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TRIASSIC FISHES

FROM

SPITZBERGEN

BY

ERIK A:SON STENSIÖ

UPSALA

PART I

INTRODUCTION

SOME REMARKS ON THE GEOLOGY OF THE TRIASSIC OF
SPITZBERGEN

DESCRIPTIONS OF THE FAMILIES CESTRACIONIDAE, COELA-
CANTHIDAE, PALAEONISCIDAE AND CATOPTERIDAE

WITH 35 PLATES AND 90 FIGURES IN THE TEXT

VIENNA

ADOLF HOLZHAUSEN

1924

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Div. of Invertebrate
Paleontology & Palaeobotany

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PRINTED WITH SUBSIDY FROM LÄNGMANSKA KULTURFONDEN

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INTRODUCTION.

Fish remains from the Trias of Spitzbergen were described for the first time in 1873 by HULKE among the material collected by A. E. NORDENSKIÖLD during the expeditions of 1864 and 1868.

In 1896 a few Triassic fish remains and a Labyrinthodont skull (*Aphaneramma rostratum* A. S. WOODWARD) were found by GREGORY and GARWOOD (WOODWARD 1912, p. 292) in the Sassen Valley, and in 1898 fragments of fishes were discovered by NATHORST in the Trias at Bell Sound (BÖHM 1912, p. 12).

In 1908 WIMAN found a horizon which, owing to the common occurrence of fishes, has been called by him the fish horizon (WIMAN 1910, p. 126; 1914 b, p. 1)¹⁾ and from this horizon a collection was brought to Upsala both that year and the following one, when a small expedition was sent out by WIMAN under the leadership of BERTIL HÖGBOM (WIMAN 1910, p. 124). As this expedition was mainly devoted to the collecting of Saurians the fish material collected was, however, rather limited. The fish material both of 1896 and of the Swedish expeditions in 1908 and 1909 was described by WOODWARD in a paper published in 1912.

During the summers of 1910 and 1911 too B. HÖGBOM had the opportunity to make collections of Triassic vertebrates, though his time was mostly occupied by practical work in the coal fields. From the summer of 1910 there are in addition a few fish remains from the Trias, discovered by Dr. J. OPPENHEIMER and Professor Dr. W. SALOMON during the excursions of the XIth Geological Congress (cf. STOLLEY 1911, p. 115).

The material on which this monograph has been based was, however, mainly brought together by the small expeditions, which on the initiative of Professor WIMAN were sent out from Upsala in the summers of 1912, 1913, 1915, 1916 and 1917 (WIMAN 1914 b, pp. 1—3; 1916 b, pp. 209—210; 1917, p. 229; STENSJÖ 1918 a, pp. 65—66). Furthermore a smaller collection was made in 1918, and finally in 1820 a few specimens were purchased.

In 1917 HOEL and RÖVIG discovered a bone-bed with Triassic fish remains at the north-east corner of Horn Sound; the material from this locality was kindly sent over to me for investigation by Professor KLAER in Kristiania (STENSJÖ, 1918 b, p. 75).

For the acquisition of the material not only of fishes but also of Labyrinthodonts Saurians and plants from the Triassic deposits in Spitzbergen we are in the first place indebted to Professor C. WIMAN at Upsala. He is not only the initiator of all the expeditions that have started from Upsala from the year 1909, but he has to a very great extent made these expeditions possible by his personal experience and by procuring

¹⁾ This horizon in fact coincides, as later investigations show, with the *Posidononyra* horizon.

money for them. He even delivered a special series of lectures on the geology and natural conditions of Spitzbergen and on the equipment of Arctic expeditions so as to prepare the members of the expeditions in the most careful way for their tasks.

I am personally very greatly indebted to Professor WIMAN, in the first place for the great confidence he has shown in me by entrusting to me the leadership of the Spitzbergen expeditions from the year 1912, and for his very obliging action in handing over to me the investigation of the large material of fishes. For all the kindness I have experienced during my work and for all the stimulus that I have received from him I must also tender him my most hearty thanks, but I feel especially grateful to him for his close personal friendship and support during the years I have had the pleasure and privilege of being his pupil.

I am also greatly indebted to the friends and colleagues who accompanied me on the expeditions to Spitzbergen; several of them have not only been members of the expeditions in the ordinary sense but have at the same time helped to defray the expenses connected with the expeditions. The following is a list of their names arranged according to the expeditions in which they took part.

- 1912: Lieutenant Count HUGO B. M. HAMILTON, Fil. Mag. FOLKE SJÖSTRAND, Kand. TOR SJUNNESSON.
 1913: Docent Dr. ERIK ASPLUND, Pharm. Kand. AXEL STENSIÖ.
 1915: Docent Dr. ERIK ASPLUND, Dr. BIRGER SJÖSTRÖM.
 1916: Pharm. Kand. AXEL STENSIÖ.
 1917: Kand. ADAM REUTERSKIÖLD, Fil. Mag. and Theol. Kand. SVEN YDÉN, Fil. Kand. CARL SAMUELSSON.

To Professor A. G. HÖGBOM, who kindly allowed me the use of a room for my work at the Geological Institute and who has always followed my work with interest I wish to offer my most sincere thanks.

I obtained much help and good advice and information with regard to the expeditions from Professor G. DE GEER and Dr. BERTIL HÖGBOM, of Stockholm, whom I should like to thank most sincerely for their kindness.

Through my respected teacher, Professor A. WIRÉN, I obtained from the collections of the Zoological Institute very valuable material of recent ganoids and both for this and for the interest he has otherwise taken in my work it is my very pleasant duty to tender him my very best thanks. A valuable collection of recent fishes for the purpose of comparison was also obtained from Docent S. BOCK, whom I have also to thank for much good advice and many interesting views. In this connection I should like also to thank most respectfully Professor G. HOLM, who in the most obliging manner put the Spitzbergen Collections of the State Museum at my disposal.

During our expeditions I received much kind assistance from Mr. K. BAY, Director of the «Store Norske Spitzbergen Kulkompani», and Mr. J. BAY, manager of the «King's Bay Kulkompani», and it is a great pleasure to offer them my most sincere thanks. I received great support during the expeditions from Swedish quarters as well, in the first place from the Isfjorden-Bellsund Company and later in 1918 from the Aktiebolaget Spetsbergens Svenska Kolfält and I must express my gratitude for this support especially to Director E. KINANDER, Director B. GRANHOLM, and B. JOHNSON, engineer.

I wish finally cordially to thank Dr. E. WIRÉN and Phil. Mag. L. FAXÉN for their good cooperation during the Spitzbergen expedition of 1918. I am also very much obliged to Dr. WIRÉN and my brother Pharm. Kand. A. STENSIÖ for a small collection of Triassic fossils made during the summer of 1920.

During my work on the Triassic fishes it proved to be necessary to undertake a closer study of the primitive fossil fishes in general and for this purpose I made special journeys to the following museums and institutions.

British Museum of Natural History, London (1916); Museo Civico di Storia Naturali, Milan (1916); Alte Akademie, München (1916, 1919); The Geological Institute of Tübingen (1919); The Naturalienkabinett of Stuttgart (1919); The Geological Institute of Heidelberg (1919); The Senckenberg Museum at Frankfurt am Main (1919); Museum für Naturkunde, Berlin (1916, 1919); The Geological Institute of Greifswald (1919). In addition I had the great advantage to study the very fine collection of fishes from Muschelkalk belonging to Redacteur H. KÖNIG of Heidelberg.

During my investigations of these collections I have continually experienced the very great kindness and it is exceedingly pleasant duty for me to acknowledge here my very deepest gratitude. This is especially great in the case of Dr. A. S. WOODWARD, who in the most obliging way made it possible for me to go through the unique collections of the British Museum. I wish to thank him and Dr. F. A. BATHER especially for all the other kindness shown to me by them. It was through them that I had an opportunity to become acquainted with a great deal of English scientific activity and I also had an opportunity of discussing with them many questions outside the region of pure science. Moreover, during my stay in London I had the great privilege of being a guest in Dr. BATHER's family and it is impossible for me adequately to express my gratitude for all the kindness I experienced there. The period I spent with this family remains as one of my brightest and most pleasant memories.

The originals of the text figures in this work — with a few exceptions (figs. 6, 11, 20) for which I have to thank Dr. O. ZDANSKY — were drawn by Miss AINA LAURELL, who also took a great many of the photographs for the plates. For all this troublesome work I wish to thank her most sincerely. I have to thank my friend Kand. A. REUTERSKIÖLD for much valuable help with the typewriting of the manuscript and in proof reading.

The work has been translated by Mr. H. ALEXANDER, Lecturer in English at the University of Uppsala, to whom my best thanks are also due.

SOME REMARKS ON THE GEOLOGY OF THE TRIASSIC OF SPITZBERGEN.

Historical.

In his work «Beiträge zur Geologie der Bären-Insel, Spitzbergen» etc. NATHORST (pp. 350—360) gave a summary of the literature published up to 1910 on the Trias of Spitzbergen and at the same time communicated his own important observations. During 1910 and after this year papers dealing with the Triassic formations of Spitzbergen were published by DE GEER (1910), WITTENBURG (1910, 1912), STOLLEY (1911), BÖHM (1912), WIMAN (1914a, 1914b, 1916a, 1916b, 1917, 1920), DIENER (1916) and myself (1918b).

Scarcely any detailed attempts to draw parallels between the Triassic of Spitzbergen and that known in other regions were made before 1886, when MOJSISOVICS published his large work «Arktische Triasfaunen», in which the ammonites especially are dealt with. MOJSISOVICS then came to the conclusion that the series of Spitzbergen Triassic strata that consisted of black shales was equivalent to the Muschelkalk. He also included in this series the horizon with *Posidonomya*, but felt a little uncertain whether this horizon could be older. He confused the evertbrate-bearing horizons situated in the sandstone series above the shaly series, partly because of the incorrect determination of *Halobia* cf. *neumayeri* as *H. zitelli* by LINDSTRÖM¹⁾ and partly because of the incompleteness of NATHORST's information as to the localities of the finds. He first takes these upper horizons to be of Karnic age (cf. BÖHM, 1903, p. 73) and later on (1886, p. 152) of Noric.

With BÖHM's work, published in 1903, on the Triassic fauna of Beeren Eiland a fixed starting-point was also obtained for a more exact parallelization of certain of the strata in the Triassic of Spitzbergen. For it appeared that in the *Myophoria* strata of Beeren Eiland there occurred, inter alia, the forms known from the upper Triassic series of Spitzbergen, *Lingula polaris* LUNDGREN, *Pecten Öbergi* LUNDGREN and *Lima spitzbergensis* LUNDGREN. The upper Triassic series of Spitzbergen ought thus, at least to some extent, to correspond to the *Myophoria* strata of Beeren Eiland and, like them to be of karnic age. Later on WITTENBURG (1910) was able to show in material collected from East Spitzbergen that the number of common forms in the upper Trias of Spitzbergen and Beeren Eiland is rather considerable.

¹⁾ Cf. BÖHM, 1903, p. 73.
Stensid, Triassic Fishes from Spitzbergen.

In 1904 and 1907 SMITH took the *Daonella* and *Posidonomya* beds of Spitzbergen to be homotaxous with the middle and lower Muschelkalk respectively.

In 1905 (p. 221) NOETLING gave the following scheme for the horizons then known from the Ice Fjord:

Upper Trias	{	Noric stage . . Limestone with <i>Halobia</i> cf. <i>neumayeri</i> , <i>Spiriferina lundgreni</i> and <i>Pseudomonotis spitzbergensis</i> .
	{	Karnic stage . . Limestone with <i>Lingula polaris</i> and <i>Lima spitzbergensis</i> .
	{	Ladinic stage . Limestone with <i>Halobia Zitelli</i> .
Middle Trias	{	Limestone with <i>Daonella</i> (<i>D. lindströmi</i>).
	{	Limestone with <i>Posidonomya</i> .

In 1910 (p. 126) WIMAN published the following section measured in the Ice Fjord district by B. HÖGBOM. The lowest horizon in this section is denoted by o. The other figures indicate the height of the different horizons above this horizon.

Probably Jurassic.

Triassic.

Mainly yellow sandstones.

Bed of sandstone.	504 m
Rhaetic? fauna of Bivalves	about 450 »
Bed of sandstone.	345 »

Mainly black shales.

Diabase	315 »
Ironstone.	300 »
Daonella shales proper, with <i>D. lindströmi</i> (Upper saurian horizon)	220 »
Horizon with «aufgeklappter» <i>Daonella</i>	210 »
Fauna of Bivalves	205 »
Lower saurian horizon	184 »
Fish horizon (<i>Posidonomya</i> shales)	170 »
	157 »
	93 »
	o »

The names upper and lower Saurian horizon and fish horizon are chosen by WIMAN because of the abundant occurrence of Saurians and fishes respectively. With regard to the lower Saurian horizon WIMAN says that even if stratigraphically it should belong to the *Posidonomya* shale and thus be homotaxous with the lower Muschelkalk, yet it cannot belong to the older part of this. WIMAN points out in the *Posidonomya* shale the occurrence of a flat «*Ceratites*»-like ammonite, which, as we shall see, is of considerable interest from a stratigraphical point of view.

NATHORST in his account of 1910 (pp. 350—360) follows MOJSISOVICS with regard to the age of the different horizons. He considers, however, that he has found that a

plant-bearing horizon, discovered in 1909 in the upper series above the black shales, was of Rhaetic age. In addition he points out the incorrectness of Mojsisovics's statement that the fossils from series of black shales as a rule are derived from limestone, and finally he also quotes the preliminary results at which BÖHM had arrived in his investigations of the evertbrate material from Bell Sound. BÖHM had then distinguished:

Upper Trias: with *Pseudomonotis spitzbergensis* BÖHM, *Aviculopecten wimani* BÖHM, *Avicula* cfr. *sola* ÖBERG, *Pseudomonotis ochotica* KAYS.

Middle Trias: » *Halobia de geeri* BÖHM, *Lingula lindströmi* BÖHM, *Monotis albertii* GOLDF. sp. var.

Lower Trias: » *Meekoceras (Gyronites) nathorsti* BÖHM, *Posidonomya* sp. and *Lingula* sp.

In 1911 STOLLEY, who the previous year had had the opportunity of taking part in the excursion of the Eleventh International Geological Congress to Spitzbergen, published an important paper on the Trias strata at Middelhook in the Ice Fjord. He came to the conclusion that the fauna described from the *Posidonomya* shale was not a unit, but that it came from two different horizons. Thus, according to his observations, *Ceratites costatus* ÖBERG belongs to a horizon above the *Posidonomya* shale, and in his opinion the same is true of *C. vega* ÖBERG and *C. lindströmi* MOJSISOVICS. The *Posidonomya* shale proper is characterized, he says, especially by the smooth *Arctoceras* species, *Meekoceras (Gyronites) aplanatum*¹⁾ WHITE and a form resembling *Prionolobus waageni* HYATT et SMITH, i. e. species that support the view that in this case we are most probably concerned with deposits of lower Triassic age.

In connection with this he emphasizes the view that the *Posidonomya* bed did not represent the bottom of the Triassic deposits in the Ice Fjord district, but added, however, that no details could be established with regard to the boundary between the Permian and the Triassic. He also mentions that Prof. W. SALOMON found in the upper part of the «Permian» a bone-bed, which, as we shall see below, is of no little interest from a stratigraphical point of view.

In a horizon situated somewhat above the *Daonella* beds he was able to ascertain the occurrence of some *Nathorstites* species, including, among others, probably *N. lenticularis* BÖHM. This, he holds, makes it possible to conclude (p. 120) «daß das Nathorstiten-Niveau am Middlehook Spitzbergens dem Schieferniveau mit *N. lenticularis* J. BÖHM am Urdberg der Bäreninsel entspricht und daß der fossilreiche sandige Myophorien-Horizont nur den oberen, auch am Kap Thordsen vorwiegend sandigen, aber fossilärmeren Schichten, mit denen er *Lingula polaris*, *Lima spitzbergensis* und *Pecten Oebergi* gemeinsam hat, zu parallelisieren ist.» And at another place (pp. 117—118) he adds: «Die Vermutung NATHORST'S, daß die untersten 140 m dunkler fossilleerer Schiefer am Urdberg usw. der Bäreninsel ihren Platz zwischen den Daonellen-Schichten und dem *Lingula*-Sandstein Spitzbergens haben möchten, kann also nicht zutreffen; vielmehr müssen erstere den tieferen Triassschichten vom Kap Thordsen entsprechen und können nicht obertriadischen, sondern nur mittel-

¹⁾ This is apparently the flat «*Ceratites*» form mentioned by WIMAN (1910, p. 127).

triadischen und vielleicht z. T. auch noch untertriadischen Alters sein. Es scheint mir noch keineswegs wahrscheinlich, daß der Bäreninsel die untere Trias völlig fehlen sollte; mindestens müssen aber Äquivalente der Mitteltrias in dem unteren mächtigen Schichtenkomplex enthalten sein. Auch kann ich in dem Komplex des Myophorien-Sandsteins und des 44 m fossilführenden Schiefers unter ihm, deren Fossilfauna von J. BÖHM beschrieben worden ist, keinen faunistisch und stratigraphisch einheitlichen Horizont sehen, sondern halte ihn für das Äquivalent aller oberen Horizonte der Spitzbergener Trias.»

STOLLEY's views on the whole with regard to the different divisions of the Triassic of Ice Fjord can be summarized as follows:

Upper Trias	{ Carnic stage . . Horizon with <i>Lingula polaris</i> etc. » » <i>Nathorstites</i> etc.
Middle Trias	{ Ladinic stage . <i>Daonella</i> beds. Fauna of Bivalves. Lower saurian horizon. Horizon with <i>Ceratites costatus</i> and possibly also <i>C. vega</i> and <i>C. lindströmi</i> .
Lower Trias	{ <i>Posidonomya</i> horizon characterized especially by <i>Gyronites aplanatum</i> and weakly sculptured <i>Ceratites</i> species.

In 1912 appeared a paper by WITTENBURG in which «Werfener Schichten» were shown to exist on the Axel Island. The same year BÖHM also published his investigations on the Triassic evertbrates from Bell Sound; his paper does not, however, contain anything new of importance beyond his preliminary communication to NATHORST in 1910.

In 1914 WIMAN (1914 a, pp. 17—22), in connection with the description of the Carboniferous Brachiopods of Spitzbergens, dealt with the series of strata up till then taken to be Permian. After a detailed examination of the fauna in this series of strata he comes to the conclusion that the question of the age must still in the main be considered an open one. He considers, however, that we most probably ought to look upon a part of the series of strata above the *Hustedia* limestone as lower Triassic. In a paper on the Stegocephalians from the Triassic of Spitzbergen published the same year WIMAN gives (1914 b, pp. 3—9) a number of newer stratigraphical observations and makes important contributions to our knowledge of the fish horizon (*Posidonomya* bed) and he also mentions a new vertebrate-bearing horizon in the uppermost Triassic at Mt Lundbohm. Two year later (1916 b) WIMAN still continues to uphold his view of 1910 as to the upper and middle Triassic. With regard to the lower Triassic he holds the same view as in 1914. In 1917 WIMAN published some fresh additional stratigraphical observations.

In 1916 DIENER in a rather long treatise dealt, among other things, with the Trias of Spitzbergen. He criticises (pp. 413—414) the view put forward by STOLLEY as to the age of the *Daonella* beds and follows MOJSISOVICS with regard to them. On the other hand he adopts STOLLEY's view as to *Posidonomya* strata. His views as to the conditions of age of the different strata may as a whole be summarized in the following table:

- Rhaetic stage Horizon with plant fossils.
- Noric » Horizon with *Pseudomonotis spitzbergensis*, *Halobia* cf. *neumayeri*, *Spiriferina lundgreni* etc.
- Karnic » Horizon with *Lingula polaris*, *Halobia zitteli* etc., *Nathorstites* etc.
- Anisic » *Daonella* beds.
 (Muschelkalk) Fauna of Bivalves.
 Lower Saurian horizon.
 Horizon with *Arctoceras costatum*.
- Skytic stage *Posidonomya* beds.

I have myself mentioned (STENSJÖ, 1918b, p. 75) the occurrence of Triassic fishes in the bone-bed found by SALOMON in 1910 (STOLLEY 1911, p. 115), which, as has already been pointed out, was formerly considered to belong to the Permian. WIMAN's assumption that at least certain of the strata between the *Hustedia* limestone and the fish horizon in the Ice Fjord region belonged to the Triassic has thus been shown to be correct. With regard to the fish fauna in the fish horizon I pointed out on the same occasion that on the whole its composition was of such a nature as rather to suggest lower Triassic age.

When in 1910 NATHORST published his «Beiträge zur Geologie der Bären-Insel, Spitzbergens» etc. Triassic strata were known in the following regions in Spitzbergen.

A) *Ice Fjord region*, comprising the south side and the inner end of Sassen Valley and the south side of Sassen Bay, the south part of Dickson Land, the field west of Ekman Bay between Cape Svea and Sefströms glacier, a sweep of raised strata on the west side of the Ice Fjord extending down towards Bell Sound.¹⁾

B) *Bell Sound region*. A sweep of raised strata on the north side of Van Mijens Bay, on the Mitterhuk and the south side of Van Keulen Bay at Reindeer Point and Cape Ahlstrand.

C) *Stor Fjord region* comprising Stans Foreland (Edge Island), Barents Lands, the stretch of coast on the north side of the inner end of the Stor Fjord and on the peninsula between this end and the south part of the Hinlopen Strait.

D) *North East Land region* comprising a part of the south-east corner of North East Land at the southern end of Hinlopen Strait.

On the basis of material collected by HOEL and RÖVIG during the Norwegian expedition to Spitzbergen in 1917 I recorded in 1918 (STENSJÖ, 1918b, pp. 75—77) the occurrence of Triassic strata in the north-eastern corner of Horn Sound, and in this cases it seems evident that we have here a continuation of the Trias sweep at Bell Sound.

Finally with regard to the relation between the Triassic series of Spitzbergen and other occurrences of Triassic I shall only give a very brief account. As we know, MOJSISOVICS (1886, pp. 147—153) grouped the Trias formations of Spitzbergen together

¹⁾ The geological map published by G. DE GEER in 1910 is important for our knowledge of details concerning this region.

with those at Olenek and Verchojansk and the circumpacific ones, into a great Arctic-Pacific faunistic province. Later on (p. 154) when he enters on the question of the relations between this province and the one he calls the Mediterranean he makes the following statements:

«In den norischen Ablagerungen der mediterranen Triasprovinz finden sich nur einige wenige arktische Typen (aus der Gruppe der *Dinarites spiniplicati*) und von arktischen Typen derivierte Gattungen (ein Teil der Arpaditen). Auch konnten wir umgekehrt konstatieren, daß einige mediterrane Gattungen zur norischen Zeit in die pazifischen Gewässer eingedrungen waren. Es haben also jedenfalls zeitweise Verbindungen zwischen den beiden Territorien bestanden, welche Wanderungen der pelagischen Tiere gestatteten. Es ist aber bezeichnend für den Zeitpunkt des Bestandes dieser Verbindungen, daß nur Gattungen und Typen der unteren Abteilungen (der Olenekschichten und des unteren Muschelkalks) die Verbindung der mediterranen und der arktisch-pazifischen Trias anzeigen.»

In 1904 SMITH (pp. 331—333, 365—367) came to the conclusion that the Triassic strata in Idaho, California and British Columbia did not belong to the Arctic-Pacific Triassic province as Mojsisovics had maintained, and he is also doubtful whether this province otherwise formed a faunistic unit. He groups the Triassic strata in Idaho, California and British Columbia into a province by themselves and with regard to this he states that its fauna showed an admixture both of Mediterranean-Oriental and Arctic elements. According to his opinion there existed communications in lower and middle Triassic between the region he calls Oriental on the one hand and the Arctic-Pacific on the other.

NOETLING (1905, pp. 206—208) lays great stress on the faunistic differences between the Triassic series of Spitzbergen and those of North Siberia and comes to the conclusion that they must belong to different faunistic provinces, a view that was contested later on by DIENER (1916).

