlippe zwischen nasalis-Bündel und erreicht nicht die Nasenflügel.

M. buccinatorius (Fig. 5) hat einen oberflächlichen und einen tiefer liegenden Teil. Die obersten Bündel des oberflächlichen Teiles inserieren sich an Maxilla über den hintersten Præmolaren; die tieferen Bündel bilden eine kräftige pars rimana (*rb*), sowie eine pars supralabialis (*slb*), die als selbstständiger, sich an die Maxilla inserierender Muskel auftritt. Sehr interessant ist es, dass der distale Teil von pars rimana, der den paarigen Muskel unter septum nasi begegnet, an dieser Stelle zu einem kräftigen, fleischigen Muskel anschwillt, der als integrierender Teil in m. nasalis übergeht. Der ventrale Teil des Muskels verliert sich fächerförmig in der Unterlippe. Der tieferliegende Teil von m. buccin. läuft von tuber maxillare zum Mundwinkel.

M. nasalis (Fig. 5 und 6 *n*) hängt, wie erwähnt, mit m. buccin. eng zusammen. Er hat hier wie bei allen von mir untersuchten Pinnipediern eine kolossale Entwicklung erfahren. Der Muskel entspringt vom Oberkiefer über dem Eckzahn, dem Zwischenkiefer und dem untersten freien Rand des septum cartilag. nasi. Von hier gehen die Bündel fächerförmig aus: die innersten legen sich dicht an den Gaumenknorpel, die Nasenschleimhaut und den Zwischenkiefer an und gehen ganz hinauf zum Nasenrücken, die äusseren hingegen mehr oder weniger winkelrecht hinaus an die Haut zwischen der Basis der Sinushaare. Da die Schnauzenpartie hier stark gewölbt ist, liegen die nasalis-Bündel wie die dichtgestellten Radien eines Kugelausschnittes. M. nasalis ist aus m. buccinatorius entstanden zu betrachten.

M. mentalis (Fig. 3 *m*) besteht aus einer Anzahl mehr oder minder isolierter Bündel, die vom Unterkiefer in verschiedenen Richtungen an die Haut gehen. Viele der Bündel könnten sehr wohl als m. recti lab. infer. angesprochen werden.

M. recti nasi (Fig. 6 *rn*) erscheinen hier als ein geschlossener, individualisierter Muskel; er entspringt hauptsächlich von der Schleimhaut zwischen der cartilag. navicul. und dem proc. lateral. dors.; die Bündel gehen von hier schräg nach oben, winkelrecht auf die Haut und keilen sich zwischen nasalis-Bündel ein.

Nervus facialis. Betreffs der Verzweigung dieses Nerven wird auf Fig. 7 hingewiesen, die genügend Aufschluss über das Lagerungsverhältnis der Verzweigungen zu den Muskeln geben dürfte, deren Umrisse (jedoch nur die oberflächlich liegenden) punktiert sind.

Die Funktion des Schnauzenkomplexes bei Zalophus soll bei Besprechung der sehr ähnlichen Verhältnisse bei Phoca besprochen werden.

Phoca vitulina.

Der Schnauzenknorpel bei Phoca (Fig. 8) ist kurz und flach verglichen mit den Verhältnissen bei Zalophus, indem hier der Schnauzenknorpel nicht über den Zwischenkiefer hinausragt.

Der Schnauzenknorpel (Fig. 9) erinnert, wie zu erwarten, einigermassen an jenen bei Zalophus. Der Eingang zur Nasenhöhle ist auch hier eine schräggestellte Spalte, indem der Processus later. dors. (*pld*) nach unten gebogen ist, dem Septum parallel und dicht angelegt. Es ist ein cartil. navicul. (*cn*) vorhanden. Der Processus lateralis anterior ist wohl entwickelt (*pla*).

Platysma (Fig. 10 *pl. pld.*) zeigt nicht die bei Zalophus vorkommende »Kontinuitätstrennung«.

Sphincter profundus (*sp*) ist im wesentlichen auf dieselbe Weise wie bei Zalophus gebaut, doch fehlt eine portio oris.

M. orbicularis oculi (*oo*) ist ein ausserordentlich wohl abgegrenzter und wohl entwickelter Muskel, der sich, wie bei Zalophus, eng an die portio palpebralis sph. prof. anschliesst. Der post- und präorbicularis sowie ein m. horizontalis fehlen.

M. naso-labialis (*nl*) entspringt von der Mittellinie des Stirn- und Nasenrückens, geht von da ventro-oral in parallelen Bündeln, die sich stark verdicken und sich an den hintersten Zweidrittel der Oberlippe zwischen deren Muskeln anheften.

M. maxillo-labialis (*ml*) ist wie bei Zalophus in eine port. super. und eine port. infer. geteilt, deren gemeinsamer Ursprung auf einer recht ausgedehnten Basis liegt: von einem Punkt gerade unter dem foramen infraorbitale bis zur lateralen Fläche des Jochbogens. Die port. inferior. liegt wesentlich an der Oberfläche, ihre Bündel verlieren sich fächerförmig zwischen den hintersten Sinushaaren. Die port. superior. liegt tief, ihre Bündel enden im hintersten Teil des dicken Wulstes der Oberlippe. Wie bei Zalophus empfängt man auch hier den Eindruck, dass der m. nasalis durch seine kolossale Entwicklung gleichsam verhindert, dass der distale Teil des m. maxillo-labialis in die eigentliche Schnauzenpartie hinausreicht.

M. buccinatorius (*rb*) ist recht schwach entwickelt. Der longitudinale Teil hinter dem Mundwinkel ist schmal und dünn. Die pars rimana (*rb*) schliesst in der Oberlippe ab etwas über der Mitte derselben; in der Unterlippe ist sie etwas kräftiger, die dorsalen Bündel reichen beinahe bis zur Symphyse des Unterkiefers.

M. nasalis ist hier ein ganz selbstständiger Muskel; seine Lagerungsverhältnisse und Entwicklung sind im übrigen ungefähr wie bei Zalophus.

M. recti nasi erreichen hier ihre kräftigste und komplizierteste Entwicklung. Sie entspringen von der Schleimhaut zwischen dem process. dors. lateral. und der cartil. navicul., vom vordersten Teil der lateralen Fläche dieses Knorpels, sowie aus der Schleimhaut unmittelbar vor diesem Knorpel; von diesem ganzen Gebiet strahlen recti-Bündel etwas divergierend in die Haut hinaus.

Mit Bezug auf den Nervus facialis, wird auf Fig. 11 hingewiesen.

Was die Funktion des besprochenen Komplexes anbelangt, so konzentriert sich das Interesse auf das Oeffnen und Schliessen der Nasenlöcher. Meine Auffassung derselben ist folgende: Weder bei Zalophus noch bei Phoca (Halichoerus grypus) sind die Seitenwände der Nasenlöcher elastisch; wenn alle Gewebe schlaff sind (bei toten Tieren nach dem Aufhören des Rigor mortis) sind die Nasenlöcher beinahe, aber nicht ganz geschlossen. Unter Wasser schliessen sie sich sicher durch den Druck des Wassers, aber unter der Funktion der Schnauzenmuskulatur beim Fischfang würde dieser Druck allzu leicht in einem solchen Grad aufgehoben werden können, dass sich die Nasenlöcher vielleicht trotzdem ein wenig öffneten. Eine Muskeltätigkeit ist daher zum Schliessen der Nasenlöcher notwendig; und das Schliessen wird von den innersten Bündeln der m. nasalis besorgt, die fast sphincterartig von dem vordersten, untersten Rand von septum an beiden Seiten des Schnauzenknorpels zur Mittellinie des Nasenrückens gehen. Die Oeffnung der Nasenlöcher wird von dem m. recti nas. und nicht etwa von m. maxillo-labialis oder andern Muskeln der Oberlippe besorgt.

Cystophora cristata ♀.

An der Schnauze (Fig. 12) ist besonders bemerkenswert ein Rudiment des Aufblähungssackes des Männchens: ein kleines Kissen aus Bindegewebe über dem Nasenrücken von zwei Transversalfurchen begrenzt.

Der Schnauzenknorpel (Fig. 13) weist im Prinzip die gleichen Bau auf, wie bei Phoca. Das septum (*s*) ist eine kräftige Knorpelplatte, die mit Vomer unbeweglich verbunden ist; es reicht nicht so weit vor, wie der Zwischenkiefer; es hat einen kräftigen proc. later. anter. (*pla*). Der proc. lateralis dorsalis (*pld*) geht nur von den letzten zwei Dritteln des septum aus; der vordere senkrechte Teil ist durch einen Einschnitt von dem wagrechten getrennt, wodurch eine dreieckige Knorpelplatte entsteht, die parallel mit dem septum in geringem Abstand von demselben liegt. Eine cartil. navicularis ist als ein ventraler Anhang zu der dreieckigen Platte entwickelt.

Die Schleimhaut, die über dem genannten Einschnitt in proc. later. dors. liegt, hat eine Ausstülpung von 1—2 cm. in dorsaler Richtung, anscheinend dem grossen Aufblähungssack des Männchens entsprechend.

Die Muskulatur (Fig. 14) erinnert sehr an jene beim Phoca. Erwähnenswert ist folgendes: Platysma ist so geteilt, dass ein dorsaler Abschnitt (*pld*) sich etwas über einen ventralen Abschnitt (*pl*) hinüberlegt. M. nasalis ist grösser und komplizierter als bei Phoca, was u. a. damit zusammenhängt, dass nasalis-Bündel von fast der ganzen dorsalen Kante des Zwischenkiefers entspringen und dieser hat bei Cystophora eine mächtige Ausdehnung dadurch, dass die äusseren Nasenöffnungen des Schädels weit nach hinten gerückt sind; sonst sind die Lagerungsverhältnisse der Muskel im wesentlichen wie bei Phoca. Ein kräftiger m. mentalis ist vorhanden. Betreffs m. facialis wird auf Fig. 15 hingewiesen.

Cystophora cristata ♂

Die Form der Schnauzenpartie ist wahrscheinlich am besten aus Fig. 16 zu ersehen, die nach einem Alkohol-Präparat gezeichnet ist.

Der Aufblähungssack ist der stark erweiterte vorderste Abschnitt der Nasenlöcher: nach oben erweitert dadurch, dass die Höhle gleichsam von dem grossen Raum in die Höhe gehoben wird; und nach hinten dadurch dass die Schnauzenknorpel einigermassen verkürzt worden sind; und ausserdem ist eine Ausstülpung der Nasenschleimhaut über dem Dach des Nasenknorpels vorhanden, also zwischen dem processus lateral. dors. (tectum nasi) und der davor liegenden Haut; es entstehen also auf diese Weise zwei kurze Blindsäcke (im Schnitt Fig. 19 zu sehen). Die laterale Wand des Sackes ist unten am dicksten und wird nach oben gleichmässig dünner.

Im Schnauzenknorpel (Fig. 17) ist das septum cartil. (*s*) sehr hoch, aber so kurz, dass es nicht zur Spitze des Zwischenkiefers reicht; es lässt sich nicht nach den Seiten verschieben. Der wagrechte Teil des processus lateral. dors. ist hinten am breitesten; nur nach hinten zu ist ein abwärts gerichteter senkrechter Teil entwickelt; durch einen Einschnitt ist er vom wagrechten Teil getrennt, nur nach hinten durch einen schmalen, bindegewebigen Streifen verbunden und erreicht dadurch eine grosse, selbstständige Beweglichkeit; wenn er eine Stellung einnimmt, die seinem Ursprung entspricht, d. h. also mit seiner Fläche parallel zum septum, ist, wie aus Fig. 17 ersichtlich, die Oberkante keineswegs parallel der Kante des proc. lat. dors, sondern die vorderste Ecke ragt weit hinauf, (vergl. Fig. 13. Schnauzenknorpel des ♀). Er kann aber auch zur Seite geklappt werden zu einer Stellung, die in Fig. 22 II illustriert wird. Man sieht hier, wie der Knorpel mit dem Dorsalrand in lateraler Stellung liegt, statt nasal gerichtet zu sein; die Nasenhöhle kann deshalb an dieser Stelle sehr weit werden. Ein cartil. navicul. mit an den proc. later. dors. geheftetem Bindegewebe ist vorhanden, er hat kaum selbstständige Bedeutung. Ein proc. later. ant. ist kräftig entwickelt.

Die Muskulatur (Fig. 18). Der dorsale, hinter dem Ohr liegende Teil des Platysma ist als eine halbwegs selbstständiger Muskelschicht (*pld*) entwickelt; im Uebrigen sind die Lagerungsverhältnisse aus der Abbildung ersichtlich. Der sphincter profundus (*sp*) ist gut entwickelt, ungefähr wie bei den anderen Pinnipediern mit einer portio auricul., einer port. interm. (*pi*), einer port. palpebralis (*pp*) und einer port. oris. (*po*). Orbicularis oculi (*oo*) ist stark entwickelt. M. naso-labialis (*nl*) ist ein kräftiger Muskel, der beinahe bis zu den dorsalen Sinushaaren reicht; dorsal mischen sich seine Bündel mit jenen von nasalis, die hier aus der Tiefe zur Oberfläche gehen; einige tief liegende Bündel reichen ganz hinunter zu buccinat.

und inserieren sich in die Schleimhaut der Oberlippe. M. maxillo-labialis teilt sich wie gewöhnlich in eine port. superior, die bis zur Basis der Sinushaare hinausreicht, zwischen welchen sie sich verliert ohne die Oberfläche zu erreichen, und in eine port. infer. (*ml*), die die Oberfläche erreicht gerade hinter den hintersten Sinushaaren; sie liegt dicht über dem Mundrand in der Oberlippe; die beiden Teile von maxillo-labialis sind von m. naso-labialis getrennt. M. buccinatorius ist tief gelegen; er reicht in der Oberlippe nicht hinaus bis in die Schnauzenspitze; hingegen reicht seine pars. rimana als kräftiger fächerförmiger Muskel in die Unterlippe hinaus bis ganz in die Unterkiefersymfyse. M. nasalis (*n*) erreicht eine ganz kolossale Entwicklung, was daher kommt, dass er der vornehmste Muskel des Sackes geworden ist. Sein Ursprung ist vom proc. lateral. ant., dem ganzen Zwischenkiefer, (der bei Cystophora eine grosse Ausdehnung hat) sowie angrenzenden Teilen des Oberkiefers. Von dieser ganzen Basis strahlen die Bündel fächerförmig vorwärts, aufwärts, rückwärts. M. recti nasi (Fig. 19—20) gehen vom proc. later. dors., von der dorsal angrenzenden Schleimhaut, sowie von der lateralen Wand des Nasenloches vor den Seitenknorpeln aus; die Richtung ist von hier winkelrecht zur Haut. Eine Anzahl kräftiger Muskelbündel liegt in der weichen Nasenscheidewand, winkelrecht an die Haut hinausgehend. Ein m. mentalis ist vorhanden, ebenso m. recti labii infer.

Im Uebrigen geben die beiden Schnitte (Fig. 19—20) mit beifolgender Figurenerklärung weitere Anfklärungen über die Anordnung der Muskeln. Der Schnitt (Fig. 19) ist der hinterste der beiden; er geht hinter dem Mundwinkel und im vordersten Teil des eigentlichen Nasenloches hindurch. Der Sack ist in dem Abschnitt getroffen, der sich dorsal über den Schnauzenknorpel gelegt hat. Fig. 20 stellt einen Schnitt dar, der den vordersten Teil des septum cartil. nasi sowie den Zwischenkiefer getroffen hat; man sieht an diesem Schnitt, welche kolossale Entwicklung m. nasalis hat, wie er unter anderem die Nasenhöhle dorsal umgibt.

Ueber nervus facialis gibt Fig. 21 Aufschluss.

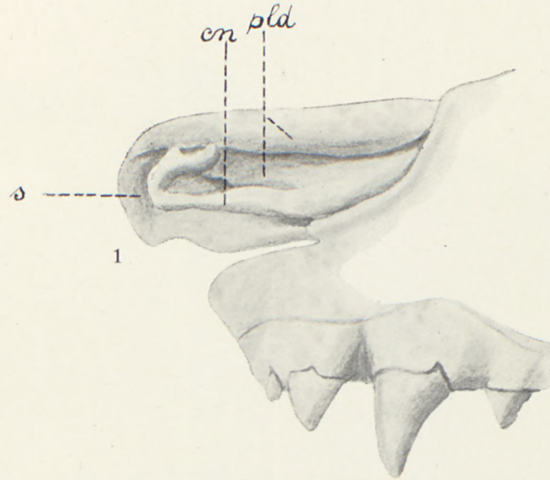
Ueber die Funktion des ganzen Komplexes ist folgendes zu bemerken. Wenn die Luft aus den Lungen den Sack ausdehnt, so steigt der Druck in demselben; die Nasenlöcher müssen darum mit grosser Kraft geschlossen werden können: dieses Schliessen besorgen die Bündel von m. nasalis, die von proc. lateral. anter, in die Wände der Nasenlöcher hinausgehen; diese Bündel begegnen sich dorsal, wirken daher als sphincter. Die Gefahr einer Sprengung des Sackes wäre vorhanden, wenn seine Wände nicht von Innen mit Hilfe von Muskeln dem Drucke entgegenwirken könnten. Solche Muskeln sind jedoch vorhanden, nämlich wieder starke Bündel von m. nasalis, die sich vom Zwischenkiefer dorsal in die Wände des Sackes erstrecken ganz über die Mittellinie hinauf; durch die Kontraktion dieser Muskel kann der Sack wieder in seinen normalen Zustand zurückgeführt werden. Unter der Aufblähung tragen die m. recti nasi dazu bei, den vordersten Teil des Nasenraumes zu vergrössern, indem sie den freien Teil des proc. lateral. dors. zur Seite ziehen können, ihn wie eine Flügeltür 90° aus seiner normalen Stellung (Fig. 22 I und II) drehend.

TAVLER

TAVLE I

Fig. 1. Snudebrusken fra Siden hos Zalophus in situ. *cn*, cartilago navicularis; *pld*, processus lateralis dorsalis; *s*, septum.

— 2. Overfladisk Lag af facialis-Muskulaturen, set skraat ovenfra, af Zalophus. *ao*, m. auriculo-occipitalis. *h*. m. horizontalis. *nl*. m. naso-labialis. *oo*, m. orbicularis oculi. *pi*, portio intermedia sph. prof. *pl*, platysma. *pld*, dorsale Del af platysma. *po*, portio oris sph. prof. *pp*, portio palpebralis. *scu*, m. scutularis, *sp*, sphincter profundus.



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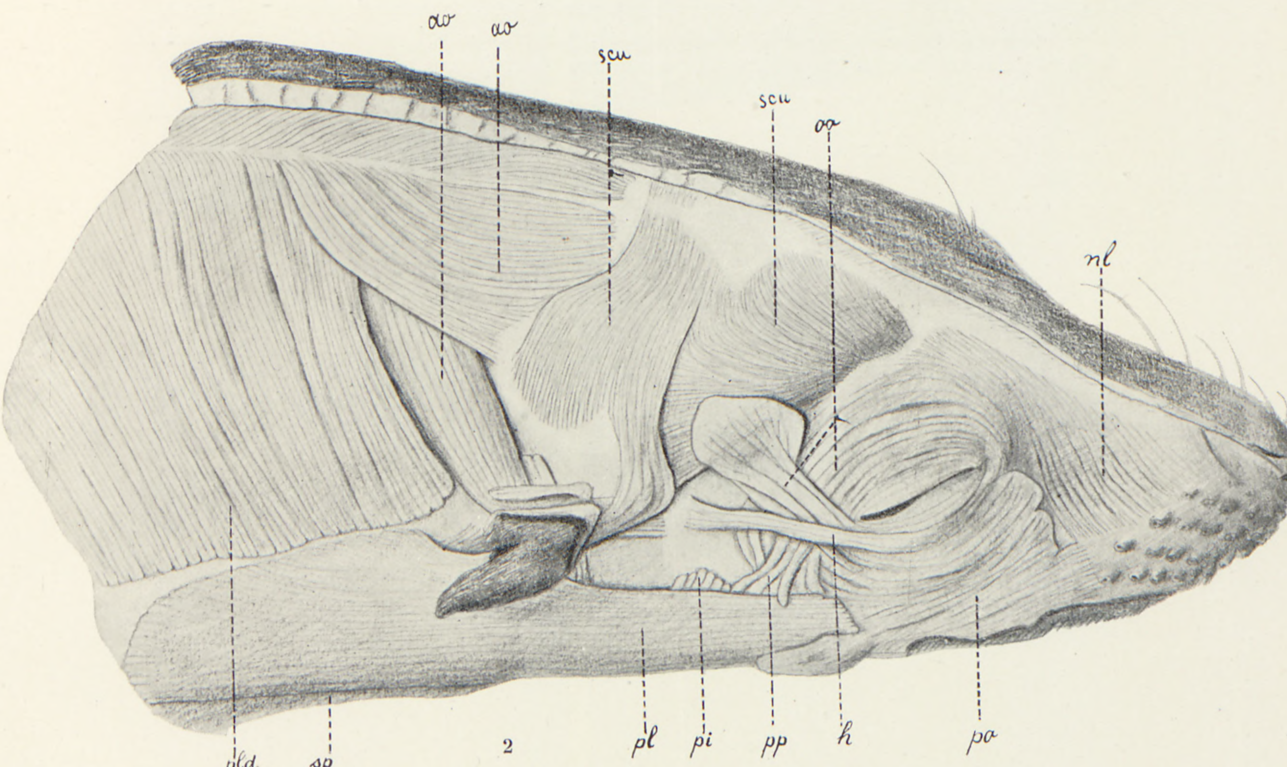

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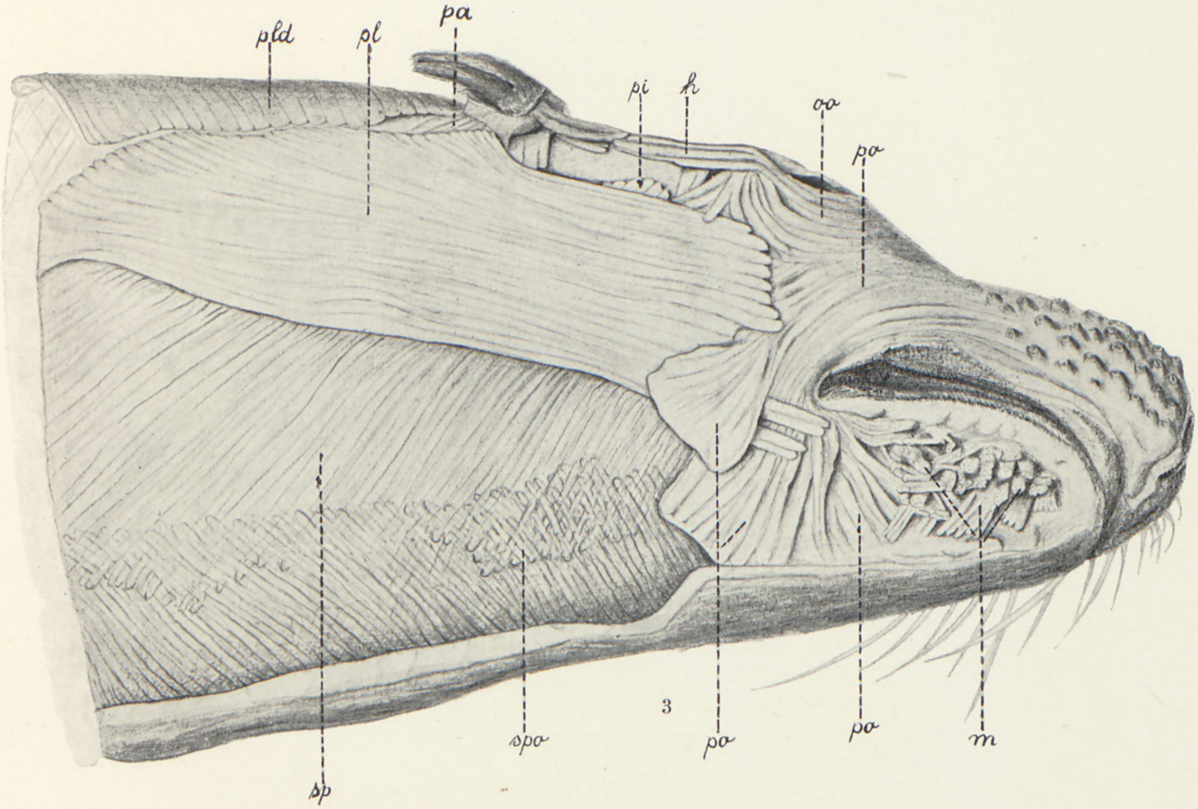
TAVLE II

Fig. 3. Overfladisk Lag af facialis-Muskulaturen, set skraat nedenfra, af Zalophus. *h*, m. horizontalis; *m*, m. mentalis; *oo*, m. orbicularis oculi; *pi*, portio intermedium sph. prof.; *pl*, platysma; *pld*, dorsale Afsnit af platysma; *po*, portio oris sph. prof.; *sp*, sphincter profundus; *spo*, overkrydsende Bundter af sph. prof.; *pa*, portio auricularis sph. prof.

— 4. Skematisk Fremstilling af Deltagelsen af port. palpebralis sph. prof. (*pp*) og m. horizontalis (*h*); Dannelsen af m. orbicularis oculi hos Zalophus.



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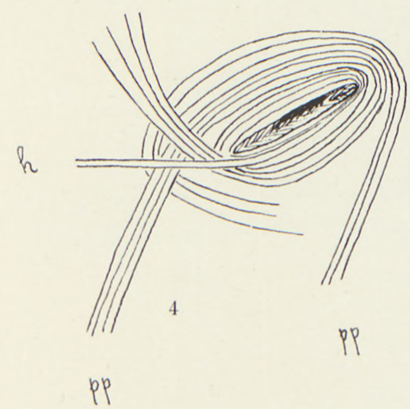

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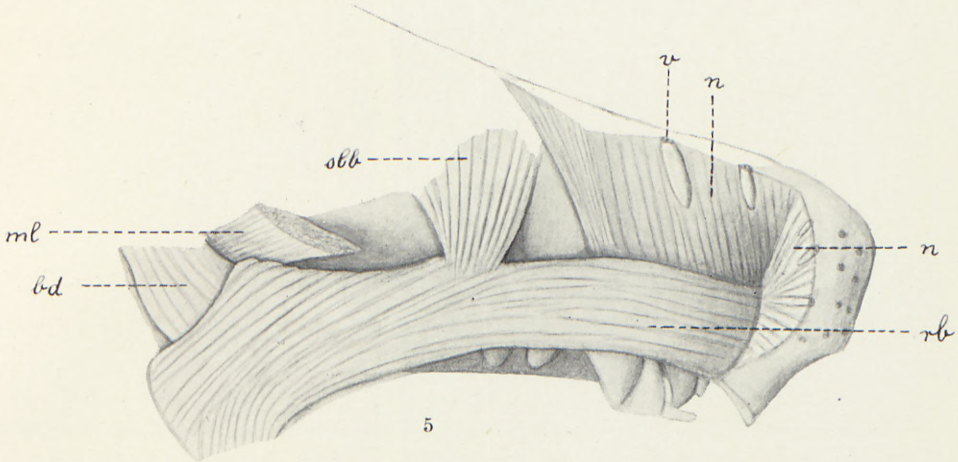
TAVLE III

Fig. 5. Dorsale Del af m. buccinatorius med m. nasalis; af denne sidste er der borttaget en caudo-lateral Del for at blotlægge pars rimana. *bd*, dybere, longitudinale Del af m. buccin.; *ml*, m. maxillo-labialis; *n*, m. nasalis; *rb*, pars rimana m. buccin.; *slb*, pars supralabialis m. buccin.; *v*, sinus vibrissarum.

— 6. Dorsale Del af m. nasalis (*n*) skaaret bort fra Mellemkæben og løsnet fra Snudebrusken, saa man ser Musklens indvendige Flade; *rn*, m. recti nasi skaaret bort fra sin Tilheftning til Snudebrusken, gennemsætter m. nasalis-Bundterne.



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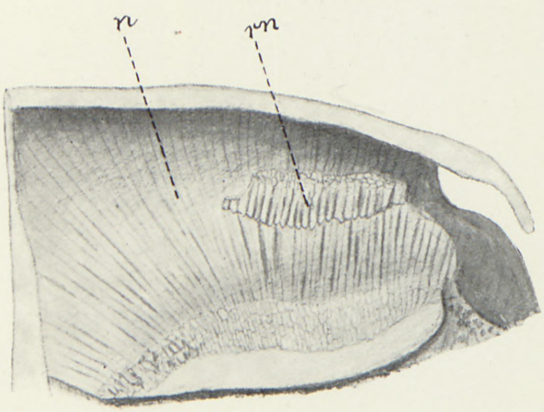

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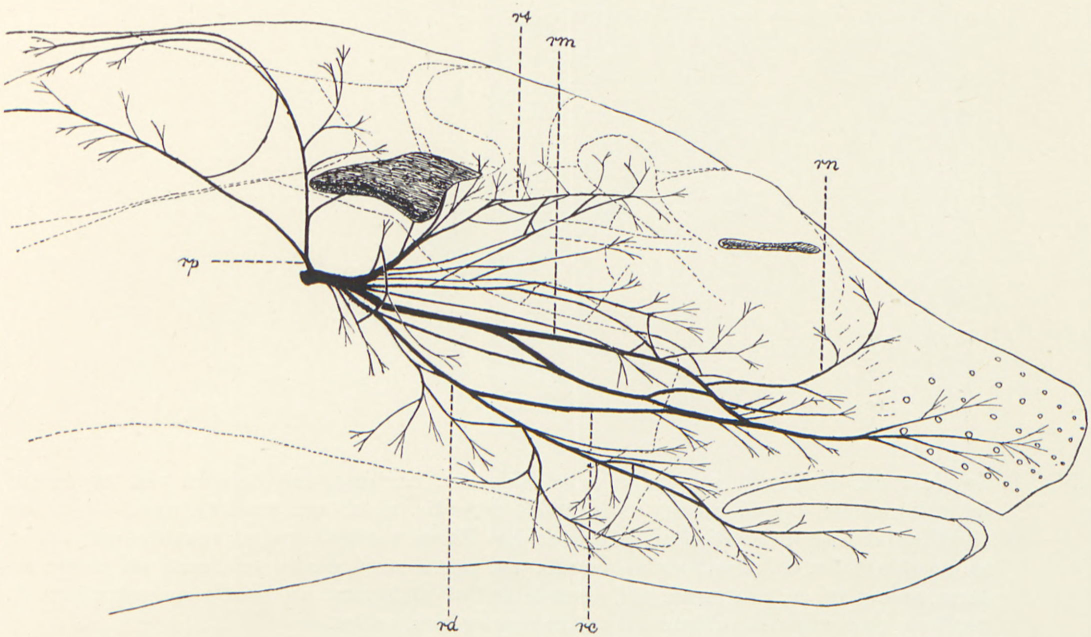
TAVLE IV

Fig. 7. Distale facialis-Forgrening hos Zalophus. *rc*, ramus communicans. *rd*, ramus mandibularis. *rm*, ramus maxillaris. *rn*, Gren til m. naso-labialis. *rp*, ramus post-auricularis. *rt*, ramus temporalis.

— 8. Snuden set forfra af Halichoerus grypus.



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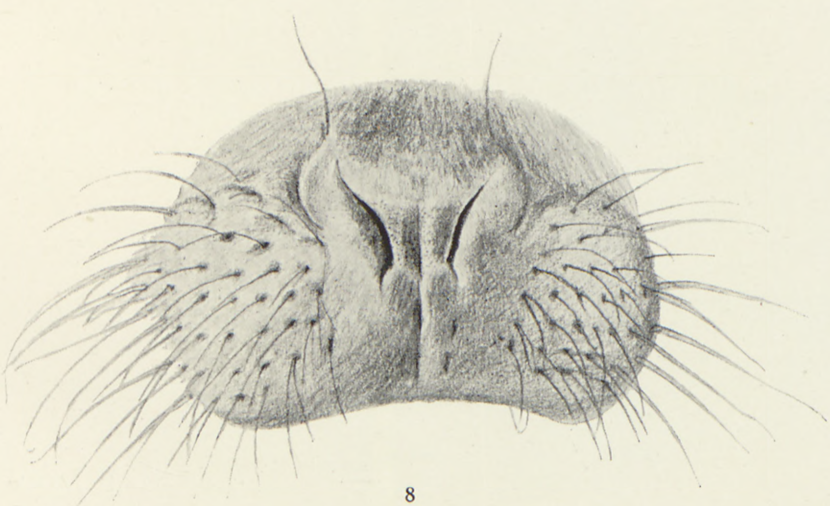

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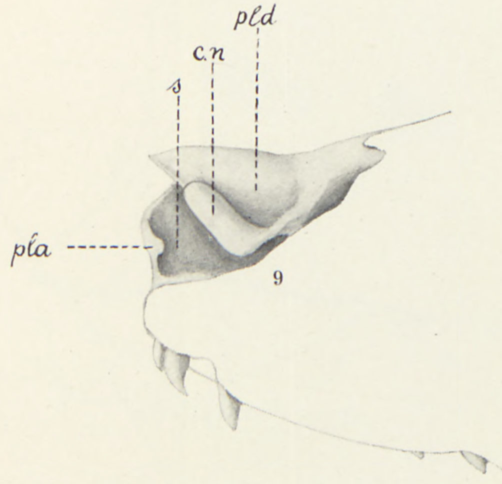
TAVLE V

Fig. 9. Snudebrusk af Phoca set fra venstre Side. *cn*, cartilago navicularis. *pla*, processus lateralis anterior. *pld*, processus lateralis dorsalis. *s*, septum cartilag. nasi.

— 10. Overfladisk Lag af facialis-Muskulaturen hos Phoca vitulina. *ml*, m. maxillo-labialis. *nl*, m. naso-labialis. *oo*, m. orbicularis oculi. *pa*, portio auricularis sph. prof. *pi*, portio interm. sph. prof. *pl*, platysma. *pld*, dorsale Del af platysma. *pp*, portio palpebralis sph. prof. *rb*, pars rimana m. buccin. *sp*, sphincter profundus.



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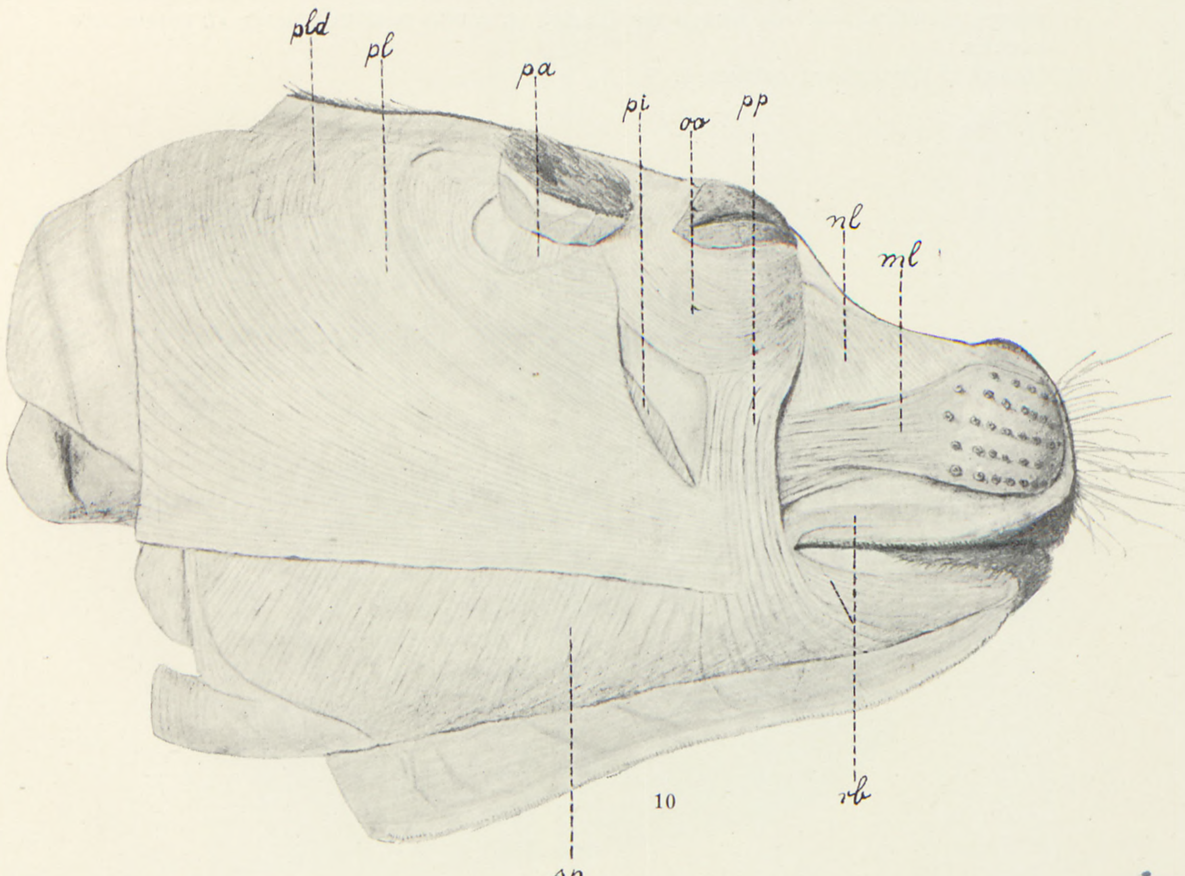

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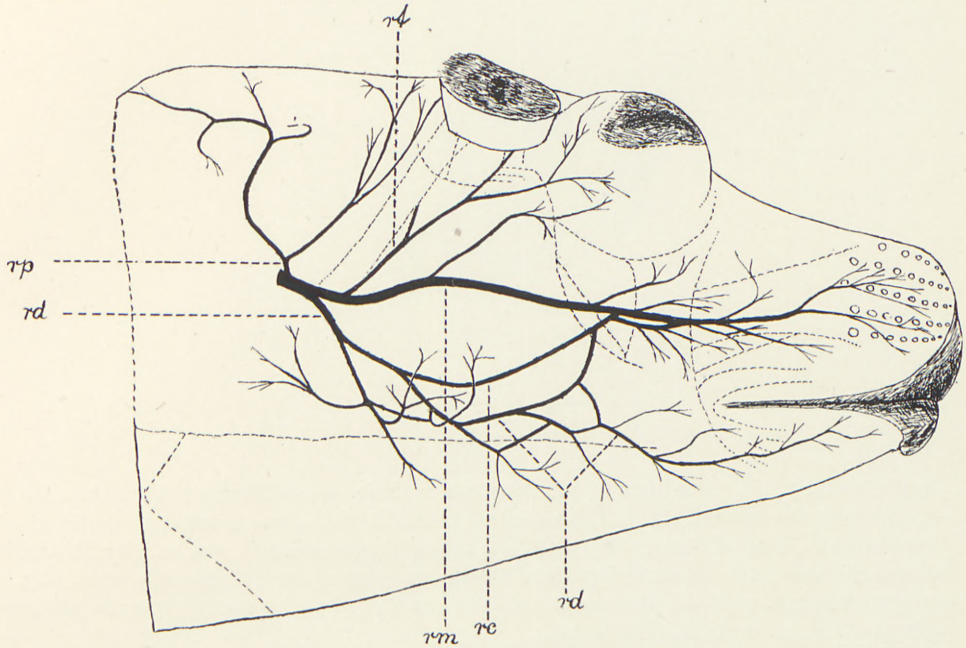
TAVLE VI

Fig. 11. Den distale Forgrening af n. facialis hos Phoca vitulina. *rc*, ramus communicans. *rd*, ramus mandibularis. *rm*, ramus maxillaris. *rp*, ramus postauricularis. *rt*, ramus temporalis.

— 12. Hoved af Cystophora cristata ♀.



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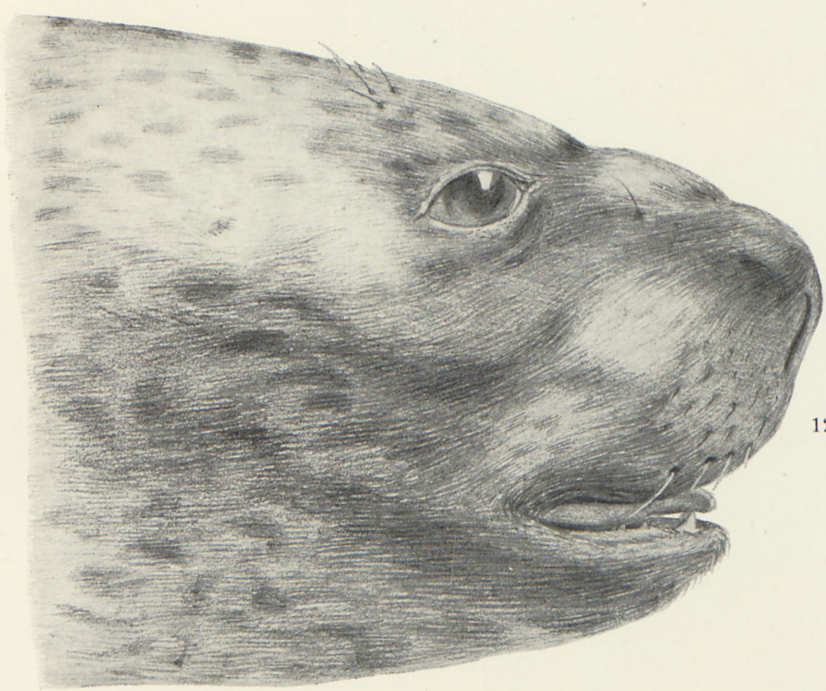

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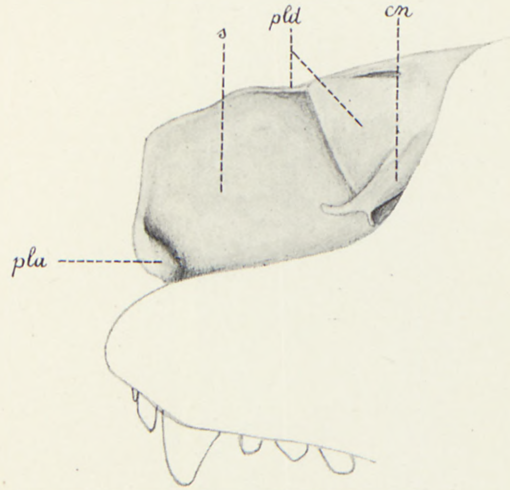
TAVLE VII

Fig. 13. Snudebrusken af Cystophora ♀, set fra venstre Side. *cn*, cartilago navicularis. *pla*, processus lateralis anterioris. *pld*, processus lateralis dorsalis. *s*, septum cartilagineum.

— 14. Overfladiske Lag af facialis-Muskulaturen hos Cystophora ♀. *ml*, m. maxillo-labialis. *nl*, m. naso-labialis. *oo*, m. orbicularis oculi. *pa*, portio auricularis sph. prof. *pi*, portio intermedia sph. prof. *pl*, platysma. *pld*, dorsale Del af platysma. *pp*, portio palpebralis sph. prof. *ri*, m. recti labii inferioris.



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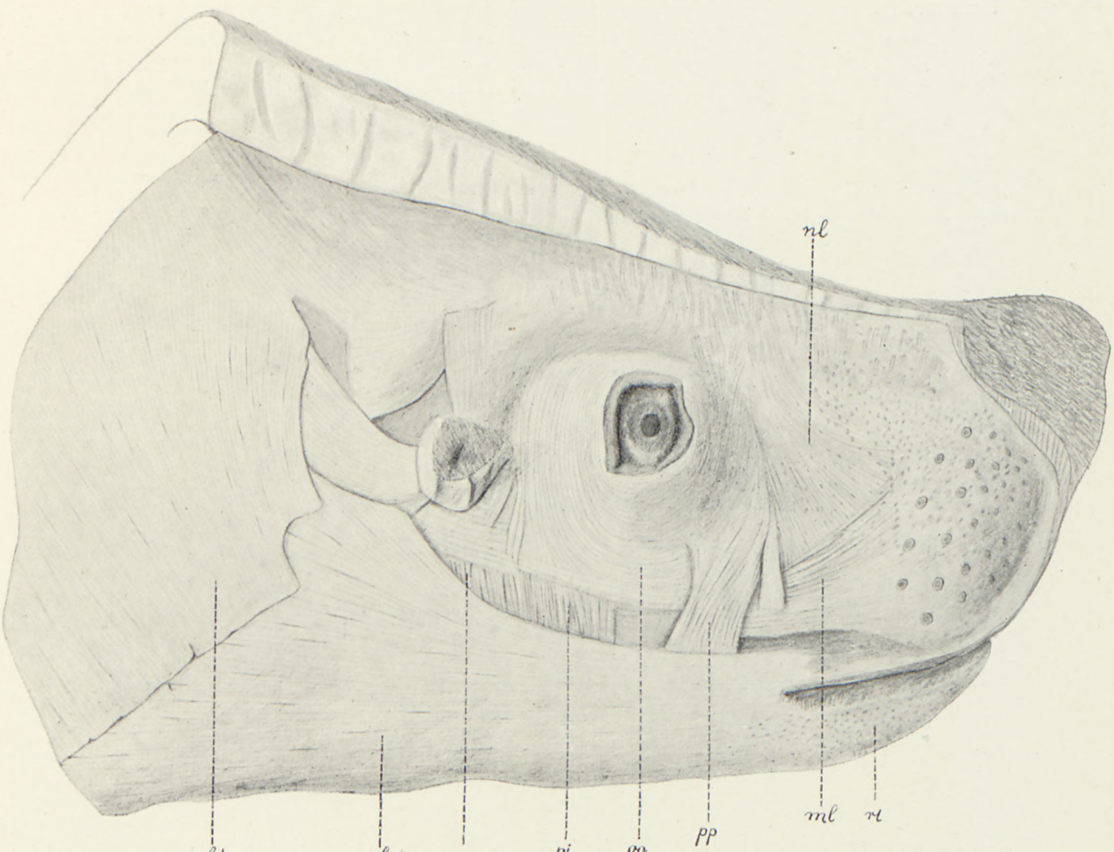

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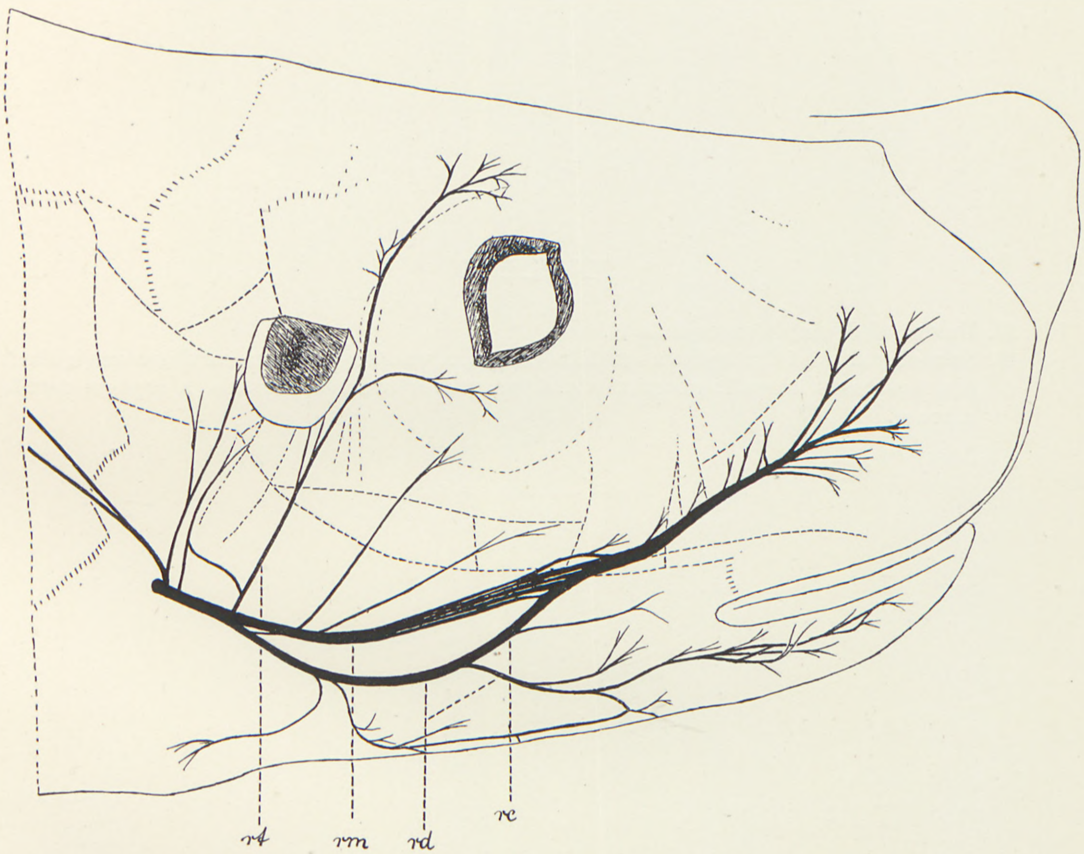
TAVLE VIII

Fig. 15. Den distale Forgrening af n. facialis hos Cystophora ♀. Muskelomridsene punkterede. *rc*, ramus communicans. *rd*, ramus mandibularis. *rm*, ramus maxillaris. *rt*, ramus temporalis.



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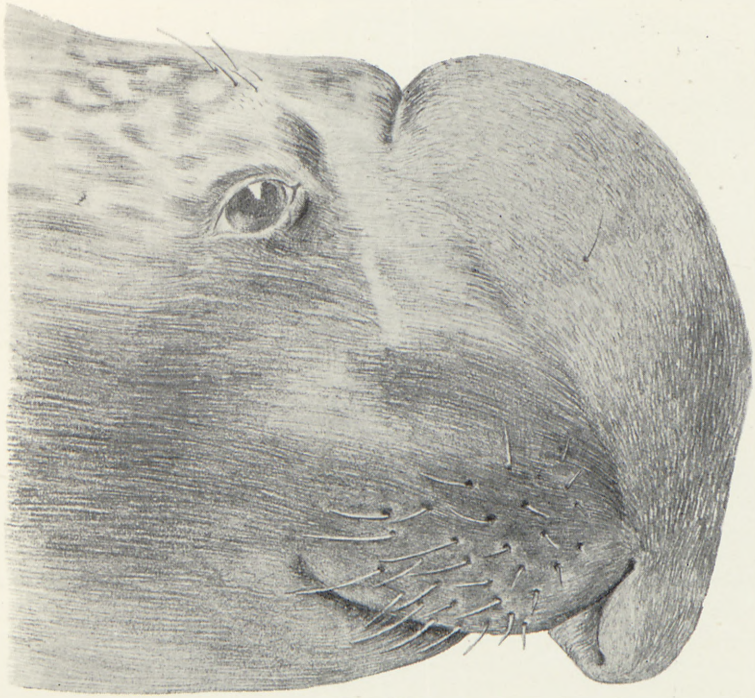
TAVLE IX

Fig. 16. Hoved af Cystophora cristata ♂.
— 17. Snudebrusken af Cystophora cristata ♂, set fra venstre Side. *cn*, cartilago navicularis. *pla*, processus lateralis anterioris. *pld*, processus lateralis dorsalis. *s*, septum cartilagineum.



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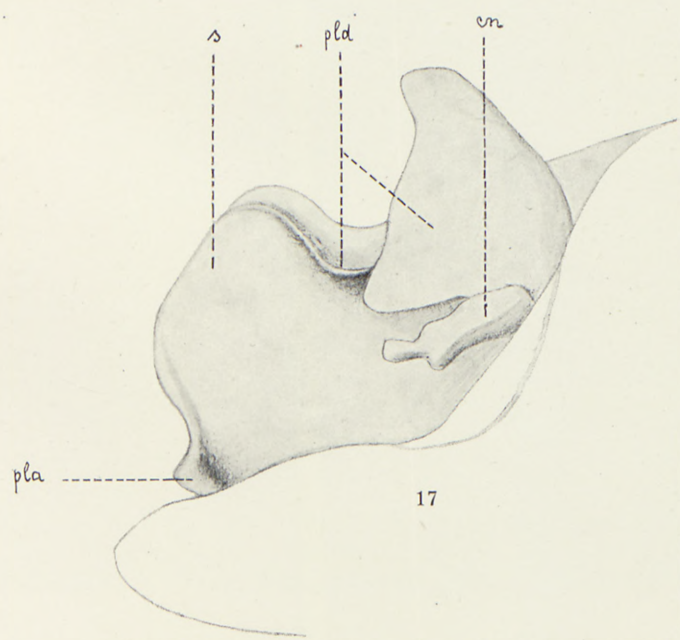

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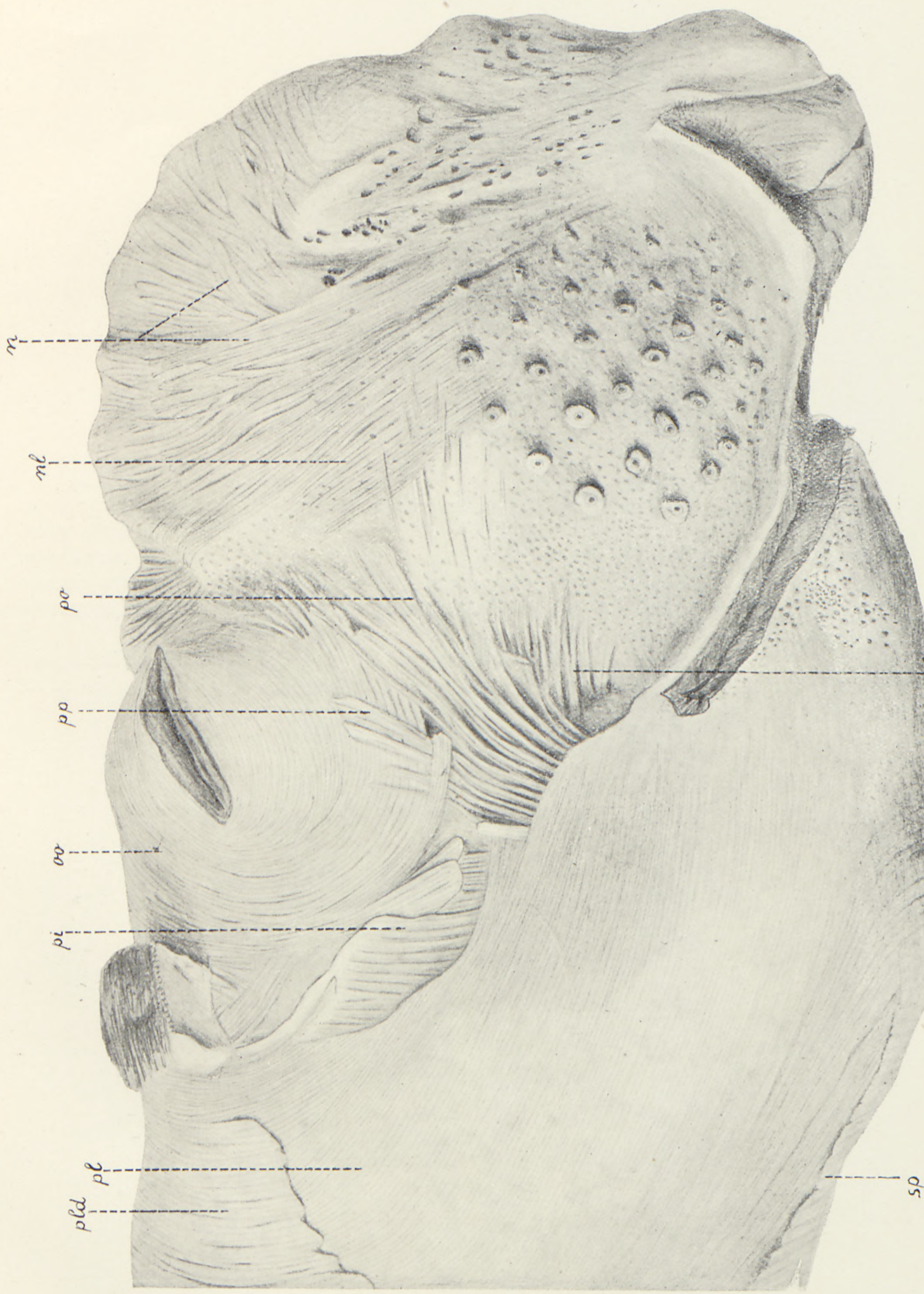
TAVLE X

Fig. 18. Overfladiske Lag af facialis-Muskulaturen hos Cystophora ♂. *n*, m. nasalis. *nl*, m. naso-labialis. *oo*, m. orbicularis oculi. *pi*, portio interm. sph. profund. *pl*, platysma. *pld*, dorsale Del af platysma. *po*, portio oris sph. prof. *pp*, portio palpebralis sph. prof.



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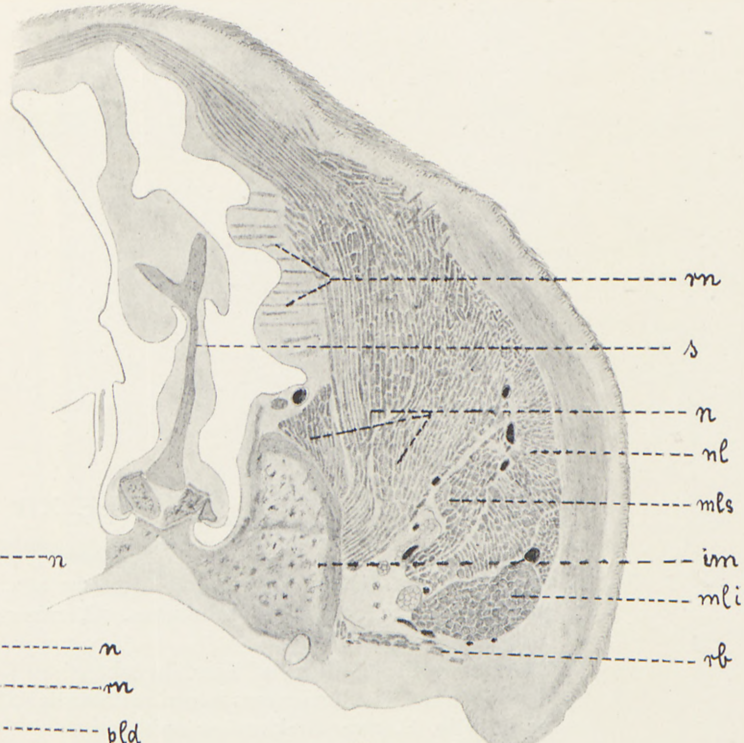
TAVLE XI

Fig. 19. Tværsnit af Hoved af Cystophora ♂ I. *b*, m. buccinatorius. *cn*, cartilago navicularis. *ethm*, Mesethmoidet. *mli*, m. maxillo-labialis port. inter. *mls*, m. maxillo-labialis port. super. *mtu*, Hulhed, hvori forreste Del af maxilloturbinale har ligget. *n*, m. nasalis. *nl*, m. naso-labialis. *o*, Overkæben. *pld*, processus lateralis dorsalis. *rb*, pars rimana m. buccinat. *rn*, m. recti nasi. *s*, septum cartilag. nasi. *sk*, Oppustningssækken. *po*, portio oris sph. prof. *pl*, platysma.

— 20. Tværsnit af forreste Del af Hovedet af Cystophora ♂ II. *mli*, m. maxillo-labialis port. inferior. *mls*, m. maxillo-labialis port. superior. *n*, m. nasalis. *nl*, m. naso-labialis. *rb*, pars rimana m. buccinat. *rn*, m. recti nasi. *s*, m. nasalis. *im*, intermaxillare.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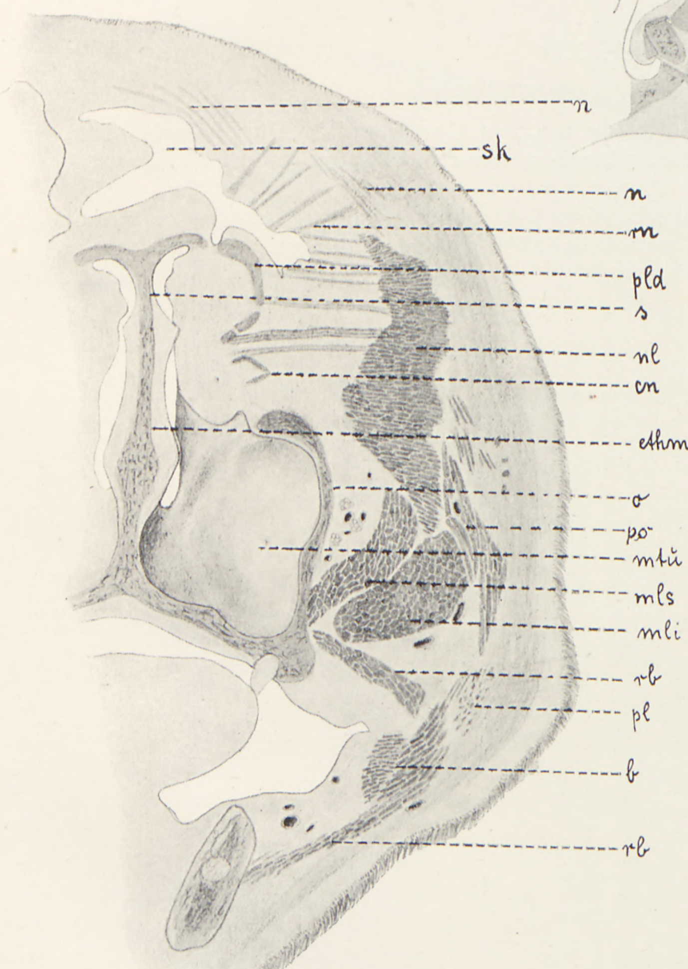
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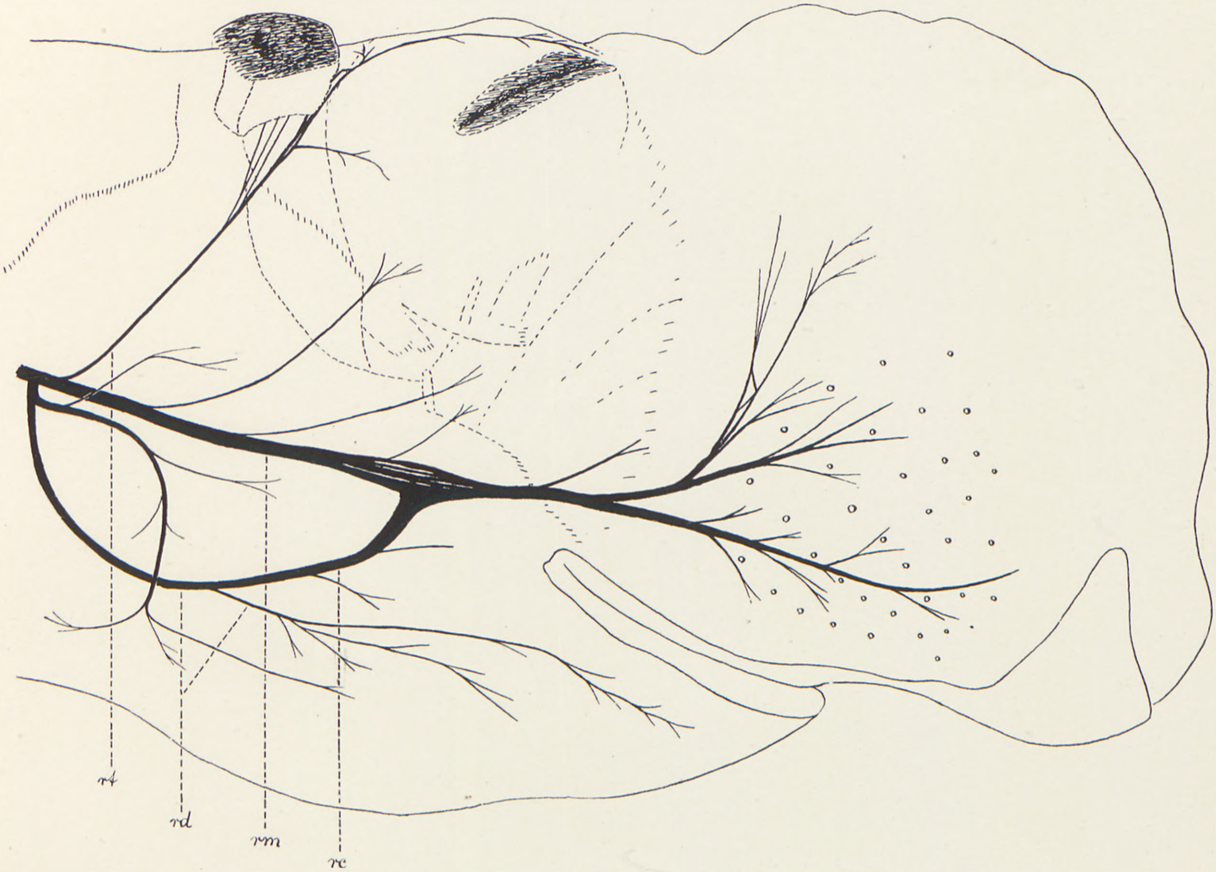
TAVLE XII

Fig. 21. Skema af den distale Forgrening af n. facialis hos Cystophora ♂. Muskelomridsene punkterede. *rc*, ramus communicans. *rd*, ramus mandibularis. *rm*, ramus maxillaris. *rt*, ramus temporalis.

— 22. Skematisk Fremstilling af Snudebrusken hos Cystophora cristata ♂ set ovenfra, med den lodrette Del af processus lateralis dorsalis (*pld*) i sine Yderstillinger. I, naar Sækken er i Hvile, II, naar Sækken er opblæst.



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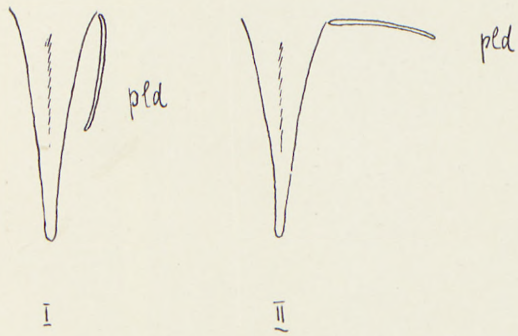

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CONTRIBUTIONS

TO THE

DEVELOPMENT OF THE TREMATODA DIGENEA

PART I

THE BIOLOGY OF LEUCOCHLORIDIUM PARADOXUM

BY

C. WESENBERG-LUND

WITH 6 PLATES AND 7 TEXTFIGURES

D. Kgl. Danske Vidensk. Selsk. Skrifter, naturvidensk. og mathem. Afd., 9. Række, IV. 3

KØBENHAVN

HOVEDKOMMISSIONÆR: ANDR. FRED. HØST & SØN, KGL. HOF-BOGHANDEL

BIANCO LUNOS BOGTRYKKERI A/S

1931

Preface.

Originally it was my intention to publish the first part only of this paper, my contributions to the biology of *Leucochloridium*.

As early as 1900—1908, while studying the plancton of the Danish freshwaters, I had observed that cercaria played a very prominent rôle in the plancton of our ponds and lakes. Being much occupied with other studies, however, I could not spare the time to undertake investigations on this interesting subject.

After an application from me in 1930 The Carlsberg Foundation purchased a house at Hillerød and equipped it as a laboratory for experimental studies relating to freshwater organisms. This laboratory is provided with numerous aquaria having air supply, thermostats at different constant temperatures, a very fine photographic outfit and a chemical balance. It is well supplied with the best microscopes and all the necessary instruments for limnological studies. It also contains a large library. On a site 2 km distant there are about 30 cemented open air aquaria. Owing to this magnificent grant it is now possible to keep cercaria-infected molluscs for months in the aquaria, to accelerate or retard the development of the parasites, and to transfer them experimentally to fishes and frogs. These excellent conditions for the study of freshwater organisms have revived my old interest in the biology of the development of the Trematoda, and I hope to be able to add a second part to the present paper later on.

It is my pleasant duty to tender my respectful thanks to the Trustees of the Carlsberg Foundation who, from the very beginning, have with the greatest generosity subsidised the investigations of our freshwaters. By this new great grant, left entirely at the disposal of the study of our freshwaters and freshwater-organisms, they have enabled us to extend our investigations to fields which have hitherto, in our country, been very little studied.

The author.

Hillerød, 20. Oktober 1931.

Chapter I.

Observations in Nature and in the Laboratory.

During my excursions along the rivulets and borders of our lakes I have very often found *Succinea putris*, which is very common in all localities of this kind. Where the snails have been abundant I have almost always gathered some hundreds of them, wishing to find the parasite *Leucochloridium paradoxum* which is now and then found in our country, but always only in a very limited number.

At last, at the borders of Tjustrup Lake in the middle of Seeland, only about one kilometre from the summer laboratory for freshwater biological investigations, I had the good fortune to find a single individual in July 1926. During the years 1927 and 1928 *Leucochloridium* was the main object of my investigations.

Since Heckert, in his admirable paper of 1889, has given a full account of the historical development of our knowledge of this very peculiar organism, it would seem superfluous to do this once more; a very short account will suffice.

In an old engraving from Halle Carus (1835) found a figure of a *Succinea*, the antennae of which showed several vividly coloured *Leucochloridium* sacks.

Ahrends (1810, p. 292) and Ramdohr (1810, p. 295) found and described *Succinea* infested with *Leucochloridium*. Ramdohr regarded the organism as a worm, and the contents of the sacks as eggs. Carus (1835) gave the parasite its name; he saw that the great green sacks were connected with a "Convolut weisser, unregelmässig angeschwollener, mit ästigen Enden fest gewurzelter Röhren von verschiedener Grösse" (pag. 92) and that this envelope was lying in the liver. He further saw that trematodes were found in the sacks; still, he was inclined to regard the contents as eggs, and supposed that the eggs were developed in the forepart of the sacks. He regarded the parasite as a worm, but supposed that it was derived from a generatio æquivoca, owing to the power of the liver to produce maladies "infolge eines Übermasses bildender Kraft". — Steenstrup (1842, p. 56) regarded the whole organism as "Amme", denied an origin from generatio æquivoca, and maintained that the parasite took its origin from small oval vivid cilia-covered organisms living in the tentacles of *Succinea* and of a similar structure to *Opalina ranarum*. On this latter point Steenstrup was mistaken, the organisms which he saw being most probably really *Opalina*. In 1845, p. 479 Dujardin created the name sporocyst, the name always used afterwards for this stage in the developmental history of the Trematoda. Siebold (1853, p. 425) showed that the sporocyst is an organism sui generis, being in no direct connection with the snail; the contents of the sacks are not eggs but germ-spheres ("Keimkörper") later on developing into larvæ which in the fully developed stage resemble *D. holostomum*. He supposed that the final host was to be found among waders and swimming birds, especially *Rallus aquaticus*. Seeing that the distoms in the sacks are motionless, whereas the sacks themselves are very mobile and furthermore of a very vivid colour, he supposes that the main task of the sacks is to allure birds and cause them to swallow the snails.

ZELLER (1874, p. 564) showed that it is at all events not water birds alone which swallow the snails; he ascertained experimentally that songbirds such as *Erithacus rubecula, Fringilla spinus, Sylvia atricapilla, Motacilla flava* tear the sacks out of the tentacles and then swallow them. He further showed that the ripe cercaria in the snails, when it has arrived in the alimentary canal of the redbreast and other songbirds, in the course of six days there develops into *Distomum macrostomum;* ZELLER as well as later authors (LÜHE 1909, p. 145 a. o.) have not been able to distinguish the two species *D. holostomum* and *D. macrostomum* from each other, and *D. macrostomum* is now stated to be found in water birds (*Rallus aquaticus, Gallinula chloropus, Orthygometra porzana*) as well as in long series of songbirds.

In 1889 HECKERT found the miracidium and gave a long, very valuable series of observations relating to the growth of the sporocyst, the infection of birds etc. It was shown that it was only possible to infect young birds, not older ones, furthermore that eggs were found in the layer of urine surrounding the faeces about 14 days after the infection with *Leucochloridium* sacks. In the eggs were found the miracidium larvæ. Leaves with excrements of birds were then given to the snails, and ten to fifteen minutes later miracidia were found in the alimentary canal of the snail. Later on the sporocysts were observed in the liver; a sack takes about three months to become fully developed. Curiously enough LÜTKEN in his little known work: "Snyltelivet og Snyltedyrene" 1895, (p. 56), writes: „Smaller birds such as nightingales and other songbirds hatch only the largest sacks so that the smaller ones get the opportunity to reach maturity; larger birds such as *Rallus* swallow the whole snail." This may be right, but as far as I know the view is based more upon suppositions than upon observed facts.

It must further be added that the *Leucochloridium*-sacks observed by HECKERT and all other observers were of a green colour with the apex of the sacks vividly red. A single time HECKERT found a sack with brown pigment. This brown form was found again by MAGATH (1920) and described as a new species, *Leucochloridium problematicum*. Its hosts were *Planorbis trivolvis* and *Succinea retusa*. The pigment was said to be of a "deep golden red colour" (1920, p. 110). Later on (1922) brown sacks were again found in Switzerland by MÖNNIG who gives a very thorough description of the histological structure of the organism. According to MÖNNIG the colour of the band is brown. The figures (Pl. VII, Fig. A by MAGATH and Pl. I, Fig. 3, by MÖNNIG) show almost quite the same colour; that of MAGATH is only a little brighter. That of MAGATH is a young sack; that of MÖNNIG an old one. The name *Leucochloridium paradoxum* Carus could in reality only be given to the sporocyst, the only sporocyst, as far as I know, which has a special name. When MONTICELLI (1888) dissolved the old genus *Distomum* Retzius he created the new genus

Urogonimus for all those species whose genital porus was terminal; the name of the parasite was then *Urogonimus macrostomus*. The genus *Urogonimus* was admitted by Loos (1899) and others. In the following we will use the name *Leucochloridium macrostomum* for the ripe stage, the parasite being best known under this name throughout the zoological world. See also Witenberg (1926, p. 226). As we shall often return to the papers of Heckert and Mönnig, we will restrict ourselves to the short remark that none of these two authors has found in the sporocyst the slightest trace either of any excretory organ or of a nervous system. With regard to the histological structure of the sporocyst I refer the reader to the two last-named scientists.

a. Investigations in Nature.

In the outskirts of Suserup Forest, along the borders of Tjustrup Lake in Middle Seeland, the sloping sides of the shore are covered with a dense carpet of *Petasites*, the stalks of the leaves being almost of a man's height (Textfig. 1). Small rivulets run among the leaves. The locality is very moist; the ground is covered with stones; in the copse bordering the forest and in the *Scirpus-Phragmites* zone of the lake there nest and live many birds belonging to the genera *Sylvia*, *Turdus*, *Fringilla* and others. The leaves of the *Petasites* are covered with numerous excrements, surrounded by white urine. After a long period of drought the leaves often look white-spotted. Very many snails live on the plants; *Helices* and *Succinea putris* are abundant in the locality from May, when the leaves grow up, until the latter part of September when the withered leaves sink to the ground and cover the stony soil with decaying matter. A great many of the leaves are eaten by the snails, greater and smaller holes giving evidence of their activity. — *Succinea putris*, especially, is found in three age-classes in the latter half of August. One very small yellow one with the viscera shining through the shell, a middle sized one, and a very large one, the two last-named sizes being of a homogeneous colour, dark greyish, or reddish yellow. Later on in the year, but also especially in spring, only the two last-named classes exist. The first class comprises the young brood of the year; those of middle size are one year old, and the last class at all events two years old, and it may perhaps also include three year old snails. During the autumn a great many of these old snails die, and the middle sized class predominates. Eggs are laid twice a year in the latter part of May, and in the middle of July; a sharp limit between the two egg-laying periods does not exist. During the two periods snails in copula are found everywhere upon the leaves. It was rather peculiar to see the great difference in size of the paired specimens; very often snails which were only one year old paired with those which were at all events two years old.

In the first hours of the day when the dew was still lying on the leaves, the snails were found upon the upper side. Shortly after the sun had begun to fall on the leaves the snails slowly disappeared. Creeping over the edges of the leaves or very often, especially in autumn, through the holes made by the Helices feeding on them, they arrived on the under side and fastened themselves there. — In periods of drought they crept down along the stalks; in very long periods of drought they totally disappeared from the plants and were then only found beneath the stones on the ground. The greatest activity was always displayed on warm moist summer days with a continuous fine drizzling rain, and with a temperature of about twenty to twenty-two degrees. On such days the upper side of the leaves would carry 15 to 20 snails and often about 10 *Succinea;* and on such days there was an enormous perforation of the leaves. In the autumn, at temperatures about 12 degrees, the snails were also

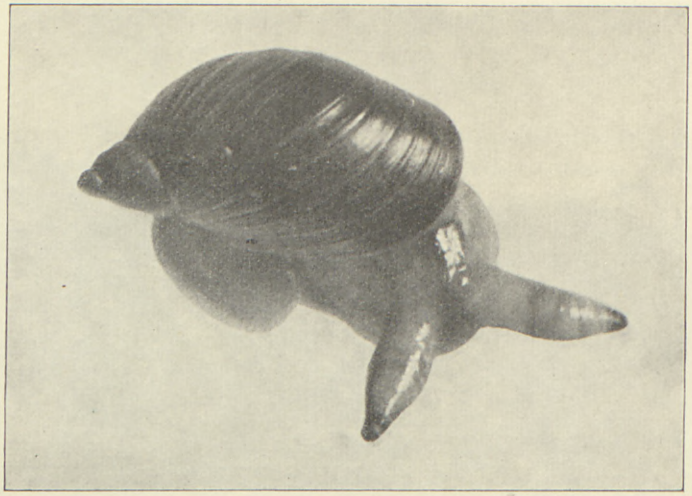
Textfig. 1.
The *Petasites* forest along the borders of Tjustrup Lake. (Berg phot.)

found upon the surface of the leaves on dark cloudy days but then they moved very slowly and mostly sat with the antennae drawn in. In stormy weather, even if it rained, and in thundershowers, no snails were found upon the upper surface.

Owing to the great leaves being commonly almost horizontal the excrements dropped by the birds, especially in the periods of drought, remained for weeks on the leaves. In rainy weather the excrements were washed off; most of the water followed the nerves of the leaves, reached the point where the stalk was fastened to the leaf and, following the stalk, finally reached the ground. Very often a little moisture was gathered round the attachment of the stalk; this moisture was very often of a greyish colour; in reality it was only the diluted excrements of birds. Just here, and in addition almost always on the excrements, snails could be observed eagerly sucking up the greyish fluid. *Limax, Helix arbustorum, Succinea putris* were here sitting side by side. The food material was the same for all the different species of snails, namely excrements, in which I several times found *Distomum* eggs, and in a few cases the distomes themselves; as far as hitherto known, only the *Succinea* are infested. Very often I have seen four *Succinea* sucking from the same excrements.

One day in July 1926, passing by the *Petasites* forest, I saw the first *Succinea* with a *Leucochloridium;* during the following three years I found about 150 specimens.

The locality was visited at all times during the period from May 1st to October 1st. During 1926 the *Succinea*, and especially those harbouring *Leucochloridia*, were only found in a very small part of the *Petasites* forest, that nearest to Suserup Forest, and



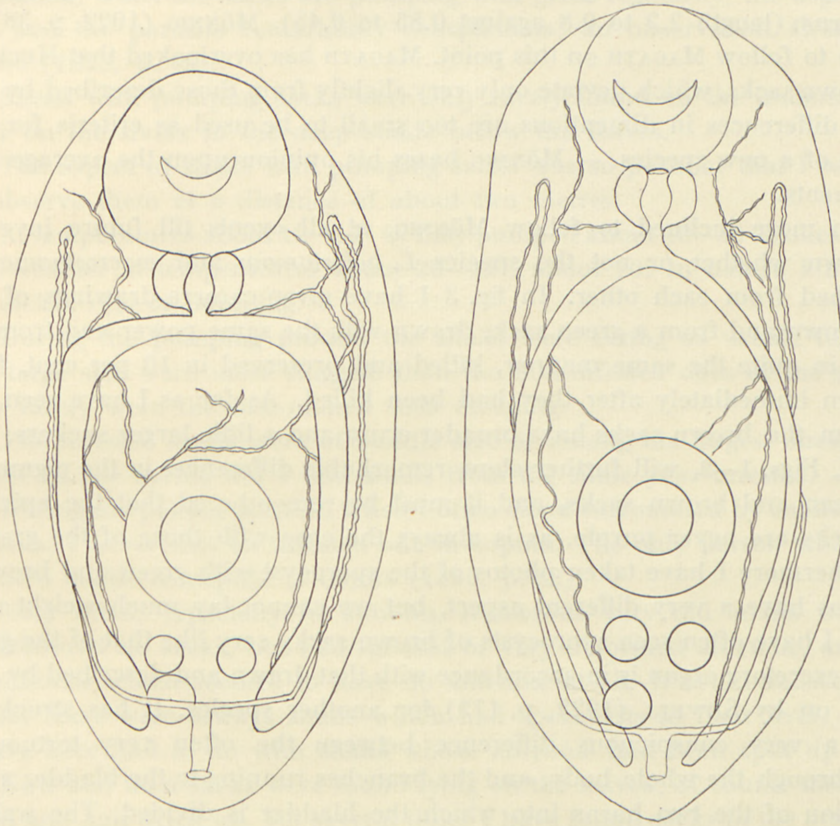
Textfig. 2.
A creeping *Succinea* with two pulsating sacks in the antenna. (Berg phot.)

where the beeches were hanging out over the *Petasites* leaves; the whole locality was most probably not more than about a few hundred square metres. During the two following years, and especially in 1928, the *Succinea* were found upon the whole of the *Petasites* forest, and those with *Leucochloridia* were also found there. The greatest number were, however, always found below or nearest to the beeches where the white spots of excrements were most abundant. During the years 1929 and 1930 the number of parasitised snails diminished.

As is well known, two forms of sacks, the green and the brown sacks, occur. In my locality I had, in 1927 and 1928, only found brown ones. In the beech forest itself near the borders of the lake, in a locality where small streams fall into the lake, the *Succinea* also occur. Very often I have searched for *Leucochloridium* here, but always without any luck. Then in August 1929 a single specimen was found, but this was green; later on in the same locality I found three other specimens, all green. In the main locality only the brown ones were found. It is rather peculiar that the two forms are restricted, each to its special locality.

HECKERT has mainly found and worked with green sacks, MAGATH (1920) and later on Mönnig (1922) with brown ones. Heckert (1889, p. 14) found both brown and green sacks in the same snail. Most probably they belonged to two different sporocysts.

As far as I can see, the green sacks are a little more slender; the most conspicuous difference is that the green sacks have a red eye spot at the apex of the sacks, whereas the brown ones lack this. The pigment bands on the green sacks are



Textfig. 3.
Cercariæ from a brown and a green sack.

of a blue-green or dark blue-green colour, on the brown ones of a brown colour. There is very little difference to be found in the arrangement of the bands in the brown and the green sacks. As Mönnig (1922, p. 11) has observed, the rings in the brown sacks show a series of small elevations. In both cases the rings are most compact in the anterior part of the sacks and may here in old sacks be almost confluent, so that the whole anterior part almost looks brown; at the apex the rings may, as shown in the figure (Pl. I, Fig. 1) present themselves as a framework of small strings. No two sacks have the same arrangement of the rings. The older the sacks are, the more numerous, and more conspicuous are the rings. As mentioned above, Magath

(1920, p. 110) has tried to create a new species: *Leucochloridium problematicum* for the *Leucochloridium* with brown sacks. This *Leucochloridium* is said to differ from *Leucochloridium macrostomum* in the following points. 1) The sacks of *L. problematicum* are brown, those of *L. paradoxum* green with a red apex. 2) The lateral intestinal crura are 0.55 mm. in diameter in *L. problematicum*, in *paradoxum* they are much smaller. 3) The cercaria (= agamodistomum) of *L. problematicum* is larger than that of *L. paradoxum* (length 2.2 to 0.8 against 0.85 to 0.45). MÖNNIG (1922, p. 38) has not been able to follow MAGATH on this point. MAGATH has overlooked that HECKERT also found brown sacks, which deviate only very slightly from those described by MAGATH.

The differences in dimentions are too small to be used as criteria for the establishment of a new species. — MÖNNIG bases his opinion upon the average of twelve measurements.

I am more inclined to follow MÖNNIG, at all events till future investigations have shown whether or not the species *L. holostomum* and *macrostomum* can be distinguished from each other. In fig. 3 I have given camera drawings of cercariæ from a brown and from a green sack, drawn with the same power and from animals prepared in quite the same manner, killed and preserved in 10 per cent. formaline and drawn immediately after they had been killed. As far as I have seen, the cercariæ from the brown sacks have broader crura and a little larger suckers. A glance at Plate I, Figs. 1—2, will further show remarkable differences in the pigment bands of the green and brown sacks, and it must be remembered that the apices of the brown sacks are never purple, as is always the case with those of the green sacks.

Furthermore I have taken photos of the sporocyst with green and brown sacks. The photos have a very different aspect, but we cannot lay much weight upon this point, for I have often seen sporocysts of brown sacks very like that of the green one.

The excretory organ is in accordance with that drawn and described by HECKERT and later on by SEWELL (1922, p. 172) for another species. It has struck me that there is a very conspicuous difference between the often very tortuous canals running through the whole body, and the branches running to the bladder as a direct prolongation of the two horns into which the bladder is divided. The walls of the former have a glandular structure with very many nuclei; the others are quite straight, the walls are smooth, and no nuclei have been observed. I have not been able to see any pulsation in these rami (MAGATH 1920, p. 111). The flame cells are very difficult to see, and I have not ventured to draw them; HECKERT makes the same observation, and so does SEWELL with regard to *Leucochloridium assamense* (1922, p. 172).

After finding the first specimen, I gathered 500 snails from my locality and took them into the laboratory. The result was very meagre; not a single one showed *Leucochloridia* in the following days. During the first few days when the snails were examined in the locality, the result was the same; the weather was cloudy. On the other hand, on a rainy warm day I rather quickly gathered 13 infested specimens.

In the following I have collected my observations in nature of the infested specimens. The locality was visited 45 times, commonly for two or three hours every time.

1. It seems as if infested snails seek the light; they are very often seen balancing on the borders of the leaves, or sitting on the underside of the leaves with only the antennæ infested with the *Leucochloridium* protruding from the borders of the leaves; in this position, when the sacks are pumping with great regularity, the aspect is very peculiar, and the parasite remarkably conspicuous; an observation already made by Mönnig (1922, p. 49).

2. Snails with pumping sacks were only rarely found on the underside of the leaves, or on the stalks in the deep shade below the leaves.

3. The aspect of snails with pumping sacks was so peculiar that I was always able to observe them at a distance of about two metres.

4. At temperatures about 12—14° C. they pumped about 40—50 strokes a minute, in warm weather at temperatures about 20—22°, about 70. In nature I have never seen a quicker rate of pumping.

5. During the pumping process the snails were eating as usual; the infested snails of large size were more sluggish than the non-infested ones of the same size, and only rarely were the first-named seen creeping.

6. The infested snails were of middle size or among the largest ones, but only three times in late spring did I find snails from the same year infested.

7. During the pairing periods, when I often stood surrounded by snails in copula by hundreds, I never saw an infested one in copula. The only person who has ever seen infested snails in copula is Carus (1835, p. 88).

8. Very often, especially in autumn, numerous very old snails were found which harboured no sacks, but had inflated or very deformed antennæ, and further some specimens which seemed to have no antennæ at all. It could subsequently be shown that these were always snails which had sporocysts in their liver. I suppose that I have here had to do with snails whose antennæ had been split up by birds.

9. Now and then sacks were found lying on the leaves; of course most of them were dead and half dried up, but several times I have found sacks in the act of pumping on the moist surface of *Petasites* leaves.