WIMANS description of the Triassic Ichthyosaurians of Spitzbergen in 1910 clearly showed that the Saurians are also of considerable interest from a faunistic and stratigraphical point of view and as early as 1911 MERRIAM published a paper on this subject, in which he arrives at the following conclusion (p. 327): «On the whole, such evidence as is available suggests that the saurian fauna of the Spitzbergen Triassic is not far removed in time from the *Cymbospondylus* fauna of the Middle Triassic of Nevada, and that it is also near the age of the *Mioxosaurus* fauna of the Besano Beds of Italy. It may also be assumed that at the period in which these faunas flourished there was free communication between the sea areas of the Spitzbergen, Nevada, and north Italian regions.»

In 1916 the same subject was dealt with in detail by WIMAN (1916 a, pp. 71—72) who also points out the difference between the Saurian fauna in the Triassic of Spitzbergen and that known in other Triassic regions. In the chapter below on the composition and the stratigraphical distribution of the vertebrate fauna I shall have a further opportunity to discuss the views put forward by MERRIAM and WIMAN with regard to the vertebrate fauna.

Finally in 1916 DIENER (1916, pp. 412—424) grouped the circumpolar Triassic formations — including those in Alaska and British Columbia — into a «Boreales Reich», and he says that the fauna in this indicates the existence of a communication of the

Arctic ocean with that of the Pacific region over Bering Strait and the east of Asia. He is of the opinion that this communication was developed already in the Skytic time.

While during the Anisic time this would have been the only communication even for a region situated as far to the west as Spitzbergen, with regard to the Skytic time, on the other hand, he comes to the conclusion that, to judge from the conditions in Spitzbergen, at least a second one was then in existence, namely with the ocean of the Mediterranean region. He writes as follows about this (pp. 514—515): «Die Entwicklung der Untertrias auf der Axelinsel (Spitzbergen) stimmt vollständig überein mit der Werfener Entwicklung im Mediterrangebiet, die ihren östlichsten Vorposten bis in das Quellgebiet des Jenissei am Zusammenfluß der Teplaja und des Uss aussendet. Es ist nicht ausgeschlossen, daß jenes Meer, das während eines so langen Zeitraumes der Anthrakolithischen Periode das zentrale Gürtelmeer Eurasiens über Nowaja Semlja mit dem Arktischen Meere verband, selbst während der skythischen Epoche noch nicht vollständig trocken gelegt war. Ein schmaler Meeresarm am Ostabhang des Urals mag, ähnlich wie im Oberjura, an der Perm- und Triasperiode den Angarakontinent von Fenoskandia zeitweilig getrennt haben. Zur Zeit der anisischen Stufe war eine solche Meeresverbindung zwischen Russisch-Turkestan, beziehungsweise dem Gouvernement Jenisseisk, und dem Polarmeer durch die Obi-Niederung, wofern sie während der skythischen Epoche überhaupt bestanden haben sollte, jedenfalls erloschen.»

During the Skytic time he does not consider it impossible either that there was a second communication between the ocean of the Arctic and Mediterranean regions much farther to the west (p. 535). «Ein solcher Zusammenhang würde», he says, «die mit der alpinen so außerordentlich nahe übereinstimmende Entwicklung der Werfener Schichten auf der Axel-Insel (Spitzbergen) erklären». He considers, however, that this communication ceased during the Anisic time.

Stratigraphical observations made by the author.

My own work on the Triassic formation was devoted chiefly to collecting vertebrates from the fish horizon, and it was therefore on the whole only more or less in exceptional cases that I had opportunities for stratigraphical studies. Consequently the account given below makes no claim at all to completeness.

General remarks. — All the Triassic localities investigated by me belong to the Ice Fjord district and are as follows: The tract of land on the west side of Ekman Bay between Cape Svea and Sefström's Glacier, Dickson Land, the south coast of the Sassen Bay, and the land surrounding the Sassen Valley. The position of these places is shown by the sketch map in fig. a, which also contains the names of the most important localities of the finds. These are as follows, enumerated from west to east:

Mt Bertil, Mt Lundbohm, Cape Svea (the cuttings of the streamlets on the tundra) Mt Congress, Mt Tschermak, Mt Sture, Mt Saurie, Mt Rotunda (with student Valley), Corrie Down (the mountain between De Geer Valley and Flower Valley)¹, Mt Marmier,

¹) The name of this mountain was introduced into the literature already by CONWAY in 1897 but, curiously enough, it has not been accepted by DE GEER, who leaves the mountain unnamed both on the map of 1910 and that of 1912. In many other cases too DE GEER has omitted several names introduced by CONWAY.

Fig. a. — Sketch map showing the extension of the Trisatic strata in the inner parts of the Ice Fiord, according to my own and earlier observations on the basis of G. de Gein's maps of 1910 and 1912 and Wimmer's map of 1914 (1914, b).

Mt Viking (Mt Hamilton WIMAN 1914)¹⁾, Mt Sticky Keep, Mt Trident, Mt Milne Edwards, Mt Andersson (WIMAN 1914 b)²⁾, Mt Wallenberg.

The Trias strata are on the whole all undisturbed in the localities mentioned above. Important disturbances have occurred only west of Mt Bertil and Mt Lundbohm, where the strata are a little affected by folding, in Flower Valley, where a large fault has taken place in the direction from north to south, and finally east of Mt Andersson on the north side of Rabot's Glacier, where a rather large fault from north to south can also be observed.³⁾ The fault in Flower Valley has a certain interest as it presumably forms the direct continuation southward of the one that has affected the southwest corner of Bünsow Land and the west coast of Billen Bay (STENSIÖ 1918 a, pp. 79—80; cf. also the map text fig. a in the present work). A number of smaller faults are found at the north-east corner of Mt Bertil and Mt Milne Edwards.

West of Ekman Bay the complex of strata has on the whole a slight dip towards the south-west. At Dickson Land this dip is practically in the same direction, but is still weaker, and this is also the case along the south side of Sassen Bay until one arrives at the fault line in the Flower Valley. On the eastern side of this line the dip has on the whole a southerly direction with a certain tendency to the south-east as far as about to the valley between Mt Trident and Mt Milne Edwards, where it turns and becomes slightly south-westerly once more.

The lower Triassic series. — As I have already pointed out in 1918 (1918 b, pp. 75—76), a part of the sandstones below the black shales must now also be ascribed to the Triassic. This lowest Triassic series is, however, little exposed and is therefore still only slightly known. So far I have found in most accessible in Dickson Land.

On the steep shore there about half-way between Mt Congress and Mt Tschermak about 1 m above sea-level I found a calciferous stratum of sandstone with *Discina spitzbergensis*, a *Lingula* and a number of other poorly preserved evertbrate fossils, which seems to show that we have here a horizon equivalent to the *Hustedia* limestone and *Pseudomonotis* shales (cf. NATHORST 1910, p. 349). Immediately above this horizon there follows another consisting of shaly sandstone with remains, probably of Palaeoniscid fishes. There then follows higher up still more shaly sandstone with beds of harder light sandstones, sometimes with ripple marks. Concretions occur in certain of the lower strata but do not seem to contain fossils. Bright coloured loose sandstones are found highest up towards the fish horizon and the transition between them and the rock of the fish horizon takes place gradually, the sandstones becoming darker (bituminous) and more shaly upwards and beginning to contain concretions. Farthest downwards the concretions have no fossils, but ammonites and especially *Posidonomya* soon begin to appear in them in great quantities. The rocks which form the main part of the fish horizon and in which the concretions are embedded consist as a rule of rather sandy shales more closely resembling the underlying series of sandstone than the real black Triassic shales, from

¹⁾ Called Mt Viking already in 1911 by DUBOIS and the name Mt Hamilton proposed by WIMAN 1914, (1914 b, p. 4), is therefore not to be used.

²⁾ The name Mt Andersson also seems inapplicable, as there seems to be a mountain with this name on the east coast of Spitzbergen (cf. WITTENBURG 1910, p. 33), although I have been unable to find it on any map.

³⁾ This fault is probably the same as that discovered by the «Vorexpedition» to Spitzbergen of W. FILCHNER in 1910 (PHILIP, 1914, pp. 15—17).

which they are in the field bounded in a strikingly sharp manner. The vertical height from the *Hustedia* limestone to the upper boundary of the fish horizon at the locality in question is, according to barometric measurements, about 90 m. It was not possible to find any bone-bed corresponding to the one discovered by SALOMON in 1910 (STOLLEY 1911) not far from this place. The fish horizon, which seems to coincide with the *Posidonomya* shales, probably has an approximate thickness of about 15 m or more.

The series of strata between the *Hustedia* limestone and the fish horizon seems to show a development that is similar on the whole in all the Ice Fjord region to that just described in Dickson Land. Detached blocks from a bone-bed with Triassic fishes were found by Dr. E. WIRÉN and Pharm. Cand. A. STENSJÖ during the summer of 1920 on the

east side of Mt Bertil and the character of the blocks shows that the bone-bed must have been situated somewhat beneath the fish horizon in the bright sandstones.

The fish horizon is very well characterized by its abundant fauna of both evertebrates and vertebrates. It seems to be thickest and most rich in fossils in the mountains of the Sassen Valley district. It is thinnest and least rich in fossils at Mt Bertil. It also contains very sparsely with fossils

Text fig. b. Part of Mt Bertil from Ekman Bay. Photo A. STENSJÖ, 1920.

Upper Carboniferous in the steep shore. Then a slope, covered with vegetation and consisting of Permo-Carboniferous strata, after which comes the so-called Permian and the lower Triassic (the lightest part forming the base of the real mountain-cliff). The lowest line denotes the upper boundary of the fish horizon. The other two the approximate position of the lower and upper Saurian horizon respectively. N. B. shaly bed above the fish horizon.

and is probably rather unimportant at Mt Högskolan and the most northerly parts of the field at Dickson Land. It is on the whole rather sandy, as on the west side of Dickson Land, but in spots, as on the south side of Sassen Bay, it may have a more purely shaly character. Sometimes, as on the east side of Mt Marmier, a couple of rather thin bone-beds are found in it.

Its upper boundary is everywhere sharply marked by a black shaly cliff, which is also very well seen in the topography (see text figs. b, c, in which the upper boundary of the fish horizon is marked).

Like the underlying sandstones the fish horizon is seldom exposed or accessible in a firm cleft. It is therefore only possible as a rule to collect loose weathered concretions, split off by frost and mostly scattered about after sliding down the rather steep slopes. The finds are consequently almost always fragmentary. The appearance

under normal conditions of the fish horizon itself is shown in text fig. c, where we can see fragments of shale, limestone and concretions on the slope.

The occurrence and state of preservation of the fossils from this horizon were described by WIDAN in 1914 (1914 b, pp. 8—10).

With regard to the evertbrate fauna of the same horizon I have little to say, as the material of evertbrates brought home during the last few years has not been investigated. It is noteworthy, however, that *Gyronites aplanatum* WHITE is very common. For the vertebrate fauna I may refer to my account in the next chapter.

Middle Triassic series. — In this work I have like STOLLEY provisionally reckoned the middle Triassic series from the upper boundary of the fish horizon, a view which,

Text fig. c. Part of Mt Trident with Sticky Keep in the background. In the nearest foreground is the fish horizon, bounded above by the shaly cliff. In the portions of the mountain farther back the upper boundary of the fish horizon and the lower and upper Saurian horizons is marked.

as we shall see, is supported also to some extent by the vertebrates. In order to decide with full certainty whether the boundary is to be drawn in this way we need, however, a more detailed knowledge of the evertbrate fauna than we have at present.

In the middle Triassic series the rocks consist mainly of black or more or less bituminous shales that often easily split into thin laminae. Here and there limestone beds appear in the shales and these may contain phosphorite, especially up towards the upper Saurian horizon. Below the lower Saurian horizon there also appear in certain strata numerous large and rather flat concretions, often situated so close together that they form real banks (Mt Congress, Mt Tschermak, Mt Bertil), some of which are often rich in fossils. The fossils are chiefly Ichthyosaurians, which are always, however, in a bad condition because of frost weathering, so that scarcely anything but the vertebrae

can be identified. Two of these horizons seem to be especially rich in fossils — one situated 61 m, the other 82 m above the fish horizons at Mt Viking.

Of the real bone-beds known in the middle Triassic series one that is apparently of a rather local nature is found at Mt Viking and Mt Marmier at a height of about 33 m above the fish horizon,¹⁾ while another, which coincides approximately with the lower boundary of the Saurian horizon, has been found with certainty from Sticky Keep in the east to De Geer Valley in the west. Both these bone-beds are situated in a thin stratum of sandstone.

The lower Saurian horizon seems to have been rich in fossils only at Dickson Land. At Mt Bertil, Mt Lundbohm, Mt Viking, Sticky Keep and Mt Andersson I have not found any vertebrates in the corresponding level.

A short distance, about 18—20 m beneath the upper Saurian horizon there follows, at least at Mt Congress and Mt Bertil, a stratum with «aufgeklappter» *Daonella*.

The proper upper Saurian level consists of calciferous shales and beds of limestone. At the top is found a bed with very large concretions, not infrequently containing Ichthyosaurians. The Ichthyosaurians occur most abundantly, however, in the calciferous shales. *Daonella* and ammonites are, on the other hand, most frequent in the strata of limestone and in the concretions. Only in more exceptional cases are they found in shale. The horizon seems to be thickest in the mountains of the Sassen Valley, where in Mt Viking, for instance, it is about 14 m, while at Dickson Land and at Cape Svea it is not 10 m.

Upper Triassic series. — I had no opportunity of studying in any detail the boundary between the upper and middle Triassic series.

Above the upper Saurian level we soon get very soft shales with nodules of ironstone and these shales form an important part of the lower half of the upper series. They alternate, however, with beds of sandstone, which become predominant towards the top. In the very uppermost part at Mt Bertil and Mt Lundbohm I found a bed of green very soft shale.

The vertebrates collected in the upper Triassic have not yet been investigated thoroughly and little can therefore be said as to the horizons in which they appear. They seem however, as NATHORST has stated to be mainly restricted to two horizons.

The plant horizon already noticed by NATHORST is, as WIMAN 1914 (1914b, p. 8) mentioned, discovered at Mt Bertil, Mt Tschermak and Sticky Keep. In 1916 Dr. E. LUNDSTRÖM found a plant-bearing horizon in the upper Triassic at Mt Trident as well, but it is uncertain whether this is the same horizon as the earlier known one.

As the south end of Mt Tschermak, the only locality where I have been able to measure it in profile, the plant horizon is situated at a height of about 134 m above the upper Saurian level between the horizon with *Lima spitsbergensis*, *Pecten Öbergi*, etc. and the horizon with *Spiriferina lundgreni*, etc.

Some centimetres above the plant horizon²⁾ we find a thin band of coal and otherwise the conditions are as follows:

¹⁾ cf. foot-note on p. XXI.

²⁾ The plant fossils have been sent to the Palaeobotanical department of the Royal State Museum at Stockholm for investigation but have not yet been described.

Sandstone	
Soft sandstone	11 cm
Yellow clay	2 »
Coal	5 »
Yellow clay	2 »
Grayish clay	15 »
Horizon with plants (in sandstone)	25 »
Sandstone	

In the uppermost part of the upper Triassic series two bone-beds are known, one of which is found at Mt Bertil and Mt Lundbohm at a height of 350 m above the fish horizon, the other only at Mt Bertil about 263 m above the fish horizon. The former of them was mentioned by WIMAN in 1914 in connection with his description of the Stegocephalians (1914 b, p. 8)

Profiles. — I publish here some of the profiles that have been measured during the expeditions of recent years, but must preface them with the remark that the statements as to the thicknesses cannot lay claim to any very great degree of accuracy, as all the measurements are made with ordinary aneroid barometers.

Mt Viking.

Upper Triassic	Sandstone and shaly sandstone with ironstone . .	66 m
Middle Triassic	Upper Saurian horizon	14 »
	Black shale	151 »
	Sandstone with bone-bed	0'03 »
	Black shale	48 »
	Sandstone with bone-bed	0'02 » ¹⁾
Lower Triassic	Black shale	33 »
	Fish horizon (<i>Posidonomya</i> bed)	15 ? »
	Soft sandstone	?

Corrie Down.

Upper Triassic	Bed with <i>Pecten Öbergi</i> , etc.	?
	Sandstone and shales with ironstone	100 »
Middle Triassic	Upper Saurian horizon	14 »
	Black shale with phosphorite and a fauna of Bivalves	63 »
	Black shale	50 »
	Bone-bed in sandy shale	0'02 »
	Black shale	50 »
Lower Triassic	Fish horizon (<i>Posidonomya</i> bed)	15 ? »
		?

¹⁾ By a mistake on my part this bone bed has been given by WIMAN, 1918 (p. 81) as being situated merely 18 m above the fish horizon.

Mt Tschermak.

	Diabase	?	
	Sandstone	23	m
	Bed of calcareous sandstone with Brachiopods (probably the horizon with <i>Spiriferina lundgreni</i> etc.	11	"
	Horizon with plants	0'25	"
	Bed of sandstone, partly calcareous and containing <i>Pecten Öbergi</i> , <i>Lima spitzbergensis</i> , etc.	18	"
Upper Triassic	Argillaceous sandstone with interstratified beds of harder sandstone and sometimes shales with ironstone	33	"
	Shales with ironstone passing into argillaceous sandstone at the top	66	"
Middle Triassic	Upper Saurian horizon	?	

Mt Congress.

	Upper Saurian horizon	6	"
	Black shales with beds of black limestone and thin strata of phosphorite	145	"
	Lower Saurian horizon	5 ?	"
	Black shales with thin beds and nodules of limestone	66	"
	Fish horizon (<i>Posidonomya</i> bed)	15	"
Lower Triassic	Soft sandstone and somewhat shaly sandstone, sometimes with ripple marks	75	"
?Permian	<i>Hustedtia</i> and <i>Pseudomonotis</i> bed	?	

Mt Bertil.

	Sandstone	17	"
	Green very soft shale and sandstone with bone-bed	3 ?	"
	Mainly sandstones	79	"
	Sandstone with <i>Lingula polaris</i> and bone-bed.	0'03	"
	Sandstone interstratified with shales containing ironstone nodules	83	"
	Upper Saurian horizon	5 ?	"
	Black shales with beds of black limestone and thin strata of phosphorite	11	"
	Stratum with «aufgeklappter» <i>Daonella</i>	1 ?	"
	Black shales	113	"
	Lower Saurian horizon	?	
	Black shales with thin beds and nodules of limestone	50	"
	Fish horizon (<i>Posidonomya</i> bed)	?	
Lower Triassic	Soft sandstone and somewhat shaly sandstone	?	

Composition, stratigraphical distribution and relations of the vertebrate fauna.

Altogether, including the fishes, no less than 60 species of vertebrates are now known from the Triassic of Spitzbergen. The species are as follows:

Reptiles.

	<i>Phalarodon nordenskiöldii</i> (HULKE)
	<i>Pessosaurus polaris</i> (HULKE)
	<i>Pessopteryx nisseri</i> WIMAN
<i>Ichthyosauria</i> ¹⁾ 2) . . .	» <i>arctica</i> WIMAN
	» <i>pinguis</i> WIMAN
	» <i>minor</i> WIMAN
	<i>Ichthyosaurus</i> sp.
<i>Sauropterygia</i> ³⁾ . . .	A vertebra of a Plesiosaurian.
<i>Parasuchia</i> ⁴⁾	A <i>Belodon</i> -like vertebra.
<i>Incertae sedis</i> ⁵⁾ . . .	<i>Omphalosaurus</i> .

Amphibia.

	<i>Lyrocephalus euri</i> WIMAN
	<i>Lonchorhynchus öbergi</i> WIMAN
	» sp.
	<i>Aphaneramma rostratum</i> A. S. WOODWARD
	<i>Platystega depressa</i> WIMAN
<i>Stereospondyli</i> ⁶⁾ . . .	<i>Tertrema acuta</i> WIMAN
	<i>Capitosaurus polaris</i> WIMAN
	<i>Cyclotosaurus?</i> <i>spitzbergensis</i> WIMAN
	<i>Peltostega erici</i> WIMAN
	A number of remains of indeterminate species.

Pisces.

	Family Cestracionidae.
{	<i>Hybodus rapax</i> n. sp.
	» <i>sasseniensis</i> n. sp.
	» <i>microdus</i> n. sp.

¹⁾ WIMAN, 1910; 1916 b; 1920, p. 12.

²⁾ HUENE, 1916, *Pachygnosaurus*, p. 39, fig. 70; BROILL, 1916, p. 494.

³⁾ WIMAN, 1916, *Bull. Geol. Inst. Upsala*, Vol. XIII, 2, pp. 223—226.

⁴⁾ WIMAN, 1918.

⁵⁾ MERRIAM, 1911; MERRIAM and BRYANT, 1911; WIMAN, 1916 a.

⁶⁾ WIMAN, 1914 a; 1916 b; 1917; MOODIE, 1915, *Journ. of comp. neurol.* vol. 25, pp. 319—322; HUENE, 1920.

	<i>Acrodus spitzbergensis</i> (HULKE)
	» <i>vermiformis</i> n. sp.
<i>Elasmobranchii</i>	» <i>scaber</i> n. sp.
	» <i>oppenheimeri</i> n. sp.
	<i>Polyacrodus pyramidalis</i> n. sp.
	» <i>angulatus</i> n. sp.
	<i>Palaeobates polaris</i> n. sp.
	» sp.
	Various Selachian species undefinable in detail.
<i>Dipnoi</i>	<i>Ceratodus</i> sp.

Fam. **Coelacanthidae.**

	<i>Winania sinuosa</i> n. sp.
	» ? sp.
	» ? <i>multistriata</i> n. sp.
	<i>Sassenia tuberculata</i> n. sp.
	» ? <i>guttata</i> (A. S. WOODWARD)
<i>Crossopterygii</i>	<i>Axelia robusta</i> n. sp.
	» <i>elegans</i> n. sp.
	<i>Myliacanthus lobatus</i> n. sp.
	» <i>spinosus</i> n. sp.
	<i>Scleracanthus asper</i> n. sp.
	Certain undefinable fragments probably referable to new species.

Fam. **Palaeoniscidae.**

	<i>Birgeria mougeoti</i> (AGASSIZ)
	» sp.
	<i>Glaucolepis gyrolepidoides</i> n. sp.
	<i>Pygopterus de geeri</i> n. sp.
	<i>Boreosomus arcticus</i> (A. S. WOODWARD)
	» <i>reuterskiöldi</i> n. sp.
	» sp.
	» ? <i>scaber</i> n. sp.
	<i>Acrorhabdus bertili</i> n. sp.
	» <i>asplundi</i> n. sp.
<i>Actinopterygii</i>	» <i>latistriatus</i> n. sp.

Fam. **Platysomidae.**

<i>Platysomus nathorsti</i> n. sp.
« sp.

Fam. **Catopteridae.**

<i>Perleidus woodwardi</i> nomen nov.

Fam. **Saurichthyidae.***Saurichthys ornatus* n. sp.« *wimani* (A. S. WOODWARD)« *hamiltoni* n. sp.« *elongatus* n. sp.Fam. **Semionotidae.**

An undefinable species.

The species referred to are distributed in the Ice Fjord district in the following way in the different horizons.

Bone-bed in the lower Triassic, Mt Congress.

(Discovered by SALOMON in 1910.)

Hybodus sasseniensis?, *Acrodus scaber*, *Polyacrodus angulatus*, detached dermal denticles, detached scales of *Glaucolepis gyrolepidoides*, *Boreosomus* spp., and detached teeth of *Birgeria mougeoti* and *Saurichthys* spp.

Bone-bed in the lower Triassic Mt Bertil.¹⁾

Hybodus cf. *rapax*?, *Acrodus spitzbergensis* (teeth most closely resembling those from Horn Sound), *Acrodus scaber*? and *Saurichthys* sp. (detached teeth).

Fish horizon.