10. The eastern part of the *Petasites* forest was often mixed with *Glyceria spectabilis* and *Cyperaceæ*. Of course *Succinea* were also found here, and often in still greater number than on the *Petasites* leaves. Nevertheless I have never found infested snails upon them, I suppose mainly because excrements falling on these plants without horizontal surfaces are immediately washed away by the downpour, and do not lie for days upon the plants in a rather soft condition after the rain. In this connection it must be remembered that the parasitised snails are extremely sluggish in all their movements. If not disturbed, they most probably live on one single plant during a whole season, only moving from the leaf to its stalk and vice versa according to the moisture of the air. The probability of infection is therefore much greater on a *Petasites* plant than on grasses.

11. Curiously enough, however often I visited the locality, and though I often sat for hours in the vicinity, I never saw any bird sitting directly upon the leaves. Nor do I know why they should. Insect larvæ were hardly ever found on the leaves. Last autumn only, I found, in a very limited number, a small Lepidoptera larva, almost black with yellow rings. The birds were perched in the overhanging beeches and in the small alders. The redbreast, the blackbird, and the blackcap in the beeches, the wagtail at the borders of the lake, and the reed bunting in the *Phragmites* forest between the *Petasites* forest and the lake were the commonest. The excrements were dropped from the branches or when the birds were flying over the *Petasites* leaves. For my own part I could have snails with *Leucochloridia* before my eyes for hours. The birds were singing only a few metres from them, but nevertheless I never had the good fortune to see the birds take the parasites. I confess that this fact has always troubled me a good deal. For it must be kept in mind that hitherto no one has ever seen a bird in natural conditions attack a snail infested with *Leucochloridia*, nor pick out a sack from the antennæ. That the birds do so in captivity is not an absolute proof that they also do so regularly in nature. I have always thought that an observation of just this kind could not be said to be quite superfluous.

On the wall of my laboratory I had the nest of a redbreast, containing 6 young ones. As these left the nest, they began hopping round the garden walks searching for food. In the course of eight days I had made them so tame that they came on to the veranda of the laboratory and picked up crumbs of bread and insect larvæ thrown out only half a metre from my seat. I then covered my veranda with leaves of *Petasites,* and distributed six snails with *Leucochloridium* sacks, all pumping eagerly, over an area of one square metre. Some of the snails had one sack in each of the antennæ. To my eyes they were conspicuous at a distance of more than two metres. The redbreasts arrived as usual; three of them were hopping about the veranda simultaneously, and more than once I saw the birds sitting on the very leaf which carried the snails with pulsating sacks. Nevertheless they did not take the slightest notice of the sacks. I have repeated the experiment three times; the result was always the same.

Of course these observations are not in the slightest degree able to weaken the excellent studies by Zeller and Heckert. Nevertheless they have puzzled me a little, and I confess I have been sorry for all the wasted efforts of the sacks pumping and pumping at a rate of about 70 strokes a minute. It must, however, be admitted that my redbreasts were all young birds which had only left the nest a few days before. It is a reasonable conjecture, therefore, that the skill and attention of the old birds may be larger than that of the young ones. As shown in the following a large number of old snails possess old sacks shrivelled up behind the antennæ and without any pulsating power. This seems to show that at all events very many sacks never reach their destination.

12. It is difficult to say how great the infestation of the colony really was; at any rate it was not very great. Once my eye was adjusted to the object, I think that I soon discovered the infested snails available on that day; all infested snails were

commonly found during the first half hour of research, none later on. When it is borne in mind that I could often observe many hundred snails simultaneously, and that the greatest harvest of infested specimens on a single day was only 13, a one per cent. infestation would seem too high, one per mille probably being nearer the mark.

13. During the years 1927—1930 I gathered 500 snails every year, took them into the laboratory and there studied them for two or three days. Only one or two of these 500 snails were infested. After observation the snails were again placed on the *Petasites* leaves.

b. Investigations in the Laboratory.

All infested snails were taken into the laboratory; here they were isolated and given a substratum of leaves of different plants, *Petasites, Taraxacum, Circium* and others. A separate record was kept of each snail from day to day, from the moment of capture to the death of the snails. Some of the snails were under regular observation from June 15th to April 15th. As many as 25 cultures have been started simultaneously. Until November 1st the cultures were kept in my work-room, later on they were taken into a room which was never heated, and where the temperature oscillated between +2 to 8 degrees C. When the snails were dying, they were killed and conserved in formaline and sublimate. Very often they were taken at a moment when the snail was really dead, but the great sacks were still pumping behind the invaded antennæ.

Of course it would be too tedious to reprint all the 70 different records kept for a period of from one to ten months; but before trying to summarise the observations of the laboratory in a short sketch, it may perhaps be suitable to give a few of them.

No. 16 is a large snail, at all event two years old, most probably more. It was found on $^{12}/_{8}$ 27, having at that time two large sacks. It shows the sacks the following days, and the snail keeps on feeding the whole of August; nevertheless from $^{16}/_{8}$ sacks are never seen. On $^{16}/_{9}$ the snail fastens itself to the glass by a secretion, and is now fastened to the vessel till $^{17}/_{1}$. During the time $^{16}/_{8}$ to $^{16}/_{9}$ the snail is very sluggish, showing very deformed antennæ. On $^{17}/_{1}$ it is found creeping about slowly; the antennæ are thickened and deformed, quite as before the winter sleep. During the rest of January it creeps about slowly but takes very little food. Sacks are never seen. On $^{1}/_{2}$ it is again found agglutinated to the glass and remains there till $^{11}/_{2}$ when it dies. During half a year it has never shown sacks, but the antennæ have all the time been very deformed. The section shows two very large and very old brown sacks; they are quite motionless, and are infiltrated in the connective tissue of the snail from which they have been unable to liberate themselves. The sporocyst is very large and furnished with 5—6 smaller and greater sacks; the cercariæ are living and moving, both in the sporocyst itself and in the large sacks here surrounded by thick brown envelopes.

No. 22 is a large snail, at all events two years old. It was taken on $^{13}/_{8}$ 27, at that time showing two small sacks in the right antenna. On $^{27}/_{8}$ one of them is voluntarily thrown off; during the period $^{7}/_{9}$ to $^{7}/_{10}$ no sacks are observed, and on the latter date the snail is cementing itself to a stone. On $^{19}/_{3}$ I put the vessel in my laboratory (tp. 12—20° C.). On $^{22}/_{3}$ the snail is creeping about; the antennæ are as thick and irregular as on $^{7}/_{10}$. On $^{23}/_{3}$ two sacks are seen, one in each of the antennæ; they are very small and peculiarly acute. During the time $^{23}/_{3}$ to $^{25}/_{4}$ the snail feeds and makes large quantities of excrements. Simultaneously the sacks are uninterruptedly increasing in size and are extremely large in the latter part of April. From $^{20}/_{4}$ to $^{25}/_{4}$ the snail is sitting on the glass, it takes very little food during the last two days, the antennæ are withdrawn, and no sacks are seen; on $^{25}/_{4}$ it dies. During the period $^{25}/_{3}$ to $^{22}/_{4}$ the sacks are incessantly pumping, always with the same incredible force and regularity, c. 50—60 strokes a minute. We shall deal with this later on (p. 123).

No. 24 is a large snail, at all events about two years old. It was found on $^{15}/_{8}$ 27. The antennæ are deformed, but no sacks are observed. On $^{6}/_{9}$ it shows one in the right, and on $^{13}/_{9}$ one small one in the left antenna. During the time $^{13}/_{9}$ to $^{3}/_{10}$ it often shows sacks, now one in the right, now one in the left antenna; sometimes simultaneously one in each. During $^{7}/_{10}$ to $^{5}/_{1}$ the snail is agglutinated to a stone. From $^{5}/_{1}$ to $^{18}/_{1}$ it is mainly motionless but not agglutinated; it takes no food.

On $^{18}/_{1}$ it is dissected in the living state. It shows one very large sack and two smaller ones, absolutely motionless. A thin smaller sack shows feeble motion. The three sacks have all very long brown threads whose lumen seems quite obsolete; in addition there are a number of small sacks. All sacks show living cercariæ.

The two snails No. 16 and No. 24 have both very deformed antennæ which are by no means healed during the winter sleep. Nevertheless it seems as if the snails possess sight; they draw back the antennæ when arriving at objects about 1 or 2 mm. distant, and alter their direction.

No. 25 is a snail only one year old. It was found on $^{12}/_{9}$ and at that time had two thick very deformed antennæ. No sacks are seen. On $^{7}/_{10}$ the snail has agglutinated itself to the glass and has never shown any sacks all the time; it awakes from its winter sleep on $^{23}/_{1}$; no sacks. On $^{28}/_{1}$ it shows a small sack. On $^{28}/_{1}$ the snail is taken into a warm room; now it feeds and gives off many excrements. It is regularly fed and now shows two small sacks which grow steadily larger; they are rather large on $^{12}/_{2}$ and very large on $^{2}/_{3}$. Day after day the sacks are always pumping, always increasing in size, and the appetite of the snail is enormous. The rate of pumping is about 50—60 strokes a minute. On $^{15}/_{1}$ the snail has thrown off one of the sacks; it is still alive and lives for three days. On $^{18}/_{3}$ it dies.

No. 31 is a large specimen, at all events two years old. It was found on $^{12}/_{9}$ and had very thick deformed antennæ. No sacks are seen, and up to $^{12}/_{10}$ when the snail has cemented itself to a stone, it has never shown any sacks. On $^{4}/_{1}$ the snail wakes; the antennæ are as thick as on $^{12}/_{10}$, and immediately a small sack is seen pumping in the left antenna. On $^{19}/_{1}$ it is taken into the laboratory, the snail feeds vigorously; the sack is commonly withdrawn, but when exposed to strong light, the sack comes out but does not pump. Slowly the sack increases in size and from about $^{29}/_{1}$ it is always in the antenna and always pumping. On $^{6}/_{2}$ there are two sacks, one in each antenna, and almost of the same size. On $^{12}/_{2}$ both sacks are very large; on $^{13}/_{2}$ the snail throws off the one voluntarily, on $^{17}/_{2}$ the other; on $^{20}/_{2}$ the snail dies.

No. 32. The snail is large, at all events two years old. It was found on $^{12}/_{9}$ and had two thick very deformed antennæ, no sacks were seen. On $^{2}/_{10}$ it shows a very thin, very small sack in the left antenna. On $^{7}/_{10}$ the snail cements itself, sitting in the same place till $^{18}/_{2}$, then it creeps about till $^{28}/_{2}$. Food is offered but not taken. On $^{28}/_{2}$ it cements itself again, and dies about $^{20}/_{3}$, during the winter sleep. The antennæ have always been very deformed, but except during the days about $^{2}/_{10}$ the snail has never shown any sacks.

No. 42 shows quite the same course of life, but the snail is very small, only one year old, and it is perhaps questionable if it is not from the same year. It was found on $^{12}/_{9}$; it has thick deformed antennæ and has never shown sacks; it cements itself on $^{15}/_{10}$ and sleeps till $^{19}/_{2}$. Then it creeps slowly about or is out of the shell till $^{28}/_{2}$ when it cements itself again; about $^{20}/_{3}$ it dies during sleep.

No. 49 is a large snail, at all events two years old. It was found on $^{12}/_{9}$, and had thick deformed antennæ. Sacks are never seen; it cements itself on $^{15}/_{10}$, and now sleeps till $^{4}/_{1}$. It creeps about slowly and on $^{5}/_{1}$ shows a very small, very thin sack in the left antenna. It refuses to eat and dies on $^{19}/_{1}$.

In the following we will try to combine the different observations derived from studies in the laboratory; all accounts relate to infested snails.

1. With regard to the snails it may be said that from the middle of June till the middle of September they feed vigorously on the leaves of *Taraxacum*, *Petasites*, lettuce which are laid before them. This is especially the case with the young ones; the old parasitised snails are more sluggish. The leaves may be moist, but not excessively so; if the snails lie in water at the bottom of the vessel, they swell and will very often die. In the middle of September they are very sluggish, cease to eat, and commonly remain in the same place with the antennæ retracted, and half withdrawn into the shell. In the first part of October they cement themselves to stones or to the sides of the vessel. In the room where temperatures below $+5°$ have most probably never been reached, they often break off the winter sleep in the first part of January. If then taken into a warm room, they immediately begin to feed and may be as lively as in summer. When taken back to rooms with a temperature of about five degrees Celsius, they do not eat and again go into their winter sleep, which is not broken before the middle of April. Old dying snails usually sit several days with the antennæ withdrawn; they take no food at all. If laid with the shell mouth upwards, they are not able to turn round. The borders of the foot get blackish and crenelated; for some hours the snail still reacts to pricking with a needle; then it dies. Snails from the year before, or which are one year old, hibernate very easily in terraria, even if they harbour *Leucochloridia*, whereas the largest sized very often die during the winter sleep. Many infested snails die before the winter sleep, commonly as soon as they cease to eat. Only the peculiar antennæ show that the snails are infested.

2. Snails, especially those of the largest size, are able to exist with *Leucochloridia* for even a very long time without ever showing sacks in the antennæ; old snails have been kept for more than 6 months, and have never shown sacks during a dry period, i.e. in the period in which the snail has taken no food. The very long time the snail may exist with the parasite is rather remarkable. It has been maintained by many authors that infested snails die in captivity much earlier than non-infested ones (SEWELL 1922, p. 16, and others). This is often in accordance with my own observations, but on the other hand, I have had snails infested with the *Leucochloridia* more than a year, and am, therefore, inclined to suppose that a great number of snails which have once been parasitised carry the parasite during the whole of their existence, and that their lives are not much curtailed on that account. That the snails may in some cases get rid of the parasite and, as far as I can see, recover, is a fact which will be dealt with later on.

3. The abnormal structure of the antennæ almost always shows if the snail is infested. MÖNNIG (1922, p. 48) says: "Nach der Ueberwinterung sind die Schneckenfühler ganz normal.... Nach der Entfernung der Schläuche, wenn die Regeneration der neuen etwas lange dauern, geht der Fühler auch wieder in seinen normalen Zustand zurück." On this point my observations are not in accordance with MÖNNIG's. As far as I have seen, especially old snails never get normal antennæ again; those of the young ones always remain a little inflated. In very many cases I have observed and gathered snails in nature which did not show sacks in the antennæ; they were only abnormal. When taken into the laboratory, they would never show sacks for weeks or months, but when dissected, it could be shown that they were in reality largely infested with them. Old snails are very often found which either seem totally to lack every trace of the antennæ or in which the antennæ are only present as very small knobs. This may be due to the fact that birds have taken the sacks and injured the antennæ, but it is beyond doubt that snails which show thick antennæ before the winter sleep in October, and show no sacks before April, have the same thick antennæ in spring when they awake. Furthermore, sacks may be taken out of the antennæ, but even if the snail lives a whole year after, the antennæ will always be abnormal. In many snails the antennæ seem almost normal. A closer examination will, however, show that the one antenna is a little inflated and slight transparent. This is especially the case with young snails of very small size, and originating from the same year. If these specimens are taken into the laboratory, they may be kept for weeks before the very thin extremely acute sacks appear for the first time. Sometimes I have thought that an inflation of the antennæ precedes the intrusion of the sacks, but of course it is impossible to say if the sack has not in reality forced its way into the antenna at an earlier stage.

4. With regard to the nourishment of the sacks, the following observations may be made.

From $^{20}/_{6}$ to $^{15}/_{7}$ a snail had had a very large sack in the left antenna. It was taken into absolute darkness on $^{15}/_{7}$ and was kept there till $^{5}/_{8}$. Slowly the water in the vessel dried up and the snail agglutinated itself to the vessel. Brought into the light on $^{5}/_{8}$ the vessel was furnished with wet leaves of *Taraxacum,* and the snail came out in the course of half an hour and began to eat. Only five minutes later the sack appeared, but curiously enough it could now be shown that the sack was only half its former size. Killed and dissected, the snail showed only one ripe sack, so that there could be no doubt that it was the very same sack which had diminished in size.

It has been observed several times that snails which have thrown off their sacks and have had none for months suddenly show a long, slender, very acute sack in one of the antennæ. This is for instance the case with No. 25 which had never shown sacks from $^{12}/_{9}$ to $^{28}/_{1}$, furthermore with No. 31 with which the same was the case from $^{12}/_{9}$ to $^{11}/_{1}$. Both snails suddenly showed very thin, acute sacks, the one on $^{28}/_{1}$, the other on $^{11}/_{1}$. Both snails then fed vigorously and during the time from $^{29}/_{1}$ to $^{15}/_{2}$ and from $^{11}/_{1}$ to $^{30}/_{2}$ the sacks increased enormously. The same observation was made in the case of a snail in March—April (Pl. III, figs. 6—7). Figs. 22 and 25 show a snail, drawn with the camera on $^{23}/_{3}$ 27 and on $^{7}/_{4}$ 27.

That the very thin-walled central parts of the sporocyst creeping over the surface of the liver is nourished endosmotically by means of the fluids of the snail through the body-wall is of course beyond doubt. On the other hand it is not easy to understand how the old sacks are nourished. The above-mentioned observations show that the development of the sacks is dependent upon the health and strength of the snail. If the snail gets no food, the ripe sacks diminish in size, if the snail feeds vigorously, the sacks increase enormously in size. These fully developed brown-ringed strongly pulsating sacks never, however, have their place in the liver; they lie free of all organs in the body-cavity behind the antennæ, and can get no other fluids than those which are found in it. The walls of the sack are much thicker than those of the central parts of the sporocyst and, especially in old ones, brown and of a leathery consistence. As long as the sacks lie pulsating in the enormously distended antennæ, it seems rather improbable that they can get nourishment through the walls, whereas this may be the case when they are withdrawn and lie right behind the antennæ. — From a certain period in the life of the sacks, which may unquestionably be extended over months, nutriment from the mother sporocyst owing to nutritive fluid flowing from behind into the sacks through the stalks may be regarded as out of the question. The stalks turn brown, lose their lumen and brown cercariæ with very thick walls are often found attached, stopped in their wandering from the central part of the sporocyst into the sacks. In the life of the sacks a moment will come when the permeability of the walls being diminished, the pulsating power diminishes simultaneously, the turgidity also, and the result is the rather flabby, very brown sacks, often kneed, lying behind the antennæ.

When the snail has been withdrawn for some time and again begins to creep about, the sacks can be seen below the skin, dorsally, behind the antennæ. We then see the sacks pumping themselves into the antennæ, which are often distended to an almost incredible extent, being in some cases almost as long as the snail itself.

5. If there is only one sack, it is the left antenna which is most commonly infested; this is quite intelligible because the opening for the sexual organs is on the right side, and the large penis, the spermatheca and the albumen gland mainly fill out the right side of the visceral cavity of the snail. If the snail has two sacks, it very often creeps about with one in each of the antennæ, but often only one is out; the other lies within. In very old snails with very deformed antennæ large sacks are often seen lying behind the antennæ; nevertheless the sacks are never seen in the antennæ. Dissection shows that they have become enveloped in the tissues of the snail, or are lying twisted round the rudimentary penis, having got a kneed form with the knee lying just between the opening for the antennæ (Pl. IV, Fig. 1). It may very often be observed how two or more sacks, lying behind the opening for the antennæ, compete with each other; when one of the sacks has been pushed out into the antenna, another may be found lying in the posterior third of it.

6. When the snail dies, the sacks still keep moving, but always very slowly; it is especially the tip of the sack which preserves its feeling motion. When the putrefaction of the snail begins, the large old sacks keep intact for some time in spite of the destructive forces, and keep the cercariæ alive, the other parts of the sporocyst decompose and give off their cercariæ which are either lying in their cysts or creeping about freely in the dissolved viscera of the snail.

7. If one of the antennæ is cut off just at the moment when it is stretched out, still without showing any sack, the sack is not, as might have been expected, thrown off through the wound. The snail of course reacts by a violent contraction, and remains in the shell a few days; the two sacks now both go to the remaining left antenna, commonly lying behind each other.

8. As already observed, in natural conditions the large sacks are often thrown off almost voluntarily by the snail. Owing to the enormous distension of the antennæ and their viscous surface the slightest contact causes the skin to burst. Suddenly the sack lies pulsating on the substratum, at the same time, so to speak, tethering the snail. Immediately after the expulsion the snail draws in its antennæ and will now sit for hours, sometimes for days, half withdrawn in its shell without eating. I have seen 5 sacks thrown out voluntarily one after the other, all connected with the sporocyst within (Plate III, Fig. 8), and all in lively pulsation.

9. There still remains a fact to which I wish to draw attention and which has puzzled me a good deal for rather a long time.

On dissecting a number of snails parasitised by *Leucochloridia* we find in one snail only one, often enormous, sack, in another 6—8 sacks not so large, in a third perhaps no developed sacks at all, whereas the antennæ of the snail show that sacks have been developed. Why has one snail only one large sack, another 6—8 smaller ones? The snails may be of the same size. The transverse section in Plate VI will show why. Fig. 9 shows a transverse section of a snail not parasitised at all; to the right lies the very large liver, to the left the immense sperm-oviduct with a large albumen gland, and further the alimentary canal. The section in Fig. 10 shows a snail whose sporocyst carries one single enormous sack; the liver is much smaller and so also is the sperm-oviduct. Between the sack and the liver there lie a number of rings. These are transverse sections of a number of small sacks. At the very moment when the large sack is taken by a bird or voluntarily given off, an enormous space in the middle of the body-cavity will be empty (Fig. 11) and the great number of small sacks will get room to develop. Instead of one large sack we then get 6—8 sacks almost of the same size (Fig. 12). The transverse sections are from snails which were first anæsthetised and later put into sublimate.

When a young snail is parasitised, the sporocyst at first only develops a single sack; if this is not taken by a bird, it may grow up to the above-named enormous size. If it is liberated in some way, the numerous compensation sacks will simultaneously be developed. If the first sack has been taken at a rather early stage, there is never very much room in the body-cavity, and only a fewer number of sacks will then simultaneously reach full size. Sporocysts which carry 6—8 sacks, almost always carry in their central parts one or two short, very brown stalks with a rather sharply cut off terminal face; it is the rest of the thread which has carried one of these sacks formerly thrown off or taken by a bird.

Heckert (1889, p. 51) maintains that small snails carry small sacks, larger ones large sacks. This is not quite in accordance with my own observations; I have several times found snails which were only about half a year old carrying a single enormous sack, and very large snails with small acute sacks. When, therefore, Heckert says that the correlation in the size of the parasite and the host confirms the fact often found in the animal kingdom that "die Grösse des Tieres in einer gewissen Correlation steht zu der Ausdehnung seines Wohnortes" I do not think this interpretation is correct in this case. In the first place the sack is not the whole parasite but only part of it, and a large sporocyst may just as well carry many small sacks as a small one may carry one large sack. The size of the sack is in the first place dependent upon how long the time is from the moment the pulsation begins to the moment when it is taken by a bird.

10. The pulsation of the sacks is quite correctly described by Heckert and Mönnig. Heckert (1889, p. 15) says "Ist der Schlauch jung, so zeigt er eine von der Spitze nach der Basis sich fortpflanzende peristaltische, ist er älter, eine rhytmische Bewegung. Diese besteht in einem in regelmässigen Zeitabschnitten wiederkehrenden Zusammenziehen und Wiederausdehnen so dass man das Ganze mit einem Pulsieren vergleichen kann. Dasselbe findet eigentlich nur in der Gegend der beiden vorderen, dunkel gefärbten Ringe statt."

Mönnig (1922, p. 50) says: "In jungen Schläuchen bei denen Pigment eben erscheint, tritt die Pulsation in Form unregelmässiger peristaltischer Kontraktionen auf, welche von der Schlauchspitze nach hinten verlaufen. Sobald das Pigment weiter ausgebildet ist, ändert sich der Pulsationsmodus in eine rhytmische Kontraktion, welche hauptsächlich am stark pigmentierten vorderen Schlauchabschnitt stattfindet, wobei der Inhalt im hinteren Teil zurückgedrängt wird. Dieser Pulsationsmodus ist vielleicht besser geeignet das Eindringen in den Schneckenfühler zu ermöglichen."

As far as I can see, we have neither any real understanding of the physiological processes according to which the pulsation of the sacks takes place nor of their significance for the organism. What I can add to the understanding of these difficult matters is but little, a combined cytological and physiological investigation is greatly needed.

That light, as mentioned above, is essential for the pulsation is a fact beyond doubt which has been corroborated by all earlier authors. It ceases in total darkness. In accordance herewith we rarely in natural conditions find sacks in the antennæ of snails sitting below the *Petasites* leaves or on their stalks. Bad light conditions not only stop the pulsation but also often, though not always, cause the withdrawal of the sacks from the antennæ. On the other hand, if there is sufficient food and if the degree of humidity is great, darkness does not cause the withdrawal of the snail itself, at all events not during summer. This shows that the two organisms, the host and the parasite, at all events with regard to environmental conditions, are not fully adapted to each other.

However, whereas the pulsation is conditioned by l i g h t, it is the t e m p e r a t u r e which determines the r a t e of pulsation; as mentioned above, in nature it may range from about 40 to about 75 times a minute, in the laboratory much greater oscillations may be observed. In vessels with great humidity and high temperatures (about 30° C.), which are standing in the sun, the pulsation may rise to 120 to 125 a minute. When autumn comes, only 30 pulsations a minute are observed, and likewise during winter at temperatures of 4—6° C. When the snails awake now and then during the winter sleep, the pulsations are extremely slow, not more than 2 to 5 a minute.

The activity of the sacks is enormous, especially in the summer months and in humid air. I have had snails, which, as far as I could see, had pulsating sacks uninterruptedly for weeks. They pulsated at $10^1/_2$ in the evening, at 1 o'clock at night, and at 4 o'clock in the morning; when observed again, they were still pulsating. In our luminous summer nights it is highly probable that the pulsations go on without interruption. In nature pulsation is unquestionably dependent on climatic conditions. Thus in periods of drought the pulsation may cease for weeks during the day, and in warm humid periods it may never cease.

From a physiological point of view the sacks, as far as I can see, are some of the most peculiar bodies in the whole animal kingdom. This is also the view of HEMPELMANN (1926, p. 152). For it must be remembered that in the *Leucochloridium* we are concerned with an organism in which we have never found either the slightest trace of a nervous system or a blood system, nor any sensitive organs of any kind.

From this very organism, which always lies motionless in the interior of the snail, parts are developed (the sacks) connected with it by means of long thin threads, the lumen of which seems to be obliterated, and whose skin, especially in old specimens, seems so thick that its permeability to nutritive juices from the host seems rather problematic. These very same sacks, in contradistinction to the other part of the sporocyst, though quite like it without any trace of a nervous system or sensitive organs, react very considerably to influences from without such as light, temperature and humidity. To some degree their expressions of life are dependent upon those of the snail. When the snail is withdrawn in its shell, the sacks are forced to keep quiet; they must sleep their winter sleep when the snail does so. And when the snail has cemented itself to a stone in a period of drought, there is no possibility of motion. On the other hand, the snail may creep about for weeks, eagerly taking food; nevertheless, even if the snail lives an active life, the sacks may be observed to keep quiet behind the antennæ, now and then slowly pulsating, and then they may suddenly push forward into the antennæ and pulsate daily for weeks. As far as I know, we know of no other organism which is able to produce parts of itself without sensitive organs or a nervous system of any kind which after a resting period of months, as soon as light strikes them, are suddenly able to react in the course of a few minutes, producing effects which it is not in the power of the other part of the organism to produce. In this connection it must, however, be remembered that in the miracidium stage of the trematode as well as in the cercaria stage we find a well developed nervous system as well as sensitive organs; the sporocyst may be regarded as the metamorphosed miracidium. Even if we have not found any trace of a nervous system in the miracidium of *Leucochloridium*, it seems to me rather problematic to deny any trace of a nervous system in the sporocyst, especially because we know that in the agamodistom stage and the ripe trematode it is as well developed as in other trematodes. Furthermore Loos (1900, p. 212) found a nervous system in sporocysts of other trematodes, even if it was of a very simple type.

It is Loos (1892, p. 166) who has advanced the opinion that the differences between the miracidium, sporocyst and redia are all nothing but gradations. They are homologous; in all stages the same plan of structure is found. This view has been further developed by Sewell (1922). At p. 301 he says: "In fact we can quite easily form a graded series. Commencing at one end with an undoubted sporocyst, which appears to be devoid of all structure, and passing through forms in which certain organs are partly developed and which might be considered to be either sporocysts or rediæ, we get, at the other extreme "rediæ" with a highly developed alimentary canal, a complicated excretory system, definite nervous system and genital organs, and active locomotor processes." A sharp division between sporocysts and rediæ cannot be made. "They are homologous stages in a line of parthenogenetic development, in which the process of degeneration has proceeded to a varying extent." I suppose Sewell is right when he says that the greater our knowledge regarding the various forms, the more certain it appears that no hard and fast boundary can be drawn between them.

It is of course very strange that such skilled observers as Heckert and Mönnig have not been able to find the slightest trace of a nervous system. Nevertheless with the above-named view in mind it will be understood that it will not be correct to deny nervous elements even in the sporocyst of the *Leucochloridium*, even if a nervous system has not been found.

As mentioned above, what we know and are able to show experimentally is that light is essential for the pulsations, furthermore that their number depends upon the temperature. How these outer stimuli cause locomotion of the sacks, we do not know. As is well known, the heart muscle of a developing chicken when it has no nerve-cells at all, is, like the sacks, able to perform rhythmical contractions (Starling 1920, p. 985). On the other hand there is this great difference between the sacks and the heart, that the sack may be set out of motion regularly during the night, during drought and for months in hibernating periods, and nevertheless in the course of a few hours, or perhaps in a still shorter time dependent upon the activity of the snail, be capable of renewed rhythmical motion.

Also in the mode of reaction to external stimuli, especially light, the above-named heart and the sack differ very much, a certain power of light being a condition sine qua non for the pulsation of the sack whereas the heart is quite independent of this factor.

How independent the movement of a sack is of the mother sporocyst, and how much it depends upon light is best shown in the following manner. If a sack as soon as it is thrown out of a snail is put into a physiological NaCl solution and placed in diffuse daylight, it may live there for three days. During the first day it will pulsate slower and slower; during the following two days it will keep quiet, but if pricked with a needle it will react. The first day it will further be seen how the sack, pulsating steadily, is revolving round its own axis, and in this way rolls from one side of the vessel to the other. On the other hand, if the vessel is put in the dark no motion of any kind is observed. This shows as plainly as possible that the primus motor of the motion is the light. Pl. II, Fig. 3a—e shows the same sack drawn with the camera and in the course of 10 minutes. The figures illustrate how extremely variable in form the sack is, and that the greatest form variations take place in the anterior part of the sack. Fig. 3f is the same sack killed in formalin.

The pigment in the sporocyst of *Leucochloridium* is in itself a very peculiar thing. Only very few pigmented sporocysts are known (*Cercaria cotylura* (Pagenstecker 1863), *Cercaria cystophora* (Wagener 1866, p. 145), sporocysts of *Gasterostomum* and *Echinostomum* (Haswell 1903, p. 279)), but in none of these cases is the pigment restricted to special parts of the sporocyst, and we do not know anything with regard to its significance.

Mönnig has supposed that the strong development of pigment in the ripe sacks which alone have the power of pulsation, and the absence of it in the young ones which do not possess this power, makes it probable that it is really this pigment which may in some way be able to transfer stimuli from the light to the organism, and then cause the rhythmical contractions of the muscular system.

Furthermore Mönnig (1922, p. 19) has found in the sacks a myoblast syncytium which he describes in the following manner. "Dieses Syncytium setzt sich aus grösseren kernhaltigen Partien, die zuweilen bis fünf Kerne enthalten, und die mit einander durch kernlose Protoplasmastränge verbunden sind, zusammen.. Es herrscht hier also kein Monopol eines Myoblasten über seine Fasern; alles ist mit einander verbunden und dadurch sind auch die Faser selber alle mechanisch mit einander in Kontakt gebracht. Ob dieses aussergewöhnliche System vielleicht mit der merkwürdigen Pulsationfähigkeit der Schläuche zusammenhängt, indem die Reize durch das Myoblastemsyncytium geleitet werden, ist schwer zu sagen." From these observations it may provisionally be permissible to suppose that light in some way acts as a stimulus upon the pigment, from which it is transferred to the muscles. How the stimulus is conducted to the muscle systems, the myoblast muscles, the longitudinal, and ring muscle layer, and how they interact is an open question; it need only be added that in the sacks we find that the muscles have a spiral striation not commonly found in the Trematoda, and here in *Leucochloridium* most probably connected with the enormous amount of work demanded by the sacks.

11. If it is difficult to understand the real manner in which the pulsations take place, it is not much easier to understand the purpose of the motions. As far as I can see the purpose is threefold: a. They cause the intrusion in the antennæ of the snail; b. they pump the cercariæ out of the sacks; c. they allure the birds.

a. When infested snails are kept in darkness and then suddenly exposed to the light, they will begin to creep. It may then be seen that the sacks behind the antennæ begin to pump, whereupon they commonly glide into the antennæ; this always takes place when the snail is fully stretched out. As far as I can see, the intrusion in the antennæ is dependent partly upon a certain pressure in the body cavity of the snail, partly upon the pulsations which may perhaps help a little, especially owing to the ring walls in the forepart of the sacks which to some extent act like the well-known ring walls in woodboring larvæ (*Cerambycidae* etc.). But the motion in the snail is also dependent upon the pressure in the sack itself. If a sack is punctured with a needle, it will very soon from a stiffened body be altered into a flabby one. It will behave like a caterpillar which has been pricked. The turgescence is of the greatest significance for the motion. In very old brown sacks this turgescence is lost; the pulsations are very small and the sacks lose their power of forcing their way forward. They then lie behind the antennæ and are often handicapped by younger ones which push past them. The old ones are then very often entangled in the tissues, are kneed, or get very irregular forms. They are loaded with agamodistomes mainly deposited in the posterior part, which is much the broadest; anteriorly they are provided with a small sharply marked almost black part which only possesses slight power of pulsation, whereas the posterior part is quite motionless.

b. More than once I have observed a peculiar phenomenon in the pricked sacks. The pricked sacks continue the pulsations for some minutes. For every pulsation an agamodistome is pumped out of the little hole. The result is that the mass of agamodistomes lie like a milky cloud round the hole. The pulsation of the sacks may perhaps have a secondary purpose, that of pumping the cercariæ out of the sack. For it must be remembered that the sack is most probably swallowed whole, either by the mother bird or by the nestlings, to whom it is brought in the beak of the mother. The walls of the sacks are very solid, we suppose that the gastric juice of the mother bird is not sufficient to dissolve the cysts of the cercariæ, but as far as I know, no one has taken into consideration the fact that in many cases it is the sack itself which must be dissolved before the cysts surrounding the cercariæ can be dissolved. When almost all the cercariæ are pumped out, the flabby sack lies motionless. I have preserved such sacks, with their gathering of cercariæ lying in a clump round the little invisible wound.

c. According to the common opinion the main purpose of the sacks is to draw the attention of birds to the parasitised snail, and so cause the bird to split the antennæ of the snail and fly away with the sack. This would demand an almost incredible power of adaptation on the part of the parasite. We shall return to this point later on.

12. With regard to the central parts of the sporocyst[1]) a few remarks would seem appropriate. The methods employed were the following. In many cases the snails were vivisected. In this way it is possible to see the young distoms through the skin of the young sacks before encystation, and to follow their wanderings into the sacks. In most of the cases the snails were narcotised by means of chloral and when fully narcotisised drenched with warm sublimate formaline. Then the shell was broken off, and the mantle cavity opened. In this way it was possible to study the whole sporocyst lying in its quite natural position often with the sacks halfway out in the antennæ.

The parasite is in the first place a typical liver parasite, nourished by this organ. As far as my experience goes, the sporocyst always lies in the same place in the second winding, covering the surface of the liver. As soon as the shell is broken off, the white sporocyst is seen shining through the skin. Its threads may come near the hermaphrodite gland, but they only rarely enter into it and have no direct contact with the sperm-oviduct. On opening living snails, a bunch of long threads are seen floating in the body cavity (Plate VI, Fig. 8); on fixed material the sporocyst lies as a broad white comb pressed against the liver (Plate VI, Fig. 2). As a rule it is not in contact with the alimentary canal of the snail. Now and then two well separated sporocysts are found; this was already ascertained by Heckert and Mönnig. As it may be expected that the snail, when infested by eating the excrements of birds, or creeping over the place where egg-infested excrements have been thrown out, has got many eggs into its alimentary canal, it is rather peculiar that the actual number of sporocysts is almost always one, very rarely two, and, as far as is known, never more than that. Most probably this may be interpreted to mean that even among the parasites in the same host there is a struggle for existence, in other words, the specimen which has obtained the best place with regard to food supply and shelter will be victorious.

[1]) I do not agree with Maggath (1920 p. 110) who uses the name sporocyst only for the sacks and describes the rest of the parasite as knob-like projections connected by thread-like processes. The whole organism may be designated as a sporocyst. The ripe sacks and the thread-like processes cannot be distinguished from each other, the first named are only a later stage in the development of the lastnamed.

Heckert (1889, p. 13) describes the sporocyst as a "Sporocystenfadenwerk" "eine mehr oder minder grosse Masse reich verzweigter Fäden, die wie die Äste eines Baumes von einem gemeinsamen Mittelpunkte aus ihren Ursprung nehmen und mit abgerundeten Spitzen endigen". Most of the other authors give the same description. Only Mönnig (1922, p. 9) deviates from this commonly accepted conception. He maintains that the sporocysts "zeigen immer einen deutlichen Zentralkörper und eine Anzahl davon abgehender Schläuche".. "Die Sporocyste setzt sich aus diesen beiden histologisch und funktionell von einander verschiedenen Teilen zusammen. Der Zentralkörper.. stellt die Keimstätte der Cerkarienbrut und sorgt auch für die Ernährung des ganzen Körpers. Die Schläuche sind secundäre Bildungen; aus ihrer Wandung habe ich nie Keimzellen hervorgehen sehen; sie dienen lediglich zur Verbreitung der Brut." I must confess that the description of Heckert and others is much more in accordance with my own observations than that of Mönnig. Notably I may maintain that I have never seen a sporocyst of the form which Mönnig figures in Fig. 1, Plate I. Only in very old, almost dying, sporocysts may sacks be found of the form which Mönnig has drawn. (See also Textfigs. 4 and 5).

There is a great difference between the very young just ramified sporocyst and the very old ones, whose power of reproduction is almost exhausted (Plate II, Fig. 1). It is almost impossible to see with certainty whether or not a snail which has never shown sacks, and whose antennæ are normal, is infested. After vivisecting 25 specimens I had the good luck in two snails of very small size to find two whitish spots on the surface of the liver; they were sporocysts whose threads were only 1—2 mm. None of them contained ripe cercariæ, and the whole sporocyst was only about one sq. mm. They were found on $^{4}/_{9}$; as the time used for the full development of the sporocyst is maintained by Heckert to be about three months, this is in very good accordance with the supposition that the snail has emerged from the egg in the first part of June, and has most probably become infested in the first part of July. At all events, in these young sporocysts a "Centralkörper" is not separated as a special part from the sacks. The threads carry branches of the second order; these are always very short.

The sporocysts of very old and very large snails which have been infested perhaps for years, differ very much from those just described (Pl. II, Fig. 2). There are extremely few ramifications; the formation of sacks has ceased; from the large, very little ramified, central part there issue only a few long white sacks like threads, often of the same breadth at the base and the apex. These are sacks arrested in their development. Furthermore there are some brown very short knotty threads (Fig. 2) which at an earlier period have borne sacks and others still bearing a few very dark sacks, without the power of pulsation. The formation of germ-spheres has ceased. In the central part of the sporocyst there occur only a very few cercariæ (agamodistomes); in the long white threads hardly any; in the old sacks they are, however, numerous. Their envelopes are very thick and almost intransparent. Some of the old sacks are extremely irregular, containing very few agamodistomes; in these old sacks the agamodistomes are often arranged serially so that the sacks resemble a string of pearls (Pl. I, Figs. 3—4). The agamodistomes have here very thick walls, often so thick that they are quite opaque.

Between these two types of sporocysts, the very young ones and the very old

Textfig. 4.

Textfigs. 4—5. Two sporocysts with very young sacks and some free lying agamodistomes. (Berg phot.)

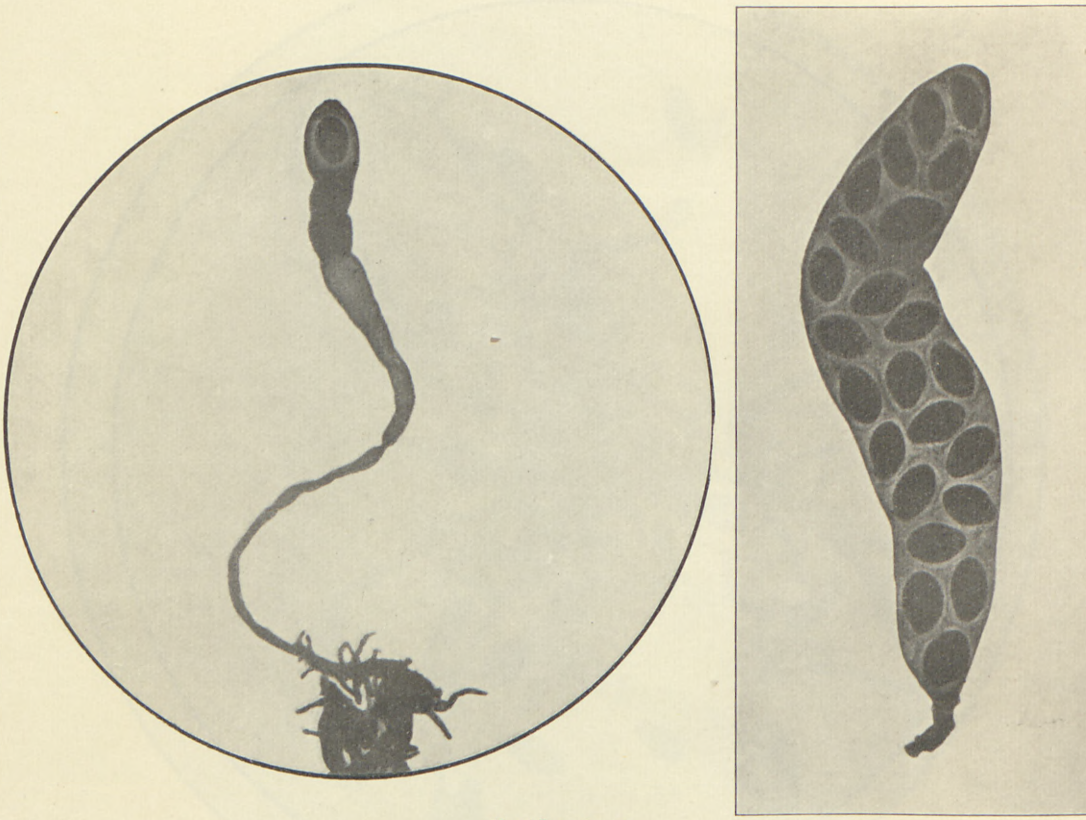
ones, there are all the intermediate stages, the strongly ramified sporocysts with 2—8 fully developed sacks, the long threads more or less altered into sacks, threads with branches of the second order, and threads without branches.

I will not venture to decide if the sharp distinction which Mönnig makes between the central body and the sacks is correct. In my specimens I have not been able to see it, at all events not in sporocysts with brown sacks. Nor do I consider his assertion correct that only the central body of the sporocyst is able to produce the cercaria-brood, whereas the sacks should only be of significance "zur Verbreitung der Brut". Heckert also (pp. 18—20) has not maintained this very sharp distinction.

Textfig. 5.

In a sporocyst in full vigour and carrying 2—6 large pulsating sacks one will in its interior as well as in the numerous not fully developed sacks find germ spheres of all sizes, from very small globular bodies to almost fully developed agamodistomes. Only in the large pulsating sacks we find no germ spheres. When the sacks have reached the antennæ, the brown rings have become conspicuous and the musculature enormously developed, no germ spheres are developed, perhaps owing to lack of sufficient food as the permeability of the walls gets smaller.

In the ramified central parts of the sporocyst, and in the young slender sacks, fully developed agamodistomes, but without any conspicuous envelope, are found. They creep about rather briskly, bending and stretching the body in all directions, living in the serous fluid which fills the sack, and by which they are nourished. Many begin to wander out into all the club-shaped fully developed sacks. A single time,



Textfigs. 6—7.
Two sacks. Fig. 6 a very young one only containing a single agamodistome. Fig. 7 a much older one containing agamodistomes but still without bands and pulsating power. (Berg phot.)

when I had opened a living snail and immediately brought the sporocyst under the microscope, I found a long club-shaped sack with faint bands of pigment, a sharp distinction between the sack and the thread, and with slight pulsating power. The thread was filled with numerous wandering cercariæ which moved upwards into the sack. In the very narrow lumen of the thread the cercariæ were altered into extremely slender, threadlike bodies, 6 times longer than broad. They were gliding over each other and all in the same direction. Upon arrival in the sack itself the body was contracted and the length was then only about $1^1/_2$ times the breadth. — This enormous power of elongation and contraction of the body resembles what is known with regard to the rediæ.

Just like the rediæ, they are able to increase the length of the body very considerably and pass through very narrow strings and openings. Cort (1915, p. 23) says that the rediæ belonging to *Cercaria diastropha* may augment the length of the body 5—6 times; he (1915, p. 21) makes a similar observation with regard to *C. inhabilis.* The wandering cercariæ of *Leucochloridium* do not possess the locomotoric winglike processes characteristic of the rediæ, but on the long threadlike bodies which I saw wandering through the threads of the sacks I distinctly saw how the body on the side of the acetabulum was dilated to form conspicuous flaps which were again withdrawn. At first this observation troubled me a good deal; but a closer examination showed that the body near the acetabulum was always broadest, and that the forepart of the body, when it was lying still and the posterior part was drawn forwards, was pressed downwards and round the acetabulum, which gave it the appearance of winglike flaps.

Heckert has shown that at the bottom of the sack there is found a peculiar closing mechanism (Plate I, Fig. 5), preventing the agamodistomes from getting back into the lumen of the threads again during the pulsations. The closing mechanism consists of a large number of threads projecting from the inner side into the lumen of the sack and closing it behind. They may be found in every ripe sack; when they are formed, the peculiar sausage-shape of the sack is sharply marked off from the stalk.

In these fully developed sacks the agamodistomes may lie in so great a number that their envelopes become hexagonal owing to pressure (Pl. II, Fig. 4). The agamodistomes in a number of 100 to 200 are here always surrounded by their very thick cuticula; this cuticula derives from a double ecdysis. It remains with the larva, forming a protective covering round it. The suckers are connected with the cuticula and between it and the larva is a very transparent fluid. The large numbers of agamodistomes mentioned by Carus (300) (1835, p. 90) and others I have never observed (Heckert). The agamodistomes lie so closely packed together that there is hardly any space between them. They may lie there for months, perhaps for years, their membrane getting steadily thicker and more opaque.

As for the rediæ they do not always take food endosmotically; they are also able to take food through the mouth opening. Rossback (1906, p. 382) a. o. have seen the rediæ by means of the muscular pharynx nip off small portions of the "Keimkörper" lying in the interior of the sporocysts, as well as portions of the liver and other parts of the body of the snail. I have especially in many rediæ belonging to the echinostomes cercariæ found the long stomach filled with yellowish brown particles which can only belong to material nipped out of the liver. With these observations in mind I tried to discover whether the cercariæ, when creeping about in the interior of the sporocyst, would take food through the mouth opening i. e. swallow the "germ-spheres" which were lying free in the fluid. This has never been observed. It may be supposed that the serous fluid in the sporocyst, passing endosmotically from the snail into its interior, is either swallowed directly by the mouth opening or once again passes endosmotically through the skin of the cercariæ. When they are lying in the sporocyst enveloped in their thick walls, it is questionable if they get any food at all. The only sign of life is from the contractile vesicle, which is emptied at regular interrvals, in the summer several times a minute. In the threads of old sacks very opaque dark cercariæ are often found; the stalks are swollen before and behind them; they fill up the whole lumen, and hinder any new invasion of cercariæ into the sack. Simultaneously the threads get a brown knotted aspect. We are unquestionably right when, from a biological point of view, we compare the agamodistomes in the sacks with the encysted stages of other Trematoda. With regard to the envelope there is only the difference that, in the last-named case, it is formed of exudations from cystogeneous cells, while in *Leucochloridium* it is the skin itself.

14. It is a well-known fact that we possess a long series of investigations relating to the influence of the Trematoda upon snails. I here refer especially to the works of FAUST (1920), AGERSBORG (1924), and HURST (1927), and to the literature cited by these authors. All these investigations, however, never deal with *Leucochloridium*, and it is open to question whether the results gained from other Trematoda will also apply in the case of this parasite upon the snail.

In all the other cases the parasites either as sporocysts, as rediæ, as cercariæ or in incysted stages, may be distributed over the whole snail; as rediæ they are able to nip off parts of the tissue of the host; sporocysts do not take this nutriment. Many cercariæ, especially monostomes, are liberated from the sporocysts at a very early developmental stage. They are then nourished directly from the host, and live for weeks or perhaps more, free in the body-cavity and organs of the host. The *Leucochloridium*-sporocyst never invades the organs of the snail with thousands of parasites. The progeny is developed in its own interior and this progeny never comes out into the snail itself. It is the same single organism, the steadily growing miracidium, which from the first day of its life to the last nourishes the whole progeny, and the nourishment only takes place endosmotically. In its whole life *Leucochloridium* is a true liver parasite. From the liver it may send its sacks into the hermaphrodite gland and into the body-cavity, but as far as I have been able to see, the organs are not intervowen and filled with a parasitic mass as is the case with organs infested with developmental stages of other Trematoda.

A more elaborate study relating to the influence of *Leucochloridium* upon the tissues of the snail is still a desideratum. In spite of the fact that I possess many sections through parasitised and non-parasitised snails, I fear that my results have not sufficient validity, and I hope that others will take up the work that has been left undone. I only wish to call attention to a single point.

It has often been maintained that parasitised snails assume another colour, owing to parasitation, and that such snails may be distinguished by their colour. Thus BIEHRINGER (1884, p. 1) says with regard to the large *Limnæa* that heavy infestations cause a peculiar yellowish white colour in the apex of the snail. According to my experience this is especially the case with snails strongly infested with *Tetracotyle*. HURST (1927, p. 335) says that a dirty grayish colour with a more or less yellowish or orange shade in the region of the viscera is characteristic of parasitised snails, and maintains that healthy snails are usually much darker in colour than unhealthy ones. The change in colour is caused by a reduction of the pigment of the snail, and by the appearance of the pigment of the parasite itself.

As mentioned in my Furesø Studies (1917), one of the most characteristic snails is the very large *L. ovata* characterised by its bright yellow colour; black pigment spots in the skin shine through the shell. Among a large material dredged from five to six metres' depth I found a single very large snail which was of a very peculiar pitch-black colour. When the animal was taken out of the shell, it could be shown that it was the shell itself which was black, only the columella was a bright white. Also the animal itself was not yellow like most of the other specimens, but much darker. The animal was infested to a degree which I have never seen before. In reality it was almost only one enormous living mass of sporocysts, producing incredible numbers of Furcocercaria.

In the following months I saw that very many snails were black at the top of the shell. When the material was large, it was an easy matter to form a series of snails typically yellow at one end of the series and totally black at the other. When dissected, it was shown that the degree of parasitation was proportional to the melanisation of the snail itself and of the shell.

The same was the case with regard to the bright yellow *Bithynia* from the same locality, whereas the *Valvata*, also heavily infested with Furcocercaria, showed no conspicuous variations in colour. In the second part of this paper I shall return to the pelagic Furcocercaria-fauna af our lakes.

As far as I can see, the *Succinea*, even if heavily infested, show no conspicuous variations in colour. As is well known, the snail in itself is commonly dark, often black, whereas the shell has its well-known amber colour. Sections through the liver of parasitised snails show an enormous deposition of pigment, but the shell itself, even if the snail is heavily infested, is always a bright amber colour. Now and then, we find peculiar grey-coloured *Succinea*. I thought that this was perhaps the result of a parasitation, but sections showed that this was not the case.

In this connection it may perhaps be pointed out that the excreta of the progeny of *Leucochloridium* are never deposited in the host itself as often may be the case with other Trematoda. In *Leucochloridium* they are deposited in the mother sporocyst. Further investigations must show whether it is not these very same excreta which the sporocyst in any way uses to build up the bands of pigment in the ripe sacks, hitherto unknown among all other sporocysts.

15. During the sexual periods, when standing in the *Petasites* forest, I was often able to observe about 20 snails in copula. On rainy days copulating individuals could be found by the hundred. During the four years of my observations I have never seen copulating individuals carrying sacks in the antennæ. When kept in terraria, my snails very often laid eggs, but I never saw a single parasitised individual which had laid eggs. Curiously enough, Carus (1835, p. 88) maintains that he has

observed a parasitised egg-laying individual. From my own observations I supposed that *Leucochloridium* affected the snail sexually, and that in this as in so many other cases we have to do with a parasitic castration.

For the purpose of studying this phenomenon, snails, when dying, were given chloral, they were then put in sublimate and dissected. Later on they were opened and camera drawings were made, a series of camera drawings being often made during the dissection. The sexual organs were not touched until the whole sporocyst with all its sacks had been laid bare; they were then taken out and drawn by themselves. Several of the snails were studied for months while alive, and regular notes made every day.

Firstly a short description of the sexual organs of a non-infested snail must be given. The hermaphrodite gland is relatively large and almost black. The hermaphrodite duct is black or greyish, always very much twisted and only rarely provided with more than one black vesiculum seminalis; the male and the female part of the sperm-oviduct are always quite distinct. The female part of the sperm-oviduct is strongly folded and provided with an albumen gland whose size varies extremely according to the season of the year and the age of the individuals; the free part of the oviduct carries upon a stalk a globular spermatheca; the vas deferens is long and thin; where it reaches the penis is found a retractor which is commonly cleft into branches attached to the diaphragm. The penis itself is relatively long. Neither penis nor the free oviduct possesses appendages of any kind. Vagina is situated just above the opening for the male organ. The results of the sections will be given in the following.

Snail No. 2 (Plate IV, Fig. 6) was found on $^{25}/_{6}$ and on that day showed one large sack. On $^{16}/_{8}$ it shows two; the second one is rather small; on $^{6}/_{9}$ the second one has almost reached the size of the first; during the time from $^{16}/_{8}$ to $^{15}/_{9}$ it has every day shown one or two large pulsating sacks, often pulsating about 100 strokes a minute in bright sunshine; during the time from $^{15}/_{9}$ to $^{25}/_{9}$ the snail is often withdrawn, and even if the very deformed antennæ are out, it shows no sacks; it is very sluggish and will not take food. On $^{25}/_{9}$ it is narcotised and dissected. It shows two very large sacks of which especially the one is very large, curved and so placed that it has most probably been impossible for it to get out into the antennæ; the sporocyst has only produced these two sacks; the outer side of the liver is covered with a large framework only containing very young, short, ramifications, in which only a few "germ-spheres", but a fair number of fully developed cercariæ are found. The hermaphrodite gland seems untouched, the albumen gland seems to be quite obliterated, the oviduct is rather well-developed but less folded than normally; the male part of the sperm-oviduct is strongly reduced, and the penis and vas deferens remarkably slight. — The spermatheca is present but very small. Both parts of the sexual organs are affected, the most conspicuous feature is the total loss of the albumen gland.

No. 3 (Plate IV, Figs. 1—2) is a very old snail, at all events three years old. It was found on $^8/_7$, at that time presenting two sacks, one in each of the antennæ. During the time from $^8/_7$ to $^{15}/_9$ the sacks pump uninterruptedly the whole day, but from $^{20}/_8$ only one very large sack is seen, the other is lying behind the antennæ and often pumping in a peculiar manner which I do not understand. From $^{16}/_9$ to $^{22}/_9$ they are often withdrawn and the snail sits cemented to the vessel without taking any food. When brought back to the leaf, the extremely thick antennæ are stretched out, and suddenly one of the sacks appears in the left antenna; suddenly this antenna is extremely distended. The next day the snail is again sitting half withdrawn in its shell. It seems very feeble; on $^2/_{10}$ it only reacts very slowly to the needle. The snail is now faintly narcotised and dissected. It shows two very large sacks, of these one is kneed. The sacks are seen pulsating below the skin behind the antennæ, and that in such a way that the knee fills up almost the whole space in front of the opening to the antennæ (Pl. IV, Figs. 1—2). It has become rigid in this position, and cannot be stretched out without breaking. The foremost part is pulsating. The other sack is peculiarly curved and extremely thick in its hindmost part. Of the sporocyst only very little is left; it is very old and its power of producing new sacks is unquestionably almost exhausted. — The generative organs of the snail are very greatly reduced. The hermaphrodite gland is but small; of the sperm-oviduct a small black portion is left; the rest is only a straight string and so also are the two separated parts, the oviduct and the vas deferens. There is no albumen gland. The penis is also much reduced; a small spermatheca is present. — The two sacks contain all the cercariæ of the sporocyst, about 500 altogether. If the snail had died a natural death, they would have become free during putrefaction.

No. 9 (Plate III, Figs. 3—5) is a very young snail; most probably not a year old, it was found on $^8/_7$ and at that time had one sack in each of the antennæ. On $^7/_8$ I amputated the right antenna; the sack did not come out but was always seen lying behind the sack of the left antenna. This had increased enormously in size by $^{20}/_8$. From $^{25}/_8$ to $^6/_{10}$ the snail never shows sacks; but several large sacks are seen pulsating behind the antennæ; it creeps about very slowly, but does not eat anything. On $^3/_{10}$ the snail is dying, and on $^6/_{10}$ in the morning it dies. Section is carried out while the sacks have still the power of motion. It shows that the body cavity of the snail consists almost entirely of *Leucochloridium*; it contains six large sacks all pigmented and all pulsating. The moment a small slit is made, all six sacks dart out. The sporocyst is very large; it lies on the outer side of the liver and sends a number of small threads into the body cavity. Of these threads five are relatively large white sacks, rather sharply set off from the thread; they contain cercariæ and numerous germ spheres. Of the genital organs only the hermaphrodite gland is fairly well developed, but all the rest of the organs are reduced to very thin strings; the albumen gland does not exist; there is not the slightest swelling of the sperm-oviduct; it is a simple string. The spermatheca is only represented by a string very slightly distended at the blind end. On comparing the figure of the *Leucochloridium* (Plate III, Fig. 4) with that of the shell, it seems almost incredible that the enormous parasite has had room in the snail Fig. 5, and that it has been able to live with it. It is rather peculiar that all these six sacks are pigmented. It would seem that the light shining through the skin of the snail is sufficient to produce the pigmentation of the sacks.

No. 12 (Plate V, Figs. 8—10) is also a young snail of middle size and most probably not more than one year old. It was found on $^{28}/_{7}$ and at that time showed two large sacks, one in each of the antennæ; during the time from $^{28}/_{7}$ to $^{26}/_{8}$, one or two sacks were always seen pulsating. On $^{26}/_{8}$ a very large pulsating sack is found lying on the leaf. Already on $^{8}/_{9}$ the snail again shows two large pulsating sacks. From $^{12}/_{9}$ to $^{17}/_{9}$ the snail is always entirely withdrawn in its shell; the foot only reacts very feebly to a needle. The snail was narcotised and killed in sublimate formaline on $^{25}/_{9}$ and then immediately dissected.

It showed two enormous fully developed sacks almost as long as the whole snail and extremely thick, two others almost fully developed, and some smaller ones. The sporocyst was situated in the liver and also in the hermaphrodite gland; of the albumen gland there was not the slightest trace, but the dark part of the sperm-oviduct showed some small windings; the rest of the organs were only thin strings; the spermatheca had almost become obliterated. When the large sacks were taken out of the body cavity, this was almost empty, containing only the alimentary canal and the liver, much reduced in size. It is rather peculiar that the penis sack is so greatly reduced and only present as a very thin string.

No. 15 (Plate V, Figs. 3—4) is another very young snail, most probably not one year old. It was found on $^{28}/_{7}$ and at that time showed two sacks, that on the left side being very small. From $^{16}/_{8}$ it shows only the large sack, and from $^{7}/_{9}$ to $^{6}/_{10}$ when the snail is dying, none. When taken for dissection, the snail shows one large sack and three smaller ones, but all pigmented and pulsating, besides two smaller ones and a rich net of ramifications in the upper part of the liver. Of the sexual organs only the hermaphrodite gland is not much affected, all the rest are only very thin strings; the penis is extremely thin. The parasite is an example of an extremely rapid development, most probably causing the death of the host even in natural conditions. In Fig. 4 is drawn the shell with the same power as Fig. 3. It will be understood what an enormous parasite the *Leucochloridium* really is.

No. 24 (Plate VI, Fig. 8) is an older snail, most probably two years old. It has been mentioned at p. 120. It was dissected without killing it. It showed one enormous sack and two smaller ones; the first showed no motion at all, the other two only slight motion; the sporocyst exhibited a great number of rather short club-shaped threads, some of them a little larger than the others. The hermaphrodite gland was present, but the sperm-oviduct as well as the male and female part of it were reduced to simple strings; no albumen gland was present. On the other hand, the penis had its normal size and appearance, and the spermatheca was also well developed. I think that these facts must be interpreted to mean that the snail has been infested rather late, most probably after the sexual organs have been functioning some time.

No. 28 (Plate IV, Figs. 3—4) is an old snail found on $^{12}/_{9}$. It shows two short thick antennæ but no sacks. During the time from $^{12}/_{9}$ to $^{30}/_{10}$ it never showed sacks; from $^{7}/_{10}$ to $^{30}/_{10}$ it was sitting cemented to the vessel, when it was taken for dissection. It exhibited two large sacks, one of them, evidently very old, was bent, dark brown, and strongly pigmented. Most probably it had formerly been larger. The sporocyst itself had only few other sacks, some of them were of a very peculiar, irregular form; it only contained cercariæ, no germ spheres; it was evidently very old and near the end of its power of reproduction. It was dissected out of the liver with all its branches and some of it drawn in Fig. 2., Plate II. In the central part, at the lower edge, are seen the two dark branches which have carried the two large sacks. It is of a rather yellow colour, not white like those in full vigour. The sexual organs showed a peculiarly high developmental stage. The hermaphrodite gland was well developed, as also the upper part of the black sperm-oviduct; the albumen gland was rather small, but the female part of the sperm-oviduct remarkably well developed, and with rather large windings. It contained balls of living spermatozoa. The spermatheca was almost normal, the penis sack somewhat reduced, especially in its upper part. It would seem as if the parasite here, in the lifetime of the snail, perhaps as an intermediate stage, was about to alter a hermaphrodite organism into a one-sexed one, and in this case into a male; we will return to this point later on.

No. 45 (Plate VI, Figs. 5—7) is a large snail, at all events two years old. It was found on $^{8}/_{7}$ and at that time showed only one medium-sized sack. On $^{16}/_{8}$ it showed two, these had grown up to two very large ones on $^{6}/_{9}$. From $^{16}/_{8}$ to $^{15}/_{9}$ one or two sacks were always pulsating; from $^{15}/_{9}$ to $^{22}/_{9}$ they were only rarely visible; the snail was half withdrawn and was unquestionably very weak. It was narcotised and dissected. It showed seven sacks, all of almost the same size; the sporocyst was large, filling up the greater part of the liver, but had no medium-sized sacks. It seemed as if the whole content of the snail consisted almost entirely of the *Leucochloridium*. The genital organs were extremely reduced. This will best be understood if fig. 5 (Plate V) is compared with a drawing of the normal sexual organs (Plate V, Figs. 1—2). — They are drawn with a high power in fig. 6, Plate V. The hermaphrodite gland is much reduced; the sperm-oviduct is only a thin string; there is almost no albumen gland, the oviduct shows no windings, only some irregular diverticula, and the vas deferens is but a very thin string. The penis is strongly reduced and the spermatheca almost obliterated.

No. 47 (Plate III, Figs. 8—10) is a medium-sized snail. It was found on $^{13}/_{8}$ and brought into the laboratory. Upon arrival here, it voluntarily threw off five large sacks which were all hanging out of the snail, all connected with the sporocyst by means of their threads. All were fully pigmented and all simultaneously pulsating. The aspect of the snail with these five pulsating sacks, which, taken together, almost took up as much space as the snail itself, was very peculiar. The snail was killed in warm sublimate formaline and then dissected. Taken out of the shell, it harboured, in addition to the five already mentioned, two other sacks, almost fully developed, and both strongly bent (Fig. 10). The sporocyst was very large, lying normally on the liver and giving off several long white club-shaped threads. The hermaphrodite gland was remarkably large, there was almost no albumen gland; the sperm-oviduct was rather well-developed with some well-defined windings, but the two separate parts of the sperm-oviduct were only two narrow strings, and so also was the penis; a spermatheca was strongly reduced. The genitalia of the snail are given with a higher power in Plate V, Fig. 7. In this case it seemed as if the body cavity almost only contained the parasite. Only the hermaphrodite gland was well developed.

No. 48 (Plate VI, Figs. 1—2) is a very large old snail found on $^{12}/_{9}$. It immediately showed one large and a smaller sack. It was very sluggish. It was narcotised, fully stretched out, and later on dissected; it had four free sacks, one of which was large, and several small ones only slightly pigmented. Furthermore on the outer side of the liver were found two rather large sacks strongly bent in and over each other, and very hyaline. The pigment was only faintly developed. The sacks contained a great number of agamodistomes (Plate VI, Fig. 2). As the sacks were rather narrow, not broader than the cercariæ, these were arranged regularly transversely to the long axes of the sacks and on a line. The curious thing was that the snail, in spite of the enormous development of the parasite, had rather well-developed sexual organs (Plate VI, Fig. 1). The hermaphrodite gland was almost of the normal size; there was a remnant of the albumen gland, and the sperm-oviduct showed a series of rather well-developed windings; only the two separate ducts and the penis were rather feebly developed but a spermatheca was present.

No. 5 (Plate VI, Fig. 3) is a little snail, at all events only one year old. It was taken on $^{13}/_{8}$ and then showed one large sack in the left antenna; the sack was almost always pulsating. On $^{7}/_{9}$ another, very large, sack was observed in the right antenna. During the time from $^{12}/_{9}$ to $^{17}/_{9}$ the large sacks were often withdrawn and often pulsating. From $^{17}/_{9}$ to $^{25}/_{9}$ the snail sat half withdrawn in its shell and took no food. On $^{25}/_{9}$ it was found dead and immediately taken for dissection. It contained two very large sacks, one of them bent and not capable of being straightened out without being broken. — The sporocyst was very large but only had these two large sacks. The sexual organs were only in part well preserved, this was especially the case with the sperm-oviduct; the rest were mainly thin strings; this applies especially to the penis. The spermatheca was but slight and there was no albumen gland.

No. 21 (Plate III, Fig. 2) is a rather large snail, most probably two years old. It was found on $^{13}/_{8}$ and on $^{16}/_{8}$ showed a large sack in the left antenna; on $^{7}/_{9}$ it had a smaller one in the right one; during the whole time from $^{16}/_{8}$ to $^{27}/_{9}$ it was always pulsating either with one or with two large sacks. On $^{27}/_{9}$ it was narcotised and immediately dissected. It shows one large sack; two smaller ones, all pigmented; the sporocyst is very large; it has reached the hermaphrodite gland. There is no albumen gland. The sperm-oviduct seems at the first glance to be normal, with many deep and conspicuous windings. A closer examination shows, however, that it is in reality in a peculiar stage of decomposition. It is gelatinous, contains no spermatozoa, and dissolves into a yellow or blackish-white matter as soon as it is touched.

The rest of the organs are merely strings, the penis is the best preserved part; there is a small spermatheca.

No. 22 (Plate IV, Fig. 5) is the snail mentioned on p. 99. It was kept under observation for more than eight months. When cementing itself for hibernation, it had two small sacks which increased steadily in size from $^{23}/_{3}$ to $^{20}/_{4}$. On $^{20}/_{4}$ the snail ceased to eat and died on $^{25}/_{4}$. When dissected (Plate IV, Fig. 5) it showed the two large sacks, curiously irregular, evidently very old; this at all events is the case with one of them, because it was observed already on $^{13}/_{8}$. But behind these two large sacks lies another of very irregular form with a peculiar knob on the foremost part, and vertical to its longitudinal axis; the form is somewhat like a bag pipe; it does not show the slightest trace of pigmentation, but in volume it is almost as large as one of the other two large sacks. The strength of the sporocyst itself is evidently almost exhausted; there are no young club-shaped sacks, and the whole framework is but slightly developed.

The liver is very small and the whole sexual system almost reduced to nothing; it shows quite the same stage of reduction as Fig. 5, Plate V; the hermaphrodite gland is present, but the albumen gland and the spermatheca have disappeared and the sperm-oviduct and the two separate canals as well as the penis sheath are all reduced to mere strings. — I tried to count the number of cercariæ in the whole sporocyst with its three sacks. It was not so very high, at the lowest 400, and not exceeding 500.

No. 50 (Plate VI, Fig. 4) is a very young snail, perhaps not one year old; it was found on $^{20}/_{7}$. During the time from $^{20}/_{7}$ to $^{15}/_{9}$ it almost always showed one single, steadily increasing very large sack, which, when fully distending the antenna, almost seemed as long as the snail itself. The last days of its life the snail was sluggish and ceased to eat. It was narcotised and dissected and then showed a single enormous sack lying above the alimentary canal and partly covering the liver; it took up more than half of the volume of the body-cavity. Only two other, small, sacks were found. The sexual organs were still rather well-developed, though certainly not able to function; the albumen gland was strongly reduced, and the windings of the sperm-oviduct not fully developed. The snail is a peculiar example of the fact that a sporocyst, when it is young, most probably begins with the development of a single sack which may reach an enormous size, and must be removed before there can be room for the development of new sacks. As soon as a bird has taken this large sack, there is plenty of room in the body-cavity and a whole number of sporocyst sacks may be developed, which again causes the total destruction of the sexual organs.

No. 51 is a very old snail, most probably more than two years old. It was found $^{20}/_{7}$ and at that time had very large, thick antennæ. During the period from $^{20}/_{7}$ to $^{5}/_{9}$, when it died, it never showed any sacks; it was always very sluggish; commonly it sat with the antennæ withdrawn and did not eat anything. On $^{5}/_{9}$ it died and was then taken for dissection. It showed highly interesting facts. It contained remnants of a single very large sack, very irregularly twisted; of the liver there was hardly the slightest trace, only a small portion in the uppermost winding round the hermaphrodite gland. But in the place of the liver there lay a large quantity of agamodistomes entirely free; of the sporocyst no trace could be observed. This was evidently the last stage in the development of the parasite, which caused the agamodistomes, when the snail was decomposed, to flow out on to the leaves. The snail almost exclusively contained agamodistomes. The hermaphrodite gland was present, but the rest of the sexual organs were merely strings.

No. 75 (Plate III, Fig. 1) is a very old snail; it was found on $^{12}/_{9}$ 26. The antennæ were very thick. It died on $^{15}/_{10}$ and never exhibited any sacks in the antennæ. During the whole time the snail was extremely sluggish and would never eat. When dissected, it showed no less than six sacks all pigmented, all almost of the same size, and all rather small. Most probably we have here an example of the fact that the snail has got rid of one or two very large sacks, and in the free space of the body-cavity six sacks have been simultaneously developed. Of the liver only very little was left; the hermaphrodite gland was small and the rest of the genital organs reduced to mere strings.

From the above observations it is possible to draw the following conclusions.

a. As mentioned above, the sporocyst only rarely sends its threads directly into the hermaphrodite gland, and I have never found them in the other parts of the sexual organs. These are not in direct contact with them, but nevertheless they are often very extensively destroyed. Apparently the snails behave in a very different manner in this respect. Snails may be found whose sexual organs are rather well developed and which nevertheless carry a large sporocyst; furthermore I have often found snails with hardly any sexual organs at all and with a very slightly developed sporocyst. Undoubtedly the age, state of nourishment, season and other factors, such as the disengagement of old sacks must be considered.

The albumen gland is the part which seems first of all to be affected; it is reduced in size, and may totally disappear.

Then the sperm-oviduct is affected; through a stage of decay in which it gets a jellied structure, it shrinks into thin strings.

The spermatheca wastes to a very inconspicuous appendix.

Penis is altered to an extremely thin string.

Finally the whole sexual apparatus is reduced to the hermaphrodite gland; and the sperm-oviduct, which is normally very thick and furnished with numerous windings, is reduced to a very thin thread.

b. The hermaphrodite gland continues the production of spermatozoa and, however thin the strings may be, spermatozoa seem always to be present. On the other hand, the production of eggs often seems to cease; they do not get down into the sperm-oviduct, and at all events get no material from the albumen gland.

With some right it may be maintained that many parasitised snails pass through a male stage or, in other words, that the parasite alters a hermaphroditic organism into a male. As a rule this stage does not last long, and most probably the animals never function as males.

In this, as in so many other cases, we have to do with a parasitic castration.

c. Several times I have found very old large snails with very deformed antennæ, though they never exhibited sacks. When they were dissected, it could be shown that the sporocyst was very old; no sacks were developed, or the snail contained one or two leathery, twisted, flabby sacks. In these cases the snails almost always showed well developed sexual organs. As far as I can see, we are here concerned with a case which is otherwise well known in parasitism, viz. that the castration, if the parasite succumbs, may cease, and normal conditions reappear. The more pronounced the parasitism is, the more must the snail draw upon its metabolic products for the nourishment of the parasite. Simultaneously the breaking down of the albumen gland goes on; this may most probably be regarded as an organ in which material is stored up for the brood; it may best be sacrificed and drawn into the metabolism for the benefit of the parasite. The demands of the parasite are enormous, and force the animal to consume great amounts of nourishment.

On the other hand, when the parasite perishes, the metabolism changes and the snail is able to work and to build up its sexual organs again.

Whether the snails will again be able to function is questionable, but it is beyond doubt that the hermaphrodite gland again begins to produce eggs as well as sperma; the sperm-oviduct again acquires its wrinckled appearance, and the albumen gland increases in size.

d. There is no doubt that the infestation with the parasite is extremely harmful to the snail. There is not the slightest trace of a static relation between parasite and host; the latter is forced to work extremely hard if it is to satisfy the demands of the parasite; the host must provide food for two and dispose of the waste products of two, the snail itself and its parasite. On the other hand, here, as so often, it seems as if the parasite is only rarely the direct cause of the death of the host, which would, indeed, be detrimental to the parasite itself. If only copious nourishment is given, the snail may live for months and often for years with the parasite. Snails which were unquestionably at least two years old, have been found with two large sacks in the latter part of June 1928; they have lived in the laboratory from June 1928 to the latter part of April 1929. Knowing that the development of the sporocyst to the stage when it is able to produce the large pulsating sacks takes at all events about three months (Heckert), we are justified in concluding that the snails must have become infested the preceding year (1927), and have hibernated twice with the parasite, i.e. about two years. That they have hibernated in 1929 is certain, and that they have hibernated twice is highly probable, since in 1928 three months before they were found, they were in the hibernating stage, and the majority of birds able to throw the eggs of the parasite had not arrived.

How enormous a parasite *Leucochloridium* really is in comparison with the snail will best be understood if we cast a glance at Plate V, figs. 3—4. Perhaps this will appear even more plainly from a study of Plate IV, figs. 7—8. The two sacks and the shell are drawn with the same power. The snail was kept alive for a month and then killed. It contained a large sporocyst, many small sacks, and the two large ones (Fig. 7); the rather well developed sexual organs are drawn in fig. 8. When the snail was killed and the two sacks were dissected out, I tried to put them into the shell again; it was, however, almost impossible to get room in the shell for the two sacks alone.

Johnston (1920, p. 363) has observed that the mass of developmental stages of *Echinostoma revolutum* may be so heavy that in quantity it was about onethird the size of the viscera of the snail.

At my request Dr. Berg has been kind enough to determine the weight of the *Leucochloridium* in comparison with that of the snail. The weighing was carried out on the aperiodic weight of the laboratory. The animals were first weighed in the wet condition, later on the dry stuff of snail and *Leucochloridium* was determined.

The snail was taken out of the shell, and the sporocyst with all its ramifications and sacks dissected out of the shell. Snail and parasite were then laid on filtering paper till all fluids which could be sucked out had disappeared. They were then removed from the paper and put in a cup.

The result was as follows:—

In the wet condition:		Dry stuff of snail and *Leucochloridium*:	
Snail ÷ shell + cup	1.1538 gr.	Snail + Cup	6.8385 gr.
Cup	0.8830 -	Cup	6.7948 -
Snail	0.2708 gr.	Snail	0.0437 gr.
Leucochloridium cup	1.8231 gr.	Leucochloridium + Cup	1.7755 gr.
Cup	1.7675 -	Cup	1.7675 -
Leucochloridium	0.0556 gr.	Leucochloridium	0.0080 gr.

It will be seen that in both cases the weight of the *Leucochloridium* was about $^1/_5$ of the total weight. The weight of the shell was 0.0715 gr. I am quite sure that the weight of the *Leucochloridium* might constitute a much greater part of the total weight.

Hurst (1927, p. 362), with regard to *Echinostoma revolutum*, arrives at the result that the highest percentage of parasites was that "in which they made up approximately one fifth of the total weight; furthermore (1927, p. 363) that in a healthy snail the soft parts are heavier in proportion to the weight of the shell.

As mentioned above, we are with regard to *Leucochloridium*, as far as I can see, concerned with a "castration parasitaire indirecte" best known through the investigations of Giard and Bonnier (1887) (Les Epicarides). Caullery (1922, p. 255) quotes as another example the *Liriopsis* parasitising *Peltogaster*. In *Peltogaster* which carries *Liriopsis* the oocytes in the ovary are always degenerate; when *Liriopsis* is fullgrown, it ceases to take food, and when it is dropped off, a hole remains in the body of *Peltogaster*; through this hole *Liriopsis* has been fastened to it. The *Peltogaster* which have been infested with *Liriopsis* again begin to develop their sexual products. In other words, it is exactly as in *Leucochloridium*, the parasite uses for the building of its own body the material which the host should have used to develop its ovaries. When parasitation ceases, the metabolic processes change, and the host can once more begin to develop its sexual products.

The snails with which we are concerned are hermaphrodites. The parasite treats the hermaphrodite gland in such a way that the oocysts are first and most thoroughly destroyed. In the life history of host and parasite a moment may arrive when the hermaphrodite is more of a male than a hermaphrodite. As is well known, SMITH (1910—11) has shown that male *Inachus* which have carried *Sacculina* are able to develop the sexual products again when parasitation has ceased; in this case, however, not male but female sexual products are produced. Simultaneously the secondary sexual characters, the broad tail and the legs which are to carry the eggs, assume the aspect of female organs. The same has been observed in *Paguridæ* carrying *Epicaridæ*.

As far as I know, the *Leucochloridium* is the first example we know of a parasite which, when living in a hermaphrodite, causes it to become unisexual, whilst the snail, when parasitation ceases, may again become a hermaphrodite. If it is really able to act as a hermaphrodite is questionable, but it seems fairly certain that the hermaphrodite gland and the sperm-oviduct acquire their normal aspect again. With the researches on intersexuality in mind, a more thorough investigation of these matters with regard to snail and *Leucochloridium* would seem of interest.

Chapter II.

Some theoretical Remarks.

Merely the slightest study of the life history of the Trematoda will give the observer an impression of the enormous power of adaptation possessed by the organism. It seems as if there is an ever active interplay between the trematode and its host, its morphological structure, habitat, and customs. Apart from a few mainly marine exceptions in the development of the Trematoda, only one thing seems fixed, the first host must almost always be a mollusc, commonly a snail. If this mollusc is lacustrine or marine the development may present great variations in detail, but broadly speaking the normal scheme of development of all these Trematoda is as follows. From the egg thrown off in the water with the excrements is developed a miracidium, which, going in search of a mollusc, pierces its skin, whereupon it is there developed into a sporocyst. This sporocyst produces either daughter sporocysts or rediæ, daughter rediæ or cercariæ; sooner or later the cercariæ will normally leave the first host, live in the free state for a short time whereupon they encyst either in a secondary intermediate host, or upon the vegetation. Sooner or later they will reach the final host, where they mature, whereupon the eggs are again given back to the water with the excrements. The variations from the normal scheme are mainly adaptations in accordance with the structure and habits of the final host. We shall return to this point in the second part of this work.

A few Trematoda accomplish their development in molluscs which are terrestrial; of the development of all these Trematoda our knowledge is extremely restricted.

The more terrestrial the snail is in its habits, the more the trematode must alter its development and habits; very peculiar life histories are the result. However different their development is, a feature common to most of these aberrant forms is the loss of a free-living cercaria stage. The slightest adaptations occur in those cases where the land snail belongs directly to the diet of the final host. This is the case with the two living in *Erinaceus europæum*, viz. *D. leptostomum* and *D. spinulosum*, whose parthenogenetic generations are passed in species of the genus *Helix*, *Succinea* and *Arion*. The miracidium is not liberated from the egg till it arrives in the alimentary canal of the snail. From there it wanders into the liver, and is transformed into a ramified sporocyst in which cercariæ are developed. Later on these wander into the kidneys and are there developed into an agamodistome stage (*Cercariœum*). As such they remain till the snail is eaten by the hedgehog. Here the adult stage is reached, whereupon the eggs, passed out with the excrements, again proceed on their way to the intestine of a snail. The cercariæ are partly furnished with a short tail, partly they have no tail at all (HOFMANN 1899, p. 176).

Highly remarkable conditions were found by MOULINIÉ (1856, pp. 187—191). In *Limax rufa* and *L. cinerea* are found cercariæ with a very reduced tail, which is used as a sucker during the creeping motion. They develop into sporocysts which, according to MOULINIÉ, in contrast to all other sporocysts force their way through the skin and are found as white dots partly upon the skin of the snails, partly in the slime from the slugs. The snail is said to deposit about 50—60 per day. The dots contain the cercariæ with an extremely short tail; deposited on plants they are said to live for several days. Sections show that the snail harbours in its organs numerous sporocysts of quite the same appearance as those which were found outside the body of the animal; notably they are common in the liver. MOULINIÉ supposes that the sporocysts are devoured directly by other slugs, and that there is no other host at all. In this case the sporocysts are therefore supposed to play a similar role as a distributing factor as the cercariæ in the life history of other Trematoda. These observations, now about 80 years old, have, as far as I know, never been corroborated later on, and renewed investigations are greatly needed.

In those cases where there is no connection at all between the primary and the final host, i. e. where the primary host is not food material for the final one, it is the trematode which must bring about such a connection, and this is just what the *Leucochloridium* does by means of its constantly pulsating and coloured sacks.

In this connection it may be added that even in those cases where the final terrestrial host is not voracious but lives on vegetable matter, the development of *Collyricum faba* seems to show that the normal scheme of development of the Trematoda can be altered so much that in that case too, an adaptation to these highly aberrant life conditions has been possible (JEGEN 1917, p. 460; TYZZER 1918, p. 267).

With regard to the *Leucochloridium* it is beyond doubt that it is to the sporocyst that the problem is committed of attracting the attention of the bird to such animals as do not always belong to their normal diet. For it must be remembered that many of the small songbirds which are to take the sacks of the *Leucochloridium* are never snail-eaters and are quite unable to swallow a *Succinea*. As this problem, as far as we know, has not been solved by any other sporocyst, it is easily understandable that just this sporocyst may differ greatly both structurally and biologically from all others.

How much it differs will be best understood if we cast a glance at the sporocyst as it is known in other Trematoda.

In the life of the trematode the sporocyst in the first place plays the following role. Starting from a single miracidium it so to speak overflows all organs of the snail by means of its propagation, and creates an enormous number of specimens which, by fresh acts of propagation, again augment these numbers, often to such a degree that the snail, shortly before its death, seems almost changed into one enormous living mass of parasites, and the water is coloured milky when the offspring from this same single miracidium is given off.

1. The propagation of the sporocyst is of a twofold kind, partly a division combined with the detachment of buds, partly parthenogenetic propagation (mother sporocysts, rediæ or cercariæ). The first-named form is maintained by many older authors (FILIPPI 1854, p. 331, PAGENSTECKER 1857) and also by many more recent authors (THOMAS 1883, p. 108; BIEHRINGER (1884, p. 108); HOFMANN 1899, p. 191; REUSS (1903, p. 469), FUHRMANN 1928, p. 80, BRAUN (1893, p. 806). Only SINITZIN (1909, p. 669) maintains that all reports of asexual propagation in the sporocyst are grounded upon insufficient observations. I do not think that this supposition is correct. I shall return to the question in the second part of this work.

The sporocyst of *Leucochloridium* has no propagation by means of division. From a miracidium there is never developed more than one single sporocyst; this, however, is of an enormous size. From the spot where the miracidium has fastened itself, the sporocyst grows, forms its long threads and club-shaped bodies which slowly expand over the whole surface of the liver. A *Leucochloridium* sporocyst may grow one or two years old, but during all that time it is the very same sporocyst, developed from the single miracidium which long ago made its way to the anchoring place which it has never left since.

2. Another difference is that the sporocyst in contradistinction to almost all other sporocysts is ramified. Ramified sporocysts are found in *Harmostonum leptostomum* from *Helix arbustorum*, where the sporocyst occurs as "netzförmig verzweigte"

organisms, which form "wahre Rasen" (Hofmann 1899, p. 186); they have also been found in other landsnails by Ercolani (Braun 1893, p. 806); in *Limnæa stagnalis* (Leuckart) developing in *cercaria ornata*. Also in the development of *Bucephalus polymorphus* do we find strongly ramified sporocysts (figured and described by Lacaze Duthier 1854, p. 294; Tennent 1906, p. 635 and by Ziegler 1883, p. 537). Recently in *Panopistus magnus* from *Gastrodonta ligera* (Sinitzin 1931 p. 799).

From sporocysts of this form there is an easy transition to sporocysts whose threads cannot be disentangled, and whose extremely fine threads are interwoven to form white spots lying on or in the infected organ of the mollusc. Sporocysts of this nature always, as far as is known, give rise to furcoid cercariæ. It may be questionable if we are not here originally concerned with ramified sporocysts.

Even if ramified sporocysts are known from other Trematoda that of *Leucochloridium* deviates in its power of producing the pulsating, irregular, pigmented and coloured sacks, which force their way into the antennæ, into which the cercariæ wander, and where they are deposited. In this respect *Leucochloridium* is unique among all Trematoda. With regard to the pigmentation of the sporocysts in other Trematoda, and the role which the antennæ of the snails play as organs through which the parasites enter or leave the snail, either as miracidia or as cercariæ, I refer the reader to the second part of this work.

3. In most of the other Trematoda we see the sporocyst develop either daughter sporocysts, rediæ, daughter rediæ or cercariæ which leave the snail. In *Leucochloridium* the sporocyst only develops tailless cercariæ, which remain in the sporocyst and sooner or later pass into a stage which, from a biological point of view, is identical with a cyst.

With regard to the peculiar origin and structure of the envelope of the agamodistomes in *Leucochloridium* this seems at first to be an almost unique feature in the Trematoda. When during the last few years I had an opportunity of studying many *Tetracotyle* stages in *Limnæa stagnalis* and became acquainted with the literature of Faust (1918a, p. 69), Scheuring and Everbusch (1926, p. 41); Hughes, la Rue and others (see list of lit.), I was struck by the great similarity between the envelope of the agamodistomes of *Leucochloridium* and the envelope of *Tetracotyle*. Later on when, in 1930, I became acquainted with the paper of Szidat (1929, p. 685) I saw that he had quite the same view. The two above-named structural peculiarities, ramified sporocysts and the conformity in the structure of the envelopes in *Tetracotyle* and the agamodistome stage in *Leucochloridium*, are just those characters which Szidat (1929, p. 685) among others has used to establish a closer relationship between the families *Harmostomidæ* and *Holostomidæ*.

4. Another great peculiarity in the sporocyst is the relatively extremely small number of cercariæ it is able to produce. Most probably it may be computed at only a few thousand. If we remember that a single *Limnæa stagnalis* or *Planorbis corneus* day after day is able to colour the water in our vessels or the small spaces among waterplants milky with xiphidioid-cercariæ and cloudy with Furcocercariæ, and that

Fuhrmann (1928, p. 90) in the course of four successive days has counted the following numbers of Furcocercariæ thrown out by a single snail (8000—5400—13300, and 15900), numbers which I can confirm and to which I shall return, it will be understood that the progeny of the *Leucochloridium* sporocyst is in reality very limited in number. Hence, as far as I can see, it is not correct when Bittner and Sprehn (1928, p. 107) maintain that the sporocyst of *Leucochloridium* "im Innern ungezählte Keimballen enthält".

5. Another peculiarity with regard to the *Leucochloridium* sporocyst is that the cercariæ never come out of the sporocyst, but remain here until the final host liberates them. The cercaria stage has entirely lost its significance as a distributing factor. (With regard to the cercariæa stages developed in watersnails (*C. paludina impuræ*) see the second part of this paper).

An approach to this highly interesting peculiarity is, however, found in those cases where the cercariæ have a well developed tail but nevertheless the whole development takes place in the snail. In these cases, too, the power of distribution of the cercariæ is often much restricted. In numerous cases the cercariæ, the very moment they have been expelled from one snail, plunge into another lying near the first; and very often, if no other snails are present, they fasten themselves on the snail which they have just left. The tail is thrown off, whereupon they pierce a hole in the skin. Cort (1915, p. 37) shows that echinostome cercariæ (*cercaria trivolvis*) may use the same animal (*Planorbis trivolvis*) both as their primary and their secondary host (see also Faust 1917b, p. 35; Moulinié 1856, p. 137; Fuhrmann 1928, p. 88).

The last stage which, from a biological point of view, is very nearly related to what we find in *Leucochloridium*, is represented by those cases where the cercariæ never leave the mother organism in which they are developed. Johnston e.g. (1920, p. 362) has found in *Echinostoma revolutum* 58 rediæ with cysts, and very often rediæ which contain both rediæ and cysts. He maintains that, in the *Echinostomata*, encystment in the same host in which sporocysts and rediæ have been developed will be a common family character. Loos (1894, p. 48) has found as many as 40 cysts in the same sporocyst, and Lebour (1907, p. 102) has found in *Cardium edule* a sporocyst which contained cercariæ as well as cysts; she furthermore observed that the cercariæ in the sporocyst throw off their tail and that the tail moved for a time after being thrown off. With regard to my own investigations and experiments on this subject I refer the reader to the second part of this work.

In all these cases the significance of the cercaria as a distributing factor in the life of the parasite is lost, nevertheless the stage is retained. Here as so often the species is altered biologically before being transformed morphologically. From a developmental and morphological point of view there may very well be differences between the encysted stages in the sporocysts of watersnails and the agamodistomes in the sporocysts of *Leucochloridium* but from a biological point of view the significance is the same.

Even if we can find related traits in the structure and behaviour of other sporocysts, there is no doubt that the *Leucochloridium* sporocyst in its structure and development deviates more from the normal than any other sporocyst hitherto known.

For years I have worked with *Leucochloridium* from a conviction that our knowledge of the development of *L. macrostomum* is in reality very sporadic, and that the whole development in *Succinea*, from being originally an abnormal, almost a pathological, phenomenon, has at last become normal and useful for the species; the original normal development may perhaps still be going on, but of its details we know nothing. For years I have tried to prove this theory; I confess, without the slightest result. The working theory may be wrong; but I am not sure that it is so. My failure may be due to the fact that the theory cannot perhaps be proved in our latitudes, the proof of its correctness belonging to more southern countries. It is especially with this supposition in mind and hoping that the theory will be tried in other latitudes, that I take the liberty of setting forth the considerations on which the working theory has been based, and the way I have gone to support it.

ZELLER's and HECKERT's investigations show that the agamodistomes in the sacks of *Leucochloridium* reach maturity when transferred into the alimentary canal of Passeres.

If the developmental possibilities of *L. macrostomum* were exhausted with this, it must be admitted that with regard to the development of *L. macrostomum* nature has solved problems which might *a priori* be regarded as insoluble.

The problem which the sporocyst so to speak had to solve and really has solved, was to remodel the antenna of a snail, an organism in which the bird was not normally interested, into an organ which, in the eyes of the bird, should look like an insect larva and in this way alter it into desirable food material. The antenna now causes a reflex action on the part of the bird, owing to which the snail now, in spite of earlier experience, attracts the attention of the bird, whereupon it is also, itself, through the sack as a transitional stage, transformed into desirable food material. For it must be remembered that even if it is only the sack which attracts the bird, it cannot be unaware that this sack is in some way connected with the impression of a snail. Furthermore it must be kept in mind that this process, which is highly remarkable from a morphological and biological as well as from a physiological point of view, is a result of mimetic phenomena, and that in a group of animals where mimetic phenomena, as far as we know, have never been observed before.

Finally these mimetic phenomena occur in an organism whose place is in the interior of the snail, and whose organisation is of the greatest simplicity. As mentioned above, as far as we know, it has no nervous system and no sensitive organs of any kind. Nevertheless it reacts to stimuli from without (variations in light and temperature), and localises this power in special parts of the body which are capable of locomotion in a quite special way.

If we further remember that no one has hitherto, in natural conditions, seen a bird split the antenna of the snail and fly away with the sack to the nestlings, it cannot be denied that there is still room for some doubt. Especially with this latter point in mind, it may be allowable to suppose that our knowledge of the life history of the trematode is not fully exhausted with the feeding experiments of ZELLER and HECKERT. In my opinion this will be even more obvious if we take some other points into consideration.

Our knowledge of the tribe *Leucochloridea*, its species and their systematical relations, has always been extremely restricted. The new treatment of WITENBERG is, as far as I can see, by no means able to dispose of heterodox opinions.

WITENBERG (1926, p. 227), in his treatment of the family *Harmostomidæ*, maintains that there exist at all events four species of the genus *Leucochloridium* (*Urogonimus*) one of which is undetermined. The other three are *L. macrostomum* (Rud.), *L. insigne* (Loos) and *L. turanicum* (Soloviev). Other species described as *L. cercatus* (Monticelli), *L. assamense* (Sewel) are either insufficiently described or larva stages. It was RUDOLPHI (1802, p. 26) who created the species *Distomum macrostomum* found in *Motacilla*. When in 1819 (p. 94) he found new specimens in *Fulica atra*, he referred these specimens to a new species *D. holostomum*. According to the description it seems that the only difference is a difference in size: *D. macrostomum* is smaller than *D. holostomum*. BRAUN (1901, p. 500) who has studied the type specimens, arrived at the result that the two species were identical and, as far as I know, all later authors who have made *Leucochloridium* the subject of a more thorough study, have arrived at the same result (HECKERT, MÖNNIG and MAGATH).

If this view is correct, this would in other words mean either that we must expect to find the *Leucochloridium* sporocyst in real water snails, or that the waterbirds get their parasite from feeding on *Succinea*.

WITENBERG, however, arrives at the result that the two species *D. macrostomum* and *D. holostomum* differ from each other. ("Indes gehören zweifellos die Exemplare von der Bachstelze und vom Wasserhuhn zu verschiedenen Arten" p. 233.) As far as I can see, he gives no other reason for this supposition than that they are found in birds belonging to different orders, perhaps also because we know a series of sporocysts, of which those with green and brown sacks are parasites in *Succinea putris*, whereas those with yellow and golden-red ones are parasites in *Succinea retusa* and water snails (species belonging to the genera *Vivipara*, *Planorbis* and *Limnæa*). WITENBERG (1926, p. 228) further maintains that all those older species are insufficiently described; on this point WITENBERG is certainly quite right. How insufficient our knowledge of the species actually is, will best be understood from the fact that the species with which HECKERT has worked, according to WITENBERG (1926, p. 232), is neither *L. macrostomum* nor *L. holostomum* "sondern irgend eine andere, wahrscheinlich *L. insigne*" (Loos).

L. insigne is found in *Actitis hypoleucos*, *Totanus ochropus* and *T. glareola*. This means, in other words, that, since HECKERT got his specimens from songbirds[1], this

[1] "Als die eigentlichen und natürlichen Träger des geschlechtsreifen *Distomum macrostomum* möchte ich aber meinen Erfahrungen zufolge die Sylvien in Anspruch nehmen". 1889, p. 26.

species should be able to live in Passeres as well as in waterbirds. As far as I can see, WITENBERG himself has given a proof of the incorrectness of his supposition that "jede aus den 3 von mir bezeichneten Arten einer spezifischen Gruppe der Wirte entspricht".

If BRAUN, HECKERT, MÖNNIG are right in their contention that *L. macrostomum* and *holostomum* is the same species, it is found in a long series of insect-eating *Passeres* as well as in many waterbirds e.g. *Rallus aquaticus, Porzana porzana, Gallinula chloropus*, birds which find their food in localities where *Succinea* may be found, which are really snail-eaters, but mainly live of typical water snails and swallow the snails whole. They are therefore by no means specially attracted by pumping sacks. — But more than that, the ripe stage is also found in a long series of typical seed-eaters such as *Passer montanus, Fringilla coelebs. Pyrrhula pyrrhula, Carduelis linaria.*

How is it possible to understand that these birds, which are neither snail nor larvæ feeders, should split the antennæ of *Succinea* and so become infected. As hosts are also stated *Garrulus glandarius, Corvus corone*, further *Picoides tridactylus(?)* and *Dryobates martius*(?). Even if the two first-named might get the parasite when eating nestlings in the nests of *Sylvias*, how can we explain that the two last-named get it?

Recent investigations furthermore strengthen the view that what we know with regard to the d e v e l o p m e n t of the different *Leucochloridium* species is extremely little.

MAGATH (1920, p. 110) found a new species of sporocysts in a Succinea (*S. retusa*) as well as in *Planorbis trivolvis*; LUTZ (1921 a, *L.* sp.) in *Hapalonyx*; FAUST (1924, p. 258) another sporocyst *L. millsii* in *Limnœa plicatula*. This shows that the development of the *Leucochloridium* species may take place in typical water snails. When *Leucochloridium* species are found in waders, which mainly live on water snails, and these cannot be distinguished from those in *Sylvias*, it may be permissible to suppose as a working theory that the development of the same species may take place in typical water snails as well as in *Succinea*, furthermore that the development in the first-named may take another course than hitherto known. The latter supposition is somewhat strengthened by an observation by SEWELL, which, however, stands greatly in need of verification. SEWELL (1922, p. 171) maintains that he has found young specimens of a species of *Leucochloridium*, which were "discovered in gelatinous yellow cysts in the thick edge of the mantle in specimens of *Lecythoconcha lecythis* and *Vivipara oxytropis* obtained by Dr. ANNANDALE in the Laktak Lake, Manipur. The cysts measured $1^1/_2$—2 mm. in length and about 1 mm. in breadth, and each communicated with the external surface of the mantle, that is, the surface in apposition with the shell, through a small pore. They contained immature *Leucochloridium*, measured 2—3 mm. in length and the hinder part of the body was of an orange-red colour". The trematode is described and figured on Pl. XVII, Fig. 3. SEWELL (p. 172) maintains that the structure of these forms agrees very closely with the description of *L. macrostomum* (Rud) given by HECKERT (1889). In accordance with this SEWELL quite correctly comes to the result" that the development of the *Leucochloridia* is not always the direct simple process that occurs in *L. para-*

doxum. In the present stage it seems certain that the sporocyst stage is followed by a free-living period, in which the cercariæ leave the original mollusc host, and migrate into and encyst in an intermediate mollusc host".

As far as I can see, our knowledge of the systematics and development of the group *Leucochloridea* is so restricted that it may be supposed that the last word with regard to the development of *L. macrostomum* has not yet been said. Furthermore, as stated above, it seems reasonable to see an abnormality in the hitherto known development of the species, which has been useful to the species in some of its areas of distribution, whereas the normal development, following the common scheme of development of Trematoda, in other of its areas is still going on. In my opinion this supposition is further strengthened if we take two other points into consideration.

1. In the history of helminthology two old theories of development have been set forth; both were very soon stigmatised as heretical; nevertheless it seems very difficult to do away with them. Again and again they turn up, each time in a new dress. The one is the theory of ERCOLANI (1881, p. 237) that the same trematode larva could, during accommodation in different hosts, develop into what we should be apt to regard as different species. The other is that of FILIPPI (1854, p. 275) that "un bon nombre de Trematodes aient cessé d'exister à l'état parfait ou ne se montrent dans cet état que rarement de temps en temps en des circonstances presque exceptionelles et que leur espèce ne se maintienne qu'à l'état imparfait".

The theory set forth by ERCOLANI is of course too massive in form. On the other hand it cannot be denied that the views of LOOS (1899, p. 521) are related to those of ERCOLANI. LOOS maintains that though flukes found in birds and mammals may be morphologically identical, they may be regarded as physiological varieties or species. The different habitat and different metabolic processes in birds and mammals would produce the differentiation. FUHRMANN (1928, p. 95) calls attention to the fact that in such different forms as birds and cats we have found species (*Opistorchis geminus* and *Opistorchis sinensis*) which it is impossible to distinguish from each other. In that case we are obliged according to FUHRMANN to suppose that we are here concerned with species which are anatomically identical but differ physiologically. We find related ideas set forth by LEUCKART (1889, p. 171), who maintains "das nämlich durch Anpassung an fremde oder falsche Wirte neue Arten entstanden sein können". LEUCKART thinks, that the parasites offer an extremely interesting field for investigation in this respect. It is a well-known fact that wherever we meet physiological races, we regard this as the beginning of a species-making process and that a closer examination has in fact more than once revealed small morphological differences between the races lasting as long as the races live under the same conditions of life.

I cannot see better than that these theories, set forth by LEUCKART, LOOS and FUHRMANN, are in reality only another, more modern, expression of ERCOLANI's old theory, or at all events nearly related to it. It is with these theories in mind that I consider it allowable to suppose that *L. macrostomum* may develop in other snails than *Succinea*, and that the development here may take another course than that known to us. It may be added that the opinion of Loos is not endorsed by Faust and Nishigori (1926, p. 121).

Even if the theory of Filippi cannot be maintained in its full extent it has at all events an element of correctness. For numerous species there may exist areas where the species may only or mainly occur in the parthenogenetic generations. In these areas the first and the intermediate host may again and again be re-infected, whereas the infection of the final host is very problematic; furthermore, in very many cases the developmental stages may find their way into or be taken up by hosts for which they are by no means destined. In many cases the result will be death, but in many others life is possible, and the new habitat gives rise to physiological and morphological races.

The more bound to the soil the first host is, the more sharply delimited it is from a systematical standpoint, the more the migratory instinct is developed in the final hosts, and to the more deviating systematical unities they may belong, the more we may expect cases in which the development of the parasite may be begun but not completed. Furthermore we may expect that metamorphoses may begin and may be completed but give rise to new physiological forms, perhaps morphologically deviating from the normal forms, especially with regard to size (dwarf forms, giant forms, variations in the strength of the organs of attachment etc.).

If we wish to understand the development of all those Trematoda which live as ripe stages in migrating birds, there is one factor, bird migration, which must always be taken into consideration. Only few have paid sufficient attention hereto; in the first place may be mentioned some American authors (Ward 1909, p. 1, and Johnston 1920, p. 369); further Sewell (1922, p. 12) with regard to India. Whereas in Europe (especially owing to the investigations of Zschokke (1902, p. 118), we are well aware of the relation between fish parasites and migration phenomena, we have not, as far as I know, studied the influence of migration upon the life of bird parasites. Only Loos has some remarks on this subject (1899, p. 522).

For 12 years Ward (1909, p. 5), aided by students and friends, made systematic collections of parasites from the migrants belonging to vast swarms of wild ducks of numerous species, which breed, some within the northern limits of the States, but mostly much farther north. Ward has made the very important observation that the parasites found in the birds going south are radically different from those they harbour on their way north some four or five months later; only a certain small percentage of the parasitic fauna of the two seasons is identical. Whether this element is acquired in both regions, or whether it is characteristic of one only and persists beyond the period of stay, is left undecided. One factor tends to confuse the results. Many of the birds which travel south in the autumn are young, having been hatched in that summer's brood; of course they are only infected by the parasitic fauna of the north. "But they are also in large part the parasites of immature age, and do not recur in the full-grown birds, even though the latter have passed the summer in the same environment". As far as I know, this extremely interesting account has not been followed up by a more elaborate investigation.

To accomplish a similar investigation of the songbirds in this country would most probably be an impossibility. All our songbirds are rigidly protected the whole year round, and their capture in nets or in any other way in which birds could be got in great numbers would not be allowed. Only during the passage from the light-houses could material perhaps be acquired, but in this case difficulties of another kind would arise. As is well known, *Succinea putris* is rather local in its distribution; the migrating songbirds use numerous localities as resting places during migration, in which *Succinea* are never to be found; enormous numbers of eggs may never reach their destination. Hitherto *Succinea putris* has not been found farther south than the northern coasts of the Mediterranean. As enormous numbers of ripe stages of the trematode may cross the Mediterranean in the cloaca of migrating birds, it would be of the greatest interest if it could be elucidated whether the African species of *Succinea* harbour *Leucochloridia*. Professor STEENBERG has kindly told me that Africa harbours many and large species of the genus *Succinea*. From Marocco is recorded 1 species, from Algiers, from Northeast Africa 16, from Congo 6, from the Cameroons 1, from Niger and Lake Chad 2, from German East Africa 2, from Portuguese East Africa 3, and from South Africa 16.

If the life history of *Leucochloridium* were fully elucidated with the investigations of ZELLER and HECKERT, its course of life would be so sharply delimited, that it would seem almost unintelligible how the species could keep its place in nature. This is especially obvious if we remember the relatively very small numbers of cercariæ which are produced by the sporocyst, the enormous amount of sacks which never reach their destination, and that the final hosts are mainly or partly migrating birds.

With the above named ideas in mind I have examined many hundreds of *Planorbis* gathered in many localities, especially the lakes of Sorø and Esrom where *Fulica atra* are present in great numbers, (in Esrom Lake by thousands), and where *Gallinula chloropus* is common (in Sorø Lake). Nevertheless I have never had the good luck to find the parasite in these snails.

On the same *Petasites* leaves upon which I found my *Succinea* infected with parasites I always found *H. nemoralis, hortensis* and *arbustorum* in great numbers. But more than that: On the leaves of *Petasites* where the birds had dropped their excrements which contained eggs of Trematoda I very often found simultaneously and upon the same mass of excrements a *Succinea* as well as two or three *Helices* sucking. We are bound to suppose that the result for *Succinea* as an excrement-eater is that it gets its ramified *Leucochloridium* sporocysts in this way. The conjecture that *Helix* could also be infested was so much the more allowable, since the Helices also harbour ramified sporocysts with tailless cercariæ which develop in *Erinaceus* *europœus* to *Harmostomum leptostomum* (HOFMANN and others) and belong to the same family to which *Leucochloridium* belongs. With these facts in mind I have taken 50 *Helix nemoralis* and *arbustorum* from the same *Petasites* leaves from which the infested *Succinea* were gathered and from the same excrement masses upon which the *Succinea* were sucking and kept them for months, but nevertheless not a single infested *Helix* was found.

Since very old snails, which had not shown sacks for months, but whose antennæ were deformed when dissected, showed cercariæa lying free in the liver, I supposed that the cercariæa could perhaps grow ripe in the snail and the bird be eliminated from the life history of the parasite. From recent years we have examples of trematodes, whose whole development is really passed in a single host (*Lecithodendrium chilostomum* in *Phryganea*; *Pleurogenes medians* in *Gammarus* and perhaps *Collyrichum faba* and Trematoda from slugs). With this thought in mind I have dissected about 50 infested *Succinea*, but always without result.

It must be frankly admitted that my above-named working theory, which has occupied me for more than two years, has by no means been verified. Nevertheless I feel convinced that it contains some grains of truth, and that the failure on my part is due to the fact that only investigations in other, more southerly, latitudes can prove its correctness.

Postscript.

After my paper was almost printed two papers by HALÍK and SINITSIN have appeared. The first paper deals especially with the pulsation of the sacks. There is only a single passage on which I take the liberty of offering some remarks. HALÍK writes (p. 462) "Diese Interpretation (of SIEBOLD) ist deshalb interessant, weil wir hier das seltene Beispiel im Tierreich haben, dass ein Tier ein anderes durch Färbung und Bewegung nachahmt, nicht um geschützt sondern um gefressen zu werden, da nur auf diese Weise die *Leucochloridium*-Schläuche den nächsten Entwicklungsstadien, den Zerkarien, einen neuen Wirt und somit das Fortkommen einer neuen Generation sichern."

This remark is not new however. ZELLER (1874, p. 577) has already put forward quite the same interpretation. He writes: "Wo wir sonst von "Maskierung" oder Nachahmung hören, soll diese immer zum Schutz und zur Erhaltung des betreffenden Tieres oder doch irgendwie zu seinem Nutzen dienen. Für unser *Leucochloridium* wird die Änlichkeit mit einer Insectenlarve nur zum Verderben. Denn was anderes wird durch dieselbe erreicht, als dass die Aufmerksamkeit eines Insecten fressenden Vogels erregt und dieser veranlasst wird, das *Leucochloridium* aus der Schnecke herauszufressen . . . Eine solche Absicht aber für seine Brut die eigene Existens zu opfern wird gewiss Niemand unserem *Leucochloridium* zutrauen wollen." He further says: "Unser Fall ist recht geeignet einen Beweis gegen die Annahme eines solchen Vermögens und die Anschauung, als ob die Thiere bei ihrer Maskierung eigentlich mit Bewusstsein handelten, zu liefern."

Zeller's view was well known to me; nevertheless I have not mentioned it, because in my opinion it is not right. Now that I find the same view advanced in a recent paper, I take the liberty of calling attention to the following fact. Whatever supposition we generally may have with regard to mimetic processes, and more especially as to those which should have produced the resemblance of the *Leucochloridium* sack to an insect larva, one thing is beyond all doubt. The sack itself is not an organism, it is only part of an organism, and this organism persists for years after the liberation of the sack. Zeller is not right when he says that "die Ähnlichkeit mit einer Insectenlarve nur zum Verderben für unser *Leucochloridium* wird", nor is Halík right when he says that *Leucochloridium* is an example of the peculiar fact "dass ein Tier ein anderes durch Färbung und Bewegung nachahmt nicht um geschützt sondern um gefressen zu werden." The liberation of the sack is an unquestionable advantage to the sporocyst, and the whole process is viewed by Zeller and Halík from a decidedly wrong angle.

In many respects the liberated pulsating sacks are almost without parallel in the animal kingdom. From a biological point of view, as far as I can see, the *Leucochloridium* sporocyst can best be compared with those organisms which develop special parts of their body in which sexual products are deposited and which, provided with the power of locomotion, are loosened from the mother organism and are for a short time able to live an active life. The detached arm of the *Argonauta*-male, the loosened buds of the chains of some of the pelagic *Syllidæ* and other *Polychæta*, the pulsating sacks of *Leucochloridium* are all parts, detached from the mother organism and all play a role in the propagation of the species. At a first glance the comparison seems farfetched, but from a biological point of view a closer inspection will show that it is right.

To the interesting paper of Sinitsin I shall return later on.

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EXPLANATION OF PLATES

All plates reduced one third.

All figures are drawn with a Zeis microscope or with Zeis lupes and with a camera. Where the power or lenses are not indicated the power is 3—4.

Plate I.

Fig. 1. A *Leucochloridium* sporocyst with brown sacks .... a*. Sucherocular

- 2. A *Leucochloridium* sporocyst with green sacks .... a*. Sucherocular

The size and form of the pigment bands are subject to very great variation, and the differences in the arrangement of the bands in the brown and the green sacks are not always so large as the figures show. The apex of the brown sacks is always brown; that of the green, as far as hitherto known, always red.

- 3.} Show two sacks from very old sporocysts; all pigmented sacks are thrown off;
- 4.} the production of germ spheres is stopped, the sacks are but small, very irregular in form, and contain only a very few agamodistomes; these are all opaque with very thick walls. In the strings, which are dark brown and without lumen, is found a single agamodistom which has not been able to force its way to the sack. It has blocked up the passage for other agamodistomes and is itself quite opaque.. a*. Oc. 4

- 5. Section through a sack showing the arrangement of the agamodistomes .... a*. Oc. 4

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Plate II.

Fig. 1. A very, young sporocyst found in a young snail which had never shown sacks in the antennæ and which had lived for three months in the terrarium .... Obj. 16. Oc. 4

- 2. A very old sporocyst. At the lower edge is shown two dark branches which have carried large brown sacks. The other sacks are all small, very irregular in form, and carry branches of the second order. The production of germspheres has ceased, and fully developed agamodistomes are not present .... a*. Oc. 4

- 3. a.—e. The same sack drawn from a living specimen. The drawings show the great form variation, most conspicuous at the apex, f. is the same sack drawn immediately after it had been killed in formaline.

- 4. Transverse section of the sack. To show that the agamodistomes are lying so closely packed that the envelope gets pentagonal or hepagonal......... Obj. 16. Sucherocular

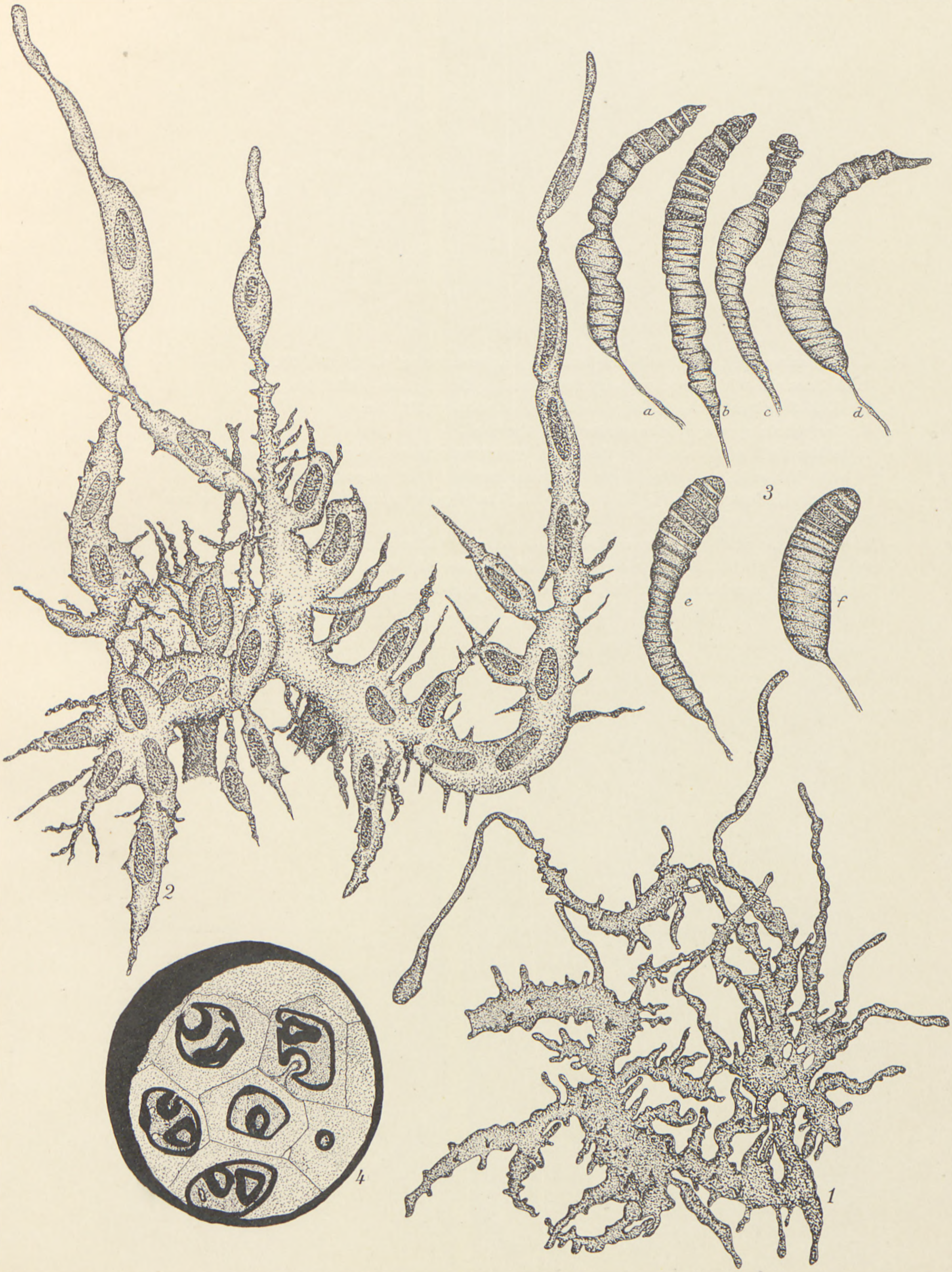

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Plate III.

Fig. 1. A *Succinea* wiith six well-developed sacks. Description p. 124. No. 75.
- 2. A *Succinea* with three well-developed sacks. Description p. 122. No. 21.
- 3—5. A *Succinea* with six large sacks. Description p. 119. No. 9.
- 4. The whole sporocyst dissected out of the shell.
- 5. Is the shell of the snail to show the enormous size of the parasite in comparison with the snail, and how large the space is which the parasite occupies.
- 6.–7. A snail drawn on $^{23}/_{3}$ 27 and $^{7}/_{4}$ 27. The figures show the growth of the two sacks in a fortnight.
- 8.–10. The same snail. In 8 drawn before dissection, 9 after the mantle cavity has been opened. In 10 all the viscera have been dissected away, only the genital organs and the parasite remain. Of the five free lying sacks only some have been drawn. Description p. 121. No. 47 . . . . × 6

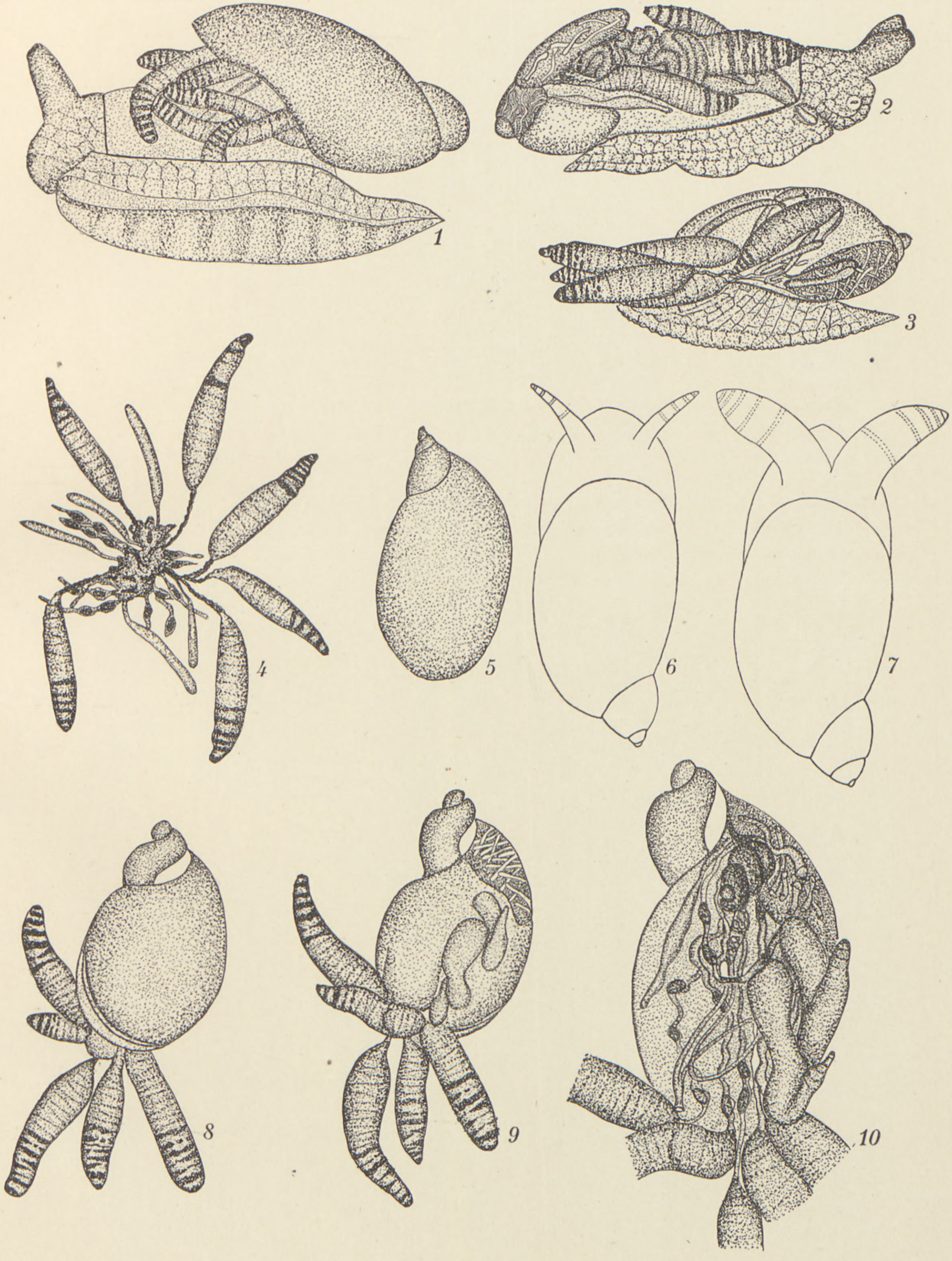

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Plate IV.

Fig. 1.⎫ A snail with two large sacks; in Fig. 2 part of the genital organs are seen.
- 2.⎭ Description p. 119. No. 3.
- 3.⎫ A snail with two large sacks. In Fig. 2 the genital organs are seen. Description
- 4.⎭ p. 121. No. 28.
- 5. A snail with three very irregular sacks. Description p. 123. No. 22.
- 6. A snail with two large sacks. Description p. 118. No. 2.

Figs. 7—8 shows a shell of a *Succinea*, the two sacks, and the genital organs of the snail... × 6

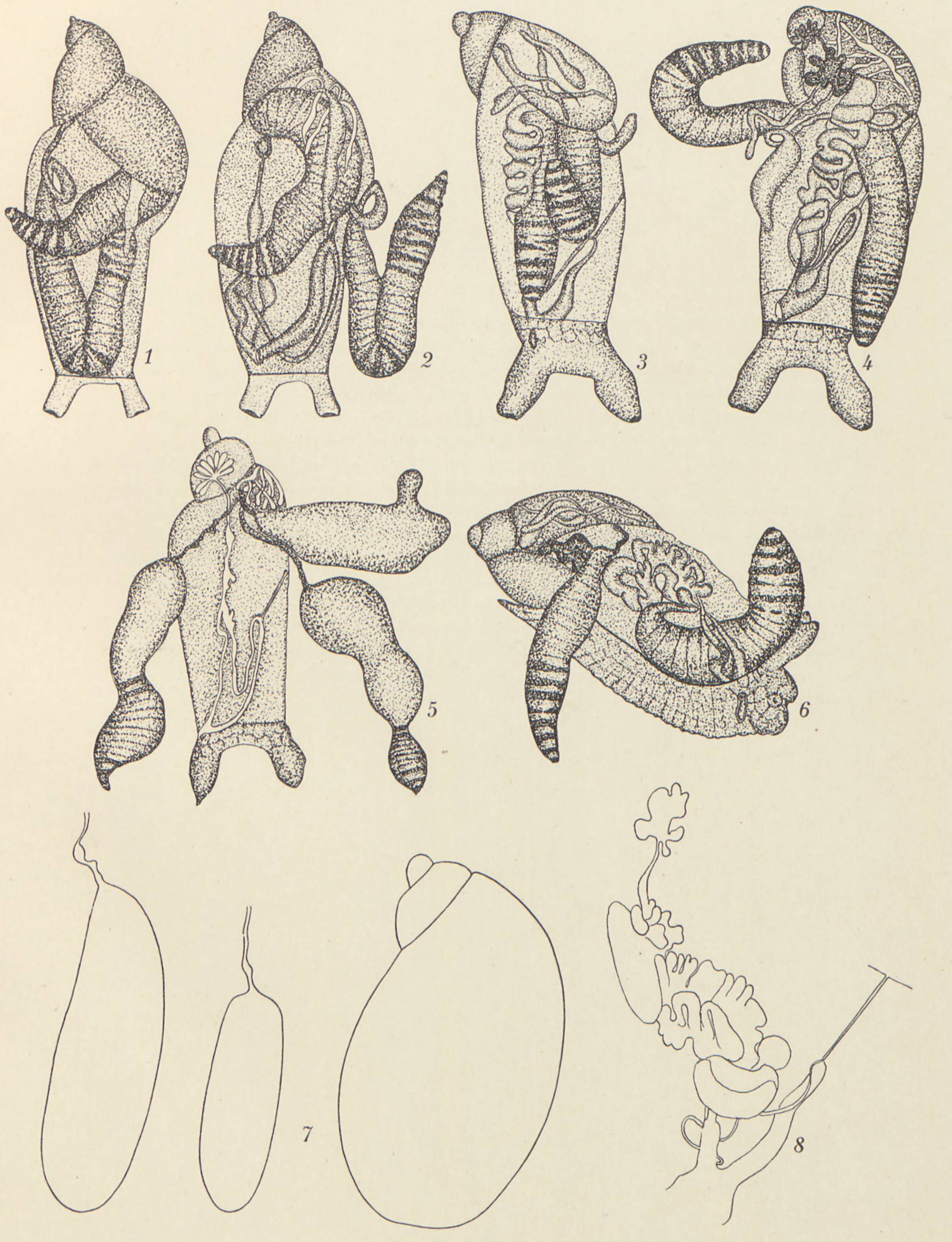

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Plate V.

Fig. 1. Normal genital organs of *Succinea putris*, seen from the inner side.

- 2. The left part of the figure, seen from the outer side. hg. hermaphrodite gland; vd. vesicula seminalis; ab. albumen gland; so. sperm-oviduct; o. oviduct; vd. vas deferens; m. muscle; p. penis; r. c. spermatheca. . . . . a*. Sucherocular
- 3.} A sporocyst with 6 sacks in different stages of development. 4 The shell of the young
- 4.} snail which has contained the enormous parasite. Description p. 120. No. 15.
- 5. The sexual organs of the snail drawn in Figs. 5—7, Pl. VI, p. 121. No. 45. The figure shows how enormously the sexual organs may be reduced by the parasite. . a*. Sucherocular.
- 6. The same sexual organs as figured in Fig. 5, but drawn with a high power (a*. Oc. 4). The albumen gland has almost disappeared and the rest is reduced to mere strings.
- 7. Sexual organs belonging to the snail No. 47 figured on Pl. III, Figs. 8—10 and described p. 121. . . . . 121 a*. Oc. 4
- 8. Snail without large sacks; and some smaller ones. Description p. 120. No. 12.
- 9. The shell which has harboured the enormous parasite.
- 10. The same snail; the sacks are dissected out and the genital organs of the snail are seen. They are almost at the same stage as those figured in figs. 5—6.

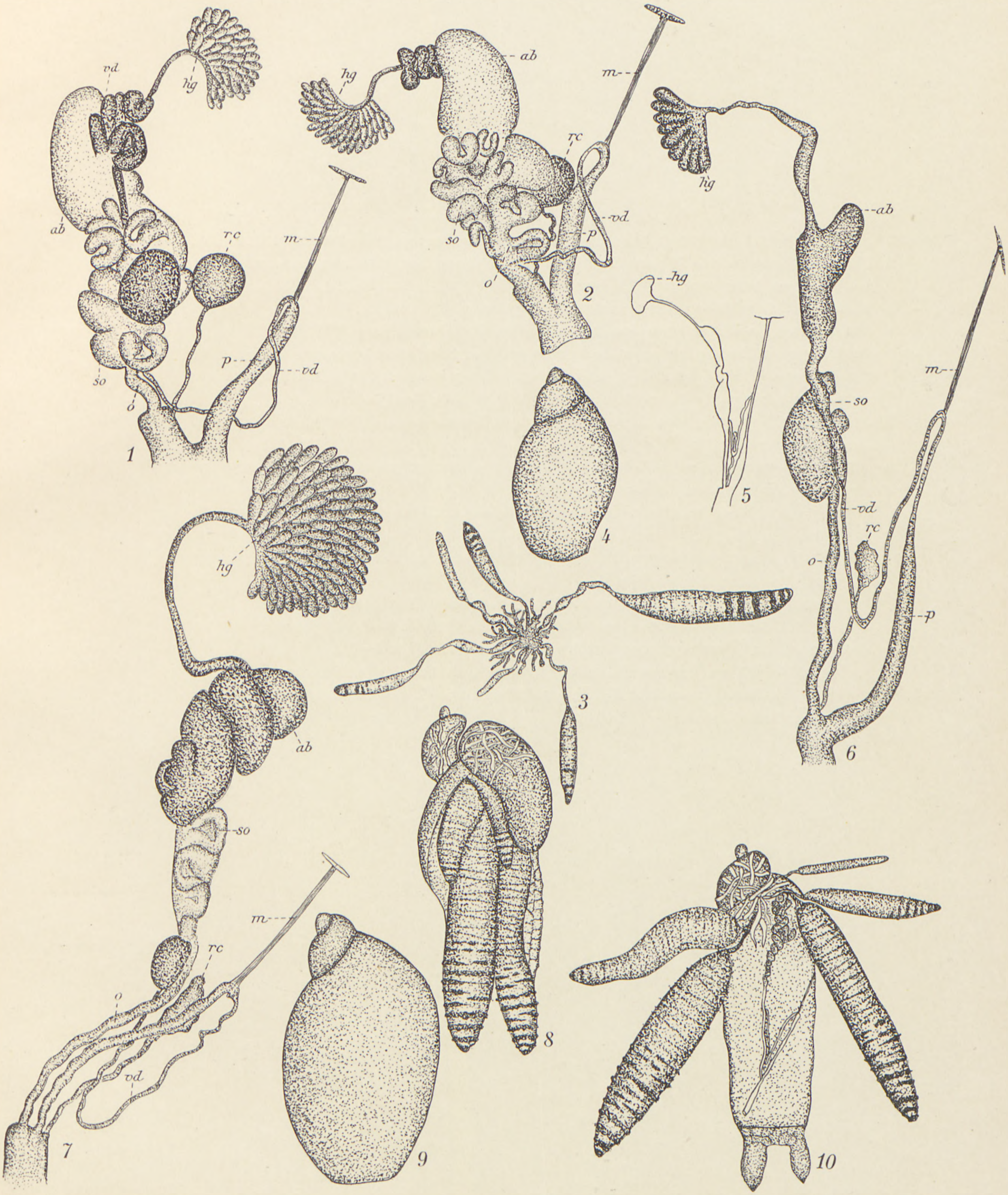
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Plate VI.

Fig. 1. Snail with four sacks and rather well developed sexual organs. Description p. 122. No. 48.

- 2. Liver of the same snail; seen from without. It shows how two long immature sacks are lying on the surface of the liver. *8
- 3. A small snail with two large sacks. Description p. 122 No. 5.
- 4. A small snail with an enormous abnormal sack. Description p. 123. No. 50.
- 5—7. A large snail showing seven sacks all ripe. The three drawings were made during the dissection, Fig. 5 after the snail had just been opened, the genital organs are reproduced in figs. 5—6 on Pl. V. Description p. 121. No. 45.
- 8. A large snail showing one large and two smaller sacks and a lot of smaller ones. Description p. 120. No. 24.
- 9—12. Four sections of a snail to illustrate the causes why one snail has only one large sack and another six or more sacks.

  Fig. 9. Section through a snail not parasitised. Figs. 10—12 sections through parasitised snails.

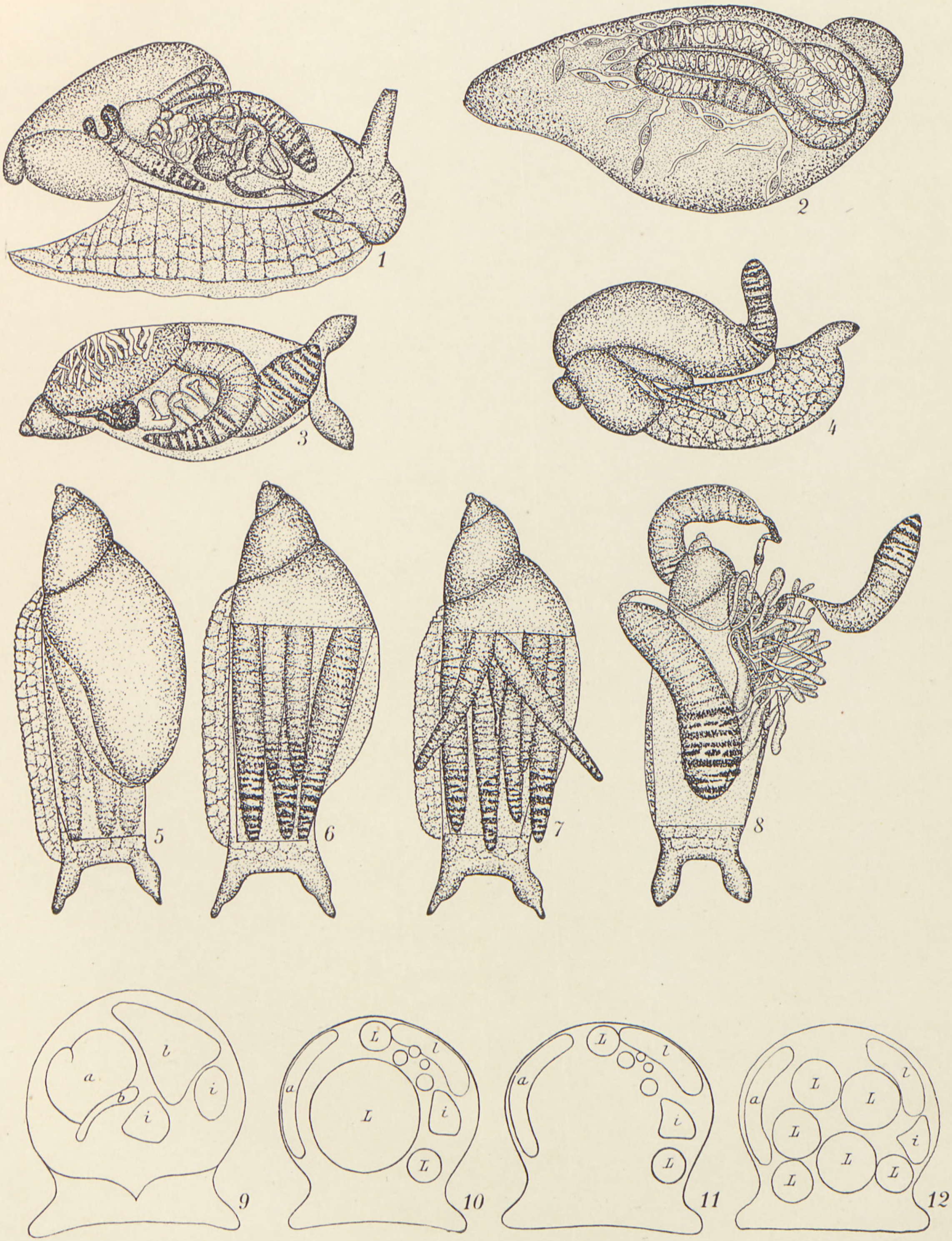
  Fig. 10 shows one large sack and 6 smaller ones of which one is lying below the strongly reduced liver (Fig. 4).

  Fig. 11. Section of a snail which has got rid of the large sack.

  Fig. 12. Section of a snail in which the small sacks in fig. 11 have grown up and occupied the empty space left by the large one (Figs. 5—7).

  Figs. 10—12 are camera drawings from animals fixed in sublimate.

  Fig. 10 corresponds to Fig. 4; Fig. 12 to Fig. 5—7. a-b. Sexual organs; l. Liver; i Intestine. L. sacks.



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NEW CONTRIBUTIONS

TO

THE KNOWLEDGE OF THE CIDARIDS

I–II

BY

TH. MORTENSEN

WITH PLATES I—XIII

D. Kgl. Danske Vidensk. Selsk. Skrifter, naturvidensk. og mathem. Afd., 9. Række, IV. 4.

KØBENHAVN

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BIANCO LUNOS BOGTRYKKERI A/S

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Not many years ago the Cidarids were thought to be only a small remnant of a once, in the Jurassic and the Cretaceous periods, flourishing tribe. More recent researches have given another result. It is true that several forms of Cidarids, which were predominant in those former periods, like *Rhabdocidaris* and *Diplocidaris*, have nearly or completely disappeared; but then other forms, particularly the Goniocidarids, have started developing and have become very richly represented in the seas of our days. Thus the stem of this great and noble family of sea-urchins is as vigorous as ever, only now one branch, now another has taken the lead.

In my Monograph of the Echinoidea, Part I, Cidaroidea, published in December 1928, some 150 species and varieties of recent Cidarids were described, but I expressed (p. 355) the expectation that a good many more Cidarids would be found to exist in the seas of recent days. Already now, three years after the publication of the said work, I can add some new forms, and even a new generic type.

The voyage which, owing to liberal grants from the Carlsberg and the Rask-Ørsted Fund, I could undertake in 1929—30 to Java and South Africa, Mauritius, and St. Helena, afforded opportunities for making extensive collections in those seas, particularly of Echinoderms. During the visit to Java I was enabled to undertake investigations in the Bali-Sea, the Government of the Dutch East Indies placing at my disposal for 12 days the S.S. "Dög" for this purpose. As distances are not great in this area, a good deal of work could be done, and important results were achieved. As regards the Cidarids the most important was the discovery of a new, fine *Goniocidaris* species. The record by DE MEIJERE of *Goniocidaris florigera* from this very locality in the "Siboga" Echinoidea, based on a single, old spine, is herewith shown to be erroneous, the spine belonging to the new species here described, *Goniocidaris florigera* being till now known only from the Kei Islands.

At Mauritius the dredgings I could undertake at depths of some 200—300 metres off Port Louis, by means of the excellent tug "Mauritius" placed at my disposal by the Colonial Government, yielded some fine results in regard to Cidarids, viz. numerous specimens of *Stylocidaris badia*, hitherto known in five specimens only, two very fine specimens of *Chondrocidaris gigantea*, one of them being the largest specimen known of all recent Cidarids; further some specimens of a fine new variety of *Stylocidaris bracteata*, and a few young specimens of *Acanthocidaris curvatispinis*, hitherto known in two specimens only.

In the South African Seas I did not find any Cidarids; particularly I was very disappointed in not finding any specimens of the *Goniocidaris*-species which I have indicated to exist there (Monograph, p. 154, Note). But then I had the great pleasure of receiving, after my return from the voyage, some specimens of a Cidarid from Captain E. Pace of the Trawler "Disa", which proved to be a new species of *Stereocidaris*, the existence of which was also indicated in my Monograph, p. 270. Further I found in the collections of the Fisheries Laboratory of Cape Town a specimen of a Cidarid, which proved to represent an interesting new generic type, and in the collections of the South African Museum another fine Cidarid, which proved to be *Histocidaris elegans*, not hitherto known from South African Seas. In the Durban Museum I found a specimen of *Acanthocidaris maculicollis* likewise not hitherto known from South African Seas.

At St. Helena a rich material of *Tretocidaris spinosa* and *Eucidaris clavata* was obtained besides *Cidaris cidaris* var. *meridionalis*, not hitherto known from so far South.

In the material of Ophiuroids and Asteroids returned to me after the death of my lamented friend Professor R. Koehler, Lyon, to whom it was entrusted for reporting on, there was found also a couple of Cidarids, viz. a young *Stylocidaris albidens* and another specimen which proved to be an unknown species, most probably of the genus *Stylocidaris*. It is described here under the name of *Stylocidaris cingulata*.

A number of Cidarids were collected in the Sagami Sea in 1930 by my friend Dr. Torsten Gislén, who very kindly placed them at my disposal. This material, however, proved to contain only the well known species *Goniocidaris mikado, G. biserialis, Rhopalocidaris rosea*, and *Stylocidaris Reini*.

I have further had an opportunity of examining in the Zoological Laboratory, Leiden, the material of Cidarids (and other Echinoids) collected in the Malay Archipelago by my friend Professor H. Boschma during the "Willibrord Snellius" Expedition in 1929—30. As no dredgings or trawlings were undertaken in deep water it was hardly to be expected that new or rare forms would be contained in this collection. The more agreeably surprised I was in finding in this collection a large fine specimen of a new Cidarid allied to *Phyllacanthus*, but representing a separate subgeneric or generic type. This new form is, however, not included here. The description thereof will appear in the Reports of the said expedition.

The report on this rich material of Cidarids, partly new, partly insufficiently known, forms the main part (I) of the present paper. To this are added (II) some remarks on fossil Cidarids.

I beg to express here my sincere gratitude for all the help received; from the Governments of Java and Mauritius, from Dr. Cyril van Bonde, Director of the South African Fisheries Survey, Dr. K. H. Barnard, Assistant Director of the South African Museum, Dr. E. C. Chubb, Director of the Durban Museum, and Captain E. Pace of the "Disa"; further to Dr. Torsten Gislén and Professor H. Boschma for placing their material at my disposal. But above all my thanks are due to the Carlsberg Fund and the Rask-Ørsted Fund for the grants enabling me to undertake the said voyage and thus to bring together this highly valuable new material.

I.

Notes on some recent Cidarids.

The species mentioned here are the following:

1. *Histocidaris elegans* (A. Agassiz).
2. *Goniocidaris balinensis* n. sp.
3. *Stereocidaris squamosa* Mrtsn.
4. — *excavata* n. sp.
5. *Cidaris cidaris*, var. *meridionalis* Mrtsn.
6. *Tretocidaris spinosa* Mrtsn.
7. *Acanthocidaris curvatispinis* (Bell).
8. — *maculicollis* (de Meijere).
9. *Stylocidaris badia* (H. L. Clark).
10. — *bracteata*, var. *mauritiana* n. var.
11. — *cingulata* n. sp.
12. *Kionocidaris striata* n. g., n. sp., with var. *teretispina* n. var.
13. *Eucidaris clavata* Mrtsn.
14. *Prionocidaris pistillaris* (Lamk.).
15. *Chondrocidaris gigantea* A. Agassiz.

Literary references are not given under the various species. I have thought it sufficient to give reference to the place where they are mentioned in my Monograph, complete lists of literature being given there.

1. **Histocidaris elegans** (A. Agassiz).

Monograph of the Echinoidea I. Cidaroidea, p. 72.

During a visit to Cape Town in 1929—30 I found exhibited in the South African Museum a Cidarid which was at once seen to be a *Histocidaris*. Unfortunately the specimen was without locality, but Dr. K. H. Barnard told me that there was no doubt that it belonged to the "Pieter Faure" collections and thus had been taken somewhere in the S. African seas. Not being able to undertake a careful study of the specimen there, I asked Dr. Barnard to send it to Copenhagen to me after my return from the voyage, which he did. I have thus had an opportunity of studying the specimen at leisure, and have come to the result that, in spite of some minor differences, it is to be referred to the species *Histocidaris elegans* (A. Ag.).

The specimen is a large one, measuring 66 mm h. d., 25 mm v. d. There are only 9—10 I. A. plates. The character of the test is as in typical *H. elegans*. The primary spines are rather stout, ca. 3.5 mm in diameter; none of them are complete. The large pedicellariæ are of the type shown in Pl. LXXVI, 10 of the Monograph.

What gives this specimen a rather unusual appearance for a *Histocidaris elegans* is the stoutness of the primary spines; also the somewhat smaller number of I. A.

contributes to give the specimen a somewhat coarser aspect than is usual in *H. elegans*. But as the species is, on the whole, rather variable, these small differences cannot afford sufficient reason for distinguishing this specimen as a separate variety of *H. elegans*, at least not for the present. If, when one day a richer material comes to hand, it be found that the characters here pointed out are constant, it may be better to regard it as a distinct variety — as also other forms now referred to *H. elegans* may ultimately prove to represent distinct varieties (cf. Monograph, p. 77). But that is for the future to decide.

To find this species in S. African Seas is not surprising, as it is otherwise so widely distributed in the Indo-Pacific region. But it would seem probable that it has been taken in the more northern parts of the S. African Seas, off Natal, where so many other Echinoderms of the tropical seas have been found.

2. **Goniocidaris balinensis** n. sp.

Pl. I, figs. 1—5; Pl. XI, fig. 7; Pl. XIII, figs. 11—14.

h. d.	v. d.	Apical system	Peristome	Number of		Longest spines
				I. A.	A. pro I. A.	
30 mm	22 mm	13 mm (43.3 % h. d.)	11 mm (36.6 % h. d.)	7—8	10—11	56 mm
24 -	16 -	11 - (45.8 % - -)	10 - (41.7 % - -)	6—7	10—11	50 -

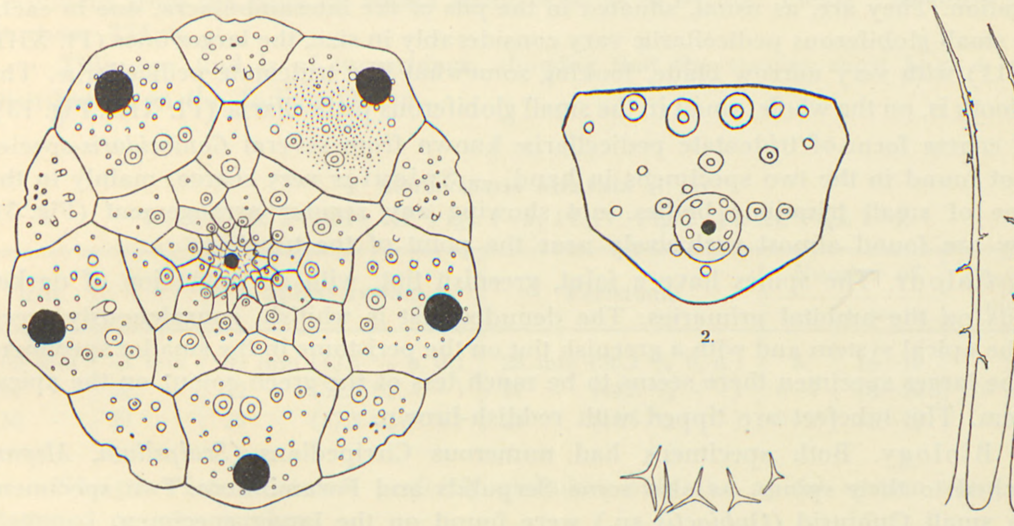
Test flattened above and below, sides subvertical; circumference round. Ambulacra distinctly sinuate. Interporiferous zone twice the width of a pore zone, sloping very gently towards the midline. Marginal tubercles rather widely separated, the inner part of the ambulacral plates covered with small tubercles of uniform size, irregularly arranged. Horizontal sutures distinctly grooved; median suture rather distinctly naked and also somewhat sunken (Pl. XI. Fig. 7).

Interambulacra. Areoles rather deep, only the two proximal ones confluent; the wall between them very narrow, except the one between the two uppermost areoles. There is a fairly conspicuous radiating striation in the outer (adradial) half of each areole. The subambital ones slightly transverse oval. No trace of crenulation observable. The median area very narrow, not half the width of an areole, slightly sunken along the midline. The scrobicular tubercles fairly conspicuous, halfmoon-shaped. Outside the scrobicular circle comes a circle of smaller tubercles, about half the size of the scrobicular ones, and then some few miliary tubercles fill up the rest of the space, leaving no naked median line, but only a small, but distinct groove or pit at the median end of each horizontal suture; no deepening at the outer, adradial end of these sutures. At the adradial side of the areoles there is hardly room for any tubercles outside the scrobicular circle.

The apical system a little less than half h. d., subpentagonal, almost flat. Ocular plates all insert; their sides rather conspicuously sinuate. Genital plates with 2—3 larger tubercles on the inner part, otherwise covered with several small tubercles.

A rather broad naked border on both genital and ocular plates. The genital openings large, near the outer edge. The specimen from which the figure of the apical system was drawn, is probably a female, in spite of the fact that its genital pores are distinctly smaller than those of the other specimen[1]. (Fig. 1). There are some scattered plates in the membrane covering the genital pore (Fig. 2), but not such a close pavement as is found in *G. florigera* (Monograph, p. 168, fig. 54). The periproctal plates with a larger tubercle at their inner edge.

Peristome somewhat smaller than the apical system, almost flat. There are 12—13 ambulacral plates in a series. The ambulacra do not join proximally, thus



1. 2. 3. 4.

Figs. 1—4. *Goniocidaris balinensis*. 1. Apical system. × 6. 2. Genital plate of female specimen, showing plates in the membrane of the genital pore. × 8. 3. Spicules from tubefeet. × 165. 4. Hairs from primary spines. × 65.

leaving free access to the mouth edge for the interradial series, which consist of 8 more or less regularly arranged plates.

The primary spines have a well developed basal disk, usually confined to the aboral side of the spine. Beyond the basal disk more or less numerous coarse thorns, which show no arrangement in longitudinal series; the basal ones are not widened so as to form repetitions of the basal disk. The shaft does not attenuate towards the point, where it widens into a distinct, star-shaped crown, which is the largest on the apical spines. The shaft may be slightly downward curving. The surface of the shaft is (in intact spines) covered by a coat of rather long, fine, non-anastomosing, somewhat thorny hairs (Fig. 4). The oral primaries are rather coarsely serrate; the third or fourth one is transitional to the ambital spines.

[1]) As the specimen had been dried before I noticed the difference in the size of the genital pores of the two specimens, I could not ascertain the sex of the specimen with the smaller pores.

Secondary spines. The scrobicular spines are 3 mm long, scarcely narrowing towards the straight cut end, which is, particularly in the larger specimen, somewhat thickened. They are slightly concave on the outer side, as seen in side view, a little thorny at the base. The marginal ambulacral spines are 2 mm long, much narrower than the scrobicular spines, likewise a little thorny at the base. At the proximal end of the ambulacra they are somewhat widened and excavate at the point. The miliary spines are very minute, not granule-like (Pl. XIII. Fig. 12).

Pedicellariæ. The large globiferous pedicellariæ almost spheroid, as is typical of *Goniocidaris.* The valves (Pl. XIII. Fig. 14) have scarcely any tubeshaped prolongation. They are, as usual, situated in the pits of the interambulacra, one in each. The small globiferous pedicellariæ vary considerably in size, the larger ones (Pl. XIII. Fig. 11) with very narrow blade, looking somewhat like tridentate pedicellariæ. The endtooth is, on the whole, small in the small globiferous pedicellariæ (Pl. XIII. Fig. 13). The coarse form of tridentate pedicellariæ known from several *Goniocidaris*-species is not found in the two specimens in hand. — Spicules very scarce, mainly in the shape of small triradiate bodies, not showing any regular arrangement (Fig. 3). They are found almost exclusively near the point of the tubefeet.

Colour. The spines have a faint, greenish tint, with an indication of darker bands on the ambital primaries. The denuded test is whitish, conspicuously green on the apical system and with a greenish tint on the peristome in the smaller specimen. In the larger specimen there seems to be much less of the green colour on the apical system. The tubefeet are tipped with reddish-brown.

Biology. Both specimens had numerous Cirripedians (*Scalpellum, Alepas*) attached to their spines, as also some Serpulids and Foraminifera. Two specimens of a small Ophiurid (*Ophiactis* sp.) were found on the larger specimen.

Occurrence. The two specimens were taken in one and the same haul in the Bali-Sea, at 7°30′ S. 114°30′ E. ca. 150 m, on a sandy-muddy bottom, 11/IV. 1929, on board S. S. "Dog".

Remarks. This species is the nearest related to *Goniocidaris florigera,* from which it is, however, distinguished at a glance by the colour of its primary spines. A notable difference from *florigera* is also the larger number of ambulacral plates on the peristome, 12—13, against only 8—9 in the said species. It also differs markedly from it in the shape of the apical disks, which in the present species are regularly star-shaped, in the other species eccentric, shield-shaped disks. There is then no doubt that we have here another distinct species of the genus *Goniocidaris,* so richly represented in the Malay Archipelago.

In the "Siboga" Echinoidea de Meijere records an isolated spine of *Goniocidaris florigera* from the Bali-Sea, 298 m ("Siboga", Station 12). I had an opportunity of seeing this spine when studying the Goniocidarids for the Monograph and came to the result that it might well be an old spine of *G. florigera,* (Monograph, p. 171). This new *Goniocidaris*-species having now been found very near the locality, where the said spine was found, it becomes much more probable that it belongs to this latter species, with the spines of which it has likewise much resemblance. But a definite result can scarcely be arrived at. The main thing is that *G. florigera* is not actually known from any other place than off the Kei Islands, where the two known specimens were taken, one by the "Challenger" the other by the Danish Expedition to the Kei Islands.

3. **Stereocidaris squamosa** Mrtsn.

Monograph of the Echinoidea I. Cidaroidea, p. 245.

One specimen in poor condition, but otherwise in perfect accordance with the specimens from the Saya de Malha Bank, was taken by the "Pickle", 32 miles E. of Durban, 374 m.

This new find is of importance, showing that the species must have a wide distribution in the Indian Ocean.

4. **Stereocidaris excavata** n. sp.

Pl. II. Figs. 1—2; Pl. III. Figs. 1—5; Pl. IV. Fig. 2; Pl. XI. Figs. 1—2.

h. d.	v. d.	Apical system	Peristome	Number of		Longest spines
				I. A.	A. pro I.A.	
69 mm	54 mm	30 mm (43.5 °/₀ h. d.)	25 mm (36.2 °/₀ h. d.)	8	18—19	?
61 -	44 -	32 - (52.5 °/₀ - -)	27 - (44.3 °/₀ - -)	6—7	18—19	70 mm
55 -	40 -	26 - (47.3 °/₀ - -)	23 - (41.8 °/₀ - -)	6—7	18—19	?

S h a p e of t e s t almost perfectly globular, only the apical system somewhat flattened or even sunken.

A m b u l a c r a rather conspicuously sinuate, even down to the peristome, particularly in the smallest specimen. In the largest specimen they are almost straight at the aboral end. Interporiferous zone about twice, in the largest specimen even a little more than twice the width of a pore zone. Marginal tubercles not very prominent, contiguous, forming a quite regular series throughout in the largest specimen, whereas in the smallest there is a slight irregularity near the peristomial edge, some of the marginal tubercles being pushed inwards. The space inside the marginal tubercles is completely filled with secondary tubercles, not distinctly serially arranged, in the largest specimen; in the smallest, where these tubercles are less numerous, those along the marginal series form rather distinct longitudinal series. The interporiferous zone is slightly sunken towards the midline, more so in the largest specimen. Pore-zones not much sunken. In the largest specimen the inner pore is distinctly the larger. The wall and ridge not much raised (Pl. XI. Figs. 1—2).

I n t e r a m b u l a c r a. The areoles are deeply sunken, widely separated, at most the two proximal ones confluent. The scrobicular edge is not at all raised, the scrobicular tubercles — which are conspicuously larger than the surrounding tuberculation and the marginal ambulacral tubercles — being placed halfway down the areole.

The boss is very low. There is no trace of crenulation. The median area is, in the largest specimen, as broad as an areole, in the smaller somewhat less. The tuberculation is very close and uniform, leaving no naked or sunken median line; but there are a number of horizontal lines across the area, from areole to areole, producing an arrangement of the tubercles in more or less regular horizontal series. Also on the outer side of the areoles such horizontal lines are distinct in the largest specimen, and there may also be some lines radiating from the upper side of the upper areoles. Pits (impressions for the large globiferous pedicellariæ) are distinct along the upper horizontal sutures — there may be a whole series of them — and may also occur along the vertical suture.

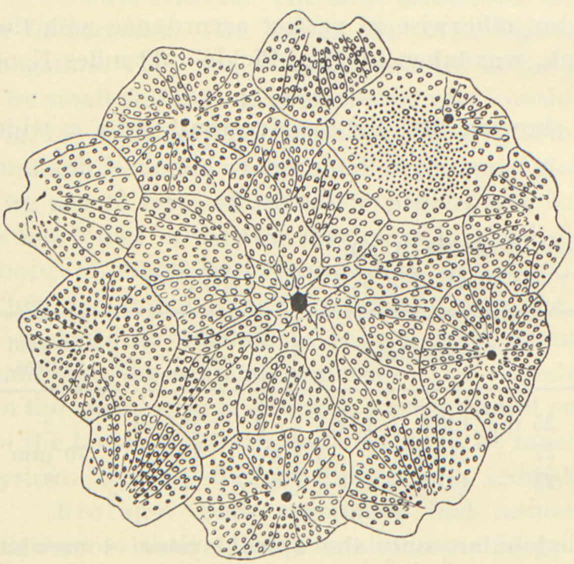


Fig. 5. Apical system of *Stereocidaris excavata*. ♀ × 2.6.

The apical system is very peculiar in the genital and ocular plates, as well as the outer periproctal plates, being conspicuously concave or rather excavate (Pl. III. Fig. 2). This is very pronounced in four of the specimens in hand, less so in the largest specimen. The oculars are all rather broadly insert. The genital plates not very large, particularly in the smallest specimen not much larger than the oculars. The genital pores are situated about in the middle of the plate, on a fairly conspicuous elevation; they are of moderate size in the female, very small in the male. Radiating lines produce a more or less conspicuous linear arrangement of the tubercles which are very close-set and of uniform, small size (Fig. 5).

The peristome is almost pentagonal, slightly elevated. There are ca. 18—20 ambulacral plates in a series; the pores form a single series, with a little irregularity here and there. The interradii are covered by a great number of small plates, arranged in transverse rows of 3—4 plates, or — in the largest specimen — not at all arranged in transverse rows, a feature rather unique in Cidarids. The interradial plates do not reach the mouth-edge.

Primary spines slender, cylindrical, with ca. 12 finely serrate, low ridges, the surface between the ridges covered by a close coat of branching, anastomosing hairs. Towards the point the ridges become somewhat more prominent, the point being thus fluted, but — on the upper spines — not crown-shaped widened. There is a conspicuous, shining, white neck, about twice the length of the collar, which latter distinctly increases in thickness towards the rather inconspicuous milled ring. The subambital primaries may be more conspicuously widened in the point; the oral primaries are simple, more or less flaring at the point. The transition to the ambital spines is very gradual.

Secondary spines. The scrobicular spines are strongly appressed, in accordance with the position of the scrobicular tubercles. They are rather thick, 4—5 mm long, slightly narrowing towards the point which is, on the whole, square cut. They are generally more or less chisel-like excavated at the point. The marginal ambulacral spines are of the same main shape, only shorter, ca. 2—3 mm. The miliary spines are scale-like, appressed, evidently without ampullæ. The transition from the scrobicular to the miliary spines very abrupt. The miliaries remain of the same small size to the very edge of the peristome.

Pedicellariæ. The large globiferous pedicellariæ are rather numerous and conspicuous, rising above the close covering of squamiform secondary spines. They may particularly form a conspicuous line along the upper horizontal sutures. Both globiferous and tridentate pedicellariæ very closely resemble those of *Stereoc. microtuberculata* (Monograph, Pl. LXXXII. 2—4). — Spicules of the tubefeet of the usual Cidarid type.

Colour of the denuded test a creamy white; there is a faint greenish tint on the apical system. The primary spines also of a creamy-white colour, only the collar is brownish. The scrobicular and marginal ambulacral spines are of a greenish-olive colour.

Occurrence. The specimens in hand were taken off E. London, S. Africa, at a depth of ca. 120 metres, by Captain E. Pace of the trawler "Disa", who very kindly sent me these and several other interesting species of Echinoderms. I beg herewith to express my very great indebtedness to Captain Pace, whose interest in these forms also previously resulted in the discovery of a fine new Echinoderm, the seastar *Anthosticte Pacei*, which I described in my paper "On some Echinoderms from S. Africa" (Ann. Mag. Nat. Hist. 9. Ser. XVI. 1925).

It can scarcely be doubted that the large test of a S. African *Stereocidaris* figured in the Monograph, Pl. XXVII. Fig. 4 (p. 270) belongs to this species.

Anomalies. Besides the three specimens described above there are two more specimens which are more or less anomalous. Both of them have the periproct raised into a rather high rounded cone, which has much the appearance of a transformation due to some parasite, of which I have, however, been unable to find any trace on the dried specimens. In both of them also the upper part of the test is misshapen on one side.

Affinities. It is beyond doubt that this species is very nearly related to the Japanese species *Stereocidaris microtuberculata* (Yoshiwara) (cf. Monograph, p. 257). The characters of the apical system and peristome, however, offer such marked differences from the said species that it seems quite necessary to regard them as separate species. Also in the secondary spines there is a marked difference, these having in *microtuberculata* a very well developed ampulla, whereas in the S. African form there is — judging from the dried specimens in hand — no such ampulla. Then the fact that one is known from the Japanese seas only, the other from S. African seas, is against regarding them as identical. If ultimately *St. microtuberculata* should be found to occur also in the Indian Ocean (or *St. excavata* be found to be distributed also over the Indian Ocean) it might perhaps be preferable to regard the S. African form merely as a local variety of *microtuberculata*; but with our present knowledge it seems to me the only justifiable course to regard it as a distinct species.

5. **Cidaris cidaris, var. meridionalis** Mrtsn.

Monograph of the Echinoidea. I. Cidaroidea, p. 298.

Six fine specimens were taken 2 miles E. of Bay Point, St. Helena, in 480 m. 24/II. 1930. They are perfectly conform with specimens from the Bay of Biscay, and I can thus have no doubt in referring them to this variety.

Considerable zoogeographical interest attaches to this find, the said variety being thus found to be distributed over the whole Eastern part of the Atlantic, from the Bay of Biscay to St. Helena. I may also mention here, quite preliminarily, that several other Echinoderms of the N. E. Atlantic were found during my researches at St. Helena in February 1930.

6. **Tretocidaris spinosa** Mrtsn.

Pl. IV. Figs. 6—12, 15; Pl. XIII. Fig. 3.
Monograph of the Echinoidea. I. Cidaroidea, p. 317.

This species was found to be quite common at depths of ca. 50—60 metres along the N. W. coast of St. Helena, particularly off Jamestown, where it was found in all sizes from fully adult and old, worn specimens down to quite small ones. The largest was 56 mm h. d., thus not quite as big as the one of 57 mm from Ascension mentioned in the Monograph, p. 317. But this, evidently, is about the maximum size of this species. Specimens of a size of ca. 50 mm h. d. generally look old and worn.

The type specimen, of 49 mm h. d. has 9—10 plates in each interambulacral series. This is rather unusual, specimens of that size having generally only 8 interambulacral plates in a series; but I have one specimen of 48 mm h. d. with 9—10 interambulacral plates, and in a specimen of 53 mm h. d. there are even 10—11 interambulacral plates.

Very noteworthy is the variation in the length of the primary spines. In adult specimens they are mostly about equal to the horizontal diameter of the test, but sometimes they are up to twice the diameter of the test. On the other hand they may be much shorter than the diameter, thus in a specimen of 48 mm h. d. they are only ca. 34 mm long. This difference in the length of the spines becomes the more conspicuous through the fact that the longer spines are on the whole more slender than the shorter ones, and the terminal widening either absent or much less conspicuous than in the short form of spines. In the more short-spined forms the spines are often distinctly cup-shaped (Pl. IV. Figs. 6—12), recalling, in fact, the spines of the fossil *Cyathocidaris cyathifera* (Agass.) (Monograph, p. 484, fig. 150. 1), which may indicate that the fossil genus *Cyathocidaris* is a near relation of *Tretocidaris*. — Such short, cup-shaped spines may also occur singly in specimens with the other spines long and slender.

The peculiar double tubercles on the upper interambulacral plates found in the largest specimen (Monograph, p. 319, Pl. LXVII. 9) are not seen in any of the present specimens. It is therefore beyond doubt that this duplication is only an anomaly.

In the description of the ambulacra (Monograph, p. 317) it is stated that "in the specimens there is, however, at the ambitus, more or less regularly a second inner tubercle higher up on the plate, obscuring thus the regular series arrangement". It should, of course, have been "in the larger specimens". Otherwise I have nothing to add to the description of the test given in the Monograph.

Tridentate pedicellariæ are exceedingly scarce, in by far the majority of the specimens entirely absent. They are very much like those of *Tr. Bartletti*, only the slight widening of the edges in the proximal part of the blade, rather characteristic of the latter (cf. Pl. 17. 1 of my paper "On some West Indian Echinoids". Bull. U. S. Nat. Mus. 74, 1910) is not found here (Pl. XIII. Fig. 3).

The colour of the denuded test is usually a light pinkish-red, the apical system of a more intense red-brown colour.

The smallest specimen found is 7 mm h. d., with 4—5 I. A. The genital pores appear at a size of ca. 15 mm h. d.

The young specimens with the rather conspicuously brownish banded spines show a considerable general resemblance to the young specimens of *Stylocidaris badia*. But under the microscope they are very easily distinguished, particularly by the characteristic large globiferous pedicellariæ which are well developed already in the youngest specimens.

A very curious anomaly was found in a primary spine which ends in three points, there being two small side branches, each ending in a small crown like the normal point (Pl. IV. Fig. 15).

From the rich material of this species now in hand from the type locality, St. Helena, it appears that the specimens from Ascension and those from St. Helena are identical, the peculiar features in which the type-specimen differed from the Ascension-specimens (Monograph, p. 319—320), viz. the more numerous coronal plates and the terminal widening of the primary spines in the type-specimen, being only individual variations. Only I find the secondary spines of the St. Helena specimens on the whole darker than those of the Ascension specimens, and also the primary spines more distinctly banded in the adult Ascension specimens. At most the Ascension specimens can be regarded as a local colour variation.

7. Acanthocidaris curvatispinis (Bell).

Pl. V. Figs. 1—5; Pl. XI. Fig. 4; Pl. XII. Fig. 8.
Monograph of the Echinoidea. I. Cidaroidea, p. 323.

My hope of getting fresh material of this splendid, but rare and little known Cidarid by the investigations off Mauritius was only partly fulfilled. In spite of all efforts only some young specimens, five in all, two of them broken, were obtained off Port Louis, at depths of ca. 200 m. Like *Chondrocidaris gigantea* and *Prionocidaris pistillaris* it must evidently be rare, or perhaps occur in more isolated spots difficult to find, not scattered all over the bottom, as is the case with *Stylocidaris badia*. Although the two specimens previously known were taken on hooks by fishermen fishing in deep water outside the reef, it seemed to be entirely unknown to the fishermen of Mauritius at present; but then there is not so much deep-sea fishing done now as there was in former times.

h. d.	v. d.	Apical system	Peristome	Number of I. A.	Number of A. pro I. A.	Longest spines
22 mm	13 mm	10 mm (45.5 % h. d.)	9 mm (40.9 % h. d.)	6—7	10—11	55 mm
21 -	12 -	9.5 - (45.2 % - -)	8 - (38.1 % - -)	6—7	10—12	50 -
15 -	8.5 -	7 - (46.6 % - -)	6 - (40 % - -)	5—6	9—10	55 -
15 -	9 -	7 - (46.6 % - -)	5.5 - (36.6 % - -)	5—6	9—10	50 -
15 -	8.5 -	7 - (46.6 % - -)	6.5 - (43.3 % - -)	5—6	9—10	38 -

In general these specimens fit very well with the description given in the Monograph (loc. cit.). Only some minor differences, due to the different age, are to be noticed.

In the ambulacra the inner series of tubercles is not yet complete, the tubercle having appeared mostly only on one side, more or less alternating (Pl. XI. Fig. 4). The primary interambulacral tubercles are conspicuously crenulate, not only on the adapical side.

The apical system (Fig. 6) is distinctly elevated, forming a rounded cone. Already in the youngest specimens the oculars are all insert. The tubercles along the inner edge are elongate, which becomes the more conspicuous by their greenish colour against the whitish ground colour of the plate. The genital pores are beginning to appear in the youngest specimens. In these specimens there are 7—8 ambulacral plates in a series on the peristome, and 2—3 interradial plates.

The primary spines are, in the three smallest specimens, of a very light colour, whitish with conspicuous bands of reddish-brown; in the two larger specimens they are darker, but still distinctly banded, in the largest one also with numerous small spots of the same reddish-brown or purplish colour. In all the specimens the collar is thus spotted, the spots alternating with the white elevations on the longitudinal ridges. The secondary spines are whitish, with only a narrow, faint, greenish midline.

The denuded test is whitish, with a slight greenish tint, particularly distinct between the upper areoles and on the apical system. The interporiferous zone of the ambulacra greenish-olive.

Of pedicellariæ only the small globiferous form is found, and a few tridentate ones; these latter present a rather characteristic appearance on account of the broad space devoid of holes along the margins (Pl. XII. Fig. 8).

The spicules of the tubefeet are more thorny than in *A. maculicollis*, more of the usual Cidarid type. The genital organs are, as in *maculicollis*, slender tubes with some long nearly smooth spicules (cf. Monograph, fig. 96, p. 331). The long and straight genital duct is mailed with thick, fenestrated plates. Also the Stewart's organs are thickly studded with irregular, triradiate spicules. Spicules of intestine as in *A. maculicollis*.

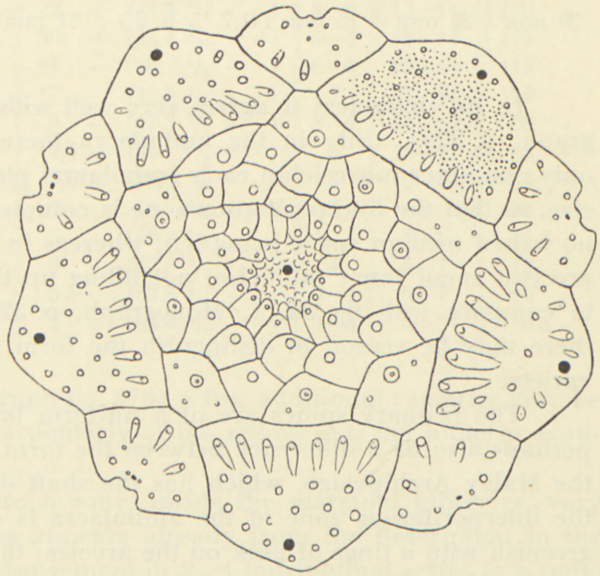


Fig. 6. Apical system of *Acanthocidaris curvatispinis*. × 8.

8. **Acanthocidaris maculicollis** (de Meijere).

Pl. V. Fig. 6; Pl. XI. Fig. 5.

Monograph of the Echinoidea. I. Cidaroidea, p. 329.

On a visit to Durban in August 1929 I found in the Museum there a specimen of an *Acanthocidaris*, unfortunately in a poor state of preservation and without exact locality. But it must have been taken off the S. African coast, probably off Natal. As I could not there undertake a more detailed examination of the specimen, I asked the Director of the Durban Museum, Dr. E. C. Chubb, to let me have the specimen sent to Copenhagen for study, which he very kindly did. I beg here to express my cordial thanks for this favour.

On studying the specimen more closely I found to my surprise that it was not, as might be expected, the Mauritius-species, *A. curvatispinis*, but *A. maculicollis*. This species was hitherto known from the Sagami Sea, the Bonin Islands and the Malay Archipelago; Koehler ("Investigator" Echinoidea. III. p. 23) has recorded it from the Indian Ocean, but without definite locality. It is then of considerable interest now to have it from off the African coast — proof that it must be distributed all over the Indo-Pacific Region, from Japan to the African Coast.

The specimen has the following dimensions:

h. d.	v. d.	Apical system	Peristome	Number of I. A.	Number of A. pro I.A.	Longest spines
36 mm	22 mm	15 mm (41.7 % h. d.)	14 mm (38.8 % h. d.)	7—8	12—13	95 mm (broken)

In its characters it agrees very well with the description of the species (Monograph, p. 329). Only in the ambulacra there is a marked difference, there being only one inner tubercle on each ambulacral plate, at the lower corner, of rather large size, so that the interporiferous zone is completely filled up by these inner tubercles, no naked median space being left, whereas in a large specimen from Amboina there are two small inner tubercles, not filling up the interporiferous zone (Pl. XI. Fig. 5 to compare with fig. 92. 1, Monograph, p. 326). If this difference proves constant there may be reason to distinguish the form from the Indian Ocean as a separate variety.

The primary spines are of a uniform brownish colour, not banded; this may perhaps also be a difference between the form from the Indian Ocean and that from the Malay Archipelago, which has the shaft distinctly banded. On the denuded test the interporiferous zone of the ambulacra is dark olive, the interambulacra faintly greenish with a tinge of pink on the areoles; the apical system a darker greenish olive. The specimen is a male, the pores being small as in fig. 94, Monograph, p. 330. Of pedicellariæ only a few samples of the small globiferous form could be found.

As no figure exists of the denuded test of adult specimens of this species, I give here a figure of the present specimen, with the test partly denuded.

9. **Stylocidaris badia** (H. L. Clark).

Pl. IV. Figs. 1, 16; Pl. VI; Pl. IX. Figs. 1—3; Pl. XII. Figs. 9—10.

Monograph of the Echinoidea. I. Cidaroidea, p. 376.

A very rich material of this species was collected at Mauritius, off Port Louis, at depths of ca. 200—300 metres outside the reef. It was evidently quite common, nearly every haul bringing specimens up, sometimes as many as 8—10 at a time. Also all different sizes were represented, from quite young ones to such as are evidently old and have reached their full size, their spines being much overgrown with sponges, Bryozoans, Foraminifera, worm-tubes, and other foreign organisms.

As hitherto only the five specimens mentioned in the Monograph (p. 376) were known it may be desirable to give here measurements of a number of specimens of the largest and the smallest sizes; measurements of specimens of medium size (38—25 mm) are given in the Monograph.

The specimen of 58 mm h. d. is the largest of all and evidently represents about the maximum size to which the species grows.

h. d.	v. d.	Apical system	Peristome	Number of		Longest spines
				I. A.	A. pro I.A.	
58 mm	38 mm	28 mm (48.3 % h. d.)	25 mm (43.1 % h. d.)	9	13—14	112 mm
55 -	37 -	26 - (47.3 % - -)	22 - (40 % - -)	8—9	13—14	135 -
49 -	35 -	24 - (49 % - -)	22 - (44.9 % - -)	8—9	13—14	100 -
46 -	30 -	22 - (48 % - -)	20 - (43.4 % - -)	6—8	13—14	115 -
45 -	32 -	21 - (46.6 % - -)	18 - (40 % - -)	8—9	13—14	115 -
41 -	27 -	19 - (46.3 % - -)	17 - (41.5 % - -)	7	12—14	110 -
19 -	10 -	10 - (52.6 % - -)	8 - (47.5 % - -)	5—6	10—12	60 -
16 -	8.5 -	8 - (50 % - -)	7.5 - (46 % - -)	5	10—11	63 -
14 -	7.5 -	7.5 - (53.6 % - -)	7.5 - (53.6 % - -)	5	10—11	49 -
12.5 -	7.2 -	7 - (56 % - -)	7 - (56 % - -)	5	8	20 -
10 -	5 -	5.5 - (55 % - -)	5 - (50 % - -)	4—5	7—8	21.5 -
8 -	4 -	5 - (62.5 % - -)	5 - (62.5 % - -)	4	6—7	13 -
6.5 -	3.2 -	3.5 - (53.8 % - -)	3.5 - (53.8 % - -)	3—4	6—7	12 -
4.5 -	2.5 -	3 - (66.6 % - -)	3 - (66.6 % - -)	3—4	4—5	6.5 -

To the description in the Monograph (p. 376) a few additional remarks may be made; also some additional figures, particularly of the naked test, not hitherto available, are given (Pl. IX. Figs. 1—3).

The tubercles of the interporiferous zone, inside the marginal tubercles, vary to a rather considerable degree, — as appears already from the description in the Monograph — from a quite regular arrangement in 2—4 longitudinal series to a quite irregular arrangement. There may also, though rarely, be a distinct, naked median space, the more conspicuous because of the white colour of the ambulacral midline.

The crenulation of the upper primary tubercles is rather variable, often it has completely disappeared, particularly in the larger specimens; it is, on the whole, more distinct in the younger specimens. The median interambulacral space may, in the largest specimens, be almost as wide as the areoles; it is almost completely covered with small tubercles.

The genital pores are quite small, also in the females, corresponding to the fact that the eggs are quite small. The pores are about to appear in specimens of ca. 15 mm h. d. In specimens of this size the oculars are still distinctly exsert, or just beginning to touch the periproct. In a specimen of 10 mm h. d. I find, however, Ocular V just in touch with the periproct and Oc. I. nearly so.