Lyrocephalus euri, *Lonchorhynchus öbergi*, *Lonchorhynchus* sp., *Aphaneramma rostratum*, *Platystega depressa*, *Tertrema acuta*, *Cyclotosaurus?* *spitzbergensis*, *Peltostega erici*, *Palaeobates polaris*, remains of hybodontid fin-spines, *Wimania sinuosa*, *Wimania?* sp., *Wimania?* *multi-striata*, *Sassenia tuberculata*, *Sassenia guttata*, *Axelia robusta*, *Axelia elegans*, *Myliacanthus lobatus*, *Myliacanthus spinosus*, *Scleracanthus asper*, *Birgeria mougeoti*, *Glaucolepis gyrolepidoides*, *Pygopterus de geeri*, *Boreosomus arcticus*, *Boreosomus reuterskiöldi*, *Boreosomus?* *scaber*, *Acrorhynchus bertili*, *Acrorhynchus asplundi*, *Acrorhynchus latistriatus*, *Platysomus nathorsti*, *Platysomus* sp., *Perleidus woodwardi*, *Saurichthys ornatus*, *Saurichthys wimani*, *Saurichthys hamiltoni*, *Saurichthys elongatus* together with a couple of forms not definable with certainty.

Scattered occurrence of vertebrates not high above the fish horizon.

Detached dermal denticles, undefinable bones of Coelacanthids, *Saurichthys elongatus*.

Bone-bed 33 m above the fish horizon, Mt Viking and Mt Marmier.

Ichthyosaurians (detached bones), one vertebra of a Parasuchian, remains of a small undefinable Tetrapod, *Hybodus rapax*, *Hybodus sasseniensis*, *Hybodus microdus*, *Acrodus spitzbergensis*, *Acrodus vermiformis*, *Palaeobates* sp., dermal denticles, fin-spines

¹⁾ The material from this bone-bed was brought home in the autumn of 1920 by Dr. WIRÉN and my brother Kand. Pharm. A. STENSIÖ when my description of the Selachians had already been sent to the press, and it could therefore not be taken into consideration.

and cephalic spines of Selachians, *Glaucolepis gyrolepidoides*, *Boreosomus? scaber*, *Birgeria mougeoti* and a number of undeterminable remains of ganoids.

Two fossiliferous horizons between the lower saurian horizon and the bone-bed 33 m above the fish horizon at Mt Viking.

As far as is known, these horizons contain only Ichthyosaurs and *Omphalosaurus*.

Bone-bed immediately below the lower Saurian horizon.

Ichthyosaurs, dermal denticles of Selachians, *Ceratodus* sp., tooth-bearing plates of *Coelacanthids*, *Glaucolepis* sp., *Boreosomus? scaber*, *Saurichthys* sp.

Lower Saurian horizon.

Omphalosaurus, *Pessopteryx nisseri*, *Pessopteryx arcticus*, *Pessopteryx pinguis*, *Pessopteryx minor*, *Acrodus spitzbergensis*.

Upper Saurian horizon.

Phalarodon nordenskiöldi, *Pessosaurus polaris*, *Acrodus oppenheimeri*, fragmentary bones of gigantic *Coelacanthids*, *Boreosomus* sp.

Lower bone-bed in the Upper Triassic of Mt Bertil.

(Horizon with *Lingula polaris*.)

Polyacrodus pyramidalis, *Birgeria* sp.; scales of a *Boreosomus*-like type.

Upper bone-bed in the Upper Triassic of Mt Bertil.

A number of undefinable bone-fragments, at least partly of Stegocephalians.

Uncertain horizons.

Vertebra of a Plesiosaurian and *Capitosaurus polaris*, both of which probably come from the upper Triassic; the former seems to originate from some stratum of shale with ironstone and the latter from a bank of sandstone.

In this connection it may also be of interest to have a list of the fossils in the bone-bed of the Horn Sound Triassic and so I give one here:

Vertebrates of the Horn Sound Triassic.

Hybodus sasseniensis? *Acrodus spitzbergensis*, *Palaeobates* sp., *Boreosomus arcticus*, *Glaucolepis gyrolepidoides*, *Saurichthys* sp.

* * *

If we first glance at the Ichthyosaurians it is exceedingly noteworthy that they could not be established within the series of the Triassic that I took as the lower one. A statement made by WIMAN (1910, p. 127) to the effect that they occur even in the fish horizon is incorrect, but is due to the fact that a number of gill-arches and sclerotic fragments belonging to giant Coelacanthids (*Wimania? multistriata*) were formerly interpreted as Ichthyosaurian remains. As is known, Ichthyosaurians are not known outside Spitzbergen either earlier than in the middle Triassic.

As has been pointed out by different authors (MERRIAM 1911, MERRIAM and BRYANT 1911; WIMAN 1916a; HUENE 1916), a large number of resemblances exists between the marine Saurian fauna in Spitzbergen and the corresponding fauna in Europe and America. It is specially noteworthy, inter alia, that the genus *Omphalosaurus*, whose systematic position is very uncertain (cf. WIMAN 1916a, pp. 70—71), seems, like *Phalarodon* as well,¹⁾ to be common to Spitzbergen and America.

If the resemblances between the Saurian forms of Spitzbergen and America are thus very great, there are also, however, as WIMAN (1916a) points out, considerable differences as well, and WIMAN continues his argument thus (1916a, pp. 71—72): «These differences appear among the ichthyosaurians. In western North America are found numerous species of the genera *Cymbospondylus*, *Toretocnemus*, *Merriamia*, *Delphinosaurus* and *Shastasaurus*, which do not appear in Europe or Spitzbergen. The Central European Muschelkalk no doubt also contains one or two specific types and *Pessosaurus* and *Pessopteryx* are characteristic of Spitzbergen.»²⁾

«If we turn to other reptile groups that are not adapted to pelagic mode of living in such a high degree as the ichthyosaurians the dissimilarities of course become greater. In the Alpine Trias two nothosaurians, *Pachypleura* (*Neusticosaurus*) from Besano and the somewhat younger *Lariosaurus* of Perledo, are found. In the middle European Muschelkalk are found numerous nothosaurians and placodonts. The marine Trias beds in Spitzbergen also contain several evidently marine labyrinthodonts, and in western North America are found thalattosaurians to which one now here has found any analogy.»

The labyrinthodonts in the Triassic of Spitzbergen are, as WIMAN (1914b) pointed out, all marine ones. Except for *Capitosaurus polaris* the more closely definable ones are from the fish horizon. *Capitosaurus* and *Cyclotosaurus* are quoted from South Africa (BROOM 1909 b, p. 286) in addition to Spitzbergen and the continental Triassic of Europe. Although even the other labyrinthodonts of the Spitzbergen Triassic show rather close relations to certain forms from Europe especially, a number of them show, however, a striking tendency to a marked lengthening of the snout, to which may also be added that in almost all of them the eyes are, independently of the width of the head, farther displaced from each other towards the sides than is generally the case in other forms (WIMAN 1914b, pp. 25—26). WIMAN is of the opinion that these characters have arisen in connection with specialization for a marine mode of life.

¹⁾ According to WIMAN's observations on recently prepared material (WIMAN 1920, p. 12).

²⁾ In a work published in 1916 VON HUENE considers that he found *Pessosaurus* in the lower Muschelkalk of Germany. His material is, however, insignificant and his determination seems, as in various other cases, to be not quite reliable (cf. BROILI, 1916).

Finally if we turn to the fish fauna we are immediately struck by the fact that it lacks almost entirely or even perhaps quite entirely forms belonging to the *Protospondyli* and *Isospondyli*, while the *Coelacanthidae* and *Chondrostei* play a very important part in it. This gives it a character that is on the whole rather ancient.

In the fauna of the fish horizon this ancient character is especially striking owing to the appearance of the genera *Platysomus* and *Pygopterus*, both of which are late Palaeozoic. Their appearance seems to me an argument in favour of the view put forward by STOLLEY in 1911 and adopted by me, namely that the fish horizon (*Posidonomya* bed) ought to be assigned to the lower Triassic. With regard to the *Platysomids* it is noteworthy in this connection that they are now known from lower Triassic in South Africa (BROOM, 1913 a, pp. 4—5) and from formations that are either of late Palaeozoic or lower Triassic age both at Madagascar (LEMOINE 1911, p. 5) and in Canada (LAMBE 1914, pp. 17—23). On the other hand they are hitherto not found in the middle Triassic. *Pygopterus* is, as we know, a form that really belongs to upper Permian in Europe, although, according to recent observations, it seems to occur in the Bunter Sandstone of Germany as well (cf. STOLLEY, 1920, p. 81).

In its relation to other known Triassic fish faunas the one described here from Spitzbergen undoubtedly shows the closest relationship to that of the Alpine and continental Trias of Europe, a fact that is shown especially by such common forms as *Palaeobates* (cf. JAEKEL 1889, pp. 327—330; WILCKENS 1909, pp. 187—188), *Polyacrodus* (cf. JAEKEL 1889, pp. 321—326), *Pygopterus* (STOLLEY 1920, p. 81), *Birgeria* (cf. STENSIÖ, 1919, pp. 177—181) and *Perleidus* (cf. DE ALLESSANDRI 1910, pp. 49—51). The genera *Hybodus*, *Acrodus*, *Ceratodus* and *Saurichthys* are certainly also common to the Triassic strata of Spitzbergen and Europe, but we cannot ascribe to them the same value in deciding the relationship between the faunas as to the above-mentioned genera, since, as is known, they have a very extensive geographical distribution (cf. WEMPLE 1906; JORDAN 1907; BROOM 1909 a, b; STROMER 1910; WOODWARD 1890 a; 1895 b). It is obvious, however that all the *Hybodus* species, certain of the *Acrodus* species, and the *Ceratodus* species from the Triassic of Spitzbergen are most closely related to the species from the Triassic deposits of Europe.

On the other hand the number of fish genera that are known exclusively from the Trias of Spitzbergen is considerable, and the fauna has on the whole a rather special character. The most characteristic of these genera are *Axelia*, *Myliacanthus* and *Scleracanthus* among the *Coelacanthids* and *Boreosomus* and *Acororhabdus* among the *Palaeoniscids*.

As will easily be seen from the facts given, the fish fauna in the lower Trias of Spitzbergen forms a very strong argument in favour of DIENER'S view (1916) mentioned above, that during the Skytic time the Arctic Ocean was in communication with the ocean in which the Alpine and continental Triassic strata of Europe were deposited. That at the same time the Arctic Ocean was also in communication with the Triassic Ocean covering the west of America seems to be beyond doubt from certain elements in the evertbrate fauna (*Gyronites aplanatum*, etc.). In opposition to DIENER I suppose in accordance with MERRIAM (1911) that both communications persisted also during the Anisic time.

DESCRIPTION OF THE FISH FAUNA.

Subclass Elasmobranchii.

Family Cestracionidae.

Genus *Hybodus* AGASSIZ.

Synonyms: See WOODWARD, A. S., The Wealden and Purbeck Fishes, etc. Palaeontogr. Soc., Vol. 69, p. 3.

Under the generic name *Hybodus* AGASSIZ grouped together (1837, vol. 3, p. 41, p. 180) a number of species which he had established on the basis of a material consisting mainly of detached teeth and fin-spines. As the state of preservation only allowed him in exceptional cases to decide with certainty which teeth and fin-spines belonged to the same species, he described them separately under different names.

The knowledge of the genus *Hybodus* increased rather slowly during the four decades after AGASSIZ's description. The most important works during this period are those of EGERTON (1845, pp. 197—199) and DAY (1864, pp. 57—65). It was not until the beginning of the eighties that the knowledge of this genus began to increase more rapidly. 1889 was a particularly important year in this respect, as WOODWARD then published the first volume of his large «Catalogue of Fossil Fishes in the British Museum», in which both the genus *Hybodus* and the fossil sharks in general were thoroughly treated on the basis of an abundant material. In the same year there appeared JAEKEL's valuable work on the *Selachii* in the upper Muschel-kalk of Lorraine (1889, pp. 294—309), in which *Hybodus* forms were also dealt with in detail.

Among the numerous works that further have followed during the last thirty years I may mention those of JAEKEL (1890; 1898; 1906a), FRAAS (1889), BROWN (1900), KOKEN (1907), BROOM (1909a), VIDAL (1915) and WOODWARD (1915; 1917).

As has been pointed out by DAY (1864) and WOODWARD (1889a, pp. 267, 279, 300), *Hybodus* is closely related to *Acrodon*. Certain of the teeth may be developed fairly similarly in both genera, and in the case of detached cephalic spines and fin-spines it is impossible to decide to which of the two genera they belong.

The earliest representatives of the genus *Hybodus* appeared in the Triassic¹⁾. They occur frequently in the continental Triassic of Germany, France and England. They have been shown to exist in the alpine Triassic deposits (DE ALESSANDRI, 1910, pp. 31—34; ZUGMEYER, 1875, pp. 79—80; BITTNER, 1898, pp. 323—326; WILCKENS, 1909, p. 188)²⁾ though

¹⁾ A tooth from the Kupferschiefer of Germany is described by GEINITZ (1861, p. 27, pl. IV, fig. 4) as belonging to *Hybodus*, but his determination may be doubted. As far as one can judge from his figure the characters of the tooth seem to point to a relation with *Polyacrodus*.

²⁾ The species described by BITTNER as *Hybodus austriacus* cannot really be a *Hybodus*. It seems also certain that it cannot belong to *Polyacrodus*, as WILCKENS (1909) has supposed. Probably it may represent a new genus.

they are only rarely found there. Isolated finds of *Hybodus* species are also described from the Triassic of North-West America (WEMPLE, 1906, pp. 72-75; JORDAN, 1907, pp. 98-99) and South Africa (BROOM, 1909a, p. 252), and I have myself shown the existence of a species in the Triassic of Spitzbergen (STENSIÖ, 1918b, p. 76). In the Jurassic the genus is represented by numerous species and in the lower Cretaceous several species still seem to have existed. With a few exceptions the Jurassic and Cretaceous species are all described from Europe.

Almost all the better known *Hybodus* species are obtained from the Jurassic and the Cretaceous (Wealden). Among the Triassic ones *H. africanus* (BROOM, 1909a) is the only one that is somewhat completely preserved and that shows the general shape of the body with parts of the axial and fin skeleton. In all the Triassic species the dentition is so far known only from detached teeth, and there is consequently not a little uncertainty about this in several respects, a fact that has caused and still causes great difficulties for the determination of the species.

As we know, AGASSIZ had originally grouped together a number of rather different types of teeth from the Triassic into one common species, for which he chose the name of *H. plicatilis*. When later on, some remains of jaws of the Jurassic species *H. reticulatus* came into his hands, he was struck by the fact that the teeth on these remains appeared to be of a very homogeneous character. Under these circumstances he considered that it was impossible to retain the species name *H. plicatilis* in its earlier sense. He limited it to one of the types of teeth and suggested for the others the names *H. mougeoti*, *H. polycyphus* and *H. angustus*. In addition of these species he also described a number of others from the Triassic; of these *H. longiconus*, *H. obliquus* and *H. cuspidatus* ought to be mentioned in this connection.

At the present time there is certainly agreement in considering AGASSIZ's division as being carried too far in this case and that some of the names proposed by him ought to be regarded as synonyms, but with regard to the actual limits of species there is still a great difference of opinion. SCHMID has suggested (1861, pp. 18-20), if I understand his exposition correctly, a grouping of all the Triassic species, described by AGASSIZ, under the name of *H. plicatilis* and this view is maintained later on by FRECH (1903, pp. 10-11). WOODWARD, on the other hand, proceeds more cautiously. Thus in his «Catalogue» of 1889 we find that of AGASSIZ's species he has adopted *H. plicatilis* and *H. longiconus* under the common name of *H. plicatilis* and in the same way *H. mougeoti* and *H. obliquus* under the name of *H. mougeoti*, while the other species are provisionally retained as defined by AGASSIZ 1843. At the same time WOODWARD emphasized the impossibility of arriving at any certain view as to the precise character of the dentition merely with the help of detached teeth. JAEKEL (1889) incorporated *H. plicatilis* in its restricted signification with *H. longiconus*. He also established two new species, *H. multiconus* and *H. multiplicatus*, but remarks that there was really no objection to a fusion of these with *H. longiconus*; he unites *H. polycyphus* and *H. mougeoti* into one species, on which he bases the new genus *Polyacrodus*. In a later work (1898) he has definitely decided to unite the three species *H. longiconus*, *H. multiconus* and *H. multiplicatus*. Another view is held by SALVAGE (1883, pp. 495-496) and still other views could be mentioned, but what has already been

said ought to be sufficient to show the difficulties in dealing with *Hybodus* material consisting only of detached teeth.

From the preceding it is clear that JAEKEL already in 1889 had tried to undertake a partial revision of *Hybodus* as a genus. Nine years later (1898) he submitted the same genus as a whole to a closer investigation. He then suggests that the name *Hybodus* should be used only for fin-spines while the teeth should be divided among the genera *Polyacrodus* JAEKEL, *Orthybodus* JAEKEL, *Nemacanthus* AGASSIZ and *Parhybodus* JAEKEL.

KOKEN in 1907 justly objects that JAEKEL has gone too far in his revision. He holds that *H. reticulatus* must be taken as the type species for the genus *Hybodus*, and that the name *Hybodus* must therefore not be restricted in the way maintained by JAEKEL. Nor has WOODWARD followed JAEKEL, but considers, like KOKEN, that *H. reticulatus* is the type species for *Hybodus* (1915, p. 4). Finally SCHLOSSER (1918, p. 58) has adopted the genus *Polyacrodus*, though with a somewhat more restricted significance than JAEKEL. Apart from this he retains in other respects the genus *Hybodus* as limited by AGASSIZ.

The view I have arrived at myself with regard to this question and that I have applied in this work agrees fairly well with that of SCHLOSSER. Like him, I consider, as will be seen from my exposition below, that we ought to restrict the genus *Polyacrodus* to teeth from the Triassic alone. It is beyond all doubt that the name *Hybodus* ought not to be used as JAEKEL suggested and still seems to uphold in 1911 b (p. 19). I am therefore quite in agreement with KOKEN and WOODWARD in considering the Jurassic species *H. reticulatus* as the type species for the genus *Hybodus*, so that this genus should comprise in the first place Jurassic and Wealden species. Our present knowledge of *H. africanus* seems to show that the species described from the Triassic ought, at least temporarily, to be also included in this genus. This seems perhaps to be contradicted by the fact, pointed out in the literature, that the Triassic species have a more heterodont dentition than the geologically younger ones. But with regard to this it must be remembered that even certain Jurassic species, e. g. *H. delabechii*, have teeth that have a rather different shape according to their position in the jaws (cf. WOODWARD, 1888, pp. 58—60; 1889a, pp. 259—264).

In the Triassic of Spitzbergen there occur *Hybodus* teeth together with those of *Acrodus* in various bone-beds. In the same bone-beds one also finds fin-spines, cephalic-spines and dermal denticles, a number of which probably belong to *Hybodus*. In no case, however, have I found them together with teeth in such a way that their connection with these could be established, and I have described them in a special chapter after my accounts of the *Hybodus* and the *Acrodus* teeth.

Finally in this connection it is worthy of mention that the *Hybodus* species from the Triassic of Spitzbergen seem to be closely related to certain of the species from the continental Triassic strata in Central Europe, while on the other hand they seem to be more decidedly differentiated from the American ones.

Hybodus rapax n. sp.

(Pl. I, figs. 1, 2.)

Of this species there are only two detached teeth (*P. 41 a*, *P. 41 b*) which are both defective.

The dimensions of these in their present state of preservation are as follows:

	<i>P. 41 a.</i>	<i>P. 41 b.</i>
Height (with the principal cone partly preserved) . . .	32 mm	30 mm
Length	23 "	35 "
The greatest height of the root	11 "	11 "
The breadth of the root at the middle	— "	15 "
The breadth of the crown at the middle	10 "	10 "

It is certain, however, that both the height and the length have been considerably greater than is indicated by the above measurements. The real height may be estimated at about 35 mm and the length at least 40 mm (cf. Pl. 1, figs. 1 a, b). It is thus evident that these teeth are larger and more powerful than any other *Hybodus* teeth so far found.

Text fig. 1.

Hybodus rapax n. sp.

A. Transverse section through the tooth *P. 41 a.* 1/1. B. Section through a lateral part of the tooth, *P. 41 b.* 1/1. The lateral side of the teeth in the two figures is situated to the left.

The crown on both teeth is bent basally in such a way that its lower margin is strongly concave, as is shown by Pl. 1, figs. 1, 2. The greatest breadth and height of the crown are at its middle part and decrease from there continually towards the ends. The lateral cones are quite absent. The principal cone, on the other hand, is strong and seems to have occupied a nearly symmetrical position. It is, however, not vertical but inclined somewhat backwards and at the same time also medially. It is flattened in the latero-medial direction and a horizontal section through it consequently becomes ellipsoidal in shape. A sharp longitudinal keel is developed along both its anterior and posterior edges, but to

judge from specimen *P. 41 a.*, this keel extends only on the posterior side right out to the point. On the anterior side it fairly soon becomes more delicate and finally disappears altogether. From the principal cone the keel continues out over the rest of the crown to each of its ends.

The sculpture of the crown consists of numerous vertically running striae, all of which issue from the basal margin. These striae are coarser on the medial surface of the crown than on the lateral one and, as a rule, longer too and have a distinctly thickened proximal end. On the principal cone they extend on the medial surface up to about the middle, while dorsally of this the sculpture is quite lacking. In front of and behind the principal cone several of the striae of the medial surface reach the longitudinal keel. On the lateral surface, on the other hand, the striae are short throughout the whole length of the crown and limited to its basal parts; the rest of this side is smooth. The other characteristic features of the sculpture are clearly shown in Pl. 1, figs. 1, 2.

The root is high and powerfully developed. Seen from the lateral or medial side it appears, like the crown, to be bent so that its basal border is concave and its distal border convex to a corresponding extent. The curvature of the root seems, however, to be somewhat weaker than that of the crown. The root has its greatest height at its middle part; toward the ends it gets gradually lower. It is considerably wider than the crown, and, as the latter is not situated right above it, but more above its lateral part, the medial part appears as a powerful torus on the medial side (text figs. 1 A, B).

On the root one can distinguish a medial, a lateral and a basal surface. The last-mentioned surface is divided lengthways into two fields (text figs. 1 A, B), a medial and wider one, above which the axis of height of the principal cone is situated vertically, and a lateral one, which forms an angle of about 45° with the former. The lateral surface is fairly low and a little concave from the distal to the basal border (text figs. 1 A, B). The medial surface on the contrary is convex in the same direction and is developed especially at the ends in such a way that we are quite justified in speaking of two fields there, a medial and a dorsal one (text fig. 1 B).

With regard to the microscopical structure the two teeth now described do not differ in any respect from other typical ones (cf. JAEKEL, 1889; KÖKEN, 1907¹). On the root numerous Haversian canals with rounded pores open in the usual way.

* * *

Remarks. — *H. rapax* undoubtedly resembles the type of teeth that was described and figured by AGASSIZ (1843, vol. 3, Pl. 24, figs. 19, 20, 21, 23), PLENINGER (1844, Tafel XII, figs. 54, 56) and QUENSTEDT (1852, Tafel 13, figs. 30, 31) and others under the name of *Hybodus longiconus*, as it differs from that type only by its larger size and the extension of the ornament on the lateral side of the crown. With the type of teeth for which JAEKEL 1889 has chosen the name *Hybodus longiconus*, on the other hand, the species in question from Spitzbergen does not agree so well.

Hybodus rapax in several respects also seems nearly related to the new species *Hybodus sasseniensis* described below, and we must therefore take into account the possibility that in future with more complete material it may perhaps show itself to be identical with the latter.

Geological occurrence and locality. — A bone-bed about 33 m above the fish horizon, Mt Viking.

Hybodus sasseniensis n. sp.

(Pl. 1, figs. 3–10.)

Synonym: 1918. *Hybodus* sp. STENSJÖ E. A: SON, Norsk Geol. Tidsskrift, Bd. V, p. 76.

I have established the species *H. sasseniensis* for six detached teeth (*P. 39 a–f*), five of which (*a–e*) are in a comparatively complete state of preservation. To this species may be added with a fairly great degree of probability three more teeth (*P. 38, P. 40, P. 633*) and, at least provisionally, the tooth from Horn Sound previously described by me (STENSJÖ, 1918 b) and another tooth, mentioned at the same time, from Middle Hook in the Ice Fjord, which is the property of Prof. Dr. W. SALOMON in Heidelberg. — The tooth from Horn Sound belongs to the Palaeontological Collection of the University of Christiania.

The largest (*P. 39 b*) of the six teeth given as typical of the species in question is about 12 mm long, the smallest (*P. 39 f*) about 6 mm. The height can only be

¹) It may be mentioned here that JAEKEL 1889 and several other palaeontologists have used the term vasa-dentine for the tissue we now call osteo-dentine (TOMES, 1914, p. 102) or trabecular-dentine (RÖSE, 1898, p. 42) in the teeth of Selachians.

ascertained in the case of one tooth (*P. 39 a*), which, including the principal cone, is 9 mm high. All the other teeth have their principal cone more or less defective.

The best preserved tooth is the one figured in Pl. I, figs. 3 a and 3 b (*P. 39 a*). The crown on this is low with an almost straight basal margin. The principal cone is considerably high and is sharply pointed at the distal end. It is not situated vertically but is inclined both posteriorly and medially. The lateral cones are low but distinct. There are three of them in front of the principal cone. Behind it the tooth is somewhat injured and only one of the lateral cones is preserved there. The lateral cones are all of a bluntly conical shape.

The principal cone is somewhat flattened in the latero-medial direction and a horizontal section of it is consequently elliptical in shape. Its anterior and posterior edges are furnished throughout their length with a sharp cutting keel, which continues as a longitudinal keel forwards and backwards to the ends of the crown.

The sculpture of the crown consists, as usual, of striation. The striae run from the basal margin nearly straight upwards as in *H. plicatilis*. They reach both in front of and behind the principal cone to the longitudinal keel. The principal cone itself is only striated throughout its height on the medial surface. On the lateral surface it is smooth in its distal third. It is also noteworthy with regard to the principal cone that the striae are more numerous and more close on its lateral than on its medial surface.

The root is fairly low, but is strongly developed. Seen from the medial or the lateral side it is straight, like the crown. It is considerably wide and forms on the medial side a projecting longitudinal torus («Wulst») in the usual way (cf. JAEKEL, 1889). The basal surface is large and broad and practically quite plane. The axis of height of the principal cone meets it at an angle of about 45°.

A tooth agreeing in most respects with the one just described is figured in Pl. I, figs. 4 a, b (*P. 39 b*). The two ends are here preserved but the principal cone is missing to a great extent. It is clear, however, that it has been situated on the middle of the tooth. Both in front of and behind it there are remains of two lateral cones. There are two more teeth of the same type (*P. 39 c, d*; Pl. I, figs. 5, 6); one of these, however, (fig. 5) has had the principal cone situated more vertically than the other. All three resemble the types that JAEKEL, 1889, called *H. plicatilis* (1889, Pl. VII, fig. 3) and *H. longiconus* var. *minor* (1889, Pl. VII, fig. 7).

The tooth figured in Pl. I, figs. 7 a, b (*P. 39 e*) represents in various respects another type than the preceding ones. Both the root and the crown of it are bent in the way that they both have concave basal and correspondingly convex distal outlines. The principal cone is broken off but it has apparently had an almost vertical position. It seems to have a narrower shape than that of the other teeth. The lateral cones are low and not very prominent, but at least on one side of the principal cone no less than four can be observed. It is also probable that one or more was present on the other side, but the tooth is incomplete there and no remains of these are now preserved. With regard to sculpture and other details the crown agrees entirely with those of the previously described teeth. The root is relatively higher and narrower than in these. — As far as can be judged from the present state of preservation this tooth resembles most closely the form called *H. longiconus* by JAEKEL 1889.

The tooth *P. 40* is of rather considerable size but is only preserved as an impression of the lateral side, which in its turn is incomplete and weathered (Pl. 1, fig. 10). If it was developed symmetrically, its length may probably have been about 20 mm.

The crown is bent in the same direction as that of the preceding tooth but not quite so much. The principal cone is sharply pointed but strikingly short in relation to the presumed length of the tooth. The lateral cones on the preserved end are relatively high and slender. They are six in number. With regard to sculpture the crown shows complete agreement with the typical teeth. The root is low, especially towards the ends, and is characterized in addition by its straight basal line.

The tooth just described bears a resemblance to the types distinguished by JAEKEL under the name of *Hybodus multiconus* and *H. multiplicatus* and has probably been situated fairly far back.

The tooth *P. 633* (Pl. 1, fig. 9) is better preserved than the former one. Only the principal cone is broken off. But its medial side is fixed to the stone and it is therefore accessible for investigation chiefly from the lateral side. It is scarcely 9 mm long. Both the crown and the root are curved in the same way as in tooth *P. 39 a*. The principal cone is short and inclined somewhat backwards. The lateral cones are small, bluntly shaped, and are four or five in number. The sculpture consists of relatively coarse and rather sparse striation as on the typical teeth.

The root is low and very broad. The axis of height of the principal cone has a vertical position in relation to the basal surface.

The tooth *P. 633* shows in several respects an approach to *Acrodus*. The root clearly shows, however, that we are concerned with a *Hybodus* species. Owing to its elongated shape, the feeble development of the principal cone and the comparatively large number of lateral cones it resembles most closely tooth *P. 40* and seems to have occupied a position similar to this or has probably been situated still farther backwards.

Specimen *P. 38* agrees rather well, as Pl. 1, fig. 8 shows, with the type form, but the sculpture is very much more sparse and delicate.

Of the teeth that I have included, with more or less hesitation, under the name *H. sasseniensis*, the one from Horn Sound is, as I have mentioned, figured and described earlier (STENSIÖ, 1918b). The tooth from SALOMON's bone-bed (text fig. 2) is incompletely preserved, but appears to bear the closest correspondence in shape to JAEKEL's *H. longiconus* type. The root and the crown both seem to be nearly straight. The lateral cones on the end that is preserved are comparatively low and blunt. The principal cone is only a little inclined backwards and medially. The sculpture of the crown consists of vertical striation as in the typical teeth, but the striae are more sparse and comparatively coarser.

* * *

Remarks. — The types that have been grouped here in a common species — *H. sasseniensis* — show a close resemblance to several of those that JAEKEL, 1898 (p. 143) includes under the name *Parhybodus longiconus*. In the Spitzbergen types, however, the lateral cones are generally lower and blunter and resemble more those of the *H. cuspidatus*

Text fig. 2.

H. sasseniensis n. sp.
From bone-bed in the
sandstone series below
the fish horizon. Orig.
belongs to W. SALOMON,
Heidelberg. 4/1.

type. Other clear differentiating characters are difficult to state, but, in spite of that it seems fairly certain, from what I have been able to make out by direct comparisons, that the Spitzbergen types described here represent a new and independent species for which I have suggested the species name *sasseniensis* after the place of discovery of the type-teeth, Sassen Valley.

Geological occurrence and localities. — The six typical teeth (*P. 39*; *a-f*) all are obtained from the bone-bed, found 33 m above the fish horizon, Mt. Viking. From the same locality and horizon the teeth *P. 38*, *P. 40* and *P. 633* also originate. Of the two others, about whose determination I am not quite certain, one, as has been mentioned, was found at Horn Sound, the other at the Ice Fjord in a bone-bed which was discovered by SALOMON in the sandstone series below the fish horizon during the excursion of the Geological Congress to Spitzbergen in 1910 (STOLLEY, 1911, p. 115).

Hybodus microdus n. sp.

The available material of this species consists of two crowns of teeth (*P. 53*, *P. 54*).

Both teeth have been very small. The length of the crowns is only 1.5 mm and the height about 1 mm.

The crowns are somewhat bent, as shown in text figs. 3 A and B. Their principal cone is strikingly powerful, with a broad base and a sharply pointed distal end, and

Text fig. 3.

Hybodus microdus n. sp.

Teeth A, after *P. 53*; 4/1.

B, after *P. 54*; 6/1.

seems to be fairly flattened from both the medial and the lateral side. In addition it is somewhat inclined both in posterior and medial direction and has a sharp anterior and posterior edge. On the tooth *P. 53* lateral cones seem to be absent in front of the principal one, but this fact may be due to the state of preservation, which in this part does not seem to be quite perfect. Behind the principal cone two lateral cones are found on the same tooth, and this is the case on the other tooth both behind and in front of the principal cone.

The tooth *P. 54* in quite smooth, at least on the lateral surface. On the other tooth some long striae can be observed on the corresponding surface; they reach almost to the distal end of the principal cone. Neither tooth has the medial side accessible for a close investigation.

* * *

Remarks. — *H. microdus* resembles in several respects both *H. minor* AGASSIZ and *H. apicalis* AGASSIZ (cf. AGASSIZ, 1843, vol. III, p. 183, Pl. 23, figs. 21–24; p. 195, Pl. 23, figs. 16–20), but seems, however, to be related most closely to the latter. It is characterized especially by the smallness and slight ornamentation of the teeth.

Geological occurrence and locality. — Both teeth were found at Mt. Viking, in the bone-bed about 33 m above the fish horizon.

Genus *Acrodus* AGASSIZ.

Synonyms: See WOODWARD, A. S., The Wælden and Purbeck Fishes, etc., Palaeontogr. Soc. Vol. 69, p. 14.

The genus *Acrodus* was established by AGASSIZ, 1838 (vol. III, p. 139). Many investigators have since helped to extend our knowledge of this genus and among them we may

specially mention DAY (1864, pp. 57—65), ECK (1865, pp. 60—62, 116—118), JAEKEL (1889, pp. 310—329; 1898, p. 145), v. MEYER (1849 b, pp. 229—233), PLIENINGER (1844, pp. 115—117), SAUVAGE (1883, pp. 493—494), SCHMID (1861, pp. 15—18), and WOODWARD (1889 a, pp. 279—306).

The material at AGASSIZ's disposal consisted practically entirely of detached teeth. Only a couple of fragments of jaws with a number of teeth in situ seem to have been known to him. Although the finds made after his time have thrown some new light on the organization of these sharks, still our view about them is very incomplete. Remains of *Acrodus* species are certainly not infrequent in several horizons of the mesozoic formations in Europe (cf. WOODWARD, 1889 a, loc. cit.; DE ALESSANDRI, 1910, pp. 34—35; ZUGMEYER, 1875, pp. 79—80), but the state of preservation of these remains, as we know, makes it impossible in most cases to study them in detail and in many cases even does not permit of any certain determination.

AGASSIZ considered that there was a close relationship between *Acrodus* and the recent *Cestracion*, for which reason he included *Acrodus* among his «Cestraciontes», while *Hybodus* was put in another family. This view was for a long while the prevailing one and it is still found as late as in ZITTEL's «Handbuch» (1887—1890, pp. 67, 76). There had however been earlier authors (CHARLESWORTH, 1839, p. 245; OWEN, 1845, p. 57; MACKIE, 1863, p. 243) who maintained that *Acrodus* ought to be connected with *Hybodus*, but it can scarcely be said that any proof of this was put forward before DAY (1864, pp. 63—65). More recent investigations, especially those of WOODWARD and JAEKEL, have now fully made it clear that this latter view is the correct one. — JAEKEL has also pointed out the relations between *Acrodus* on the one hand and the genus *Polyacrodus* founded by him on the other (1889, pp. 321—324).

The genus *Acrodus* is known with certainty earliest in the Triassic¹⁾ and in the definition given it by WOODWARD it seems to have persisted nearly to the end of the Cretaceous formation. The great majority of species are known from Europe, where, as I have mentioned, they occur in all three mesozoic formations. Only one species has previously been found in Spitzbergen (HULKE, 1873, p. 10; STENSIÖ, 1918 b, p. 76); three species are described from the Triassic of North America (JORDAN, 1907, p. 100; WEMPLE, 1906, pp. 71—72) and one from its Cretaceous; finally one species is known from the upper Cretaceous of South America (WOODWARD, 1889 a, p. 297).

On account of the fragmentary state in which they are preserved the *Acrodus* species have always been and still are, as has already been pointed out, difficult to treat from a systematic point of view. Just as in the case of the *Hybodus* species the different authors are very different opinions with regard to the actual limits of species. Now-a-days, especially in the case of the Triassic ones, there is, however, a tendency to consider, with good reason, that a number of species names proposed by AGASSIZ and several succeeding authors may to a considerable extent be regarded as synonyms.

From the Spitzbergen Triassic we now have, as the subsequent description will show, four species, of which one, *A. spitzbergensis* HULKE, is, as has been pointed out above, already known previously. The relationship between these four and the other known ones is of course not yet fully ascertained, but as far as can now be seen,

¹⁾ PHILIPPI and FRECH (1903, p. 11) also refer *Woodnuka althausi* (MÜNSTER) to *Acrodus*. Although the genus *Woodnuka* is undoubtedly closely related to *Acrodus*, at least at present it seems as if it ought not to be included in the latter.

Stensiö, Triassic Fishes from Spitzbergen.

A. oppenheimeri, one of the newly-established species, resembles in certain respects the tooth-type from the continental Triassic of Europe which is called *A. gaillardoti* AGASSIZ, while *A. spitzbergensis* and the other species seem to resemble more closely the North American forms.

As has been pointed out above in the introductory description of the genus *Hybodus* (p. 3), fin-spines, cephalic spines and dermal denticles of this genus and of *Acrodus* are often found detached in the same horizons as the teeth. But these conditions of occurrence of the spines and dermal denticles do not of course permit of any decision as to which of them ought to be referred to *Acrodus* or *Hybodus*, since, as we know (DAY, 1864; WOODWARD, 1889a; JAEKEL, 1889), they are similarly developed in both these genera. Because of this I have described them all below in a special chapter (p. 25).

Acrodus spitzbergensis HULKE.

(Pl. 2, figs. 1—19.)

Syn. 1873. *Acrodus spitzbergensis* HULKE, I. W., Stockholm K. Vet. Akad. Handl. Bih., Bd. 1, no. 9, p. 10.
1889. *Acrodus spitzbergensis* WOODWARD, A. S., Catalogue of Fossil Fishes in the B. M., Part I, p. 299.
1918. *Acrodus spitzbergensis*? STENSIÖ, E. A:SON, Norsk Geol. Tidsskrift, Bd. V, pp. 76—77.

In the material of the Triassic vertebrates collected by A. E. NORDENSKIÖLD during the Spitzbergen expedition of 1864 HULKE (1873, p. 10) was able to recognize a tooth of an *Acrodus* species also, which he described under the name of *A. spitzbergensis*. His description is as follows in extenso: «A single, but characteristic tooth 0·9 inch long and having a greatest breadth of not more than 0·12 inch, imbedded in a thin piece of limestone labelled (95 Is fj. 1864, Saurie Hk.) plainly belonged to an *Acrodus*. The striae rather coarse, and separated by proportionately wide intervals, pass off from the lips of a sunken groove instead of from a raised line as in all hitherto known species. I am indebted to Mr. DAVIES, Senior, for calling my attention to this distinguishing character, and a comparison which I made of this spitzbergen fossil with a large series of *acrodus* teeth in the British Museum, has confirmed its distinctiveness.» The tooth in question belongs to the State Museum in Stockholm, but could not be found, having either got lost or being missing at the time.

The material of this species now available shows that the distinguishing character of the type tooth, the longitudinal groove from whose raised lateral «lips» the striae issue, is as a rule only found on the teeth of the posterior and median transverse rows of each jaw. Those of the anterior transverse rows are developed, as we shall see, with a number of cones and sometimes have a decided resemblance to those of *Hybodus*.

I have provisionally grouped under the name of *A. spitzbergensis* about 20 detached teeth from the Ice Fjord district (*P. 98 a—m*, *P. 99 a—e*, *P. 100*), all belonging to the Palaeontological Institute of Upsala. I have previously described with some hesitation a number of teeth from Horn Sound under the same species name (STENSIÖ, 1918 b), and the view I put forward then has been confirmed on the whole, at least by the facts known up to the present. The teeth from Horn Sound, which I shall deal with again here, belong to the Palaeontological Collection of the University of Christiania.

Teeth of the anterior transverse rows. — The transition between the teeth of the anterior and middle transverse rows of each jaw apparently takes place gradually,

which is probably also the case between those of the middle and posterior transverse rows. For practical reasons, however, I have grouped here under the heading «teeth of the anterior transverse rows» all those teeth that have somewhat distinct lateral cones, while the rest are described as belonging to the middle and posterior transverse rows. It is true that it sometimes happens (cf. *A. annungiae* Woodward, 1889a, p. 293, text fig.; Pl. XIV, fig. 4, Pl. XV, fig. 1) that small lateral cones are found developed even on the teeth of the middle and posterior transverse rows, but in the species under consideration there seems to be no risk of this being the case, as the sculpture on the teeth of the anterior transverse row is, as we shall see, developed in another way than in those of the posterior and middle ones.

I take the teeth *P. 98 a*, *P. 99 a-c* (Pl. 2, figs. 1-7) and one tooth from Horn Sound as belonging to the anterior transverse rows. To this category I have also referred the tooth *P. 98 b*, though not without hesitation.

The tooth *P. 98 a* (Pl. 2, fig. 1) is defective at one end, otherwise it is well preserved. In its present state of preservation it is 10 mm long. Its greatest height is about 7 mm. If it has been developed symmetrically there seems to be no reason why it should not have belonged to the unpaired symphyseal row.

Seen from the lateral or medial side the crown is much bent in the way that its distal outline is convex from end to end, while its basal one, on the other hand, is concave (Pl. 2, figs. 1 b, c). Another special characteristic of the crown is the low and blunt, but nevertheless powerful principal cone and the distinct lateral cones, four of which are preserved on one side of the principal cone and one on the other. The appearance of the crown as seen from above is shown in Pl. 2, fig. 1 a.

From one end of the crown to the other there passes off over all the cones a longitudinal crista (Pl. 2, fig. 1 a) and over the principal cone a distinct transversal crista is also developed. The latter crista reaches both on the lateral and the medial surface of the tooth almost entirely to the basal border of the crown, in the neighbourhood of which it is ramified. Laterally of the longitudinal crista (Pl. 2, fig. 1 c) this ramification is considerably stronger than medially of it (Pl. 2, fig. 1 b). Apart from these cristae the principal cone has no ornament. Anterior and posterior to this cone both on the lateral and the medial surface there is on the basal half of the crown a rather coarse vertical striation. None of the striae on the lateral surface reach the longitudinal crista, but there is a fairly smooth interspace between their distal ends and that crista; on the medial surface, on the other hand, there is for each lateral cone a stria longer than the other ones, extending from the basal margin of the crown to the longitudinal crista. Short fine striae issue from this crista both on its lateral and medial side, without becoming attached to the longer ones described, which are mainly developed on the basal halves of the crown (Pl. 2, fig. 1 a).

The root is high, especially its middle part, but rather thin in comparison with the height. It is bent in the same way as the crown, though not quite so much. The lateral and the medial surface meet basally, forming a rounded angle, so that one cannot speak of any real basal surface. — A cross section through this tooth, clearly showing this and the relation between the root and the crown, is seen in text fig. 4 A.

A tooth which, although considerably smaller (about 2 mm in length), is very like the one just described, occurs among the material from Horn Sound.

The tooth *P. 99 a* (Pl. fig. 2) is rather fragmentarily preserved and under these circumstances one cannot get any exact idea of its shape. In its present state of preservation it is about 5 mm long.

The crown was almost straight with a somewhat powerful principal cone and prominent lateral cones. A longitudinal crista is developed as on the tooth before, but a transversal crista is here not only a distinguishing feature of the principal cone, but is also present on the lateral ones. Between each pair of the latter cristae there are one or two short striae, which do not reach as far as the longitudinal crista.

The two teeth *P. 99 b* (Pl. 2, fig. 3) and *P. 99 c* (Pl. 2, fig. 4) are also of a type similar to the one just described. The former differs somewhat, however, by being more bent and having smaller lateral cones. — With regard to a third tooth, *P. 99 d*, which also resembles in shape the teeth of the anterior transverse rows, it does not seem to be possible to decide with certainty, from the development of the crown (Pl. 2, fig. 5), whether it belongs to *Acrodus* or *Hybodus*. But the root clearly indicates that the former alternative is the correct one. The principal cone of this tooth is certainly broken off, but all the same it is evident that it did not have a vertical position, but has been inclined somewhat towards the caudal end of the tooth. The sculpture of the crown is considerably finer than on that of the other teeth.

An evident transition type between the anterior teeth and those following them farther posteriorly is seen in the tooth *P. 99 e* (Pl. 2, fig. 6). This is 14 mm long and its greatest height is about 4 mm. Both the crown and the root, seen from the lateral and medial sides, are bent in the usual way, so that their dorsal contour is convex from one end to the other and the basal contour is concave to a corresponding degree. The bend is most evident from the lateral side (Pl. 2, fig. 6 c).

The principal cone is scarcely discernible here except as a marked angle above the middle of the tooth. Lateral cones are present but are very small. Seven can be observed on one side of the principal cone, six on the other. Between both ends of the crown extends the usual longitudinal crista, which, for the reason given immediately below, I call the primary longitudinal crista. On the principal cone there is, in addition, a well developed transversal crista. This is not ramified medially until near the basal margin of the crown, laterally, on the other hand, its ramification already begins at the place where it crosses the primary longitudinal crista and, as the ramification is abundant, the principal cone obtains a rather dense sculpture on this side (Pl. 2, fig. 6 c). From the primary longitudinal crista there issues on the medial surface one or two sharp striae for each lateral cone; these striae pass off to or close to the basal margin of the crown. Between them appear other shorter ones, which are not connected to the primary longitudinal crista. On the lateral surface practically all the striae end in a similar way a short distance from the primary longitudinal crista, so that there arises a sculptureless surface close to this almost throughout the whole length of the tooth. On one half of the tooth — it is not possible to decide whether it is the posterior or the anterior one — all the striae of the lateral surface have their distal ends curved in the direction of the principal cone and are then attached to each other, so that a

secondary longitudinal crista is formed, which passes along the primary one and nearly parallel to it. We thus find here the character developed that is specially characteristic of HULKE's type-tooth. On the other half of the lateral surface of the tooth this tendency to curvature of the striae is evident only close to the principal cone. In other respects the striae on this half have a rather vertical position and fairly often reach, especially towards the end of the crown, the primary crista, so that under these circumstances the smooth longitudinal zone does not exist at this place.

The root has its basal surface placed horizontally in relation to the axis of height of the principal cone.

The tooth *P. 98b*, which is represented only by a small part (Pl. 2, fig. 7), has had a rather large number of lateral cones, all of which, however, seem to be very small. A tendency towards the development of a secondary longitudinal crista can be observed laterally of the primary one. Between both there is a sculptureless longitudinal groove. The root is low and the basal surface is developed in correspondence with that of the tooth just described.

Teeth belonging to the middle and posterior transverse rows. — Under this heading I have grouped together the teeth *P. 98c—m*, *P. 100* and in addition some of those found at Horn Sound.

The tooth *P. 98c* (Pl. 2, fig. 8) has been comparatively large. Its length especially seems to have been considerable. What is now preserved, however, is only an end part, and consequently it is impossible to obtain any exact idea of the appearance and proportions of the tooth as a whole. Both the root and the crown are curved as in the tooth *P. 98a*, but the curvature is much less. The crown has a primary longitudinal crista clearly developed, and in addition there is a rather long secondary longitudinal one present laterally of the former. Between the two the surface of the crown is slightly sunk and forms, as in the tooth described by HULKE, a real longitudinal groove. The rest of the sculpture consists of transverse striation. On the medial surface the striae are restricted to the neighbourhood of the basal margin of the crown except for a few that issue from the primary longitudinal crista. They are all very short. On the lateral surface the striae are coarser and longer, but are discontinuous at the middle part, so that proximal stumps of them are situated close to the basal edge of the crown, while the distal ones are attached to one another and form the secondary longitudinal crista (cf. Pl. 2, fig. 8a). — The appearance of the crown and the root in cross section is seen in text fig. 4B. The basal surface of the root is placed obliquely so that it faces ventro-laterally.

The tooth *P. 98d* (Pl. 2, fig. 9) is very incompletely preserved, but, as far as can be seen, it has resembled *P. 98c*. It differs from this only by having some of the transverse striae attached to the primary longitudinal crista both on the lateral and medial side and in not having any secondary longitudinal crista developed — at least not on the small part present.