In the largest specimens there are ca. 18 ambulacral plates in a series on the peristome, and 8—9 mostly very regular interradial plates. In a specimen of 10 mm h. d. there are 7—8 ambulacral and 3—4 interradial plates. As a rule the peristome is conspicuously conically elevated.

The length of the primary spines varies to a rather considerable degree, as appears rather strikingly from the above measurements, where in the specimen of 14 mm h. d. the longest spines are 49 mm, while in the specimen of 12.5 mm h. d. they are only 20 mm. In a specimen of 34 mm h. d. the longest spines are 85 mm, while in the specimen of the same size recorded in the Monograph the spines reach the length of 103 mm. Such relatively short-spined specimens are, however, exceptional.

As the spines measured are always fully formed, and cannot, therefore, grow any longer, one may perhaps wonder how the spines can attain the much greater length in the larger specimens than do those of the younger specimens. The explanation is the very natural one that the spines which are the longest in the young and the old specimens are not the same. Thus in the specimen of 10 mm diameter the longest spine is no. 4 from below; in the specimen of 19 mm it is no. 5, and in the specimen of 55 mm the longest spine is no. 7. When, however, in this latter specimen spine no. 4 has a length of ca. 50 mm, no. 5 a length of ca. 80 mm, thus rather longer — at least for no. 4 — than what can be accounted for by the normal amount of variation, this must mean that these spines have been regenerated. As a matter of fact, young regenerating spines are often seen among the old spines in adult specimens. Whether the old spines are directly cast off, through autotomy, by the sea-urchin itself, or they are lost through injury of some kind, is, as a rule, not to be ascertained. But that such autotomy does take place is beyond doubt (cf. Monograph, p. 27).

Secondary and miliary spines without glandular ampulla.

The large globiferous pedicellariæ are, on the whole, very scarce, and in adult specimens more often totally absent; in younger specimens they are more common. The tridentate pedicellariæ are richly developed, particularly in the younger specimens; they are in two forms, one with shorter valves, slightly outward curved in the basal part and therefore very widely apart, joining only in the point, the other with the valves curved inward above the base and therefore much less apart (Pl. XII. Figs. 9—10); the valves are also somewhat coarser in the former, in which also the stalk is very much shorter than in the second form. — The spicules of the intestine of the form typical in the genus *Stylocidaris*.

The naked test, when well cleaned with hypochlorite of sodium, is of a creamy white colour, in remarkable contradistinction to the dark colour of the test as covered with its skin and spines; there may be a more or less distinct pinkish tint on the upper part of the corona, particularly in the peripheral part of the areoles. The marginal tubercles of the ambulacra somewhat darker, greenish-olive, the tubercles inside the marginal ones may be pinkish, but generally the interporiferous zone is whitish. The apical system is somewhat darker, reddish-brown or more olive. It is rather more intensely coloured in the young than in the adult specimens.

Several specimens were opened on October 12th and found to be unripe; but it looked as if the eggs would be very small and clear, which might indicate that this species has a pelagic larva. — In the intestine I have found remains of hard-shelled bottom organisms, particularly of Bryozoans; also sponges.

A curious anomaly was observed in a primary spine, it being bifid at the point (Pl. IV. Fig. 16), much like the one of *Schizocidaris assimilis* figured in the Monograph, Pl. XVII. 9.

The species is only known to occur at Mauritius.

10. **Stylocidaris bracteata**, var. **mauritiana** n. var.

Pls. VII—VIII; Pl. IX. Figs. 10—11; Pl. XII. Figs. 3—5, 7.

h. d.	v. d.	Apical system	Peristome	Number of I. A.	Number of A, pro I. A.	Longest spines
45 mm	28 mm	21 mm (46.6 % h. d.)	18 mm (40 % h. d.)	8—9	12—13	91 mm
42 -	28 -	21 - (50 % - -)	17 - (40.5 % - -)	8	14—15	ca. 80 -
39 -	23 -	19 - (48.7 % - -)	15 - (38.5 % - -)	8	14—15	81 -
38 -	22.5 -	18 - (47.4 % - -)	16.5 - (43.4 % - -)	7—8	13—14	86 -
33 -	19 -	17 - (51.5 % - -)	15 - (45.5 % - -)	7	14—15	81 -
32 -	19 -	16 - (50 % - -)	15.5 - (48.4 % - -)	7	13—14	94 -
26 -	15 -	13 - (50 % - -)	11 - (42.3 % - -)	6—7	13—14	73 -

In regard to shape and structure of test and spines this form agrees so closely with the typical *Stylocidaris bracteata*, as described in the Monograph (p. 359) that it would be quite superfluous to give a full description of the present form; it will suffice to state the few points in which there is any noticeable difference.

The size appears to be, on the whole, somewhat larger in the Mauritius-form than in the typical *bracteata*, which latter hardly exceeds 35 mm h. d., whereas the present form attains a size of at least 45 mm h. d., and probably more, since the uppermost spines in the specimen of that size are as yet quite young and undeveloped. In conformity with this larger size the median space of the interambulacra is somewhat wider than in the typical form, and the part adradially to the areoles is broader with more numerous small tubercles, but this difference is simply due to the difference in size.

The only real differences from the typical form are in the colour and in the pedicellariæ. The primary spines are banded on the shaft, and spotted on the collar as in *bracteata*, but whereas the bands and spots are red or red-brown in the typical form, they are brownish-olive in the present form and also the ground colour is greenish, in the typical form cream-whitish or yellowish. The larger primaries are rather distinctly curved (the concavity on the oral side), but this is also indicated in the typical form, only less distinctly on account of the smaller size. The secondary spines are pinkish, more conspicuously so than in the typical form. More conspicuous is, however, the difference in the colour of the naked test. Whereas in the typical form the interporiferous zone of the ambulacra is a dark olive, forming five conspicuous, dark, radiating lines, in the present form the interporiferous zone is a light pinkish. Also the apical system has a faint pinkish tint, not olive-purplish as in the typical form. Further the peristome is simply whitish, whereas in the typical form it has a distinct greenish tint.

As in the typical form there is a conspicuous brownish spot at the median and outer end of each horizontal interambulacral suture and at the corner of each ocular plate; sometimes there is a series of such spots along the interambulacral midline and along the edges of the genital plates. These spots are very resistent and remain distinct even after the test has been cleaned with hypochlorite of sodium.

Large globiferous pedicellariæ, which in the typical form occur rather frequently at the brown spots in the interambulacra, could not be found in any of the specimens at hand of the present form. On the other hand, there is generally found at these spots a peculiar form of tridentate pedicellariæ, short-stalked and with widely gaping valves which, in the larger samples, are coarsely dentate (Pl. XII. Fig. 4); this kind of pedicellariæ is not found in the typical form. Sometimes, however, the usual, more slender-valved tridentate pedicellariæ (Pl. XII. Fig. 3) occur at the brown spots, as elsewhere on the test. This latter form of tridentate pedicellariæ is more like that of the typical form, though in the latter the valves are generally more apart (Pl. XII. Fig. 6); as a rule they are also much smaller in the typical *bracteata*, but they may also here reach a considerable size, up to ca. 1.5 mm length of head, as in the Mauritius-form, only in the latter those of such large size (or even up to nearly 2 mm) are much more common. The irregular globiferous pedicellariæ found in the typical form (Monograph, p. 361, Pl. LXXXV. Figs. 4—5) were not found in the Mauritius specimens.

A parasitic Gastropod (*Mucronalia* sp.) is found rather commonly on this Cidarid, attached at the base of the primary spines, mainly those on the oral side. Also a crab, *Eumedonus* sp., was found on one of the specimens.

13 specimens of this Cidarid were taken at depths of ca. 200—300 metres off Port Pouis, Mauritius, in October 1929. They are all of them very closely alike in all their characters, so that it is quite evident that we have here a very well marked form. It is, in any case, very closely related to *Stylocidaris bracteata;* perhaps it should rather be regarded as a separate species, but as the differences from *bracteata* are rather unimportant, I think it preferable to designate it only as a variety of that species. Whether it is merely a local variety or it is widely distributed over the Indian Ocean remains to be ascertained through future investigations.

11. **Stylocidaris cingulata** n. sp.

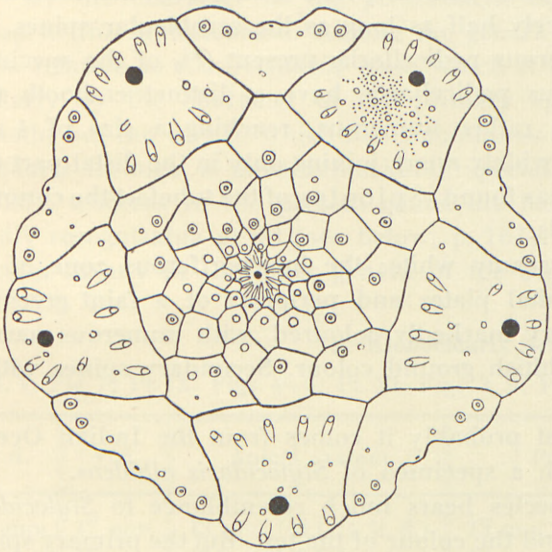
Pl. I. Fig. 6; Pl. XI. Fig. 6; Pl. XIII. Figs. 8—10.

h. d.	v. d.	Apical system	Peristome	Number of I. A.	Number of A. pro I.A.	Longest spines
22.5 mm	13 mm	12 mm (53.3 % h. d.)	11 mm (49 % h. d.)	4—5	14—15	46 mm

Test much rounded, only the periproct conspicuously raised.

Ambulacra rather broad, $^2/_5$ the width of the interambulacra, distinctly sinuate. Interporiferous zone about the width of a pore zone. Marginal tubercles not very prominent, nearly contiguous. A single small secondary tubercle occurs rather irregularly at the lower edge of the plates, often together with a miliary tubercle, the two being sometimes placed so close together as to form one elevation. Median line slightly sunken. The pores are rather distant, the outer one distinctly the larger. The wall is broad, of a somewhat unfinished character, flattened in the lower part, raised, sometimes into a more or less sharp edge, in the upper part; the ridge low. The lower furrow is straight and sharp, a somewhat unusual feature (Pl. XI. Fig. 6).

Interambulacra. Areoles rather large, not at all sunken; the upper ones are widely separated, and even the proximalmost ones are not confluent. No trace of crenulation on the primary tubercles. Scrobicular tubercles not prominent. Median area narrow, only about half the width of an areole; there is thus very little room for secondary tubercles outside the scrobicular circle, there being in the main only a single circle of them, alternating with the scrobicular tubercles; on the adradial



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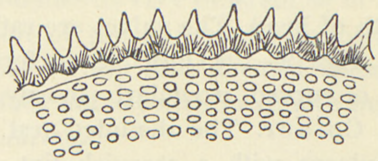


8.

Fig. 7—8. *Stylocidaris cingulata.* 7. Apical system. × 6. 8. Part of section of primary spine. × 100.

edge there are no secondary tubercles outside the scrobicular circle. The scrobicular circle of the uppermost fully formed plate is somewhat drawn out adapically.

Apical system (Fig. 7). The genital plates are rather narrow, corresponding with the unusual width of the ocular plates, which latter are all broadly insert. Tubercles are, on the whole, scarce on the apical system. There is a series of tubercles along the outer edge of the oculars, and some conspicuously elongate tubercles along the inner and outer edge of the genital plates. Otherwise these plates are almost bare, excepting the madreporite, which has several tubercles scattered among the hydropores. Genital pores of moderate size, not close to the edge; very probably the specimen is a female, and apparently it is fullgrown. Periproct conspicuously elevated, with numerous well-sized plates, most of them with a single tubercle each.

Peristome somewhat smaller than the apical system, slightly raised. There are 12 ambulacral plates in a series, the pores forming a regular series. 5—6 regularly shaped interradial plates, the series widely excluded from the mouth edge.

Primary spines up to twice as long as the diameter of test, tapering gently to a simple point. They are very smooth; in the specimen in hand they are rather worn, but in places they show the surface intact; it is very finely striated, without any hairs. As seen in sections (Fig. 8) the striæ are so close together that there is no room for hairs. Towards the point of the spine there are usually some low, quite smooth ridges. The collar is about one millimetre long, slightly widening towards the inconspicuous milled ring. There is no distinct neck. The oral primaries are quite simple, scarcely flattened or widened, but with rather conspicuous ridges, particularly spine no. 2 is distinctly ridged in its distal half.

The secondary spines are 3—4 mm long, of the normal, simple shape, flattened, slightly narrowing towards the rounded point. The marginal ambulacral spines of the same main shape, scarcely half as long as the scrobicular spines.

Pedicellariæ. No large globiferous pedicellariæ present ($^3/_4$ of the specimen was denuded). The small globiferous pedicellariæ have a distinct endtooth (Pl. XIII. Fig. 8). Tridentate pedicellariæ rather numerous, reaching a size of 1 mm length of head. The valves are rather widely apart, joining only in the distal part (Pl. XIII. Figs. 9—10). Only this one form was found. Spicules of the tubefeet the common type of curved, irregularly thorny rods.

Colour. The denuded test a creamy white; the interporiferous zone of the ambulacra with a greenish tint. Genital plates and periproct of a faint greenish-olive tint. The primary spines are very markedly coloured, with numerous narrow bands of red, alternating with the whitish ground colour. Secondary spines with a narrow median greenish-olive stripe.

The locality is uncertain. Most probably it comes from the Indian Ocean, as indicated by its lying together with a specimen of *Stylocidaris albidens*.

Remarks. Superficially this species bears much resemblance to *Stylocidaris tiara*, both in regard to the structure and the colour of the test. But the primary spines are so strikingly different from those of that species, and, indeed, of any other known species, that there cannot be the slightest doubt that we have here a distinct new species. Also the tridentate pedicellariæ differ conspicuously from those of *St. tiara*, as seen on comparing the figures here given (Pl. XIII. Figs. 9—10) with those of the latter species (Monograph, Pl. LXXXV. 24—25).

In the absence of large globiferous pedicellariæ it cannot be ascertained definitely whether this species belongs to the genus *Stylocidaris*, but its general appearance makes it rather certain that it does belong to that genus. At least, there is nothing to disprove it.

The only other species with similar red bands on the primary spines, *Stylocidaris annulosa* Mrtsn., is in every other regard so different from the present species that it is entirely out of question that there could be any nearer relation between them.

Kionocidaris[1]) n. g.

Pores not conjugate, the wall slightly elevated. Pores on peristome in a single, regular series. Primary tubercles perforate, the upper ones crenulate. Madreporite not enlarged. Primary spines thick, slightly tapering, perfectly smooth, finely striated, with regular series of pores in the outer part of the shaft. Large globiferous pedicellariæ without endtooth; (limb on stalk?). Small globiferous pedicellariæ strongly developed, with small opening and a small endtooth. Tridentate pedicellariæ slender.

Genotype: *Kionocidaris striata* n. sp.

By the character of the pedicellariæ this genus is shown to belong to the group of the *Stylocidarina*. Among the genera of that group it would seem to have some relation to *Centrocidaris*, from which it is, however, distinctly separated, particularly by the character of the primary spines. In both genera the spines are smooth, but the way in which this smoothness is obtained is very different — in *Centrocidaris* through a most remarkable specialisation of the hair-coat (Monograph, p. 426), whereas in the present genus the hair-coat on the fully formed spines is hardly recognisable at all (see below, p. 167). It does not seem to have any nearer relation to any of the other genera of the *Stylocidarina*.

12. Kionocidaris striata n. sp.

Pl. V. Fig. 7; Pl. IX. Figs. 4—6; Pl. XI. Figs. 3, 9; Pl. XII. Figs. 1—2; Pl. XIII. Figs. 4, 6—7.

h. d.	v. d.	Apical system	Peristome	Number of		Longest spines
				I. A.	A. pro I. A.	
1. 27 mm	17 mm	13 mm (48.1 % h. d.)	13 mm (48.1 % h. d.)	6—7	12—13	36 mm
2. 27 -	17 -	12.5 - (45.5 % - -)	12 - (43.6 % - -)	6	12—13	56 -

Specimen no. 1 is the type; specimen no. 2 is the var. *teretispina* Mrtsn.

Test rather low; in the type slightly flattened above, but not below; in specimen 2 also flattened below. Sides beautifully arched. Circumference regularly round.

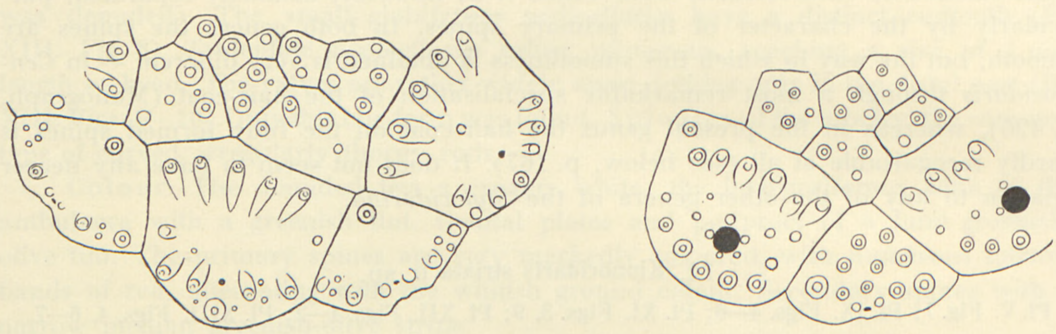
Ambulacra narrow, distinctly sinuate. Interporiferous zone about twice the width of a pore zone. Marginal ambulacral tubercles in a perfectly regular series, fairly prominent, contiguous, somewhat indistinctly mamelonate. The space inside the marginal tubercles very narrow, leaving room only for a single, incomplete series of tubercles, placed now on one, now on the other side of the midline. As a rule there is a miliary tubercle (bearing pedicellariæ) at the lower, inner side of each marginal tubercle. Pore-zone not sunken. The pores are small, equal-sized; the separating wall narrow, slightly elevated; the ridge low, indistinctly set off (Pl. XI. Fig. 3).

Interambulacra. Areoles not at all deepened, well separated, only the two proximal ones confluent; even these latter hardly at all transversely elongate. The two to three uppermost primary tubercles rather large, the following ones diminishing

[1]) ὁ κίων-column.

markedly in size downwards, the proximalmost ones being very small. The two or three upper ones distinctly crenulate on the aboral side. Scrobicular circle not at all raised, the tubercles scarcely larger than the marginal ambulacral tubercles. Outside the scrobicular circle only a few scattered small tubercles, the midline being naked, and also rather distinctly sunken. There are also in the type specimen, at the ambitus, some few small tubercles between the adjoining scrobicular circles on the wall separating the areoles. On the adradial side of the areoles there is scarcely room for any tubercles outside the scrobicular circle. The median area is, at the ambitus, scarcely half the width of an areole.

Apical system. (Figs. 9—10). Oculars all narrowly insert. Both genital and



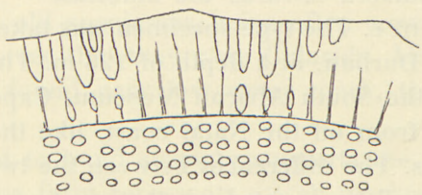
9. 10.

Figs. 9—10. Part of apical system of *Kionocidaris striata*, type specimen (9) and of the var. *teretispina* (10). × 6.

ocular plates in the type specimen rather bare; there is a series of tubercles (spines) along the outer edge of both and along the inner edge of the genital plates, and a single tubercle at the inner end of the ocular plates. Otherwise the plates are bare and there is thus a conspicuous bare belt all round the apical system, interrupted only by the madreporite, which has spines all over. This latter plate is not larger than the other genital plates. In specimen 2 the genital and, particularly, the ocular plates are more closely tuberculate. The tubercles at the inner edge of the genital plates are very conspicuously elongate. Genital pores at a fair distance from the outer edge of the genital plates; they are very small in the type specimen, which must then, evidently, be a male. The size of the pores is so unusually small that they convey the impression that they are just about to be formed; but with the size of the specimen this would mean an appearance of the pores so late as to be perfectly unique in the whole Cidarid family, which is very improbable. (Usually the genital pores appear at a size of 12—15 m h. d., in some forms much earlier). Specimen 2 has genital pores a good deal larger; evidently this is a female. — The periproct is somewhat raised; each plate carries a number of tubercles.

The peristome, which is of the same size as the apical system, is rather conspicuously elevated. There are 10—11 ambulacral plates in a series, and 4—5 interradial plates in a regular series, not reaching the mouth.

The primary spines are comparatively thick and robust, of a very characteristic column-like appearance, tapering gently towards a simple point; they are perfectly smooth (Fig. 11), but longitudinally striated with ca. 25 fine, low ridges without any kind of serrations. Between the ridges the surface of the shaft, in fully formed spines, is very finely porous, the pores being arranged in fairly regular longitudinal series (Textfig. 12; Pl. XI. Fig. 9). In the basal (thickest) part of the shaft the pores disappear. This peculiar pore-structure originates through the fine longitudinal striæ, elevations from the outer layer, joining at more or less regular intervals. In not fully formed spines (best seen in specimen 2) the striæ have not yet united to form the pores; they carry along their free edge numerous fine, hair-like outgrowths; these "hairs" it is which gradually widen and coalesce with those from the neighbour-striæ, leaving holes — the pores — between them. In such not fully formed spines the spaces between the ridges may still be rather deep. At the point of the spines the ridges become somewhat more prominent; the point is, however, not widened; it has a small central peg. Towards the base the spine decreases a little in thickness, but forms no distinct neck; the collar is short, ca. 1 mm long. The milled ring is not prominent. In specimen 2 the primary spines are more slender (and longer).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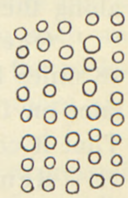

12.

Figs. 11—12. *Kionocidaris striata*. Part of transverse section of primary spine (11). Arrangement of pores on surface of spines (12). × 100.

Oral primaries simple, slightly flattened, striate, but not serrate; transition to the ambital spines quite gradual.

The secondary spines are of quite simple shape, flat, narrowing a little towards the rounded point. The scrobicular spines are ca. 4 mm long, the marginal ambulacral spines ca. 2 mm long. They are not strongly appressed.

Pedicellariæ. The large form of globiferous pedicellariæ is very scarce; only the isolated valves of one sample were found in the type specimen among the pedicellariæ dissolved by the treating of part of the test by means of hypochlorite of sodium. The stalk could not be identified with certainty, and thus it remains uncertain whether it has a limb of free, projecting rods. The valves are small, but of the form typical of the *Stylocidarina* (Pl. XIII. Fig. 6). The small globiferous form is strongly developed, both as regards number and size, up to nearly 1 mm length of head; the stalk varies very considerably in length, from quite short up to 2 mm. The valves (Pl. XIII. Figs. 4, 7) have only a small opening, with a small endtooth. In specimen 2 they are more elongate and with the endtooth more strongly developed and also usually with some serrate crests in the blade, which are not found in the type (Pl. XIII. Fig. 5). The tridentate pedicellariæ reach a considerable size, up to 1.5 mm length of head. They occur in two, not very distinct, forms, one with narrow blade, slightly incurved above the base, the other with somewhat widened blade and not incurved above the base (Pl. XII, Figs. 1—2). In specimen 2 only small samples of the form with the narrow valves were found. The spicules are irregularly spinous rods of the typical Cidarid form.

Colour of the denuded test of the type specimen white, only the upper primary tubercles and the apical system of a more creamy colour. A small dark spot in the middle of the genital plates. Primary spines of the type specimen of a uniform creamy colour, in the second specimen they are more white, with a faint indication of pink bands. The secondaries white, with a narrow median stripe of greenish-olive. In specimen 2 the apical system is a uniform olive colour, a tinge of this colour continuing along the ambulacra towards the ambitus.

Occurrence. The type specimen was taken by the "Pickle" off the Natal coast, 18 miles E. of Durban, at a depth of 126 m. The second specimen, which I received later on from the South African Museum, Cape Town, is labelled only "Durban". That it comes from off the Natal coast, like the type, can hardly be doubted.

Remarks. The differences between the two specimens are rather considerable, so that it may well be doubted whether we have not here in fact two separate species before us. It is particularly in the primary spines that we find noteworthy differences, as described above. As a matter of fact it is only in one of the spines of the second specimen that the pores, so characteristic of the type, are faintly observable. Then the colour of the primary spines and of the test is different from the type; also the globiferous pedicellariæ offer a considerable difference. Thus there is much that speaks in favour of the two specimens representing two different species. It is the fact that there are only two specimens, one of them, specimen 2, being in a rather poor condition, which makes me hesitate in making each of them the type of a separate species. Under normal conditions I should have left them simply in the same species until further material should come to hand and show whether they are really two species or individual variations of the same species. But as we must reckon with the existence of a man like Prof. Embr. Strand, whose main "scientific" activity consists in finding in other people's works descriptions of aberrant specimens, which he then names with his own name attached as the author (nom. nov. Strand) to make himself famous by establishing so many names, I shall think it better to prevent his doing so in this case and shall designate specimen 2 as the type of a separate variety, **teretispina** n. var., leaving it to the future to decide whether it represents only an individual variation (? sexual difference), a variety, or a separate species.

13. **Eucidaris clavata** Mrtsn.

Pl. IV. Figs. 3—5.

Monograph of the Echinoidea. I. Cidaroidea, p. 408.

This species I found to be very common at St. Helena at depths of ca. 20—60 metres, particularly off Jamestown. In places the bottom is here at depths of ca. 20—30 metres covered with large colonies of the sponge *Chondrosia plebeia* O. Schmidt, and this appeared to be a favourite locality for the Cidarid, which was usually found lodging in the larger holes and cavities of the sponge. But the Cidarid was also common on all other kinds of bottom, e. g. among the mussels *Arca* sp. overgrown with *Cirripathes* which cover the bottom in places at depths of ca. 40—50 metres. The specimens found here generally had their spines much overgrown by incrusting Lithothamnions or similar red algæ. Specimens from shallower water usually had their spines much overgrown with various small algæ, old specimens being often covered to such an extent that it was difficult enough to see that they were Cidarids. Also on the rocks specimens of the Cidarid could be found near low water mark, though more exceptionally.

The rich material thus brought to hand strongly supports the view expressed in the Monograph that this St. Helena form represents a well marked species, quite distinct from the West Indian — West African *Eucidaris tribuloides*, characterised above all by its thick, club-shaped, uniformly dark-brownish coloured primary spines. Only in the few specimens from the rocks at low water mark the spines are somewhat more slender than usual, but in these specimens also they are more or less club-shaped, and there can be no doubt that they belong to *E. clavata*, not to *E. tribuloides*.

The largest specimen found measures 51 mm h. d.; this specimen, as also the specimens of ca. 40—45 mm h. d., looks very old and worn, so that a size of ca. 50 mm h. d. is evidently the maximum size of this species. It is quite curious to see in these old specimens among the old spines totally covered by foreign organisms, particularly incrusting Lithothamnions, here and there a quite fresh spine, newly regenerated. In all probability then this species, as is the case in at least some other Cidarids, is able to drop such spines as are too much worn, and to form new ones instead.

The youngest specimen found was 3 mm h. d., with 4 I. A. plates in a series. The specimen of 51 mm h. d. has 9—10 I. A., which is also the maximum number, as is evident from the fact that the spines of the uppermost plates are fully formed, while no sign of young spines is found adapically to them. The genital pores appear at a size of ca. 13 mm h. d.

I have nothing to add to the description given in the Monograph, except that I have now found the tridentate pedicellariæ also. They are, however, exceedingly scarce, not at all represented in by far the majority of the specimens. They are quite like those of *E. tribuloides* (Monograph. Pl. LXXXVI. 16).

A curious anomaly has been observed in some few cases, one or other of the primary spines being bifid (Pl. IV. Figs. 3—5). In one specimen a Polynoid worm was found on an ambulacrum near the peristome, such as was also found on one of the "Scotia" specimens (Monograph, p. 411).

14. **Prionocidaris pistillaris** (Lamarck).

Pl. IX. Figs. 7—9; Pl. XI. Fig. 8.

Monograph of the Echinoidea. I. Cidaroidea, p. 452.

This species was found to occur fairly commonly among the rocks at the breakwater of the Durban Harbour, where it could be collected at good low tide. It is very noteworthy that only this species, not *Pr. baculosa*, occurs here. The latter then evidently has its southern limit farther north; exactly where is not known.

The new material of *pistillaris* thus available fully bears out the result reached in the Monograph (loc. cit.) that *pistillaris* is a distinct species, well separated from *baculosa*. To the characters pointed out in the Monograph I may now add some characters from the test, good preparations of denuded tests being now available (Pl. IX. Figs. 7—9).

In the ambulacra the interporiferous zone is somewhat broader than in *baculosa*, fully twice the width of a pore-zone in *pistillaris*, scarcely twice that width in *baculosa*. More conspicuous is, however, the difference in the interambulacra, the primary tubercles being well separated, even the proximalmost ones, the scrobicular tubercles on the separating wall not smaller than the others, and both circles remaining distinct; in *baculosa* the separating wall is much narrower, and the tubercles thereon markedly smaller than the others (Pl. XI. Fig. 8, to compare with Pl. LIII. 8 and 11 of the Monograph). Also the median area of the interambulacra is somewhat broader than in *baculosa*.

One specimen from Durban is remarkable in its primary spines being flattened in the distal part and slightly widened, so as to be perfectly oar-shaped.

The colour of the denuded test also differs conspicuously from that of *baculosa*. The primary tubercles are a beautiful pink in *pistillaris*, cream-coloured or greenish in *baculosa*. The marginal ambulacral tubercles are of the same light greenish colour as the interambulacra and apical system, the pore zones reddish-brown; in *baculosa* the marginal ambulacral tubercles are dark olive, usually much darker than the test, and the pore-zones more brownish-olive.

During the investigations at Mauritius, spines of *Prionocidaris pistillaris* were usually found in the dredgings in deep water, ca. 200—300 metres, outside the reef, and mostly large and fine samples of spines — but never a living specimen of the sea-urchin itself. This shows that it probably lives in very restricted localities in the deeper water, not scattered all over like *Stylocidaris badia*.

15. **Chondrocidaris gigantea** A. Agassiz[1]).

Pl. III. Fig. 6; Pl. IV. Figs. 13—14; Pl. X. Figs. 1—2.

Monograph of the Echinoidea. I. Cidaroidea, p. 492.

During my visit to Mauritius in September—October 1929 I had the pleasure of dredging two large specimens of this species off Port Louis, a little outside the reef, at a depth of ca. 200 metres. Whereas loose spines were found very often, it was only one haul that yielded any specimens, and that gave both the specimens, hanging in the tangles. Both specimens are very large, larger, in fact, than any specimens hitherto recorded; one of them, 115 mm in diameter of test, is even the largest specimen of any recent Cidarid recorded till now, the largest one hitherto recorded being a *Phyllacanthus irregularis* of 110 mm h. d. in the Western Australian Museum, Perth (Monograph, p. 522).

I shall give here the dimensions of the two specimens.

h. d.	v. d.	Apical system	Peristome	Number of		Longest spines
				I. A.	A. pro I.A.	
115 mm	73 mm	48 mm (41.7 % h. d.)	39 mm (33.9 % h. d.)	10—11	15—16	125 mm
104 -	67 -	41 - (39.4 % - -)	38 - (36.5 % - -)	9—10	15—16	150 -

The largest specimen, which had lost several of its spines, has been denuded, and I think it desirable to give here some figures of this magnificent Cidarid, the more so as the denuded specimen (belonging to the Museum of Comp. Zoology) represented in the Monograph, Pl. LXIV. 1—2 is much smaller, 73 mm h. d., and, being incompletely cleaned, does not show all the details (particularly the apical system) as clearly as desirable.

It is to be noted that the apical system is distinctly sunken; in the other specimen it is not sunken, the aboral side being simply flattened. The small elevated part on the madreporite is an anomalous growth, probably due to some parasitic organism. In the interporiferous zone of the ambulacra the tubercles are very numerous, ca. 12 in a double series between each two opposite marginal series at the ambitus. There are ca. 18 ambulacral plates in a series on the peristome. The skin between these plates was thick and raised, almost cushion-like.

On p. 494 of the Monograph it is mentioned that "on a spine from the large specimen in the Paris Museum the hairs in places form a very dense velvety coat, especially on the basal part". This I find to be the case also on some of the spines of the present specimens; there can thus be no doubt that this is a character of the

[1]) In the Monograph of the Cidaridæ, p. 492, the author name of *Chondrocidaris gigantea*, A. Agassiz, is given in parenthesis, as is also that of *Chondrocidaris brevispina*, H. L. Clark, p. 497. This is, of course, a printers error for which I can offer no better excuse than that I have overlooked it. These author names should be without parentheses.

fully developed and untouched spine (Pl. IV. Figs. 13—14). It is only in the basal part of the spine, about the third part of its length, that this thick, velvety or rather woolly hair-coat is developed; then the hairs decrease rapidly in length and become quite short and simple, as shown in Fig. 157, p. 494 of the Monograph. The long hairs of the basal part of the shaft — which cover also the thorns almost to their point — are up to 2 mm long, very slender, perfectly smooth, ending in a simple point or rarely irregularly bifurcate at the point. They are more or less undulating, sometimes bent in the middle, the neighbouring hairs following each other fairly closely in their undulations or bendings so as to form a close, regular coat (Fig. 13). At the base they are slightly thickened.

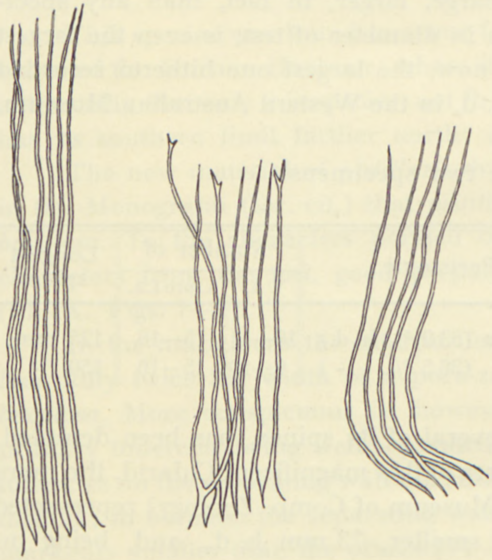


Fig. 13. Hairs from primary spines of *Chondrocidaris gigantea*. × 40.

Having found this structure to be characteristic of the spines of *Chondroc. gigantea*, we may conclude with full certainty that the thick red coat of hairs on the basal part of the shaft of the spines in *Chondroc. brevispina* is likewise the normal hair-covering of these spines, not an epizoic sponge, as it has been assumed to be (cf. Monograph, p. 498).

In none of the specimens in hand there could be found any large globiferous pedicellariæ, this kind of pedicellariæ thus being as yet unknown in the present species.

On the larger specimen were found a pair of specimens of an *Ophiothela* (probably *Ophiothela danæ* Verrill) on the base of the primary spines, inside the scrobicular spines.

The two specimens in hand corroborate the result reached by both H. L. Clark and myself, after the examination of the previously known material of this species, that it is impossible to distinguish the Mauritius specimens from those from off the Hawaiian Islands, so that, in spite of the remarkable discontinuous distribution, we must recognise the two so widely separated populations as belonging to one and the same species.

In this connection it is of considerable interest that the "Dana" Expedition found in a dredging off New Caledonia (St. 36112. 21°20′ S. 165°24′ E. 200 m) a fragment of a Cidarid spine which can with almost full certainty be identified as *Chondrocidaris gigantea;* it is merely somewhat more slender than any of the spines at my disposal. This would seem to show that the species must occur also at New Caledonia, and is thus not confined solely to the Hawaiian Islands and Mauritius.

A few additional remarks may be made here.

The Stewart's organs. When speaking of these organs in the Monograph, p. 35, I regret having entirely omitted to mention that Ludwig, in his paper "Über Asthenosoma varium Grube und über ein neues Organ bei den Cidariden" (Zeitschr. f. wiss. Zool. XXXIV. 1879, p. 29), without knowing the paper by Stewart (On certain organs of the Cidaridæ. Trans. Linn. Soc. 2. Ser. Zool. I. 1877), where these organs were first described, gave a careful description and a very good figure of these organs in *Eucidaris tribuloides*, which he designates as "radiäre Blindsäcke des Kauapparates". He has found these organs well developed in several other Cidarids which he could examine — and states (as I have also found — cf. my Report on the Echinoidea of the Swedish S. Polar-Expedition, p. 17) that in *"Goniocidaris" canaliculata* they are entirely devoid of calcareous spicules, which are otherwise generally very well developed (of the triradiate type). Also in *Diadema setosum* he has found similar, only simply sac-shaped organs. As to their function he makes no suggestion.

I must take this opportunity of mentioning and correcting a very curious — and perfectly inexcusable — lapsus which has slipped into my "Handbook of the Echinoderms of the British Isles", p. 262 and 278 (also in my book "Echinodermer" in "Danmarks Fauna", p. 166), viz. that the Echinothurids have Polian vesicles — instead of Stewart's organs! Of course, I never dreamt of claiming that these organs of the Echinothurids should have anything at all to do with Polian vesicles; it is nothing but a lapsus, caused probably by the sausage-shape of these organs in the Echinothurids, giving them a certain superficial resemblance to the Polian vesicles of Holothurians, but not a bit more excusable for that.

In speaking of the Stewart's organs of Cidarids I have mentioned (Monograph, p. 35) the erroneous statement by A. Agassiz ("Revision of the Echini, p. 694) of the occurrence of gills in Cidarids. In this connection I ought to have mentioned that the Sarasins also, in their "Anatomie d. Echinothuriden u. die Phylogenie d. Echinodermen" (Ergebnisse Naturwiss. Forschungen auf Ceylon I. 3. 1888, p. 134) suggest that the Cidarids may have gills in the young stages, likewise regarding, as did Agassiz, the five interradial slits in the peristomial membrane as "hypothetische Kiemeneinschnitte". There is not the slightest foundation for this suggestion of the Sarasins, no more than there is for the statement of Agassiz. There is no trace of gills in Cidarids, neither in the young nor in the adult specimens.

Cidaris grandis Stewart. My friend Professor H. L. Clark has called my attention to the fact that mention is not made of this name in my Monograph. I regret having overlooked this name, about which there is, otherwise, nothing to say but that it is a nomen nudum, and that there is no possibility, nor, indeed, any desirability of finding out which Cidarid is meant by it.

Enemies of Cidarids. On p. 41 of the Monograph I have mentioned the various cases known of enemies attacking Cidarids. To these a new and interesting case may be added. Professor R. Legendre, Director of the Biological Station at Concarneau, has informed me that a specimen of *Lophius piscatorius* has been taken there, which had "dans sa gueule un *Cidaris cidaris* brisé, ses piquants en partie broyés". Also the seastar *Palmipes membranaceus* has been observed by him to be eaten by *Lophius piscatorius.*

Stylocidaris affinis. In the Monograph, p. 340, it is stated that the largest specimen on record of this species is 43 mm in horizontal diameter. I was, therefore, very surprised in receiving from Professor Mercier, Caën, a specimen of 54 mm h. d. In his paper, mentioned below, p. 175 "Etude des variations chez *Dorocidaris papillata* Leske et *Dorocidaris affinis* Philippi" Mercier records a still larger specimen, of 61 mm h. d. These specimens are from the Mediterranean, where this species evidently, on the whole, reaches a larger size than it does in the West Indies, another fact speaking in favour of regarding the West Indian form as a separate variety (cf. Monograph, p. 340).

II.
Notes on some fossil Cidarids.

1. On some Cidarid names.

It appears to be a matter of considerable difficulty to attain conformity in the nomenclature of fossil and recent Cidarids (and other Echinoids also, of course). In my Monograph of the Cidarids I made great efforts to build up a sound basis for a conform nomenclature — but already now divergent views have been expressed in this regard. It is the names *Dorocidaris* — *Cidaris* — *Stylocidaris, Plegiocidaris* — *Histocidaris*, and *Phyllacanthus* — *Leiocidaris* which have come under consideration.

First I may say in general that there ought not to be any dispute about the fact that complete knowledge can be gained only of the recent forms. It is only from these that we can judge of what characters must form the foundation of classification. It has been demonstrated incontestably that, besides the characters of the test — which must, of course, remain of foremost importance — the microscopical characters of spines and pedicellariæ are of great classificatory value, and that without taking those characters into consideration it would be quite impossible to obtain a reasonable classification of the numerous recent forms. Consequently it must be acknowledged that the fossil forms in which we do not — except in very exceptional cases — know those finer microscopical structures, are only insufficiently known, and that in those, unfortunately very numerous, cases where the test structures and the spines do not afford sufficient evidence for the classificatory position, the true generic position of such species remains problematic. This refers e. g. to the numerous "*Plegiocidaris*"-species, which have only this in common that they have crenulated tubercles and non-conjugate pores.

There is, of course, nothing to blame the authors on fossil Echinoids for, when they unite all such forms in one "genus", since it is impossible to get hold of other characters by which to separate them further. Only it must be claimed that they agree that such "genera" are unnatural, mere lumber-rooms into which are thrown all such forms that cannot be further distinguished, and particularly it must be claimed that the specialists in fossil Echinoids are not competent, on the basis of the insufficiently known fossils, to interfere with the classification of the recent forms, all the characters of which are available to us.

In a paper "Etudes des variations chez *Dorocidaris papillata* Leske et *Dorocidaris affinis* Philippi. Notes échinologiques IX." (Bull. Inst. Océanogr. No. 570. 1931) by J. Mercier the genus *Stylocidaris* is not recognised but united with *Dorocidaris,* as the characters of the test do not warrant a generic distinction between them; also the characters of the pedicellariæ "assez relatives du reste" are regarded as insufficient for generic division "à plus forte raison pour la classification générale d'animaux dont la majeure partie est fossile et dont le système de vestiture a disparu". A discussion, of course, is hopeless. What has been said above covers the matter. It should only be emphasised that the characters of the pedicellariæ, particularly in the case in question, are decidedly not relative, as anybody who has ever seen a large globiferous pedicellaria of *Cidaris cidaris* (which is the true name of *Dorocidaris papillata*) and of *Stylocidaris affinis* must agree. A glance at these pedicellariæ at once distinguishes the two forms and shows that, in spite of the general resemblance of their test-characters, they are not nearer related to one another.

When MERCIER further speaks of "les difficultés que l'on recontre en n'ayant souvent à sa disposition pour la reconnaissance des Echinides actuels, que des diagnoses portant surtout sur les charactères du système de vestiture" (p. 4) I would remark that he will find all characters, from the test and the "système de vestiture", fully mentioned and figured in my Monograph. If he has not been able to consult this main work on recent Cidarids, he might perhaps rather have omitted criticising what he does not know.

In a paper by MARIA LANDI "Gli Echinidi neogenici di Montegibbio" (Giorn. di Geologia. Bologna. 2. Ser. IV. 1929) the genera *Plegiocidaris*, *Cidaris* and *Dorocidaris* (to mention only the Cidarids) are taken in the same sense as in LAMBERT & THIÉRY's "Essai de nomenclature raisonnée", thus *Plegiocidaris* being stated to be found in recent seas in worldwide distribution and at depths of 200—3550 m, and similarly *Dorocidaris* etc. Particularly *Plegiocidaris* is an obvious case. It has been proved beyond dispute that the typical *Plegiocidaris* is so strikingly characterised by its peculiar peristome and the peculiar shape of its spines that it can only be designated as nonsense to refer the recent *Histocidaris*- and *Aporocidaris*-species to it, as is done by LAMBERT & THIÉRY. But although Dr. LANDI has seen my Cidarid Monograph and quotes it, she cannot have taken the trouble to look at the status of this genus, but simply continues the absurdities of LAMBERT & THIÉRY. No wonder she finds that "tutti questi generi hanno una distribuzione cosi ampia, che uno studio su questa base non condurrebbe a resultati degni di nota". From my paper "The Geographical Distribution of Cidarids" (Arch. Zool. Ital. XV. 1930), as also from the chapter "Zoogeographical Distribution" of my Monograph (p. 529—541), Dr. LANDI will gather that the study of the geographical distribution of Cidarids, when properly distinguished, does give noteworthy results — so noteworthy, indeed, that we must see herein a very strong support and a direct proof of the correctness of my classification of the Cidarids.

I would add the remark that the statement of Dr. LANDI (p. 12) that *Dorocidaris margaritifera* Meneghini is so closely related to *Eucidaris tribuloides* that it may be regarded as "una mutazione ascendente" of the latter species, is a very bold assertion, as *Dorocidaris margaritifera* is known only from isolated spines, which are not at all so characteristic as to prove beyond any doubt its close relationship to *Eucidaris tribuloides*. Also the further statement that this latter species is now extinct in the Mediterranean is without any real foundation. There is not the slightest proof that *Eucidaris* *tribuloides* ever lived in the Mediterranean, as the erroneous identifications by COTTEAU and LAMBERT of some isolated spines as belonging to that species (cf. Monograph, p. 407) could hardly be regarded as proof of the former existence of *E. tribuloides* in the Mediterranean.

Quite lately CHECCHIA-RISPOLI ("Illustrazione di alcuni Echinidi del Maestrichtiano della Tripolitania raccolti da Ignazio Sanfilippo". Mem. Soc. Geol. Ital. I. 1931, p. 8) in discussing the names *Phyllacanthus* — *Leiocidaris* follows LAMBERT & THIÉRY in regarding the former name as not acceptable and adopts instead the name *Leiocidaris* Desor.

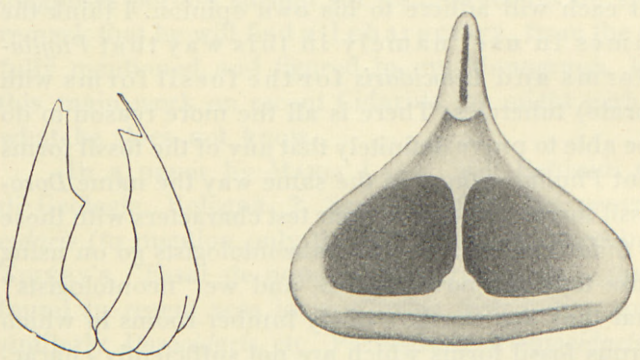
It would be quite useless here to reassume the discussion of these names, as nothing will result from it but that each will adhere to his own opinion. I think the only way will be to keep both names in use, namely in this way that *Phyllacanthus* is used for the recent forms and *Leiocidaris* for the fossil forms with conjugate pores and smooth (perforate) tubercles. There is all the more reason to do so, since we shall probably never be able to prove definitely that any of the fossil forms are really congeneric with the recent *Phyllacanthus*. In the same way the name *Dorocidaris* may be kept in use for the fossil forms agreeing in their test characters with those of the recent *Dorocidaris papillata* = *Cidaris cidaris*. Also let palæontologists go on using *Plegiocidaris* and *Cidaris* in the sense they are now used to, and we "neontologists" will take these designations for what they are worth, namely lumber-rooms in which are thrown together all those numerous fossil forms which are not sufficiently characterised by the characters of their tests and spines and, therefore, for want of the microscopical characters necessary for that purpose, cannot be classified more definitely. But, on the other hand, we neontologists must claim that the palæontologists do not interfere with the nomenclature of the fully known recent forms on the basis of their imperfectly known fossils, introducing changes which, like most of those introduced by LAMBERT & THIÉRY, are not only absurd nonsense but also give rise to no end of confusion and do great harm to science. This applies to the Cidarids as well as to those of the other regular Echinoids in which the microscopical characters of pedicellariæ and spicules are of primary classificatory importance. Neglect of these characters has led e. g. to refer to the genus *Toxocidaris* the common mediterranean sea-urchin designated by all students of recent Echinoids *Paracentrotus lividus*, an absurdity which can result only in most regrettable confusion.

As for *Plegiocidaris* it would be preferable to use this name only for such species as can be said with a reasonable degree of certainty to be congeneric with the genotype, *Plegiocidaris coronata*, so well characterised by its pluriseriate peristomial ambulacral plates and its peculiar clubshaped primary spines (cf. Monograph, p. 475), and establish a new "genus" for the numerous other forms referred to *Plegiocidaris* on account of the insufficiently distinctive characters: crenulate tubercles, non conjugate pores. But I leave that to the palæontologists.

2. On some pedicellariæ of fossil Cidarids.

In mentioning (Monograph, p. 33) the various records of pedicellariæ of fossil Cidarids I regret having overlooked the record by G. STEFANINI (Fossili terziari della Cineraica. Paleontogr. Italica. XXVII. 1921, p. 110. Tav. XVI. 1. c.) of the find of a tridentate pedicellaria in *Porocidaris Schmideli* (Münst.). I reproduce here (Fig. 14) the figure of it given by STEFANINI; it does not give any information beyond the fact that it is a pedicellaria.

In fig. 20 d—f, Monograph, p. 33, I have reproduced some figures of a very remarkable Cidarid-pedicellaria, after Dr. BRÜNNICH-NIELSEN (Nogle Echiniderester fra Danmarks Senon og Danien. Medd. Dansk Geol. Foren. VI. 29, 1925. Pl. I. 20—21, 23), stating that, unfortunately, it cannot be said with certainty to which species they belong. This still holds good; however, a reasonable suggestion can be made as to the Cidarid to which these pedicellariæ belong. Dr. BRÜNNICH-NIELSEN informs me that he finds them only in such places where *Tylocidaris baltica* is found, and he thinks they must belong to that species. This seems not at all improbable, and it would be very satisfactory to find this unique kind of pedicellariæ connected with such an isolated type of Cidarids as is *Tylocidaris*.



14. 15.

Fig. 14. Pedicellaria of *Porocidaris Schmideli*. After Stefanini. (Enlargement not stated).

Fig. 15. Valve of large globiferous pedicellaria, seen from the inside, of *Tylocidaris baltica* (?). × 20.

BRÜNNICH-NIELSEN designates it as a tridentate pedicellaria. This, however, is not correct. Through the kindness of Dr. BRÜNNICH-NIELSEN I have had an opportunity of examining more closely a few valves of these pedicellariæ, and one of them is in so fine a condition as to show the true character of this pedicellaria (Fig. 15). In the remarkably small blade there is a very distinct longitudinal slit, sharply limited below by an elevated, rounded ridge. This slit cannot be anything but the opening for the poison gland of a globiferous pedicellaria. We have thus here a very interesting type of a large globiferous pedicellaria, quite different from those of any recent Cidarid. The general shape of these pedicellariæ recalls the globular large globiferous pedicellariæ of the genus *Goniocidaris;* it is also worth recalling that a long, narrow, slitlike opening is found in the small globiferous pedicellariæ of some Goniocidarids, particularly in the genus *Schizocidaris*. But, as a whole, a type of pedicellariæ like this fossil form is unknown in recent Cidarids. By the rather isolated position of *Tylocidaris* (imperforate tubercles!) it would be quite natural to find its pedicellariæ also to be of a very unusual character. Of course, there is no certainty as yet that these pedicellariæ do belong to *Tylocidaris;* but, apart from the coincidence emphasised by Brünnich-Nielsen of their occurrence in layers where *Tylocidaris baltica* is predominant, there is another fact in favour of this suggestion. My friend, Dr. J. P. J. Ravn, has called my attention to some shallow depressions occurring sometimes among the secondary tubercles on the upper part of the test in *Tylocidaris baltica*. The idea easily suggests itself that these are places where the large, globiferous pedicellariæ were seated, as we may also in *Goniocidaris* and *Stereocidaris* find similar impressions of the large, globiferous pedicellariæ.

I have also examined the remarkable small pedicellariæ from Herfølge, figured by Dr. Brünnich-Nielsen, reproduced in the Monograph, p. 33, fig. 20 g. Though the figure is correct enough, it does not give the full shape of this pedicellaria quite correctly. It is perfectly evident that the point of the three valves is broken off; therefore they have ended in a point, not abruptly cut off, as the figure shows it, and the pedicellaria has thus been much like other Cidarid pedicellariæ of long and slender type, as e. g. of *Stereocidaris sceptriferoides*, var. *lanceolata* (Monograph, Pl. LXXXI. 9). I can scarcely doubt that the same will apply to the pedicellaria of "*Anaulocidaris*" *Faurai* represented in the same figure 20, c, of the Monograph, from Lambert's "Revision des Echinides fossiles de la Catalogne" (1927).

3. The genus **Ancylocidaris** A. K. Miller.

I 1929 A. K. Miller published in the American Journal of Science, 5. Ser. Vol. XVIII, p. 334—336 a paper "Ancylocidaris, a new Echinoid genus from the Sundance of West-Central Wyoming" containing the description of a small Echinoid from the locality named, belonging to the Jurassic period. The single specimen known is only 9 mm in diameter; it is a bare test of depressed spheroidal shape on which no trace of tubercles or other surface structures is seen, only the limits of the coronal plates and the ambulacral pores being distinct. (Fig. 16). The interambulacral plates have a very characteristic downward bend; the ambulacral plates are simple, with the pores close to the outer edge. It is named *Ancylocidaris spenceri*, and is referred to the Cidaridæ, with which Jackson appears to agree.

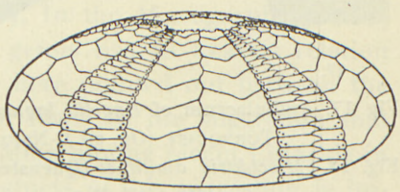


Fig. 16. *Ancylocidaris spenceri*. × 6. From A. K. Miller.

I cannot agree at all that this little Echinoid is to be referred to the Cidarids. The depressed shape of the test is most unusual for a Cidarid. The number of interambulacral plates, 15 in a specimen of 9 mm diameter is as extraordinary for a Cidarid as is their shape; and even if it is only an inner impression of the test (?) one would also expect to find at least a faint indication of the large primary tubercles which must have existed if it be a Cidarid; but not a trace of them is seen. Likewise the shape of the ambulacral plates, their produced median end, and the markedly oblique position of the pores, is very unlike any Cidarid, as also the fact that only three ambulacral plates correspond to each interambulacral plate, is very unusual.

Thus, as there is nothing in its known features which speaks for its being a Cidarid, whereas all the characters observable are most un-Cidarid-like, I cannot accept this form as a Cidarid. To what family it should be referred it is impossible to tell definitely in view of the absence of nearly all distinctive features. The arrangement of the pores in a regular single series rather indicates an Orthopsid — but until its characters become better known, its affinities must remain problematic.

4. The genus Engelia Tornquist.

This genus was established by TORNQUIST in his paper "Die Diadematoiden des württembergischen Lias". (Zeitschr. d. Deutschen Geol. Gesellsch. 60. 1908, p. 408) for *Cidaris amalthei* Quenstedt. He points out that this Diadematid is unique in uniting the imbrication of the coronal plates of palæozoic Cidarids with an ambulacral structure of diadematoid type, each plate having two pairs of pores.

LAMBERT & THIÉRY in their "Essai de nomenclature raisonnée des Echinides" (p. 195) accept the genus as belonging to the tribus *Orthopsinæ* of the Pedinids, but are of opinion that TORNQUIST mixed up two different types in it, so that in reality only the ambulacral structure of the genus is known.


17.

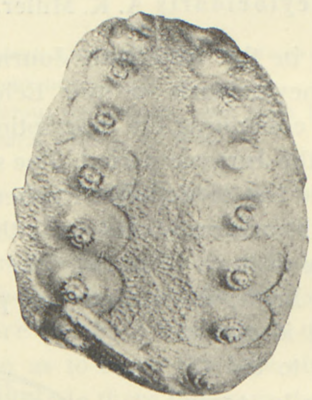

18.

Fig. 17. Ambulacrum of *Engelia laqueata* (Quenst.). From TORNQUIST (Op. cit.). Natural size.
Fig. 18. *Miocidaris amalthei* (Quenstedt). From LÖRCHER (Op. cit.). Natural size.

Recently ERNST LÖRCHER ("Neue Seeigelfunde aus dem Jura Württembergs". N. Jahrb. f. Mineral. Beilageband 64. Abt. B. 1930, p. 262) maintains the genus *Engelia* in the original sense of TORNQUIST, but as a Cidarid, related to *Miocidaris* but differing from that genus by its ambulacral structure "denn uns scheint die Ausbildung der Ambulacralzonen (as shown in the figures 3—4, Pl. XVI of TORNQUIST's paper —) Grund genug zu sein, um diese Gattung von *Miocidaris* zu trennen".

Assuredly this ambulacral structure is reason enough to separate *Engelia* from *Miocidaris*, so much, indeed, that it does not belong to the Cidarids at all, but to the Diadematids or Pedinids — as quite rightly seen by TORNQUIST and by LAMBERT &

THIÉRY. On the other hand, it is equally true that the interambulacra and the spines show it to be a Cidarid. The solution of the problem is, as well seen by LAMBERT & THIÉRY, but evidently not understood by LÖRCHER, that two entirely different forms are confounded by TORNQUIST in his diagnosis of the genus *Engelia*, viz. the interambulacrum of *Cidaris amalthei* Quenstedt, which is decidedly that of a *Miocidaris*, and the ambulacrum of a Diadematid (or Pedinid), figured by TORNQUIST. I reproduce here the fine interambulacrum figured by LÖRCHER, and the ambulacrum after TORNQUIST (Figs. 17—18).

To prove that these two widely different structures belong together it would be an absolute requirement to find them in direct connection, but this has (of course) never been done. In the original description of *Cid. amalthei* by QUENSTEDT (Die Juraformation. 1858. p. 198. Taf. 24. 42—44) only part of two interambulacral plates and some fragments of primary spines are figured. In the same author's "Petrefactenkunde Deutschlands" III. 1872—1875, p. 155 he suggests that the ambulacrum figured on Taf. 67. fig. 98, under the name of *Cidaris laqueata*, belongs together with the interambulacrum and spines designated as *Cidaris amalthei*. This suggestion is adopted by TORNQUIST (Op. cit. p. 426) and now again by LÖRCHER — but without any new evidence whatever of their belonging together. I entirely agree with LAMBERT & THIÉRY that two different types are confounded in the "genus" *Engelia*, first by TORNQUIST and now again by LÖRCHER. But I cannot agree with either of these authors in taking *Cidaris amalthei* Quenst. as the type of the genus *Engelia*. As rightly seen by both LAMBERT & THIÉRY and by LÖRCHER it is the ambulacral structure that characterises the genus *Engelia* — it is, as a matter of fact, all that is known of it. But then it must be the *Cidaris laqueata* Quenst., under which name this ambulacrum was originally described, that becomes the type of the genus *Engelia*.

5. The genus **Cyathocidaris** Lambert.

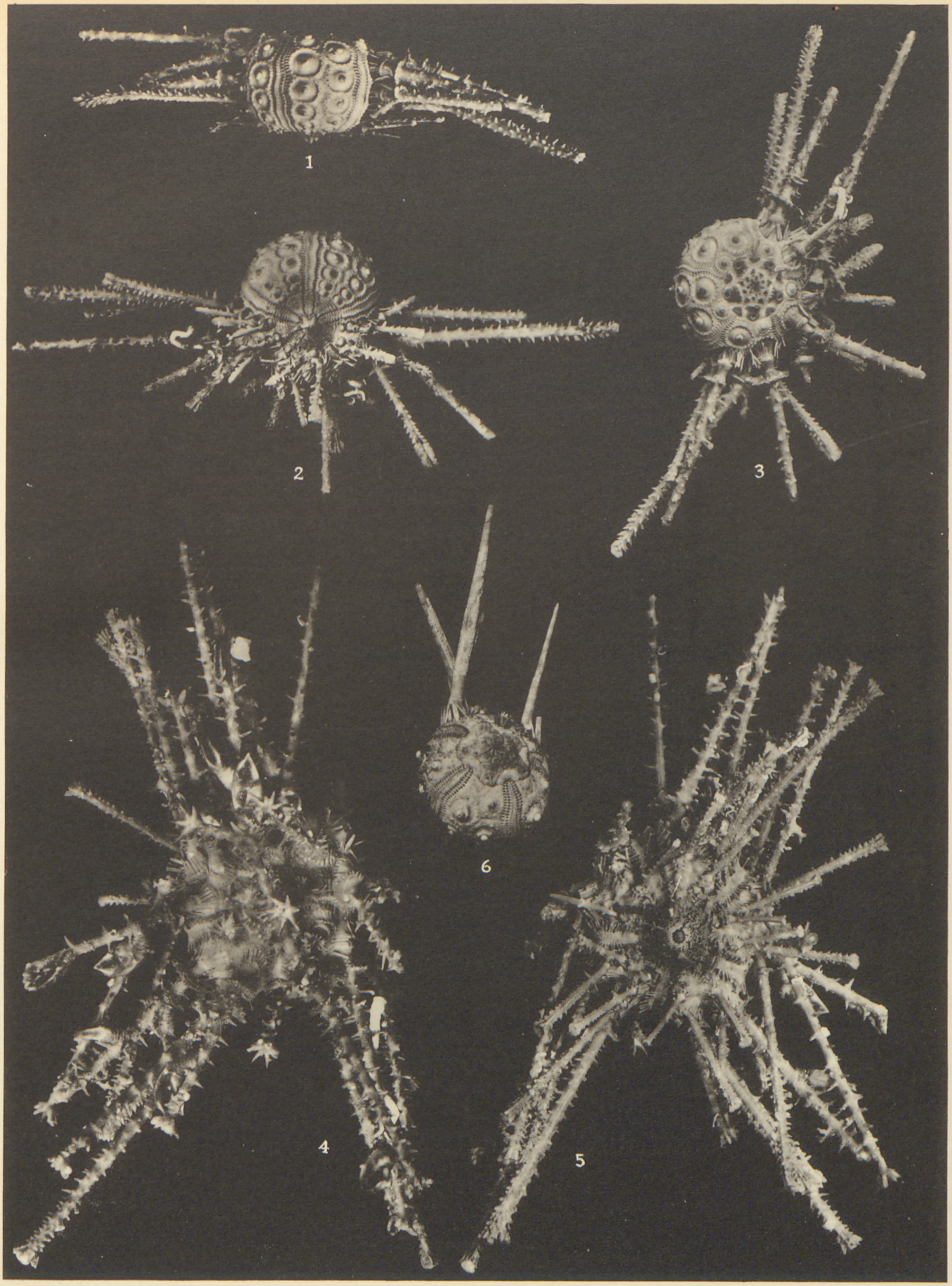
As explained above (p. 155) the primary spines of *Tretocidaris spinosa*, mainly the subambital ones, not rarely assume a shape that strikingly recalls that of the fossil, cretaceous, *Cyathocidaris cyathifera* (L. Agassiz). In the Monograph (p. 484) I have adopted the view of LAMBERT that this fossil genus has its nearest relation among recent Cidarids in *Eucidaris*. The resemblance here pointed out between the *Cyathocidaris* spines and those of *Tretocidaris spinosa* leads to the suggestion that *Cyathocidaris* may more probably have its nearest relation among recent Cidarids in the genus *Tretocidaris*. To give direct proof of the correctness of this suggestion is impossible, at present at least, on account of the insufficient knowledge we possess of the structural details of *Cyathocidaris*. But what we do know of the test structure of *Cyathocidaris cyathifera*, the only species of the genus *Cyathocidaris* of which anything at all is known of the test, is, at least, not opposed to its suggested relation to *Tretocidaris* (cf. LAMBERT. Etude sur les Echinides Crétacés de Rennes- les Bains et des Corbières.

Bull. Soc. Etudes scientif. de l'Aude. T. 22. 1911; p. 45. Pl. II. 24, 27). Since the main character distinguishing *Tretocidaris* from the other genera of the group *Cidarina*, viz. *Cidaris* and *Calocidaris*, is the peculiar reduction into a small pore of the opening of the large globiferous pedicellariæ (cf. Monograph, p. 286, 314), there is no great probability that we shall ever learn how this character was in *Cyathocidaris*. But the fact that it has now been possible to ascertain the main character of the large globiferous pedicellariæ probably belonging to *Tylocidaris*, warns us to be careful and not deny the possibility of discovering the microscopical structures so important to the classification of the Cidarids, also in the fossil forms, and thereby gradually finding out the real affinities of the numerous fossil forms, whose test characters do not afford the clue to their true place in the natural system.

Plate I.

Figs. 1—5. *Goniocidaris balinensis* Mrtsn.
1—3. Paratype; half denuded. Side view (1), oral side (2), aboral side (3).
4—5. Type specimen. Aboral side (4); oral side (5).

Fig. 6. *Stylocidaris cingulata* Mrtsn. Type specimen; half denuded. Aboral side.
All figures natural size.



J. v. Huth fot. Pacht & Crones Eftf. Fototypi.

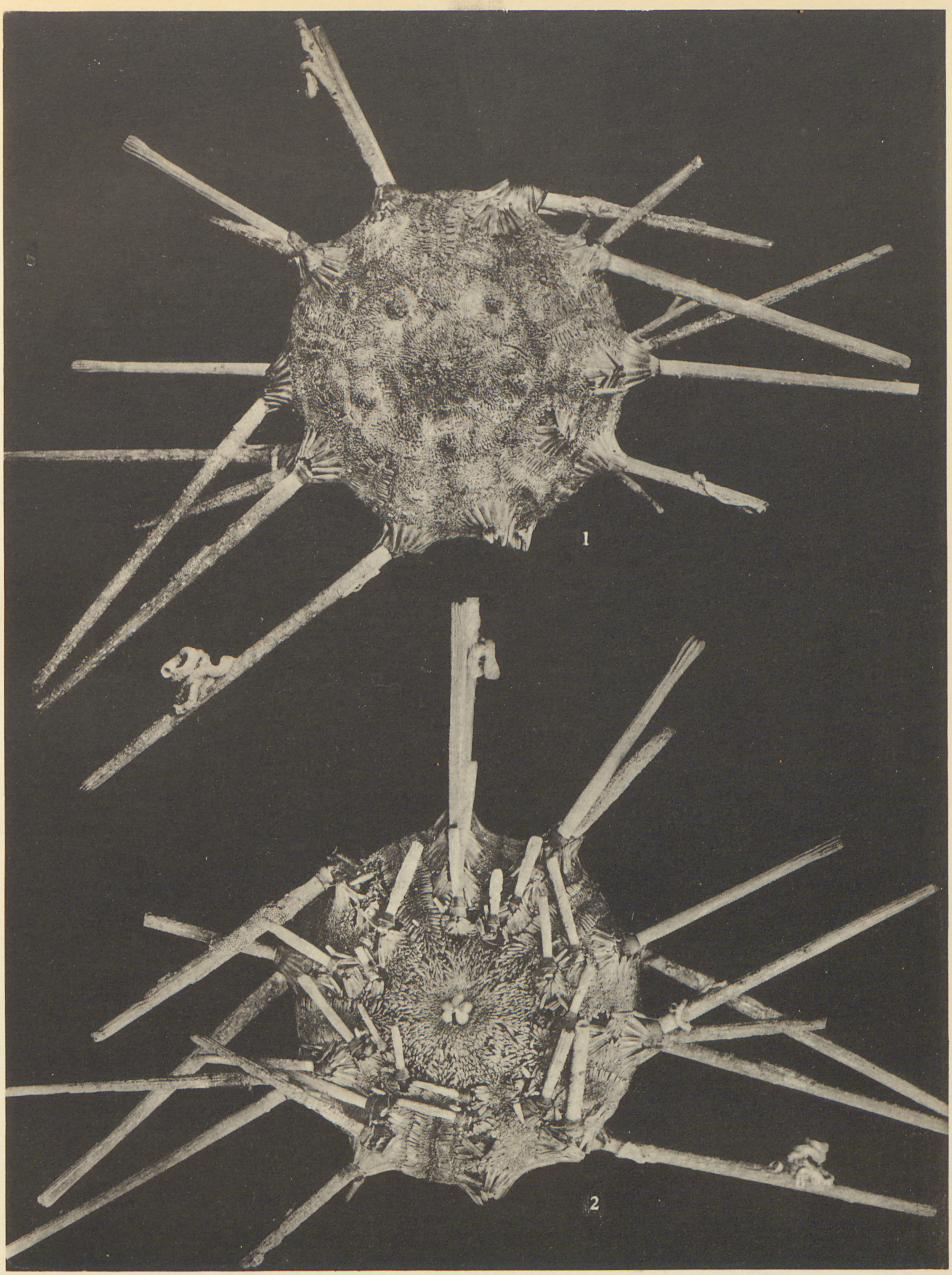
Plate II.

Stereocidaris excavata Mrtsn.

Fig. 1. Large specimen; aboral side.

- 2. Same — ; oral side.

Natural size.

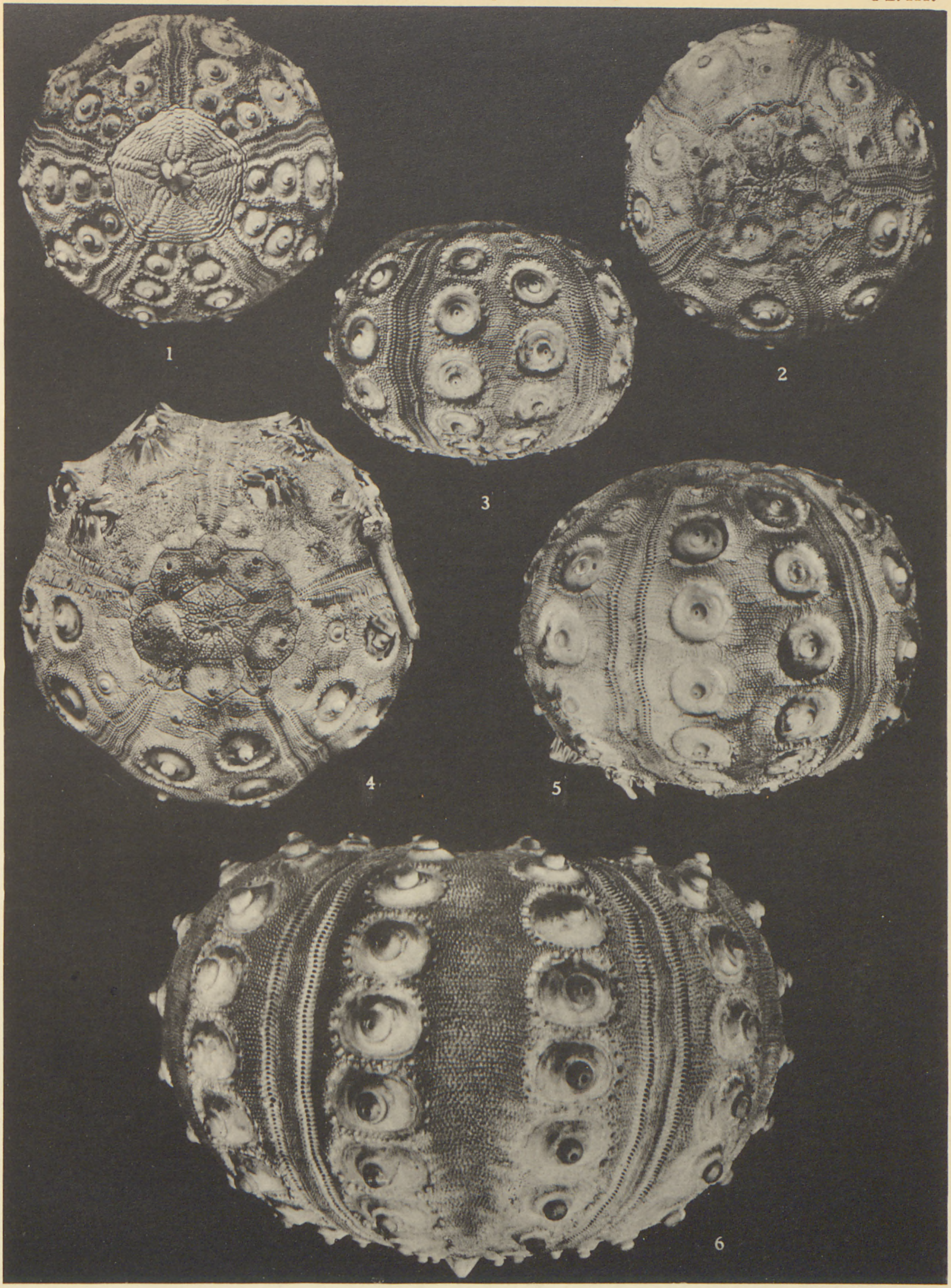


J. v. Huth fot.

Pacht & Crones Eftf. Fototypi.

Plate III.

Figs. 1—5. *Stereocidaris excavata* Mrtsn. Denuded tests.
1—3. Smaller specimen, from the oral side (1), the aboral side (2), and in side view (3).
4—5. Larger specimen, from the aboral side (4) and in side view (5).
Fig. 6. *Chondrocidaris gigantea* A. Agass. Denuded test, side view.
All figures natural size.



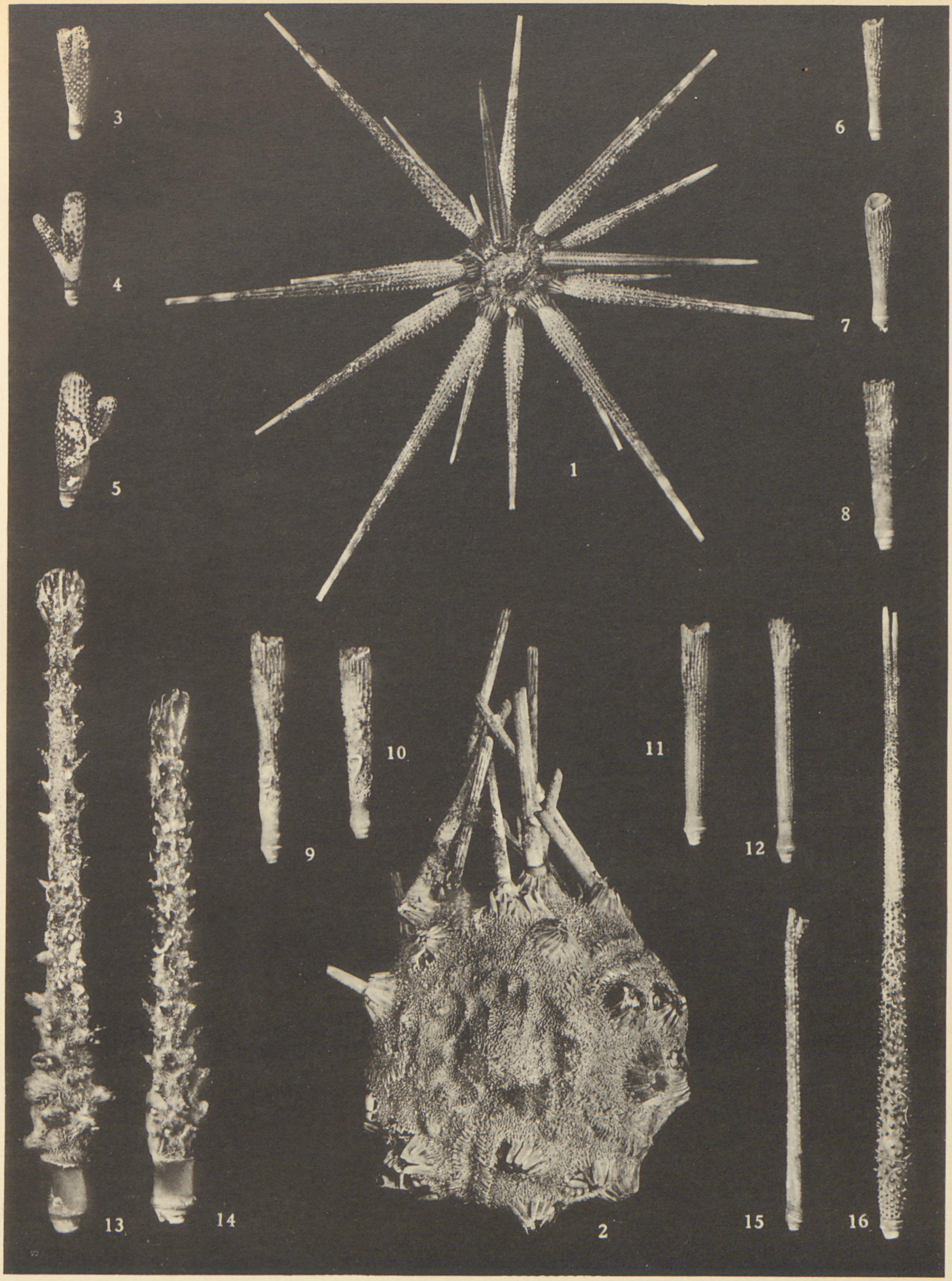
J. v. Huth fot.

Pacht & Crones Eftf. Fototypi.

Plate IV.

Fig. 1. *Stylocidaris badia* (H. L. Clark). Young specimen. Aboral side.
- 2. *Stereocidaris excavata* Mrtsn. Aboral side.
- 3— 5. Abnormal, branching primary spines of *Eucidaris clavata* Mrtsn.
- 6—12. Primary spines of *Tretocidaris spinosa* Mrtsn.
- 13—14. — — - *Chondrocidaris gigantea* A. Agass.
- 15. Abnormal, branching primary spine of *Tretocidaris spinosa* Mrtsn.
- 16. — bifid — — - *Stylocidaris badia* (H. L. Clark).

All figures natural size.



J. v. Huth fot.

Pacht & Crones Eftf. Fototypi.

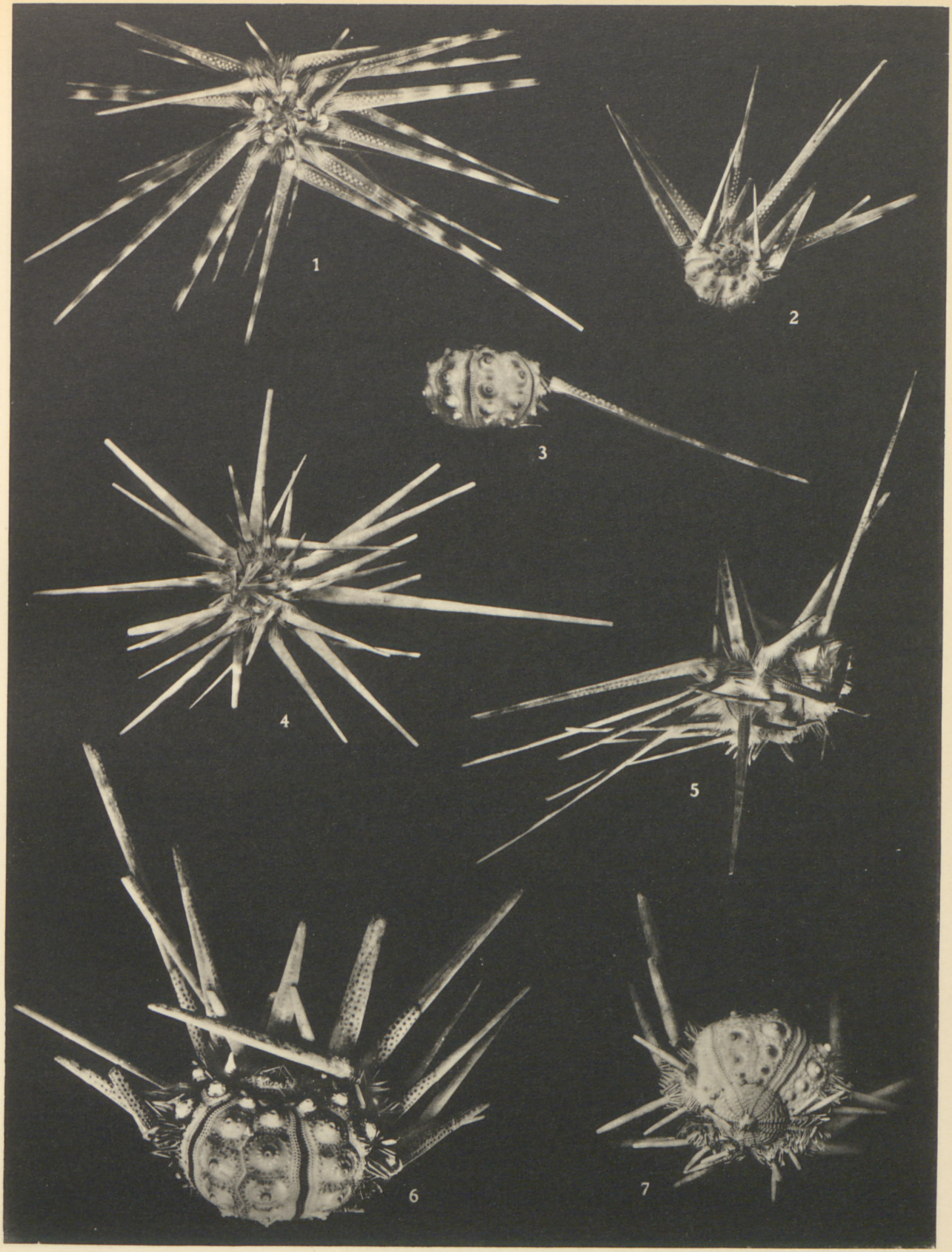
Plate V.

Figs. 1—5. *Acanthocidaris curvatispinis* (Bell). Young specimens. Aboral side (1); aboral side of half denuded specimen (2); side view of denuded specimen (3); oral side (4); side view (5).

Fig. 6. *Acanthocidaris maculicollis* (de Meijere); half denuded. Side view.

- 7. *Kionocidaris striata* Mrtsn. Type specimen; half denuded. Oral side.

All figures natural size.

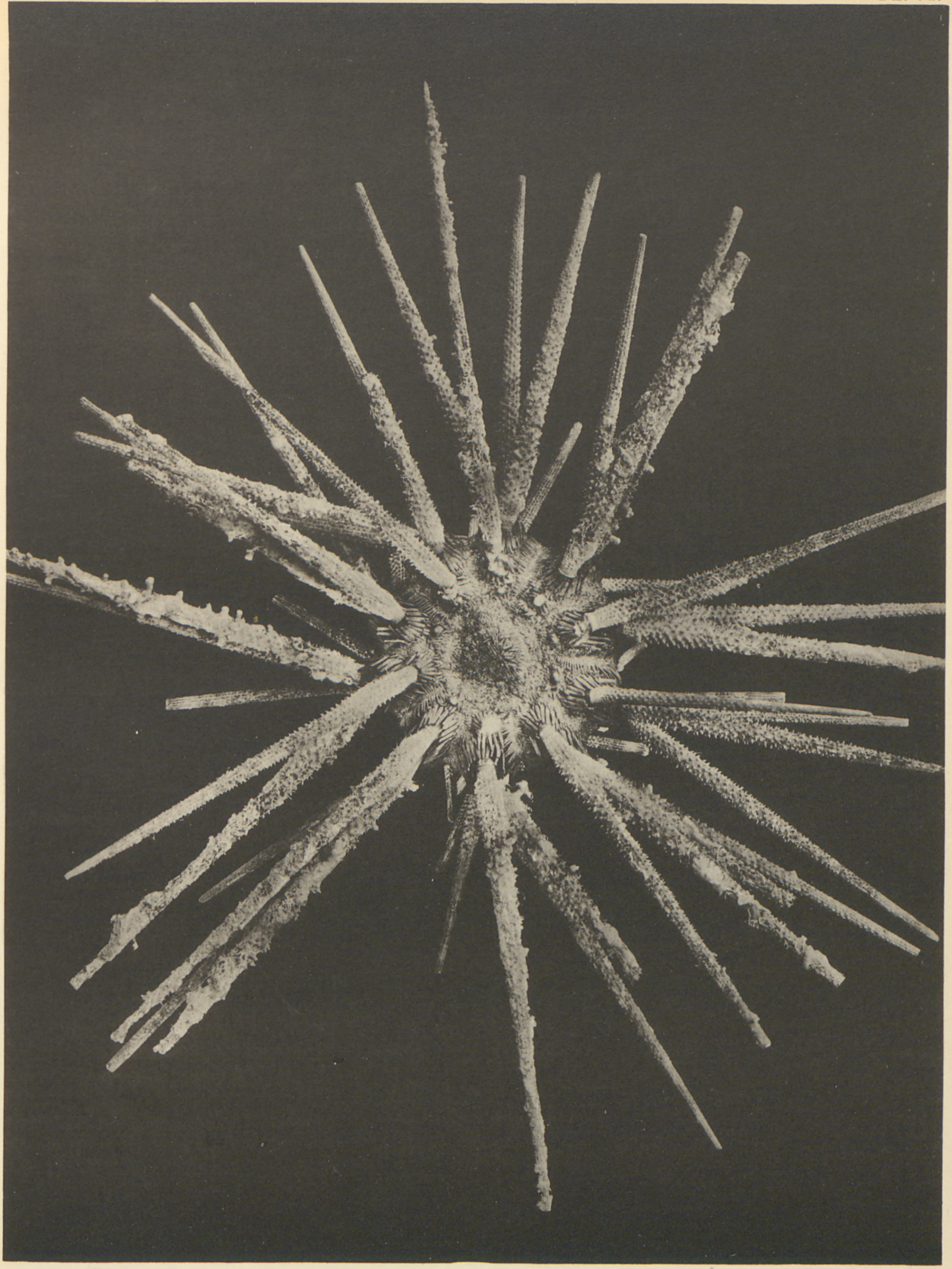


J. v. Huth fot.

Pacht & Crones Eftf. Fototypi.

Plate VI.

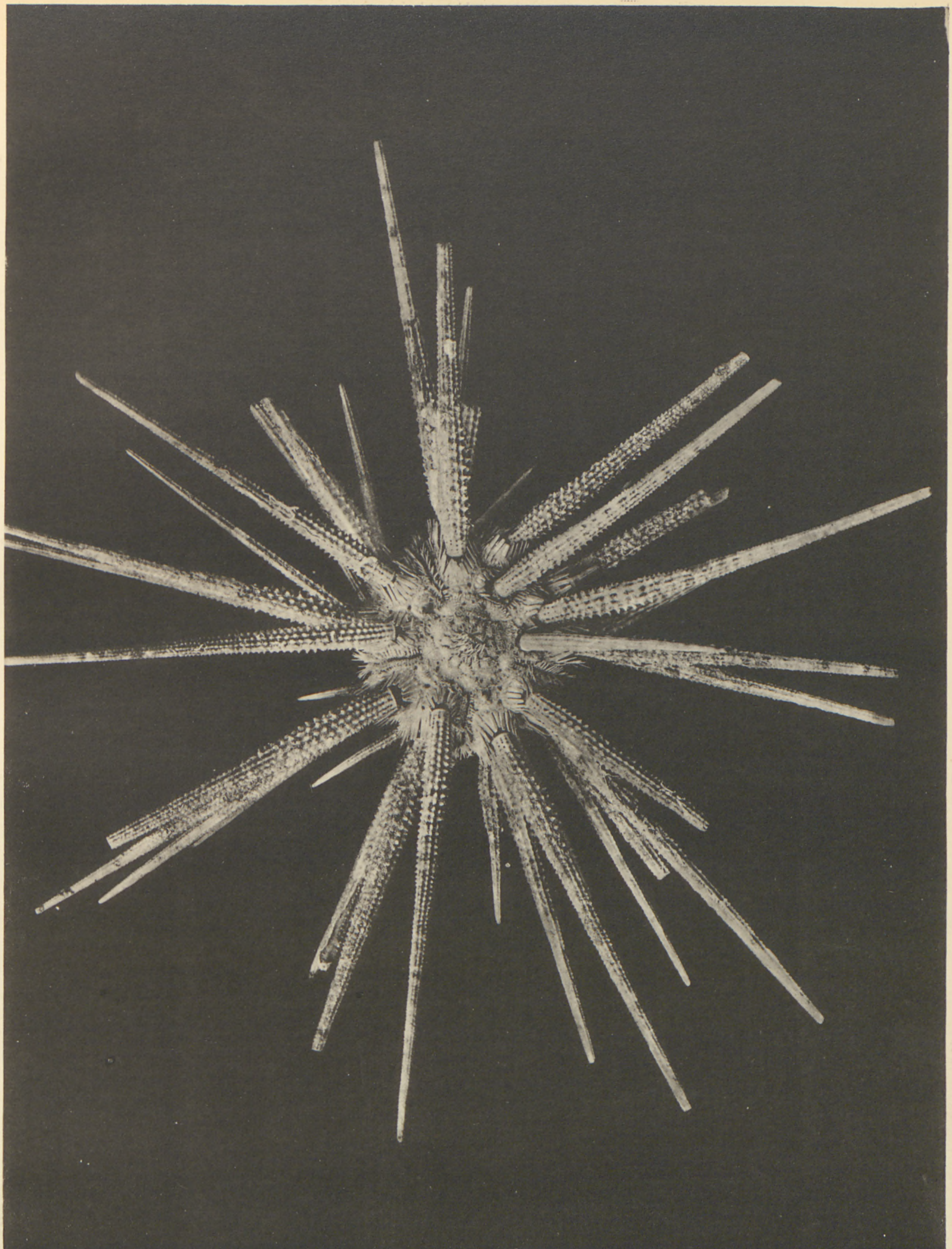
Stylocidaris badia (H. L. Clark).
Old, fullgrown specimen; aboral side. Natural size.