Of the tooth *P. 98e* (Pl. 2, fig. 10) a part is preserved that originally had a position somewhat to the side of the middle. It is impossible to establish whether this part belonged to the anterior or posterior half of the tooth. As far as can be judged, this tooth was probably about as large as *P. 98c*. Both the root and the crown seem

presumably to have been bent in the way described above for several teeth, i. e. so that the distal contour of the tooth was convex from one end to another and its basal contour was correspondingly concave. The crown is characterized in the first place by a very sharp primary longitudinal crista; a secondary longitudinal crista is not developed on the part present. Otherwise the sculpture of the crown consists of the usual transversal striae. These are strong on the medial side and a number of them extend right from the basal margin of the crown to the primary longitudinal crista, to which they are attached at almost a right angle. On the lateral side, on the contrary, they are finer and only comparatively few reach continuously from the basal margin to the primary longitudinal crista. As Pl. 2, fig. 10 c shows, the majority are developed as a rule only at the basal and distal parts, while the middle part is weak or is absent. Both the discontinuous and the continuous ones join the primary longitudinal

Text fig. 4.

Acrodus spitzbergensis HULKE

All the sections have the medial side to the right.

A, section through tooth	P. 98 a;
B, " " "	" P. 98 c;
C, " " "	" P. 98 e;
D, " " "	" P. 98 b;
E, " " "	" P. 98 i;
F, " " "	" P. 98 g;

All the sections in nat. size.

crista at a right angle, as on the medial side. It is also noteworthy with regard to the sculpture of the crown that a large number of shorter striae, which have nothing corresponding to them at the basal margin of the crown, are intercalated between the distal ends of the striae previously described and, like these, are connected with the primary longitudinal crista. The number of striae is in this way considerably larger close to the primary longitudinal crista than at the basal margin of the crown. — The appearance of the crown and root in section is shown in text fig. 4 C. The basal surface of the root is only slightly oblique.

In the material from Horn Sound I found several fragments of teeth which, apart from their small size, seem to differ from the tooth *P. 98 e* only by having almost all the striae, even those on the lateral side, extended continuously from the basal margin of the crown to the longitudinal crista.

The tooth *P. 98 f* (Pl. 2, fig. 11) also resembles *P. 98 e* considerably. It has, however, a less sharp primary longitudinal crista, a secondary longitudinal crista is present and the greater number of the striae, even on the lateral side too, are continuously developed and attached to the primary longitudinal crista, or, nearer the preserved end, to the secondary one.

The fragment of tooth *P. 98 g* (Pl. 2, fig. 12) agrees in all essentials with *P. 98 f* and no special description of it is necessary.

The tooth *P. 98 h* (Pl. 2, fig. 13) is represented in its present state of preservation only by its middle part. It has certainly been somewhat smaller than, for instance, *P. 98 c* and *P. 98 e*. An indication of the principal cone can still be detected and across it there is developed a transversal crista which sends out shorter striae to both sides and which shows rather strong ramification both at the lateral and the medial end. A fairly sharp primary longitudinal crista is present, but there are no signs at all of a secondary one, at least on the part of the tooth that is preserved. In other respects the sculpture of the crown seems, as far as one can see, to have resembled most closely that described on the tooth *P. 98 c*. — A transverse section through this tooth is shown in text fig. 4 D. This shows that the crown extended on the medial side

considerably out over the root and formed with this a rather marked notch. The basal surface of the root is oblique and faces ventero-laterally. Both the root and the crown seem to have been somewhat bent in the usual way, so that, seen from the medial or the lateral side, their basal contour was concave and the distal contour convex.

The tooth *P. 98i* greatly resembles in all essentials *P. 98h*, as is seen in Pl. 2, fig. 14, but the transversal crista is coarser, as are its ramifications too, and the striae on the lateral side of the primary longitudinal crista have their distal ends curved towards the slightly indicated principal cone and seem to have formed a secondary longitudinal crista, although this is now in a bad state of preservation.

The tooth *P. 98k* (Pl. 5, fig. 15) has the principal cone marked only by a distinct angle that is clearly seen both from the medial and the lateral side. A transversal crista is situated above this angle in about the same way as in tooth *P. 98h*. There is a primary longitudinal crista clearly developed as usual, and besides this there are two secondary longitudinal ones present, both situated laterally of the primary one. The one of these two that lies nearest the primary one is the longest and strongest. The position and extension of all the longitudinal cristae and their relation to the transversal crista are clearly shown in Pl. 2, fig. 15a. In other respects the sculpture has the usual character and the striae on the medial side reach from the basal margin of the crown to the primary longitudinal crista without interruption. On the lateral side they are also uninterrupted and near the transversal crista they run for some distance together with the lateral one of the two secondary longitudinal cristae; farther from the transversal crista, on the other hand, they join the medial one of them. The three longitudinal cristae have between them two sculptureless longitudinal grooves, whose extension and position is clearly shown in Pl. 2, fig. 15a. Otherwise with regard to the crown it is only necessary to mention that it is obviously somewhat bent in the usual way.

The root is very incompletely preserved and its conditions are rather uncertain in many respects.

The tooth *P. 98l* (Pl. 2, fig. 16) is very fragmentarily preserved as there now remains only a portion of its middle part. There is no sharp angle present, as was the case on the three teeth just described. A transversal crista is evident, however, but it is ramified both at its medial and lateral end rather close to the primary longitudinal one and consequently seems strikingly short. Its ramification is most abundant at the lateral end. — A cross section through this tooth is seen in text fig. 4E.

The axis of height through the crown seems in its prolongation to have met the basal surface of the root almost at right angles.

Another tooth that shows great agreement with *P. 98l* is *P. 98m* (Pl. 2, fig. 17). Both the crown and the root seem on this tooth to have been bent in the vertical plane through the axis of length in the usual way, although not particularly strongly. A primary longitudinal crista is clearly developed, whereas the transversal one seems to have not been prominent, owing to its abundant ramification even in the immediate neighbourhood of the former. The striae are somewhat more feeble on the lateral side of the crown than on the medial one and have their distal ends distinctly curved towards the transversal crista, so that long pieces of them run parallel to the primary

longitudinal crista. But notwithstanding this it can scarcely be said that there is any real continuous secondary longitudinal crista developed on this part of the tooth, but it is not impossible that there has been one nearer the transversal crista, i. e. towards the middle part of the tooth. On the medial side of the crown most of the striae reach continuously from the basal margin to the primary longitudinal crista. Towards the end of the tooth they run quite transversally, while more towards its middle part their distal ends are curved considerably towards the transversal crista. Under these conditions they consequently meet the primary longitudinal crista at an acute angle. In this way the middle part of the crown acquires a very characteristic feature, as all the striae converge, as it were, towards the point where the primary longitudinal and the transversal crista cross each other. The details of the sculpture are further shown in Pl. 2, fig. 17 and will be treated more thoroughly below in a similar tooth which is better preserved (*P. 98j*). On the medial side the crown projects rather considerably out over the root, with which it forms in this way a notch like that on the tooth *P. 98h*. The basal surface of the root is oblique in the usual way, so that it faces ventro-laterally.

In the material from the Triassic of Horn Sound there is a tooth which, as far as it is accessible for investigation, seems to resemble *P. 98l*. It is, however, considerably smaller.

The tooth *P. 100* (Pl. 2, fig. 18) is better preserved than the majority of those previously described and there is rather more than the one half of it present. The original length seems to have been about 24 mm. Its greatest height is about 8 mm.

The crown has a rather distinct and comparatively long, though low, transversal crista, which is abundantly ramified both at the lateral and medial ends. Curiously enough, no angle is developed at the place where the transversal crista is situated, but the outline of the actual masticatory surface is well rounded in the longitudinal direction both in medial and in lateral aspect. A primary longitudinal crista is present and at the end part of it there is on both sides a short secondary crista as well. The striation is developed approximately equally on both sides of the primary one and the striae extend continuously from this to the basal margin of the crown. Their distal ends all curve towards the transversal crista and meet the primary longitudinal one at an acute angle, as was the case with certain of the striae on the above-described tooth *P. 98m*.

Seen from the medial side, both the root and the crown have been fairly straight. From the lateral side, on the other hand, the crown seems weakly bent. The crown projects out over the root on the medial side and forms a considerable notch. The basal surface is very oblique and forms an angle of about 45° with the prolongation of the axis of height of the crown. It faces ventro-laterally in the usual way.

The tooth *P. 98j* (Pl. 2, fig. 19) is the best preserved of all the teeth that I have included here among those of the middle and posterior transversal rows. Its length may be estimated at about 25 to 28 mm and its greatest height is about 9 mm. Both the root and the crown are bent in the vertical plane through their axis of length in the same way as has already been described in a number of teeth and the curvature is strikingly strong in the case of the crown. The crown is somewhat higher and broader in the middle than towards the ends. As it is somewhat injured in the middle

part one cannot decide with certainty whether a transversal crista has existed. At any rate, however, it is certain that, if it existed, it must have been short. The primary longitudinal crista is distinct. On the medial side the striae extend continuously from the base of the crown to the primary longitudinal crista, which they meet at right angles. They are all straight on this side and equally thick throughout their length. Between their distal ends there issue here and there from the primary longitudinal crista a few very short striae. On the lateral side of the same crista, on the contrary a great number of such short striae are sent out. The rest of the striae on the lateral side are all long and their distal ends are curved towards the highest part of the crown, and run together into a few. Each of these in its turn then continues a long way towards the middle of the tooth, being in this course at first rather parallel to the primary crista, then curving towards and finally joining this crista. This relation between the striae gives us a good idea of the origin of the secondary longitudinal cristae. And, if one likes, one can here speak of a secondary longitudinal crista subdivided into several sections. All the transversal striae of the lateral side are, however, not of equal length basally. Only every second or every third one reaches right down to the basal margin of the crown (Pl. 2, fig. 19). These longer striae are apparently thickened at their proximal ends; this is due to the fact that they really send out fine branches on both sides (Pl. 2, fig. 19 c).

The root, like the crown, is highest and thickest at the middle. Its basal surface is about as oblique as that of the tooth *P. 100* and like all other teeth in which this is oblique, it faces ventro-laterally. On the medial side the crown and root form together a notch which is developed most strongly at the middle part of the tooth. — A cross section through the lateral part of the tooth in question is shown in text fig. 4 F.

Microscopical structure. — The teeth included here under the name of *A. spitzbergensis* show normal conditions of microscopic structure a fact that it is important to observe, as the teeth in question are partly rather distinctly differentiated from the usual *Acrodus* type by their macroscopical appearance (cf. JAEKEL, 1889).

* * *

Remarks. — Although the teeth described above sometimes show rather great mutual deviations, there seems to be no doubt, in my opinion, that the majority of them belong to the same species and, as we have seen, I think I can identify this with the species *A. spitzbergensis* founded by HULKE. A few of the teeth in question may perhaps belong to the species *A. vermiformis* described below, although with our present incomplete knowledge of this species they cannot be kept separate from *A. spitzbergensis*. It is not improbable that this is the case, for instance, with such teeth as *P. 98 b* and *P. 99 c*. If we leave out *A. vermiformis*, *A. spitzbergensis* seems to be well differentiated from most of the other known species. Such teeth as *P. 98 j*, *P. 98 l* and *P. 98 m* certainly bear a rather great resemblance to the *A. pulvinatus* type (SCHMID, 1861, Pl. 2, figs 2, 3; WOODWARD, 1889a, p. 299), but this is still too little known for us to venture to draw any conclusions as to its closer relationship to the Spitzbergen species in question. To a certain extent it also seems as if we could find some distant resemblance between,

e. g. the teeth *P. 98c* and *P. 98d* of *A. spitzbergensis* and the tooth that Miss WEMPLE (1906) has described from the Triassic of Western America under the name *A. alexandrae*.

Geological occurrence and localities. — The 13 teeth *P. 98a—m* were found by Dr. J. OPPENHEIMER during the excursion of the Geological Congress at Spitzbergen in 1910 and were kindly handed over to the Palaeontological Institute of Upsala. According to the labels they come from the lower Saurian horizon, Middlehook, which seems to indicate that they were either collected on the mountain that is called Mt Tschermak on DE GEER's latest map or on Mt Congress. The teeth *P. 99a—c* and the tooth *P. 100* were found in the bone-bed 33 m above the fish level at Mt Viking. No details are known as to the circumstances under which HULKE's type-specimen was found.

The teeth from Horn Sound were found by HOEL and RÖVIG in a bone-bed 10 m above the boundary towards the Carboniferous. The locality is at the north-east corner of Horn Sound.

***Acrodus vermiformis* n. sp.**

(Pl. 2, figs. 20, 21.)

Under the species name *A. vermiformis* I group at present only two teeth (*P. 98n*, *P. 101*).

The best and most completely preserved of these (*P. 101*) is relatively long and low (Pl. 2, fig. 20). In its present state of preservation with one end (portion) broken off it is about 24 mm long, while its greatest height does not amount to more than 5 mm.

Both the crown and the root are straight when seen from the medial or lateral side. Regarded from the crown, they are both, on the contrary, somewhat bent in the way shown in Pl. 2, fig. 20a, i. e. the median part is weakly convex at the medial side, the two ends, on the other hand, at the lateral side. The curvature of the root is weaker than that of the crown.

The crown has the same width almost throughout its entire length. At the median part it is higher than towards the ends, but the difference is, however, rather slight. A longitudinal crista which for the same reasons as in *A. spitzbergensis*, ought to be termed the primary longitudinal crista, seems to have been developed throughout the entire extent of the crown. It is somewhat stronger than in *A. spitzbergensis* and is characterized especially by its irregularly sinuated course. On both the medial and the lateral side of it there is at certain parts a discontinuous secondary longitudinal crista that is also rather strong and that resembles in its development the one on certain teeth belonging to *A. spitzbergensis*, such as, e. g., *P. 98j* and *P. 98m*, i. e. the striae running from the basal parts of the crown towards the longitudinal crista in the species in question are attached to each other in groups at their distal ends and form a number of short cristae in the longitudinal direction of the crown. Of these latter cristae each in its turn runs for a bit towards the middle part of the tooth, to finally fuse with the primary longitudinal crista, or possibly, in the case of the middle part of the tooth, with the transversal one. This latter crista most closely resembles in its development the similarly situated one on the tooth *P. 98h* (Pl. 2, fig. 13a) in *A. spitzbergensis*, but it is coarser and has a ramification that differs in its details.

Besides the longitudinal and transversal cristae the sculpture of the crown consists, as has already been pointed out, of the same sort of striation as was found in *A. spitz-*

bergensis. The striation of the medial side appears on the whole to be coarser than that of the lateral side, but otherwise it is considerably more similar on both sides than was the case in *A. spitzbergensis*. It is possible to distinguish two types of striae, short and long, which show great differences in their arrangement. The long ones have their basal ends situated close to the basal margin of the crown and extend from there in a distal direction towards the primary longitudinal crista. They are connected directly with this only farthest out at the end of the crown. Otherwise they run together in groups, as has been described, and form a discontinuous secondary longitudinal crista both on the lateral and medial side of the primary longitudinal one. The short striae, which at the same time are fine, issue from the transversal crista, the primary longitudinal crista, the stumps of the secondary longitudinal cristae and the basal parts of several of the longer striae just described. Characteristically enough, they issue from these cristae and striae as a rule almost at right angles. On the transversal and primary longitudinal crista they are generally developed on both sides, on the stumps of the secondary longitudinal cristae and on the longer vertical striae, on the contrary, only on the side that is turned from the primary longitudinal crista. As they occur in great numbers they are very prominent and help essentially to give the general sculpture of the tooth a very characteristic appearance. The notch between crown and root on the medial side is small. The root is low and the basal surface is so situated that the axis of height through the crown meets it at right angles. Text fig. 5 shows a cross section through the tooth in question.

Text fig. 5.

Acrodus vermiformis n. sp.
Transverse section through the tooth
P. 101, 1/1. Medial side to the right.

The tooth *P. 98 n* (Pl. 2, fig. 21) consists in its present state only of a fragment. It seems to agree well with *P. 101* and does not need any special description.

* * *

Remarks. — *Acrodus vermiformis* appears in several respects to be closely related to *A. spitzbergensis*, but it is still too incompletely known to be separated from this species with certainty. As I have already pointed out, it is accordingly not improbable that among the teeth that I have provisionally grouped under the species name of *A. spitzbergensis* there may also be a few belonging to *A. vermiformis*.

The species name *vermiformis* refers to the long and narrow shape of the crown, which together with the characteristic sculpture gives the teeth at a hasty glance a certain resemblance to the larva of an insect or to a worm.

Geological occurrence and localities. — The tooth *P. 98 n* was found by Dr. J. OPPENHEIMER during the excursion of the Geological Congress to Spitzbergen in 1910 and was presented by him to the Palaeontological Institute of Upsala. As is shown by its number, it was found together with teeth *P. 98 a—m* of *A. spitzbergensis* and it is therefore probable that it comes from the same horizon and locality as these, i. e. the lower Saurian horizon at Mt Congress or Mt Tschermak.

The tooth *P. 101* was found at Mt Viking in the bone-bed 33 m above the fish horizon.

Acrodus scaber n. sp.

(Pl. 1, fig. 20.)

Under this species name I have distinguished a number of fragments of teeth collected by Professor Dr. W. SALOMON of Heidelberg from the bone-bed discovered during the excursion of the Geological Congress to Spitzbergen in 1910 (STOLLEY, 1911, p. 115). All the fragments belong to the collector.

In two cases the fragments consist of fairly complete crowns. Otherwise there are mostly parts of crowns. Parts of roots are only preserved in two cases.

All the remains so far present are from small teeth. The height of the crown seems in most cases to be not much more than 1 mm. In the two cases where the length can be established with any certainty it amounts to 2 and 3.5 mm respectively, but it has often certainly been somewhat greater.

The 2 mm long crown (text fig. 6) seems to have belonged to a tooth that was situated rather far forward, though not in the foremost transversal rows. It is somewhat bent in the vertical plane through the axis of length in the same way as several of the teeth in *A. spitzbergensis* described above (text fig. 6); i. e. it is arched so that its basal contour is concave from one end to the other and its distal contour is correspondingly convex in the same direction. The highest part of the crown is situated about half way between the two ends and is not rounded but angular. A longitudinal crista is present. The rest of the sculpture, which is available for investigation only from one side, consists of a few strikingly coarse striae running from the basal margin of the crown to the longitudinal crista. Their course is, however, not entirely transversal but is oblique in such a way that their distal ends are nearer the highest part of the crown than their basal ends. Some of the striae that are situated closest to the highest part do not reach directly from the basal margin to the longitudinal crista like those situated towards the ends but fuse more or less in the way shown by text fig. 6 with their distal ends to a secondary longitudinal crista.

Text fig. 6.

Acrodus scaber n. sp.
Tooth from a specimen
belonging to Professor
Dr. W. SALOMON of Heidel-
berg. Magnification 201.

The 3.5 mm long crown is developed with a longitudinal crista and the striation is of essentially the same type as was described on the preceding tooth. The striae are, however, more sparse and feeble.

Three or four fragments of teeth resemble rather closely, as far as can be judged, the tooth *P. 98f* of *A. spitzbergensis* described above (cf. Pl. 2, fig. 11). They show, however, a coarser sculpture with sharper striae. In one of them I also observed that on one side — probably the medial one — there was a smooth surface close to the basal edge of the crown. It was also evident that the striae with their basal ends close to the smooth surface were split up into fine branches that formed a network. — On teeth of this type the root seems to be fairly high.

Finally there is also a fragment from the middle part of a tooth (Pl. 1, fig. 20) which in its general features resembles the teeth *P. 98j* and *P. 100* among those described above as belonging to *A. spitzbergensis* (cf. Pl. 2, figs. 18, 19). It has, however, a stronger transversal crista and the striae of the lateral side are considerably coarser. A further characteristic of this tooth is that the striae of the lateral side send out

numerous small branches, directed obliquely and basally, throughout their length, while such branches are sparse on the above mentioned teeth of *A. spitzbergensis* and are always restricted to the basal ends of the striae. The conditions of the sculpture on the medial side are unknown and similarly nothing can be said as to the primary longitudinal crista or possible secondary longitudinal cristae. Both the root and the crown have been rather wide.

With regard to the microscopical structure the conditions of the teeth of this species seem to have been normal (cf. JAEHEL, 1889).

* * *

Remarks. — The teeth described here are all of about the same size and have various features in common with regard to their sculpture, so I considered it proper, at least provisionally, to group them in one species. On account of their relatively strong sculpture I have suggested the species name *scaber* for them.

Acrodus scaber seems, as far as is known, to be a well defined species, resembling *A. spitzbergensis* most closely.

Geological occurrence and locality. — The material of *A. scaber* was, as already mentioned, collected by Prof. Dr. W. SALOMON in the bone-bed found by him at Mt Congress. It thus comes from the lowest Triassic.

***Acrodus oppenheimeri* n. sp.**

(Pl. 3. figs. 1—11.)

The material of this species that is present consists altogether of almost 40 teeth, most of which, however, are very fragmentarily preserved. Except for a tooth that was among the material from NORDENSKIÖLD'S Spitzbergen expedition (1864) kept at the State Museum, Stockholm, all the teeth (*P. 103—105*) belong to the Palaeontological Museum of Upsala.

Somewhat over 30 teeth occur together on a slab of slate (*P. 105*) in such a way that they undoubtedly belong to one and the same individual. It is impossible to decide whether they come from the palatoquadrate or the mandibula or from both. Together with them are found badly preserved remains of calcified cartilage and a number of dermal denticles. When nothing is said to the contrary the following description is based on specimen *P. 105*.

Teeth.

The teeth of the most anterior transverse rows are characterized, as in *A. spitzbergensis*, by the presence of a principal cone and distinct lateral cones on their crowns. In the present material there are only two such teeth.

One of them, the one figured on Pl. 3, fig. 1, is only preserved as an impression of one side and even this impression is in its turn greatly destroyed. The crown has probably had a total length of about 11 mm. It is weakly bent so that its distal contour is convex from one end to the other. Its powerful, comparatively high and sharply pointed principal cone is a very characteristic feature. On one side of the principal

cone one can observe close to it a small lateral cone and it is probable that a similar one also existed on the other side, as everything seems to indicate that the tooth was developed symmetrically. The basal margin of the crown has three small sinus appearing basally on the preserved half. The sculpture is mainly restricted to the principal cone and consists of a few fine vertical striae. — The root seems to have been comparatively low and has probably been bent in about the same way as the crown.

The other of the anterior teeth (Pl. 3, figs. 2, 3) is considerably better preserved than the former and its two sides are known. It is somewhat more than 11 mm in length and its greatest height is 5 mm. Both the root and the crown are bent in the same way as in the preceding tooth, but somewhat more strongly. The crown has a broad blunt principal cone and a very small blunt lateral cone on each side of this. The basal margin of the crown is without such sinus as are found in the above described tooth. A marked longitudinal crista extends over the principal cone from one end of the crown to the other. From this crista there issued on both sides a number of very short striae. Apart from these the sculpture consists of fine striae, situated sparsely, occurring both on the principal cone and the rest of the crown. The striae are fairly parallel to one another, vary in length, and have a transversal (vertical) course. Those on the basal part of the crown are best developed.

As far as one can judge, the root seems to be somewhat narrower than the crown. Its two ends are truncated and comparatively high. The basal edge is concave, the dorsal one correspondingly convex.

There are several teeth preserved which seem to form transitional types between the two just described and those of the middle transverse rows.

One tooth of this category is about 11 mm long. Its crown is strongly bent in the same plane as in the two teeth described above and is higher at the middle than towards the ends. A very slight bluntly rounded principal cone is present. Lateral cones on the other hand are quite absent. From the middle the crown grows continuously narrower towards the ends, which are fairly pointed. The sculpture agrees closely with that we have already seen on the two anterior teeth, but it appears to be somewhat more powerful, especially in the case of the striae that issue from the longitudinal crista.

A somewhat larger tooth measuring about 13 to 14 mm in length and with a maximum height of almost 5 mm (Pl. 3, fig. 4) shows a great resemblance in several respects to the last-described tooth. It differs from this by an asymmetrical development — its highest part is situated somewhat towards one end — and by the absence of a rounded angle. Another tooth (Pl. 3, fig. 5) of about the same size as the former is symmetrically developed, and has, as will be seen, a fairly wide crown with rather strong sculpture, which is, however, incompletely preserved. The sculpture consists on the middle part of one side — whether it is the medial or the lateral side cannot be decided — of transversal striae, extending from the basal margin of the crown up to and joining the well developed longitudinal crista. On the remaining part of the same side and probably the whole of the other there seem to be short stumps of striae issuing from the longitudinal crista, while other similar stumps were probably present close to the basal margin of the crown. The striae consequently appear to have been discontinuous in their middle.

As in the Liassic species of the genus in question *A. oppenheimeri* may probably have had two or three transversal rows among the middle ones which consisted of long and robust teeth. That this was the case is clearly shown by the comparatively considerable number of such teeth that are present in the material of the fish hitherto found. The largest of these teeth have a length of 30—33 mm, the smallest about 21—25 mm. The greatest height varies between 7 and 10 mm, and it is often as great in the shorter teeth as in the longer ones. One finds also not infrequently that the former are somewhat wider than the latter. Seen from the medial and lateral side (Pl. 3, figs. 6, 8 b, c, 9, 10), i. e. in the vertical plane through the axis of length, they are arched in such a way that their distal outline is convex and the basal one correspondingly concave. Often, however, this curvature is not strongest at their middle, but somewhat to the side of this towards one end, and in such cases the highest part of the crown is consequently situated asymmetrically. Certain teeth show in addition curvature in the horizontal plane in such a way that their middle part is convex at the medial side and correspondingly concave at the lateral side, while their end parts show quite contrary conditions (Pl. 3, figs. 8a, 10).

In the great majority of these larger teeth the crown is long and low (text figs. 7, 8; Pl. 3, figs. 6, 8, 9, 10). On several of them its width is fairly small and in several cases it is almost the same from one end to the other (Pl. 3, fig. 10). The narrowing towards the ends is, however, always continuous and gradual, so that there are no sudden contractions or similar appearances of the breadth of the crown, as is often the case in the type of teeth described in the literature under the name of *A. gaillardoti*.

The crown has no trace of cones. Its highest part is always well rounded, has never any marked angle, and, as has already been pointed out, is often somewhat asymmetrically situated towards one end.

The sculpture is rather similar on all the larger teeth in question. A longitudinal crista, which may either occupy a median position or may be situated more or less to one side, is always developed. On the other hand a transversal crista is quite absent. Numerous striae issue at right angles on both sides of the longitudinal crista. Every second or every third one of these is very short, fairly straight and always unramified. The others are long, weakly sinuated, and send out fine branches, often directed obliquely and basally. The majority of them also extend right to the basal edge of the crown both on the lateral and the medial side. On the lateral side they are not infrequently thickened close to this edge. — Sometimes on certain of the shorter teeth belonging to this category one can find a certain indication of a radiating arrangement of a number of striae on the highest part of the crown, and at the same time the rest of the sculpture somewhat resembles that of the most anterior teeth.

On the medial side the crown forms with the root a notch, often rather strong (text figs. 7 A, B, C). In most cases the root is probably at least somewhat narrower than the crown and is strikingly high in relation to the latter. Its basal surface does not seem to be oblique on the few teeth in which it can be observed.

Text fig. 7.

Acrodus oppenheimeri n. sp.
Cross-section through teeth from the middle transversal rows. Medial side to the right. A, through the tooth belonging to State Museum, Stockholm; B and C, two teeth from specimen P. 105. $\times 14$.

Finally of the teeth belonging to the posterior transversal rows only a few seem to be preserved in the material so far known. A small tooth, about 5 mm long and 2 mm high (Pl. 3, fig. 11), certainly belongs to this category and, to define it more closely, probably to the most posterior transversal row of all. The crown and root on this tooth are straight. The crown is low and has had a sculpture of delicate transversal striae. A couple of other incompletely preserved teeth, which are characterized by their weak curvature both in the vertical and horizontal plane and also by their comparatively small size, but which otherwise closely resemble the teeth of the median transversal rows in sculpture and other respects, may have possibly been situated in the transversal row next to the most posterior one or in the third one counting from the last-mentioned row (Pl. 3, fig. 7).

Text fig. 8. *Acrodus oppenheimeri* n. sp. Schematic restoration of the dentition in one half of a jaw, as indicated by the teeth belonging to specimen P. 105 and the *Acrodus* species from the Lias. 1/2.

The present material of *A. oppenheimeri* has been able, as we have seen, to afford us a more certain and complete knowledge of the dentition than is usually the case in the Triassic *Acrodus* species. If we assume that this species, like certain other of the same genus that are known from the Lias, had 8 transverse rows of teeth, the dentition in it ought probably to appear about as is shown in text fig. 8. It must however be

expressly mentioned that there is still much unknown and that this figure is only intended to give an idea of the approximate position of the most important types of teeth so far known.

The teeth of *A. oppenheimeri* show the same conditions as to microscopic structure as are usual in the genus *Acrodus* (cf. JAEKEL, 1889).

Dermal denticles.

As has already been mentioned there occur together with the teeth of *A. oppenheimeri* a number of dermal denticles, practically all badly preserved. They are not conical in shape as in *A. nobilis* and *A. anningiae* (WOODWARD, 1889, p. 284, p. 289), but are as shown in text fig. 9.

Remarks. — The dentition in *A. oppenheimeri* is, as we have seen, composed partly of rather different teeth. The teeth of the anterior transversal rows possess in the comparatively strong development of the principal cone and the sculpture of the crown characters that remind us very much of *Hybodus*. Certain of them, e. g. the one figured in Pl. 3, fig. 2, have also a rather great resemblance to a number of types of teeth of *A. minimus* (cf. especially the tooth figured by SCHMID, 1861, Pl. 2, fig. 38).

The teeth of the median transversal rows and to a certain extent those of the posterior ones as well in *A. oppenheimeri* are, both with regard to their general shape

and their sculpture, closely related to the type of teeth to which AGASSIZ and the majority of the subsequent investigators have given the species name *A. gaillardoti* (WOODWARD, 1889a, p. 279), but they differ very distinctly from this, especially in the uniformly narrow and low shape of the crown.

The teeth of the middle and posterior transverse rows in *Acrodus oppenheimeri* also resemble to a certain extent the tooth to which Miss WEMPLE (1906) gave the name of *A. oreodontus*, but this has a little and prominent cone on the crown, which, to judge from her figure, has an additional special characteristic in the coarseness of its longitudinal crista. The relations between *A. oppenheimeri* and *A. wemphiae* JORDAN (JORDAN, 1907, p. 100) are still very uncertain.

Acrodus oppenheimeri is named after Privatdozent Dr. J. OPPENHEIMER of Brinn. I intended originally to name the teeth he had collected himself after him, but it turned out, as we have seen, that practically all of them were identical with HULKE's species *A. spitzbergensis*.

Geological occurrence and localities. — *Acrodus oppenheimeri* rarely occurs in the upper Saurian horizon. So far it has only been found at Mt Tschermak, Mt Saurie and south of Sassen Bay on the mountain between De Geer Valley and Flower Valley.

Text fig. 9.

Acrodus oppenheimeri n. sp.
Dermal denticles. A. From the lateral surface. B. From the dorsal or ventral edge.
Magnification 15/1.

Cephalic spines, fin-spines and dermal denticles belonging to *Hybodus*, *Acrodus* or closely related genera.

Cephalic spines.

Of cephalic spines only a basal plate (*P. 351*) has been found so far. Its appearance and size are shown in Pl. 1, fig. 11.

* * *

Geological occurrence and locality. — Bone-bed 33 m above the fish horizon, Mt Viking.

Fin-spines.

At present only four fin-spines are known of the type characteristic of *Hybodus* and *Acrodus* (*P. 42*, *P. 102*, *P. 282*, *P. 383*).

The best preserved of these is *P. 282*, of which only a small part is missing at each end. In its present state of preservation it is 91 mm long, but originally it was probably about 100 mm. The maximum width between the anterior and posterior edges is 10 mm. Pl. 1, fig. 17 clearly shows its shape and sculpture and makes a special description superfluous. It ought, however, to be pointed out that the ridges are better separated than the figure suggests; this is due to the fact that the interspaces could not be quite freed from stone in the preparation. For the same reason the ridges also seem here and there to be a little varicose, which as a matter of fact is not the case. They all grow gradually and uniformly narrow towards their distal ends.

The fin-spine *P. 42* (Pl. 1, fig. 18) is represented in its present state of preservation by a portion of the distal part. At the proximal end this portion measures about 30 mm

from the anterior to the posterior edge, at the distal end in the same direction only about 18 mm. The appearance of the cross section at both ends is seen in text fig. 10 A, B.

The posterior edge (Pl. 1, fig. 18 a) has been equipped with denticles, but only the basis of a few of these are preserved. The lateral surfaces are without the usual ridges and all coarse ornament, but this is probably a secondary condition and due to weathering. The fine longitudinal striation that is present and whose character is clearly shown by Pl. 1, figs. 18 a, b, is presumably found in all the fin-spines that, like this one, are built up in their external parts of trabecular-dentine.

Text fig. 10.

Cross section through fin-spine *P. 42*. 1/1.

A. Cross section through the proximal end of the preserved part. B. Cross section through the distal end of the same part. *o*, dentine of normal character (ortho-dentine); *o*, trabecular-dentine, outer layer; *o*₁, trabecular-dentine, inner layer; *p*, pulp cavity.

This outer layer of trabecular-dentine is in the present case thick and strong (*o*, text fig. 10 A). Inside it there follows a layer of ortho-dentine (*d*, text fig. 10 A), which becomes thicker towards the distal end of the spine in the way AGASSIZ has described (1843, vol. III, p. 215). The tubules of this ortho-dentine are somewhat irregularly and strongly ramified. The pulp cavity is much reduced in the part present (*p*, text figs. 10 A, B) and really consists only of a fine vertical canal. The space between this and the ortho-dentine is filled up with a layer of trabecular-dentine (*o*₁, text fig. 10 A) of the same type as in the outermost layer. As far as one can judge, this inner layer of trabecular-dentine has, however, been thinner towards the point of the spine, while, as has been mentioned, the ortho-dentine is thicker there.

According to AGASSIZ (1843, pp. 212, 215, Tab. A, figs. 8, 9) the *Hybodus*-like fin-spines lack the central layer of trabecular-dentine that was found in the fin-spine *P. 42* described above. As our knowledge of the structure of fin-spines in general is very incomplete, it is not yet possible to decide whether this layer is of any importance from a systematic point of view.

The fin-spine *P. 102* is the one mentioned by WOODWARD 1912 (p. 291). It is represented by three fragments, one of which shows the shape of the pulp cavity at its proximal part.

The spine has been rather large and its maximum width (from the anterior to the posterior edge) is, as WOODWARD states, about 30 mm. The sculpture is of the usual type. Its appearance is seen from Pl. 1, fig. 15.

With regard to its finer structure it is noteworthy that no traces of any central layer of trabecular-dentine are found. It is also worthy of mention that the layer of ortho-dentine is absent round the proximal part of the pulp cavity, while it is present further distally and becomes rather thick towards the point. — I have also been able to ascertain that at least the fin-spine *P. 282* described above has no layer of ortho-dentine at its proximal end.

The fin-spine *P. 883* is very incomplete (Pl. 1, fig. 16) and no reliable measurements can be given. The posterior edge has, as usual, a double row of thorn-like denticles. The ridges are finer than on the preceding fin-spine. The pulp cavity in the preserved part is rather large and is surrounded by a distinct and fairly thick layer of ortho-dentine.

Remarks. Of the fin-spines mentioned here *P. 102*, *P. 282* and *P. 883* belong undoubtedly to the *Hybodus* and *Acrodus* type; *P. 42* differs by having a partly diverging microscopic structure, but it is not yet possible to ascertain the importance of this. It is of course also conceivable that *P. 42* showed different conditions with regard to sculpture, etc. from the typical spines. But, at least for the present, I thought I could group it together with them.

The fin-spine *P. 282* seems to resemble rather much the spine described by JAEKEL under the name of *Hybodus laczkoi* (JAEKEL, 1911b, p. 18, text fig. 7), but it is curved in another way. It is well differentiated from *H. dimidiatus* by its general shape and the appearance of the denticles (cf. JAEKEL, 1889).

The other fin-spines are too incompletely known to be compared with the ones described earlier.

Geological occurrence and localities. — The fin-spine *P. 282* was found on the east side of Mt Marmier in a bone-bed in the fish-horizon; the fin-spine *P. 42* was found at Mt Viking in the bone-bed 33 m above the fish-horizon. The two other fin-spines belong to the material collected by Dr. B. HÖGBOM and the locality is given on the labels only as «Middelhook». *P. 883* was found some metres below the lower Saurian level and *P. 102* in the «Daonella layers», i. e. in or near the upper Saurian horizon.

Dermal denticles.

Detached dermal denticles are present in great numbers and it seems certain that at least a part of them belonged to *Hybodus* and *Acrodus*. Certain of them even resemble those described by me above in *A. oppenheimeri* (p. 24). Others, as Pl. 1, fig. 14 and text figs. 11 A, B, C show, have partly another appearance.

Text fig. 11. Dermal denticles.
A, from *P. 57¹⁰/1*; B, from *P. 77¹⁰/1*; C, from
P. 609¹⁰/1.

* * *

Geological occurrence and localities. — Detached dermal denticles are found in all bone-beds. In two of these, namely the one 33 m above the fish-horizon and the one in the lower Saurian horizon, they are exceedingly common. The one in Pl. 1, fig. 14 and the two in text figs. 11 A and C come from the former horizon, while the one in text fig. 11 B comes from the latter.

Genus *Polyacrodus* JAEKEL.

Synonym: *Hybodus* (in part) JAEKEL, 1889.

The genus *Polyacrodus* was founded by JAEKEL in 1889 (p. 321) for certain teeth from the Triassic, which were considered by AGASSIZ and subsequent authors to belong to *Hybodus*. JAEKEL's characterization of the genus at that time can be summarized as follows: The teeth agree with *Acrodus* with regard to the root. The crown in its general development is like that of *Hybodus*, with a principal cone and lateral cones, but all these cones, unlike those of *Hybodus*, have a short skittle-like shape. The crown has a longitudinal keel. The striae issuing from this on both sides and passing off fairly trans-

versally are somewhat coarse and sparse and do not reach the basal margin of the crown. Other striae, also transversal, in the neighbourhood of this margin are finer and situated closer together. There is usually a stronger stria crista running in a basal direction on the lateral and medial sides of the cones, giving these a more or less distinct pyramidal shape. — The dental crown is almost entirely formed of ortho-dentine, contrary to what is the case in *Hybodus* and *Acrodus*.

The microscopic structure of the crown is considered by JAEKEL as the most important characteristic of the genus, but he adds at the same time it may easily be thought that this structure has arisen from the one found in *Acrodus*. «Man hat eben nur anzunehmen», he writes, «daß die auch bei *Acrodus* vorhandene Dentinzone bei *Polyacrodus* sehr mächtig entwickelt ist.»

In a paper published in 1898 JAEKEL somewhat modified his original definition of *Polyacrodus*. He now limits it (pp. 137—138), as he says, to the teeth, «bei denen sich ein zusammenhängender Längskiel über sämtliche Zahnkegel zieht und die Fältelung der Seitenflächen von den Zahnspitzen ausgeht». Eight years later he considers (1906 a, p. 158) that, on account of the nature of the teeth, he ought also to include in the genus *Polyacrodus* the species from the Lias described by FRAAS as *Hybodus hauffianus*.

As has already been pointed out in this work (p. 3 above) KÖKEN found (1907) that *H. hauffianus* had the teeth developed as in the typical *Hybodus* species with regard to the microscopical structure and that *H. hauffianus* in all other respects as well could not be separated from the genus *Hybodus*. He further remarks that we must attribute a greater scope of variation not only to the outer shape of the *Hybodus* teeth but also to their microscopical structure, especially with regard to the degree of development of the dentine. In accordance with this he has considered *Polyacrodus* as a synonym of *Hybodus* in his treatise of the fishes in the second edition of ZITTEL'S «Grundzüge der Paläontologie» (1911).

Finally SCHLOSSER (1918, p. 59) has adopted the genus *Polyacrodus*, but restricted it to include teeth from the Triassic alone.

Polyacrodus has hitherto only been known from Germany and the east of France, where it has been found especially in the Muschelkalk and the lower Keuper (cf. above p. 1, note 2).

It is now very remarkable that in the Triassic of Spitzbergen two species occur which in their characters resemble both *Hybodus*, *Acrodus* and *Palaeobates*. As far as I can see they come within the bounds of JAEKEL'S definition of the genus *Polyacrodus* and I thus consider it certain that this genus ought to be maintained. At the same time it seems to me also necessary to confine it to Triassic forms, as SCHLOSSER did.

The new material from Spitzbergen affords of course a somewhat extended knowledge of *Polyacrodus* and I have therefore to add to JAEKEL'S original definition the statement that the dentition was probably rather heterodont. With regard to the ornament of the teeth it ought to be expressly stated that this may be very feebly developed or be quite absent, and that it consists of striation mainly issuing from the longitudinal keel.

In this connection it is worth nothing that one of the *Polyacrodus* species described below, *P. angularis*, resembles especially closely certain of the types of teeth that QUENSTEDT (1852, p. 179), ECK (1865, p. 118) and WOODWARD (1889 a, p. 282) have grouped together

under the name of *Acrodus minimus*. This makes it very desirable to have a microscopical investigation of all the types of teeth referred to this species. I did not have the material to carry this out myself.

***Polyacrodus pyramidalis* n. sp.**

(Pl. 1, figs. 21—26.)

The material of which I have established this species consists of 12 incomplete teeth (*P. 713*—*717*). With a few exceptions it is only crowns or parts of crowns that are present. They are usually so embedded in the stone that only one side is accessible for investigation.

The smallest tooth is scarcely 2 mm long; the maximum height of its crown is somewhat over 1 mm. In the largest teeth the length may be estimated at about 8 mm, while the crown has a maximum height of 2.5—3 mm.

The teeth that I group here under the species name *Polyacrodus pyramidalis* are of at least three types, mutually rather different, and the dentition must therefore have been rather heterodont if my view is correct. Only a very vague idea can be obtained of the position of the different types of teeth in relation to each other when they were in situ in the jaws. To judge from their shape it seems probable, however, that they were arranged in somewhat the same way as in *Acrodus* and the *Palaeobates* species described below.

The crown (*P. 717a*) figured in text fig. 12A and in Pl. 1, fig. 21 is about 2 mm long and its greatest height is somewhat more than 1 mm. Even towards the well rounded ends the height is strikingly great. The crown is not quite straight but shows, as the figures indicate, a slight bend in the vertical plane through its longitudinal axis in the same way as several of the above-described *Hybodus* and *Acrodus* teeth. It has a broad, relatively high and rather sharp principal cone, but this is situated somewhat towards one end of the crown. Between the principal cone and this end there are two fairly low, blunt lateral cones. On the other side of the principal cone there are, on the contrary, no lateral cones at all. A longitudinal keel seems, as far as one can judge, to have extended between the two ends over the three cones. On the side accessible for investigation — probably the lateral side — the sculpture consists of delicate, sparse striae, which issue from the longitudinal keel and pass off in a basal direction. They do not nearly reach the basal margin of the crown, however, but between this and their basal ends there is a sculptureless stretch. The striae often show a certain convergence towards the distal ends of the cones. — Only fragments of the root are preserved.

The tooth figured in text fig. 10B and Pl. 1, fig. 22 (*P. 714a*) resembles very closely in all respects the one just described. It is, however, larger and has lower and blunter lateral cones. The root is partly preserved. As in *Hybodus* and *Acrodus* a number of Haversian canals open on its surface.

Another type of teeth is represented by five crowns (*P. 712a*, *P. 714b*, *P. 715a* and *b*, *P. 717b*), all of which resemble each other very closely. None of them is completely preserved. The largest one was probably about 8 mm long and about 2.5 mm high, while in the case of the smallest these measurements were 6 mm and 2 mm respectively. They have all been slightly bent (text figs. 12C, D; Pl. 1, figs. 23, 26) in the same way

as in the preceding type. The curvature is strongest on the side I take to be the lateral one (text fig. 12D; Pl. 1, fig. 23c). Above or in the neighbourhood of the middle of the crown there is a principal cone, certainly rather low but all the same quite prominent, and on both sides of this there is towards each end a very blunt and low lateral cone in the way shown by the figures. The principal cone often has a markedly pyramidal shape and is in a characteristic way considerably wider from the lateral to the medial side than the crown is otherwise, so that, seen from the distal end, it appears as a distinct thickening at the middle of the crown (Pl. 1, fig. 23a). This thickening is strongest on the side that I take to be the lateral one (text fig. 12D; Pl. 1, fig. 23c), where it continues in a basal direction right to the basal margin of the crown.

The two ends of the crown are rather high and rounded. Between them a median longitudinal keel extends over all the cones. The surface of the crown both laterally and medially of this keel is divided lengthways into a dorsal and a basal half, the former of which faces dorso-medially, the latter ventro-medially. The two halves meet in a not very prominent longitudinal edge (text figs. 12 C, D). The whole appearance seems to me to indicate that a notch was developed here between the root and the crown both on the medial and the lateral side.

Text fig. 12.

Polyacrodus pyramidalis n. sp.

Teeth of the three types present. A, B, from *P. 717a* and *P. 714a* respectively; C, D, from *P. 715a* and *P. 715b* respectively; E, from *P. 716a*. All teeth with magnification 4/1.

The sculpture is most developed on the lateral side and closely resembles that described on the two teeth *P. 714a* and *P. 717a*. The striae are, however, considerably shorter (text fig. 12D). On the medial side the sculpture is limited to the principal cone and consists of a few rather coarse striae. Both on the medial and the lateral side the striae of the principal cone exhibit a slight convergence in distal direction.

Of a third type of teeth the present material contains only two crowns, *P. 712b* and *P. 716a* (text fig. 12E; Pl. 1, figs. 24, 25). The larger of these (*P. 712b*) has been about 8 mm long and its maximum height has been 3 mm; for the other the same measurements amount to 6 mm and 2.5 mm respectively. Both teeth are bent in the same way as the preceding ones and also show with regard to their shape some obvious resemblances to them. They have a strong and broad but bluntly rounded principal cone. One of them, *P. 716a* (text fig. 12E, Pl. 1, fig. 24), has on each side of the principal cone only one lateral cone, while the other, on the contrary, seems to have had two. The development and position of the lateral cones is the same as on the teeth belonging to the type described just above. As in these, so here too the principal cone is thicker than the rest on the tooth. The thickening on the medial side is, however, still more marked in this type and its continuation in the basal direction even forms a distinct swelling on the basal margin.

A notch between the root and the crown has been developed at least on the medial side.

The sculpture is nearly quite lacking, but if this is due to weathering or ought to be considered as a primary condition cannot be decided. As far as one can see it consists only of some indistinct striae on the principal cone.

On all the teeth in question the crown consists entirely, apart from its thin peripheral layer of enamel (cf. TOMES, 1914, pp. 50—59), of ortho-dentine, as in *Palaeobates*. As has already been pointed out, the root consisted of ordinary trabecular-dentine (cf. TOMES, p. 192; RÖSE, 1898, p. 42).

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*
*

Remarks. — The types of teeth dealt with here have so many common characteristics that, in spite of their rather great differences, I feel justified in combining them in one species. I have suggested the name *P. pyramidalis* for this species on account of the shape of the principal cone.

As far as is known *P. pyramidalis* seems to be most closely related to *P. angularis* described below. It is well differentiated from *P. polycyphus* (AGASSIZ) — cf. JAEKEL, 1889.

Geological occurrence and locality. — *Polyacrodus pyramidalis* is only known from Mt Bertil, where it occurs in a bone-bed belonging to the upper Triassic (the upper sandstone series). According to barometrical measurements the bone-bed is situated about 263 m above the fish level, but on account of the slope of the strata this figure is probably somewhat too low.

Polyacrodus angulatus n. sp.

(Pl. I, fig. 27.)