J. v. Huth fot. Pacht & Crones Eftf. Fototypi.

Plate VII.

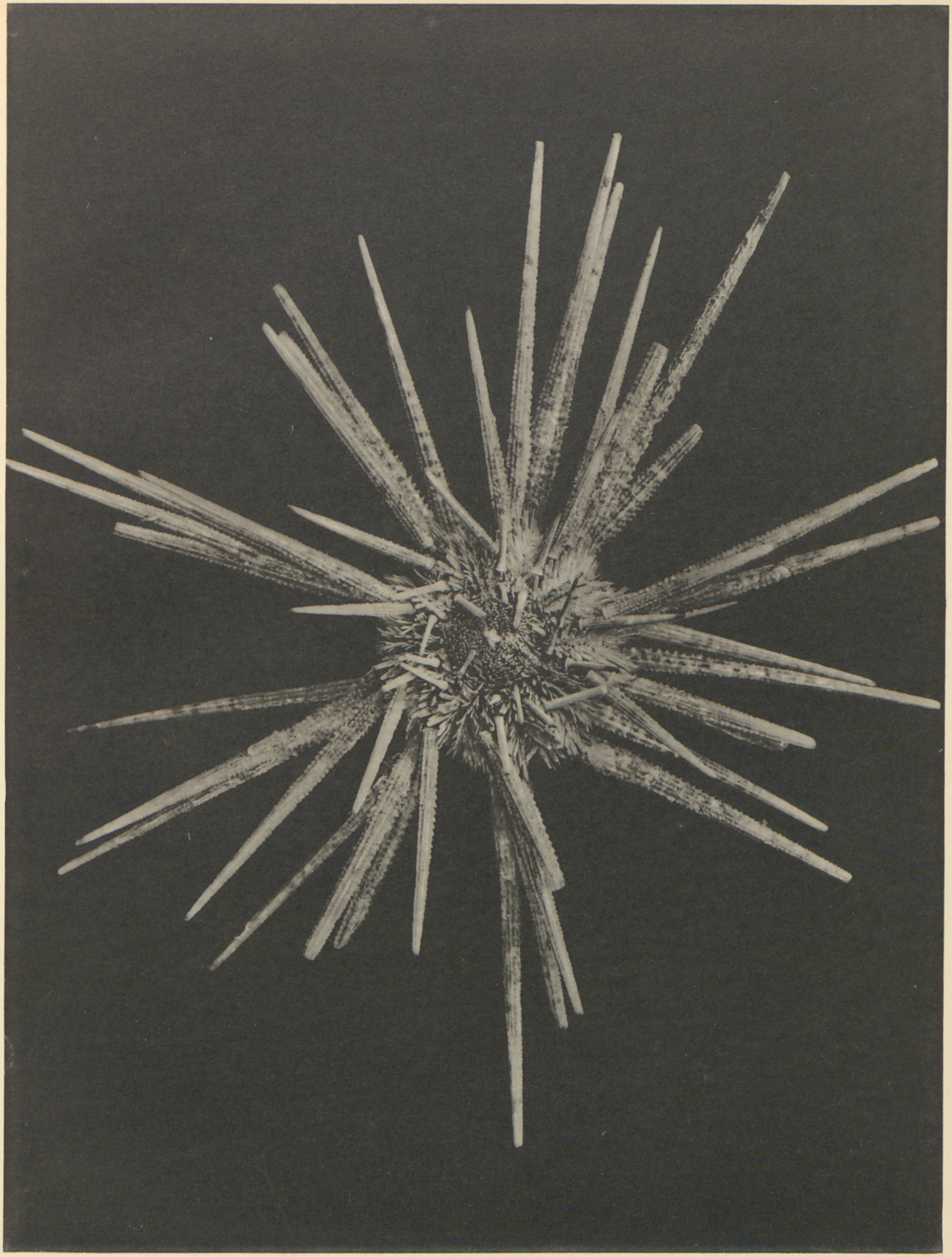
Stylocidaris bracteata, var. *mauritiana* Mrtsn.
Adult specimen; aboral side. Natural size.



J. v. Huth fot. Pacht & Crones Eftf. Fototypi.

Plate VIII.

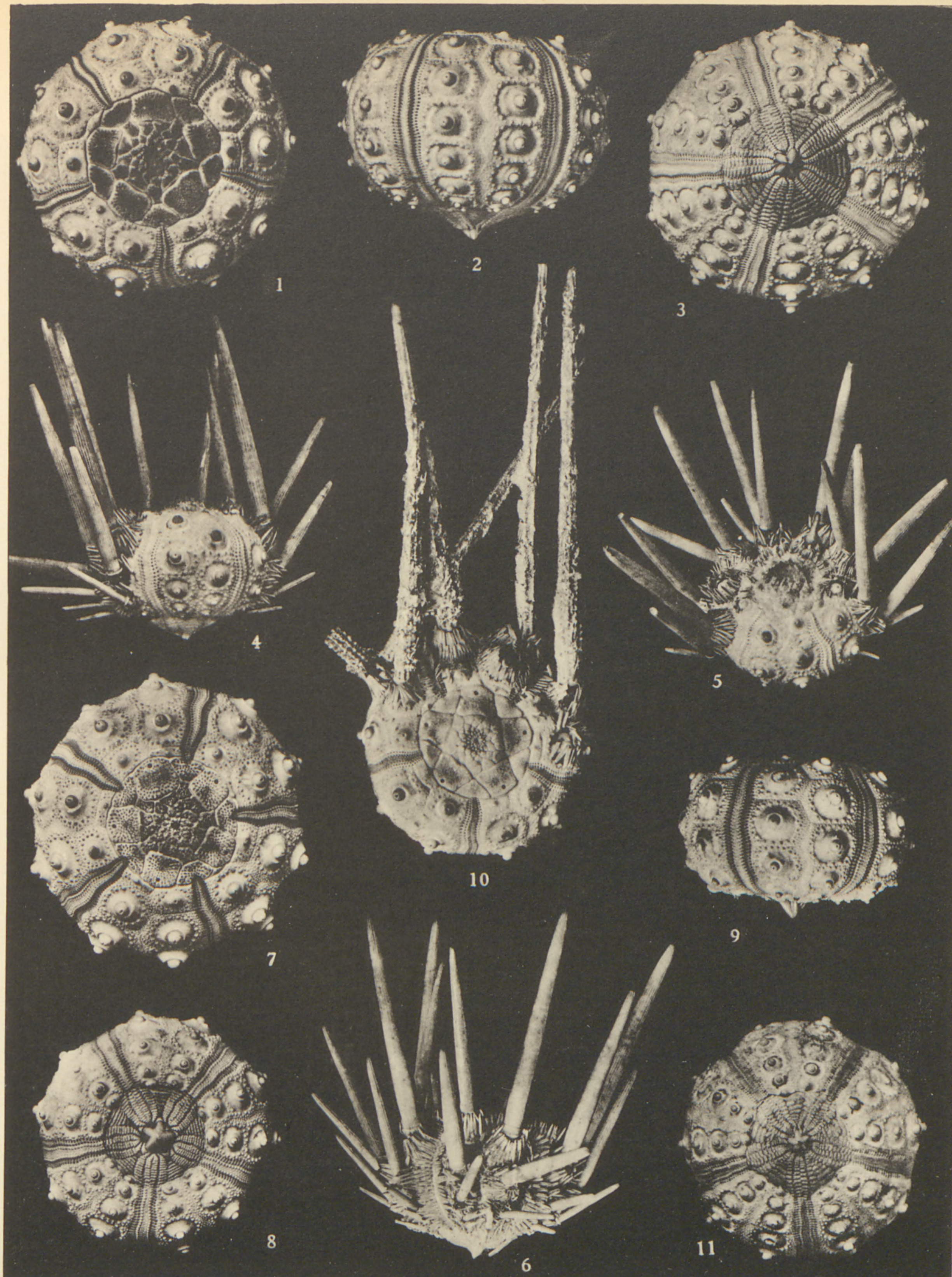
Stylocidaris bracteata, var. *mauritiana* Mrtsn.
Adult specimen; oral side. Natural size.



J. v. Huth fot. Pacht & Crones Eftf. Fototypi.

Plate IX.

Figs. 1— 3. *Stylocidaris badia* (H. L. Clark). Denuded tests.
Aboral side (1); side view (2); oral side (3).
- 4— 6. *Kionocidaris striata* Mrtsn. Type specimen; half denuded.
Side view (4); aboral side (5); side view (6).
- 7— 9. *Prionocidaris pistillaris* (Lamk.); denuded tests.
Aboral side (7); oral side (8); side view (9).
- 10—11. *Stylocidaris bracteata*, var. *mauritiana* Mrtsn. Denuded tests.
Aboral side (10); oral side (11).
All figures natural size.

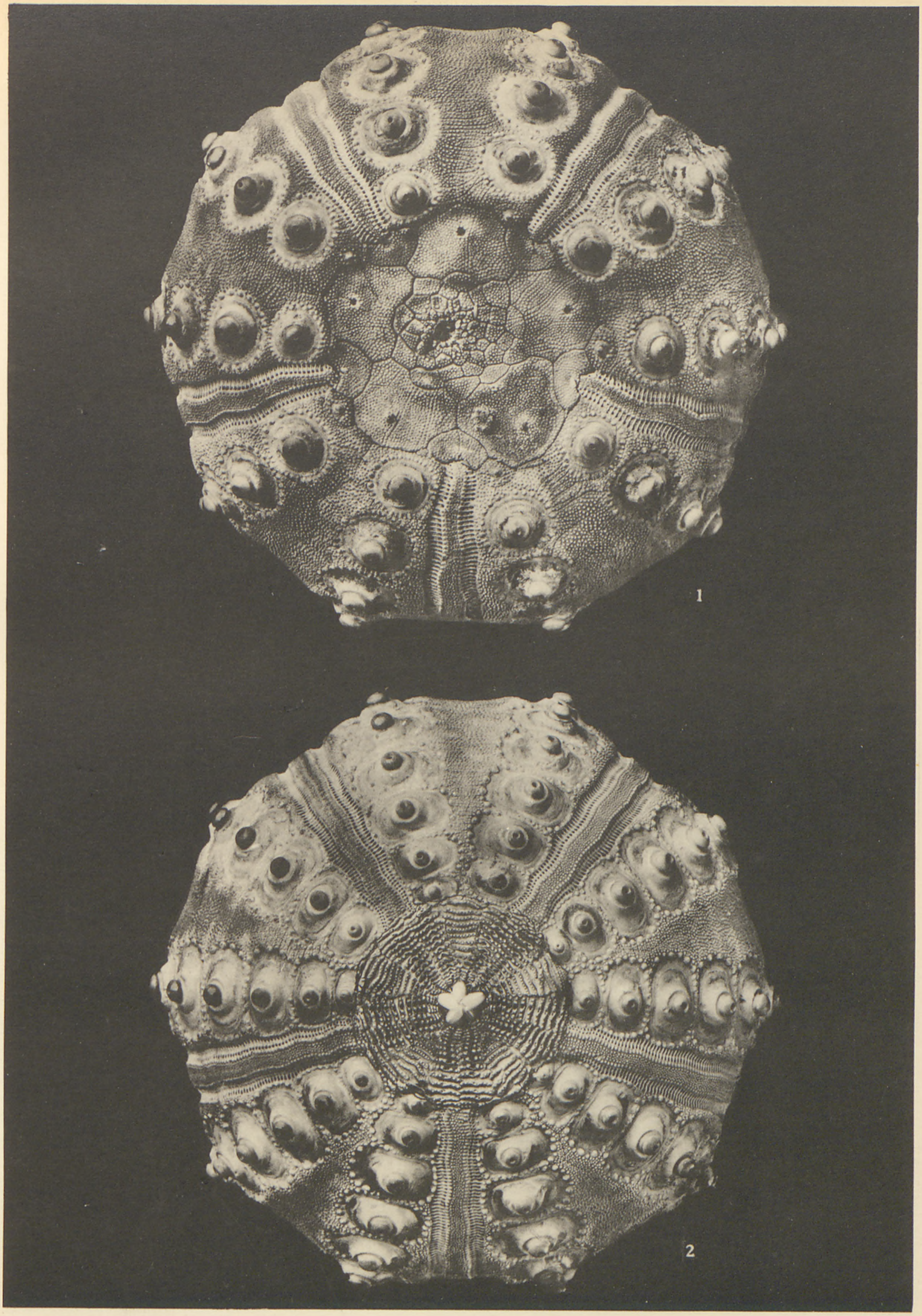


J. v. Huth fot.

Pacht & Crones Eftf. Fototypi.

Plate X.

Figs. 1—2. *Chondrocidaris gigantea* A. Agass. Denuded test. Aboral side (1); oral side (2). Reduced 1/6.



J. v. Huth fot. Pacht & Crones Eftf. Fototypi.

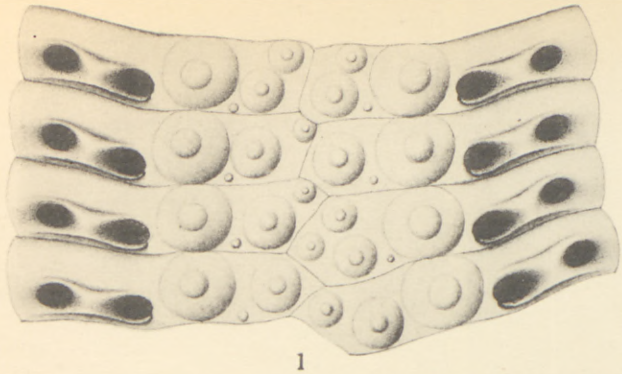
Plate XI.

Figs. 1—2. *Stereocidaris excavata* Mrtsn. Part of ambulacra of a smaller (1) and a larger specimen (2).

Fig. 3. *Kionocidaris striata* Mrtsn. Part of ambulacrum of type-specimen.

- 4. *Acanthocidaris curvatispinis* (Bell). Part of ambulacrum.
- 5. — *maculicollis* (de Meijere). Part of ambulacrum.
- 6. *Stylocidaris cingulata* Mrtsn. Part of ambulacrum of type-specimen.
- 7. *Goniocidaris balinensis* Mrtsn. Part of ambulacrum. Paratype.
- 8. *Prionocidaris pistillaris* (Lamk.). Part of ambulacrum.
- 9. *Kionocidaris striata* Mrtsn. Part of primary spine.

Figs. 1—6, 8 × 12. Fig. 7 × 50. Fig. 9 × 30.



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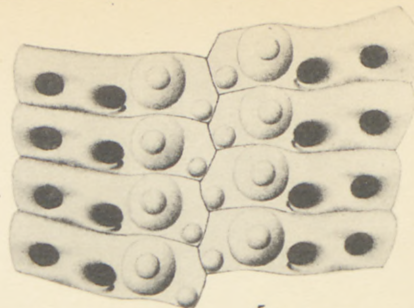

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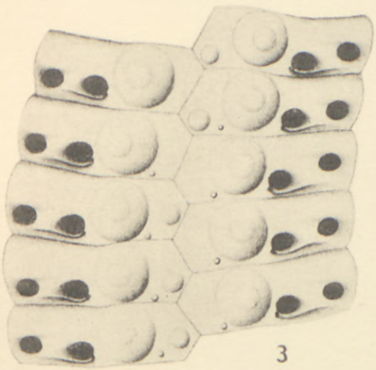

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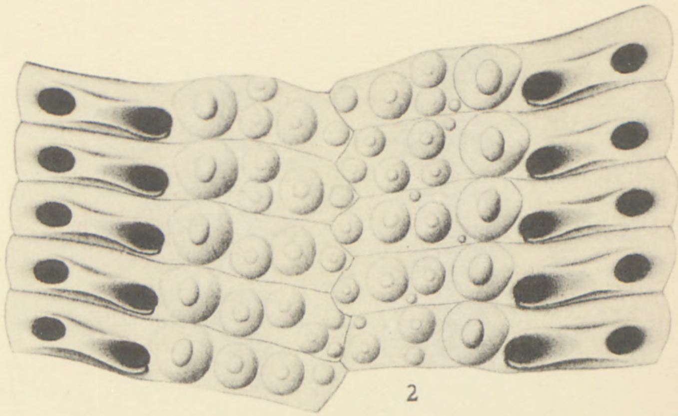

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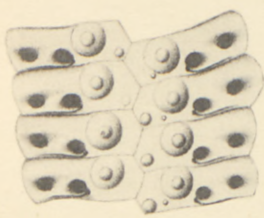

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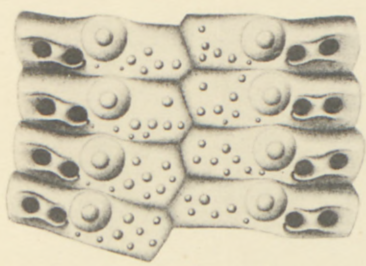

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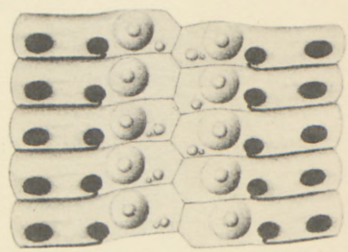

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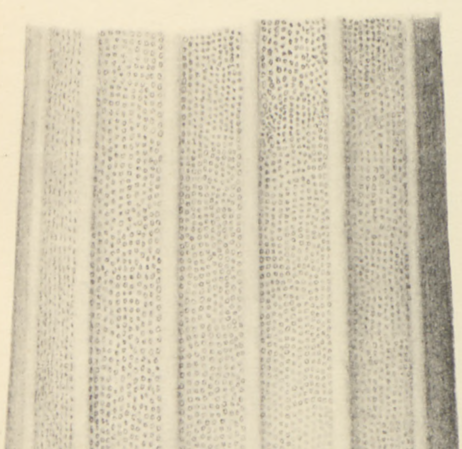

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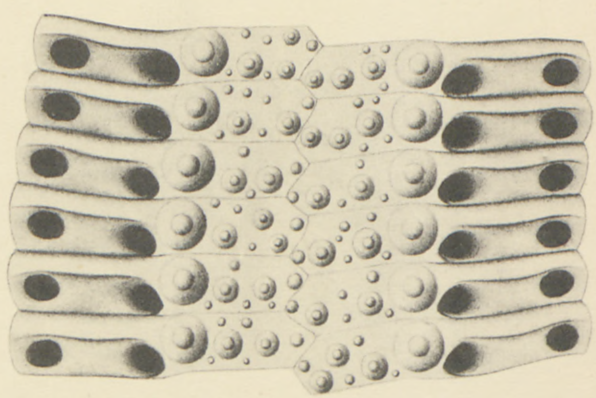

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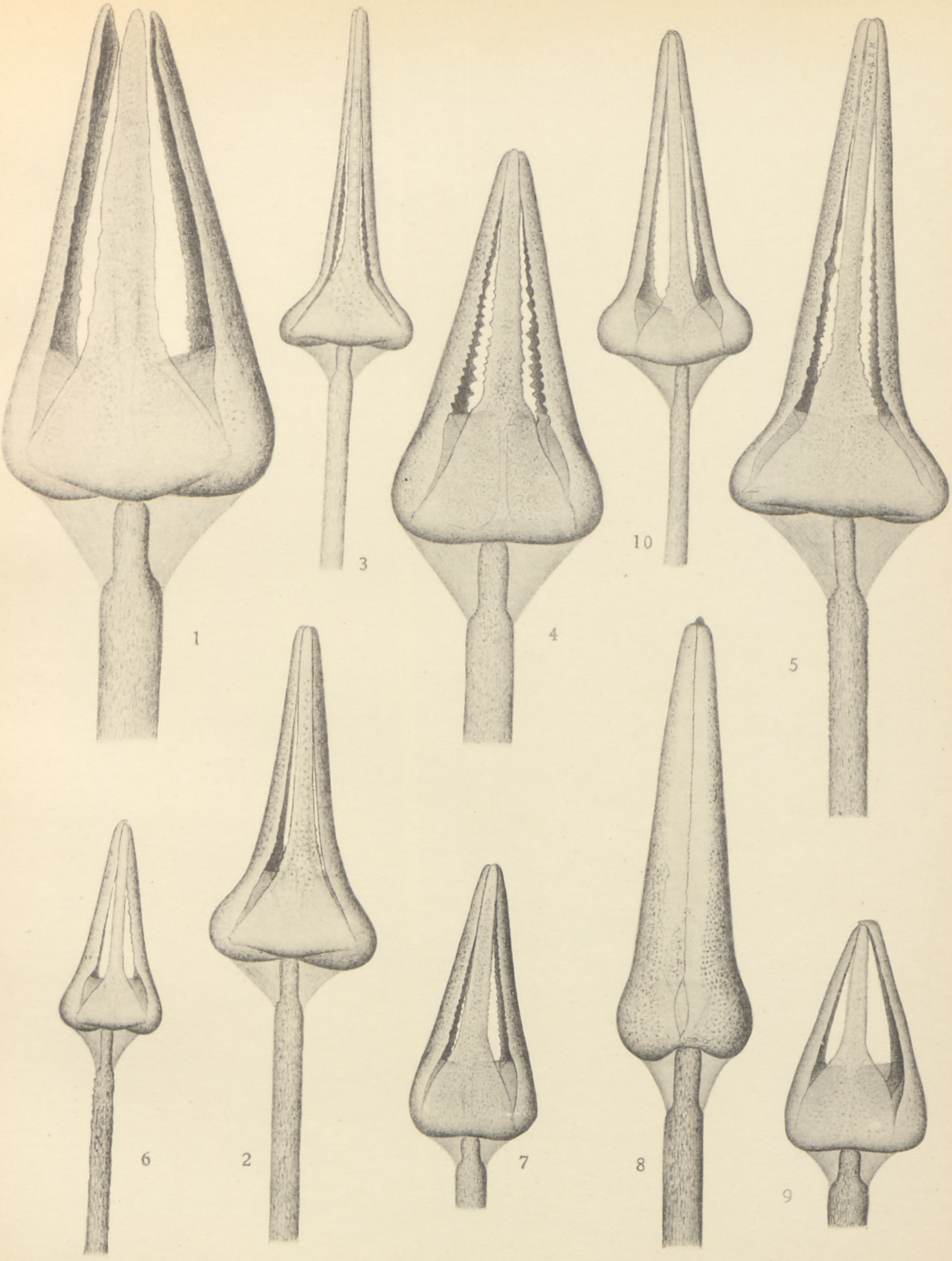
Th. M. del.

Pacht & Chrones Eftf. Fototypi.

Plate XII.

Figs. 1— 2. *Kionocidaris striata* Mrtsn. Tridentate pedicellaria, large (1) and small form (2). × 50.
- 3— 5 and 7. *Stylocidaris bracteata* var. *mauritiana* Mrtsn. Tridentate pedicellariæ. × 50.
- 6. *Stylocidaris bracteata* (A. Agass.). Small tridentate pedicellaria. × 105.
- 8. *Acanthocidaris curvatispinis* (Bell). Tridentate pedicellaria. × 50. (The underlying third valve indicated only at the point, otherwise not indicated, in order not to make the figure less clear). × 50.
- 9—10. *Stylocidaris badia* (H. L. Clark). Two types of tridentate pedicellariæ. × 50.



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Pacht & Chrones Eftf. Fototypi.

Plate XIII.

Figs. 1—2. *Stylocidaris badia* (H. L. Clark). Valves of two forms of tridentate pedicellariæ; side view. × 100.

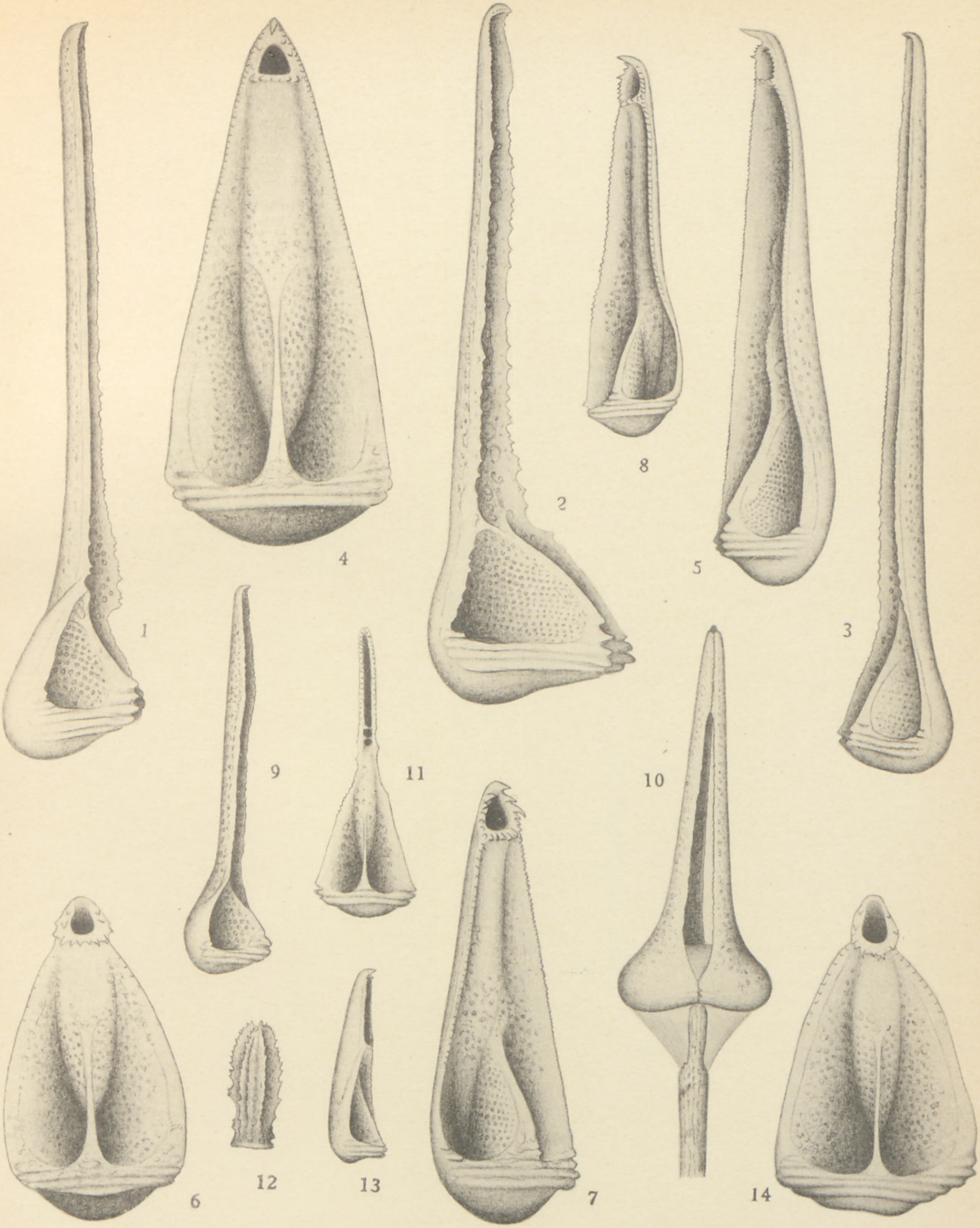
Fig. 3. *Tretocidaris spinosa* Mrtsn. Valve of tridentate pedicellaria; side view. × 95.

Figs. 4, 6—7. *Kionocidaris striata* Mrtsn. Valve of small globiferous pedicellaria, from the inside (4) and in half side view (7). Valve of large globiferous pedicellaria, from the inside (6). × 120.

Fig. 5. *Kionocidaris striata*, var. *teretispina* Mrtsn. Valve of small globiferous pedicellaria; side view. × 95.

Figs. 8—10. *Stylocidaris cingulata* Mrtsn. Valve of small globiferous pedicellaria, side view (8). × 100. Valve of tridentate pedicellaria, side view (9). × 100. Tridentate pedicellaria (10). × 68.

Figs. 11—14. *Goniocidaris balinensis* Mrtsn. Valve of small globiferous pedicellaria, elongate form, from the inside (11). Miliary spine (12). Valve of small globiferous pedicellaria, side view (13). Valve of large globiferous pedicellaria, from the inside (14). × 105.



Th. M. del.

Pacht & Chrones Eftf. Fototypi.

CONTRIBUTIONS

TO

THE PHYSIOGRAPHY OF ICELAND

WITH PARTICULAR REFERENCE TO THE HIGHLANDS WEST OF VATNAJÖKULL

BY

NIELS NIELSEN

WITH 32 PLATES AND 9 MAPS

D. Kgl. Danske Vidensk. Selsk. Skrifter, naturvidensk. og mathem. Afd., 9. Række, IV. 5.

KØBENHAVN

LEVIN & MUNKSGAARD

BIANCO LUNOS BOGTRYKKERI A/S

1933

PREFACE

The material on which the present work is based was for the most part compiled on a journey in 1927, The Second Danish-Icelandic Expedition, the members of which were:—

Pálmi Hannesson, B. Sc. (now Rector at the Grammar School in Reykjavík).
Steinþór Sigurðsson, B. Sc.
Sigurður Jónsson frá Brún, schoolmaster and farmer.
Niels Nielsen, Ph. D.

Some of the material, however, was collected on my former journeys in Iceland in 1923 and 1924, and, though it plays no great part from the point of view of quantity, those journeys have had a particularly important bearing on the work because, through them, I had become fairly familiar with the technique of travelling in Iceland and also had formed a certain concrete view of the tasks that presented themselves when we made a start on the work in the field in July 1927. I am greatly indebted to all my companions for work well done and for their enjoyable society; I would especially extend my thanks to my old travelling companion Pálmi Hannesson for a collaboration which, spread over many years, has been an inexhaustible source of knowledge to me. Nor can I omit to express my gratitude for the kindness and helpfulness I have always found among the Icelandic authorities and in Icelandic homes. Mr. W. E. Calvert has undertaken the translation in a most carefull manner.

The funds necessary to cover travelling expenses were procured from grants kindly made by the Carlsberg Foundation and the Dano-Iceland Union Foundation, while the Carlsen Lange Endowment Fund, by means of its stipend to Steinþór Sigurðsson has greatly promoted the handling of the cartographic material. The translation expenses was defrayed by the Rask-Ørsted Fund. I tender my heartfelt thanks to these institutions.

Copenhagen, October 1930.

Niels Nielsen.

A. The Landscape west of Vatnajökull.

1. Situation and History of Discovery.

The region to be dealt with in the following lies in Central Iceland in lat. 64—65 N., long. 18—20 W. Its total area is about 1600 sq. km., and the mean height above sea level is about 700 m. On the north it is bounded by Vonarskarð and Túngnafellsjökull, on the west by Þjórsá, on the south by the Túngná, and on the east by the Túngná and Vatnajökull.

Of the whole of Central Iceland this area is one of the most difficult to penetrate, because a whole series of obstacles to the forward march of man combine there; travelling through it is difficult enough — a sojourn of any duration still more so. If one attempts to come from the south and along by the glacier one meets a system of wild lava fields that are by no means easy to force. Coming from the north one must first pass through the great desolate wastes north and northwest of Vatnajökull, and thereafter one meets the glacial river Kaldakvísl, of which a great part of the upper course runs in ravines and thus forms a very effective hindrance. The easiest way into the region is from the southwest, as without much difficulty it is possible to get from the Hekla region as far as to Fiskivötn by making use of the regular ford over the Túngná at Bjallar, north of Mount Loðmundur. With this, however, the difficulties have not been overcome. The whole area is so to say bare of vegetation, and in two places only is it possible to obtain so much pasture that a number of horses can live for any length of time, viz. in Illugaver and Fiskivötn. In good summers one may also expect to find grazing in August in the small oasis Botnaver, just west of the margin of Vatnajökull; the quantity of grass there is only small, however, and can only feed five to ten horses for a few days.

At one or two other places it is possible to cross the Túngná. Both THORODDSEN and ERKES have crossed it at the bend at Námskvísl, and BJÖRN GUNNLAUGSSON indicates a ford across the Túngná southeast of Fiskivötn, probably identical with the one used by PÁLMI HANNESSON at the remarkable tuff column Tröllið, fig. 24. Both these fords, however, have the disadvantage that they are very variable and full of quicksands, so that a caravan carrying scientific equipment would if possible avoid them. Finally, it is usually possible to cross the Túngná over its tributaries in Túngnárbotnar, right up near the Vatnajökull. There the ford lies some few hundred metres above the place where the watercourse from Botnaver empties into the river, west of the highest peak of the characteristic mountain that lies just to the north of Botnaver.

These difficulties form one of the reasons why this part of Iceland has hitherto lain almost as virgin country. Another reason is that most investigators who have travelled the country — now quite a considerable number — have proceeded along the traditional, oft-travelled routes, at any rate when the object was the central highlands; the consequence is that there has been a pronounced diversity in our knowledge of that part of the country, certain routes and certain localities being comparatively well known, whereas others close by have remained terra incognita, from a scientific point of view, up to the present day.

The pass between Vatnajökull and Hofsjökull — about 35 km wide — through which the mountain path Sprengisandsvegur runs, has been travelled scores of times by explorers and sportsmen, and practically all the men of science who have made deep studies of nature in Iceland have traversed this route. Only rarely, however, have any of them attempted to go eastwards from Sprengisandur and examine the country on the west edge of Vatnajökull. The country south of the Túngná has been the scene of a very violent volcanic activity in historic times, especially in the years 1783—84, for which reason a number of investigators have visited it: HELLAND, THORODDSEN, SAPPER, RECK and several others; thanks to their researches a part of this landscape is known fairly well.

On the other hand the country north of the Túngná has been visited by only few investigators, who have remained in these inhospitable regions a few days. Nor does the peasantry of Iceland know anything of it, to the best of our knowledge, because only the most southerly part, the Fiskivötn area, has been of any value industrially. The two oases have been known in olden times, but little or nothing else.

The first to record his observations in these regions was the highly gifted Icelandic physician and naturalist SVEINN PÁLSSON, who went to Fiskivötn in 1794. His visit was quite a short one, and the report in his diary consists of an account of the main topographical features and some biological observations. The knowledge we have so far had of Fiskivötn was almost exclusively derived from a journey made in 1889 by ÞÓRVALDUR THORODDSEN, with the farms of the Hekla-region as his starting point. He worked in the area five days and thereafter went up to the edge of the Vatnajökull, discovered the oasis Botnaver, and then travelled southwards, discovered Langisjór, and went back to Fjallabaksvegur nyrðri. The accounts of this momentous journey are contained partly in the Ferðabók and partly in Geografisk Tidsskrift, Vol. 19, and both in THORODDSEN's geological map of Iceland and in his large manuals we find the results of that exploration.

Access is much easier to the regions round Túngnafellsjökull, and in fact they have been frequently travelled by investigators. In August 1839 BJÖRN GUNNLAUGSSON went through Vonarskarð, the pass between Túngnafellsjökull and Vatnajökull, and to this day his observations and measurements form the basis of our knowledge of the main topographical features of this region. He stayed two days at the oasis Illugaver, which has also been visited in recent times by several travellers, although their stay has been very brief, and there is little information about the geography of the region.

In Nýidalur, on the west side of Túngnafellsjökull, there is a small oasis where many travellers have sojourned a short time. Among them particular mention must be made of Reck and Erkes. The former went round the whole of the mountain group in 1908 and had the opportunity of making a number of valuable geological and topographical observations, to which I shall revert later.

In 1925 and 1926 the Danish minister to Iceland, F. de Fontenay, made two journeys up there. At the beginning of August 1925 he went from the oasis Illugaver to the mountain group known as Kerlingar on the edge of Vatnajökull, climbed the edge of the glacier and went round the mountain group in question. On this journey he discovered the very interesting tectonic fissure Heljargjá, established that the flow from that part of the glacier was southwards, and recorded much other information of value concerning this land, up to that time entirely unknown. In 1926 he went to Fiskivötn together with Pálmi Hannesson. There they remained for some days, but their work was greatly hampered by unfavourable weather.

In 1924, Pálmi Hannesson and I, the sun beating down upon us, stood on Hofsjökull looking out over the country between it and Vatnajökull, spread before us like a map far below. We then made a compact that our next journey should be to that region, and that it should be on such a scale that we should be able to work through practically the whole of that interesting terrain. However, it was not until 1927 that we were ready for that journey; on the other hand we were able to make a stay of about two months. The plans for the journey, the technique we used, our equipment, programme of work, etc. have already been described in my preliminary reports, to which I must here refer (Nielsen 1927 and 1928).

2. Topographical Conditions.

Our present knowledge of the topographical conditions in Iceland is of a very heterogeneous nature, and as a result the reliability and value of the various maps as aids to scientific work is also very varied. Of about half the coast lands we may say that the maps meet all the requirements of a modern, topographical survey in detail, the south, west and a part of the north coast having been surveyed by the topographical section of the Danish General Staff, whose material is represented in the form of 118 map sheets on the scale of 1 : 50,000 and 5 on the scale of 1 : 100,000. These carefully drawn and handsomely got-up maps provide most valuable material for the study of a number of geographical and geological problems, of which one, for instance, is dealt with in the closing chapter of the present work.

For the most part, our knowledge of the topography of the east and northeast coast land is based upon a triangulation made in the years 1801—15 under the auspices of the Dano-Norwegian Government. In connection with this work the Icelandic topographist Björn Gunnlaugsson (1831—43) energetically and with great skill surveyed important parts of the then entirely unsurveyed interior of the country, and these two series of surveys were then combined in a map which, for its time, was a most excellent piece of work: Uppdráttur Íslands 1844, which bears the name of Björn Gunnlaugsson (Nørlund 1930). Unfortunately, the difficulties bound up with satisfactorily coping with the task of making a map of the interior of Iceland were far in excess of the powers of one man — especially when one considers how very modest were the conditions under which Björn Gunnlaugsson worked — and so it is no wonder that the result is full of defects, as a few examples in the following will show. Nevertheless, Gunnlaugsson's was a pioneer labour of great value, and to this day it is of fundamental importance to our knowledge of these parts of the country. His method of working has been described in a small book in Danish and Latin dated 1834. The map was reproduced by Kålund in that deserving work: Bidrag til en historisk-topografisk beskrivelse af Island, Copenhagen 1877—82, and has been the foundation for the cartographical representations of Iceland during the succeeding half century.

Since then Thoroddsen, Daniel Bruun, Heinrich Erkes and others have made numbers of corrections on the basis drawn up by Gunnlaugsson and have remedied a number of its manifold defects. Thoroddsen's map has been published piecemeal in a great many special works and in its entirety in the large Handbook of 1905—06, as well as in the geological map of Iceland, scale 1 : 600,000, published separately in 1901. On his tourist map of Iceland Daniel Bruun inserted a number of corrections, most of them the results of his own observations; and finally an Icelandic commission in 1928 published an orographic wall map, which included the results of the surveys made up to about 1925.

But while a part of the coast land is thus well known topographically, it is by no means possible to say the same of the interior highlands. The maps of that part of the country are for a great part based upon purely rough sketches, drawn without the use of instruments to any great extent. As a rule they have had the character of route notes, and, as only very few investigators have remained for any length of time at one place in the interior — usually with other objects of study than topography pure and simple — the result is a very uncertain one both with regard to the course of the main topographical contours and with regard to the placing of the features of the terrain. Only in very few cases has a small area been measured with any great accuracy, and even in these cases the details are lacking in accuracy. Among them are those of Caroc in Askja, Helland's at Laki, Wunder's in Kerlingarfjöll and Oetting's in the terrain between Hofsjökull and Langjökull.

It is evident that, as far as the interior is concerned the investigator will usually have to make his own map of the region he is working in. On the 1924 journey we were only two who busied ourselves with scientific work and so we had to simplify our methods as much as possible. Our surveys were made in this manner: in each of the areas examined we set up a measuring station, and from it, using the Bussole, we measured the angles to some prominent points in the terrain, and their distance from the station was then measured with HYMAN's pocket rangefinder. On this skeleton we then drew the sketches on which the geographical and geological results were entered. We found North by means of a meridian line calculation, as the magnetic variation was subject to such great local disturbances that the compass was useless for the purpose. No general orientation in relation to the topographically surveyed region at the coast was obtained, however. A method of this sort is of course unsatisfactory, but much to be preferred to the sketch method pure and simple, without the use of measuring instruments. In 1927 we were able to check some of our 1924 measurements by triangulation, and it turned out that the topographical picture was correct on the whole, even if there were errors of up to 5 per cent. in the distances.

The object of the journey in 1927 was not essentially topographical; but if we were to place the phenomena observed, we had to procure a map of the area in some way or other. The fact is that our knowledge of the region between Túngná and Kaldakvísl was in advance very slight. The surveying work was organized in this way: one of the members of the expedition, STEINÞÓR SIGURÐSSON, with the necessary assistance from the other members, was detailed to triangulate the whole of our field of operations and to measure up as many of the prominent points in the surrounding landscape as possible for the purpose of obtaining, firstly, working sketches, and secondly, the map worked out on the scale of 1 : 200,000 for the present publication.

The base of the measurements was a line of 637.99 m., measured with the measuring tape on the plain at Vatnakvísl. To assist in sighting we built about two hundred cairns here and there on the ground. The measurements were then taken with a small theodolite, which was no heavier than that a man could climb about with it. Orientation was secured by means of sextant observations and by means of an area in the south part of the country, surveyed by the Danish General STAFF, with which we connected during the final stage of the journey. Heights were obtained trigonometrically in some cases, in others with the barometer. The aeronoid barometer used for the latter was corrected at every main station with the hypsometer, whereby we obtained confirmation of our earlier experience than an aneroid barometer, even when packed with extreme care, does not stand a horse-back journey well, as the correction was found to vary very considerably at the different stations. From four high trigonometrical stations we then measured a number of prominent points in the whole of the southern part of the Icelandic highlands, right from Langjökull to the nunataks in the south and west parts of Vatnajökull, while from two points in the north part of the region we have taken a number of sights to various points in Ódáðahraun and the highlands north of Hofsjökull.

These measurements have demonstrated that hitherto there have been various errors in the placing of the main topographical contours of the south highlands, and, as the map page . . . shows, the differences are rather great. On the map are shown the glacier boundaries and rivers as plotted on THORODDSEN's map of Iceland, and for purposes of comparison the boundaries shown by our measurements. The principal results are as follows:

The geographical length of the west edge of Vatnajökull is in all essentials correct on the earlier maps, and this means that the east to west extent of that glacier must also be correct. According to TRAUTZ (1912) its northwest corner is if anything placed too far south; Kverkfjöll, too, according to KOCH and WEGENER's measurement of the distance between it and Esjufjöll (65 km.), may be assumed to be somewhat more to the north than hitherto thought. Thus the area of Vatnajökull is scarcely less than indicated by THORODDSEN, and probably is something over 8000 sq. km.

Both the size and placing of the other inland glaciers must, however, be revised to some extent. From the observations of DANIEL BRUUN and HEINRICH ERKES we have had reason for presuming that the distance between Hofsjökull and Vatnajökull on the maps was given too short, but no exact measurement had hitherto been taken, and one could not determine where the error lay. Our measurements show, however, that the explanation is an incorrect idea of the size of Hofsjökull. The fairly primitive measurements of 1924 (cf. Map No. 2, NIELSEN 1924) already showed that the distance between the southwest and southeast corners of this glacier had been put at too high a figure, and our triangulation in 1927 has confirmed this to the full. The central point of Hofsjökull is indicated correctly, but the edges to the south, east and west have been pushed too far forward. THORODDSEN estimated its area at 1350 sq. km., but actually is it much less, in fact about half that size, as according to the present measurements Hofsjökull may be estimated to cover a surface of about 700 sq. km. It is only right to add, however, that with regard to the north edge we have not sufficiently complete measurements to enable us to outline the course of the ice margin with certainty.

For Túngnafellsjökull THORODDSEN indicates a size of 100 sq. km., but this, too, is an exaggeration. In 1908 RECK explored the mountain region and was able to state that the area of the glacier must be round about 30 sq. km. This corresponds well to our measurements, which may be incomplete, but nevertheless are sufficient to show that THORODDSEN's idea of the size of the area of this glacier does not harmonize with reality.

This brings us to another question: the mutual situation of these glaciers. Vonarskarð, the pass between Túngnafellsjökull and Vatnajökull, has practically the breadth indicated by THORODDSEN, and thus the error when drawing in the former glacier lies in the size, not in the placing. On the other hand the distance between Hofsjökull to Túngnafellsjökull has been greatly underrated, as, instead of 12 km., it must be put at 25 km.; this is a part of the aforementioned over-estimation of the area of the Hofsjökull. A similar distortion is revealed by a revision of the maps of the area between Hofsjökull and Langjökull. The big pass there, Kjölur by name, is actually much wider than earlier maps indicate; it is true that the angle of intersection between our sight-lines is rather more acute than desirable, but we believe we have established that the distance from Blágnýpa to Hrútafell exceeds 20 km. and thus is more than twice as great as hitherto believed. The correctness of these measurements has been fully confirmed by the German geologist OETTING, who in 1928 made a topographical survey of this landscape, from which it appears that the distance between the two points is about 25 km. (OETTING 1930).

There is no doubt that our maps of Langjökull also need revising, but our material contains only a single measurement that is of any interest in this connection, namely, that Hrútafell — a large and widely-visible mountain just east of the glacier — must be moved about 15 km. to the northwest. Here it must be observed that the situation of the south edge of this glacier has been established by the surveys of the General STAFF, and that there is furthermore reason for supposing (based upon BJÖRN GUNNLAUGSSON's intimate knowledge of this district) that the west edge of Langjökull has been drawn without much inaccuracy. It this supposition is correct, we arrive at the result that the north part of Langjökull is somewhat narrower than it has been taken to be, from which again follows that its size, estimated by THORODDSEN at 1300 sq.km., must be reduced somewhat. I shall not enter upon any estimate as to how much the reduction should be, but I am certain that Langjökull is larger than Hofsjökull, and that in future it will have to be given place as the second largest of the Icelandic glaciers.

It is thus evident that the main error in our past ideas of the topography of Central Iceland may be traced back to the fact that the size of the glaciers, with the exception of Vatnajökull, has been much overrated, quite a natural consequence of their completely dominating the landscape with their height and massive contours, whereas the extent of the intermediate plateaux — differing so slightly as they do in ground features — has been correspondingly underrated. I believe that the total area of Langjökull, Hofsjökull and Túngnafellsjökull has been put at about 1000 sq.km. too much by THORODDSEN.

Within the region specially explored it would be supposed that a systematic survey would lead to a far-reaching revision of our ideas of the topographical conditions; this has indeed proved to be the case. Not only has it turned out to be necessary to alter and add details, but the course of the main topographical lines: waterways, ice-margins, valleys, mountains and sea beaches, is somewhat different than hitherto believed. A comparison between the previously existing maps and the one now published makes the difference apparent at once. The most important errors in earlier maps are: Both the Kaldakvísl and the Túngná are placed too far to the south, and the direction is also erroneous, as in their upper course they both run southwest and are almost parallel; the lake group Fiskivötn—Litlisjór is wrongly orientated, the edge of Vatnajökull runs differently to what has hitherto been assumed, and, as shown by DE FONTENAY's observations in 1925, its waters run into the Túngná, which rises away up in the mountain group known as Kerlingar; the latter, too, must be moved about 10 km. further north.

The mapping of the lakes deserves some brief reference. Björn Gunnlaugsson entertained the belief — the result of information given him by Björn sal Þórvaldsson in Stóradal — that there were the following lakes north of the Túngná: Two large lakes, i.e. Stórisjór and Litlisjór, as well as a number of small ones lying together in a group and called Fiskivötn. According to Gunnlaugsson, who did not know the region personally but only through what the peasants told him, the mutual situation of these lakes was: Nearest to the glacier was Stórisjór, then next came Litlisjór, and, furthest southwest, Fiskivötn. On this question Sveinn Pálsson writes: "Of the known lakes the following are the largest: Stórisjór, furthest north, largest of all, winding, perhaps comprising several small lakes, extends further north than one has travelled .... from Stórisjór towards the southwest a river runs under "Hraunet" (the lava) to Stórafossvatn, which again empties into Litla-Fossvatn." The same names are used by Thoroddsen on maps and in travel diaries and handbooks, whereas Daniel Bruun (1925, p. 38) says that north of Græṇavatn one comes first to Litlisjór and then to Stórisjór, which previously had erroneously been called Litlisjór by some people; on the map accompanying his paper, however, he has only shown Stórisjór.

In his paper 1925 de Fontenay, p. 130, summarises the problem of Stórisjór, and comes to the conclusion that the Stórisjór of Thoroddsen and Sveinn Pálsson are identical and the same as the lake which Gunnlaugsson calls Litlisjór. Undoubtedly this is correct. Nowadays this lake is called Litlisjór by the peasants, and therefore we must give it the same name, regardless of the terminology used by the writers named. But then the question arises: Is there a Stórisjór, or, put more correctly, is there between Litlisjór and the glacier a large lake that can bear this name? Among the country people in the Hekla region one sometimes meets with this belief. Nevertheless, our investigations show that there is no such lake. It is true that there are several small lakes in that terrain, but they are all very small, rarely exceeding 1 sq.km. and thus much inferior to Litlisjór in point of size; the result is thus that there is no Stórisjór, and that the traditions both among the peasantry and in the literature about this lake are simply a myth without foundation in reality. We do not know definitely how this interesting example of myth-growth has started, but my companion Pálmi Hannesson has advanced the following theory: The lake north of Fossvötn is, and always has been, called Litlisjór, that is to say "the little sea", and this is a name that fits it very well for, seen from the south, the lake really seems to be of imposing size; later on the origin of the name has been forgotten, and it has been thought that if the ancients called the lake Litlisjór, there must also be a Stórisjór that was bigger; and where else than up in those wide and unknown wastes north of Litlisjór could such a lake be situated? Both Sveinn Pálsson and Thoroddsen, who have both been to Fiskivötn, call the largest lake in the area Stórisjór and allow the other name to fall, whereas Gunnlaugsson and Daniel Bruun believe that there really are two large lakes in that region. And so, when after his great journey in 1889

THORODDSEN has to name the big, elongated lake south of Botnaver, he calls it Langisjór because of the other names Stórisjór and Litlisjór. It is in this manner that we find the explanation of the remarkable fact that in this region there are three lake names ending in "sjór", although in Icelandic a lake is called "vatn", whereas "sjór" means "sea".

Northwest of Fiskivötn and Litlisjór is another lake, Þórisvatn, shown by BJÖRN GUNNLAUGSSON and on all later maps. His cartographic placing and outlining leave much to be desired and would seem to indicate that he did not have the opportunity of seeing it during his aforementioned sojourn in Illugaver; indeed it would rather seem that he has learned of its existence through the verbal communications of the country people. THORODDSEN, however, visited it in 1889, and we know that some other investigators have seen it since. Thus on his great journey from Arnarfell out over the Kaldakvísl in the interior, HELLAND (1883, p. 262) passed Þórisvatn, but he went astray and could find no grass; only after great privations and difficulty did he get out of the desert and bring his caravan safely down to the Hekla region. DANIEL BRUUN has also seen it, as have HEINRICH ERKES and possibly HERMANN STOLL. Among the peasants in the south country it is well known, many of them having been to it when rounding up sheep in autumn.

THORODDSEN reached the northwest shore of the lake and from the surrounding heights received a mostly correct impression of its shape, size and situation, and on this, as on so many other points, made a valuable revision of GUNNLAUGSSON's map. He considered that its area is about 100 sq.km. and that it is thus of almost the same size as Iceland's largest lake, Þíngvallavatn. DANIEL BRUUN came to the conclusion (1925, p. 39) that it is the largest; but our measurements show that this is not the case, as its area is about 80 sq.km. Þórisvatn must therefore be content with second place among the lakes of Iceland.

3. Principal Features of the Structure of Iceland.

The opinion that the structure of Iceland more than anything else is a result of the activities of volcanic forces was already advanced by one of the first of the investigators who have occupied themselves with the study of nature in that country: the Icelander SVEINN PÁLSSON, who lived in the closing years of the eighteenth and the first years of the nineteenth century. Since his time many scientists have endorsed the correctness of that view. This, however, is not the place for a general account of the developments through which our views of the geology of Iceland have passed since the time of SVEINN PÁLSSON, so much the more as the literature already contains several exhaustive dissertations on this theme, among them THORODDSEN's great collective work: Landfræðissaga Íslands, Reykjavík and Copenhagen 1892—1904, HELGI PJETURSSON: Om Islands Geologi (1905), and HANS SPETHMANN: Der Aufbau der Insel Island (1909).

Iceland forms a part of the great North Atlantic basalt region, or, as it is called with a modern term, the Thule Region or The Brito-Arctic Petrographic Province (TYRELL and PEACOCK 1927). To this region we include the whole of Iceland, the Faroe Islands, Jan Mayen, the most of Franz Joseph's Land, as well as peripheral parts of Scotland, Greenland, Spitzbergen and King Charles' Land; we may reasonably add the two submarine plateaux Rockhall Bank and Porcupine Bank in the Atlantic west of the British Isles. The whole of this region has a pronouncedly eruptive character, and the predominating rocks are basalt lavas. Iceland's peculiar feature, in contradistinction to the other parts of the region, is the occurrence of a very complicated rock series that forms such a decided contrast to the regularly deposited basalt strata that the very founder of Icelandic natural science, EGGERT ÓLAFSSON, distinguishes between "regular" and "irregular" mountains, and thus draws attention to the two predominating surface forms of the country, widely different as they are petrographically as well as morphologically.

In the course of time the "irregular" formation has been known by several names, i.a. the breccia formation, the tuff formation, the palagonite formation, and many others. The latter name especially has played a part in the literature on Iceland and is probably the one most frequently used, despite the fact that its justification has been seriously doubted. It was first used by SARTORIUS VON WALTERSHAUSEN, because he found a brown or yellow substance, palagonite, in certain of the rocks of the formation, and this he presumed to be a separate mineral. In 1879, however, PENCK showed that this was not the case, and he even went so far as to say: "Es darf gerechtfertigt sein anzunehmen, dass ein als Palagonit zu bezeichnender Körper nicht existiert." All the same, the term palagonite formation has been used by most writers right up to the present day, though with some reservation and criticism. THORODDSEN used it as late as in 1914, and v. KNEBEL-RECK even wrote (1912, p. 108): "dem Palagonittuf, wie es seit dem klassischen Untersuchungen SARTORIUS VON WALTERSHAUSENS nach einem seiner Mineralbestandteile genannt zu werden pflegt." In his earlier works Pjetursson uses the term "the glacial palagonite formation", but in later works tries to get away from it. In recent times, however, the Scottish petrographers MARTIN A. PEACOCK and G. W. TYRELL, have resumed the use of the term in the form of "The volcano-glacial Palagonite Formation". On the basis of modern petrographical examinations of the rocks they assert that, although palagonite may not be a mineral, it is a petrological substance of such a consistence that it is justifiable to set it up as a separate mineraloid, i. e. a naturally occurring, homogeneous, amorphous substance with such a constant complex of properties that it can be verified petrographically, and, even if in point of quantity it forms no great part of the rocks in question, it is so characteristic, and so important a component to our understanding of the creation of the formation, that we ought to continue to use the term without reserve.

According to TYRELL and PEACOCK, the finer-grained Icelandic tuff deposits of glacial age may be characterized either as sideromelan tuffs or as palagonite tuffs.

"Sideromelan is a black, lustrous, most anhydrous basalt which is pale coloured and translucent in thin section; it is known only in fragmental volcanic ejecta. In Iceland, sideromelan is a product of drastically chilled, sub-glacially extruded basalt magma. This mode of formation results in the invariable fragmentation of the material and the inhibition of ore-separation producing the characteristic translucency. Sideromelan tuffs are found near the margin of the present ice-sheets at heights up to 2000 feet. Sideromelan may be classed as a mineraloid.

"The palagonite tuffs are the older sideromelan tuffs which have suffered hydration, usually by submersion or by hot-spring action.

"Palagonite is the hydrogel of sideromelan. It is a yellow, colloidal material containing up to 28 per cent. of water, the greater part of which is liberated at 105 C. When hydration has taken place at low temperatures by submersion, isotopic gel-palagonite tends to form; when hydration results from hot-spring action, obscurely birefracting fibro-palagonite is the main product. The change from sideromelan to palagonite is further accompanied by a partial loss of lime and soda, an almost complete oxydation of iron and a progressive lowering of refractive index.

"Palagonite is unstable; it tends to crystallise with a partial loss of water into chlorites and zeolites." Tyrell and Peacock 1927.

According to these investigations the occurrence of sideromelan and palagonite in the Icelandic "palagonite formation" is a consequence of that series having been partly formed by subglacial eruption, sideromelan being the primary product, whereas palagonite is the product of a subsequent hydration of it, a process called by these writers palagonization, and thus it is warrantable to maintain the use of the name palagonite formation, provided that the views advanced above prove to be tenable.

A general stratigraphical treatment of the Icelandic series is an undertaking of the greatest difficulty, for it has not been possible to find even one continuous horizon that can be identified with certainty, neither by faunistic, floristic nor petrographic methods; as a consequence we lack definite guides in our stratigraphical orientation. The principal reason is that fossiliferous strata are very rare and of slight horizontal extent. It is true that the petrographic differences are considerable; we find eruptives of different types, glacial and volcano-glacial deposits, marine, æolic and lacustrine sediments, and in so far one might presume that there was a possibility of a stratigraphy on a petrographic basis; but the characteristic feature of these deposits is that they are of purely local nature as a rule and that the country has been built up by the activity of innumerable locally-governed forces. The result of working stratigraphically is thus that one's material becomes a series of elementary phenomena whose mutual relationship is very difficult to establish.

And, indeed, we find the most widely diverging opinions on the connection, chronology and dating of the Icelandic series. The main features of the course of developments are as follows:

Krug v. Nidda (1834) assumes that the western and eastern parts of the country are older than the central part, but this theory is strongly contradicted by later writers, such as Sartorius v. Waltershausen (1847), who avers that the whole country lies on a foundation belonging to the palagonite formation on which the ligniferous deposits and large layers of trachyte lie. During the next half century opinions change completely, for in that period two important features in the geological structure of Iceland have been ascertained. Although with some uncertainty, the age of the lignite deposits has been fixed at Tertiary (Miocene), and the presence of moraines and the marks of glacial erosion on the present surface of Iceland has been proved — results that are partly due to the progress made in Icelandic exploration itself and partly to the great improvement in the science of geology in that period.

The chronological sequence of the series was set up by Thoroddsen in the following schema, which appears in his work of 1899 and which is the foundation for his later writings on this subject:

a. Alluvial and diluvial deposits.
b. Preglacial dolerite.
c. Volcanic palagonite formation.
d. Basalt formation with interbedded miocene lignite deposits.

The year before, Thoroddsen had concluded his systematic travels in Iceland, the untiring and, in many respects, fundamental work of eighteen summers. The schema above gives us the results compared with the results of half a century's investigations, now revised and collected by the tremendous effort of one man. And then, the very same year the strange event occurs that the student Helgi Pjeturss(on) makes a discovery that will always ensure his name a prominent position among the scientists who have been of importance to the exploration of Iceland.

Thoroddsen, and all other investigators too, assumed that the dolerite and the palagonite formation were preglacial; but now Pjetursson, under the dolerite in the palagonite formation, found series that undoubtedly were moraines and rested on surfaces striated by ice. The necessary inference was that both the "preglacial" dolerite and the palagonite formation must be placed to the Quaternary, which of course upset Thoroddsen's schema. During the subsequent heated debate between Thoroddsen and Pjeturss(on) the latter added to his material concerning the occurrence of moraines in the Icelandic series. He observed several superimposed moraine horizons not only in the palagonite formation but also in the upper series of some basalt regions.

There is a collective account of these matters in the work of 1905, where Pjeturss(on) arrives at the following conclusions: Iceland is built of an early, regional, and a later, insular basalt formation, between which there is very great unconformability. Possibly the volcanic activity was at rest in the period corresponding to this; there was considerable erosion, and a series of marine sediments, ascribable to Crag, was deposited. Towards the end of the Pliocene period the volcanic activity started again, resulting in the insular basalt formation between whose dolerite beds one finds quaternary moraines, glaciofluvial deposits, as well as marine glacial and interglacial deposits. The considerable quantities of tuff and breccia that are found in the upper parts of the insular basalt system are the ruins of pleistocene volcanoes. The postglacial volcanism is a continuation of the pliocene. The terms regional and insular basalt formation are used as expressing the following views: The regional basalt formation is that part of the Icelandic series that was formed while the land bridge between Great Britain and Greenland assumed by many writers to have existed was still there, whereas the insular basalt formation did not appear until after the bridge was broken down and Iceland had become an island. The upper part of the regional basalt formation is built up of rather light-coloured dolerites, the grey stage, in which there are both moraines and striæ, and as that stage is assumed to be earlier than Crag, Pjeturss(on) arrives at the conclusion, surprising to the reader as to himself, that one must assume the occurrence of widespread ice-sheets in the Tertiary period, i. e. at a time when, to use his own words, one should rather have expected to find remains of great forests.

Later investigations, however, have made Pjeturss(on) doubt the tenability of these latter views. Based upon a series of observations in southwest Iceland he arrives at the conclusion that "man am richtigsten tut, die Annahme vom tertiärem Alter der Glazialbildungen der "regionalen" Basaltformation fallen zu lassen" (1907, p. 618); but, as his paper of 1908 shows, Pjeturss(on) has not entirely abandoned the idea of the tertiary (miocene) moraines, although he adds: "Unterdessen hat man noch keinen palæontologischen Beweis für ein miocänes Alter dieser Altmoränen erbringen können, und so werden wir wenigstens vorläufig zu der Annahme hinneigen, dass die ältesten noch aufgefundene Glazialbildungen Islands wirklich dem Eiszeitalter entstammen." In his 1910 work the "miocene" moraines are not mentioned, and thus it is indeed natural to abandon the terms regional and insular basalt formation and, instead, to differentiate between Tertiary and Quaternary formations, the latter then being divided into Early Quaternary and Late-Quaternary.

The result of this interesting sequence of developments is thus that, thanks to Pjeturss(on)'s works, we have arrived at a new view, nowadays generally recognized, of the stratigraphy of Iceland; its central point is that under the Quaternary we have to place not only the palagonite formation but also the latest part of the "basalt formation" which was formerly regarded as a continuous stratigraphical unity; in order to avoid the terminological difficulties arising out of such a radical rearrangement of opinions Spethmann (1908) suggests the following terms for the main grouping of the Icelandic series:

1) Postglacial systems,
2) The glacial-volcano formation,
3) The Tertiary-volcano formation

whereas Pjeturss prefers the terms "the Tertiary" and "the Quaternary basalt formation". A more detailed survey is to be found in Pjeturss' work of 1910, on which the following synopsis is mainly based.

The postglacial systems are formed partly of eruptives, both lavas and loose products, and partly of sediments of marine, lacustrine, fluviatile, æolic, glacial and organogenous origin.

The Quaternary formations may be placed in two age groups, an early and a late, both well-differentiated in a petrographical sense but otherwise imperfectly known. To the late group belong several series of glacial deposits, viz. one or perhaps several systems of quite late, unhardened moraines. Interglacial and interstadial deposits occur at the coast in the form of marine sediments, and probably the extensive, superficial, doleritous lava streams that are so characteristic of the southwest country and parts of the interior highlands, may possibly be assumed to have been formed in interglacial times. The early group is represented by a series which, according to Pjeturss, has a thickness of 6—800 m., most of which is of eruptive origin and composed of basaltic lava separated by glacial, moraine-bearing and interglacial, fossiliferous sediments.

Pliocene deposits are known as a mostly sedimentary series of a thickness of at least 700 m. (Bárðarson 1925), whose extremely fossiliferous content indicates a transition from a temperate to a boreo-arctic climate.

Pre-pliocene deposits form a thick series measuring at least 3000 m. and consisting most of all of basalt layers, intrusive rocks, loose volcanic material, and æolic (Hawkes 1916) and organogenous sediments. The latter are of vegetable origin and occur in many localities in both the northwest and east, some of them in the form of inorganic deposits with slight admixture of organic substances, and partly as pure lignites. It is held that the flora represented in them is of miocene age; but there are certain indications that the lignites in the different parts of the country are of somewhat different ages. Below the lignites are very large basalt layers, which must thus be taken to be miocene and pre-miocene, but what underlies them is not known, and there is nothing definite to work on when attempting an estimate of the time of their formation.

Roughly, the regional distribution of the different formations is: The Tertiary volcano formation or basalt formation crops out on the surface in two regions, viz. the west fjords and the east country, but in great parts of the country it is overlain by Quaternary deposits and can only be recognized where tectonic and erosive changes have exposed it. The postglacial eruptives crop out for the most part along a rather narrow zone from Axarfjöður in the north to Reykjanes in the southwest, and they are of widest extent in Ódáðahraun, the country west of Vatnajökull, the Hekla region and the Reykjanes peninsula. The distribution of the deposits on the surface is mostly symmetrical in relation to the southwest—northeast line mentioned, and is so arranged that the latest deposits lie along this zone and the earliest farthest away from it.

In the terrain west of Vatnajökull no fossiliferous deposits have been found, and the character of the rocks provides only little guidance for a definite determination as to age. Uppermost lies a series of recent rocks having the appearance of being even particularly late. Its various facies will be dealt with in greater detail when describing the landscape forms; at this point it need only be said that one mostly meets with late lava fields, loose volcanic material and rebedded sand of æolic origin; the recent moraine material is of little importance, whereas one comes across glacio-fluvial deposits of considerable extent and thickness. In contrast to these present-day deposits is a series of rocks that is exposed in the higher parts of the terrain. The stratification shows that they were deposited and hardened before the depositing of the recent series. Furthermore, in the interval there had occurred a considerable difference of level between the various parts of the landscape, mostly the result of tectonic processes. The rocks in the early series are mostly tuffs, but there are also quantities of breccia of undoubtedly volcanic origin, grey, basaltic lavas, and lava with the peculiar globular structure that is now taken to be a sign of subglacial origin. Breccia has been observed in Túngnárfjöll, in Skálafell, Þóristindur, in the regions east of Þórisvatn and at Botnaver. Basalt with globular structure is found in large quantities in the eastern part of the area, in the foreland of Vatnajökull and in the region near Heljargjá.

The rocks very closely resemble certain complexes from the palagonite formation in the southwest of Iceland, but moraines have not been found between the Kaldakvísl and the Túngná, and, if there are any there, they are at any rate insignificant. It is scarcely to be doubted that they belong to the same main group of Icelandic formations, but they have been formed in a rather different manner than the glacial volcano formation in southwestern Iceland. Finds of dolerites in the blasted debris from certain volcanoes indicate that deep down there are deposits of these, but the violent volcanic activity in the area has covered up the early deposits. On the whole the different petrographic condition of this region must be placed in connection with this volcanic activity, which has probably extended for a long period, perhaps so violently that a glaciation in the usual sense of the word could not proceed, and which has resulted in the depositing of a layer of tuff about 300 m. thick, now to be seen in the southeast part of this region. If there is any early moraine material, it is probable that in some places it has been so much disturbed by volcanic action that it is now extremely difficult to find it.

In the region round the Kaldakvísl there is another type of landscape, recalling that common to the west highlands. There one meets large, doleritous, striated layers with a southwesterly dip. The striæ run in the same direction, and overlying the dolerite is a deposit of moraine material with several boulders, dolerite as well as liparite. Fig. 26.

Conditions in Sauðafell are very interesting and call for further attention. The mountain rises about 300 m. above the plateau and is to be seen from great distances on all sides. Its ground area is about 15 sq. km., while its greatest dimension lies in a northeast—southwest direction. For the most part the rocks are tuffs, but among them lie doleritic lavas and hardened moraines. The slopes of the mountain are quite even and the profile line differs greatly from what one sees for instance in the mountain Loðmundur, which otherwise is built in quite an analogous manner. As these two mountains each represent a type in the Icelandic landscape they must be dealt with in greater detail.

Loðmundur has a ground area of about 5 sq. km. and a relative height of about 500 m. Its petrographic composition is quite the same as that of Sauðafell. Both mountains contain tuffs, breccia and hardened moraines, and at the top they both consist of tuff and breccia. The walls of Loðmundur are very steep, and are regularly so on all sides. At the top is an almost vertical surface, 100—200 m. high, running into a talus at the foot with a dip of about 45 degrees. At certain places the vertical edge is broken by some clefts where the talus runs right up to the uppermost edge of the mountain, and by means of these clefts it is possible to climb it. From a distance one does not observe these small irregularities, and the mountain looks very compact and uniform. The profile of the upper edge is serrated and sharp, and one gets the impression that the lateral superficies intersect in a sharp ridge. Having climbed it, however, one sees that on its summit the mountain has a small plateau surface of about 2 sq. km. with some small rounded hills and a few sharp pinnacles, of which the highest, reaching about 50 m., stand along the north edge of the plateau (Fig. 47 and 48). They have been formed by the weathering of a volcanic breccia. On the top one finds evidence of a temporary water erosion of the same type as that referred to later on p. 71, 253. There are several ponds, patches of snow that have withstood the summer, and traces of a lively solifluction. As already indicated, the walls are so steep that climbing is impossible in most places. The edges between the plateau surface and the sides are quite sharp, and the clefts referred to are narrow and not conspicuous in the terrain. The material carried by solifluction to some extent slides down towards the clefts, which in summer are dry, but undoubtedly lead water when the snow is melting, and this brings about a sorting of the material, the finer being washed down into the surrounding depressions while the coarser remains in washed state on the slopes and moves down at a much slower rate.

This form of mountain is extremely characteristic of large parts of South Iceland, where in certain cases the great mountain masses completely dominate the landscape. Very often they appear to be quite young, especially on account of the almost complete absence of traces of water erosion, despite the fact that swift streams are formed down the sides every year. Sometimes the formation of the plateau surface is petrographically indicated. If at the top a mountain has a cap of lava with underlying, less-resistant rock such as tuff or breccia, the subaerial denudation will not attack the upper edge of the mountain side so fiercely as further down, and in these cases there is a tendency towards an undermining of the edge, resulting in a landscape form of an habitually similar type, characterized by the occurrence of a high plateau surface with steep slopes down towards lower surfaces surrounding it. The forming of the "Tafel-Form" ("table" shape) in some cases must thus be associated with the activities of denuding forces. Loðmundur and many other mountains of the same shape, however, have no such protecting cap of lava, and, as will be explained later, one must assume that they have been formed by the activities of tectonic forces, so that they must be regarded as being horsts.

On Sauðafell there are two separate sets of traces of an ice covering which cannot be contemporaneous. One set forms a part in the structure of the very core of the mountain and is overlain by lavas, breccia and tuffs; it contains striated stones and has hardened in the manner characteristic of early Icelandic moraines. But in addition there are traces of another and later glacial activity, which has first taken place when Sauðafell rose as it does now up over the surrounding plateau surfaces. For in the higher parts of the mountain there are traces of a radial ice erosion of modest extent, but sufficiently powerful to cause veritable Botn-formations and striae that are not orientated in relation to the main direction of movement of the ice down the fall of the landscape, but appear clearly as local formations associated with a local ice-sheeting process, the direction of whose movement was governed by the difference of level between Sauðafell and the surrounding plateaux.

This duality in the ice traces is confirmed by another observation, likewise from Sauðafell. There are two mutually unconformable moraine series, and in the youngest of these there are boulders of earlier, hardened moraine material. This can only be explained in one way: that there must have been at least two glaciations, with an intervening period in which the first series of moraines became hardened and overlain by lavas. In certain places a later ice sheet has had an opportunity to erode the earlier moraines and has carried lumps of them away in the form of boulders.

In this period between two ice sheets there must also have been a difference of level between the higher and the lower parts of the present terrain. How this has happened has scarcely been laid clear in all cases, but on Sauðafell it is reasonable to assume that there have been tectonic changes. Whether or not the same interpretation may be applied to the mountains in the other parts of the highlands of Iceland has not yet been established and of course must be investigated in every case. In some, however, one must assume that it is tectonic processes that have been active.

The question of a plurality of glaciation within the borders of Iceland has already been treated on a former occasion. On the coast there have undoubtedly been pauses — and long ones at that — between the periods. This is shown by the occurrence of considerable interglacial deposits, of the presence of which we are gradually learning in various Icelandic localities, among them being especially Fossvogur and Snæfellsnes. These deposits are marine and contain so much fauna that their identity is not to be doubted. It is another matter whether several ice periods can be proved in the interior. No interglacial deposit of limnian character has been found, but there are other signs of interglacial periods. In the first place v. Knebel found in South Iceland unconformable moraines between whose deposition a very long space of time must have elapsed. It must furthermore be assumed that the great layers of dolerite must have erupted at a time when the highlands were not covered with ice over a stretch comparable with the present one. For as far as we know, streams of lava do not form under ice, while the position is that the dolerite layers rest upon moraine-bearing material and that on their own upper side they have striae and a layer of moraines. In the highlands these dolerite layers are to be found at a height of at any rate up to 5—600 m. above sea level, and to that height the land must have been free of ice — probably still higher. The lava-dome Baldheiði, east of Langjökull, with a height of about 740 m., must have been ice-free almost to its top. And not only that: if there have been still higher parts of the country, the ice moving down from them cannot have got down to the present plateau surfaces; in other words, during the eruption of the dolerite layers the ice cannot have had a much greater extent than it has at present, with the consequence that the snow line in the last interglacial period must have gone back to the same level as it has now; this corresponds very well with the conclusions regarding the climate at the coasts that can be drawn from the composition of the fauna in the interglacial, marine deposits.

4. Volcanism in the highlands west of Vatnajökull.

As has been stated, a number of circumstances indicate that volcanism in this part of Iceland has been very active during the last glacial period; its traces, however, are very difficult to find, because the later volcanic and æolic activity has been so violent that it has covered the signs. The latest eruptions in the neighbourhood are of a very youthful character and it is probable that the processes have not yet discontinued. Thus we must be prepared for further eruptions in this part of the country and, as we may take it that they will be of the same type as those immediately preceding them, i.e. mass eruptions, they will provide a most interesting study, though suffering from the drawback that the area is difficult of access.

The more recent volcanic activity is not evenly distributed over the whole region, but is concentrated in three fields that are well separated topographically, and as they exhibit typical differences with regard to the course of the eruptive processes, it will be natural to deal with them one by one. The most northerly centre is in the region east by south of Háganga syðri, and, as the recent lava fields there are known under the name of Hágönguhraun, this term will be used in this work too, despite the fact that the two mountains themselves, Háganga nyrðri, and syðri represent a peculiar type of eruption differing considerably in point of time, as well as petrographically and morphologically, from the mass eruptions in Hágönguhraun and for that reason will be dealt with in a separate chapter (d) of the present account. South of this region is a volcanic field whose most prominent topographical peculiarity is that it encloses the lake group Fiskivötn; and finally, the system of volcanic eruptions that have taken place in the northern part of Landmannaafrjettur, in the vicinity of Frostastaðavatn, must be regarded as separate. Thus the following account of the recent volcanism in the highland west of Vatnajökull may suitably be divided into four sections.

a. The Háganga Region.

This volcanic field lies between the upper course of the Kaldakvísl and the northwest corner of Vatnajökull, and comprises a number of vents, some of them in the foreland of the glacier itself, some of them in the terrain in front of it up to a distance of 15 km. from the present ice margin. For the most part the eruptions have been in the form of basalt mass eruptions with an enormous output of lava, and only in few cases have insignificant examples of eruptions of other types been found. As map No. 1 shows, the masses of lava have a very considerable horizontal spread, about 440 sq. km., and as they are also of great thickness, they have succeeded in giving character to the landscape, both morphologically and topographically, even at great distances from the vents; but, despite this enormous productivity, it is only possible by means of very close study to show whence the various streams of lava have come, because the accumulation of material round the vents is so small that they are not at all prominent on the terrain.

The pre-eruptive terrain, i.e. the terrain prior to the present eruptive activity, has had a marked influence upon the distribution of the products of the eruptions. Taken as a whole the terrain slopes to the south and west, the pass between Túngnafellsjökull and Vatnajökull representing a point on the northwest—southeast axis of elevation. This general direction of fall, however, is interrupted by two large valleys running northeast—southwest, watered by the Kaldakvísl and the Túngná respectively, both of which have exercised an influence upon the spreading of the lava.

Apart from these valleys (their effect upon the terrain will be dealt with later), the pre-eruptive landscape is built in the form of a plateau land with two different surface systems, each forming its distinctly marked terrain stage. One is formed of a continuous plateau surface, on the south lying about 500 m. above the sea and from there rising evenly towards the northeast until, in the region of Vonarskarð, it reaches a height of about 900 m. The other stage is represented by a number of separate mountain regions rising from 200 to 500 m. above the plateau surface, so that its upper part lies at a height of from 900 to 1600 m. above the sea. These mountains have steep sides, but on the top they are flat and have the form of high plateaux whose areas vary within very wide boundaries. The largest is Gjárfjall, with a plateau surface of about 100 sq. km., but it is possible to make out numerous smaller hills whose area forms only a fraction of a square kilometre; between these extremes are all possible sizes. Thus the terrain is formed of three principal elements:

1) The low surface system.
2) The high surface system.
3) The slopes between them.

As will be shown later, the difference of level between the two surface systems generally must be taken as being due to the activity of tectonic forces.

The places of eruption are not definitely associated with any one of these landscape elements, but are situated both in the high and in the low surface systems, and sometimes in the slopes between them. Regardless of their situation, however, the lava is spread on the lowest surface system whereas the high plateaux are mostly bare of it.

Most of the vents in the northern part of the region are linear eruptions, though some of the lines are quite short and thus form a smooth transition to the group of central eruptions. The material erupted is almost exclusively lava, but there are examples of stratic eruptions, as for instance at Botnaver, where, in the immediate vicinity of the edge of the ice, amid the moraines and glaciofluvial deposits from the present ice margin, there are several volcanic cones. Several of the mass eruptions have had a final phase accompanied by the eruption of adhered slag, which has been carried by the lava streams up to several kilometres from the vents; this is observable at the two fine scoria craters Gámur and Gima in the southern edge of Vatnsleysuöldur.

Between Kerlingar and Vatnsleysuöldur are at any rate three large fissure eruptions lying parallel in the direction of northeast—southwest. Two of the fissures are only a few kilometres long, but the middle one has a length of about 15 km., and is thus one of Iceland's large volcanic fissures. It is, if anything, right-lined and, as is usually the case with this sort of phenomenon, has split the terrain regardless of the hindrances that were there. Both edges of the fissure are marked by a continuous mound, formed at the concluding phase of the eruption by the ejection of lumps of plastic lava which, while coagulating, have been welded together into a porous mass. Only here and there have the mounds a height of 50 m., and their volume is thus negligible in comparison with the quantity of lava produced, so that one must design these eruptions as mass eruptions.

The lava is basalt, coal black, and torn and irregular in the forms it has assumed on cooling. In certain parts of the area of its spread, particularly close to the places of eruption, the upper layer is very porous and of a consistence resembling cinders, whereas the lower layers of the streams — 10 to 15 m. deep at any rate — have coagulated in coherent and compact form.

As a result of the direction of the fall of the terrain described above, the lava has spread very little towards the east, whereas towards the north it has gone up on to the plateau that is called Köldukvíslarbotnar and has advanced to the southern part of Vonarskarð. It is possible, however, that the lava in this area partly originates from other vents as yet unknown; but the situation is not very clear because the meltwater rivers from Vatnajökull have covered the whole of the surface with a thick layer of glaciofluvial gravel and sand. On the northwest it has spread right over to the foot of Háganga syðri, and on that stretch has forced the Kaldakvísl to turn westwards and erode a narrow gully in the very mountain side. The pass between

Háganga syðri and Vatnsleysuöldur is likewise filled with lava, and there the Kaldakvísl has formed a very shallow bed across the lava; at the south edge of it the river falls down into a deep cañon in the form of great waterfalls and rapids. The parts of the lava moving west of the Kaldakvísl have met with rather rugged terrain, where it has split up in the depressions in the form of large tongues, flowing round the higher parts of the pre-eruptive surface. Here we have an example of the commencing stage of the formation of a volcanically filled-up plateau, characterised by a net of anastomosing lava streams, between whose branches the pre-eruptive surface still emerges like islands. The edges of the streams take the form of block walls 10 to 15 m. high, and this would thus seem to be the minimum thickness in this part of the region.

The eastern edge of Vatnsleysuöldur has cut off the advance of the lava westwards, and only at the south edge has it found a way through the 7—8 km. wide pass between that mountain and Gjárfjall on the south. Through this pass, which is filled from one mountain foot to the other, mighty streams have run down into the lower land on the south and west, where they have spread right over to the Kaldakvísl.

On this stretch the course of the river has also been much disturbed by the eruptive masses. At those places where the lava has got down to the valley of the river the latter has been forced out in curves towards the west, where it has been compelled to form new courses, usually of the cañon type. Above the places where it was dammed there are areas with only a slight fall where the river branches and has deposited flat areas of gravel.

Most of the lava has, however, rounded the northwest corner of Gjárfjall and has run towards the south and southwest. The southwest part of the stream has made its way between the wide depressions down towards Þórisvatn, where the water level and outlet have been greatly influenced by lava embankments; this circumstance, of which there are parallels in many other recent-volcanic areas, will be dealt with at greater length in the chapter on hydrographic conditions. The streams that have run southwards have spread into enormous layers out over the plateau surfaces down towards Fiskivötn; the lava has not stopped until it got about 50—60 km. away from the vents, sometimes forming block walls, at other places like a slab of a few metres thickness, the smooth coagulation forms bearing evidence of the fact that the course of the lava has ended there without disturbance of any kind. The occurrence of numerous small areas of pre-eruptive surface, jutting up through the covering of lava, indicate that the thickness of the stream there in the border zone has been much less than in the central parts of the area of eruption, but nevertheless has been sufficient to conceal all the details of the pre-eruptive relief; thus the landscape appears as a **lava-levelled plane.** Fig. 3.

After this series of giant eruptions has run its course there have been a number of smaller eruptions, by which both the extent of the lava fields and the thickness of the layers have been somewhat increased. South of Gjárfjall there has been an eruption of lineal form which has produced very considerable masses of lava, although owing to the terrain their extent is slight in comparison with those just described. Another recent volcanic field has been formed in the southern slope of Vatnsleysuöldur. In this case, too, it has doubtless been a fissure eruption, but its length is very slight; nevertheless it has produced very considerable quantities of lava which, through large canals (now collapsed) has spread out over the earlier lava fields from the fissures on the east over towards both Gjárfjall and the southwest down towards Þórisvatn. The situation of the eruption fissures is marked by two very fine adhered-slag scoria craters, Gámur and Gima, of which Gámur as the largest reaches a relative height of 50—100 m. The lava as it streamed out has broken great clefts in the ring-shaped mounds of scoria and has carried enormous quantities of loose material down to the plains below, where the lava at good distances from the vents is covered with an almost unbroken carpet of loose scoria of a remarkable, distorted form.

The last mass eruption in this region came from a fissure lying to the west of the principal fissure referred to above, between it and Vatnsleysuöldur. From it the lava has exclusively spread over earlier lava fields and thus has merely increased the thickness of the layers, but not their extent. In a morphological sense this stream contains several interesting details which will be dealt with in greater length below. The spreading of the lava has been greatly affected by a tectonic disturbance which has taken place in the period between the older series of eruptions and the very recent mass eruption just referred to; it has led to the forming of a subsidence, Heljargjá, as to which more information will be given in a later chapter. When the youngest lava on its way to the southwest met this fissure, it has fallen over the brink in great cascades and has covered the whole of the northern part of the bottom of the fissure with an indescribable confusion of blocks. It is doubtless an offshoot of this same stream that has filled Heljargjá at the point where the fissure runs into Gjárfjall, and has also been able to send a long tongue of lava further along the mountain side on top of the old lava from the Háganga fissures and right down over the lava from Gámur.

With the time and labour at our disposal it has not been possible, however, to make these matters clear in all their details, as the manner in which the lava has spread and come to rest is difficult to account for in any other way than by simply following the various streams throughout their entire length, and as, owing to the torn structure of the lava fields, these journeys represent such long and wearing toil that we have been quite unable to complete them, we have had to be content to try and establish the lines of distribution by means of binocular observations from the heights of the region Háganga, Sauðafell, Vatnsleysuöldur, Gjárfjall, the mountains at Kerlingar and those at Þórisvatn; these observations have then been worked into the results of four or five journeys across the lava fields.

While the principal mass of the lava has, as we have seen, run towards the south and southwest, smaller quantities have found their way south, east about Gjárfjall through a valley along by the ice margin of Vatnajökull between Kerlingar and the mountain which DE FONTENAY has given the name of Hádegisfell. Towards the north the valley is three or four kilometres wide, but midway between Kerlingar and Botnaver it shrinks in to a very narrow port a few hundred metres wide, through which the lava has poured like a foss down towards the plains on the south. This port has probably been formed by the Túngná's northern tributary, which rises at the ice margin north of Kerlingar and follows the glacier in a curve right down to Botnaver; the lava, however, has forced the river out to the side, where it has cut itself a steep-walled channel in rock belonging to the glacial volcanic formation. After breaking through, the lava has spread into a region that is also the scene of local eruptions, most of which are isolated central eruptions with a very considerable lava output and a concluding phase in which the production of adhered slag has been predominant. Certain signs indicate that the two lots of lava are almost contemporaneous, but we have only been able to spare a very short time for the investigation of this area, and so I would not venture to attempt any definite interpretation of the events that have led to the bringing about of the conditions now prevailing. That the thickness of the lava fields is very great appears from a consideration of the subsidence areas, up to 10 m. deep, of which there are many in the terrain north of Botnaver and whose form and distribution show that it is not tectonic changes that have been the cause, but that they are subsidence holes caused by contraction or branching out in lava masses of great thickness. The pre-eruptive terrain, at any rate in the northern part of the plain, is completely effaced and the lava has spread as far south as down to the Túngná southwest of Botnaver, where at high water the river has gone up over the lava and has covered a part of it with glaciofluvial gravel.

There are small eruption fields in several other places in the terrain. Mention may be made of a small stratic field just north of Botnaver, a few hundred metres from the edge of Vatnajökull, amid the morass of water-soaked moraines and glaciofluvial deposits that here border upon the ice margin. The output of this field has been very small, and it is scarcely of much interest in a volcanological sense; but it displays the interesting circumstance that the recent volcanic activity has taken place at any rate right up to the ice margin and that at this spot the glacier has since the end of the eruption remained behind the line that is marked by the situation of this field.

The whole of this extensive volcanic region, the Háganga region, has developed with very little variation as will be seen from the above description; it has exclusively been the scene of mass eruptions, and in this respect it forms a pronounced contrast to the Fiskivötn region on the south of it, where matters are very varied as regards the nature of the eruptions. But in the most southerly part of the lava fields formed from the Háganga region there are some volcanoes, purely local and isolated, of a type that is different to those just referred to and form a transition to the volcano forms prevailing at Fiskivötn. Thus in the west edge of the lava fields at Botnaver there is an oval lake with a basin that must doubtless be regarded as a maar formation. Unfortunately we did not get so far as to make a close examination of its surroundings, and therefore no definite statement can be made; but quite habitually it is very like a maar-lake even if other interpretations cannot be rejected.

There is no room for any doubt as to two enormous maar's east of Þórisvatn in the southern part of the lava fields. Their dimensions are almost the same, the diameter of both being about 1 km. and the maximum height of the surrounding gravel mounds is about 200 m.; that on the north is circular, that on the south oval, with its greatest length lying southwest—northeast. The mounds consist partly of substratum dipping periclinally in relation to the vent of the eruption, and partly of rejected volcanic gravel of small grain; both volcanoes must be placed to the type described and set up in the following as a special type and named blast crater. It is peculiar that they both lie on the line that has been struck by the aforementioned tectonic fissure Heljargjá and that the long axis of the oval eruption coincides with the direction of the fissure. The ages of the various processes at this spot appear from the following observations: The thrust has affected both the "maar"s and the surrounding lava from Hágönguhraun, and must thus be assumed to be later than both these eruptions, while the distribution of the lava shows that both explosive volcanoes are older than it is. At the "maar" on the north conditions are especially very clear and perspicuous. Its bottom has lain much below the surface of the lava field, and consequently the stream has made its way into the already existing basin and has filled it, and, as coagulation here has proceeded under uncommonly quiet conditions, the surface has assumed the form of an unusually regular and finely developed sheet-lava, consisting of circular shields of a diameter of 20—30 m. These features show with certainty that the "maar"-basin is older than the Háganga lava. Fig. 7.

The situation of the two explosion volcanoes on the same line as the later fault naturally brings up the question of whether we may assume that there has been any direct or indirect combination of causes between the two phenomena. As the distribution directly shows, it is not probable that the fault is a consequence of the volcanic outbreaks, for there is no reason at all why two relatively small eruptions of loose volcanic material should have a tectonic, disturbing effect along a lineal zone of a breadth of 1 km. and a length of about 30 km.; furthermore, the volcanoes are at one end of the fault, and there is no trace of volcanic activity along the whole of the remainder of the fissure. Then the question remains as to whether the coincidence is merely accidental or whether in that zone, prior to the eruptions, there has been a structural peculiarity which may have tended towards the occurrence of both eruption and fault; it is possible that there may have been a previously formed line of weakness that has first served as a channel for the eruptions and thereafter as a zone of release for tectonic tensions; from the observations so far made, however, it is impossible to settle the question definitely.

Surface forms of the lava.

In the lava area that has originated from the eruption field dealt with in the foregoing the detail of the surface forms varies considerably. There is every possible stage between the smoothest plane surface sheet-lava (Icel. Helluhraun) to the wildest block lava (Icel. Apalhraun).

The impression given by a field of lava of this kind seen from a distance, whether of the one or the other type, is that the landscape is a plain of strikingly uniform structure. One sees nothing but endless black spaces devoid of valleys and heights. The fall in the direction of the lava diffusion is so slight that from a distance it is usually impossible to determine from which direction it has come. Nor can the eruption vents be seen in a mass-eruption area, as already indicated. Mostly the surface is only broken by the higher parts of the substratum which in some cases jut up like islands over the lava sea. The lava fields of the Icelandic highlands look completely desolate; no green breaks the blackness of the land, animals are very seldom seen, everything is uniformly black and dead. Fig. 4.

To the inexperienced traveller a lava field looks easy to cross — and even veteran Iceland travellers are time and again misled into underrating the difficulty of getting over even very narrow spurs.

Whereas the distant impression is one of unique constance from a landscape point of view, one's close-up impressions change rapidly. As already stated, one can distinguish between two main forms of surface: sheet and block lava, but these two forms are not sharply separated, and in many cases it is a matter of taste whether one applies the one or the other term. Fig. 7 shows the sheet lava in its pronounced form, the simple explanation of which is to be found by making a study of the circumstances under which hardening proceeded, cf. p. 28, 210. The other extreme form, typical block lava, is represented by Fig. 8. One's immediate impression is of an altogether irregular, chaotic, piled-up mass of blocks with jagged, pointed and sharp edges, heaped up pell-mell with wide intervals between the various blocks. The points and edges are often brittle and easily broken off, and even blocks weighing many tons can be made to topple over without much effort. In such a block-lava area the only means of advance is by clambering, and it is most difficult to obtain anything like a safe foothold. Even for men who are accustomed to moving about in lava fields and are quite familiar with the difficulties there, movement is most arduous and often risky, and obviously it is impossible to take a horse caravan through.

A more intimate study of this chaos of blocks, however, reveals that very often there is some regularity in the distribution of the unevennesses, which to some extent recall the waves of a storm-beaten sea. In the most disturbed areas one frequently observes an alternation of ridges and valleys running almost parallel to one another. The ridges rise about ten to thirty metres above the valleys, and the distance from one to the other is about fifty to a hundred metres. They are quite narrow-backed, like the roof of a house, and their sides are as steep as the loose piling of the blocks permits. Often they can be followed for a distance of several kilometres in this confusion of blocks from one to five metres high, which show signs of having hardened while in rapid movement; the sides that hardened last very often bear striæ from their collision with the sharp edges of other, already hardened blocks. The valleys must undoubtedly be regarded as fallen-in channels into which the lava has streamed, i.e. mass eruption's analogy to the well-known sub-surface canals of smaller streams of lava, of which such fine examples are to be seen for instance on the west slope of Hekla, where several investigators, von Knebel for instance, have observed and interpreted them. A miniature example in the Fiskivötn region is shown on fig. 17. Lava channels of this kind have, however, only been observed up to a few kilometres from the vents and they seem to be a morphological peculiarity associated with regions where warm and fluid lava streams of great depth have prevailed.

Further away from the vents the lava surface is more even as a rule, and the heights and hollows are of other types than those just described. First of all there are the hornitos formations which have been described morphologically and genetically by other writers, especially by Sapper (1908 and 1910). They form where large quantities of gases have collected in or below the masses of lava and come out into the air when these gases force their way out. Sapper (1908 p. 4) differentiates between primary and secondary hornitos; by the former he understands those formed on the vent itself, whereas those formed out on the lava fields are called secondary. In its typical form a hornitos consists of adhered slag, but sometimes a considerable element of loose slag is included. Another morphological peculiarity is, if not a hornitos formation, at any rate one that is analogous. On the lava fields one very often sees round domes having a diameter of up to 100 metres and a height of up to 10 metres. They give the impression of having been formed as one unit, but most of them are split up by deep cracks. They may be taken to be a kind of hornitos in its preliminary stage, arising when the gases working in the magma have not been powerful enough to break the surface. They can be clearly observed on lava surfaces where there has been an abundance of sand, the lower parts of them being full of sand whereas the domed parts stand out as heights with a clean-blown surface of lava. Fig. 19.

Another type of unevenness occurs when the lava surface hardens sooner than the deeper parts of the stream. As a consequence of the continued movement the surface will be broken up, and the fragments then take up all kinds of positions and coagulate in the form of oblique floes, whose fracture edges jut far out into the air and often form large penthouses while at the same time the surrounding floes are pushed out of position.

One special coagulation form occurs in lava streams of great depth but slight horizontal breadth and slow movement. In several cases the following morphological combination has been observed (figs. I—II). The edges of the stream are higher than the central parts and are pronounced block-lava; inside this marginal zone there is a belt of sheet lava, and in the middle one or more areas with deep subsidences. The figure shows an example of this kind with the height rather exaggerated in proportion to the horizontal length. The difference in height between the block-lava on the margin and the sheet lava inside it has been measured at 7 to 10 metres. These circumstances indicate a very considerable decrease of volume during the cooling process, whether due to contraction during coagulation and escaping air, a reflow of lava in the vent, or a combination of both processes — the latter being the most probable in certain cases.

The lava streams at Hagönguhraun display all these surface types in great variety of form and from place to place. The monotony that is characteristic of one's distant impression of the lava fields is thus broken up on closer examination into a wealth of different detail forms, each of which is an illustration of the course of the volcanic processes just at that spot. As a whole one may say that the lava fields south of a line from Sauðafell to the east are, although somewhat disturbed in places, sheet lava more or less easily passable for a horse caravan, whereas the whole of the northern area is more or less pronounced block-lava. This is particularly true of the youngest of the lavas originating from the very recent vent east of Vatnsleysuöldur. I have seen many quite recent streams of block lava in Iceland, but none even approximately so wild and torn. Fig. 8 gives a faint notion of the conditions, but a very faint one indeed. There are hornitos in several places, and in the vicinity of the extreme edges of the lava streams are the cracked domes shown on fig. 19. Subsidences were especially observed in the lava field north of Botnaver, where the collapsed areas are so extensive that we used them as roads through the lava because the drift sand had collected there and greatly facilitated travelling.

In many of the areas there have been post-eruptive changes. That part of Hágönguhraun that lies north of a line from Háganga syðri was on the east covered with glaciofluvial deposits from the glacial rivers. From the ice margin in Vonarskarð run two large-sized rivers that unite with two coming from the east into a very complicated net. In addition there is a large watercourse that drains the south part of Túngnafellsjökull. All this tremendous mass of water collects and forms the river Kaldakvísl just under the eastern slope of Háganga, but there, as already mentioned, the whole system has been dammed up by the lava streams. As a consequence, the fall north of that point is too gentle, and as all the watercourses carry a lot of mud, large quantities of glaciofluvial material are deposited on the surface of the lava; this again involves that the rivers are constantly changing their course, as figs. 33 and 34 show, and the result has been that the whole of this northern part of Hágönguhraun has been transformed into a plain of sand and gravel, called by Gunnlaugsson Köldukvíslarbotnar. Only here and there are hornitos and other heights visible over the plain.

In the other part of Hágönguhraun the lava surface is visible almost everywhere. Only in the hollows does one meet with deposits of drift sand of a depth of up to a few metres. This, however, holds good of the older streams only; in the young ones there are no sand deposits at all. In the southern part of the area the lava is covered with a thick layer of volcanic gravel; its origin will be reverted to later, as it comes from the volcanic region at Fiskivötn on the south.

Practically the whole of the area is sterile. For over a month we have every day passed over large and small stretches of the area without ever seeing an animal; of vascular plants there are extremely few, but here and there is an impoverished growth of moss and lichen.

The lava fields from the vents southeast of Hágöngur are of considerable size, as map No. 1 shows. Their greatest length is from northeast to southwest and is about 55 km., their greatest breadth about 20 km. The free spreading of the lava to the southwest has been hampered by Gjárfjall, which has forced the lava to make its way through the lower areas east and west of the mountain. The westerly arm is much the longer and, south of Gjárfjall, has spread out into a large continuous plain. The north part of the lava fields, north of Gjárfjall, occupies an area of about 180 sq. km., and the south part, south of that mountain, covers an area of about 260 sq. km., so that the total area is about 440 sq. km. If we assume an average depth of 30 metres — this estimate being very low, by the way — the volume of the erupted lava must be about 13 kubic kilometres.

b. The Fiskivötn Area.

I have called this volcanic region after the Fiskivötn lake group, the most prominent topographical feature in this part of the highlands of Iceland. This is so much the more warrantable as the basins of the lakes are in fact the outcome of the volcanic processes. The total size of the region is about 140 sq. km., and within that area the volcanic forces have manifested themselves very violently and peculiarly and have produced a type of landscape that is not equalled in any volcanic region of Iceland at any rate, and perhaps in any other volcanic region in the world. It is thus very deserving of a place among the units into which we are gradually being able to divide the recent and subrecent volcanism in Iceland, and it is likewise practical in this present work to treat the area separately as has been done in the following description.

The scene of the volcanic events is a landscape whose main orographical lines are orientated in the direction of southwest—northeast. On the northwest it is bounded by a chain of hills whose highest peak is the widely visible, very characteristic Þóristindur. The parallel boundary on the southeast is formed of the long, narrow plateau Túngnárfjöll, whose various sections have different names but which forms a well-marked unit as to terrain and also genetically. The volcanic activity can be traced up in the southern part of the lava fields that principally have their origin between Kerlingar and Háganga syðri and under the name of Hágönguhraun described in the foregoing chapter. The southwest boundary of the Fiskivötn region may properly be placed at the great bend of the Túngná, as at this spot the river forms a natural geographical boundary against the volcanic region at Frostastaðavatn. As will appear from the next chapter, there are furthermore such profound volcanological differences between these two adjacent areas that a distinction between them is justified.

Our knowledge of the volcanic conditions at Fiskivötn has hitherto been based upon the observations collected by Thoroddsen on his great and productive journey in 1889. This material has been published in various places, viz. Geografisk Tidsskrift Vol. 10, Ferðabók Vol. 2 Copenhagen 1914, and in the great monograph: Island, in PETERMANN's Mitteilungen, Ergänzungsheft 152, 1905—06. Like many of THORODDSEN's reports in that periodical, the article in Geografisk Tidsskrift is a publication of his diaries and as such is practically identical with the corresponding chapters of the Ferðabók. They give a very vivid picture of his method of travelling and his ability to find his bearings and assimilate a host of observations in a very short time, but they are no scientifically treated and systematically arranged account. We do find one, however, in the monograph Island 1905—06 and in Lýsing Íslands. The cartographic material was published in the geological map of 1901 and in the map accompanying the work of 1905—06. Below is the account from the latter work (p. 122) in extenso as it contains practically all we know of the region:

"Nirgends sind so viele grosze Kratergruppen auf Island vorhanden, als bei den Seen Fiskivötn im Innern des Landes, westlich vom Vatnajökull. Hier befinden sich sowohl kegelformige gröszere und kleinere Krater wie auch Vulkanspalten. Es wäre von groszem Interesse, eine detaillierte Karte von dieser Gegend zu besitzen, die aber leider nicht existiert...... Nordwestlich von den Bergen Túngnárfjöll 580—600 m. ü. M. befindet sich eine Gruppe von Seen, Fiskivötn oder Veidivötn genannt, in einer öden Gegend, von Schlackenrücken, vulkanischem Schutt, Bomben und Asche umgeben. Mehrere der Seen sind Kraterseen, aber von den gröszeren Seebassins ist jedes für sich, nicht von einem einzelnen Krater, aber von vielen Kraterringen gebildet, die miteinander verschmolzen sind; verschiedene kleinere Seen werden jedoch bei näherer Untersuchung in tiefen Kratern versteckt gefunden. Der kleine See Tjaldvatn liegt in einem alten, groszen Krater, dessen Durchmesser 2—3 km. beträgt. Der See hat viele Buchten und Wiecken, nimmt aber kaum die Hälfte des Kraterbodens ein. Die aus Lavaschutt Schlacken und Bomben aufgebauten bogenformigen Kraterränder, mit einer Höhe von 60—90 m. über dem See schliessen eine schmale Lavaterrasse ein, die einem älteren, höher liegenden Lavaboden zu bezeichnen scheint, der später gesunken ist. Die Lavaströme, welche aus der Zeit stammen, als der grosze Krater gebildet wurde, konnte ich nicht sehen, sie waren mit Schlacken und Lavaschutt bedeckt, wogegen die den Kraterboden bedeckende Lava von einer neueren Ausbruchsspalte mit mehreren kleineren Kratern herrührt, die später nicht nur diesen alten groszen Krater, sondern auch verschiedene andere, nach NO. gelegene, zerklüftet hat. In dem südwestlich vom Tjaldvatn zunächst liegenden See Skálavatn, der bedeutend gröszer und von Kratergruppen umgeben ist, befinden sich mehrere Inseln, anscheinend ausgebrannte Krater; im Boden des Sees sollen tiefe Kessel und Abgründe vorhanden sein. Nordöstlich von Tjaldvatn befinden sich auf sehr vulkanischen Terrain zwei kleinere Seen, Fossvötn; durch die Seen Skálavatn, Tjaldvatn und Fossvötn erstreckt sich die ca. 15 km. lange neuere Ausbruchsspalte aufwärts nach dem Stórisjór hin. Auf dieser Spalte findet sich eine Kraterreihe mit der Hauptrichtung nach NO., die jedoch mehrere Krümmungen macht; die kleinen, steilen, zackigen Krater bilden einen Wirrwarr und sind aus Lava aufgebaut. Viele davon sind mit Wasser angefüllt, und die zusammengeschraubten Lavamassen sind von zahlreichen Sprüngen durchzogen. Die Kraterspalte hat mehrere der alten Schlackenkrater zerklüftet und nach beiden Seiten Lava ausgegossen; nur bei den Fossvötn befindet sich eine gröszere Lavastrecke, deren Oberfläche sehr uneben ist. Das ganze Terrain um diese Seegruppe, mit einem Areal von 150—200 qkm., ist mit Kratergruppen bedeckt. Von den vulkanischen, mit Lavaschutt, Schlacken und Asche bedeckten Flächen am Vatnakvísl erhebt sich eine Reihe von Gipfeln. Ich bestieg 1889 eine der pyramidenförmigen Spitzen, welche die Umgebung um 260 m. überragte, und es zeigte sich, dasz die spitzen Anhöhen Reste von groszen, alten Kratern waren, welche die Denudation arg mitgenommen hatte. Die höchsten Spitzen des Kraterrandes nehmen sich in der Entfernung wie isolierte Pyramiden aus. In diesen aus regelmäszigen Schichten von Scorien und Bimsstein aufgebauten Kratern sind tiefe Furchen und Rinnen vom Regen ausgewaschen. Zwischen den Scorien befinden sich einzelne gröszere Basaltsteine, auch sieht man nicht selten kleine Brocken von Liparit. Die Krater haben nicht Lava ausgegossen, sondern sind unter heftigen Explosionen aufgebaut worden, bei welchen Scorien und Bimsstein sowie Stücke der Gesteine, welche warscheinlich den festen Untergrund bilden, ausgeworfen wurden. Die südlichste Krater ist von beträchtlichem Umfang und auf dem Boden desselben befindet sich ein kleiner runder See mit direktem Abflusz in die Tungná.'' THORODDSEN 1905—06, p. 122—23.

THORODDSEN's idea of the topographical conditions and the geological surface forms appears from the geological map, scale 1 : 750,000 of 1905—06. A comparison of the reproduction of a section of that map on p. . . with the map we have drawn shows that, as might have been expected, his topographical impression has been somewhat defective, as has already been shown in chapter 2 of the present work. Regarding the distribution of the various geological formations the following observations are called for: THORODDSEN has never been in the northern part of the region, and his statements in this respect are presumably based upon observations in the mountains north of Þórisvatn and on BJÖRN GUNNLAUGSSON's map of the region at Vonarskarð.

As a consequence his account of the distribution of the different surface forms is not very satisfactory, nor of the south part of the region; he indicates, for instance, a connection between Hágönguhraun and some large masses of lava south of Þórisvatn which continue across the valley of the Túngná and there run together with the lava from the Hekla region. This is not correct; there is no great lava field; Hágönguhraun ends a few kilometres northeast of Fiskivötn and is not connected with the lava fields south of the Túngná. Their origin is quite different, for they have come from a very productive volcanic region of which THORODDSEN has observed a part and entered on the map under the name of Tjörfafellsgígir. The details will be seen by a comparison of the two maps. Regarding the terminology there are the following difficulties. THORODDSEN (1905—06, p. 152) states that at Veiðivötn or Fiskivötn there are six craters with a total lava area of 1550 sq. km. These craters are Snæöldugígir, Tjaldvatnsgígur, Fossvatnagígir, Vatnakvíslargígir, Botnagígir and Hágönguhraun. In the same work, p. 144, he refers to Veiðivatnahraun, to which he credits an area of 1080 sq. km. I do not understand the connection between these names and the areas given; but as a matter of fact it is of less importance in this respect, because THORODDSEN's ideas of the topographical conditions have, as already mentioned, been lacking in accuracy. As the map shows, there is no reason for maintaining the name Veiðivatnahraun, because there is no large lava field at Veiðivötn, or, to use the other name, Fiskivötn. In this part of Iceland the dominating lava area is that which from the time of BJÖRN GUNNLAUGSSON has been called Hágönguhraun, and that name it should continue to bear.

Prior to the period of eruption that has given the landscape at Fiskivötn its present character there has been a wide valley between the Þóristindur mountain range and Túngnárfjöll. The difference of level in this region has mostly been caused by the activities of tectonic processes and it is still possible to recognize the course of a great system of fracture lines in the direction of southwest—northeast. Some of these faults occurred before the period of eruption had commenced, and in the following these are termed pre-eruptive; this expression presupposes nothing as to conditions prior to the forming of the faults. Chapter 5 deals with the tectonic conditions.

In this landscape the volcanic processes have been of great violence but the manner in which they are manifested differs greatly in the various parts of the region, the result being a volcanic landscape of very complicated and most varied structure. On this point there is a most pronounced contrast to the Háganga region just described, where, as we have seen, mass eruption is the all-prevailing form.

In the Fiskivötn region the volcanic area is especially concentrated in two elongated zones, both running southwest—northeast. The two zones are separated by a depression about 3 km. wide, through whose southwest part the watercourse Vatnakvísl runs.

The field west of the Vatnakvísl consists of nine enormous centres of eruption in two groups, one on the southwest with two, and one on the north east with seven craters. THORODDSEN observed this field and on his map showed six craters in a row with the name of Vatnakvíslargígir. He climbed one of the surrounding mounds of gravel and gave a brief description of the phenomenon (Geogr. Tidsskrift, Vol. 10, p. 14; Ferðabók, Vol. 2, p. 256), its principal features being included in the last lines of the citation on p. 33—34, 215—16.

These nine craters, Vatnakvíslargígir (i.e. the eruption vents at the Vatnakvísl) lie in a straight line about 15 km. long, running southwest—northeast. They are situated on an edge, probably a small fault, formed prior to the eruptive period. The height of the fault is greatest on the southwest, where it is rather more than 100 m.

in height, whereafter its size decreases towards the northeast as far as Crater No. 8, after which it can no longer be seen. The sunken area lies towards the southeast. The eruption intensity is greatest at No. 1 and 2 and decreases evenly to No. 9; the last traces are northeast of No. 9 and appear in the form of small heaps of gravel a few metres high. The highest of the gravel cones lying round the craters is about 290 m.; as a rule their base is oval with the longest axis in the direction of the volcano line. This feature is most prominent in Crater No. 9, which is about 1 km. across the widest part, inside measurement. The mounds round the vents are all leaning over with the exception of No. 9, and in every case they lean the same way, viz. towards the southeast, the result being that the southeast part of the mounds is about 100 m. lower than the northwest part. This gives the upper edge a very peculiar and handsome curvature that is practically the same on from No. 1 to 7; seen from a distance this produces a very striking impression of uniformity. The outer sides slope about 40° and from a distance appear to be perfectly undisturbed conical surfaces; a closer examination shows, however, that the sides are grooved by long channels of slight depth, cut by the waters of the melting snow. I cannot agree with Thoroddsen that these cones are badly broken down by erosion, as this is only the case as regards one side of Nos. 1 and 2, which have been attacked by the Túngná and the Vatnakvísl, which run just at the foot of them. The side facing the crater is usually a little steeper than the outer side. In most cases the craters are filled by a lake temporarily or permanently. No. 9 for instance has a temporary lake, Nos. 1 to 4 permanent lakes. The water is clear, slightly green, and the depth is small. No. 1 forms an exception, as its water comes from the Túngná which at high tide runs in and fills the basin with muddy glacial water from Vatnajökull.

The material forming these cones differs somewhat. In the first place it is peculiar that there are no streams of lava, so that the eruptions must have been of the explosive type. To a great extent the cones are built up of loose volcanic material that has been thrown out, but in the deepest part of the cone there are some anticlinally situated, hardened tuffs, which also occur as loose blocks in the other loose parts of the cones, and these tuffs can scarcely be other than parts of the pre-eruptive substratum. Thus the phenomenon corresponds to the Erhebungskraters described by Reck (1910, p. 316), with the difference that in the example figured (fig. 9) the phenomenon occurs in pure state, whereas here it is combined with the usual gravel-cone. It would thus seem (and corresponding observations in the region we have examined confirm it) that the upward forces of the volcano succeed in lifting the ground strata periclinally round the vent without breaking them up to any great extent.

The loose material is of varied origin. There are considerable quantities of volcanic gravel of basaltic composition, as well as sharp-edged lumps of other rocks such as hardened tuffs, basaltic lava with filled cavities, and finally lumps of liparitic lava. These must undoubtedly be taken to be broken fragments of the substratum. One peculiarity is that nearly all the material is of strikingly small grain.

It is rare that one finds blocks of more than 25 cm., and the number of bigger blocks is so small that it is difficult to find stones large enough for cairn building.

In most cases the cross section of the eruptive vent has been slightly oval, and there is scarcely any doubt that the vents, at any rate in Nos. 1 to 7, have sloped in the direction of southeast. This is confirmed through the observation of a small phenomenon of detail of a character that is interesting in another way. In No. 3 a part of the inner crater side is covered with a thin sheet of lava of a thickness of about 1 m. This covering, which lies in the form of tongues reaching from the bottom some way up the sides, is in three places. One tongue lies on the northwest side and extends about 30 m. up, the other two, on the southeast side, are more than 100 m. high and extend right up to the edge of the gravel cone. From there they can be traced on down over the outerside as a thin layer of fragmented lava that decreases in thickness as it goes downwards and forms a pronounced contrast to the gravel material that is otherwise predominant.

Fig. 14 was photographed on the southeast edge of the gravel cone. Below on the left is a part of the small lake that fills the bottom of the crater. The dark patch in the foreground is a part of the one lava sheet, then follows a belt in which the stratified gravel material appears without any covering of lava, and behind this again the second sheet of lava, whose edge on the steep slope has been somewhat exposed to solifluction with the result that large and small floes have broken loose and have glided down towards the bottom. On the extreme right of the picture is the edge of the gravel cone covered with a thin layer of lava appearing as a dark stripe. In the background are volcanoes No. 4, 5 and 6. The picture was taken looking north 30° east. Fig. 15 is a close-up picture of the southeast edge with its covering of lava. In Crater No. 1 we observed a similar formation but with only one tongue, lying on the southeast slope.

On the basis of these observations I have come to the following conclusions concerning the course of the processes. The eruptions in all nine volcanos have proceeded in almost the same manner and practically simultaneously, for in every respect the whole row gives the impression of complete uniformity, and nothing has been observed to indicate a difference of age. As there are no lava streams, the eruption must be placed to the purely explosive group. It should be observed here that one peculiar sign of ordinary explosive volcanoes is lacking, viz. the occurrence of large blocks that have been thrown out by the explosions. A comparison with the complicated "maar"s at Fiskivötn is in this respect called for, and it immediately shows the difference, as will be seen in the following account of their formation (p. 50, 232, fig. 13). On the other hand the quantity of material erupted and the periclinal tilting of the pre-eruptive surface show that the pressure has been enormous. It is difficult to imagine that there have actually been explosions; far more likely is it that the process has been in the form of an escape of gases under high pressure. In this connection it may be observed that other volcanic processes of this kind have been observed, viz. the famous eruption of pumice stone in Askja on March 29th, 1875, resulting in the forming of what the Germans called the Rudloff crater. On the course of the process THORODDSEN writes (1905—06, p. 125): "Während des Ausbruchs wurde durch die gewaltige Explosion aus dem engen Kessel wie aus einem Kanonenrohre in wenigen Stunden 3—4 cbkm. Bimsstein geschleudert." Thus there is a contrast between the "maar"s proper, where explosions are the prevailing form of manifestation, and the type observed at Vatnakvíslargígir, which differs in that the process has rather had the character of a blowing off, and thus we arrive at a differentiation between two "maar"types, viz. Explosion craters and blast craters.

In No. 1 and No. 3 the last phase of the eruption has been different, as is evidenced by the coverings of lava on the inner slopes of the craters. There is no trace of any lava in the crater, and one is therefore obliged to imagine the formation of lava fountains, an explanation that is confirmed by the distribution of the lava crust. The occurrence of three isolated tongues of a very thin sheet of lava must be the result of jets of thin lava. The two larger of these in Crater No. 3 must have been more than 150 m. in height, as they have reached beyond the south edge of the gravel cone, whence they have trickled down the outer side of the volcano in the form of a broken-up, incoherent mass. The distribution of these jets of lava also indicates that the vents have been inclined, for of the four observed three of them run towards the southeast, whereas only one — and of insignificant size — has gone to the northwest.

As the figures show, the surface of the lava is not covered with loose products and therefore we must assume that the eruptive process has concluded with the formation of the inclined lava fountains reaching a height of almost 150 metres.

In the terrain northwest of Vatnakvíslargígir there are several eruption vents lying parallel to the line of eruption just referred to. As far as can be seen now, their output has been insignificant and has resulted in the formation of several small lava streams as well as a few short rows of scoria cones. In some places one also meets with evidence of the activity of explosive forces in the form of typical "maar" formations surrounded by gravel and stone mounds. Two of these enclose a small lake. In this part of the field the effects of the volcanic processes have, however, been concealed to a great extent by a thick layer of volcanic gravel, whose origin must undoubtedly be placed in connection with the row of blast-hole formations referred to above.

Thus volcanism northwest of Vatnakvísl exhibits the following characteristic features: It is of typical linear character. Outside the lines are only few isolated "maar" formations. In this region the early phase seems to have proceeded in the form of small eruptions of a mass-eruption character connected with the volcano lines northwest of Vatnakvíslargígir. The later phase, the one that is also predominant both as to quantity and landscape, is Vatnakvíslargígir, which is a linear eruption of the explosive type. Along a straight line of 15 km. the eruption has concentrated in 9 foci. The process must have been in the form of a blowing out of relatively small-grained material, caused by gases under high pressure. Block material is absent. In two of the vents the processes have concluded with the forming of lava fountains of a height up to 150 m.

The volcanic zone southeast of Vatnakvísl: Fiskivötn zone.

As a whole this region lies parallel to the linear, explosive eruption area in the direction of southwest-northeast, but is larger, about 25 km. long, and, from a morphological point of view, much more varied than the foregoing region. For the sake of clarity it will be practical to divide the region into sections from northeast to southwest, with morphological peculiarities as the basis of the division. I will simply call the zones A, B, C and D.

Zone A, the most northerly part of the region, is an eruptive fissure about 5 km. long stretching from the remarkable extension of the volcanic zone that is taking place in the zone marked B on the map, to a nameless mountain whose south edge lies about 5 km. north of the north end of Litlisjór. The eruption has the character of a mass eruption, lava being predominant and loose material quite subordinate. It is a pronounced fissure eruption which has been productive of lava throughout almost the whole of its length. Here and there are small adhered-slag craters which make it possible to follow the course of the fissure from a distance. On the northeast it runs into the aforementioned nameless mountain, which is about 300 m. high and of the plateau form that is usual in this area. In prolongation of the fissure the mountain is interspersed with cracks, and in its southern slope one can see the results of the activity of explosive forces in the form of large blocks thrown out to long distances. The obvious course is to place these phenomena in direct connection with the volcanic processes, but they may also be partly associated with the tectonic changes that have caused the difference in the level at this spot. Possibly there is some connection between Zone A and a small eruption field north of the mountain, and, if this is correct, we may assume that the cracks in the mountain were formed at the same time as the volcanic fissure. From this fissure the lava has spread to the northwest and southeast, but mostly in the latter direction. There it has covered the plain over to Túngnárfjöll and its continuation to the northeast, Vörðufell. Between these two mountains is a pass leading down to the big valley of the Túngná. Through this port the lava from Zone A has flowed down and filled the bottom from side to side. If anything it must be characterised as block lava. The edges are somewhat sandblown, especially in the north part of the area of its spread. The total lava area is about 15 sq.km., and the average thickness is scarcely less than 20 m.

As Zone C has been formed in a somewhat similar manner it may be dealt with simultaneously. Like the foregoing it is a linear mass eruption which has emerged out of a fissure about 2 km. long, stretching from a point north of Fossvötn to a point west of Litlisjór, where the volcanic field widens out to Zone B. On this stretch of

2 km. the fissure is almost continuous and lava has been emitted all along, though not with the same intensity everywhere. The lava streams are of no great extent; to the southeast they have spread to the shore of the Litlisjór and have not succeeded in veiling the pre-eruptive relief of the landscape. It has passed along in some very handsome sub-surface canals whose roofs are now collapsed. On both sides of the fissure are fine mounds (fig. 5) the inner sides of which are often covered with a carpet of adhered slag which have been thrown up in the form of soft, sticky patches of about one metre and, during coagulation, have run down the side (fig. 16). There are also some vertical, conical lava hummocks down in the fissure near its outer side. As a rule they are about 5 m. high and about 2 m. in diameter, and consist of thin caps of more or less compact lava. They seem to have been thrown up while the lava was cooling and possibly they are a parallel in miniature to the famous Mont Pelée needle. In several places the adhered slag forms arched bridges over the eruptive fissure, which is about 50 m. wide.

The most peculiar feature of this section of the Fiskivötn area must be said to be the rich development of the adhered-slag phenomenon there. All the way along the fissure is an almost unbroken mound of the characteristic agglomerate that forms when fluid, sticky lumps of lava are thrown out of the magma containers — sufficiently sticky to adhere together without losing their individuality. At certain places the production of adhered slag has been extremely active and has formed circular mounds of a height of up to 50 m. This volcanic form is very common on Iceland and plays no small part in the landscape. Often this formation bears the name of Eldborg (fire borg), as a study of the topographical maps of the recent volcanic areas of Iceland shows. The term is thus used as a proper name for a number of vents — of a certain type, it is true; but as this type is well limited and is the outcome of a certain side of the activity of volcanic processes, it may perhaps be justifiable to use the name as a common denominator for formations of this type, as a morphological category.

An "Eldborg" is formed round a cylindrical vent when the latter throws out large quantities of adhered slag and only small quantities of loose material proper. The result is the formation of a circular mound with very steep slopes both on the crater side and on the outer side. The height is usually small, not over 100—150 m., but the steepness gives the phenomenon a very conspicuous form. The steepness of the sides, 60—70°, in conjunction with the porosity of the material and slight coherence, often make it difficult to climb over the mound, and still more difficult is the descent on the inner side down into the crater. As a rule the upper edge is only a few metres wide, very jagged and uneven, and thus from a distance has a very characteristic, serrated profile. The whole structure bears a resemblance to the very collapsed ruin of a round borg tower, and thus the name is a very apt one, as indeed are many of the Icelandic landscape names.

Zones A and C are thus regular fissure eruptions from an easily recognizable, sharply bounded eruptive fissure with a slight output of loose material. The characteristic feature of Zone A is that the lava output is so absolutely predominant, whereas Zone C is remarkable for its small lava output; on the other hand it has had a lively production of adhered slag.

There has been another type of volcanic activity in the other two zones, B and D, which on many points resemble each other, for instance in the fact that their structure is extremely complicated. While making the preliminary survey of the terrain we found the whole utterly confused and it was impossible for me to obtain any impression of the course of developments in the landscape as a whole. Only after a month's study of the conditions and a cartographical recording of the very intricate topography of the area was I able to arrive at the views which I shall explain in the following and which, I believe, can be maintained.

Zone D is a landscape 10 km. long and up to 3 km. wide, embracing the lake groups Fiskivötn and Fossvötn with the surrounding country. The longitudinal axis runs southwest—northeast and forms a direct, straight-line continuation of the volcanic line that can be followed from the northeast point of Zone A and through that zone and the subsequent Zones B and C. About one-third of the longitudinal axis of the whole Fiskivötn system thus falls in Zone D. I have put the northern boundary at the southwest corner of Litlisjór and the southern boundary at the Túngná bend; the southeast boundary lies at the foot of Mount Skálafell, and the northwest boundary at River Vatnakvísl. Accordingly the total area of this zone is about 25 sq. km.

Within it the pre-eruptive terrain is so to say completely destroyed. Our examination has shown that at least a hundred foci of volcanic activity can be established, about 25 of them at Litlisjór and Fossvötn, whereas about 75 lie in the terrain near Fiskivötn. As a whole the terrain does not rise above the surrounding country, although here and there are small gravel hills of 50 to 100 m.; but it is lower than Zone C and, what is more, much lower than Vatnakvíslargígir. This fact alone indicates that the output of volcanic material has been small, and our investigations proved this to be the case. In many places on the edge of the volcanic field there is a mound of gravel sloping gently outwards; on the inner side the slope is steeper.

While the field as a whole runs in the direction of northeast—southwest, it is only here and there that one can find a similar arrangement of the various volcanic units in the field. In certain cases five, ten or twenty eruption foci lie together in a group without any order at all, whereas in other cases a similar number may lie in a line — usually southwest—northeast. There also occur continuous linear eruptions, and, finally, it is not seldom that one meets with isolated central eruptions where no immediate connection with any other is perceptible.

It has not been possible to organize a detailed examination of all the places of eruption; much more assistance would be necessary than I had at my disposal. A monographic treatment of this kind, going into all the details, would be a very profitable enterprise, but would require the employment of much labour, time and money. In the present work my task must be confined to an account of the elementary phenomena and then to endeavour to bring them all together into a morphogenetic whole.

The course of developments, as far as can be seen now, has commenced with an explosive phase of very violent character. Traces of this activity are to be seen in various places on the outskirts of the area, for instance in the north part of the field at Fossvötn, where the volcanic area is bounded by mounds about 50 m. high, consisting of tilted layers of tuff and, overlying them, loose explosion material. Within the mounds the volcanic activity has involved the forming of a large, unbroken basin, whose presence becomes of essential importance to the further course of the processes. Analogous formations have been observed in the north part of Fiskivötn, where we find the same combination of central basins and surrounding mounds. It has been in this manner that the greater part of the basin now containing Skálavatn, Langavatn, Eskivatn and Kvíslarvatn has been formed.

Meantime the eruptive activity has continued and has given parts of the explosion area quite another character. That these processes are later appears from the fact that they are unconformable with those just described, and that they intrude in their terrain forms and disturb them. Thus we see earlier gravel mounds, parts of which have been blown away by later explosions, and earlier basins that have wholly or partly been filled with explosion material from later eruptions. Most probably it is to some extent the same material that time and again has been blown up and shattered; it has simply been moved about as the centres of the process moved.

Several of the later phases have spread out beyond the area in which one can now find the traces of the early phase. Thus on the south shore of Litlisjór there is a narrow zone with 17 vents on a plain of about one square kilometre. They lie scattered about in no sort of order, quite close together, often overlapping so much that twin craters have been formed with "spectacle-shaped" twin lakes in the bottom. The vents themselves are about 100 m. wide, 20—30 m. deep, and in towards the crater have a slope of about 45°. The mounds are about 15 m. high. The material produced is almost exclusively loose and for the most part consists of slag, thrown into the air in a state that was plastic but not so adhesive that it became welded together. Part of the material is burnt red, but in some places real adhered slag and bombs up to a size of 30 cm. have been observed. There were no lava streams, but a number of sharp-edged blocks were seen, of an old basaltic lava with cavities filled with quartz. All this small, handsomely shaped crater group provides an example of the form of volcano that is called the explosive area eruption. On fig. 11 is a view over the region. The lake has attacked one side of the eruption field, but a number of craters are still preserved. In the foreground are the remains of three of these, one being full of water. One side of them has been broken down by the erosion of the lake, and across them there is now a raised beach.

The foreground is the south side of another "maar" formation, on whose sides one can see a thick strewing of blocks, all sharp-edged lava fragments.

In the basin enclosing the two lakes Stóra and Litla Fossvatn there are traces of several older explosion centres, but the relief produced by these explosions has been greatly disturbed by both erosion and the activities of the later volcanic processes. The character of these latter has varied greatly, as there is evidence of both explosive and mixed eruptions. They have especially been concentrated in two fields, viz. at the north end of Stóra Fossvatn and at the south end of Litla Fossvatn. From the first of these a small but deep lava stream has run southwards and filled part of the basin formed by the earlier explosions. Here are innumerable indications of collapse, hornitos formation and sub-surface canals, on the whole a series of phenomena that characterises very fluid lava streams of great depth.

In the area north of Tjaldvatn there are also marked traces of an earlier, mostly explosive phase that has later on been followed by one of mixed character. The latter activity is in the form of a line and lies in the usual direction of northeast—southwest. The process has caused a crack through the mound that separates the Fossvötn basin from the Tjaldvatn basin on the south. On the side opposite to Fossvötn the eruptive intensity has been comparatively slight and has only resulted in the formation of some small adhered-slag craters; on the south side, however, the activity has been considerable. In the first place there are two deep explosion craters, belonging to the most recent phenomena in this part of the area, for their occurrence shows that they were formed after the second main phase came to an end. This corresponds in character, and probably also in time, to the effusive phase at Fossvötn and, like the latter, is characterised by a mixed output and the lively erupting of very fluid lava. The situation of the vent is marked by a series of adhered-slag craters with small, steep cones of lumps of fluid lava welded together. Close to the centres are many hornitos formations and one or two coagulation cavities, one of which, known as Tjarnarkot, has been built up as a dwelling for the trout fishers who now and then come to this group of lakes. The lava has filled the bottom of the old explosion basin and from there has spread into the basin where Skálavatn lies, while another branch of the stream has gone down into the Langavatn basin.

As to conditions here THORODDSEN writes (1889, p. 8): "Tjaldvatn lies in a very large, old crater. The lake has made irregular bays and coves, but scarcely occupies half of the crater bottom. The arc-shaped crater rims had a height of 2—300 feet above the lake; on the inner side they have a narrow lava terrace which seems to mark the place of an old, higher, lava bottom which has later been melted again and sunk in the course of renewed eruptions and drainings. The crater cone itself is principally built up of slag and drops of lava. I observed no really old lava streams dating from the time when the big crater was formed; on the contrary, the crater bottom itself was covered with later lavas."

My investigations have confirmed the correctness of these observations, but several things have escaped his attention, presumably owing to lack of time, and as a consequence his view of the whole system is somewhat defective.

If one follows the lava fields from the centres of eruption north of Tjaldvatn down towards this lake, it will be observed that from a certain zone there is a fall of about ten metres down to the level of the lake. The surface of the lava field continues, however, on the side of the Tjaldvatn basin in the form of an unbroken lava shore line which runs into the basin in which Skálavatn lies and also into the Langavatn basin. The shore line is very distinct at Tjaldvatn where, as stated above, it was observed by THORODDSEN. It is here (fig. 9) seen as a sharp edge that has acted as an arresting ledge for the masses of gravel sliding down from above. This makes a very characteristic break in the curvature of the mountain side. In many places I have removed this gravel material in all three lake basins and everywhere found an even surface of lava resting upon the side of an old explosion crater. There is no doubt that this shore line marks the presence of a continuous lake of lava which has filled all three basins; its lifetime has, however, been brief — it has not even got so far as to settle horizontally, as the shore line lies higher at the place of eruption than in the distal parts of the lava lake.

The question then is, what has become of the great mass of lava that filled these three basins up to the height of the lava shore line. One might imagine that the lake has been emptied in the manner known in other recent volcanic localities (NIELSEN 1927, p. 121, fig. 6), but in this case this possibility must be rejected. I have examined the lava shore line along all three basins and nowhere found it broken, nor have I observed any trace of streams caused by such an emptying, despite most thorough search. It must therefore be assumed that it has sunk as a consequence of coagulation contraction; possibly there has been a re-melting as indicated by THORODDSEN.

In this connection it is of interest to know the relief of the bottom of the lake and especially the maximum depth. On this THORODDSEN says l. c. "In the bottom (of Skálavatn) there are also said to be deep hollows and abysses", and further down he refers to the occurrence of deep abysses in a connection that must be presumed to apply to Tjaldvatn and the small holes south of that lake. These ideas are rather exaggerated. The depth of the lake is remarkably constant, as a rule not more than 3—4 metres, but at some few places there are depths of up to 8—9 metres. The bottom is lava everywhere, and the relief and character of its surface is just the same as that of the sunken lava fields above the level of the water, except of course at those places where the superficial feed-waters have led gravel out into the lakes, a process that in particular has had an influence upon the bottom conditions in Tjaldvatn, where the water coming from the north has brought about the forming of small deltas. Fig. 41. In Skálavatn especially is a number of islets which THORODDSEN presumed to be craters. This is not the case. They have proved to be of the same structure as the lava mounds separating the lakes. For the most part these consist of fragmented lava, but sometimes one sees a tendency towards stratified coagulation. In many places on these mounds there are steep-walled crags of a height of up to 10 m., the most prominent being the so-called Arnarsetur, so named because the sea-eagle is said to have nested there up to a few years ago. These crags consist of lava fragments lying very irregularly and are certainly not craters; they must be regarded as a kind of hornitos. Fig. 10.

On making a comparison of my observations in this part of the Fiskivötn region I have come to the following conclusions regarding the course of the volcanic processes and the product of their activity as reflected in the landscape. The foundation is three eruptions mostly of an explosive character, which have produced three basins that today are marked by the presence of the lakes Tjaldvatn, Skálavatn and Langavatn. The two first-named have the character of area eruptions of limited extent, undoubtedly resembling the local formations that occur in undisturbed condition in several places within the region and described below. The Langavatn basin has come about as the result of a linear, explosive eruption and thus must be called an explosion pit. The three basins have overlapped at the west end of Tjaldvatn. The next phase of the developments is marked by the great eruption of lava in the north corner of the system, and it must be noted that we observed nothing to indicate effusive activity elsewhere within this tripartite explosion area. The result is that all three basins are full of lava to a very considerable height, but the output has not been large enough to overflow the mounds round the old explosion basins. The subsequent collapses, whose greatest observed depth is 15 m., are markedly great and, as stated above, their cause is rather doubtful; the result is, however, that three principal subsidences were formed corresponding to the deepest parts of the three primary explosion basins. Only at the edges of this tripartite lava lake is there a narrow shore line left as evidence of the higher level of the lava. Hornitos were formed in certain parts of the lava lake (Fig. 10). The mostly deeply sunken parts at present are below the surface of the water and have in fact given rise to the forming of these lakes. The biological conditions in and round these lakes are most remarkable; both fauna and flora are relatively rich in individuals but poor in species; naturally, conditions of life are hard, and life is sparse, but when one comes from the enormous wastes on the north and west and surrounding Fiskivötn on all sides, one rejoices in this poor little oasis and feels that it is luxuriant and good place to be in.

In the northern part of the Fiskivötn area in its strictest sense it is thus possible to form a summary of the play of the volcanic forces and separate the different phases of developments. In the southern part of the area this is extremely difficult, not to say impossible, a consequence of the very complicated course of the volcanic phenomena there, as we have not to deal with eruption phases that are separable as to time, place and character. Here the explosive forces have prevailed right up to the end of the eruptive period and have so covered up the older traces of activity that it has not been possible to account for conditions throughout a long period. Volcanism has been active throughout the whole of the landscape from the foreland of Túngnárfjöll to the Vatnakvísl, and on the whole of this domain there are not many square metres of ground that have not repeatedly been uprooted and blasted away by the explosions. The actual production of material has not been great; the highest peaks are scarcely more than 100 m. above the level of Skálavatn, and the lava streams are of small extent and have, as far as can be seen, remained within the area. But never have I seen such a typical area eruption, a surface that has been knocked about to such an extent by volcanic forces, and never have I come across such a confusion of explosion craters of all possible forms. Some of them, the most recent, are quite undisturbed, whereas the earlier ones are more or less destroyed by the later explosions, with the result that the relief is most complicated and of exceeding variety.

Some examples will illustrate this variation. Right up to the foot of Skálafell is a height that at some distance looks like a simple ring-shaped crater mount. Closer inspection shows, however, that this is a "maar" that is very complicated. In this respect it forms an analogy to the large complicated "maar" at Litlisjór to be described later. Four explosion centres can be shown in it, and the surrounding cone of gravel is not continuous, but consists of four cones running into each other, their outer sides being fairly undisturbed, whereas the parts facing the centre have been blasted away by the neighbouring explosions. Details are given on p. 50, 232 and fig. IV. Just to the west of this we find a small linear eruption, with its fissure marked by three craters of the Eldborg type (cf. p. 40, 222). From this fissure there has emerged a small stream of lava, and the conditions under which it has spread show that it must have appeared after the aforementioned masses of lava on the north at Skálavatn had found their resting place. The stream has a margin of block lava, 50—100 m. wide, and inside this we find a lower lava surface where coagulation has proceeded more quietly and has resulted in the forming of a pronounced sheet lava. In the immediate vicinity of the eruption fissure there have been great subsidences, resulting in the forming of deep pits with handsome terraces. Figs. I—II show a section through the whole series; A is the subsidence basin with the terraces, B is the sheet lava, and C is the uneven marginal zone of block lava. The course of the subsidences here has been that large areas of 2—3 hectares together have sunk 5—10 m. There is another form of subsidence just south of the most southern and largest of the three Eldborg craters. We find there a round hole, 100 m. wide, leading down to a subterranean gallery about 10 m. deep and connected with another opening of similar kind.

In the rest of the field one finds a bewildering collection of vents, nearly all of an explosive character but differing greatly in a morphological sense. Some are typical central eruptions, others are linear, and others again are small area eruptions. A very fine explosion pit, about one kilometre long, exhibits the following peculiarities: The eruption fissure itself is scarcely more than 50 m. wide, and on both sides lies a continuous homogeneous mound of gravel. The eruption has been concluded with a short lava phase, during which the bottom of the pit throughout its whole length has been covered with a lava lake in whose surface one sees the usual subsidence phenomena. Fig. 12. — In the most southerly part of the field one finds especially "maar"s of the type described below on p. 50, 232, remarkable owing to the presence of explosion centres very close together. Here and there are small lava eruptions and lava phases as a concluding or intermediate stage in a series of explosions. Here the terrain is very wet and has been eroded from the Vatnakvísl and Túngná, and

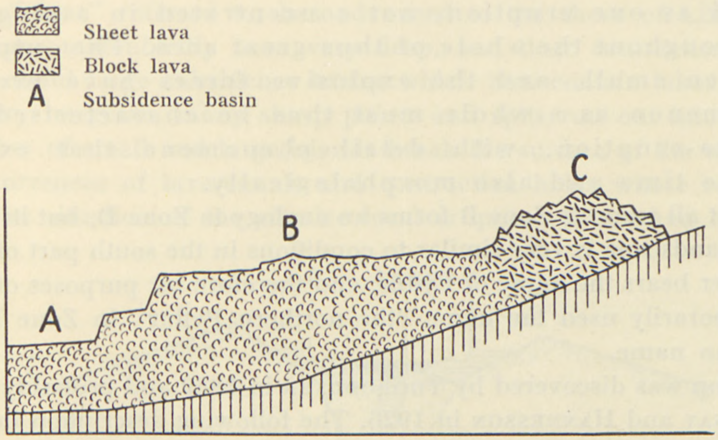


Fig. I. Section through a lava stream which has come from the left. The lava has hardened into block lava (apalhraun) (C) in the marginal zone, inside this into sheet lava (helluhraun) (B), which here and there has collapsed and formed small subsidence basins (A).

as a consequence some of the craters have been partly destroyed, usually enclosing lakes or swamps. The surrounding landscape is likewise to a marked degree charac-

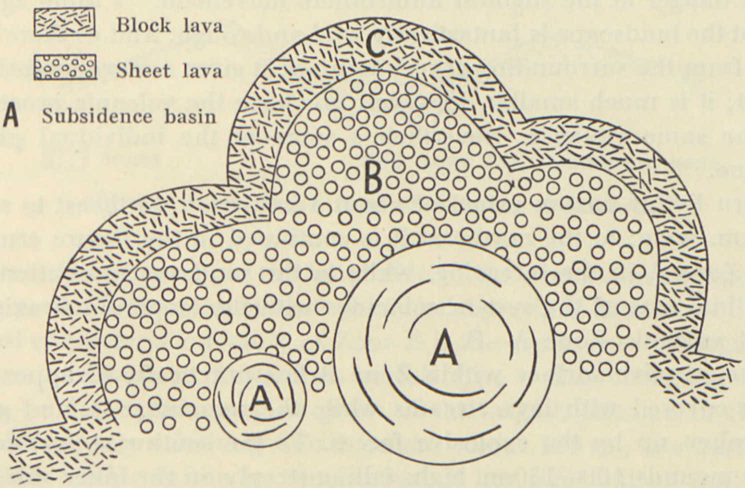


Fig. II. Three tongues of a lava stream, showing a marginal zone with block lava and a central zone of sheet lava and subsidence basins. Cf. Fig. I.

terised by the great masses of water carried down by these rivers, or originating from the considerable quantities of ground water that pass from Litlisjór down through the whole of the porous gravel masses of this volcanic field.

There is scarcely any doubt that the whole of that volcanic field, 20 sq.km., at Fiskivötn is one whole that owes its being to the same source. In reality it must be regarded as one eruption, not concentrated in a single spot but working throughout the whole of thus great area. The output of material has been small, and the explosive forces have predominated. The phenomenon as a whole must thus be characterised as an explosive area-eruption, with detail phenomena that exhibit great variety as to time and also morphologically.

In almost all respects Zone B forms an analogy to Zone D, but its area is rather smaller. The landscape is very similar to conditions in the south part of the Fiskivötn zone. The latter bears the name of Pytlur, and therefore for purposes of identification we have temporarily used the name "the northern Pytlur" in Zone B, which previously had no name.

The region was discovered by THORODDSEN in 1889 and probably was traversed by DE FONTENAY and HANNESSON in 1926. The following description in THORODDSEN may be taken to apply to the northern Pytlur (l. c., p. 11): "Such wild volcanic scenery I have rarely seen in Iceland. Many of these craters, like the old ones, are full of water, and between them the rugged and tossed masses of lava are cleft by innumerable fissures. Under the thin crust of lava are water-filled holes and crevices or long tunnels with glazed lava stalactites, and owing to these hidden dangers we had to proceed with the greatest caution, as on such a terrain the horses would get into most serious danger at the slightest unfortunate movement." I quite agree with THORODDSEN that the landscape is fantastically wild and rough. And as there is an excellent view over it from the surrounding gravel mounds, it gives a more imposing impression than Zone D; it is much smaller, however, nor have the volcanic processes had anything like the same violence. Nevertheless some of the individual phenomena are extremely fine.

Northern Pytlur has an extent of about 4 km. from northeast to southwest, and is about 2 km. wide; to the northeast it is continued in the fissure eruption that has been called Zone A in the foregoing, while to the southwest it continues in Zone C. The longitudinal axis of the system coincides with the longitudinal axis of the whole of this great volcanic Zone A—D.

The pre-eruptive surface within Zone B has practically disappeared, part of it having been covered with lava streams while the remainder — and greater part — has been broken up by the explosive forces. To the southwest and east the field is bordered by mounds 100—150 m. high, falling steeply on the inner side, but less steep on the outer side. These mounds are without doubt the remnants of gravel cones and are thus analogous to the formations at Fossvötn and Fiskivötn. On the south edge of the zone the boundary mound is broken by a large and complicated "maar" which will be described below.

The eruption field itself exhibits a combination of simple "maar"s, complicated "maar"s and explosion pits. There are also traces of an effusive activity, but its lava streams are quite short and have remained in the depressions within the field itself. There is an exception, however, in a small lava tongue which, through a cleft at the complicated "maar" referred to, has advanced to the shore of Litlisjór. Here the lava lakes have undoubtedly been very deep, and their contraction while cooling has brought about large subsidence basins which now contain lakes. Their circumference is very irregular; many sharp points and spits run out into the lakes, and a large number of small and large islands break the surface of the water. There are frequent occurrences of lava-canals and contraction holes whose roofs are as yet unbroken. The situation of the effusive local eruptions is marked by the presence

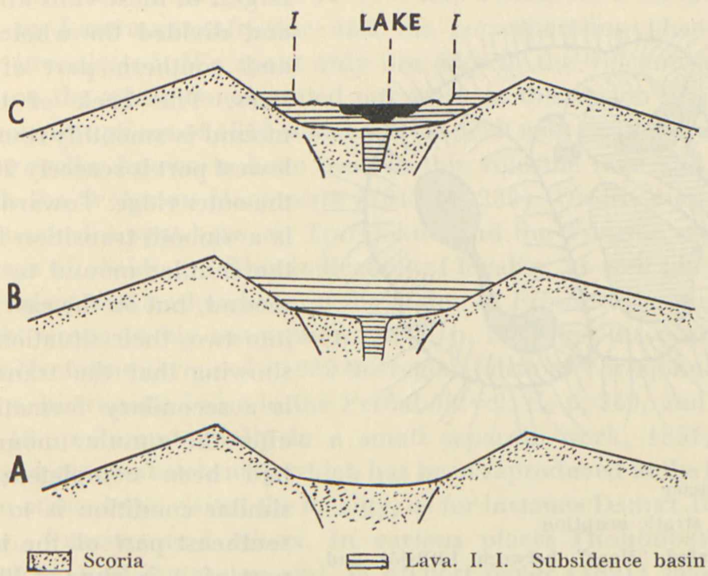


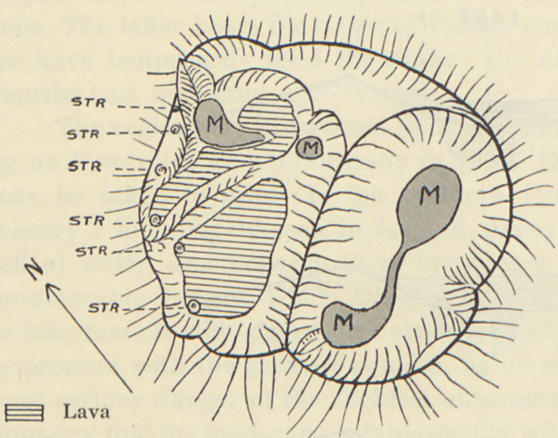
Fig. III. The evolution of a volcanic area at Fiskivötn.

of small craters. At one place on the inner side of the east boundary mound we have observed a superficial covering of lava produced by a lava fountain of about 100 m.

The most characteristic feature of Zone B is the occurrence of large, complicated "maars". As an example of formations of this type — also occurring in Zone D as stated above — a description may be given of the largest, situated in the south edge of the zone. Despite its relatively small height, about 100 m., the surrounding ring mound is widely visible in the terrain because it lies right out on the west shore of Litlisjór. Seen from the outside it gives the impression of being a simple, round, single "maar", but when one climbs up the edge it is discovered that in reality it is most complicated. Fig. IV.

The top of the annular mound is practically circular, and only at one place, on the northwest in towards the rest of Zone B, is it broken by a narrow opening. The material in the mound has partly come from the magma in the form of gravel, adhered slag and bombs, and partly originates from the substratum. Most of the blocks thrown out are of considerable size, up to 10—15 sq. m., which shows that it has been an explosive eruption proper, in contrast to the "maar" type mentioned, whose most pronounced representatives were found at Vatnakvísl and which were distinguished by the fact that the material all through was fine grained and presumably was the product of a blowing-off process. The difference appears from a comparison between fig. 13 and fig. 14.

Within the annular mound is a very complicated eruption basin, fig. IV, which is divided into several secondary basins separated by mounds of gravel. The largest of these runs almost east—west and divided the whole in a northern and southern part of almost equal sizes. The back of the transversal mound is smoothly rounded and at its lowest part is scarcely 20 m. lower than the outer ridge. Towards the west there is a smooth transition from the top of the annular mound to the transversal mound, but on the east the latter splits into two, their situation and direction showing that the transversal mound is a secondary formation, appearing after the annular mound at this spot had been completed; a somewhat similar condition is to be seen in the southeast part of the basin. The east part of it is shaped like two funnels with overlapping edges and their bottoms are occupied by a small S-shaped lake. The western half is more complicated. There is more or less direct evidence of six secondary explosion centres, each of which has formed its own funnel with surrounding mound of gravel, the youngest of them with a fine and regular appearance, whereas the older ones have been disturbed by the subsequent eruptions and can only be recognized fragmentarily. The volcanic activity has concluded with small eruptions of lava, which have been peculiarly placed. The vents — six in all — lie in the west basin but not, as might have been expected, in its deepest parts; the lava has broken out high up on the inner side of the gravel cone a short distance below the ridge. Two streams of lava have run from there down into the deepest parts of the west basin, in which the bottom of the crater-funnel is partly full of lava.



Lava
Lake
M Youngest maar
STR Secondary stratic eruption

Fig. IV. Complicated "Maar" between Litlisjór and Hraunvötn.

The characteristic feature of this type of volcano is that the explosive forces have predominated. Outwardly it appears like a simple "maar", but its crater basin is very complicated and bears evidence of the activity of at least 14 eruptive centres.

Thus it belongs to another morphological type than the simple "maar", described on p. 35—39, 217—21 and I suggest for this type the name; complicated "maar" formations.

c. Volcanism in Landmannaafrjettur.

In contrast to the volcanic regions so far described, this is relatively easy of access; and, as it furthermore occupies a conspicuous, separate position, it has fairly frequently been visited by investigators. It is outside the scope of this work to give an exhaustive account of conditions there, and I shall confine myself to a brief report of the results of the work of others in order to create a basis for a comparison between the volcanism in Landmannaafrjettur and the corresponding phenomena in the region that we investigated. We spent only one day in the volcano area at Frostastaðavatn, and on the whole concentrated our work in this region upon investigating the two little known eruptions of 1913, which will be dealt with in a separate publication.

The first traveller known to have been in this volcanic field and to have made notes about it is the Scotsman Mackenzie (1812, p. 239). On his map he has drawn his route and marked a spot between Torfajökull and the Túngná, where he writes: "Here is a stream of obsidian." This indication of locality, as well his whole description, make it evident that he has been in the region of Frostastaðavatn, and Schythe is without doubt wrong in his assumption (1847, p. 137) that the obsidian found by Mackenzie was Hrafntinnuhraun. In 1889 the region north of Torfajökull was travelled by Thoroddsen, his reports being in the Ferðabók vol. II, p. 240, and also in Geogr. Tidsskrift vol. 10, p. 7; and finally in a small separate work, 1891, he described several details and gave a sketch-map which has been reproduced in the large synopses.

Since then others have visited the locality, as for instance Daniel Bruun, Sapper, Reck, Tyrrell, Peacock and others. In various places Thoroddsen published a geological sketch-map of the region and, in a short paper (1891) gave a description of the liparitic lava occurrences. The rocks in the liparitic lava streams, Laugarhraun, Námshraun and Dómadalshraun, have been examined and described by Helge Backström (1892), and finally Sapper (1908) published a morphological analysis of the region and also a map — the best in existence both morphologically and topographically. The results of the work of Tyrrell and Peacock (1924) have unfortunately not been published yet.

The strangest thing about the volcanic forms of expression is that in post-Glacial times there have been liparitic and basaltic eruptions side by side. Sapper (1908, p. 35) goes very thoroughly into a description of the conditions, which may be briefly summarised as follows: The eruptions have to some extent occurred along a line running NNE, and thus in so far are typical; but along that line there are: 1) a large explosion crater, 2) a small basaltic fissure eruption with a considerable output of lava, and 3) two liparitic eruption fields. There is scarcely any doubt that we have here a continuous series of volcanoes despite the petrographical differences of the individual parts, and consequently one comes to the conclusion that there must be two magma-containers under this terrain, one basaltic and the other liparitic, and that it is one common cause, having nothing to do with volcanism, that has opened them. The cause is probably to be found in tectonic changes.

To the west of these two liparitic streams is a third one of the same character, Dómadalshraun — post-Glacial like the others. Our investigations of the surrounding mountains have shown that the earlier deposits in the region belonging to the Glacial-volcano formation on the north are basaltic and on the south contain liparites, and the boundary between them almost coincides with that of the present day. This observation might mean that the boundary between the two petrographic provinces is rather old and has remained unchanged throughout a considerable period.

Northwest of the liparitic region, between it and the Túngná, is a very productive basaltic, mass-eruption field that hitherto has had no mention in the literature. Lack of time, unfortunately, prevented us from examining it more closely. Its construction is fairly complicated; there are "maar"s and a large number of lava eruptions. The vents are apparently not in linear order and presumably the field may be characterised as a collective area eruption. Productivity has been very great. The masses of lava have spread west and north and fill the country between the foot of the mountain and the Túngná. It is these masses that have caused the intrusion of lava into the Túngná that will be described later and determined its course throughout the whole of the bend to the north until it joins the Þjórsá.

With very few exceptions the Tjörfafell lava forms the left bank of the river from the place where it is overlain by streams from the Hekla region. The relations between the different series of eruptive products from the two volcano fields Tjörfafellsgígir and Hekla as to deposit and age are, however, not known, and it is an extremely difficult, perhaps practically impossible task to find this out; it is probable, however, that these fields have jointly produced the enormous masses of lava that have forced their way through the valley of the Þjórsá right along to the coast of the Atlantic.

d. Hágöngur.

The names Háganga nyrðri and Háganga syðri designate two isolated mountains of truncated-cone shape, standing on the plateaux south of Túngnafellsjökull. We know only very little about them, for to my knowledge they have only been visited by Björn Gunnlaugsson in 1839, when he climbed the most southerly one and there had a topographical surveying station. As was stated in the introduction, several travellers have since passed through the region, but we know of none who have climbed or made any examination of the summits.

As both cones are widely visible and very prominent in the surrounding plateau-land they have been referred to by several writers without attempting any detailed description. Thoroddsen, who has seen them from the heights at Þórisvatn, writes (1905—06, p. 280): "Mitten auf dem Hochlande, in den Ausläufern des Túngnafellsjökull, den sogenannten Hágöngur, sind blaszrote Bergspitzen sichtbar, die warscheinlich aus Liparit bestehen, jedoch bin ich nicht an Ort und Stelle gewesen."

These two mountains are on a low ridge south of the massiv on which Túngnafellsjökull lies. The rocks in situ that are visible in this region belong to the Glacial—volcano formation (the Palagonite formation), but they differ from corresponding rocks in the surrounding areas by a frequent occurrence of liparitic intrusives. The ridge from Túngnafellsjökull runs north—south and thus, together with a mountain range east of Hágönguhraun and a cliff in Vatnajökull, forms a system of north—south lines that are in decided contrast to the southwest—northeast lines that prevail in the rest of the landscape. It is possible that just this zone represents the transition between the two main regions of the great axial fracture system, viz. the great Nordland system and the southwesterly system, of which the former is characterised by fault lines running north—south, whereas the latter is marked by faults running southwest—northeast. As yet, however, these conditions have been too superficially examined to allow of any definite statement on the problem; nevertheless, the transition must be somewhere in this region, as the north—south fracture lines are known to extend a good distance south of Ódáðahraun.

The distance between the two Hágöngur is about 3 km. The one to the south is the highest and also the widest, but otherwise they resemble each other and in their whole appearance are of a peculiarity that contrasts in a most pronounced manner with the mountain forms in the whole of the surrounding landscape. Fig. 18.

At its base Háganga nyrðri has a diameter of about 1 km. and a relative height of about 700 m., whereas Háganga syðri has a base-diameter of about 2 km. and a relative height of about 800 m. The sides are fairly steep, with an incline of about 45 deg., and this steepness increases somewhat towards the summit, where the basic rock is visible, whereas the talus at the foot has produced declivities that do not incline so much and are more varied. The summit of Háganga syðri is a plain of about 1 sq.km., forming a marked contrast to the slope, as everywhere the edge between the two planes is quite sharp. The top surface bears two low, circular domes. Ascent gives no great trouble, except that some care must be taken, especially when descending, because on the surface of the rock there is a very thin coating of loose gravel which must be removed before one can obtain anything like a safe hold. In addition the rock walls are badly weathered, and even large and apparently firm protruberances give no secure foothold, but easily loosen off and fall into the depths.

In the upper half of the mountain wall the rock is visible almost everywhere; but lower down it is also accessible for examination in the deep clefts which the mountain streams have formed in the otherwise thick covering of talus. As Thoroddsen supposed, the material all through proved to be liparitic lava, and the presence of no other material has been established. One prominent feature is a peculiar fluidal structure which seems to be associated with forms of lava with a strong tendency to split into cubic blocks measuring 10—30 cm. along the edges. There are also rocks with a faintly developed porphyric structure produced by the presence of small, angular grains of quartz; and finally there is glassy, black obsidian, although in small quantities only. In the surface of the plateau at the top is an angular, liparitic breccia.

The most astonishing feature of the building of this mountain colossus, whose volcanic origin is indisputable, is that it has not been possible to find any crater, no sign of it, morphological or petrographical, having been discovered. We are therefore compelled to assume that this is a liparitic volcano type not previously known in Iceland, a form corresponding to the "Staukuppe" known in other volcanic regions, as described for instance by Sapper in his splendid work: "Vulkankunde" of 1927.

Unfortunately, time did not permit of a closer study of these extremely interesting matters, and I would not venture to make any definite explanation of the phenomenon; all I have wished to do was to point out that Háganga syðri seems to be unique among the types of volcanoes hitherto known in Iceland.

5. The tectonic conditions.

There has been this especial difficulty in examining the tectonic structure of this region, that it has not been possible to find a single continuous horizon. The tremendous volcanic activity has resulted in the forming of a collection of elementary phenomena whose morphological association and chronological sequence have been impossible to analyse. In this respect the difficulties are increased by the circumstance that normal humid erosion is lacking, so that in the study of the tectonic conditions one has not the important assistance that is usually given by the profiles cut by the watercourses. As a consequence, one's tectonic studies have mostly to be made on the basis of observations on the terrain, and profile observations in the higher parts of the landscape can only be of a supplementary nature. That it is nevertheless possible to unravel certain of the tectonic problems here is due to the fact that the phenomena are quite recent and not yet blurred by the activity of disintegrating forces.

Briefly, the principal morphological result of the recent volcanic activity in the country west of Vatnajökull may be described in the following way: Throughout the whole of the north part of the area investigated, volcanism has produced a slightly sloping plain, uneven — very uneven — in its details (fig. 8), but in the main having a strikingly constant and slight dip (fig. 3), a surface form that is characteristic of regions where for long periods mass eruptions have been the predominating morphological factor, the volcanic filled up plateau. In the south part of the region, where explosive forces at any rate in recent times have predominated, we do find volcanogenous heights round about the eruption vents, but these gravel cones are only of slight importance in the terrain as a whole. In Vatnakvíslargígir the highest summits have a relative height of 2—300 m., but as a rule they do not exceed 150 m., and in the greatest area of them all, the great Area Eruption Zone D at Fiskivötn, the relative height scarcely exceeds 100 m. In this case, too, the local heaps round the vents are very small. Nevertheless, large masses of loose material have been released. The covering of lapilli stretches over an area that measures at any rate 300 sq.km., and, as far as can be ascertained at the moment, it is relatively evenly distributed, the region with the heaviest deposit of lapilli being at Fiskivötn, whence the thickness decreases smoothly to all sides. The gravel cones referred to are perishable formations, and it is solely due to their youth that today they play any part at all in the terrain.

The forms of erosion that are active at the present time only add to the relief in quite exceptional cases. Water erosion is almost insignificant, and the forms of subaerial and aeolic denudation smooth out and reduce the relief. It has practically been impossible to establish traces of glacial erosion on the present surface between the Túngná and the Kaldakvísl. At one single place, viz. on the northwest side of Snjóalda, I have observed at some height a few hollows that may be read as ice or snow-erosion phenomena; in one, by the way, lies a small mass of ice, a hanging glacier, partly covered with last year's snow. Otherwise on these plateaux, which rise several hundred metres above the predominating high-plateau surface, no trace of glacial radial erosion has been met with, and this must mean that the present terrain form cannot have existed at a time when the snow-line for this part of Iceland was much lower than it is now. On the other hand there is nothing to indicate that this difference in height, formed in recent times, can have been produced by the work of erosive forces; we must assume that this height-difference and peculiarity of relief is of tectonic origin: in other words, that the slopes that occur (ruptures de pentes) are faults. The correctness of this view is confirmed by means of a closer study of the conditions.

Heljargá. The most recent and most pronounced example of a tectonic disturbance is the fissure discovered in 1925 by de Fontenay and named by him Heljargá. East of Þórisvatn de Fontenay and Hannesson in 1926 came across a similar formation, and, by following it towards the northeast, they found that it was a continuation of the same fissure.

It runs from the northeast edge of Vatnsleysuöldur to the region east of Þórisvatn, and thus has a length of about 30 km. The fissure is continuous and straight, and, as the map shows, it runs from southwest to northeast. At its widest part it is barely 1 km. broad, and for the most part it only measures 5—600 m. It is peculiar that the ends do not taper off very much, as the bordering fracture lines if anything run parallel right to the point where the fissure-formation is obliterated. At the ends the depth decreases steadily, and, if one goes along the bottom of it, one comes up an even slope to the unbroken surface both north and south of it. The fault has its greatest depth in the mountain Gjárfjall, where it measures about 100 m., but at the other parts is rarely exceeds 40—50 m. The greater part of the fissure is simple and does not branch off; but at the deepest stretch in Gjárfjall complications occur, there being several small cracks parallel to the main fissure, as well as very short, inclined, lateral fissures running from both the main fissure and the secondary fissures. There the whole of the fractured zone is about 2 km. wide.

The terrain that is cut through by Heljargjá is divisible into three. To the north it runs through an arm, 6 km. wide, of the lava fields of Hágönguhraun, then follows a plateau, Gjárfjall, at a height of about 300 m., and southwest of this is the southern part of the said lava fields, which are cut through along a line about 16 km. long. In this section the fissure passes two "maars", one of which is cut right through, the fissure running like a path through it, whereas the other (the most northerly one) is only slightly disturbed. The fissure has been caused by tremendous force. The fields of lava are cleft as if along a line (figs. 20 and 19), the plateau of Gjárfall, ca. 300 metres high and steeply-walled, is cracked right through along a line 8 km. (fig. 21), and there is nothing to indicate that this obstacle has had the slightest influence on the course of the processes.

Having made a number of detail observations, it is possible to form some idea of what has happened. When one approaches Heljargjá from the side, the fissure is invisible until one is quite close to it, owing to the fact that the two fracture edges lie undisturbed at their original level; the dislocation has only affected the zone lying between the edges. In other words, the movement has been purely local. This becomes particularly clear where Heljargjá passes through fields of lava, because there a thrust can easily be detected. Thus the vertical dislocation has not taken place in the lava fields as a whole but is limited to the long, straight, narrow zone between the fracture lines; the situation is only comprehensible viewed from the standpoint that there has been a subsidence, and that the rest of the terrain has retained its level unchanged. As will be shown in another connection, this peculiarity is of fundamental significance, as a very large number of the dislocations on Iceland have proceeded in a similar manner, and in this respect they are quite different to the forms of vertical dislocation that we know for instance in Central Europe.

Where the fracture has run across a field of block lava, the latter has broken along a straight line and left an almost vertical wall. In sheet lava the lava has been broken into large blocks, some of which lie obliquely with one edge at the level of the undisturbed surface, whereas the other rests upon the bottom of the subsidence. Fig. 20. We know of a similar state of affairs in the famous Almannagjá, at Þíngvellir, which every Iceland traveller has seen. At those places where the thrust has been greatest we find another complication. The vertical movement has apparently been greatest in the middle of the pit, so that we have a kind of terrace-fissure; the subsiding area has split into blocks, of which the middlemost has sunk deepest while the side blocks lie higher up, while at the same time they have been flung in towards the median line of the fissure.

Apart from the two "maars", which are both older than the dislocation, there is no trace of volcanic activity along Heljargjá, and, from what can be judged, the cutting through of these is not due to any cause connected with their volcanic character. On the whole, nothing has been observed to indicate direct connection between the volcanic processes in the region and the forming of Heljargjá.

The edges of the fracture are quite sharp and only very slightly denuded. All the eruptions in Hágönguhraun with the exception of the very youngest series have come to an end before Heljargjá was made, and therefore the process must be of very recent date.

The fracture zone at Túngnárfjöll and the Túngná. Along that part of the Túngná that stretches from Túngnárbotnar to the bend at Kirkjufell the landscape has been disturbed by fractures in recent times. The dislocations are, in fact, so considerable that they set their mark upon the terrain.

The main topographical lines are all straight, running practically parallel from southwest to northeast. One of them, the east Túngná line, may be followed along the southeast bank of the Túngná from Túngnárbotnar to Kirkjufell, i.e. along a stretch of no less than 45 km.; along the west bank of the Túngná, from the north point of Vörðufell to the south point of Snjóalda, there is a parallel topographical border line, the west Túngná line, of 35 km., and a little further to the west is a third main line, the Litlisjór line, likewise 35 km. long in the same direction as the other two. The distance between the lines is constant, two to three kilometres.

These three main lines divide the landscape into strips of different heights, but within the same strip the height is almost constant. Between the east and west Túngná lines is the long, narrow, straight valley in which the Túngná runs, and between the west Túngná line and the Litlisjór line is a mountain ridge, with separate names for its various parts; the northern part as far as a narrow pass at the north end of Litlisjór is called Vörðufell, the middle section is called Túngnárfjöll, and the south part Snjóalda. Northwest of the Litlisjór line comes a basin in which Litlisjór and Fiskivötn lie.

The mountain range Vörðufell-Snjóalda forms a continuous wall, 35 km. long, two to three km. wide and 3—400 m. high, measured in relation to the Túngná. At only one place it is broken by a pass, viz. at the south end of the Vörðufell section; but at one or two other places, opposite Litlisjór and opposite Skálavatn, there are depressions where the ridge can be crossed on horseback.

Seen from a distance this range appears to be a narrow ridge (fig. 11); on ascending it one sees that really it is a long, narrow plateau bordered by two parallel cliff walls. The plateau is not quite continuous; in the north part it has been broken to pieces by fractures, the surface in places being crushed into fragments thrust one against the other. This thrusting has mostly been vertical, but along the walls of the ridge, the west Túngná line and the Litlisjór line, there is often an outward tilting towards the lower planes, northwest and southeast of the ridge. Fig. 23 illustrates this. The picture was taken towards the northeast and shows the cliff facing Lake Litlisjór. In the background is the broken surface of the plateau, appearing as a continuous whole, with step-like blocks on both sides. Fig. 23 shows one of these blocks. On the left of the picture is Litlisjór, to the right of the centre another water that is part of the Túngná. On its top the block bears a remnant of the plateau surface, which has leaned over towards the northwest in towards the Litlisjór basin, so that the surface lies obliquely. This phenomenon is most typical of both cliff walls and can be followed all the way along the 35 km. ridge.

The Túngná valley has been described in the chapter on hydrographic conditions, where it will be seen that between the west and east Túngná lines this valley is about 35 km. long, two to three km. wide and on both sides bordered by continuous, straight cliffs with a height of 3—400 m.

There can be no doubt that the Túngná valley and the range Vörðufell-Snjóalda as well as the basin of Lake Litlisjór are tectonic formations, and that the three main topographical lines indicate the situation of the principal fracture lines. The Túngná valley is thus to be regarded as a tectonic fissure of the same type as Heljargjá, but a little wider; the Vörðufell-Snjóalda range as a region of tectonic resistance, a horst, and the basin in which Litlisjór lies an area of tectonic subsidence.

Unfortunately I know the land southeast of the Túngná only from a distance, but there too is a number of long, narrow ridges separated by fissures and subsidence areas; one of these fissures is occupied by Langisjór. Here, too, the direction of the fracture lines is southwest—northeast.

West of Vörðufell is another mountain running southwest—northeast. It is 12 km. long, about two km. wide and about 150 m. high. The walls are steep, and almost straight; at the top is a plateau surface, broken in places into vertically thrust blocks. In every respect the form of terrain resembles Túngnárfjöll, and there can be no doubt that this, too, is a tectonic phenomenon, or, to be more correct, a region of tectonic resistance.

The landscape between Túngnárfjöll and Þórisvatn. In this landscape, too, southwest—northeast lines are so prevalent that the terrain consists of a number of narrow strips of land at different heights and with parallel borders. The various units in this system are not nearly so large as in the landscape just to the west of it and referred to above, and the height-difference between the various blocks is less too. The border lines between the blocks can rarely be followed more than about ten kilometres, and as a rule the width of the blocks does not exceed 3 km. In most cases the difference in height between two neighbouring strips is less than 50 m., although here and there it is up to 2—300 m. The largest and highest of the ridges bears the widely-visible peak Þóristindur. Travelling the country from southwest to northeast one can pass unhindered through long, flat-bottomed valleys with parallel sides, or along the planes of the intermediate strips of plateau; but were one to proceed in a direction at rightangles to the terrain lines the level would be found to change time after time, and one would be compelled to pass over a long series of ridges and valleys.

This region may likewise be regarded as a fracture area, but it is more complicated than those just described. The fracture lines are not so long, nor have they been formed at the same time. Some of the edges are fairly well concealed by denudation and aeolic deposits, as is particularly the case in the region round Þórisvatn, whereas others are quite recent. Very often the valley floors are covered with temporary lakes, others are permanently so covered, as for instance the large eastern corner of Þórisvatn. Time did not permit of a detailed tectonic mapping of the whole of this fracture area; but by the aid of sketches I have drawn the more important lines. The number of fracture lines is, however, much greater than the map indicates, and I suppose the number of well-individualized fracture lines between Fiskivötn and Þórisvatn is at any rate not under 50.

Southwest of Heljargjá is an area that is interspersed with a large number of quite short, parallel fractures in the usual direction. Fig. 22. One of the thrusts is 10—15 m. high and can be followed for a stretch of some kilometres. The others are quite short and low, but nevertheless very distinct. Very often the distance between the various thrusts is only about fifty metres, the result being that the whole terrain is divided up into blocks and strips, a repetition in miniature of the other two fracture areas at Túngnárfjöll and Þóristindur just referred to. The thrusts have taken place in very recent times and possibly were formed simultaneously with Heljargjá.

In a tectonic sense the whole landscape, from the east side of the upper course of the Túngná to the west bank of Þórisvatn, is thus very richly developed. The number of fracture lines is exceedingly great, so great that the whole area must be called a "champs de fractures" (fig. 22). The course of the fracture lines is conspicuously regular, their direction being for the most part southwest—northeast.

6. Subaerial denudation.

On the whole the landscape west of Vatnajökull lies between 400 and 800 m. above the sea, and consequently the mean temperature for the year and the summer temperature are so low that the chemical disintegration of both inorganic and organic substances proceeds slowly and incompletely. The landscape may be called a desert in a biological sense, the annual quantities of organic matter produced being very small; but where an oasis has been formed for some reason or other, one meets with organically mixed deposits with a thickness that is considerable in proportion to the density of the vegetation. Under the continuous covering of plants at Fiskivötn there is a 10—30 cm. layer of loose, crumbly, dark earth mostly consisting of incompletely rotted vegetation whose organic structure can frequently still be recognized. This layer is to be found on both a lava bottom and a gravel bottom, and sometimes it is carried by solifluction down to the lower levels and forms accumulations of great depth; as a rule, however, on account of the great porosity of the substratum it lies fairly firm and appears as a smooth, evenly distributed carpet. Where this deposit is found on a lava bottom it appears that the surface of the lava is quite unaffected below it, with all the small unevennesses characteristic of lava surfaces that have cooled in the open air. The inorganic part of the covering has thus not been formed by mechanical or chemical disintegration of the surface there, but has been carried, assuredly by aeolic means. This soil type seems to be characteristic of the central Icelandic areas of vegetation, lying on a highly porous substratum and especially well-developed in the oasis-area at Fiskivötn.

Another, and much more varied soil type occurs in some overgrown stretches that form a rather widespread facies in the landscape west of Kaldakvísl; we found its most well-developed specimen in the oasis of Illugaver. In the depression, about 10 sq.km., north and west of Sauðafell the groundwater in summer is just above the surface, and on both sides of the mountain small, slow streams have formed with irregular and shifting beds; their bottom is a morass of saturated sand and mud; although these watercourses are quite shallow they sometimes conceal unpleasant surprises to the traveller, for the elastic layer of mud on the bottom gives way time after time. Whereas the surrounding, higher moraine surfaces are so to say naked, and those running down to the depression are at any rate very sparsely covered with vegetation, the bottom of the depression is almost completely covered. The central part of it is very wet and has the character of a marsh, whereas the peripheral parts are drier and firmer and gradually become mountain heath. The wettest parts have almost a plane surface, on which in summer there are large pools of stagnant water and fairly luxuriant vegetation, so that they represent the type that in Icelandic is called *flói* (Mølholm Hansen 1930, p. 34). Round about the "flói" region is a belt of "*mýri*" vegetation, with a surface-form that has only very few unevennesses. On the transition between this and the surrounding mountain heath, which there takes the form of a very hummocky *jaðar*-ground, we find the surface and vegetation form that is so typical of certain highland regions, in Icelandic called *flá* (Nielsen 1928, p. 21). In habit it is very like a partly dug peat-bog in a temperate climate with its alternation of peat-pits and balks, i.e. narrow parts of the bog that have not yet been dug and therefore are higher. It is doubtful whether as regards the vegetation the "flá" is to be considered as a unity, as its principal peculiarity lies just in an alternation between swamp-formation of the "flói-mýri" type and large hummocks whose sides bear a chamæphyte vegetation; in addition there is still another type of vegetation, found on the top of these hummocks and, at any rate in certain parts of the highlands, characterized by *Cetraria islandica*. There is also a striking morphological difference between the hummocks and the intermediate flat stretches of swamp. The hummocks, or knolls, (Icel. rústir, i.e. ruins — an analogy from the ruins of turf-built, deserted farms frequently met with in certain parts of the highlands) are usually about a metre high with a diameter of from 2 to 10 metres. They consist on the outside of a layer, 20—50 cm. thick, of incompletely disintegrated plant remains and fine-grained inorganic material, probably brought by the winds; under this is usually a core of coherent ice, usually containing such small quantities of earth that it is not to be presumed that it was formed by the simple freezing of the marsh earth. On the other hand the flat belts of marsh between the knolls is not frozen in summer, and it is easy to stick a pole two or three metres down into the muddy bottom without encountering the least trace of ice or frozen ground.

The knolls in the "flá", the "rústir", are accordingly different from the usual arctic hummock in that they enclose a lump of ice that lasts long, and the obvious conclusion to draw is that they appear by means of a kind of ground-ice formation caused by the freezing of the ground water that rises in winter. Thus the "rústir" phenomenon would be analogous to the Siberian blocks of ground ice that are formed when the ground water in winter is enclosed by the frozen surface, but occasionally breaks out either right up to the surface like a spring or, if not so far, lifting the closed, frozen crust like a dome. In both cases the rising ground water freezes and forms a superficial covering of ice and a lenticular, underground lump of ice. The indications of the formation of the Siberian ground ice are scarcely to be doubted, as the process has been observed repeatedly; but we had no similar intimate knowledge of the Icelandic "flá" formation and a thorough investigation was most desirable. For the present we must thus assume that a certain combination of ground conditions, moisture and winter climate, brings about the formation of lenticular lumps of pure ground ice which, while being formed, raise the overlying frozen earth and make it appear as a knoll, on whose sides the oecological conditions in the subsequent periods of growth become different from those on the flats lying between the knolls. While the flats retain their "flói-mýri" character, chamæphyte families will appear on the sides of the knolls.

We thus see that the knolls in the "flá" can scarcely be regarded as being analogous to those in other Icelandic ground-forms; indeed, on the whole the effects of frost in the Icelandic landscape are very varied and produce many surface types, some of which have been dealt with in a work by Hawkes (1924).

In the outskirts of the oasis Illugaver there is an arctic mountain heath on a hummocky ground, but in the outermost border zone of the overgrown area the covering of vegetation is weaker, and there are no hummocks. There the bottom consists mostly of inorganic material that is slowly carried down by solifluction. Here and there the border zone is broken by large fields of springs lying in elongated hollows — without doubt an example of the special type of erosion that occurs through the excavating activities of spring water flowing over a flat surface. At such places ground and vegetation are naturally very peculiar and in Icelandic are called "*dý*" (Mølholm Hansen 1930).

The chemical disintegration of the rock proceeds very slowly, as already stated. On the other hand the physical disintegration is very extensive and plays a great part in the forming of the landscape. In the snowless period the naked surface, devoid of vegetation, is exposed to very considerable fluctuations of temperature, and, as most of the rocks are brittle and very frangible, their destruction proceeds at a fast rate and is observable in many ways. On many mountain sides stonefall is a common phenomenon, and it is no rare occurrence for blocks of up to several hundred cubic metres to break loose and fall into the valley. The result of the mechanical disintegration becomes very conspicuous, as large parts of the highland have no surface drainage, the consequence being that the loose material is not carried away but remains in the immediate vicinity of where it is formed.