Under this name I have provisionally grouped five detached crowns of teeth, belonging to the material collected by SALOMON in 1910 and in his possession. None of the crowns is accessible on both sides for investigation. They are all very small, their length varying between about 1.5 to 2 mm and the height between 0.5 to 0.75 mm.

As in *P. pyramidalis*, so here one finds teeth of at least three types.

The crown which is shown in text fig. 13 A is the only one known of its type. It is nearly straight and has a powerful, rather high and somewhat blunt principal cone, which is symmetrically situated between both ends of the crown. The principal cone and the part basally of it are very much thickened in comparison with the other parts of the crown and this thickened part also forms a swelling on the basal margin in the same way as in the type of tooth figured in text fig. 12 E belonging to *P. pyramidalis* though not so much prominent as in this latter. There is only an indication of a lateral cone on one side of the principal cone.

A longitudinal crista seems to be developed and probably also extended over the principal cone. On the side accessible for investigation the crown is nearly quite smooth or has at least no striae clearly discernible.

Another type is also represented by one crown (text fig. 13 B). This is bent in the vertical plane through its axis of length in the usual way, so that its base is concave in the longitudinal direction and its dorsal contour is correspondingly convex. It has a principal cone that is certainly not high but all the same very distinct; this cone is bluntly rounded and is situated somewhat asymmetrically on the side of the transversal middle axis. A lateral cone is very faintly indicated on each side of the main cone by

an angular swelling. The side accessible for investigation — apparently the medial one — is divided lengthways by means of a blunt longitudinal edge into a basal and a distal longitudinal part about in the same way as in *P. pyramidalis*.

A median longitudinal keel seems to have been present. A transversal keel is developed from the distal end of the principal cone to the longitudinal edge of the medial side. Otherwise the medial side is quite without sculpture.

The crown has been wider than the root and between them there has been a notch at least on the medial side.

The third known type of teeth is represented by three crowns, all of which are bent in the usual way in the vertical plane through the axis of length. In this case, however, the curvature is fairly strong (text fig. 13 C; Pl. 1, fig. 27). There is no real principal cone, although the crown has a very distinct angle and is strongly thickened at the place for this cone on the lateral side. Lateral cones, on the other hand, are indicated on one of the crowns and corresponding to each of them there is a thickening on the lateral side.

Text fig. 13.
Polyacrodus angu-
latus n. sp.
Three types of dental
crowns, 6/1.

A median longitudinal keel is present and there seems to be also a transversal keel over the highest part of the crown, at least on the medial side. This side, which is without any other sculpture, is developed in the same way as in the type just previously described (cf. text figs. 13 B and C). The lateral side has also been smooth. The crown has been wider than the root and a notch was formed between them, at least medially.

With regard to the microscopic structure *P. angulatus* agrees with *P. pyramidalis*.

* * *

Remarks. — I am of the opinion that the three types of teeth described here ought to be grouped under a common species name, as, in spite of a large number of differences, they still have important features in common.

Polyacrodus angulatus seems undoubtedly to be rather closely related to *P. pyramidalis*. It differs from this, inter alia, by a different development of the cones, the almost total absence of striation, and probably also by its smaller size.

It is also noteworthy in this connection that *P. angulatus* resembles to a rather great extent certain of the types of teeth that have been incorporated with *Acrodus minimus* AGASSIZ. This is true, for instance, of the teeth described by AGASSIZ (1843, vol. III, p. 146; Pl. 22, figs. 13—15) under the name of *Acrodus acutus* and also PLIENINGER'S (1844, p. 116; Pl. X, figs. 20—22, 27) so-called *Thectodus* species. Whether the resemblance extends further than the exterior is, however, not known, but this would certainly be worth further investigation.

The name *angulatus* for this species refers to the fact that the tooth crowns have not infrequently an angle developed in the highest part.

Geological occurrence and locality. — *P. angulatus* is so far known only from the bone-bed found by SALOMON in the lower Triassic at Mt Congress, where it seems to be rather common.

Genus *Palaeobates* H. v. MEYER.

Synonyms: *Psammodus* (in part) GEINITZ H. B. (ex AGASSIZ M. S.) 1837, *Strophodus* (in part) AGASSIZ 1838.

Teeth belonging to *Palaeobates* are found mentioned in the literature for the first time in 1837 under the generic name of *Psammodus* (GEINITZ, p. 22, Pl. III, figs. 6, 7; HOGARD, pp. 214, 235). In 1838 AGASSIZ considered that he ought provisionally to include these teeth in the genus *Strophodus* and in connection with this he says in his description of the teeth of *S. angustissimus*: «leur extrême petitesse qui sort des limites que l'on observe habituellement dans les dimensions des espèces d'un même genre, me porterait même à croire qu'elles proviennent d'un poisson qui constituera un jour un genre à part, quand il sera mieux connu» (1838, vol. III, p. 128).

The generic name of *Palaeobates* was introduced in 1849 by H. v. MEYER (1849 b, pp. 233—234) for those of AGASSIZ's *Strophodus* species that were known from the Triassic.

Among the investigators who have worked on teeth of *Palaeobates* may be mentioned, in addition to those already given: SCHMID (1861, pp. 6—9), ECK (1865, p. 62), WOODWARD (1889 a, p. 248) and JAEKEL (1889, p. 327; 1911 b, p. 17). JAEKEL especially has made a study of the microscopical structure of the *Palaeobates* teeth.

In his family «Des Cestraciontes» AGASSIZ included his genus *Strophodus*, comprising in it, among others, also the teeth we now distinguish under the name of *Palaeobates*, together with *Cestracion* CUVIER, *Ptychodus* AGASSIZ, *Acrodus*, *Psammosteus* AGASSIZ, *Ceratodus* AGASSIZ and a number of other genera. A similar view was also held by PICTET (1845), GIEBEL (1848) and QUENSTEDT (1852) among the older authors.

H. v. MEYER (1849 b) was of the opinion that the *Palaeobates* teeth most closely resembled those of *Myliobatis* and *Zygobatis*, i. e. that they were teeth of rays, and the same view was taken by SCHMID in 1861.

ZITTEL in his «Handbuch der Paläontologie» (1887—1889, p. 77) includes *Palaeobates* in *Strophodus*, which, together with *Cestracion*, *Orodus* AGASSIZ, *Campodus* DE KONINCK *Acrodus*, *Ptychodus* and a couple of other genera, he groups in the family *Cestracionidae*.

WOODWARD (1889 a, p. 248) placed *Palaeobates* as an independent genus among the Cestracionids, to which he also referred the genera *Orodus*, *Campodus*, *Diclitodus* DAVIS, *Sphenacanthus* AGASSIZ, *Tristychius* AGASSIZ, *Wodnika* G. VON MÜNSTER, *Hybodus*, *Asteracanthus* (*Strophodus*), *Bdelodus* QUENSTEDT, *Palaeospinax* EGERTON and *Synechodus* A. S. WOODWARD.

In 1889, after thorough investigations of teeth belonging to *Palaeobates*, JAEKEL was able to separate this genus from others better than preceding investigators, and, while emphasizing its relationship to *Acrodus*, he follows the view that it ought to be included among the Cestracionids. *Palaeobates* is now usually found among these in textbooks, e. g. in the two later editions of ZITTEL's «Grundzüge der Paläontologie» (1911, 1918), while *Orodus*, *Ctenacanthus* (*Sphenacanthus*), *Hybodus*, *Tristychius*, *Acrodus*, *Polyacrodus*, *Asteracanthus* and *Wodnika* are separated from the Cestracionids and grouped in the family *Hybodontidae*.

Palaeobates was for a long time known only from upper Bunter Sandstone and the Muschelkalk in Germany and the east of France. In 1890, however, TOMMASI (p. 3) mentioned *Palaeobates* in the Triassic of Raibl. In 1911 JAEKEL described a *Palaeobates* species from the Bakony-Wald (1911 b, pp. 17—18) and I have now myself ascertained beyond all doubt that this genus is represented in the Triassic of Spitzbergen as well.

It is also possible that the teeth from the upper Triassic in North California, described by BRYANT under the name of *Strophodus shastensis* (1914), belong to *Palaeobates*. At any rate these teeth show a rather considerable resemblance to *Palaeobates* teeth in their general shape and the same seems to be true of their sculpture. In this case the microscopic structure would certainly show quite distinctly if we were concerned with teeth of *Palaeobates* or *Strophodus*, but this is still unknown.

The material from Spitzbergen now makes it possible to give a somewhat more complete definition of the genus *Palaeobates* than previously. The characters so far known can be summarized as follows: Mandible short and high with comparatively few, probably only five or six transversal rows of teeth; possibly an unpaired symphyseal row is also present. The third and fourth transversal rows, counting from behind, each consists of long, large teeth, the rows that follow anteriorly and posteriorly consist of smaller teeth, the most posterior row having even very small teeth. The anterior teeth have a more strongly arched crown than those following posteriorly. The dentition in the palatoquadrate is not known in detail, but it possibly differs somewhat from that of the lower jaw. All the teeth, both in the palatoquadrate and the mandible, have a flattened, long and narrow crown without lateral cones, but sometimes with a principal cone. A longitudinal crista is often present, but may also be absent. The sculpture of the crown consists of fine, very much ramified striae, in certain species anastomosed with each other and forming a network. The crown has a rather thin layer of enamel, apart from which it is entirely formed of ortho-dentine; the root consists of trabecular-dentine. There is often the remains of a pulp cavity between the root and the crown.

The Spitzbergen material confirms the view that we have in *Palaeobates* a genus differing distinctly from all other known Selachian genera. It is also clear that *Palaeobates* most closely resembles *Polyacrodus* with regard to the microscopic structure of the teeth, while on the other hand, to judge from the general shape and arrangement of the teeth, it seems to occupy an intermediate position between *Acrodus* and *Asteracanthus*. If a family *Hybodontidae* is accepted with the definition of KOKEN and SCHLOSSER in the later editions of ZITTEL's «Grundzüge der Paläontologie», there is no doubt that *Palaeobates* ought to be included in this family.

Palaeobates polaris n. sp.

(Pl. 3, figs. 12—18.)

This species is represented by two specimens (*P. 107* and *P. 108*). On both there are remains of teeth and dermal denticles. One (*P. 107*) has also a number of parts of the visceral skeleton preserved.

Visceral skeleton.

The visceral skeleton is calcified in the usual way in its peripheral layers. The calcified layer seems to be about 0.5—1 mm thick.

Only small portions of the palatoquadrate are preserved. The right mandibula is fragmentary, the left, on the other hand, is almost perfect, as only its postero-dorsal corner is absent (text fig. 14; Pl. 3, figs. 16 a, b).

The mandibulae are strikingly high in relation to the length, as the length was about 10 cm and the greatest height about 4 cm. The lower margin is strongly convex and passes over without any definite corner into the posterior one. The anterior margin, on the other hand, is better defined and passes into the ventral one by means of a rounded angle. The upper margin has an obtuse-angled process in front of the articulatory fossa, otherwise it seems to have been straight and to have occupied an almost horizontal position. In the direction from the anterior to the posterior margin the mandibulae are concave on the lateral side and correspondingly convex on the medial side.

The cartilage in the mandibulae has had a total thickness of about 10 mm. Its uncalcified part is in its present state of preservation replaced by calcite.

Between the two mandibulae there is a paired, long skeleton element which is somewhat arched. It seems as if we were concerned here with the ceratohyal (*Chy*, Pl. 3, fig. 16 a).

A number of poorly preserved cartilaginous fragments, situated between, behind and ventrally of the mandibulae, have probably belonged to the gill-arches.

Dentition.

The arrangement and shape of the teeth.— Specimen *P. 107* shows on the left mandibula five transversal rows with teeth that are rather well preserved in situ (text fig. 14; Pl. 3, figs. 16 a, b). As the most anterior of these rows lies rather near the anterior edge of the mandibula, it is clear that the space for further rows in front of those that are preserved is very restricted. We can therefore conclude with rather great probability that the total number of transversal rows was at most six. It cannot be decided with full certainty whether any unpaired symphyseal row was present, but it seems very probable that this was the case.

I have denoted the most anterior of the preserved rows by the letter *a*, the one following behind it by *b*, etc. (text fig. 14, Pl. 3, figs. 16 a, b).

The tooth-row *a* is composed of at least 6 teeth, having on an average a length of about 10 mm and a maximum breadth of 2—2.5 mm. As text fig. 14 shows, they are situated rather obliquely in such a way that their anterior end is nearer the labial margin of the jaw than is the case with the posterior end. The tooth nearest to the labial margin has the masticatory surface of the crown turned dorsally, the tooth farthest from it, on the other hand, has the same surface turned ventrally. The teeth intermediate between these two occupy transitional positions.

The teeth in row *a* are fairly strongly bent, so that the masticatory surface is convex from one end to the other. The most raised part of the crown is at about the middle of the teeth or sometimes a little in front of the middle; the greatest width of the crown is also situated at the same place. The anterior half of the crown grows more narrow than the posterior half, and the anterior end is therefore rather pointed. Another characteristic of the anterior end-part seems to be that it is arched towards the medial side.

Text fig. 14. *Palaeobates polaris* n. sp.
The left mandibula, seen from the medial side with five transversal rows of teeth in situ. 1/2.

The sculpture of the crown is incompletely preserved. It is evident, however, that a longitudinal crista has been present and that this crista was situated somewhat on the lateral side of the median line of length. One can also see that dense transversal striae have issued, at least anteriorly, from the longitudinal crista to both sides.

The root, though preserved on a number of teeth in the row in question, is not accessible for any detailed investigation.

Row *b* (text fig. 14, Pl. 3, figs. 13, 16 a, b) consists of seven teeth, which are considerably larger than those in row *a*. Their length is about 14–15 mm, the maximum breadth 3–3.5 mm and the greatest height about 5 mm.

Their arrangement is such that the axis of length through each of them is fairly parallel with the labial margin of the mandibula. Their relative positions are the same as in the teeth in the row in front.

Seen from the lateral or the medial side they are bent in the usual way so that the masticatory surface is convex from one end to the other and the basal surface of the root is concave in the same direction. The curvature is strongest, however, somewhat caudally of the middle and the highest part of the crown is also situated at this place, as shown in text fig. 14.

Text fig. 15.

Palaeobates polaris n. sp.
A. Cross section through tooth belonging to the transversal row *b*. Medial side to the left. *B*, and *C*. Two teeth belonging either to one of the most anterior rows or more probably to an unpaired symphyseal row.

The caudal end of the crown is truncated. From it to the highest part the crown is of uniform width (Pl. 3, fig. 13); in front of the highest part it grows gradually narrower and the anterior end thus gets rather pointed. The crown and the root are both of about the same height. With regard to width, however, the root is far exceeded by the crown and in connection with it a very prominent notch is developed on the medial side (text fig. 15 A).

The part of the surface of the crown that forms this notch faces medially and at the same time basally and is separated by a sharp angular longitudinal edge from the real masticatory surface (Pl. 3, fig. 15). When I speak of this below I shall call it the baso-medial surface of the crown. The real masticatory surface is only weakly arched from side to side. It passes in a well rounded edge into a lateral surface (Pl. 3, fig. 14) that is fairly vertical and that I shall call in the subsequent description, the lateral surface of the crown.

On the real masticatory surface we find fairly close to the edge between it and the lateral surface a fine longitudinal stria or, if one likes to call it so, a longitudinal crista. From this there issue to both sides dense fine striae with abundant ramifications. Laterally of the longitudinal crista all the striae pass off quite transversally and continue on the lateral surface of the crown right to the basal margin. Medially of the same crista, on the other hand, they only reach the angular edge between the masticatory surface itself and the medial surface of the crown. Their course is such that their part situated nearest to the longitudinal crista bends round towards the highest part of the crown and in this way meets the longitudinal crista at an acute angle. Those situated in front of the highest part, on the other hand, are bent forwards. All the striae, both medially and laterally of the longitudinal crista, form only a few anastomoses (Pl. 3, figs. 13, 14, 15).

The root (text fig. 15 A, Pl. 3, fig. 15) has a plane, well developed basal surface, which is so situated that the axis of height of the crown meets it at right angles.

Row *c* consists of seven teeth, of the same order of magnitude as in row *b*, but somewhat narrower than these in relation to the length. Their length is generally on an average about 15 mm, while the greatest width is only 3 mm. The greatest height is 4–4.5 mm.

The majority of the teeth in this row have their anterior end situated lower than the posterior one in relation to the labial margin of the mandibula. Otherwise the arrangement is the same as in the two rows in front of them. All seven teeth are bent in the usual way, so that the masticatory surface is convex from one end to the other, while the basal surface of the root is correspondingly concave. Contrary to what is the case with teeth belonging to row *b* the curvature here is strongest in the anterior half. The highest and broadest part of the crown is consequently also in this half (Pl. 3, fig. 13).

Anteriorly the crown has a broad, truncated end (Pl. 3, figs. 13, 16 a, b) which meets with the posterior end of the teeth in the preceding row. From this end the width of the crown is maintained fairly unaltered posteriorly to its highest part and then gradually grows narrower right to the caudal end, which is rather pointed. The crown appears, when seen from the masticatory surface, to be also weakly bent in the shape of an *S*, so that its anterior half is convex on the lateral side and its posterior half on the medial side. In other respects it shows the same conditions as in the row in front, which is also true of the sculpture.

The root is also developed in a way that resembles very closely what we found in row *b*.

The five teeth in row *d* are considerably smaller than in rows *b* and *c*. The length varies between 5–6 mm, the greatest width is about 2 mm and the greatest height is 2–2.5 mm. Their position is the same as in row *c* and the curvature and the highest part of the crown also show the same conditions as in this row, i. e. they are situated nearer the anterior than the posterior end. The widest part coincides with the highest part of the crown and the crown grows narrower both to the anterior and the posterior ends (text fig. 14), but mostly to the latter end. Otherwise the shape and sculpture of the crown closely agree with what we know of the teeth in rows *b* and *c*. The root was also developed in them in a similar way.

The most posterior row, *e*, consists in its present state of three or four teeth, measuring in length about 3–4 mm and between 1.5–2 mm in height. From the medial or the lateral side both the crown and the root are fairly straight or at any rate only weakly bent. The conditions of these teeth in other respects cannot be established.

Among the number of detached teeth that occur on specimen *P. 107* there are some that, apparently, must have been situated still farther forward in the mandible than row *d* or more probably may have belonged to an unpaired symphyseal row. These teeth (text figs. 15 B, C; Pl. 3, fig. 12) are 4–5 mm in length and their greatest height is somewhat more than 3 mm. The crown is strongly bent in the way that it is convex from one end to the other, while the base of the root, on the other hand, is straight. The two ends of the crown are sometimes bent distally too in the manner shown in text figures 15 A, B and Pl. 3, fig. 12. A further characteristic of the crown is that on one side it has some round protuberances. The sculpture consists of fairly

sparse, straight and unramified striae, passing off transversally. These teeth resemble in their entire shape and development certain types of teeth belonging to *Asteracanthus*, e. g. those figured by AGASSIZ, vol. III, Pl. 17, figs. 1—5.

Nothing certain can be said as to the dentition of the palato-quadrate, but it does not seem improbable that its teeth were partly somewhat more robust than those of the mandible. There seem also to be certain reasons for believing that the shape of these teeth too may have been to a certain degree different from that of the mandibular teeth.

The microscopic structure of the teeth. — In accordance with JAEKEL's observations in *P. angustissimus* (AGASSIZ) we also find in the species under discussion from Spitzbergen (Pl. 3, figs. 17, 18) that the crown is entirely composed of ortho-dentine, with the exception of the peripheral layer, while the root consists of trabecular-dentine (cf. JAEKEL, 1889).

According to their positions in the transversal rows the teeth have of course different ages and are therefore at different stages of development. Thus, for instance, we find that in the transversal row *b* of the mandible described above only the crown is developed in the youngest tooth, and the crown there seems to consist, apart from a distinct layer of enamel, of only a very thin layer of ortho-dentine formed in immediate connection with the enamel. The crown thus has a large pulp cavity, which is open basally. On the next tooth of the same row the layer of ortho-dentine in the crown is thicker and the root is developed, although it consists only of a rather thin peripheral layer of trabecular-dentine. Its interior thus has a large pulp cavity which communicates with the still present pulp cavity in the crown. In the succeeding teeth of the same row the pulp cavity decreases more and more through the growth of the layer of ortho-dentine in the crown and the trabecular-dentine of the root, but still it does not disappear entirely in the oldest teeth (*p*, Pl. 3, fig. 17). In these it is found as a narrow longitudinal cavity between root and crown.

JAEKEL (1889, p. 329) also described and figured a longitudinal cavity of this sort in *P. angustissimus*, but he definitely denies that it has the nature of pulp. Everything clearly indicates, however, that even in this species we are concerned with a last remnant of the pulp cavity and not, as JAEKEL maintained, with Haversian canals or cavities arisen from a certain expansion of one or more of these that have met together.

Dermal denticles.

Dermal denticles occur in rather great numbers among the teeth and the cartilaginous parts, but they are poorly preserved. They are all relatively small, the length and height amounting to about 1.5 mm and 0.75—1 mm respectively. In shape they resemble nearest those described by me in *Hybodus* and *Aerodus*, but they differ from these by having the ridges on their lateral extended as rather long, slender processes backwards. The number of these processes cannot be stated with certainty, but it is probably not more than three or four as a rule.

* * *

Remarks. — *Palaeobates polaris* is well separated by the sculpture of its teeth from both *P. angustissimus* and *P. balatonicus* JAEKEL (1911 b). Both these species have a far more copious formation of anastomoses between the striae, the result of which is that the whole sculpture of the crown gets a reticulated appearance, which is not the case in *P. polaris*. It is true that a longitudinal crista also occurs, according to my observations, in a number of teeth belonging to *P. angustissimus*, but it is not found regularly as in *P. polaris*; *P. balatonicus* is still too incompletely known in this respect to be compared with the two species mentioned.

Geological occurrence and locality. — *P. polaris* is only known with certainty from the fish horizon, where it is rather rare. The two present examples come from Mt Andersson.

***Palaeobates* n. sp.**

(Pl. 1, figs. 28, 29.)

I have grouped here provisionally four teeth (*P. 96*, *P. 97* and two teeth from Horn Sound, belonging to the Palaeontological Collection of the University of Christiania). Two of these are accessible for investigation only from the lateral side (*P. 97* and one of those from Horn Sound). Of the two others one (*P. 96*) is present only as an impression of the lateral side. The other is so embedded in the stone that only the root is discernible.

In spite of a considerable difference in size the tooth *P. 97* and one of the teeth from Horn Sound are developed very similarly. The former is 8.5 mm and 2.5 mm respectively in length and maximum height, the tooth from Horn Sound 3.5 mm and 1.5 mm respectively. They are both bent so that the masticatory surface is convex from one end to another and the base of the root is concave in the same direction (Pl. 1, figs. 28, 29). This curvature is not symmetrical, but is stronger towards one end, as in the majority of the teeth described above in *P. polaris*, and at this place the crown has a distinct, blunt principal cone. This cone is most strongly developed on the tooth from Horn Sound (Pl. 1, fig. 29).

The crown of the two teeth first mentioned has a more prominent longitudinal crista than in *P. polaris*. The striae issuing from it are very much ramified and anastomose with each other with their branches, forming in this way a close network. The surface of the crown consequently gets pitted as in *P. angustissimus* and *P. balatonicus*. It is also noteworthy that the striation or, more correctly speaking, the network of striae, at least on the medial side is not developed nearest to the basal margin of the crown, but that close to this there is a narrow sculptureless region.

The tooth *P. 96* has no indications of any cone on the crown, and with regard to its shape it seems to have resembled most closely the teeth in row *b* of the mandibula of *P. polaris*. The sculpture of the crown is not preserved.

The remaining tooth from Horn Sound has an elongated shape. Its state of preservation does not permit of any detailed description.

* * *

Remarks. — The sculpture of the two best known of these four teeth shows a considerable resemblance to that of *P. angustissimus* and *P. balatonicus*. They differ from these two species by the distinct cone on the crown and a rather strong longitudinal keel. They differ distinctly from *P. polaris* both by their cone and their sculpture.

The two other teeth are, as we have seen, too incompletely known to be characterized in detail, and I have included them here because they are the only ones found at the same horizons as the two preceding ones.