The consequence is that the "original" tectonic and volcanic relief of the landscape is to some extent veiled, the steep slopes are smoothed out, the heights are broken down and converted into rounded ridges, where only here and there it is possible to recognize the permanent substratum, whereas the remainder is concealed under a thick layer of the loose material freed by the mechanical disintegration. An example of the weathering of the substratum will be seen on fig. 24, which represents the peculiar column that is called Tröllið. It stands at the exit of a pass leading from the region round Fiskivötn over Túngnárfjöll down to the Túngná. In the background is the extensive river bed, several kilometres wide here and full of deep and quite impassable patches of quicksand. Some idea of the column will be gained by a comparison with the ice-pick standing in front to the right; its helve is about one metre long. The column is thus about 10 m. high and about two metres thick. Its origin may without doubt be placed in connection with tectonic processes of recent date, and I presume it may be taken to be an analogy to the columns observable in other parts of the same mountain range, see p. 57, 239, fig. 23. At the moment it is undergoing violent attacks of weathering, as the picture shows. The large blocks lying at its foot have fallen out of the cavities that can be seen in the upper part of the column.

Another example of the brisk rate of the mechanical disintegration is shown on fig. 26, where there is a moraine boulder that has been split by the frost into a large number of large and small slabs, some of which are in situ, while others have been carried by solifluction down along an otherwise gentle slope. In the landscape west of the Kaldakvísl, Holtamannaafrjettur, one frequently meets with this phenomenon in various stages of maturity. There are all stages from moraine surfaces with intact, scattered boulders, to surfaces where the boulders have been turned into stone slabs which, by means of solifluction, have been distributed over a larger or smaller area, usually oval in form. Large parts of this landscape are in fact characterised by oval patches of frost-split slabs, separated by belts of ordinary wind blown moraine. Each of these patches originates from one or more erratic boulders, nearly all of doleritic lava. The figured specimen shows the phenomenon at a stage where the process is well advanced, but no more than that the situation of the boulder and its approximate contour can still be recognized.

Subaerial denudation plays a very great part in the shaping of the details of the relief in the Icelandic highlands, but in the long run it also succeeds under certain circumstances in marking the landscape as a whole. Fig. 32. An examination has shown that the figured landscape in Þóristungur has been exposed to the activities of very violent tectonic processes, but the consequent disturbances in the relief have been practically erased by the disintegrating forces, the result being a form of landscape characterized by soft, rounded forms produced by very rapid weathering and piling up of the freed material in the intermediate hollows. As regards subaerial denudation, a landscape like this must be said to represent a mature stage, although, as will later on be shown, it is no subaerial-denudation landscape proper, as both the effects of the wind and a peculiar, temporary water erosion have helped to give the landscape its present form.

Only in regions where tectonic and volcanic disturbances have taken place in very recent times does the relief have an undisturbedly young appearance; the unevennesses formed by tectonic and volcanic forces gradually disappear under a covering of their own products of disintegration, and in this manner the arctic desert produces an analogy to the phenomenon that we know so well, especially in sub-tropical desert regions and named by de Martonne "ennoyage desertique".

7. The æolic processes.

The climate of Iceland is on the whole very windy, and the number of storm days is large, especially in the west and south parts of the land (Thoroddsen 1914, p. 278; Þorkelsson 1924). The frequence and violence of the gales, in combination with the slight biological valence of the landscape, have the result that the effects of storms in the Icelandic highlands become a morphological and oecological factor of the very greatest significance, to which many of the writers who have occupied themselves with the study of Iceland's geography and geology have referred. Thoroddsen, both in his diaries and in his comprehensive works of handbook character, mentions a great many times the violent and destructive effect of the wind in certain parts of the inhabited country and also the grand wind-erosion phenomena that characterize large parts of the desert regions of the interior. The works of v. Knebel, Reck, Spethmann and Sapper also contain valuable contributions to our knowledge of the activities of the aeolic forces, and finally, the Swedish investigator Carl Samuelsson has dealt with these problems in two works which not only contain numerous individual observations, but in addition a reference to the interesting fact that the Icelandic region of wind erosion is the analogy of the North Atlantic to the sub-arctic, wind-erosion regions of the southern hemisphere.

The spreading and intensity of the landscape effects of the gales are limited to a certain extent by the fact that the higher parts of the country are covered with snow for a good part of the year, and of course one of the conditions of rapid wind erosion is that the ground is not snow-covered. But even if this condition is present, it is by no means certain that a storm will have any visible morphological effect. In artic and sub-arctic regions the erosive force of the wind is not only governed by its strength, but just as much by its drying power, for moist winds are only slightly erosive, whereas dry, steady winds are capable of carrying even very considerable masses of earth away.

In this connection it would be of the greatest interest to know the size of the rainfall, especially summer rainfall, in the various parts of the highlands of Iceland;

of this we know scarcely anything, however. According to the measurements made at the farm Mödruvellir we must take it that the rainfall in the northern highland is much less than at the coast, as there it only amounts to 34 cm. a year (Þorkelsson, p. 3). It is also quite beyond doubt that there is a very great difference between both rainfall and the number of rain days in the various parts of the interior. While we were in the regions west of Vatnajökull in July and August it was very striking that the Fiskivötn region had many more rainy days than the landscape to the north of it.

A common and very important type of dry wind occurs in a kind of Föhn. A north wind will usually bring rain over the stretch north of the NW—SE altitude axis of the country, and southerly winds to the south of it, whereas the descending winds on the other side of the axis are frequently dry. It must furthermore be assumed that local barometric disturbances of summer time over the ice-covered regions plays some part in this connection, a circumstance that is particularly noticeable at Vatnajökull, whereas the climatic importance of the smaller glaciers is much less marked.

The decisive factor, however, is scarcely the extent of the rainfall or its distribution, but the physical conditions of the surface of the ground, for, on account of the low temperature, the rainfall is quite sufficient to affect the climate in a humid sense. The surface, however, is in all essentials formed of highly porous rocks which allow of the rapid passage of even large quantities of water. The content of fine-grained constituents and especially of colloids is small, and therefore the ground is only little capable of holding the rain water back, so that the soil, despite fairly large quantities of rain, appears to be very dry. Only at places where the ground water appears in the immediate vicinity of the surface does it appear humid, but on the other hand this humidity is often so pronounced that the landscape assumes the character of a marsh. The transition between this type of ground and the highly porous, dry type is rather sharp, and the degree of dryness that changes gradually with the terrain, so characteristic of humid, temperate soil, is unknown in the Icelandic highlands. We have either the dry ground type or the marshy type. Only in rare cases transition forms play any greater part.

According to Richthofen and Walther the erosive activities of the wind are divided into two types: deflation and corrosion. By deflation is to be understood the removal of fine-grained material by the wind, whereas corrosion signifies the polishing effect of firm particles carried by the wind over large boulders and the naked ground. Both types play a great part in the landscape of Iceland, especially in the land west of Vatnajökull.

Deflation. When circumstances are favourable the gales become very violent, and the wind can then carry away particles of considerable size. Thus Harder (1911) states that a December storm in 1908 threw a stone like a bullet through a window in Sandfell Church, and it has often been observed that the gales roll small stones up slopes and throw them into the air from the ridge. There are, however, no exact measurements of the size of the grains carried by the wind. The deflation processes in the highlands are greatly favoured by the fact that there is no continuous covering of vegetation; as a consequence the wind has free play, its speed over the surface becomes relatively high, and, as there is transportable material almost everywhere, there is a violent sweeping across the surface. Sand storms in the highlands are sometimes most disagreeable experiences, the skin is abraded, tents, sleeping bags, food and instruments are filled with sand, and it is difficult to retain one's sense of direction. In addition there is trouble with the animals. Dogs are quite helpless, horses manage rather better owing to their greater height, but they nevertheless suffer a good deal, and keeping a caravan together in the teeth of a sand storm is a task that requires much energy and care. When conditions are difficult it is worth while tying the whole caravan in a long line, head to tail.

The transportation of the coarser material proceeds in the form of a sweeping across the ground, but the finer particles are carried in another manner, at any rate some of them. In good weather, looking out over the interior of the island from some high point, one often witnesses to the formation of large rotating columns of dust of a height of several hundred metres. Usually there are several together and they sail away at a considerable speed, but retaining their mutual positions and forcing upon the observer an impression of advancing groups of giant soldiers. These phenomena are only to be seen on relatively calm days and are especially fine at the commencement of a sandstorm. As they continue to develop the details become blurred, visibility is reduced, and the whole landscape is enveloped in a fog of dust. If one observes a sand storm from a suitable elevation, it will be seen that the mass of dust is sometimes sharply limited at the top, and in such cases it is possible to obtain a tolerably reliable measurement of its height. In this manner we succeeded in measuring the height of a dust storm south of Hofsjökull at 2—3000 m. over the plateau.

The surfaces of the Icelandic plateaux contain large quantities of material sufficiently fine-grained to be carried away by the wind. Even if the moraine material that covers large parts of the highland is fairly coarse, there is a considerable part of it with a grain that is less than the maximum size for transportable sand. Some of these glacio-fluvial deposits provide a very good working basis for deflation, as the grain varies from very coarse gravel to quite fine clay. The rapid mechanical disintegration of the rocks of the glacial-volcanic formation likewise produces large quantities of fine material (Thoroddsen: palagonite dust), and finally, in certain periods and regions enormous quantities of fine volcanic explosion material are present. There is thus an abundance of material for the deflation process, and this, in combination with the favourable climatic and terrain conditions, makes the region west of Vatnajökull a pronouncedly arctic wind-erosion region, perhaps the most pronounced in the northern hemisphere.

The result of the deflation is that the greater part of the fine material that is accessible to the wind is blown away. In this manner the moraine is converted into a stone-paved surface whose moraine character is still to be recognized owing to the varying size and petrographic composition of the stones. If there nevertheless is any doubt as to the origin of the covering of stones it is easy to ascertain by means of digging, as directly underlying it is the untransformed moraine. Glaciofluvial surfaces are transformed in a similar manner, the fine particles are blown away while the coarser ones remain, and, gradually as the process goes on, there will be a lowering of the surface. The further result in this case is that a clean-swept surface is formed, closely paved with stones; these, however, in contrast to the blown surface of the moraine, are almost uniform in size and usually not more than 5 cm. in diameter. As a rule it is also possible to recognize the pre-æolic relief, as for instance in the wind-blown moraine one can distinguish the undulating surface form that is so markedly in contrast to the glaciofluvial surfaces which, after being swept clean, are practically flat. The volcanic explosion products and weathering material undergo a similar sorting, whereby the fine-grained material is blown off, leaving the coarser particles behind.

In the lowland the effects of sand and dust storms are fainter as a rule, because the surface is more resistant, for one thing on account of the vegetable covering, and also because the strength of the wind in the lower aerial strata is less than in the highlands. In some especially disposed regions, such as the great sands of the south, the Hekla region and certain places in the north, there is, however, a very considerable and fateful sand drift, and over practically the whole country the æolic phenomena play a great part in the forming of the landscape. As has been stated, erosion is especially active in periods of descending winds of a Föhn character, and, as a consequence, the northwest—southeast axis of elevation divides Iceland into two regions which differ as regards æolic landscape-forming, viz. a northern part with south-wind erosion and a southern part with north-wind erosion.

Sand drift is usually a local phenomenon, but the fine dust spreads out over tremendous areas. With dry north winds of ordinary strength there arises a peculiar atmospheric condition in the south and far out over the Atlantic, (Icel.: mistur), characterized by a soft, yellowish-brown gleam as a consequence of the refraction of the innumerable particles of dust. Even with a cloudless sky the light is very diffused, so that the shadows are faint and pale even in full sunshine. When examining objects close at hand nothing unusual is noticed; but at only a few hundred metres away everything is seen as through a fine veil, and the remote distance is shut out entirely. This is when the dust from the plateaux is falling steadily and densely over the whole landscape.

Aeolic ablation is not equally great in all parts of the highlands, however. In certain places the activities of the wind are hampered by moisture or other factors; but in the region between Hofsjökull and Vatnajökull the gales have free play, and I know of no part of Iceland that is so storm-harried. Another significant peculiarity is that sand storms from this region have relatively easy and unhindered access to the lowlands through the large, flat-bottomed, barren valleys west of Hekla. In its mildest forms the drift in the lowlands looks like fig. 28 and 29. These two pictures show the same locality, but photographed in different directions. The person has not moved between the two exposures. Fig. 29 was taken from the south and shows how the surface is covered with an apparently continuous carpet of vegetation, in this case mosses (*Grimmia*), whereas fig. 28, which is taken towards the south, discloses that the carpet in reality is not continuous, but consists of a number of cushions, separated by wind-blown, stony flats. The various cushions display a most asymmetrical structure, with a steep, undermined north side and an evenly sloping plane towards the south. In this locality we thus have an example of the conditions that hold good for the whole of South Iceland, that it is the north winds that ravel out the covering of vegetation, whereas the corresponding processes in the north are due to southerly gales and produce similar results, except that here the erosion is from the south. It is a question whether such a ravelled-out cushion formation is to be regarded as a transitional stage between a continuous type of growth and an entirely clean-blown desert surface, or whether the cushion regenerates on the lee side at such a speed that the growth there keeps pace with the erosion on the other side. In a number of cases it must be assumed that the latter is the case, and that the intensity of growth adapts itself to a certain equiponderance governed by the interplay of the biological valence of the locality and that of the destructive forces — in this case especially the devastating activity of the gales.

In other places there is no such stability at all, and there is no question but that developments have been towards a reduction of the covered area. There is a typical example of a landscape of this kind in the Hekla region, where wind erosion in past centuries has assumed an extent not paralleled anywhere else in the country. A part of the region where this erosion is at present attacking the inhabited country is shown on fig. 30, a view from Skarðsfjall towards the southwest. The foreground is a wind-blown, stony surface which formerly has borne a metre-deep covering of quite fine, wind-deposited loose earth, as near as anything a loess. A remnant of this covering is to be seen on the right in the picture, the dark patch representing the surface before the commencement of the erosion. It has quite a luxuriant covering of grass. The wind attacks the under edge of the loose layer so that the vegetation layer is undermined and falls down. On the figure one can see the quite fresh profile made in this manner, displaying the still recognisable original stratification in the atmospherically deposited material. In the lowland, which forms the background of the picture, two different surface types can be recognized. On the right is a smooth, grass-grown, loess surface attacked from the left, i.e. from the northeast, by the wind, whereby the whole layer of loose earth with its plant covering is being peeled off. This exposes the underlayer, in this case a postglacial stream of lava, whose characteristic unevennesses mark the left side of the background. The loess-covered lava field here is of great industrial importance and forms the subsistence of a very large herd of sheep and cattle; in this locality the erosion is nothing short of a national catastrophe, as a number of farms have been laid waste and others are threatened. The principal agent of the erosion here is the sand that sweeps along the surface, undermining the loose earth; the method of putting a stop to the work of destruction is therefore this, that a number of stone dikes of blocks of lava are built at right angles to the prevailing winds in order to catch and hold the sand. On the picture are two of these dikes, one straight and the other curved.

Corrosion. The violent sweep of the sand along the surface of the land causes greater wear, both on the particles that are swept along and on the substratum, whether this consists of loose blocks or firm ground. This indirect wind erosion, corrosion, is very marked and several writers have referred to it. For instance, v. Knebel has observed the triangularly polished stones that are so familiar in other wind-erosion regions, as well as lava blocks with air pockets, whose orifices were of the form of enlarged funnels as a consequence of the corrosion (v. Knebel-Reck 1912, p. 133, fig. 15). Harder (1911) relates a very drastic example of sand-grinding. He says that a flock of sheep one stormy night were driven out into a snow drift, where they froze fast. When they were found next morning most of them were dead, and the others had to be killed, as all that showed up above the snow was bloody flesh, wool and skin having been worn entirely away by the sand and stone drift.

Outcrops are frequently smoothed off by corrosion. There is one example of this kind in a postglacial lava surface on the dome volcano Solkatla, where the uppermost layer, with the characteristic cord structure of such deposits, has been partly removed by wind erosion (Nielsen 1927, p. 107, fig. 2). It is naturally most marked on prominent edges and often gives rise to curious profile forms, in which with the application of a little imagination one can see human and animal heads and all kinds of fabulous beings. The very heterogeneous rocks are given a character of their own. The glacial volcanic formation so frequent in Central Iceland usually consists of a fairly soft basic mass of a rock that must almost be called a tuff, in which are strewn boulders of harder material. In the course of corrosion the tuff is violently attacked and is smoothed off, whereas the hard boulders are dressed and stand out as protuberances and points which offer convenient but rather unreliable holds when climbing. The landscapes that are least marked by corrosion are undoubtedly the post-glacial lava fields; there loose material to work with is lacking, and, if it should be brought along, it soon settles in the numerous cavities. Only if the surface of the lava is very smooth or the material brought very large is there any actual corrosion.

In the Icelandic wind-erosion regions we thus have a number of surface types that in all essentials correspond to the hamada phenomenon in the temperate, sub-tropical and tropical deserts. Apart from the differences produced by climatic divergences, the main difference seems to be that in the warm deserts the phenomena are frequently mature, whereas the Icelandic hamada-form is of very youthful character. This is seen, for instance, in the fact that the pre-æolic landscape phase is usually easy to recognise. One can differentiate between the moraine hamada and the glaciofluvial hamada and the weathering hamada, and below the stone paving one constantly finds rocks that have not been affected by æolic activity.

Where nothing of an unusual nature interferes, the sand freed by the wind settles in the vicinity of the eroded area. As a consequence of the climatic conditions described above, the transportation is nearly always in a direction away from the axis of elevation of the country, and thus one may expect to find sandy deserts outside the erosion regions, especially below them. But there is no parallel to the sand-dune areas of the sub-tropical desert (Sahara: erg, Asia: kum). THORODDSEN was already aware of this peculiarity, for he writes, for instance in his report from Fiskivötn: "Sand-dunes proper do not exist at all." This entirely conforms with my observations both in the regions west of Vatnajökull and in other parts of the Icelandic highlands. The absence of dune areas is without doubt due to a number of coinciding circumstances. In the first place the Icelandic landscape forms referred to are of fairly young type, and the processes have simply not been allowed to work sufficiently long to form a mature "erg" landscape. Next there is the factor that one of the predominating landscape facies in the Icelandic highlands, viz. the post-glacial lava field, is able to absorb and retain large quantities of æolic-brought sand without becoming "satiated", and this is probably the cause of the apparent disproportion between the thickness of the dust deposits in the lowlands and the corresponding sand deposits both in the highlands and on the outskirts of the wind-erosion areas of the lowlands.

In places, however, we find landscapes that must be said to be marked by wind-blown masses of sand; but even in such cases there is usually no dune formation proper. This is undoubtedly connected with the fact that the æolic activity is a temporary phenomenon, being restricted to a short period of the year, and that throughout the whole of the remainder of the year the surface of the ground is exposed to the workings of other forces which in fact level out the rudimentary dunes formed during the sand storms, a circumstance that is referred to elsewhere in this work, viz. in the hydrographic section and the chapter on the annual morphological cycle.

8. Hydrographical conditions.

We know nothing of the rainfall in this part of the Icelandic highlands, and in fact we know little of the climatic conditions on the whole. It is true that from the north we have continuous observations from two inland stations up in the hills, but a comparison between conditions north and south of the axis of elevation would be untenable, as the coast stations in the north and south return such great differences that we cannot assume that the climate of the Icelandic highlands is marked by any uniformity either.

The summer rainfall in 1927, however, was much greater at Fiskivötn than in the lowlands, which had dry weather for weeks at a time, whereas at Fiskivötn there was rain almost every day. It would seem, however, that the profensity for rainfall varies greatly in the different parts of the highlands; Sprengisandur, for instance, had much less rain than the region round Fiskivötn, and at Illugaver the rainfall was much less than at Tjaldvatn. In the latter part of August snow already begins to fall down to about 1000 m. above sea level, and throughout the whole of the winter half-year the landscape is covered with snow.

The total period when there is no snow is presumably about five months, and in that time a large part of the rainfall must thus be carried away. The output of the glacial rivers falls off very considerably in winter time, whereas the spring-fed rivers, as far as we know from other parts of the highlands, are open and productive throughout the greater part of the winter (Müller 1926, Nielsen 1928, p. 19).

The watercourses are fed with supplies that come from 1) summer rain, 2) melting snow, and 3) glaciofluvial waters. All these factors are very variable; snow melting is a spring occurrence, but it commences at different times in the various parts of the highlands; glacier melting is a high-summer phenomenon and represents a dominating regional factor in the hydrography of the landscape. The fact is that neither summer rain nor snow melting is sufficient to form the basis for the forming of a hydrographic net. In this region this is done by the glaciofluvial waters alone.

This is surprising, in so far as the volume of water produced by both summer rain and snow melting is very considerable, and this, in conjunction with the low temperatures, whose effect is that evaporation is small, ought to favour the development of a well-formed hydrographic net similar to what we normally find in regions with a pronouncedly humid climate. But, as already stated, there is none.

The cause of this peculiarity is the physical nature of the surface of the ground. As was stated in the previous chapter, the following surface forms predominate: lava fields, lapilli surfaces and glacio-volcano formation. In the region between the Kaldakvísl and the Túngná they prevail so to say to the exclusion of all others, but west of the Kaldakvísl we find moraines of relatively young age, and quite young moraines at the margin of the Vatnajökull.

The lava fields occupy about half of the surface and are all very porous. Even in periods of most violent rain there is not a drop of surface water to be seen; probably the snow melt-water also disappears immediately; at any rate in this part of Iceland I have seen no sign of ponds or streams having been formed in the lava fields. Furthermore, arctic lavas are very durable. They are snow-covered for considerable periods of the year so that there is not much subaerial denudation, water erosion nil, while vegetation is lacking. We thus see that a long time elapses before erosion can get to work at all and transform or carry away parts of the lava. All things being equal, the lava fields in these regions will retain their porosity for a long time and thus prevent the forming of a drainage system on the surface.

In the lapilli surfaces we have something of the same kind, but not so stable. They occur especially in the region round Fiskivötn and cover about 140 sq. km. These, too, are highly porous and avidly absorb rainwater and melt-water. The material, however, is not coherent, and as a rule the landscape has not the horizontality that is so typical of the lava fields, but may, all according to the nature of the substratum, be more or less markedly profiled. This favours a removal of material. In summer the lapilli fields are quite dry and usually have no superficially running water. But during the melting of the snows such considerable quantities of water are freed that a number of small brooks are formed, of a purely local character and only leading water down from the ridges towards the nearest valley. The result is that the loose lapilli material gradually disappears from the heights and accumulates in the valleys in the form of stratified deposits of great thickness. Regarding the forming of lakes in these valleys see p. 84, 266 and, as regards æolic forces, p. 63, 245.

The glacio-volcanic formation, too, in these regions is usually very porous, although not so much as the surface forms just referred to. This is probably connected with the fact that there is little chemical disintegration, and that mechanical disintegration is the prevailing form of demolition. In some cases small watercourses are formed on surfaces of this kind, but as in these regions such surfaces only occur in the form of elevated areas, jutting up over the enormous lava or lapilli plains, such small brooks reach no further than to the foot of the height, where they immediately disappear in the highly porous surface.

The least porous of the surface forms in this part of Iceland is the moraine. The fresh moraine contains a considerable quantity of fine-grained material and therefore can very well retain water; otherwise conditions in the very young moraine areas are as a rule so peculiar, hydrographically, that quite other factors predominate. The rather older moraines, such as those in Holtamannaafrjettur, are to a considerable extent subjected to the activities of the æolic forces and are thus transformed into stony plains; in the depressions, however, the water collects in lakes and marshes, from which rise brooks that in certain cases have succeeded in accumulating into a drainage system.

On account of the peculiar conditions referred to here, practically the whole of the landscape between the Túngná and the Kaldakvísl lacks superficial drainage, and thus, despite the markedly humid climate, there are surface forms that are pronouncedly arid both as regards their present condition and morphological development. All surface water percolates away or evaporates, so that there must be a very large transportation of water in the form of ground-water. This is directly observable at the great spring systems, of which the south part of the area in question has a great number, and it also appears for instance from the fact that the Vatnakvísl five kilometres from its source is so big that it can only be crossed at certain fords. It is also to be seen with great distinctness from the way Þórisvatn is fed and drained, p. 80, 262. The few spring-fed rivers that do exist are, although of some volume, quite short and play scarcely any part morphologically. The only rivers that are of any topographical and morphological importance are the two large rivers that drain the northwest part of Vatnajökull: the Túngná and the Kaldakvísl.

a. The Rivers.

The main watershed of Iceland runs in the direction northwest—southeast and divides the country into two main hydrographical provinces, a northern part that is drained into the Arctic Ocean and a southern part drained into the Atlantic. A small province is drained into Denmark Strait, and another into the ocean washing the east coast of the island.

The area that concerns us here is the northeast part of the drainage of the Þjórsá, and thus lies on the boundary of the great southern, main hydrographical province. The main watercourses in this area are the Kaldakvísl and the Túngná, which unite and immediately fall into the Þjórsá at Búðarháls. The drainage area is about 4000 sq.km., but in addition there are the parts of the Vatnajökull whose disburdening of ice takes place down towards the area in question, and of the size of this region we know nothing, no more than of the volume of the masses of melting ice. Both main watercourses have a length of about 100 km., and together they carry so much water that when they join the Þjórsá the latter's volume is almost doubled and thus becomes one of Iceland's largest rivers, if not the largest. Both the Kaldakvísl and Túngná are glacier rivers with the muddy, greyish-white water characteristic of such watercourses, but on their way they both receive large supplies of clear spring water (Icel. bergvatn).

The Kaldakvísl. The northwest part of Vatnajökull is formed of an enormous dome about 2000 m. high, from which large masses of ice glide down towards the north, west and southwest. In summer time the lower parts, up to 14—1600 m. above the sea, are subjected to very violent melting, and a great part of the water thereby freed collects in Vonarskarð into a fair-sized glacial river which must be regarded as the main source of the Kaldakvísl; but it is just as difficult to point to any definite source for this river as for so many other Icelandic watercourses.

In a hydrographical region where the watercourses are fed by the groundwater it is mostly possible to determine the exact position of the source of a fluvial system, and the same can be done with the ice-born rivers in an ice-sheet region of Alpine character, as the subglacial terrain, in conjunction with the abundance of cracks and fissures in the ice, favour the formation of large collective subglacial drainage systems which come to view through glacier ports; as a rule it is said that the river has its source at this spot. At most of the Icelandic glaciers, however, the draining assumes another form. It is true that at ice-margins in the Icelandic highlands there are numerous glacier ports, but their importance as drainage channels is relatively small. For there the freeing of the meltwater mostly proceeds diffusely along the whole of the margin, and as a consequence it collects into an enormous number of small streams which only gradually turn into large watercourses. In such cases we may therefore only say that a watercourse rises in this or that district, but we cannot point to any definite spot. But where the terrain favours it, as at some of the ice-margins in the south there are also examples of the Alpine drainage type.

On its way through Vonarskarð the Kaldakvísl receives a number of tributaries from the Vatnajökull and a corresponding series from the western part of Túngnafellsjökull, and on leaving that pass the watercourse is already of considerable size. There it runs out on to a plateau lying about 800 m. above the sea, called Köldukvíslarbotnar, which is the name of the landscape between the foreland of Vatnajökull and the Háganga mountains. Here the substratum consists of lava, as the enormous mass eruptions to the south have pressed the lava streams northwards right up to the foot of Túngnafellsjökull. It is possible that there have also been eruptions in this area, but we do not know the landscape with such certainty that this can be decided. Thus, as far as is known the substratum in Köldukvíslarbotnar is the extreme northerly offshoot of Hágönguhraun. The eruptions of lava have affected the course of the Kaldakvísl, it having been forced towards the north and west by the advancing masses and in quite recent times been compelled to form a new bed in the edge of the lava field.

In this region the Kaldakvísl receives several large tributaries, all glacial rivers, one of which comes from Túngnafellsjökull. It drains the southern part of the glacier and makes its way through a number of deep gullies down on to Köldukvíslarbotnar where, over a large, flat gravel cone it joins the Kaldakvísl. The draining of the margin of the Vatnajökull proceeds over the lava field, where in the course of time the various rivers have changed their beds again and again. The result has been that the lava is covered with a continuous layer of gravel and sand and the landscape transformed into a fluvioglacial plain, where the underlying lava can only be recognized here and there. In 1927 there were three main watercourses, one from the ice margin just at Vonarskarð and two from that part of the margin that lies behind the great forelands north of Kerlingar. Fig. 33.

The fall in Köldukvíslarbotnar down to Háganga syðri is slight, and, as the surface owing to its origin is almost flat, the watercourses frequently change their beds. This is to be seen on fig. 33, which was photographed from the top of Háganga syðri, i.e. about 800 m. above the plain. In the background there is a glimpse of Túngnafellsjökull and the river coming from it; from the background to the right comes the Kaldakvísl, and from the right edge several small streams which are branches of the three rivers referred to. It will be seen that the Kaldakvísl splits up into a confusion of small arms which join together again further down. Furthermore, the lighter zone to the left of the ramified part of the Kaldakvísl marks a bed that has only recently been left and where the river has formed a system of ramifications corresponding to the present one. Under these circumstances of course a very brisk deposition of sand and clay is proceeding over the whole plain.

At the foot of Háganga the Kaldakvísl receives its last afflux of glacier water, and immediately afterwards it pours down at rushing speed through a narrow ravine which the river has cut out of the foot of the mountain itself. There the lava embankment has been extremely strong, the lava streams have come like waves towards Háganga's slope (fig. 18), where they have been broken and turned to the north and to the west. Just at this point is where the Kaldakvísl breaks through, and the effects are magnificient. The river runs in against the side of the mountain and again out on to the lava field, then it forms two fine falls, after which it continues more smoothly in a deep ravine. Here we have the explanation of the formation of the whole of the great area of deposition in Köldukvíslarbotnar as described above.

The course from Háganga to where it meets the Túngná is much quieter and uniform, though there are certain disturbances too. On the stretch as far as Þórisós the river is in several places intruded upon by offshoots from the great lava fields on the east. At the places where the lava is visible in the valley the course is usually through a ravine and the fall is steep, with whirlpools and small waterfalls; but above such narrows the course is quiet and not uncommonly the bed is ramified. At these places the river is easy to ford. The relation of drainage to lava at Þórisvatn will be dealt with when describing this lake.

On its course from Háganga to the Túngná the Kaldakvísl receives considerable quantities of clear water (Icel. bergvatn), for instance, from Þórisvatn through its outlet Þórisós and from Holtamannaafrjettur. From this landscape run a number of streams, and also along the valley bottom of the Kaldakvísl there is an almost continuous spring horizon which is especially marked on the left bank. It is characteristic of this part of the Kaldakvísl that the flow of water to it varies greatly. In many places ravines and river valleys of insequent character are observable, practically dry in summer but, while the snow is melting, carrying considerable masses of water. They have in fact modelled the relief so much that, when travelling in the direction northeast—southwest, one cannot very well follow the river but must direct one's route at some distance from it, five to ten kilometres. On the stretch from Þórisós to the Túngná the valley is wide and open, with long, gently sloping sides. There the river receives a number of tributaries, of which the largest is the Klifshagakvísl which drains the southern part of Holtamannaafrjettur.

The Túngná. On his journey in 1889 Thoroddsen followed the Túngná from Vörðufell to Botnaver, and in describing that journey he says that the Túngná rises in a plain north of Botnaver, which he calls Túngnárbotnar, and there on his map he indicates the source of the river. When de Fontenay in 1925, after a laborious wandering over the wild lava fields of Hágönguhraun, came to Kerlingar, he observed a small glacial stream running southwards, rising in the region north of Kerlingar, which he called Ulfaldakvísl. From all appearances this must run into the Túngná, and on his map of Iceland of 1927 Daniel Bruun marked a small stream running from Kerlingar to the Túngná. This was confirmed during a journey undertaken in 1927 by de Fontenay and the writer of the present work, and the river coming from Kerlingar proved to be so large that it is justifiable to place the source of the Túngná to the plain in front of Kerlingar.

The Túngná drains the ice margin of the Vatnajökull from a point north of Kerlingar to Gamelsfjöll, i.e. a stretch of 15 to 20 km. Along this stretch the glacier slopes smoothly and almost uncreviced. The subglacial drainage is slight and the glacier ports small. On the other hand there is a parallel system of meltwater streams down over the ice, by which means enormous volumes of water are carried to the ice margin; from the margin itself, too, and the numerous dead blocks of ice in the foreland, much water is freed, and the moraines and glaciofluvial plains in front are consequently saturated and form, at any rate sometimes, an almost impassable, bottomless morass. From this rise numbers of muddy brooks which collect into bigger watercourses.

One of these systems of small streams is formed on the plain before Kerlingar, whence, in the form of a deep river, they pass to the south. Almost midway between Kerlingar and Túngnárbotnar the river passes through a deep, narrow cleft between two mountains belonging to the glacial volcanic formation. There the river's course has been violently disturbed by recent volcanic processes. From the north a thick stream of lava has run down and filled the gully, with the result that the river has had to erode a new bed for itself. This has been done in the manner typical of such processes (fig. V) (Bjerring-Petersen and Nielsen 1925, p. 228, fig. 2). The forming of the new bed has proceeded at the outer edge of the lava, but mostly outside it in rocks from the glacial volcanic formation. From there the river runs in a gully on the edge of the lava field down to the edge of the lava at Túngnárbotnar. At this stretch the river is quite narrow but deep, and very swift with many small waterfalls.

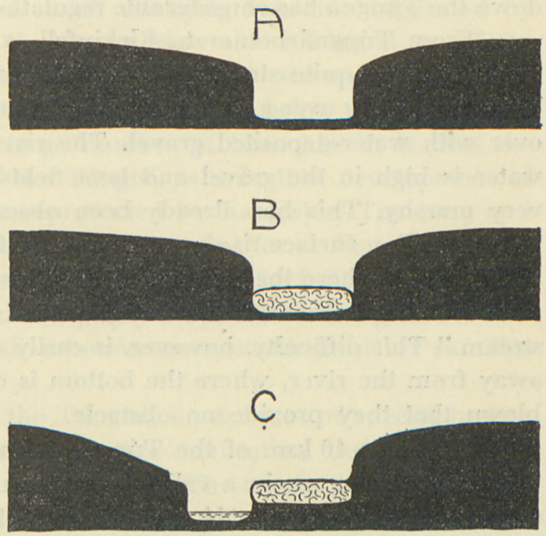


Fig. V. River valley filled up by a lava stream. The river has been forced to erode a new bed at the edge of the lava.

The whole of Túngnárbotnar may be characterized as a moraine morass with a number of ponds, and before it a fluvioglacial plain of clay and gravel, with only a few boulders and craters rising out of it. Numerous meltwater rivers ramify over this terrain. They differ greatly as to volume, strength of flow and bed; some are hard and stony at the bottom, others are full of quicksands and very difficult to cross. The principal water, the Túngná itself, is difficult to ride over at this point, and the fords change from day to day. Normally, however, it is possible to cross the river just a little way below the outlet of the lava-dammed gully at the spot where it begins to branch out, and a little more to the south towards the isolated mountain. Below this place the whole of the mass of water from the Vatnajökull gathers into a wide, quiet, muddy stream, with numbers of quicksands. Like all glacial rivers, the Túngná here is very variable. In cold periods it shrinks, but on warm days, and especially when rain is falling over the glacier, it swells violently and forms new beds in an astonishingly short time. Under such conditions large parts of Túngnárbotnar are under water and are practically impassable. The same oscillations are of course observable in the lower parts of the river, but the amplitudes are less, because further down the Túngná has considerable regulating basins in the form of lakes and swamps.

From Túngnárbotnar to Kirkjufell, a distance of about 50 km., the course of the Túngná is quite straight in a southerwesterly direction. For the first 10 km. the river runs freely over a wide plain, doubtless an old lava field which has been covered over with water-deposited gravel. The river branches a good deal, and the ground water is high in the gravel and lava fields to the west, which to a great extent are very marshy. This has already been observed by THORODDSEN, who writes (1889, p. 15): "The surface is here covered with angular, coarse lava gravel and drift-sand, and, as there the lava lies at the same level as the Túngná, it is saturated with water so that here we have to fight against an unusual obstacle — a swampy lava stream." This difficulty, however, is easily avoided by simply going two or three km. away from the river, where the bottom is dry and firm and the lava fields so sand-blown that they provide no obstacle.

The next 40 km. of the Túngná's course are morphologically very interesting. There the river runs in a valley which must be taken to be a tectonic fissure of the same type as the Heljargjá and others of this kind described elsewhere. The width of the valley is two to four km., the sides are steep, continuous mountain walls of a height of three to four hundred metres. On the side looking northwest the valley is bounded by the mountain chain Vörðufell, Túngnárfjöll and Snjóalda, which form a wall about 35 km. long, 2—3 km. wide and about 300 m. high. Its origin must be placed in connection with the activities of tectonic forces and has been dealt with elsewhere in the present work. In some parts this mountain wall has a pass, viz. between Vörðufell and Túngnárfjöll just opposite the north end of Litlisjór, and also opposite Skálavatn at the remarkable rock (fig. 24) that is called Drangur or Tröllið (i.e. the troll). Several parts of the southeast wall of the valley are broken by water-courses which make their way through gullies to the Túngná; this side of the valley, however, is also straight and steep, and, with the exceptions named, continuous for a stretch of almost 40 km.

Out on the bottom of the valley lie several isolated rocks, and here and there it is interrupted by transversal ridges of a height of about 100 m. Throughout its entire length the valley is dominated by the Túngná. From one side to the other it is covered with soft sands and clay deposited by the river at various times. The transversal ridges have played an important role in the course of developments in the terrain, for they have formerly been dams against the waters of the river and have thus given rise to the formation of at least two lakes. The basins of these lakes have presumably occupied an area about 20 km. in length but only two to three in width, so that there has been a lake formation in every way similar to the Langisjór discovered by THORODDSEN on the east of it. In the course of time the Túngná has succeeded in breaking through these ridges by means of a narrow gate, whereby the water level in the lake above has been lowered; it is still possible, however, to see remains of one of the lakes and there is still an unevenness in the fall of the river. The current in the gates is very swift, whereas the river above spreads over an area two to three km. wide, with thousands of small, changing branches separated by bottomless patches of sand and clay. Fig. 35 shows a view of the Túngná seen from the top of Túngnárfjöll from a height of about 300 m.; one can see one of the transversal ridges with the breach, where the river is very narrow; below it spreads over a considerable area and splits up into a large number of branches. It is thus the obvious thing to do to regard this part of the Túngná as a further development of a system of the same type as nowadays is represented by Langisjór. The base is a tectonically-formed fissure of characteristically long, narrow form. For a time this was filled with glacial water to a height that was governed by the height of the dam; after this had been eroded down the lake was partly emptied, resulting in the formation of a flat sand and mud-covered valley bottom over which the river ramifies in a large number of branches.

Throughout the whole of this stretch the Túngná, on account of special hydrographic conditions which will be dealt with in another connection, does not receive a single tributary from the right, but a few from the left. The two largest of these fall into the Túngná opposite Drangaskarð and at Kirkjufell just by the first bend.

Hitherto the Túngná has run southwest, but at Kirkjufell it runs right into the great mountain region whose highest part is represented by Torfajökull. This forces the river to make a bend of 90° to the right, and in that direction it runs for about one km.; then, however, it meets another obstacle in the form of a volcanic ridge which, from the neighbourhood of Frostastaðavatn, runs up towards Fiskivötn. This compels the river to bend again at right angles, and over a short stretch it now lies in a bed parallel to the course north of Kirkjufell, but running in the opposite direction. Another small complication arises by the fact that the river is nipped in between the outermost offshoots of Snjóalda and a large, elongated "maar", thus forming two right-angled bends; after that, however, the river runs northeast towards Fiskivötn. There it bends again 180° and runs south of the most southerly of the volcanoes in the Vatnakvíslagígir. This mountain's enormous gravel cone has been partly eroded by the Túngná; one side has been completely removed, so that the Túngná and the lake in the bottom of the crater are connected. Thereafter the Túngná describes a wide curve towards the north and west. It follows the edge of the masses of lava that came from the basaltic mass eruptions at Frostastaðavatn and from the northeast eruption centres of the Hekla region. Here the river's course is violently disturbed by lava, and the same applies to a long stretch of the Þjórsá after meeting the Túngná. West of the ford at Bjallar there are several high waterfalls, and the greater part of the river as far as the Þjórsá runs through ravine.

On the stretch from Kirkjufell the Túngná receives large tributaries. The largest is the Námskvísl, which drains a part of Torfajökull and the surrounding mountain region. It is a deep and swift glacial river with a large volume of water, and over some extensive gravel plains it joins the Túngná just at the second bend. From the northeast come two large tributaries, the Vatnakvísl, draining the Fiskivötn region, and the Blautakvísl — very short but conveying a lot of water and, as the name indicates, swampy and soft. These tributaries both bring clear water exclusively.

As has been indicated previously, the Túngná presents rather serious obstacles to the traveller. Throughout the whole of the 80 km. stretch from Botnaver to Þjórsa it is only passable at few places, viz. 1) at Drangaskarð, 2) above Námskvísl and 3) at Bjallarvað. The first two fords are very unreliable and variable; they are full of quicksands and therefore difficult to cross. On the other hand Bjallarvað is constant, as there the river lies permanently on a single bed, the bottom is hard and not too stony, but the ford is rather deep.

During a survey of the course of the Túngná we find a number of the features that are so characteristic of the hydrography of that part of the island where post-glacial volcanism and tectonic activity have been the predominating morphological factors. In fact, the various sections of the Túngná each represent a type. At the highest part as far as the south edge of Túngnárbotnar there is a typical glaciofluvial collecting area, then comes the straight course to Kirkjufell, determined by tectonic factors, and finally the lower course from Námskvísl to where it joins the Þjórsá, a stretch that has been influenced by volcanic activity. A glance at the map will show that the difference is also conspicuous from a purely topographical point of view.

b. Lakes and Marshes.

In a terrain where volcanic and tectonic forces have been active right up to the present day, the presence of a large number of closed basins may be expected, and thus in the country between the Kaldakvísl and the Túngná one may expect to find good orographic conditions for the formation of lakes. As moreover we have no hydrographic net and consequently no normal erosion either, these basins will generally not be exposed to having the embanked barriers cut through, so that we may expect to find lakes of fairly stable character.

The principal lake basins in the region may be genetically divided according to the following plan:

Glacigenous lakes	Extra-marginal ice-margin lakes.
	Lakes in basins from dead ice.
	Moraine lakes.

Volcanogenous lakes.......	"Maar"-lakes, simple and complicated. Lakes in explosion pits. Lava-subsidence lakes. Lava-dammed lakes. "Maar"-dammed lakes.
Tectonic lakes.	

We can make another classification if we take regard to the water circulation. Some lakes have ever-running, superficial tributaries, but most of them have none and receive their supplies of water partly from ground water, partly from temporary local tributaries (snow-melting streams). Drainage areas are likewise variable, for some have constant, superficial streams, others temporary superficial streams, and again others (most of them) have no surface outlet. This again involves a difference as to water level. Those with constant outlets naturally have a constant water level, whereas the others are exposed to greater or smaller fluctuations of the level and consequently of their area. The extreme case is represented by the purely temporary lakes, which only exist a short period of every year — after the snow has melted. As the following will show, this type plays a great part in the landscape. This little survey makes no pretence at being complete, and is merely given for the purpose of providing some sort of systematic guide to the following description of a number of typical cases.

Þórisvatn has an area of about 80 sq. km. and thus is the second largest lake in Iceland, much larger than any other in the region now under review. Its basin is in two parts, a main basin of about 70 sq. km. and a branch of about 10 sq. km. The main basin has its longest dimension in the direction of NNE, where it measures 14 km., while the breadth is three to five km. The side basin has its longest dimension running NE, about 8 km., while the breadth is 1 to $1^1/_2$ km. Here and there are small indentations. There are no islands except a few very small ones near the shores.

The shores of the lake are mostly cliff walls rising steeply from the water edge, though part of the west shore is less steep, and on the northeast the basin opens with a gate 3 km. wide towards the great plateaux that are covered by Hágönguhraun. There is not much trace of erosion by the lake on the shores, and as a rule no beach has been formed; here and there are small spits across the coves, but the present water level seems to be a phenomenon of recent date. No earlier, higher shore lines were observed, but it is not precluded that such traces may be found; time did not permit of a thorough examination. Only at one place was there observed a spit of considerable size, near the eastern end of the small basin; from the southeast shore a spit of about 1 km. runs over towards the other shore, so that a small part of the bay is almost entirely shut in.

At most places the shore is so steep that it is difficult to get down to the water edge on horseback. This is connected with the fact that the lake has no superficial tributary; as far as we could see the heights round the lake have no permanent watercourse; the only ones we saw were some small brooks rising from springs in the slopes and no wider than that one can jump over them. At some places we also observed unbroken spring horizons. The result is that there are no erosion gullies leading down from the surrounding high land to the lake, such as would normally be the case (fig. 40).

The outlet stream Þórisós is on the north, i.e. towards the normal fall of the land, and forms a fairly big river, about 5 km. long, ending at the Kaldakvísl. This implies that the lake must have fairly large but invisible supplies of water. Experience elsewhere may perhaps justify the assumption that the supply of water mostly comes through the great lava fields which, through the aforesaid northeast gate, stretch right up to the shore of the lake and must be taken to be the subterranean drainage channel for a large part of the water that falls over the extensive lava fields in Hágönguhraun; nor is it impossible that part of the melt-water from Vatnajökull has also made its way there.

In broad outlines the origin of the lake may be taken to be the result of the development sketched in the following. Both basins must have been tectonically formed. As is usually the case in Iceland there is no trace whatever of folding. It is not a volcanic basin, and it is true of at any rate part of the basin that it cannot have been formed by erosion. The small, narrow basin, for instance, cannot be other than a tectonic fissure. Long and narrow, with steep parallel walls, it recalls in every way the fissures of tectonic origin that are so frequently met with in this part of the country. The only kind of erosion that could produce a terrain of similar type is ice erosion, but this possibility must be rejected, as at the side towards the ice the basin is closed by a steep wall, and on the whole there is no trace of this small basin ever having been filled with ice. On the other hand it is possible that ice had some part in the forming of the large basin, but the fact that it is open towards the north and closed by a cliff on the south does not indicate that in this we have to do with a glacially-formed basin.

There is, however, another factor that has helped in the forming of the present appearance of the lake. As has been said, Hágönguhraun runs right down to the northeast shore of Þórisvatn. Lava has forced the outlet aside up against a ridge which forms the partition between the basin and the valley in which the Kaldakvísl flows. Thus we may take Þórisvatn to have been tectonically formed, but with the complication that in recent times there has also been a damming up by lava; erosive forces, on the other hand, have played only a slight part in the formation of the basin.

It is quite curious to see the almost complete analogy which, in a genetic sense, characterises Þíngvallavatn and Þórisvatn. The former is likewise a tectonic lake which at some time or other has been dammed by lava. The two lakes have very much in common in a landscape sense, except that the different height above the sea involves a number of biological differences, especially that the shores of Þíngvallavatn have vegetation whereas those of Þórisvatn are almost sterile.

Litlisjór is the second largest lake in this region, occupying an area of about 9 sq.km. On its longest axis, running northeast—southwest, it measures about 7 km., and its greatest breadth is about 3 km. It occupies a part of the bottom of the great tectonic subsidence area lying just to the west of Túngnárfjöll. Its shores are very different. On the southeast the lake washes the foot of Túngnárfjöll and the shore line is practically the same as the fracture line along which one of the principal movements in the system has taken place. Some large blocks have, however, loosened themselves from Túngnárfjöll and have been flung northwest out into the subsidence area, fig. 23, and in that way have formed a part of the small projections of the shore.

The greater part of the southeast shore is steep, some of it cliff and some steep talus. Only at a few places is there a little flat beach. At the north shore we find a very low and flat sandy beach running smoothly into the extensive sandy plains which, like a wide trough, continue right up to Vatnajökull. The west and southwest shores are mostly of volcanic explosion material, and on this long stretch the lake for the most part washes the outer side of volcanic gravel ridges, of which the most northerly originate from the volcanic region at Hraunvötn, i. e. Zone B of the Fiskivötn region, and the most southerly from Zone D.

We may take it that the basin of the lake was formed in the following manner. The primary cause was the occurrence of the large tectonic basin on the west side of the mountain chain of Snjóalda-Vörðufell. It is to be regarded as a formation analogous to the long tectonic fissure in which the Túngná runs. In the southern part of this subsidence occur a number of complicated volcanic phenomena which have previously been described under Fiskivötn — zones A—D. The explosion phenomena in Zones B and D have created a continuous rampart of tipped substratum and loose volcanic gravel, and this rampart forms the embankment of Litlisjór. Thus genetically it is characterisable as a tectonic lake which in addition is "maar"-dammed.

Litlisjór has neither superficial tributary nor superficial drainage. As a consequence the water level is subject to annual variations which seem to amount to one or two metres, for it is possible to trace numerous systems of higher water marks all round the lake. In the lake itself are several islets. The banks are extremely poor in vegetation and thus form a decided contrast to those of Fiskivötn described below. The cause may be found in the circumstance that the water level is variable and that the whole of the beach (and probably the greater part of the bottom) consists of sand and gravel and not of lava. It is inhabited by numerous families of loons and thus may be assumed to have a stock of fish.

Fossvötn is the name of two small lakes lying southwest of Litlisjór, separated from it by a barrier that has probably been formed by explosive eruptions. Stóra Fossvatn covers about 1 sq.km; its outline is irregularly winding, the sides are steep slopes. There are several peninsulas and a triangular island connected with the shores by two barriers of stone and sand. Over one of these runs a lively stream. Litla Fossvatn is a small, round crater lake in whose steep walls there are traces of secondary eruptions.

The water circulation is very large in proportion to the size of the area. From Stóra to Litla Fossvatn there is a short but deep and swift channel; at the outlet of Litla Fossvatn there is a fall, about 10 m. high (fig. 36) just on the edge of the lake. Fossvötn has no superficial tributary, and the surplus water must thus come to it through subterranean channels. It is possible to observe a little of this up in the lava field which THORODDSEN has called Fossvatnahraun, where in the numerous lava holes the water can be seen streaming slowly down towards Stóra Fossvatn. This water undoubtedly comes from Litlisjór, which thus seems to be drained through the aforementioned barrier of gravel. This explains why Litlisjór has no superficial drainage and why the water from the very small Fossvötn is of such an imposing volume. The shores of Fossvötn have a biological valence that for these regions in considerable; large parts are covered with continuous vegetation of great luxuriance; the lakes abound with life and are particularly well stocked with trout.

Fiskivötn or Veiðivötn. This name signifies a group of at least 50 lakes and ponds, whose situation I have described in another connection, p. 32, 214. The two largest bear the names Græenavatn and Snjóölduvatn and they both have an area of about 2 sq. km. Several cover about 1 sq. km., viz. Ónýtavatn, Skálavatn and the two variable lakes Breiðuvötn on the lower course of the Vatnakvísl. The remainder are smaller.

I have already accounted for a number of the morphological factors which have led to the formation of the lake district, p. 39, 221, but shall add a few details here. As I have stated, the formation of the lakes must be directly or indirectly placed in connection with volcanic activity, but the various lake basins genetically and habitually represent a number of different types.

Græenavatn and Ónýtavatn form a unit by themselves; they lie in a common basin having its greatest length southwest—northeast. This basin seems to form an analogy to the basin in which Litlisjór lies. On the southeast it is bounded by Túngnárfjöll and is cut off from the deeper part of the valley system on the west by the gravel mounds that have been produced by the explosive eruptions referred to on p. 42, 224. Tectonic and explosive eruptions have thus in community formed the basin. Græenavatn runs into Ónýtavatn and therefore has a constant water level. It is not a lava or crater lake with steep shores like most of the others in the area, but is surrounded by flat marshy land with a continuous and luxuriant *Cyperacée* vegetation which provides good grazing. The Ónýtavatn, however, has no superficial drainage and therefore its water level is very variable. It is surrounded by gravelly slopes displaying many water marks, but it has no vegetation and on the whole seems to be deficient in life.

Snjóölduvatn is, as THORODDSEN observed, a complicated crater lake. It is connected with the Túngná by a short channel. North of this lake is a landscape that is given the name of Pytlur. It contains a very large number of small lakes of volcanic origin. Simple and complicated crater lakes, some partly full of lava and thereby reduced to small, crescent-shaped basins, explosion craters with lakes in the bottom, lava-subsidence lakes, and so on, and as these phenomena everywhere overlap, there is a great abundance of forms. Drainage from this part of the group is exclusively subterranean.

A special group is represented by Skálavatn, Tjaldvatn and Langavatn. Their genesis has been referred to on p. 45, 227. They are fed by springs which can be seen in some places. In the north end of Tjaldvatn, for instance, there is a most productive spring area with numerous openings, and in the slopes east of Skálavatn there is another large spring area. Skálavatn is drained subterraneously through the lava to Tjaldvatn, and from there a brook runs down into Langavatn, whence drainage continues through Eskivatn and Kvíslarvatn to the Vatnakvísl. In the first three lakes, bottom and shores consist of lava, which, however, in certain places and in parts of Langavatn and Tjaldvatn is overlain by a thin deposit of gravel and sand. The presence of lava seems to have a very favourable effect upon conditions of life, which here seem to be especially good. The fauna in the lake is rich, the stock of trout large and well nourished, and on the shores, which are covered with a low but continuous vegetation (fig. 43), a number of birds breed.

Eskivatn and Kvíslarvatn are both "maar" lakes whose encircling walls of gravel are broken and eroded by both tributaries and drain-water. The water level has once been higher, and up the slopes one can still see systems of old shore lines on a level with the upper edges of the embankments.

The lower part of the Vatnakvísl, i. e. from Vatnaskarð downwards, is connected with two lakes called Breiðuvötn. They lie at almost the same level as the river and are surrounded by low, extensive stretches of marsh which have probably been formed by deposits from the Vatnakvísl. Their depth seems to be slight and their form and size variable, but the whole terrain is so marshy that movement in it is very difficult. In the edges of the marshes there are very good grazing places.

Other volcanic lakes. In the region of Hraunvötn there is a form of landscape that corresponds to the southern part of Fiskivötn. We find here again the same changes in the terrain, with numerous undrained small basins, many of which contain lakes, p. 48, 230. Thus there are very fine examples of complicated "maar" lakes with gravel shores and very fluctuating water levels; there are also lava-subsidence lakes with the very irregular outline and not very high, but steep shores that are peculiar to such formations. Here as elsewhere it is obvious that the lava lakes offer the best conditions of life. The shores are densely covered with vegetation and the water teems with small animals and fish. In most of the large "maars" in this region there are crater lakes, fig. 11, but their effect upon the landscape is small. In the eruption vents belonging to the mass-eruption types, however, I have not found a single crater lake.

The temporary valley lakes, on the other hand, are an important morphological feature in that part of the landscape which is not covered with lava. As there is no superficial drainage system, the valley structure is discontinuous, i. e. there are no evenly sloping passes from one valley to another, and every hollow forms a separate, closed basin. During the melting of the snow the valley bottoms are turned into lakes, whose water level is determined by the quantity of melt-water. During the course of the summer the water percolates away and evaporates, and thus the level gradually falls. This can be directly read from the shore lines or watermarks, whatever one may call them, surrounding valleys of this kind. In spring these lakes may have an area of several square kilometres, but in the late summer they have diminished greatly and many of them dry up entirely. The difference in the water level may be more than 5 m., and it will be understood that these lakes form an important part in the water circulation of the district. Their shores are always devoid of vegetation, a fact that must be placed in connection with the fluctuating level of the water. For when the water falls the surface comes under the influence of the destructive effects of the wind and any germs are immediately swept away. Shores of lakes having a variable water level are therefore practically sterile, as several examples in this account have shown, whereas shores with a constant water level are overgrown. The same applies as a rule to the edges of the lava lakes where the possibilities of shelter seem to be the condition that is vital.

Especially well developed temporary valley lakes are to be found in the regions round Þóristindur. The largest one observed, lying in the valley west of this peak, seems to have an area of about 10 sq. km. in spring. In the landscape east and northeast of Þóristindur too drainage proceeds in the manner described above.

At the bottom of the lakes proceeds a very lively accumulation of washed-down gravel, which forms finely stratified, horizontal beds of great thickness, at any rate up to 25 m. In addition, considerable quantities of loess, which is caught by the surface of the water and precipitated. This causes a raising of the bottom, while at the same time permeability decreases, and there are various circumstances that argue that such temporary lake basins may under certain conditions develop into a kind of marsh of a type that is for instance to be found in the landscape Þóristúngur, southwest of Þórisvatn. Fig. 45.

Moraine lakes. The recent moraine deposits on the west edge of Vatnajökull are not very large, but, where they do exist, they naturally have lakes. A frequently occurring type is formed when the ice margin on its retreat exposes a hollow between an older moraine and the new margin. There has been just such a retreat in recent times at that part of Vatnajökull that lies between the Túngná and the Kaldakvísl, and therefore we find many of these extra-marginal lakes. In Botnaver there are many traces of dead ice, both in the glaciofluvial plains and in the moraine. This brings about a quantity of small lake basins which, however, generally do not seem to last long as they are quickly filled with sand and clay and are transformed into mud holes.

In those areas where the terrain is characterized by glacial-deposit forms as in Holtamannaafrjettur we have moraine lakes that are not much different to the corresponding lakes in other parts of the Icelandic highlands.

9. Annual cycle of denudation.

The activities of the disintegrating forces in the Icelandic highlands are subject to a very characteristic, annually recurring variation. Winter is signified by a covering of snow — permanent as far as we know — lasting six to eight months, and in this period the morphological changes in the earth's surface must be quite minimal. In the time from May to July inclusive most of the snow melts and in the saturated earth there occurs a lively solifluction which has a very marked, flattening effect upon the relief. The output of melt-water, however, is so great that even highly porous surfaces are unable to absorb it all, and the surplus has to run off in the form of streams. In loose, sterile soil these streams are able to cut furrows a metre deep and they transport large quantities of the loose surface layer down on to the lower parts of the terrain. The meltwater streams, however, are not sufficiently voluminous to form a permanent hydrographic net. They usually end blindly in the depressions, where they give rise to the formation of large, shallow lakes whose water in the course of the summer is greatly diminished or disappears entirely through percolation or evaporation. Patches of snow that last throughout the summer may be met with down to 7—900 m. far below the snow line at places where the winter depth has been especially thick or where melting has been especially slow, as for instance on northern slopes. Year after year one finds summer patches at the same places, and this gives rise to a concentration of the erosive activity of snow-melting, which in the long run produces a very peculiar form of landscape which plays a great part in the Icelandic highlands.

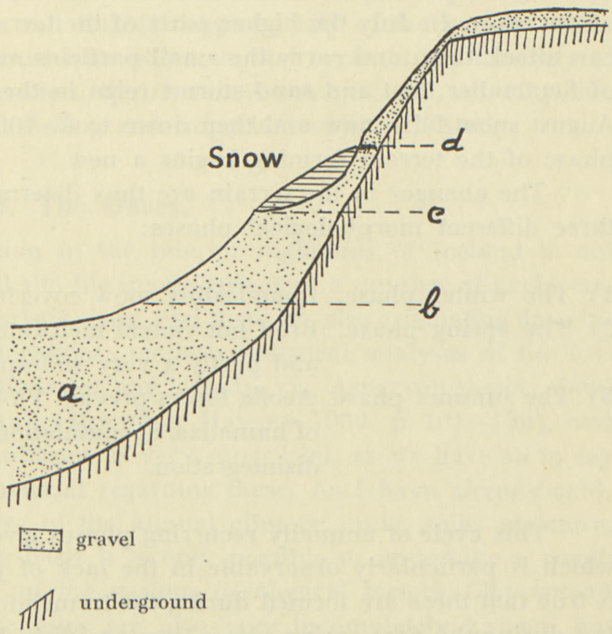


Fig. VI. Slope with an oversummering snow patch.

Fig. VI represents a vertical section through a slope with one of these summer snow patches. Above it the surface is smooth and dry. Below the snow itself a small hollow will form because the bottom is always wet and therefore inclined to shrink downwards. The material thus displaced forms a small mound at the lower edge of the snow patch. On the part of the slope lying below the snow the percolating meltwater will always keep the soil moist and, in periods when melting proceeds quickly, furrows will form in the surface. The total result of the process is that there is a considerable displacing of material under the snow and for some distance below it, thus producing a hollow at the side of the slope. Fig. 42.

After the meltwater has percolated or evaporated away and the surface has attained the necessary dryness, the æolic forces come into play, and, on account of the great porosity of the surface, this takes place shortly after the disappearance of the snow. In July the higher parts of the terrain are already so dry that the wind can attack them and carry the small particles away, and from that time till the end of September dust and sand storms reign in the highland wastes. But at the end of August snow falls, now and then down to 6—700 m. above sea level, and the winter phase of the terrain forming begins a new.

The changes in the terrain are thus determined by the alternating activities of three different morphological phases:

1) The winter phase. Long-lasting snow covering. Slight morphological change.
2) The spring phase. Brief but violent meltwater activity, partly local water erosion and partly a very widespread solifluction.
3) The summer phase. Aeolic forces prevail. Violent deflation and corrosion, forming of hamadas, accumulation of sand and dust, rapid mechanical disintegration.

This cycle of annually recurring phases gives the landscape a special character which is particularly observable in the lack of purely æolic forms of deposition. It is true that these are formed during the tremendous sand and dust flight in summer, but during the next spring phase they are disturbed and obliterated again. The lack of dune formations in the highlands is very typical. Instead we have sandy flats with slightly undulating surfaces. In the lowlands, however, where the climatic conditions in many respects are otherwise, there are numerous examples of dune formations of considerable expanse, whereas the wind-deposited material in the highlands is rebedded by the temporary water and snow erosion in combination with solifluction. These forces by their united efforts push the loose material — both that formed on the spot and that carried there — down into the hollows where it is accumulated in the form of thick, handsomely stratified series.

An important section of the annual morphological cycle is the forming of the aforementioned temporary lakes. For on their bottom it is not only the material brought by the meltwater streams that is deposited, but also a quantity of sand and dust that is caught by the surface of the water during the passage of the sandstorms throughout the summer and gradually deposited on the bottom in fine argillaceous layers which form the arctic analogy to the "Schwemmlöss" that we know in other parts. When during the course of the summer the lake disappears partly or entirely, the bottom appears as a clay flat which, after drying, is subjected to a lively deflation and supplies a voluminous contribution to the dustladen air of the late-summer storms.

Under these conditions the annual variation in the morphological processes is very marked, but it is a question whether one ought, to an extent greater than is now the case, to turn one's attention to the corresponding variations in other climes too. In a temperate, humid region such as Denmark for instance, there must be very important differences in the erosive and transporting capacity of the various water courses at various seasons. There must also be an annual cycle in the intensity of solifluction, the mechanical disintegration, the chemical changes, etc., all of which are questions that embrace most interesting and important objects of study.

10. The Oases.

Our knowledge of the vegetation in the interior highlands of Iceland is not very satisfactory. It is true that, thanks to the investigations of a number of explorers, the country is very well known in a floristic sense, and there are also orientating descriptions of the formations of various localities; modern statistical analyses of the formations, however, have only been made for one locality, viz. Arnarvatnsheiði, about 500 m. above s. l., west of Langjökull (MØLHOLM HANSEN 1930, p. 101—120), and our knowledge of the œcological conditions is very superficial, as we have so to say no complete, reliable observation material regarding these. As I have already said, we know very little about the course of the annual climatic cycle, soils, moisture, snow fall, etc. and on this insecure basis it is only possible to undertake a rough examination of the relative valence of the various oecological factors. The spread and distribution of the vegetable colonies are also very incompletely known, but some of them: a mýri-growth with *Carex* and *Eriophorum* as the predominating families, play so great a part to the traveller, that we must assume we know all the more important occurrences in the Icelandic highlands.

The highlands west of Vatnajökull, as has been stated in the foregoing chapters, bear a plurality of surface types with very profound morphological and genetic differences. Among the recent rocks — which form the greater part of the surface — lava and lapilli fields predominate, whereas moraines and glaciofluvial material are more subordinate. There are also extensive areas where the very varying rocks of the glacial volcanic formation, also called the Palagonite formation, crop out, but we lack — at any rate as a surface layer — the older, striated, doleritic lava streams with a very thin coating of moraine that are so widespread in the other highlands. If all these surface types, despite great differences, nevertheless bear a certain common stamp, it is due i.a. to the fact that they have the common property of being sterile, as the land is practically bare of vegetation.

In the lower parts of the Icelandic highlands earlier lava fields in their hollow shelter an impoverished growth of lichens and mosses, with scattered vascular plants; but throughout the greater part of the lava fields between the Kaldakvísl and the Túngná conditions are so bad that there is practically no macroscopic life unless special conditions prevail, and conditions are at least just as severe on the lapilli surfaces and on the greater part of the moraine and the recent, glaciofluvial deposits.

Only in especially favoured parts are the conditions of such a nature that it has been possible for a continuous vegetable covering to develop, and there oases have formed, with a luxuriance that is only modest, it is true, but still forming a striking — and very pleasing — contrast to the enormous wastes surrounding them.

The area of the ice-free land between the Túngná and the Kaldakvísl is about 1600 sq. km., and of this only about 10 sq. km. is covered with a vegetable growth, distributed in the following oases:

Fiskivötn and Fossvötn....................	circa 5 sq. km.
Northern Pytlur	— 2 —
Botnaver..................................	— 1 —
Þóristúngur...............................	— $^1/_2$ —

In addition there is a small growth at Þórisós, whose size I do not know, and small overgrown patches at Blautakvísl and on the spit that blocks the innermost cove of Þórisvatn. Otherwise the land is practically naked.

According to the surroundings in which they occur these oases represent four types:

1) Oases in lava fields.
2) Oases on lake shores with constant water level.
3) Oases on recent, glaciofluvial plains.
4) Oases on moraine land with high ground water.

When dealing with the morphology of the landscape I have several times referred to the patches of vegetation, as for instance when describing the volcanism at Fiskivötn and in the chapters on subaerial denudation, the aeolic conditions and the annual cycle of denudation; I shall here present some supplementary and summarizing observations.

As a rule the lava oases are associated with the edge of the subsidence basins that are so characteristic of the volcanic regions at Fiskivötn, Fossvötn and Northern Pytlur. At any rate physiognomically the vegetation is dominated by dwarf bushes, especially *Salix* species, and thus is of little value for grazing. The favours offered by nature here seem capable of being summarized in two groups, viz. a suitable ground-water level and protection against the destructive forces of the gales. The deeper parts of the subsidence areas are usually full of water, and in the lower parts of the lava the ground water is near the surface. In itself the irregular relief of the lava offers a fairly effective protection from the gales, and the volcanogenous gravel mounds lying round the fields are certainly of some importance in this respect. On the other hand, as already stated, conditions in the usual lava fields that have come from the great mass eruptions are not sufficiently good, and very few living things succeed in withstanding the destructive work of the hostile elements.

The second type of oasis, the lake oases, have grown on the shores of those lakes that have a constant water level. As a rule they are flat expanses of marsh with continuous vegetation, whose character changes with the conditions prevailing in the various arts of the area. The predominating families there are *Carex* and *Eriophorum*, which provide good fodder. There are examples of this type of growth beside the most easterly of the lakes in the Fiskivötn group, especially at Grænavatn and Breiðuvötn.

The glaciofluvial oases are poorly represented on the west margin of Vatnajökull, as for the present we only know one, viz. Botnaver in the southern corner of Túngnárbotnar. Poor and small is this patch of vegetation, only about 1 sq. km. in extent, but it gives a charming impression to visit this green little vale just under the ice margin, far away from other life. The soil consists of sand, which throughout the summer is soaked by springs and meltwater from Vatnajökull. Most of the area has the character of a "mýri", in which spring-water predominates and which is sheltered from the gales by the surrounding mountains. In several other parts of the highlands this type of oasis is the principal one (Nielsen 1928), and is especially well developed at the southeast margin of Hofsjökull, where the area of vegetation is at least 100 sq. km. Fig. 46.

Moraine oases are also weakly developed in the land between the Túngná and the Kaldakvísl. In Þóristúngur there is a small patch of this type, but it seems to be perishing. There is a typical example of this form of oasis in Illugaver, just west of the Kaldakvísl. In the chapter on subaerial denudation I have dealt with certain soils and, in connection with them, some peculiarities of vegetation in that locality, which embraces a whole series of vegetation types, various "flói" and "mýri" types, "flá", "jaðar", "mó", and transitions between these.

Conditions throughout the whole of this part of the Icelandic highlands are so severe that, in a biological sense, it must be called a pronouncedly border region; the question is, however, whether this poverty is associated with any one of the oecological factors or whether it must be regarded as a result of a general impoverishment of the conditions. Even without knowing any figures as to the volume of rainfall and its distribution, it may be asserted that the volume of summer rainfall, combined with the water freed by the melting snows, is more than sufficient to maintain a continuous covering of vegetation under the prevailing temperature conditions. Nevertheless it is a fact that the quantity of surface water in great parts of the highlands is very small, and one of the hydrographical and morphological results of this is that drainage almost exclusively proceeds along subterranean channels, whereas there is no normal, superficial, hydrographic net. This is undoubtedly connected with the great porosity of the surface and its poverty in colloids, a peculiarity that stamps many of the polar surface forms. The great majority of Central Icelandic types of vegetation are consequently xerophilous, not only in the localities where the ground is very wet and cold, but also in the comparatively high, well-drained areas of vegetation. Thus both soil and vegetation bear evidence of a dryness that cannot be directly governed by the climate, but must rather be described as a pedologically governed aridity.

Naturally, the temperatures leave their mark upon the intensity of the vegetation, but it is scarcely the failure of the thermal conditions of life that set a boundary to the diffusion of life in the Icelandic highlands. This view is supported by the fact that we find extensive oases, some of the largest and most luxuriant we know — for instance those at Hvítárvatn and the southern margin of Hofsjökull — on high localities just under the ice margin. Naturally, a vegetation living in the conditions prevailing in this region must be poor, but neither rainfall nor temperature are of such a character that the formation of a continuous covering of plants is precluded for that reason, and so the cause of the poverty of the landscape must be looked for in other directions.

The feature common to the oases is that they are associated with localities where the destructive work of the wind is rendered difficult in some way or other. In some of them — as in the lava oases — it is a direct lee-protection, in other cases the moisture of the soil is so great and so constant throughout the summer that the gales do not succeed in pulling the plants up. The desert formation in Central Iceland must thus be regarded from the following angle: Low summer temperature, in combination with the poor water-economy of the soil, makes for slight intensity of vegetation; and yet conditions in these respects are not so bad that the formation of a continuous growth is precluded for that reason, but the vegetative power is too small to withstand the destructive activities of the gales, especially the dry gales. In this part of Iceland the deserts must therefore be called gale deserts.

B. Iceland's Volcanism and Tectonics in the Light of the Wegener Theory.

1. Types of Volcanic Landscapes.

Iceland having for the most part been built up by the activities of eruptive forces, the primary volcanic landscape must be one of the most important starting points for a study of the morphology of the country. As is often stated in the literature, regions characterized by eruptions contain a plurality of surface types whose differences are founded upon an interference between a number of colliding factors, namely:

1) The properties of the magma.
2) The nature of the earth's surface at the place of eruption, and
3) The character of the medium or media that cover the earth's surface at the place in question.

We thus differentiate between mass eruptions with mostly effusive outbreaks of very hot, thin lava, explosive eruptions with a predominating production of loose materials, and eruptions of mixed or stratic character, with alternating output of lava and solid products corresponding to effusive and explosive phases respectively.

The course of volcanic activity is furthermore governed by a number of dimensions such as the shape of the magma container, its size and distance to the surface, and the shape of the vent, which again depends upon a very complicated set of physical factors in the earth's crust. Finally, a volcanic eruption will proceed very differently according to whether the earth at that place is covered with air, water or ice.

In the recent Icelandic volcanic region, mass eruption is the predominating form of eruption, whereas stratic and explosive forms play a subordinate part, and this balance is of vital importance to the line of development in the recent moulding of the relief. The predominance of the eruptive and terrain-forming mass eruption is, however, not only a present day phenomenon, but has, as far as we know at present, extended through by far the greater part of the period of the geological development as to which the now accessible Icelandic series give us any information, and in addition it seems to have been the prevailing morphological factor during the forming of the other parts of the North Atlantic volcanic region (the Thule Region). It is therefore of importance to arrive at an understanding of the direct effect of such an eruption on the terrain.

We often meet with the view that the activity of volcanic forces produces an increase of the unevenness in the terrain in which they work; the validity of this view is, however, very restricted. It is wrong, for instance, when talking of mass eruptions, and as these — not only in the Thule Region but in many other earlier and later volcanic regions — have been and are still predominant, it would perhaps be most correct to allow the view to drop entirely. If a mass eruption takes place in an uneven terrain, the masses of lava will find their way to the lowest parts and wholly or partly fill them, with the result that a smoothing out takes place, simplification of the relief, which tends towards the forming of a plateau. An example of such a process has already been described on page 25, 207 of the present work, and it is there pointed out that, as regards the terrain, the places of eruption mean very little indeed, because the accumulation of material round them is slight, so slight in fact that it is not uncommonly a matter of difficulty to find them. Here and there in recent-volcanic Iceland we find more or less completely formed, recent volcanic lava plateaux, of which the largest and, as regards degree of filling up, most well developed is Ódáðahraun. The stratification in the greater part of the quaternary and tertiary formations shows, however, that there has been an enormous number of these volcanic plateau surfaces in which there have constantly occurred disturbances arising from the activities of non-volcanic forces, but that, parallel with the destruction of the plateaux, there has been a regeneration of them, produced by the filling-up activities of the ever-recurring mass eruptions; Iceland's surface forms have, throughout the greater part of the period in which we know the geological development of the country, been determined by this very cooperation between these two processes. T h e volcanic filled-up plateau is thus the most important structural basic form in the Icelandic landscape.

During explosive eruptions the greater part of the gravel material is distributed fairly evenly over the landscape, without regard to the pre-eruptive forms; but as soon as erosion, especially solifluction (so violent in arctic and sub-arctic regions) begins to work, we get a lively transportation of loose material towards the lower parts of the terrain and, as a consequence, a flattening out of the relief. Only if the volcanism is concentrated in pronouncedly stratic eruptions will it have much effect in a relief-increasing and mountain-forming direction; but this type of volcano, which elsewhere in the world is so conspicuous that it has been regarded as the paradigm of volcanic activity, plays a very small part in Iceland.

The series dating from the Glacial Ages — the interglacial periods and interstadial epochs — occupy a special position. Interstadial and interglacial eruptions do not differ much from the other subaerial eruptions, and the large sheets of lava thrown up are usually of doleritic character; but the terrain over which they have spread has been affected by the ice sheet in different ways. Subglacial eruptions have played a great part, but so far we know too little about the course of these processes to say anything with certainty about the primary morphological results. It is true that similar processes are going on at the present time, under Vatnajökull and under Mýrdals-Eyjafjallajökull, but they unfold themselves with such violence that it is very difficult to get near them and make the necessary observations, and there is no report of any scientific investigation of such an eruption. That something extraordinary is going on is beyond all doubt when it is remembered that the temperature of the lava must be assumed to be above 1100°, and that large quantities of this material are being pushed up under an ice sheet of very considerable thickness. Part of the ice melts, and the freed water makes it way through and over the ice-masses below, whereas another part of the water sinks down upon the glowing lava and is converted into steam with tremendous explosions; simultaneously the lava is burst into pieces and thrown high into the air in the form of ash, much of which is washed away by the freed water. The whole of this mixture of water, lumps of ice, volcanic ash and gravel then rush down the slopes and spread over the flatter parts. The present-day form of these processes is called volcanic glacier runs, or perhaps better glacier "jumps" (Icel. jökullhlaup), and are among the most violent natural catastrophes which the earth's surface can show at the present time. They have time after time devastated the coast plains in southern Iceland and have stamped this part of the island both morphologically and economo-geographically.

In those periods when the country was covered with ice, processes of like kind must have gone on to a much greater extent, and some of the rocks from the glacial volcanic formation or Palagonite formation were undoubtedly made by subglacial eruptions. We do not know much about the character of the resulting landscape forms, but the extent of the formation shows that there has been a very considerable diffusion of the material produced, even if it is beyond doubt that in certain cases there have been local accumulations of eruptive products to such an extent that increases of the relief — and very pronounced increases — have resulted.

With these deviations — immaterial on the whole as they are — the Icelandic rocks are remarkable for their almost horizontal stratification, and the dominating form of landscape is the plateau.

2. The Tectonic Disturbances.

The whole of the North Atlantic volcanic region, and especially the Icelandic part of it, distinguishes itself by the occurrence of a large number of tectonic disturbances. The most striking peculiarity of the Icelandic tectonic processes is that there is no trace whatever of folding, and that the dislocations have formed themselves exclusively as fractures. The course of the tectonic processes in the earlier part of the country's geological development are unfortunately little known; we know that there have been great and numerous thrusts, but there is no systematic investigation of Iceland's early tectonic development; as a matter of fact it is a very difficult subject for, as stated above, through the constant flattening out of the mass eruptions the unevennesses caused by the fractures have been concealed. On the other hand, Iceland's later tectonic development, especially the recent, is easily accessible and readily studied and has been subjected to examination by several investigators. For the fractures are so large and so recent that in many cases the physiognomy of the country is determined by the course of the tectonic processes, and therefore it is possible to apply purely topographic-morphological methods of investigation.

The distribution of the fracture zones is remarkable for an arrangement in great continuous systems with a conspicuously common stamp.

The more recent Icelandic faults of morphological importance may be divided into a few, perspicuous groups. The earlier systems are more difficult to grasp, because their morphological effects in the neo-volcanic region have to some degree been erased by later eruptions and, in the older part of the surface of Iceland, by the glacial and humid erosion. In the latter region there is for instance a possibility of confusing "ruptures de pentes" of tectonic origin with those produced erosively. The quaternary and post-glacial fracture zones are divisible into two main systems, which one might call the Westerly System and the Axial Southwest—Northeasterly System. The former group is represented by the great depressions in Breiðifjörður, Faxafjörður and the southwest lowlands, all of which are topographically conspicuous. Among the writers who have occupied themselves with the morphology of Iceland there is a fairly unanimous opinion that these three great basins are tectonic and that at any rate the latter two are very recent; the processes have probably not come to an end yet, as for instance appears from the great seismicity of the regions. In all three cases the boundary of the tectonically affected region lies near the present highland boundary, and the fracture areas run into one another only slightly, being separated by two long, narrow areas of resistance, Snæfellsnes and Reykjanes. In a geographical sense their difference is considerable; Breiðifjörður is a large, two-armed gulf, whose innermost part is shallow and studded with islands, Faxafjörður is a wide bay with no great indentations and no islands, and the third fracture area for the greater part lies above the surface of the sea; with a submergence of about 50 m., however, Faxafjörður would be increased by the landscape Mýrar, which would thereby be converted into an archipelago, and with a little more submergence we would have a completely analagous transgression area in the southern lowlands. There are no similar landscapes at all in East Iceland, and thus we have the characteristic asymmetry in the Icelandic coast line and landscape-forming that, in practically every respect, is a prominent geographical feature in the regional division of the country. Probably one formation that corresponds to the three fractures is the large indentation Ísafjarðardjup, which can be followed from the central parts of the great northwest peninsula to a depth of 200 m. on the submarine plateau. This narrow, curved channel is undoubtedly tectonic and probably belongs to the same system of fractures, even if with regard to age and form it may differ somewhat from the other three.

The axial main system of tectonic disturbances is in two sections. It can be followed from the southwesterly corner of Iceland, Reykjanes, across the country to a depth of about 300 metres out in the northern Arctic. The southwesterly zone runs from Reykjanes to a stretch in Central Iceland, almost from the northern margin of Langjökull to a point northwest of Vatnajökull. In this zone the fracture lines are with small deviations orientated southwest—northeast, whereas in the northern part of the system they run north—south, likewise with small deviations. The fault lines of the south land are very distinct on the Danish General Staff's topographical map-sheets of this part of the country; topographically they appear very clearly and in several localities they lie so closely together that the areas concerned may be characterized as "champs de fracture". The fracture lines of the north land are of very different ages and in this they form a contrast to those of the south land, which for the most part are quite recent: late-Quaternary or post-Glacial. In the north country they occur principally in the sides of the great gulfs. Húnafloi, Skagafjörður, Eyjafjörður, Skjálfandi and Axarfjörður are all wide, deep depressions which can be followed about 100 km., sometimes more, into the highland plateaux and at least just as far out into the northern Arctic, whereas the peninsulas lying between them continue as shoals out from the present coast line. These fracture lines are undoubtedly of Quaternary age, as they cut through rocks belonging to the earlier parts of the glacial volcanic formation, and as the situation of the later glacial erosion valleys shows that at that time the fractures already had been formed. Later, and even recent, fracture lines with the same direction exist in the regions east of Eyjafjörður, where they very pronouncedly give character to the terrain.

3. Tectonics and Volcanism.

One peculiarity of the Icelandic tectonics is its close association with the volcanism. On the whole the volcanic processes are lineally orientated, and, even if there are numerous exceptions from this rule, the phenomenon is so consistent that the circumstances are most striking in the landscape. As a rule the volcanic lines are not particularly long, rarely more than 20—30 km.; in some places, however, one sees volcanic zones stretching over wide expanses, but in such cases the lines do not lie in prolongation of one another but in parallel displacement. This feature occurs in nearly all the new-volcanic regions of any considerable output, Reykjanes, Þingvalla-region, Hekla region, the regions west of Vatnajökull and Ódáðahraun. The probability is that the great mass eruptions bring about mass disturbances, which result in a kind of tectonic movement, and indeed we see that a series of mass eruptions in a district is followed by tectonic disturbances; the phenomenon is met with so often that we must assume a causal-connection between the volcanic processes and certain subsequent tectonic changes. The fracture lines then formed in certain cases become determinative of the situation and form of the next series of eruptions in the region, and in that way we have an interference between the volcanic and tectonic processes which seems as if it would continue through long periods.

Observations of this kind have led some writers to the assumption that the tectonic activity is a phenomenon arising out of the volcanism, and that the volcanic activity in this respect too is the fundamental morphological feature.

To this it must be observed, however, that the tectonic movements of Iceland proceed according to such great common main lines that they can scarcely be placed in direct causal-connection with the volcanism, whose tectonic after-effects must be of local extent. There is thus little probability that a volcanic eruption for instance in the Hekla region can have any tectonic after-effect that stretches far beyond the rather limited area in which the eruption takes place. The tectonic processes are, however, much more widely diffused and are not associated with the volcanic regions alone. Nor would there be any reason why the tectonic changes should retain their right-lined course if they were not due to a cause independent of volcanism, or, more correctly, if they were not inter alia under the influence of forces which indicated this right-lined course and which did not directly stand in causal connection with volcanism. On the whole it does not seem to me possible to advance the eruptions as the explanation of the arrangement of the fracture lines; much rather must it be assumed that both groups of phenomena are under the influence of a common, mighty force of regional character. However, before going further into this problem I shall deal briefly with one or two other matters that are important in this respect.

One of the fundamental problems in the creation of forms of the tectonic landscape is: What is the direction of the movements that have involved the forming of the fractures, and how have these movements proceeded on the whole? In advance there are three or perhaps four possibilities that must be taken into consideration: 1) The process may have been this, that the present highest parts (the horsts) were pushed upwards while the other parts have lain still. 2) Both the highest and the lowest parts may have moved, but in opposite directions. 3) The present lowest parts may have sunk and the higher parts retained their position, and finally, there is the possibility 4) that the whole surface has sunk or risen, but unequally.

All that is directly accessible to observation is usually that a once continuous surface has become discontinuous, that "ruptures de pentes" have formed along the fracture lines; but it is rather difficult to fit every single concrete case of tectonic movement into the above system and decide the direction of the movement. And yet, in certain cases it is possible to do it with some certainty. At the forming of the great, recent tectonic fissure Heljargjá, west of Vatnajökull, what has happened is this, that a small right-lined zone with a width of rather less than a kilometre and a length of about 30 km. has sunk, while the surrounding terrain has retained its position unchanged. Similar phenomena are to be seen time after time in the Icelandic landscape, recognizable by the fact that the two edges of a fissure lie at the same level; why should they do so if the movement has not been localized to the fissure and the two sides have remained firm? This has in addition given us a determination of the direction of the movement which, as far as I am aware, in all cases investigated has revealed itself as a subsidence.

Another circumstance may help to clear up this problem, namely, the stratification of the Icelandic horsts. As shown above, the Icelandic series distinguish themselves by a mostly horizontal stratification, signified by a course of mass eruptions with intermediate deposits of tuffs and subordinate, sedimentary series. Now it appears that the positions of the strata in the Icelandic horsts have in a strikingly large number of cases retained their horizontality even after the tectonic disturbances. Early horst formations will naturally be rather severely eroded, and the difference between the orientation prior to and after the tectonic processes can only be determined by the dip of the strata; in the very young horsts, however, we have still another indicator, viz. the terrain. On their upper sides the young horsts have plateau flats which are the remains of the pre-tectonic surface, and in most cases this proves to have retained its horizontality. These young horsts are very common in the south land and in parts of the interior highlands, and they are also to be found in that part of the north land where there are recent tectonic disturbances. As typical examples I may name the Ingólfsfjall, Vörðufell and Skarðsfjall. As the map shows (No. 2), Ingólfsfjall is bounded by steep walls 3—400 m. high, with sharp edges both towards the plain at the foot of the mountain and towards its upper surface, which is in the form of a plateau with slightly rugged terrain forms. Humid erosion has only affected this flat and its edges in the slightest degree and the plateau surface is almost unbroken. Vörðufell (map 4) is exactly the same; on its plateau it bears a small lake whose drainage to the south has formed a very small gully. Both mountains must be very young, otherwise Ingólfsfjall would be cut up by erosion gullies and the little lake on Vörðufell would have disappeared long ago, emptied by the deepening of the erosion gully. A more exact estimate of the age may be obtained by a comparison with the landscape shown in map 5, on the east of Skagafjörður on the peninsula lying between that fjord and the Eyjafjörður to the east of it. The section of the map shows a volcanic plateau land, mostly built up of lava beds; but in between the uppermost of these Helgi Pjeturss has shown moraines and striated horizons, so that we must assume that the lower part of the system is Tertiary, while the upper part is Quaternary. The valley formation at this place must therefore be later than the early ice-sheet. The forms of the valleys, however, display a most distinct glacial erosion, partly in the principal valleys shown in the map section and partly in the form of a number of cirques lying in an almost continuous row along the upper edge of the valley, each of which has eaten away a small piece of the plateau. The principal valley must therefore have existed during the last Glacial period.

There is a type of landscape of somewhat similar origin in the mountain region of Súlur (Botnssúlur) in Southwest Iceland. Pjeturss(on) has explored it geologically and morphologically and has come to the probably incontestible conclusion (1904) that the mountain is the ruin of a strato-volcano, the formation of which has taken place at any rate partly in Quaternary times, as the products of the volcano rest upon ice-striated and moraine-bearing horizons, whereas today the volcano appears as a mass badly broken down by a post-eruptive glacial erosion. Map 6 shows that the mountain is split up into a collection of peaks and ridges with steep walls, leading down to characteristic Botn formations. Photograph No. 51, was taken from the highest summit on the map, Point 1095, and the high pinnacle in the middle of the picture is Point 1035. The two Botn-formations on the right and left side of the picture meet at the rounded ridge whose lowest point on the map bears the Cote 888. The peak in the middle of the picture, Point 1035, is probably an old crater canal. This type of terrain and the land east of Skagafjörður have this in common, that they both contain moraine-bearing material, and that prior to the last great glacial period there has been a difference in the level of the landscape, which has given rise to a violent, glacial erosion under the last ice sheet. That they are so different as the map shows, despite this fundamental likeness, is a result of petrographic differences, Súlur being built by the activity of stratic eruptions, whereas the land at Skagafjörður is a lava plateau which in all essentials has received its form by a long series of Quaternary mass eruptions' having flooded the land with streams of lava.

If we now compare the illustrated and described forms of landscape, we arrive at the conclusion that they represent two main morphological types. One, represented by maps 2 and 4, distinguishes itself by the fact that the terrain forms look young, as there is no trace of a glacial erosion after the occurrence of the difference of level, while the traces of humid erosion are sparse and very faintly developed. The other type, maps 5 and 6, displays landscape forms with a similar difference of level, but this has already existed under the last ice-sheet. We must therefore date the formation of Ingólfsfjall, Vörðufell and many other mountains to post-glacial times, and this assumption is strengthened by one more observation. The plateau surface on Ingólfsfjall and several other similar mountains such as Skarðsfjall and Hrafnabjörg (fig. 50) bear traces of glacial erosion, including striae; these are peculiar in that they run in the direction of the natural fall of the country, regardless of steep slopes and the now-existing difference of level between the plateau surfaces and the lowlands at the foot of the mountains, and they are to be found right out to the edges of the plateaux, in fact on the marginal boulders which in certain cases during the tectonic processes have been loosened from the mass and displaced from it outwards and downwards. The cliffs on these mountains must thus be younger than the striae on the plateaux. Another question is whether these striae date from the last great glacial covering, and this seems to me to be much the most probable explanation, for, if this were not the case, one would find on the edges of the rock traces of local ice movement and small cirques produced by the erosion of ice and snow; as the maps clearly show, there are none.

Conditions at the present time indicate that one must regard the faults not as instantaneous processes but as interrupted movements that take place throughout a short or long period, but whose duration in a geological sense seems to be fairly short. For the present we do not know sufficient about the tectonic processes in Iceland to definitely fix the duration of the various fault systems, but, as shown in the foregoing, one can in certain places arrive at an approximate dating of the processes, roughly as follows: The great fjords in the west country seem to have been formed in Quaternary and post-Glacial times, the north-country fjords are Quaternary, and the principal faults now identifiable in the south country must be taken to have been formed in late-Quaternary and post-Glacial times.

4. The Tectonics of Iceland and the Alpine Foreland.

When considering the forms of movement that have caused these fractures it will not be out of place to undertake a comparison between the Icelandic faults and the corresponding movements in the Alpine foreland, where there is also a system of young — some of them recent — tectonic processes.

According to several writers, the northwesterly Alpine foreland between the Alps and the North Sea is remarkable in that it consists of a large number of blocks of great size (Schollen), each of which turns on its own axis while at the same time an axial change seems to be in process. Certain parts of the blocks are rising, others sinking, and in this manner occur a number of inclined planes dipping in various directions, varying from one block to another. The characteristic morphological feature in this part of Europe is thus that the pre-tectonic horizontality is being broken.

In this respect there seems to be a profound difference between the tectonic processes in the Alpine foreland and the processes in the Icelandic fault region, where we find that the fundamental morphological peculiarity is that horizontality is retained during the tectonic processes. It is true that there are inclined planes in the Icelandic fault country, seemingly caused i.a. by a general subsidence in towards the new-volcanic zone. Another form of inclination occurs at the edges of the tectonic-resistance regions. We see this in recent fractures when these for instance have affected the lava streams, causing the gjá-formations described by several writers, on the borders of which one frequently sees large tilted blocks with one edge resting upon the upper edge of the fault and the other on the sunken surface. We know of a corresponding example on a larger scale on the mountain Esja at Reykjavík (THORODDSEN 1906, p. 209), where the principal tectonic element, the mountain itself, is horizontally orientated whereas the smaller blocks to the south of it have tilted away from the highest part of the fault area. We know of similar conditions in the great fault area west of Vatnajökull, where tilted marginal blocks have played a very considerable part in the forming of the terrain. On fig. 23 is a horst, Túngnárfjöll, in the centre; on the right and left are long, narrow subsidences, one of which is filled by the big lake Litlisjór, which is shown on the picture. On the side towards Litlisjór very large boulders have loosened themselves from the horst and have been flung out towards the subsidence; the process has taken place so recently that it is still possible to recognise remains of the plateau surface on the upper side of these blocks which, on account of their tilting, forms an inclined plane in contrast to the almost horizontal surface of the main block.

In all cases known to me, in which it has been possible to determine the direction of movement during Icelandic tectonic processes, there has been a subsidence of certain parts of the terrain, whereas other parts have remained stationary. We have thus to do with a one-sided movement and not a tilting like that characteristic of the Alpine foreland. The great western fjords have already been assumed to be subsidence areas, and the correctness of this view can scarcely be disputed. The great north-country fjords must likewise be taken to be subsidence areas, whereas the peninsulas lying between them may be regarded as areas of resistance. What it is that brings about this contrast between subsidence and resistance areas, what it is that holds parts of the tectonic units of the landscape up when the other collapse, we can say very little about at present. PJETURSS(ON) (1904, p. 257) was perhaps the first to get the idea that "the volcano itself is often regarded as being less exposed to fracture than its immediate surroundings". HANS RECK later (1922) reviewed this problem and propounded the theory that the regions in which volcanic eruptions have taken place, probably on account of the stiffness of the magma are firmer than the surrounding country and, moreover, anchored so deeply that they get these very peculiarities during a tectonic breaking up of the country. He gives a number of examples, especially for the north country, of landscapes whose formation is explainable on the basis of this theory, and on the whole it seems to me possible to apply this view as a working hypothesis when considering the formation of a number of the Icelandic horsts.

As I have stated above, we find the surprising circumstance that in most cases horizontality has been preserved in the later Icelandic horsts. This would scarcely be imaginable if these horsts had been formed by upheaval processes, at any rate not as a common feature. For in that case what would undoubtedly have happened is that they would have been tilted. There are thus a number of circumstances that argue that the tectonic processes in Iceland have mostly been in the form of subsidences, and that the movements for the most part have been vertical.

5. Iceland and the Wegener Theory.

In explanation of these remarkable features in the Icelandic tectonic region I have gradually arrived at the following theory, which may be of some importance as a working hypothesis in the further exploration of this territory, which contains so many valuable objects of study for tectonic morphology. My theory aims at setting the activity of the volcanic and tectonic forces in association with the theory of the horizontal Contintal displacement as formed by ALFRED WEGENER in his famous work: "Die Entstehung der Kontinente und Ozeane" (Ed. 1, 1915, Ed. 4, 1929) which in so many ways has stimulated geographical and geological science. WEGENER drew attention to the fact that the conspicuous unity in the North-Atlantic basalt region finds an explanation in the westerly movement of the American continental group. Accordingly, the various earlier basalt regions are regarded as parts of a split-up basalt plateau of Middle-Tertiary age, of which the various parts have later on been subjected to transformation by erosive tectonic and eruptive processes.

The foregoing account of the Icelandic tectonics has shown that the great common features are the following: We have a number of great, curved subsidences in the west and a large system of almost right-lined faults in the direction southwest—northeast and north—south. These two systems may be regarded as the result of a pull from west to east which has simply split the land into innumerable fissures. When deeper-lying, firm material is removed, cavities occur, and these collapse, thus providing an explanation of the peculiarity of the Icelandic tectonics that subsidences are the main feature. Where such fissures meet a magma and go so far down that this can make its way out, we get the fissure eruptions and the other linear eruptions; and likewise a magma extending from below upwards will, just through the effects of the constant pull, be inclined to break out along a linear zone at rightangles to the pull. This relieving of the magma containers will then produce new subsidences of secondary character with on the whole the same orientation, governed partly by the situation of the relieving zones and partly by the tendency accompanying the pull to form cracks at rightangles to the pull.

The Swiss Alpine school (Argand, Staub and Collet, etc.) have earlier placed the Alpine folding and its accompanying formation of faults in the Alpine foreland in connection with the Continental movement and have regarded the whole of this process as a result of a collision between European masses and Gondwana masses. The construction of these ideas has been presented in a number of works of great ingeniousness and beauty. The characteristic feature of the whole of this tectonic unity is the pressure, in the central parts of the geosynclinal region manifested as nappes with gigantic overthrusts, and in the foreland manifested as a breaking up of the land into blocks which tilt and turn about different axes. The whole of this system is a typical example of what with a common term one might call the pressure tectonics. In contrast to this the Icelandic tectonics must be regarded as the result of a tension, a tearing asunder, and in this manner we get a distinction between two forms of tectonic movement that genetically and morphologically are very different: pressure and tension.

It must be regarded as certain that there is a profound difference between these two tectonic types; whether the explanation I have set up is tenable is another matter, but it is to be hoped that future investigations will throw more light over these fundamental morphological problems. For the present I hope that this collective point of view of the variegated crowd of individual phenomena in Icelandic tectonics and volcanism will prove to be fruitful to further research.

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Fig. 1. Old, hardened moraine, Tillit, in Suaðafell. The stones have been graved by the subaerial denudation.

Fig. 2. Hardened, stratified, volcanic tuff that has been broken up by a recent dislocation, Heljargiá, and thereafter eroded by the wind. Among the blocks is wind-borne sand.

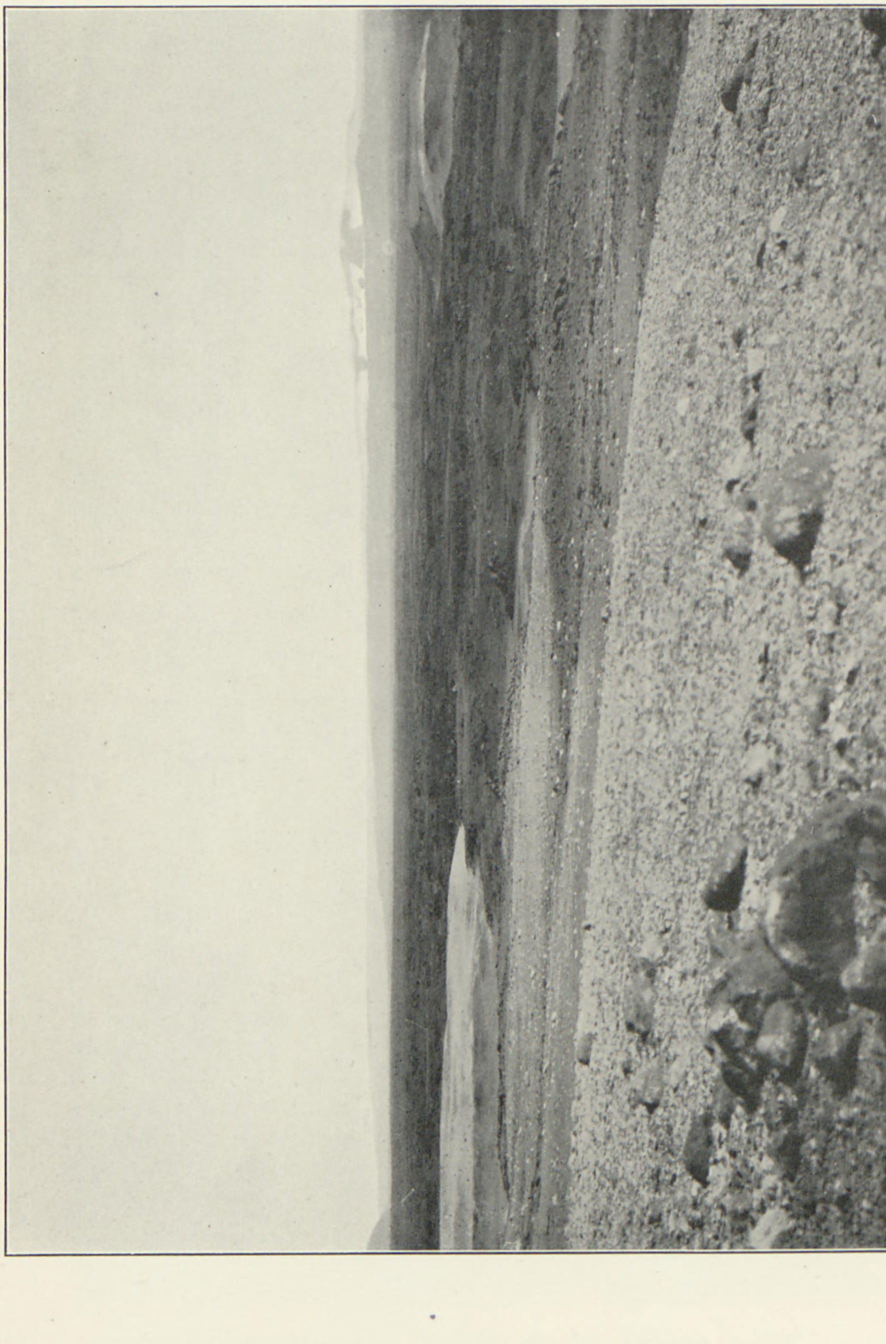


Fig. 3. Hágönguhraun, seen from Ljóshólar. Lava-levelled plane caused by lava eruptions from fissure vents almost in the middle of the lava field. Cf. fig. 4 and 8.

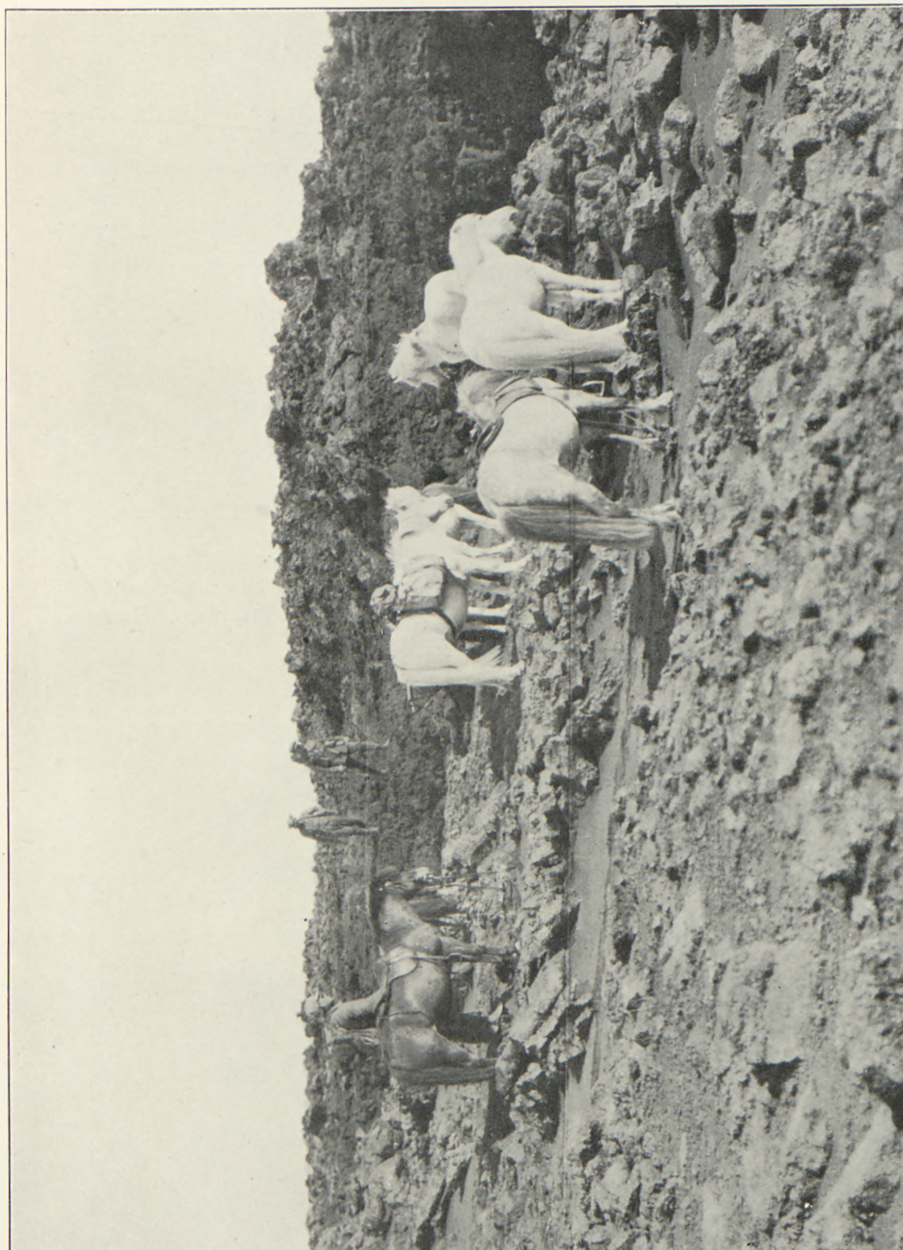


Fig. 4. Terrain details on Hágönguhraun. The horses are standing on a rather sand-swept, older lava surface which has been covered by a very recent stream of block lava. The two men are walking on the later covering, the edge of which is clearly seen in the picture.

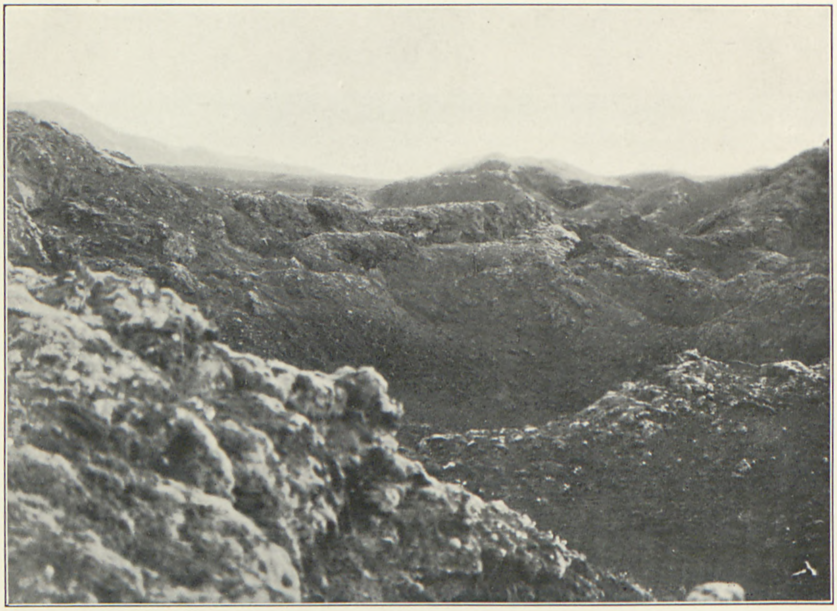


Fig. 5. The vent of a linear mass-eruption, in Zone C of the Fiskivötn region. The fissure itself is full of a chaos of slag mounds, cf. fig. 16. The slag mounds along the edges of the fissure are quite low, rising only about 15 metres above the surrounding terrain.

Fig. 6. "Maar" in Pytlur. After the conclusion of the explosive process a small lava stream has come from an adjacent effusive vent and filled about half of the maar basin. The whole surface of the surrounding landscape is interspersed with explosive areal-eruptions.

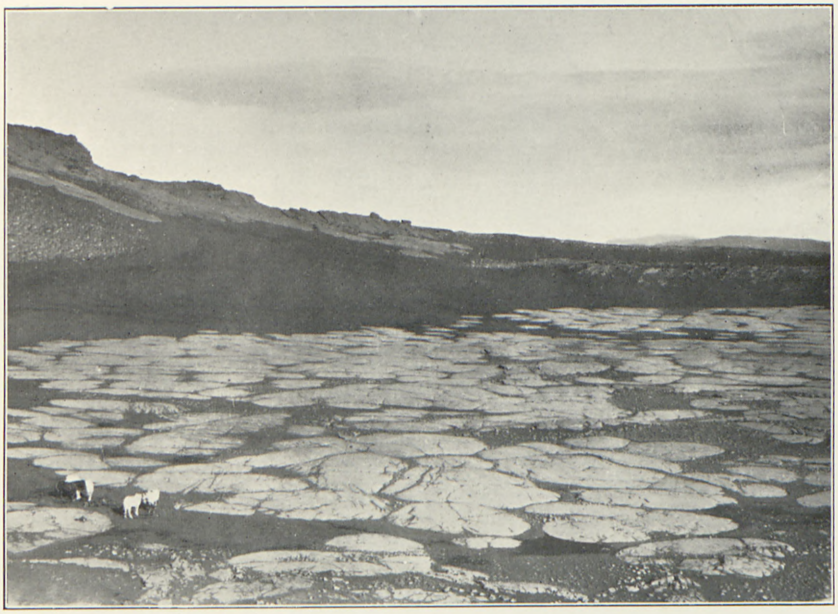


Fig. 7. An explosive volcano, the crater partly full of "foreign" lava which has hardened under very quiet conditions in the form of sheet-lava (Icelandic: helluhraun). The size of the various domes may be estimated from a comparison with the four horses.

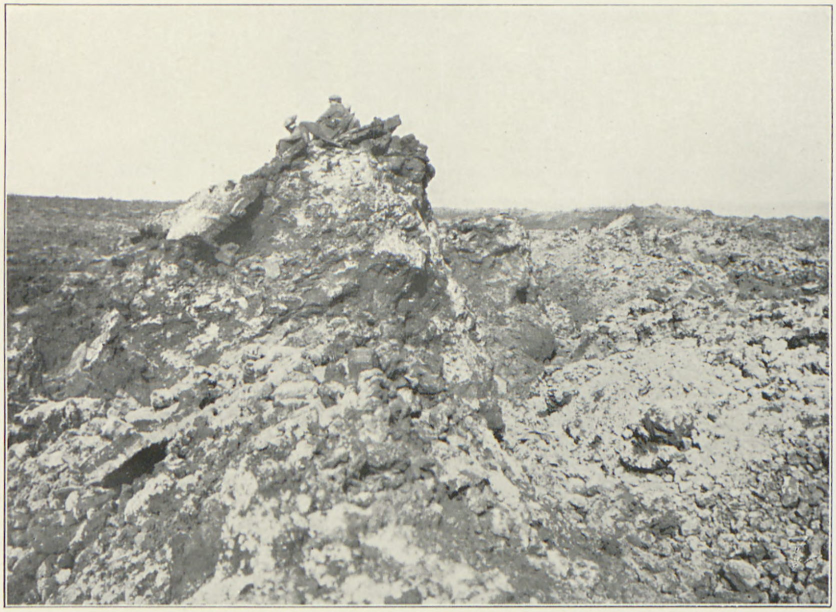


Fig. 8. Terrain detail from Hágönguhraun. Characteristic block lava (Icel. apalhraun). Cf. fig. 3, a general view of the same locality.

Fig. 9. Landscape at Fiskivötn. On the left is Lake Tjaldvatn. The basin in the foreground was formed by the collapse of a deep lava lake, of which a remnant of the surface may be seen in the "shore line", which appears in the right side of the picture and — farther back — in its left edge.

Fig. 10. A corner of Lake Skálavatn, formed in a subsidence basin, on the banks of which are two hornitos of lava fragments. The largest is known as Arnarsetur.

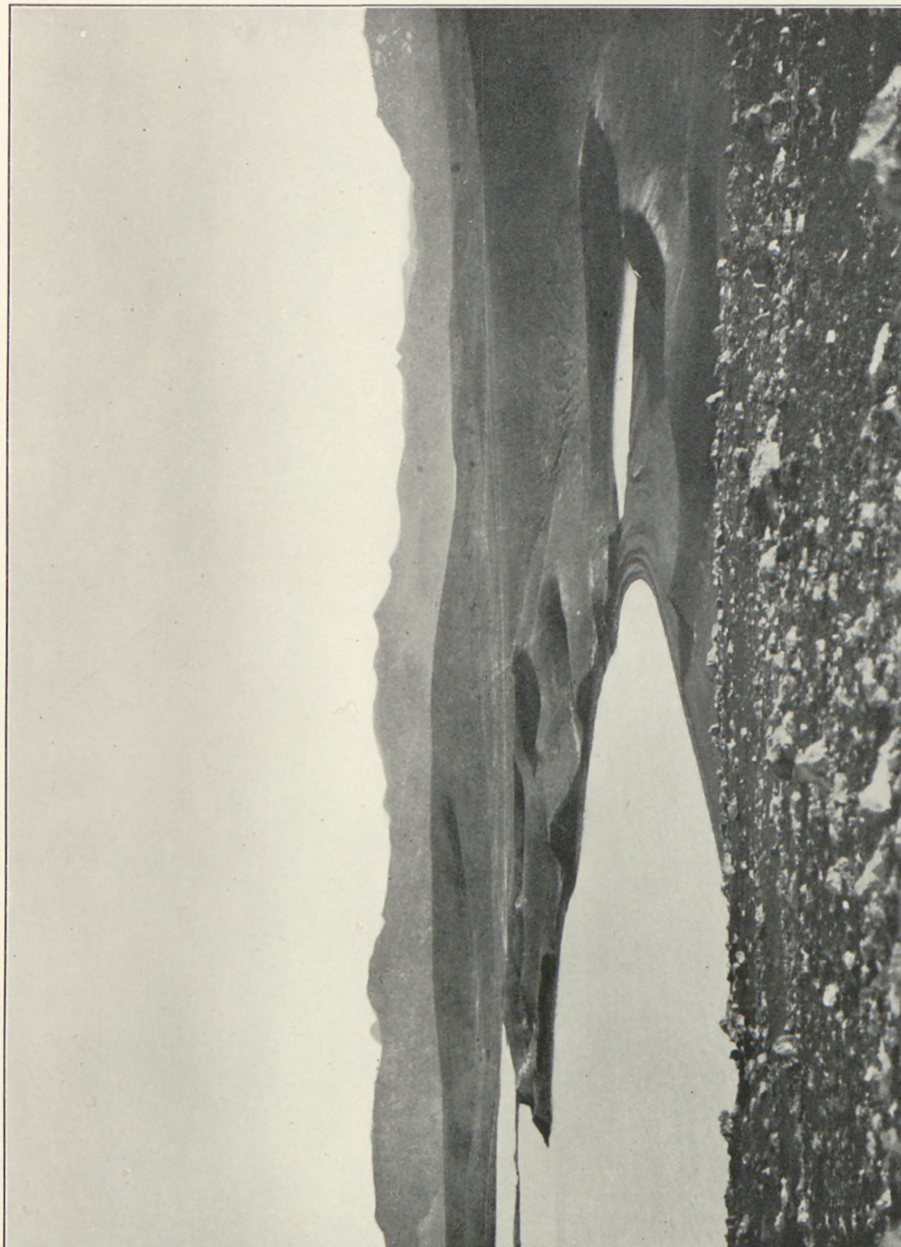


Fig. 11. The southwest end of the large lake Litlisjór. On the shore is an explosive areal-eruption. Note the water-marks which indicate the high water-table when the spring thaw is on. The foreground is of material from an explosion crater. Behind the craters is a landscape with a lapilli surface, converted by solifluction combined with temporary water erosion. In the background is a part of the long, narrow horst Túngnárfjöll.

Fig. 12. Explosion pit in Pytlur, looking along the pit, which is split up by low gravel mounds. After the explosive phase, lava has risen up in the fissure, but only to a certain height, and there have been subsidences during the solidification process.

Fig. 13. A genuine explosion volcano on the banks of Litlisjór, seen from the outside of the gravel cone. Its peculiarity is the presence of large blocks, and thus forms a contrast to the blast crater shown on fig. 14.

Fig. 14. Blast crater in Vatnakvíslagígir, photographed almost from the ridge-top of the gravel cone; in the background are two other volcanoes of the same type and belonging to the same line of eruption. The deepest part of the crater contains a lake, and the cone consists of rather fine-grained material, visibly stratified; cf. fig. 13. The dark, elliptical covering of the inner wall of the cone consists of lava and came from a lava jet which must have been about 150 metres high and which seems to have brought the eruption to a close.

Fig. 15. The edge of the same cone as in fig. 14. Close-up picture of the top of the gravel cone covered with broken up lava from the jet referred to under fig. 14.

Fig. 16. Coherent slag ("Schweiszschlacken") from the innerside of an "eldborg". The splashes of lava have been thrown up on the inner side of the crater in such a state that they have stuck together before cooling, but without losing their individuality.

Fig. 17. Sub-surface canal in the lava at Fiskivötn. The orifice of the canal is seen in the foreground of the picture, the roof having partly fallen in. The lava sheet is covered with a carpet of incompletely decomposed organic remains originating from the characteristic vegetation-covering of moss (Grimmia) and dwarf bush (Salix lanata).

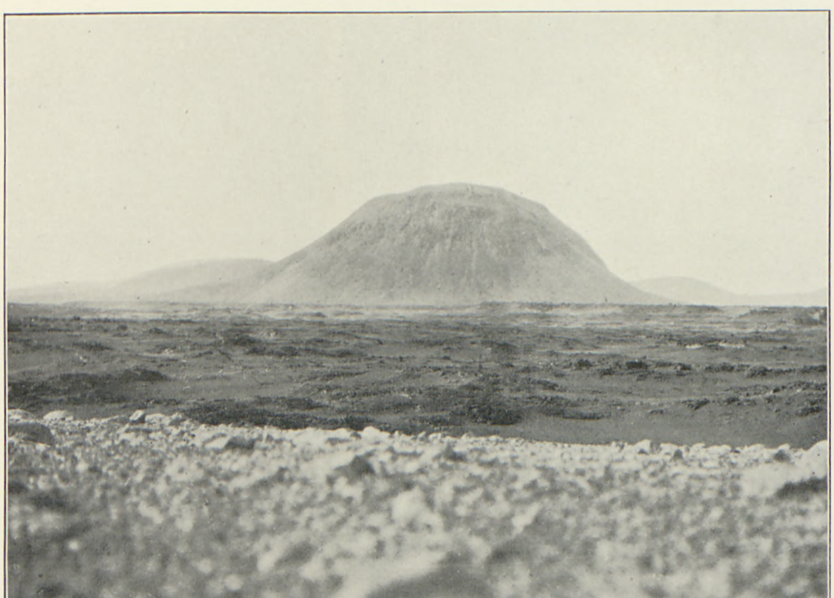


Fig. 18. Háganga syðri, a craterless, liparitic "Staukuppe"?, about 800 metres high. In the foreground is wind-eroded moraine, in the middle distance basaltic lava.

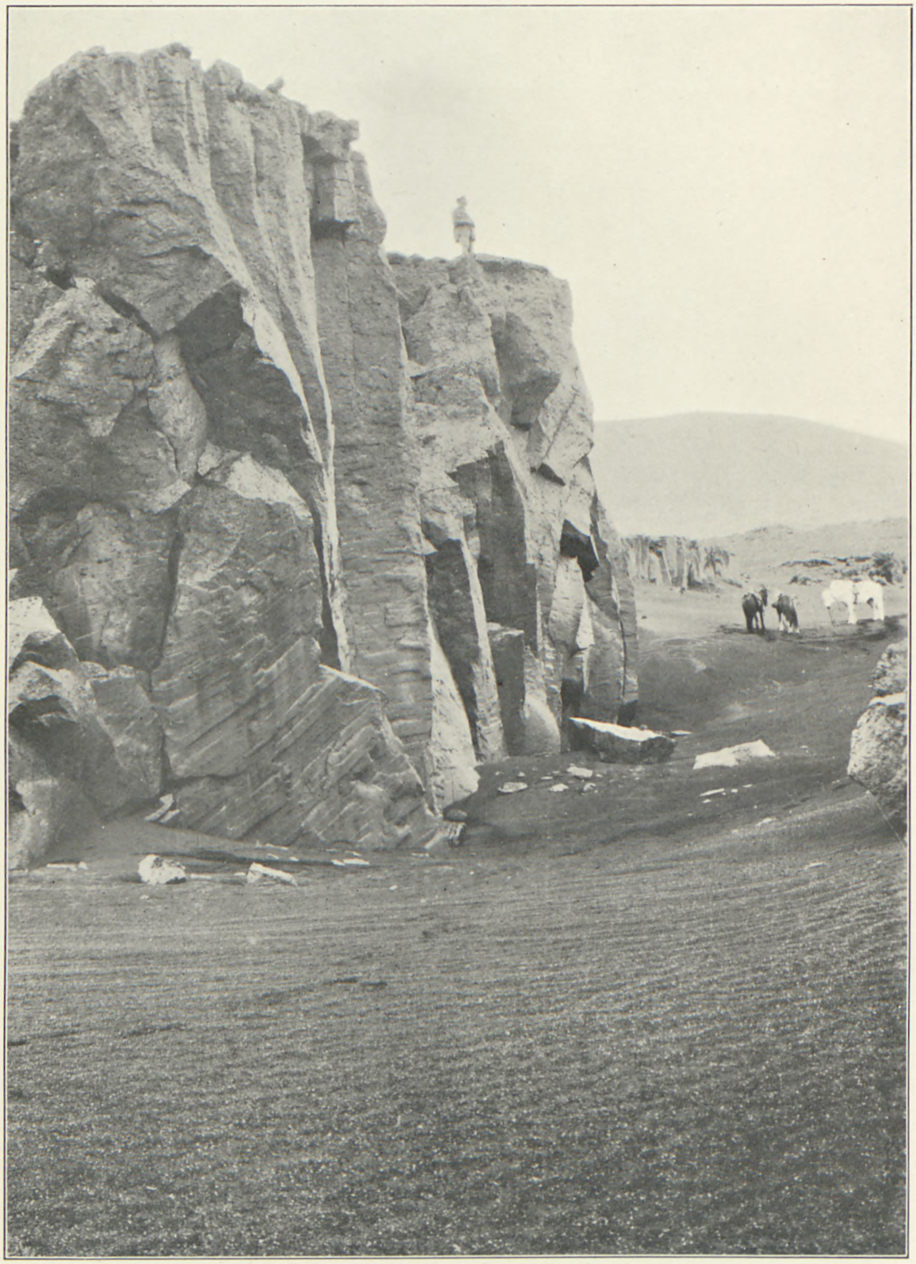


Fig. 19. Heljargjá, a recent tectonic fissure west of Vatnajökull, looking along one edge, which here runs through a field of sheet-lava. The picture is taken from the subsidence depression, the man standing on the extreme edge of the undisturbed lava field. In the foreground wind-borne sand.

Fig. 20. Heljargjá at a spot where the fissure extends through slab lava. The edge of undisturbed lava surface is seen on the right, the subsidence area to the left. During its movement a large slab of lava has tipped over towards the subsidence.

Fig. 21. Heljargjá in Gjárfjall. Here the fault is about 100 metres deep. At the top the edge of the fissure is quite sharp, at the bottom concealed by tipped blocks and later by aeolic material. The wavy line is the track of the caravan, made while descending to the bottom of the fissure.

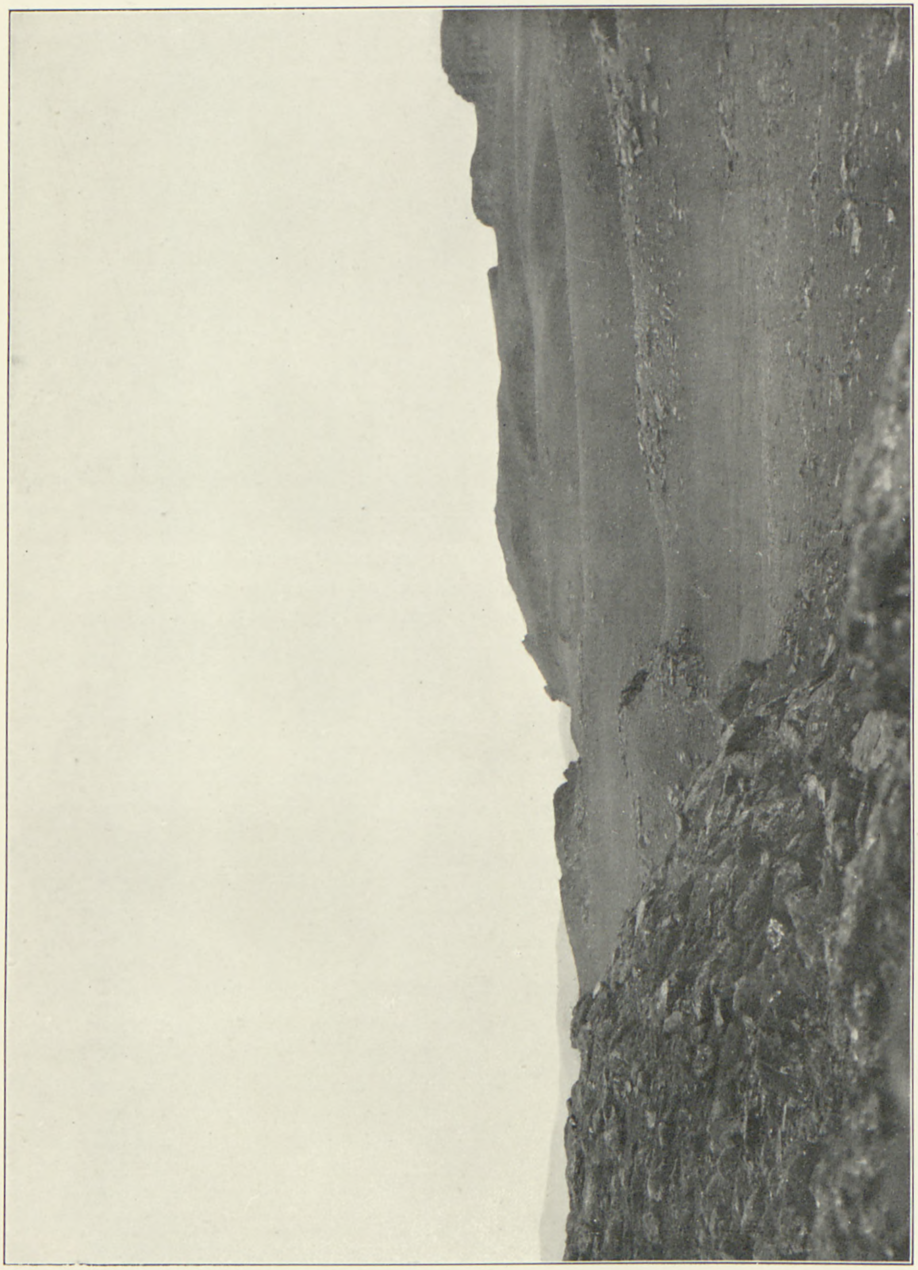


Fig. 22. Recent “champs de fracture” with a close system of parallel fracture lines, which have divided the landscape into narrow, straight-sided strips. The area east of Þórisvatn.

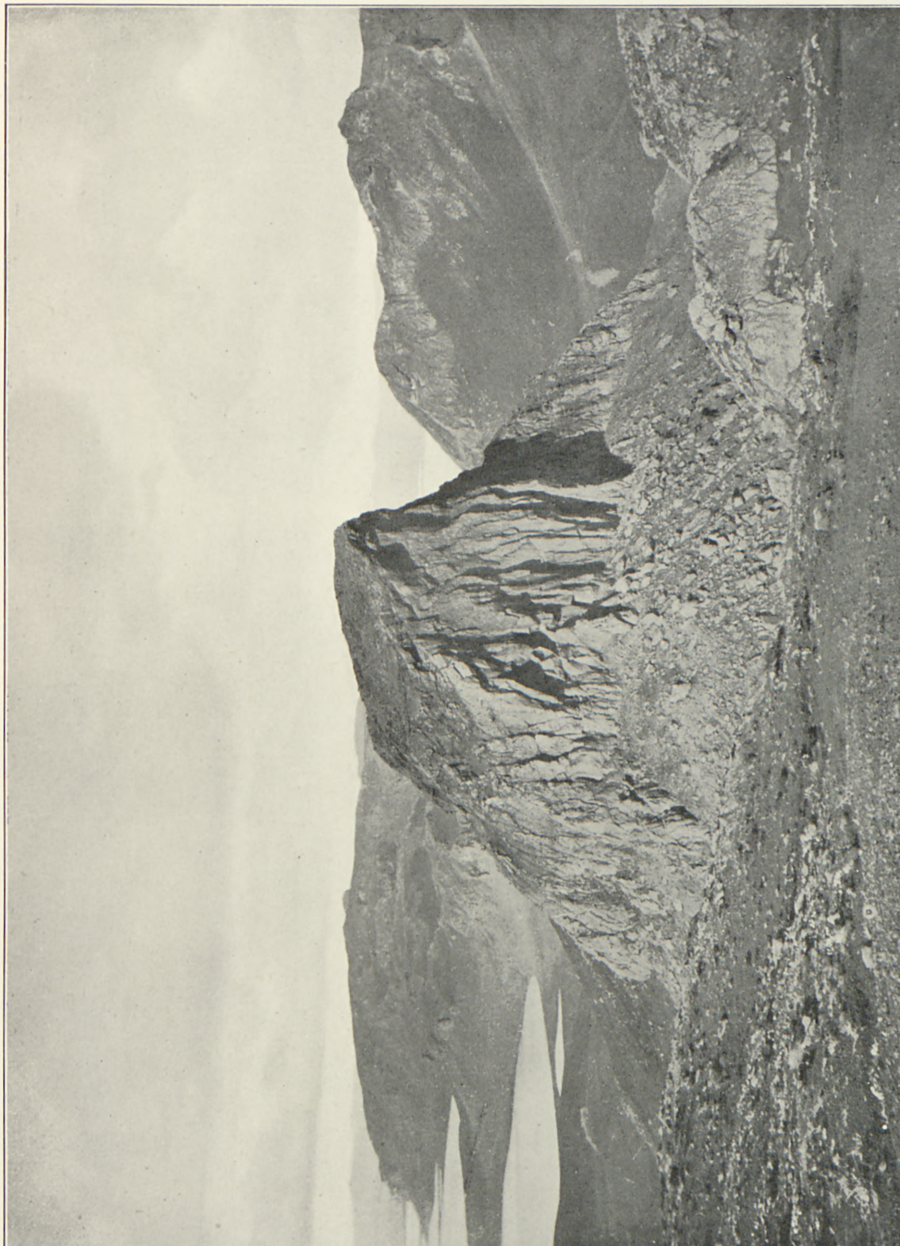


Fig. 23. Túngnárfjöll, photographed towards the northeast. On the left Lake Litlisjór, on the right a part of the bed of the Túngná in a tectonic fissure 2—3 km wide. In between is a view of Túngnárfjöll, a horst about 25 km long, 2—3 km wide, its steep wall forming the right bank of Litlisjór, and its plateau surface distinctly visible. The block in the foreground has on the top an inclined plane: a small plateau surface which has got into its present position through being tipped to the left out towards the subsidence area in which Litlisjór lies.

Fig. 24. A column, over 10 metres high, called Tröllið, probably formed by a combination of tectonic and subaeric processes. The stick in front of the column measures about 1 m. Sterile lapilli surface with an incline of about 12°. Traces of the local and temporary spring water erosion, which has produced a dense, consistent system of melt-water channels 0.3 to 1 m deep. No terracing, cf. fig. 25. In the background Túngná, with one of the transversal barriers (see fig. 35), through which the river has cut a gateway.

Fig. 25. Solifluction surface with terraces at Fiskivötn. Dip about 8°. In the background are steeper slopes with meltwater channels, but without terracing. The landscape is a small part of an explosive area-eruption, the depression on the right being a secondary crater. The material is partly lapilli, but mostly the explosion debris repeatedly referred to in the text.

Fig. 26. Windblown, sterile moraine surface on Holtamannaafrjettur. A doleritic boulder has been split into slabs by the frost; some of the slabs are seen in situ, whereas others have been carried by solifluction down towards the observer. The stick is 1 m high. In the background are several other blocks, similarly disintegrated and split.

Fig. 27. Storm-devastated lapilli surface at Fiskivötn. Almost in the middle of the picture is a small, stunted Armeria in bloom.

Fig. 28. Overgrown lava surface in Þingvallahraun, looking south. Most of the vegetation is Grimmia, its carpet having been torn up by the north gales, which gives the cushions a steep destruction-face towards the north. Cf. fig. 29.

Fig. 29. The same locality as fig. 28, photographed towards the north. The man has not moved between the two exposures. The carpet of moss is apparently continuous and intact, whereas it is actually being torn up by the dry north winds, as fig. 28 shows.

Fig. 30. Wind-erosion from the north-east (the left) in Hekla farming area. View from the southwest end of Skarðsfjall towards the southwest, from a point about 100 metres above the plains. In the left half of the picture is the wind-eroded surface, where the lava has been laid bare; the right half is covered with loess and grass. On the border line between these two surface-forms the local inhabitants have built long dykes of lava blocks, two of which are seen on the picture, one straight, the other curved.

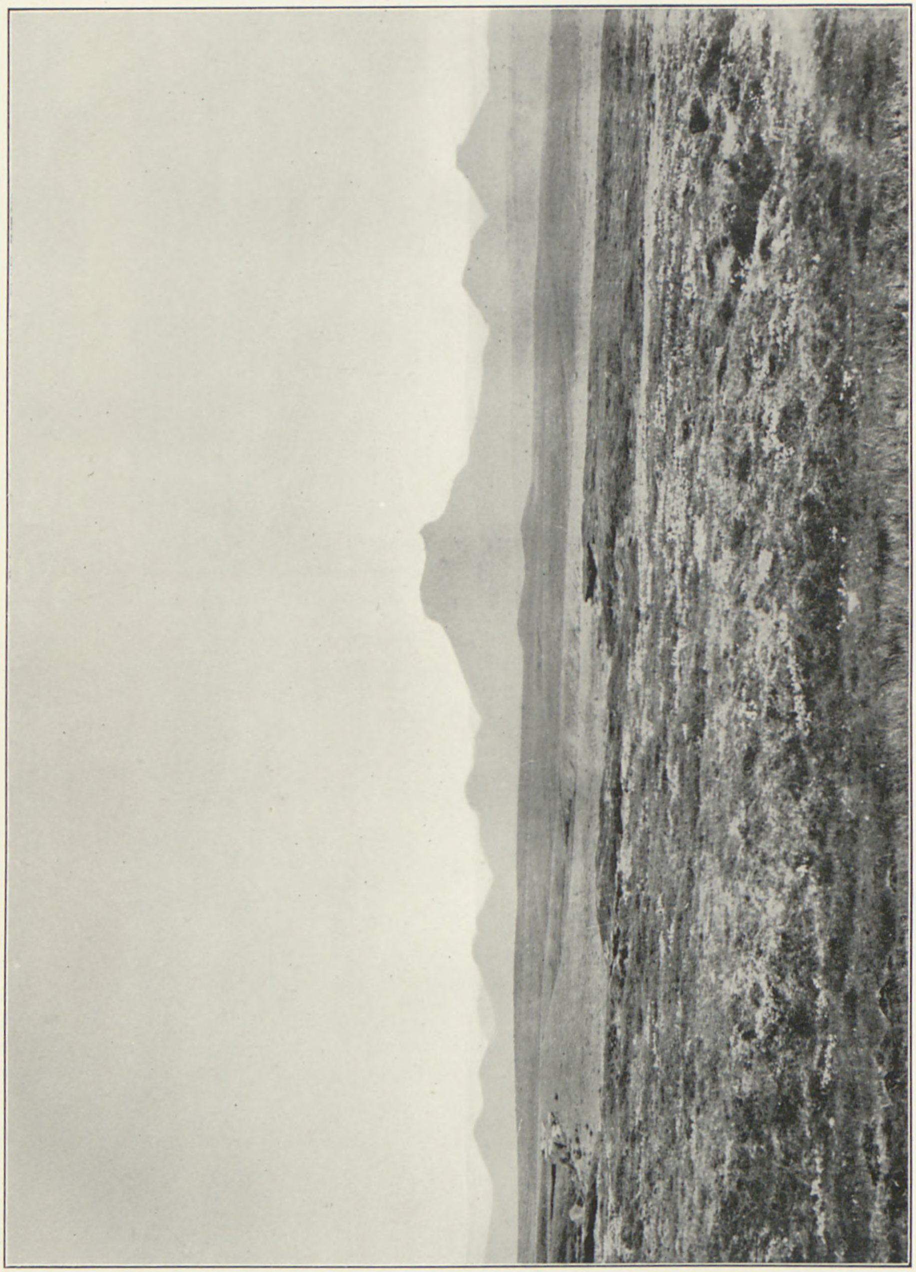


Fig. 31. Wind-erosion in the highland east of Langjökull. In the foreground a patch of continuous vegetation, the edge undermined by the gales. Behind are enormous wind-eroded surfaces, with very sparse vegetation. The surface of the plateau has been raised to the present level by lava of inter-glacial age, eroded by ice during the last glaciation and covered with a thin cap of moraine. The hills in the background, Jarlhettur, appear to be Quarternary volcano ruins. Behind them is a glimpse of Langjökull.

Fig. 32. Polar storm-waste in the high-land west of Vatnajökull. The surface is very modified moraine, the relief is mainly tectonic in origin, but the details are the result of subaeric denudation and aeolic forces in combination with a temporary and local solifluction and snow-melting erosion. A typical example of polar "ennoyage desertique".

Fig. 33. View from Háganga syðri (relative height about 800 metres) over the jökull-river Kaldakvísl's upper course, which is remarkable on account of its great change-ableness. On the left edge of the picture is a recently abandoned bed. In the background Túngnafellsjökull.

Fig. 34. Köldukvíslarbotnar, seen from Háganga syðri (relative height about 800 m). In the background Vatnajökull. The plain is a lava field overlain by recent glaciofluvial deposits. Numerous abandoned river beds.

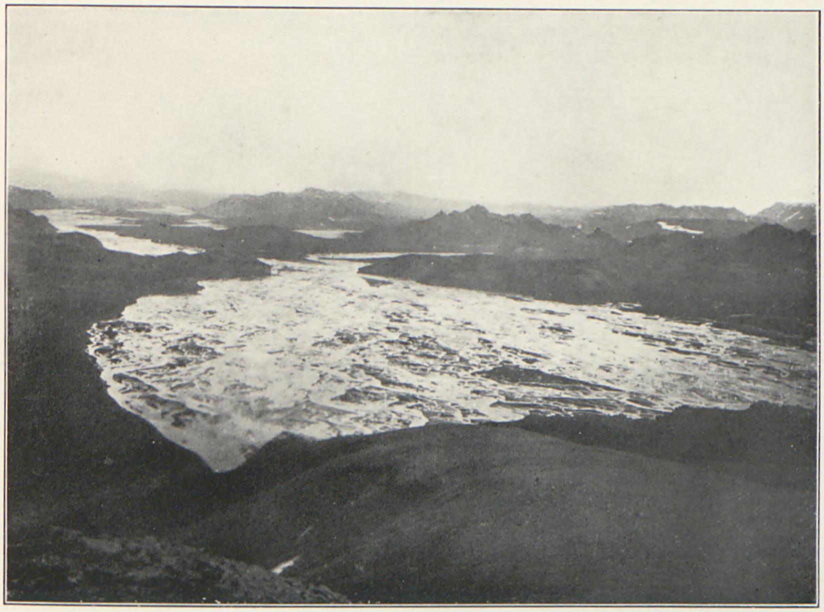


Fig. 35. View over the valley of the Túngná from Túngnárfjöll, showing one of the breaches in a transverse barrier referred to in the text; below it the river spreads out in a large number of arms which enclose very variable quicksands. In the background a region broken up by tectonic processes. The valley is about 2 km wide.

Fig. 36. Outlet from the crater-lake Litla Fossvatn. The waterfall is right in the shore of the lake.

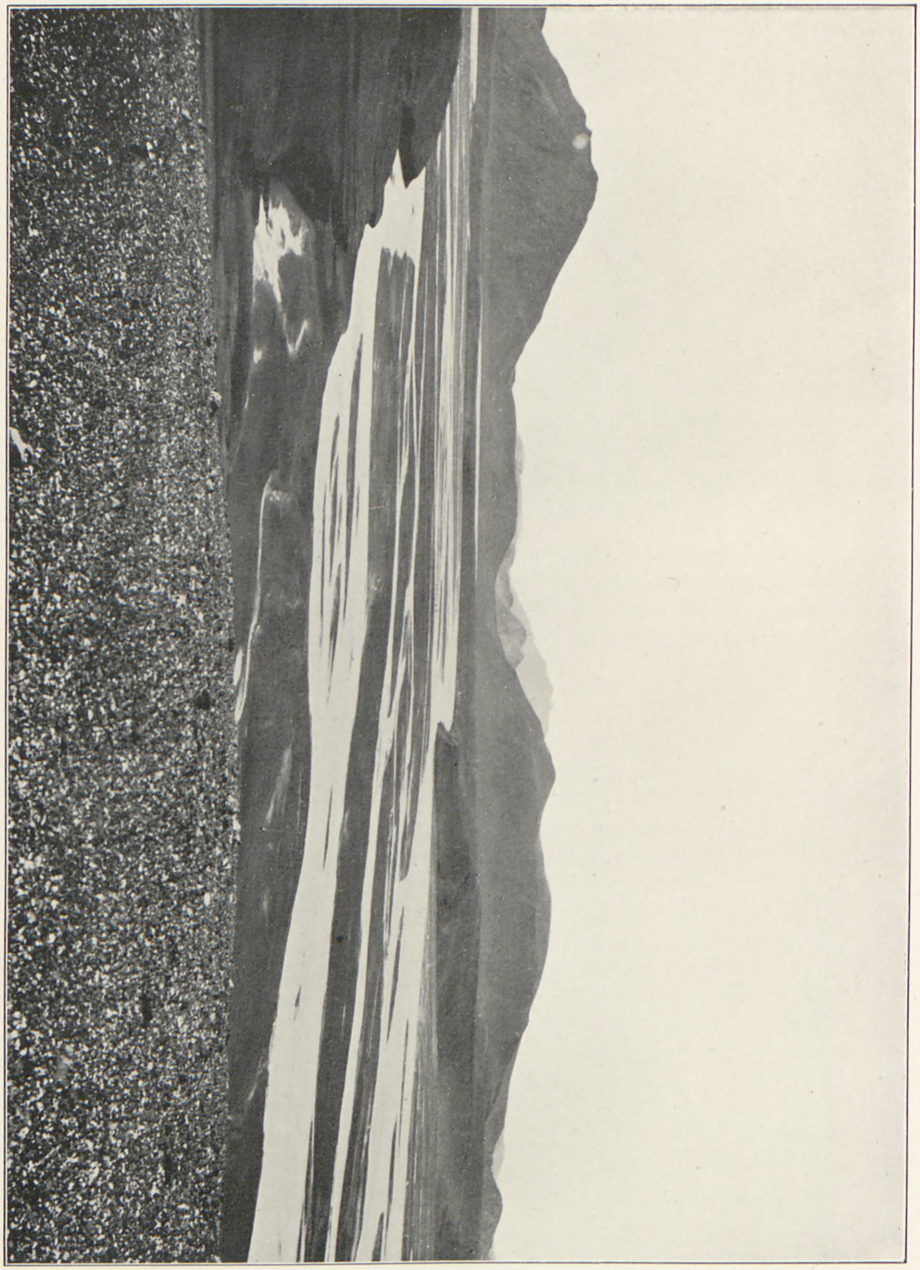


Fig. 37. The Túngná, below where it joins the Námskvísl. The bed is about two kilometres wide. Several arms with intermediate, variable sandbanks. Both the arms and the banks are full of quicksands.

Fig. 38. Hraunvötn west of Litlisjór. The depression is an explosive area-eruption, which has been secondarily filled to a certain height by lava which, while solidifying, has formed numerous subsidence basins which now contain lakes.

Fig. 39. Litlisjór, seen from Túngnárfjöll. The lake has no superficial feed or outlet, and water table is variable and the shores sterile. The basin was formed by the damming up of an explosive eruption in a tectonic basin, one border line of which passes along the mountain foot in the right side of the picture.

Fig. 40. Þórisvatn, seen from the northeast. Only a small part of the main basin is visible; most of the area belongs to the eastern arm, which is a tectonic fissure, its inner part being cut off by a tongue of sand. Almost in the middle of the picture is Þóristindur, and on the right of it Loðmundur.

Fig. 41. Part of Fiskivötn. The foremost lake is Tjaldvatn, and behind it on the left is Skálavatn, on the right Langavatn. The peaks in the background are the great blast craters in Vatnakvíslagígir.

Fig. 42. Snow erosion at Fiskivötn. The snow lies long in the inclined depression which runs from the foreground up to the right of the stick, and thus the bottom is kept moist and moveable untill well into the summer. The mound on which the stick is standing glides down a little every year towards the left edge of the picture.

Fig. 43. Lava oasis at Fiskivötn. Certain lavas provide good shelter, where a continuous covering of vegetation grows, with various forms of growth. The heights in the background are wind-blown and sterile.

Fig. 44. Illugaver, a swampy oasis in a moraine country. A high ground-water table prevents wind-erosion. In the central part of the swamp are many ponds. Drainage to two sides, both right and left in the picture.

Fig. 45. Moraine oasis in Þóristúngur. Purely locally the ground-water table is high enough to prevent wind-erosion. In the foreground is wind-exposed moraine.

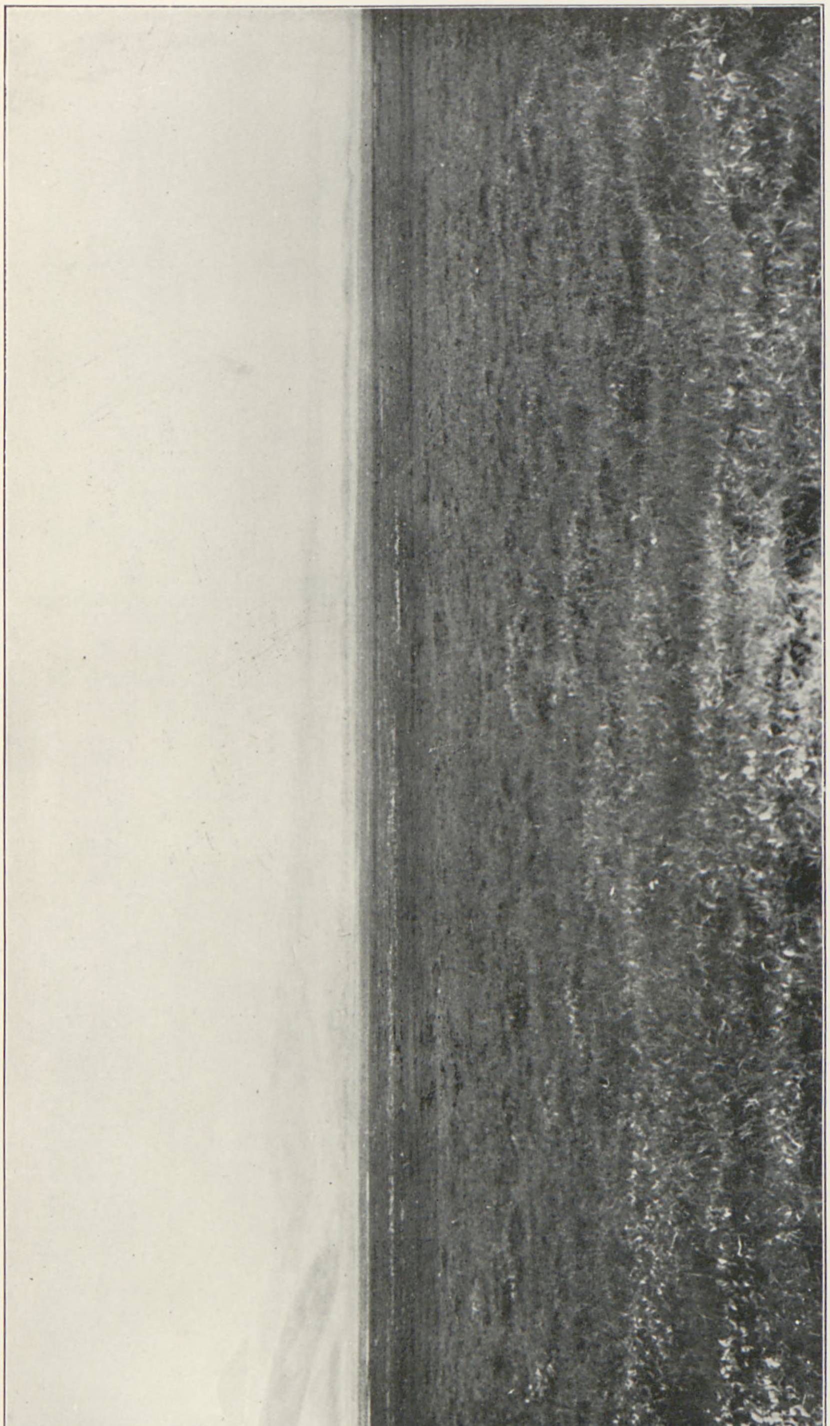


Fig. 46. Glaciofluvial oasis as the south edge of Hofsjökull. High ground-water table, part of it meltwater from the "jökull", prevents wind erosion and creates a possibility for the formation of very large overgrown surfaces. In the background "the jökull" can just be seen.

Fig. 47. The mountain Loðmundur á Landmannaafrjetti. Type of a young horst. The walls are steep, not much attacked by erosion, without a trace of glacial erosion. At the top is a plateau. Cf. the following picture, fig. 48.

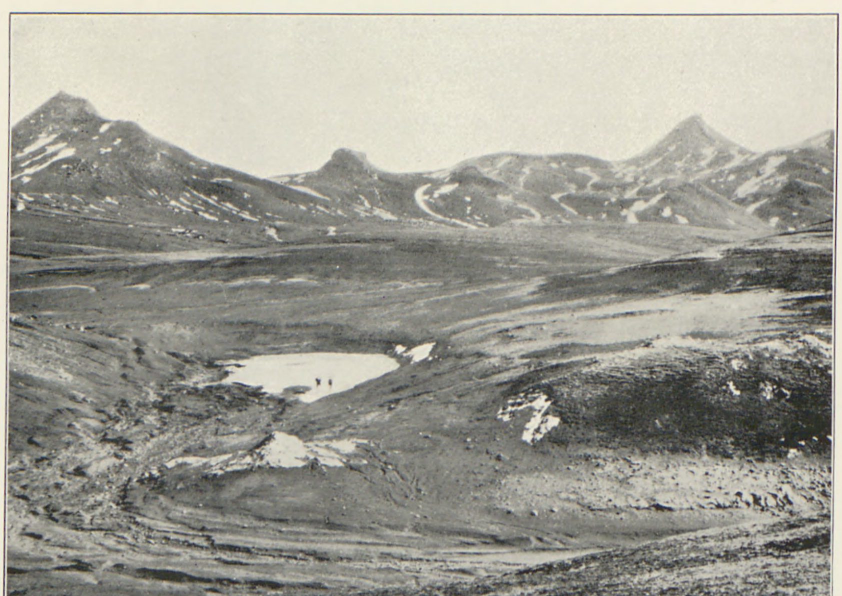


Fig. 48. The plateau on the top of Loðmundur. An impression of the size is given by the two men on the snow surface.

Fig. 49. View northwards from Hengill in Southwest Iceland. In the right background is Þingvallavatn. The surface marked by many straight-lined, parallel faults which have split the terrain into narrow strips.

Fig. 50. Hrafnabjörg, NE of Þingvellir. A young, possibly post-Glacial horst, with steep sides and a striated plateau surface on the top practically untouched by erosion. In the foreground post-tectonic lavas.

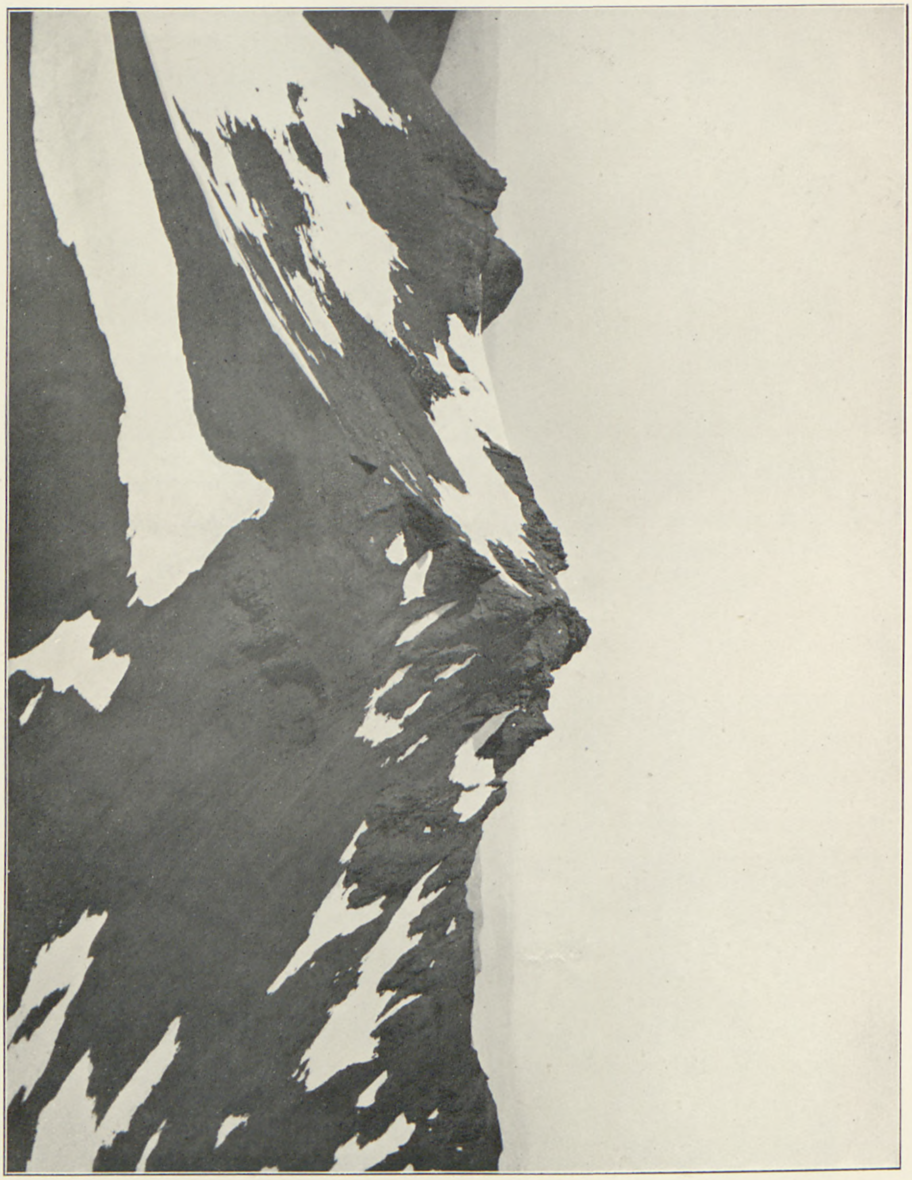
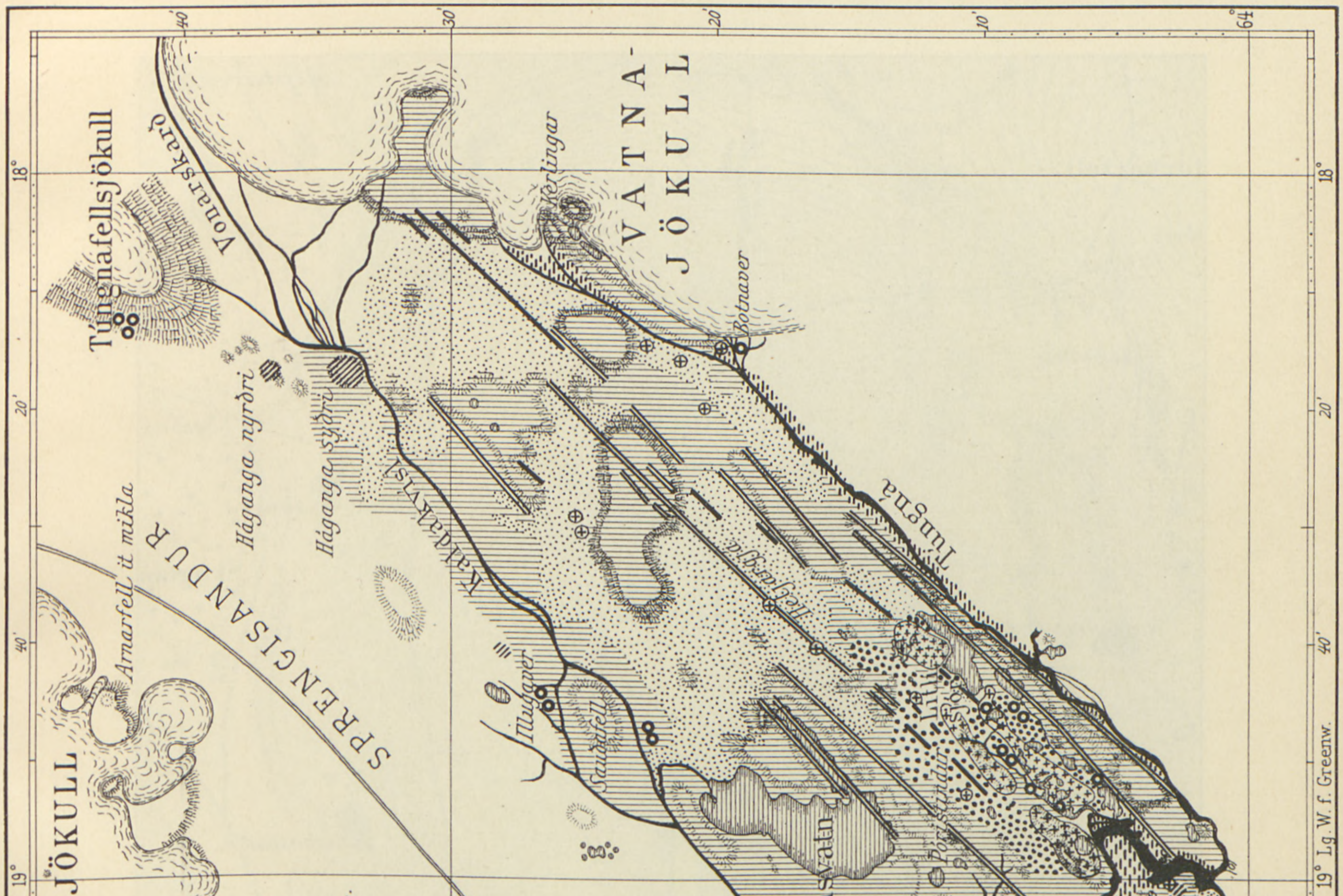
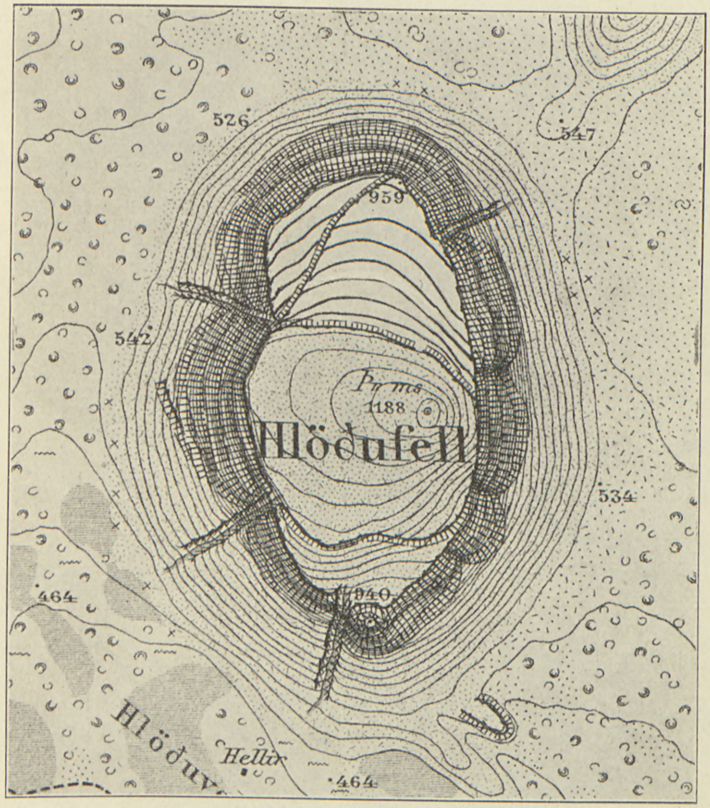


Fig. 51. The mountain Súlur (Botnsúlur) in Southwest Iceland. Ruin of a Quarternary strato-volcano with strong evidence of glacial erosion. The peak in the middle of the picture is probably an old crater pipe.

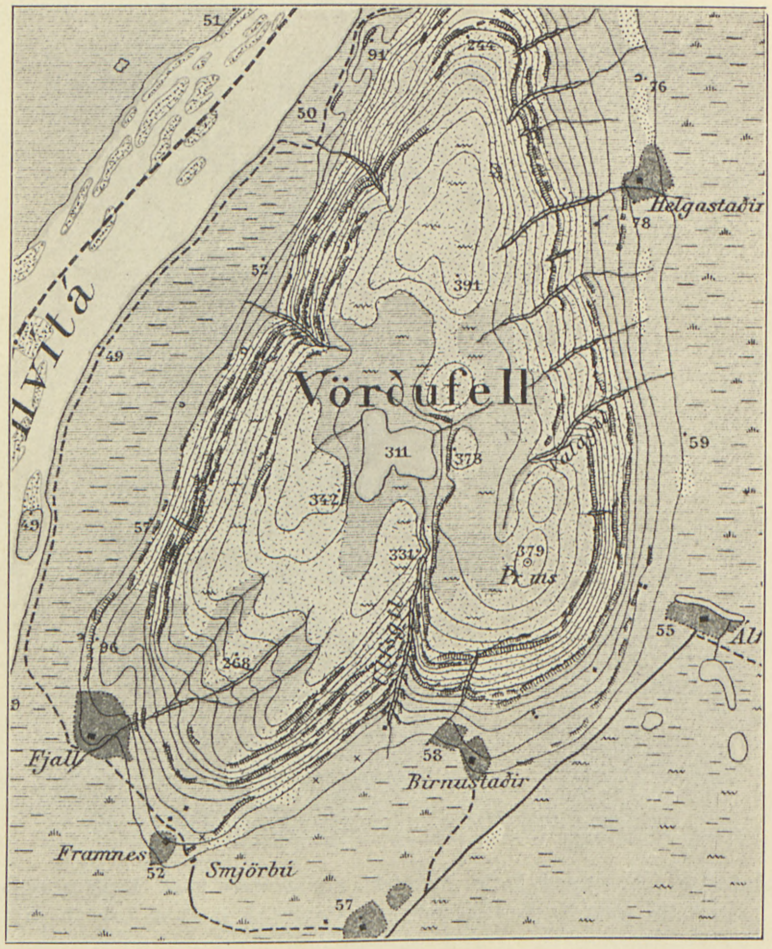


Map Nr. 1. Geological map of the region West of Vatnajökull. Topographical survey by Steinþór Sigurðsson, geological survey by Niels Nielsen.

Map Nr. 2. Ingólfsfjall in S.W. Iceland. Scale: 1 : 50 000, Equidistance 20 m. Explanation see p. 97, 279. Reprinted from Nr. 37 Hengill S. A. Geodætisk Institut. København.

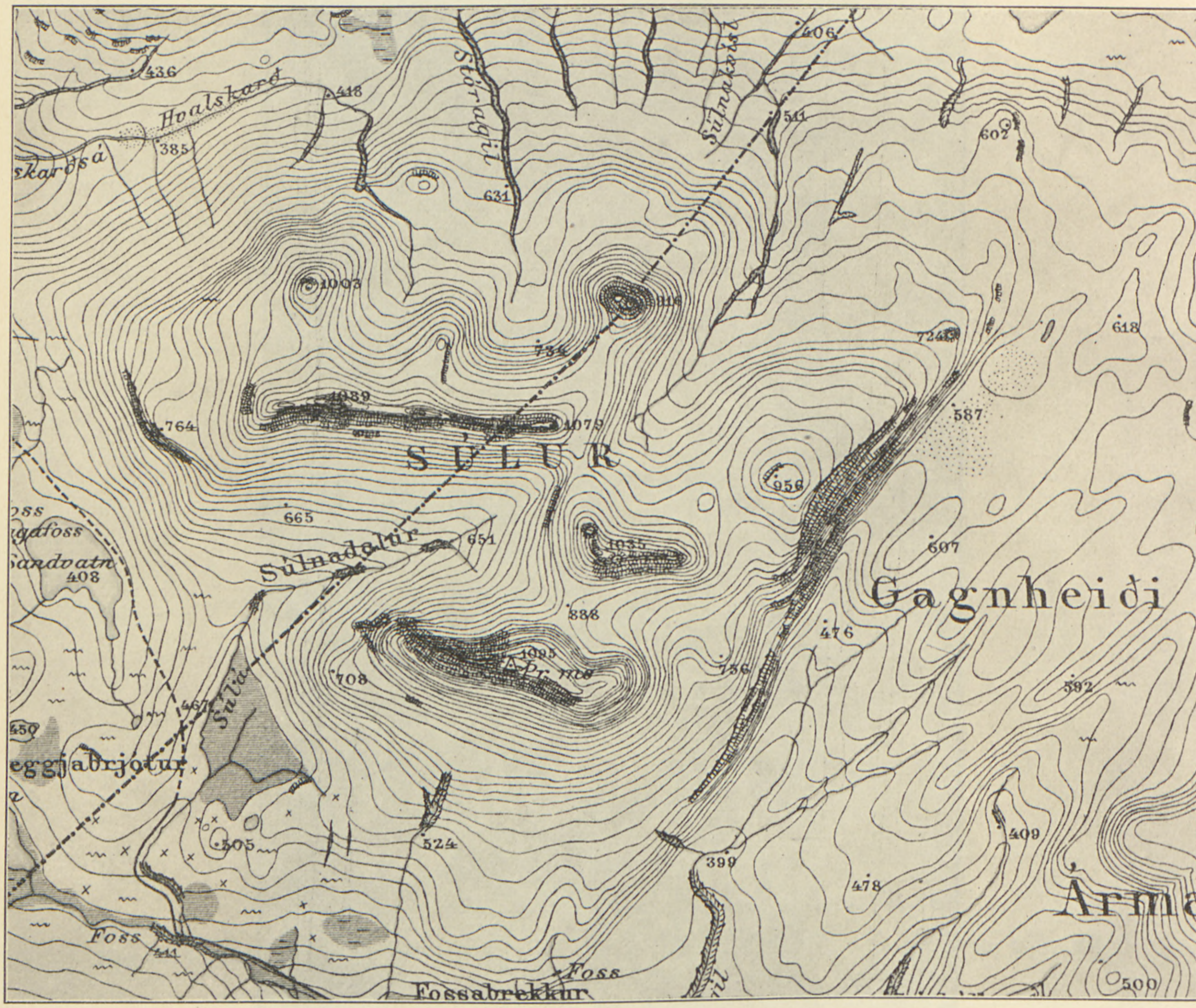


Map Nr. 3. Hlöðufell in S.W. Iceland. Scale: 1 : 50 000, Equidistance 20 m. Explanation see p. 97, 279 ff.
Reprinted from Nr. 46 Hlöðufell S. V. Geodætisk Institut. København.



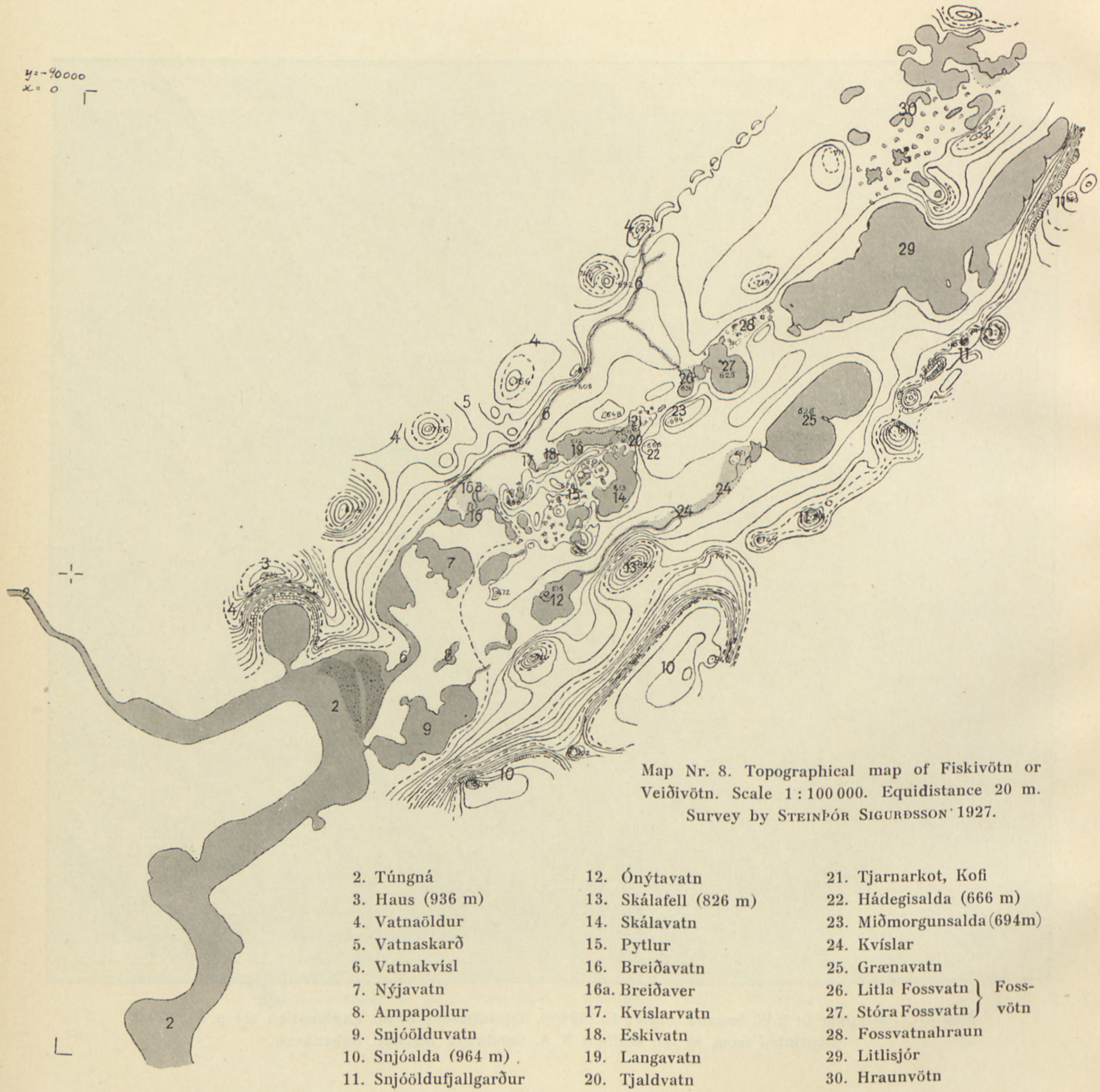
Map Nr. 4. Vörðufell in S.W. Iceland. Scale: 1 : 50 000, Equidistance 20 m. Explanation see p. 97, 279.
Reprinted from Nr. 47 Skálholt S. V. Geodætisk Institut. København.

Map Nr. 5. Landscape on the East of Skagafjörður, North Iceland. Scale: 1 : 240 000, Equidistance 20 m.
Explanation see p. 97, 279.
Reprinted from Nr. 52, Skagafjörður. Geodætisk Institut. København.



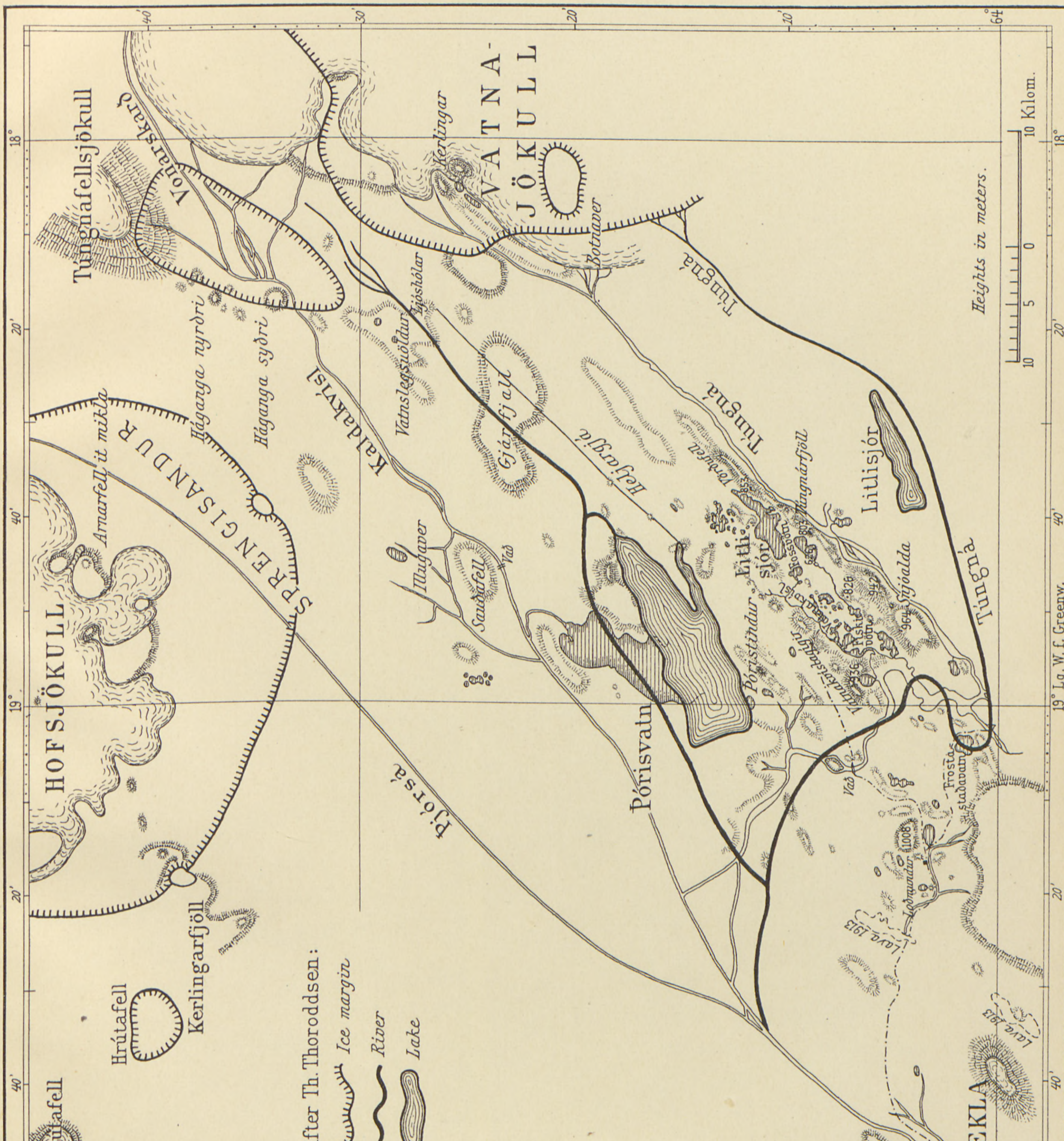
Map Nr. 6. Súlur (Botnssúlur) in S.W. Iceland. Scale: 1 : 50 000, Equidistance 20 m. Explanation see p. 97, 279 f. Reprinted from Nr. 36 Botnsheiði S. A. Geodætisk Institut. København.

Map Nr. 7. Hreppar in S.W. Iceland. Scale: 1 : 130 000, Equidistance 20 m. Explanation see p. 95, 277 ff.
Reprinted from Nr. 47 Skálholt N. A. Geodætisk Institut. København.



Map Nr. 8. Topographical map of Fiskivötn or Veiðivötn. Scale 1 : 100 000. Equidistance 20 m. Survey by Steinþór Sigurðsson 1927.

2. Túngná
3. Haus (936 m)
4. Vatnaöldur
5. Vatnaskarð
6. Vatnakvísl
7. Nýjavatn
8. Ampapollur
9. Snjóölduvatn
10. Snjóalda (964 m)
11. Snjóöldufjallgarður
12. Ónýtavatn
13. Skálafell (826 m)
14. Skálavatn
15. Pytlur
16. Breiðavatn
16a. Breiðaver
17. Kvíslarvatn
18. Eskivatn
19. Langavatn
20. Tjaldvatn
21. Tjarnarkot, Kofi
22. Hádegisalda (666 m)
23. Miðmorgunsalda (694m)
24. Kvíslar
25. Grænavatn
26. Litla Fossvatn } Fossvötn
27. Stóra Fossvatn } Fossvötn
28. Fossvatnahraun
29. Litlisjór
30. Hraunvötn



Map Nr. 9. Main topographical features of the region West of Vatnajökull as drawn by Steinþór Sigurðsson compared with Thoroddsen's map