It seems impossible as yet to decide whether we are concerned here with a new species, as so far we scarcely know anything about the dentition of the palatoquadrate in *P. polaris*, and it also seems as if there were certain indications that this was somewhat different from that of the mandible. We must consequently always take into account the possibility — even if it does not seem probable — that the teeth described here could have belonged to the palatoquadrate in *P. polaris*.

Geological occurrence and localities. — The teeth *P. 96* and *P. 97* were found at Mt Viking in the bone-bed 33 m above the fish horizon.

The two teeth from Horn Sound belong to the material collected by HOEL and RÖVIG in 1917 and come from the north-eastern corner of this fjord, where they were collected about 10 m above the upper limit of the Carboniferous.

Generically indeterminable fin-spines of Cestracionids.

(Pl. 1, figs. 12, 13, 19.)

In the present material of Elasmobranchii from the Triassic of Spitzbergen there are also fin-spines that differ in a number of respects from those of *Hybodus* and *Acrodus*. So far remains of three of these (*P. 35*, *P. 43*, *P. 44*) have been found, representing two different types.

Text fig. 16.

Cross section through fin-spine *P. 35*, 1/1.

The section runs through the proximal end of the exposed part of the spine. c, enamel list on the anterior edge; p, pulp cavity.

The best preserved of these fin-spines (*P. 35*; Pl. 1, fig. 19) is the single representative of its type. In its present condition, with a part of the root and the point missing, it is 43 mm long, but its total length was probably at least 50 mm. The maximum width of the spine, from the anterior edge to the posterior surface, lies within the basal half and is about 8 mm. The maximum thickness from one lateral surface to the other lies immediately in front of the posterior surface and is approximately 4 mm.

The fin-spine in question is only slightly arched backwards. It grows gradually and uniformly narrower distally and has apparently passed off in a rather sharp point. Its cross section is triangular (text fig. 16). The anterior edge is rounded, the postero-lateral edges are sharp, and the posterior surface is consequently well marked off from the lateral ones. All the surfaces are nearly plane.

The anterior edge apart from that of the root is covered with a wide list of enamel, which also reaches out somewhat over the adjacent part of the lateral surfaces, in the way shown in Pl. 1, fig. 19 b and text fig. 16. The exposed part of the lateral surfaces following caudally of this is furnished with rounded tubercles of enamel, arranged in rather distinct longitudinal rows. These rows, six or seven of which are

found close to the root, run parallel to the anterior edge of the spine, the result of which is that the most posterior ones are rather short, as in their course distally they meet the postero-lateral edge fairly soon. The number of rows of tubercles thus gradually decreases in this way towards the distal end of the spine.

It is noteworthy with regard to the tubercles that on closer inspection they appear to be flattened, with an obvious point, directed postero-dorsally. They also have a sculpture of fine ridges and in all respect much resemble dermal denticles.

It is specially worthy of attention that the posterior surface is quite without denticles or formations corresponding to these. It is impossible, however, to decide whether this condition is primary or is due to the state of preservation. The pulp cavity opens on the basal half of the posterior surface in the usual way.

The outer layer of the spine consists of trabecular-dentine and, at least in the root, this layer is the only one present, as was also the case in certain of the fin-spines described above belonging to *Hybodus* and *Acrodus*. As in these, so here too the layer of trabecular-dentine has on its surface the usual fine striation that is due to the microscopic structure.

The two remaining spines (*P. 43*, *P. 44*) are poorly preserved (Pl. I, figs. 12, 13). The most complete one of them (*P. 44*) consists of a fragment of the root with an adjacent piece of the exposed part. The other is represented only by a fragment from the anterior half of the exposed part. Both belong in the same species.

The spine *P. 44* has a maximum width (measured from the anterior to the posterior edge) of about 10 mm and a maximum thickness (measured from one lateral surface to the other) of about 5 mm. The greatest thickness is situated in the posterior half of the spine. The other spine seems to have been smaller, but it is impossible to obtain any certain measurements of it.

A transverse section through the spine *P. 44* at the proximal end of the exposed part (text fig. 17) shows that all the edges — both the anterior one and the postero-lateral ones — are only slightly marked and the different surfaces consequently merge into each other without any very distinct boundaries. The same cross section also shows that the posterior surface is strongly convex in the transversal direction.

The anterior edge has no enamel list. The lateral surfaces have on the exposed part a tubercular sculpture closely resembling that described on the fin-spine *P. 35*, although it differs from that by being developed quite close to the anterior edge (Pl. I, figs. 12, 13). Further differences are that the tubercles in the two fin-spines discussed here are coarser than those of the spine *P. 35* and that, contrary to what was the case in this spine, they do not seem to be arranged in distinct rows.

The posterior surface has no trace of denticles, at least in the preserved part, but it cannot be decided whether this condition is primary or secondary.

With regard to the microstructure we find that the basal part of both the spines consists only of trabecular-dentine around the large pulp cavity. Farther distally the spine *P. 44* shows a rather reduced irregular pulp cavity (*p*, text fig. 17), which is almost surrounded by a thick and, to judge from the macroscopical appearance, compact

Text fig. 17.
Cross section through
fin-spine *P. 44*, 1/1.
The section has proceeded
through the proximal end of
the exposed part of the spine.
p, pulp cavity; *d*, trabecular-
dentine; *o*, layer consisting,
at least most centrally, of
ortho-dentine.

layer (*d*). It is probable that, at least at its most central part, this consisted of orthodentine. Outside the more compact layer the trabecular-dentine follows in the usual way, and text fig. 17 shows that this was developed especially thickly in front of the pulp cavity.

* * *

Remarks. — The fin-spine *P. 35* closely resembles both *Nemacanthus* (cf. Woodward, 1891b, pp. 115—117; JAEKEL, 1892, pp. 145—151; etc.) and certain of the spines described under the generic names *Cosmacanthus* and *Geisacanthus* (DAVIS, 1883, pp. 355—358; ST. JOHN and WORTHEN, 1875, pp. 440—442; WOODWARD, 1891b, pp. 111—113; EVANS, 1904, pp. 397—402). Until it has been decided whether denticles were present in its posterior surface or not its relations will, however, remain very uncertain.

The two fin-spines *P. 43* and *P. 44* seem to belong to a rather special type, but they are not sufficiently well preserved to be fully compared with previously known types.

If one might venture to express a supposition as to the teeth to which the fin-spines described here belong, it looks most probable that these are *Polyacrodus* and *Palaeobates*.

Geological occurrence and locality. — All three fin-spines (*P. 35*, *P. 43* and *P. 44*) come from Mt Viking, where they were found in the bone-bed 33 m above the fish horizon.

Subclass Teleostomi.

Order Dipnoi.

Genus *Ceratodus* AGASSIZ.

Ceratodus sp.

(Pl. 3, fig. 19.)

The material hitherto discovered consists of a right mandibular tooth (*P. 350*), on which the lateral part with the processes is broken off (Pl. 3, figs. 19 a—d). The tooth is still connected basally with a piece of the so-called splenial (*Spl*, text fig. 18).

It seems to have agreed very well in size with the mandibular teeth in *C. sturii* TELLER (1891, pp. 22—31; Pl. III, figs. 3—6; Pl. IV, fig. 4). It has had the usual triangular shape, and its medial and caudal borders meet at a marked angle, the so-called angulus internus.

As in *C. sturii* and *C. kaupii* (STROMER and PEYER, 1917) the medial part of the masticatory surface is fairly plane. Laterally of this three distinct ridges gradually rise. A fourth, farthest posteriorly, is only slightly indicated. The first and the third have their axes of length converging towards a point situated just antero-medially of the angulus internus. The axis of length through the second runs so that the medial prolongation passes some distance behind the angulus internus. The fourth ridge is situated close to the caudal margin of the tooth and runs about parallel to the third. The groove between the first and second ridge is in the usual way wider than that

between the second and the third (STROMER and PEYER, 1917). In addition it is worthy of note with regard to the former groove that it extends farther medially and is deeper than the others.

The medial surface of the most anterior ridge faces also much dorsally, which, according to PEYER (1917, p. 54), is one of the more constant characters by which the teeth of the mandibles differ from those of the palatines. Text fig. 18 shows the different ridges in transverse section and this figure, like Pl. 3, fig. 19 a as well, indicates that a pulp cavity (p_1 — p_4) was developed under every ridge.

The masticatory surface has the «narbenähnlichen» depressions, often found in the *Ceratodus* teeth. Nothing is preserved of the enamel. On the medial border, just in front of the angulus internus, can be seen a small facette (a, Pl. 3, figs. 19 b—d), with which the tooth came into contact with that of the opposite side.

Concentric lines of growth are clearly seen on the part of the tooth that extends downwards and covers the inner side of the so-called splenial ventrally of the medial and caudal borders (Pl. 3, figs. 19 b—d); on the transverse section a similar striation can also be distinguished (text fig. 18).

Remarks. — The tooth described here seems in all respects to agree closely with the correspondingly situated teeth of *C. sturii* and *C. kaupii*. It is not possible as yet to decide whether it represents a distinct species or is identical with either of the two species mentioned.

Geological occurrence and locality. — The *Ceratodus* tooth P. 350 was found in the bone-bed of the lower Saurian horizon at Mt Viking (Mt Hamilton).

Text fig. 18. *Ceratodus* n. sp.
Section through tooth. p_1 — p_4
Spl., so-called splenial; p_1 — p_4 ,
the pulp cavities of the different
ridges.

Order Crossopterygii.

Family Coelacanthidae.

Historical.

In G. MANTELL'S work, «The fossils of the South Downs» (p. 239), published in 1822, we probably find the first description and reproduction of the remains of a Coelacanthid fish under the name of *Amia? lewesiensis*. In 1829 SEDGWICK (p. 118) mentions and figures a Coelacanthid form under the indefinite term «Fossil fish», and another one, also unnamed, is described three years later by BERGER (1832, p. 18). In 1834 MÜNSTER (p. 539) introduces the generic name *Undina* for a species from the white Jurassic of Bavaria; in 1835 we find *Amia? lewesiensis* of MANTELL under the generic name *Macropoma*¹⁾ in AGASSIZ'S «Feuilleton», to his «Recherches» (Feuilleton additionnel p. 55), and the year afterwards, also in the «Feuilleton» (1836, p. 83), the generic name *Coelacanthus* is used for the first time. It was not until 1844 (vol. II, part 2, pp. 168—180), however, that AGASSIZ published

¹⁾ The name *Macropoma* is already used by AGASSIZ 1833 («Recherches», vol. II, part 1, p. 2), but there is no statement to the effect that this name refers to the so-called *Amia? lewesiensis* (see WOODWARD and SHERBORNE, Catalogue of British Fossil Vertebrata, p. XXV).

a description of the two genera and in connection with this established his family «des Coelacanthes». As the name itself indicates, the type genus for this family was *Coelacanthus*.

Among his «Coelacanthes» AGASSIZ now includes a number of different forms. Besides *Coelacanthus* and *Macropoma* he mentions the following genera: *Holophrychius* AGASSIZ, *Glyptosteus* AGASSIZ, *Phyllolepis* AGASSIZ, *Glyptolepis* AGASSIZ, *Psammolepis* AGASSIZ, *Hoplopygus* AGASSIZ, *Uronemus* AGASSIZ, *Undina* MÜNSTER, *Ctenolepis* AGASSIZ, and *Gyrrosteus* AGASSIZ. The forms mentioned were for the most part preserved in a very fragmentary manner and the definition of the family that AGASSIZ was able to give was consequently, as he points out himself, very incomplete. For this reason alone it is therefore easy to explain why the family should have a certain heterogeneous composition, apart from the principles on which AGASSIZ in other respects based his classification. It is curious, however, that he considered it possible to incorporate *Macropoma* with the «Coelacanthes» only with hesitation, while he places even Placoderms among them without any reservation. He certainly points out the considerable analogies between *Macropoma* and *Coelacanthus*, but at the same time he believes he can show differences between them of a profound nature. The close mutual relationship between *Coelacanthus*, *Undina* and *Macropoma* was thus not clear to AGASSIZ, a fact that appears still more in a later work, his «Monographie des poissons fossiles du vieux grès rouge» (pp. 59—109), published in 1844.

In this work AGASSIZ considers that he has gained a somewhat deeper insight into the organization of his «Coelacanthes». He puts forward as their most important character the cycloid «enamel-coated» scales and the «hollow» nature of the bones. In other respects he finds them closely connected with his «Sauroids». From the latter he has now also transferred the following to the «Coelacanthes»: *Platygnathus* AGASSIZ, *Dendrodus* OWEN, *Lamnodus* AGASSIZ, and *Cricodus* AGASSIZ; and from the Cephalaspids *Chelonichthys* AGASSIZ, which he now gives under the name of *Asterolepis* EICHWALD. *Glyptosteus* is now called *Bothriolepis* EICHWALD and *Psammolepis* is termed *Psammosteus* AGASSIZ. He does not restrict himself in this connection to asserting more decidedly his previous views on *Macropoma*, but goes considerably farther. It is not only *Macropoma* that in his opinion fits in badly with the real «Coelacanthes» but also *Undina* as well, and he is also doubtful whether a number of other forms such as *Bothriolepis*, *Asterolepis* and *Psammosteus*, did not in fact represent a special type, quite different from the *Coelacanthus*-type.

In an appendix, published in the work just mentioned together with the last part of the description of the «Coelacanthes», AGASSIZ, 1844, pp. 107—109, considers that he could with certainty add to them even the recent genus *Arapaima* and probably the similarly recent genera *Heterotis*, *Osteoglossum* and *Amia*, as well, a view that is emphasised more strongly by VOGT in 1845 (pp. 53—68). Moreover AGASSIZ has in letters expressed the opinion that *Ceratodus* AGASSIZ too would belong to the «Coelacanthes» (GÜNTHER, 1871, p. 559). Finally EGERTON in 1861, pp. 51—55 adds to the «Coelacanthes» as defined by AGASSIZ *Tristichopterus* EGERTON and *Dipterus* SEDGWICK and MURCHISON.

In 1845 PICTET (pp. 231—236) closely follows the views put forward by AGASSIZ in his «Recherches». On the other hand GIEBEL (1848, pp. 219—227, 270—280), three years later, had apparently already perceived to some extent the heterogeneous character of the «Coelacanthes» as conceived by AGASSIZ. The fossil forms included among them by the latter are thus found in GIEBEL'S «Fauna der Vorwelt» divided among three

different families, «*Holothychii*», «*Dipterini homocerci*», and «*Dipterini heterocerci*». It is also obvious that GIEBEL had a certain feeling of the close mutual relationship between *Coelacanthus*, *Undina* and *Macropoma*, in as much as these three, together with *Ctenolepis* and *Gyrosteus*, are the only genera that are brought together in his «*Dipterini homocerci*». The genus *Libys*, founded by MÜNSTER (1842, p. 45), as to whose relations MÜNSTER himself felt uncertain, is placed by GIEBEL (1848, p. 209) hesitatingly among the representatives of his «*Monostichii*». In 1852 QUENSTEDT (1852, p. 219, pp. 228—231) places *Macropoma* among his «*Ganoidae homocerci*», while the other «*Coelacanthes*», to which, curiously enough, he also seems to assign *Saurichthys*, is referred in his appendix to the ganoids.

The first who really strongly emphasizes the mutual relationship between *Coelacanthus*, *Undina* and *Macropoma* is, however, THOLIÈRE 1858 (pp. 782—793). He also points out how these three genera form together a natural family, for which he suggests the name «*Ortho-coelacanthes*». Together with HUXLEY, who, three years later (1861), in revising the classification of the Devonian fishes, arrived at a similar result, he may therefore be looked upon as the founder of the family *Coelacanthidae* in its modern signification. In addition REIS (1888, 1892) and WOODWARD (1891 b, 1898 a, b; 1907 a, 1908 b; 1909; 1910 b) especially have made important contributions to our knowledge of the anatomy and classification of the *Coelacanthidae*. Besides these authors GÜNTHER (1871, 1880), HEINECKE (1907), SCHMALHAUSSEN (1913), WELLBURN (1902) and ZITTEL (1887) deserve mention.

The differentiation of the various genera of the family *Coelacanthidae* seems in many cases to have caused rather great difficulty. Thus in 1866 HUXLEY (p. 16) feels rather uncertain as to the difference between *Coelacanthus* and *Undina*, and in 1869 WILLEMOES-SUHM (1869, p. 86) gives *Undina* and *Graphiurus* KNER as synonyms of *Coelacanthus*, while *Holophagus* EGERTON and *Macropoma* are considered as distinct and independent genera. With regard to the relation between *Diplurus* NEWBERRY on the one hand and *Coelacanthus*, *Holophagus* and *Macropoma* on the other, NEWBERRY in 1888 (p. 71) makes the remark that if all these genera occurred in the same geological formation we should hardly be justified, with our present knowledge, in regarding them as more widely separated than different species of the same genus, a view which was put forward by LÜTKEN already in 1868 (p. 61). ZITTEL in his «*Handbuch*» (1887, pp. 171—176) retains the genera *Coelacanthus*, *Diplurus*, *Graphiurus*, *Heptanema* BELOTTI, *Undina*, *Holophagus*, *Libys*, *Coccoderma* QUENSTEDT and *Macropoma*, and at the same time he gives a short and clear definition of these. REIS (1888, p. 5, pp. 68—73) in his monograph on the *Coelacanthids* of the white Jurassic, published in 1888, also maintains the same genera as ZITTEL, but with the difference that he restricts the generic name *Coelacanthus* principally to the Permian forms, while for the great majority of the Carboniferous ones he introduces the new generic name *Rhabdoderma*¹⁾.

WOODWARD, on the other hand, adopts in 1891 (1891 b, pp. 394—423) a point of view partly different from that of REIS. He incorporates *Holophagus* with *Undina*, but does not accept *Rhabdoderma*. He considers that *Graphiurus*, *Diplurus* and *Coccoderma*

¹⁾ Among the genus *Coelacanthus* REIS (1888, p. 5, p. 71) also placed one Carboniferous species, *C. elongatus* HUXLEY (cf. WOODWARD, 1891 b, p. 406).

are, as far as one could judge from the facts then known, distinct from *Undina* only in certain less important characters. His clear and concise definitions of the different genera have made it possible to remove many of the earlier difficulties in the determination of the genera, and his opinions have been adopted by the majority of later investigators, such as, for instance, ALESSANDRI (1910), EASTMAN (1907), KOKEN (1911) and SCHLOSSER (1918). In a paper published in 1900 REIS (p. 191) however, defends his old point of view with regard to the genera *Coelacanthus* and *Rhabdoderma* and seems to have arrived at about the same view as NEWBERRY and LÜTKEN as to the mutual relations of the various genera. «Es ist kein Zweifel,» he says, «daß, wenn man die Gattung *Macropoma* aufrecht erhält, man auch das gleiche bei *Rhabdoderma* etc. tun muß; der Systematiker der Zukunft wird wahrscheinlich, um die Verhältnisse richtig auszudrücken, nur eine Gattung gelten lassen und die übrigen Gruppen als Untergattungen anreihen.»

In 1907 WOODWARD established the genus *Mawsonia* (1907 a, pp. 134—137) and the same year EASTMAN (1907, pp. 259—264) described, under the name of *Palaeopichthys*, an eel-shaped fish which, on very weak grounds, he places provisionally among the Coelacanthids.

Our view of the systematic position of the Coelacanthids and their affinities with other fishes is of course very closely connected with the development of the classification of fishes in general. AGASSIZ's classification was based, as we know, in many cases on a few characters, taxonomically of little importance, and it fairly often connected widely separated forms with one another. We have already seen above that in this case the forms brought together by AGASSIZ under the term «Coelacanthes» were no exception. His conception as to the relationship of his «Coelacanthes» with his «Sauroids» has also been sufficiently emphasized in the preceding.

No really clear view as to the relations of the Coelacanthids to other Teleostomes was obtained before 1861, with HUXLEY's revision of the classification of the Devonian fishes. HUXLEY then placed the Coelacanthids as an independent family together with five others¹⁾ in his now established order «*Crossopterygidae*», which at that time also comprized a number of forms now assigned to the *Dipnoi*. He expresses his view as follows: «The *Coelacanthini* as thus understood, are no less distinctly separated from other fishes than they are closely united to one another. In the form and arrangement of their fins; the structure of the tail and that of the cranium; the form and number of the jugular plates; the dentition; the dorsal interspinous bones; the pelvic bones; the ossified air bladder; the *Coelacanthini* differ widely from either the *Sauropodipterini*, the *Glyptodipterini*, or the *Ctenodipterini*; but, on the other hand, they agree with these families and differ from almost all other fishes, in the same respects as those in which the several families just mentioned have been shown to agree with one another; viz., the number of the dorsal fins, the lobation of the paired fins, the absence of branchiostegal rays, and their replacement by jugular bones.

Their special affinities among these three families appear to me to lie chiefly with the *Ctenodipterini*: the scales, the arrangement of the teeth, and the form of the lower jaw in the two families presenting many curious analogies.»

¹⁾ *Polypterini*, *Sauropodipterini*, *Glyptodipterini*, *Ctenodipterini* and *Phaneropterygini*.

HUXLEY also finds in certain cases a considerable agreement between the Coelacanthids and *Lepidosiren*, and, moreover, as he included *Dipterus* in the family «*Ctenodipterini*» and with hesitation *Ceratodus* and *Tristchopterus* as well, he apparently considered the Coelacanthids to be most closely related to the forms we now look upon as primitive *Dipnoi*.

LÜTKEN 1868 (pp. 60—64) considers the Coelacanthids most closely related to his «*Cyclodipterini*», to which he assigned, among others, *Dipterus*, *Glyptolepis*, *Holoptychius*, *Gyropterychius* M'COY, *Rhizodopsis* YOUNG, *Rhizodus* OWEN, *Strepsodus* YOUNG and *Phaneropleuron* HUXLEY.

The discovery of the recent *Ceratodus* in 1870 played an important part in the conception of the relationship of the Coelacanthids. KREFFT (1870) already considered *Ceratodus* as being most closely related to *Lepidosiren*, and in 1871 GÜNTHER definitely proved it to be a dipnoan. At the same time GÜNTHER (p. 557) also showed that at least one of the forms included by HUXLEY among his «*Ctenodipterini*», namely *Dipterus*, had to be placed among the *Dipnoi*, a view that was confirmed some years later by TRAQUAIR (1878, pp. 1—12). GÜNTHER (1871) also includes the genus *Phaneropleuron* among his *Dipnoi*, although with hesitation.

In connection with this revision GÜNTHER also enters on the question of the relationship between the Coelacanthids and other fishes. After first criticizing the family «*Coelacanthi*» in the definition given to it by AGASSIZ he continues (p. 559): «THIOLLIÈRE and HUXLEY have independently come to the conclusion that AGASSIZ's family of Coelacanthids comprises too many heterogeneous forms to allow us to regard the affinities of a fish as determined by its being referred to it. Both have limited the term to the genus *Coelacanthus* as type and a few other forms closely allied to it. The family thus restricted appears to me even more remote from the *Dipnoi* than the other «*Crossopterygians*». Fin-rays in definite numbers, joined to the interspinous bones, obtuse paired fins as in *Polypterus*, a double pelvis, developed upper jaws with small conical teeth, external nostrils, are characters sufficient to prevent us from associating *Ceratodus* and its allies with the *Coelacanthids*, which form not only a distinct family, but belong, according to my view, to a distinct suborder»¹).

In 1873 LÜTKEN (pp. 46—49), in accordance with the new facts, excluded *Dipterus*, *Ctenodus* AGASSIZ and *Phaneropleuron* from his «*Cyclodipterini*». With regard to the Coelacanthids he has nothing to add and in his new synoptic table of the ganoids, as well as in the earlier one, they are put immediately after the «*Cyclodipterini*». ZITTEL later on (1887) in his «Handbuch» placed them between «*Phaneropleurini*» and «*Cyclodipterini*».

Curiously enough, even as late as 1888, when publishing his «Monographie» REIS seems to have been unaware of the discussion on the systematic relations of the Coelacanthids that had been introduced into the literature in consequence of the discovery of *Ceratodus*. At least he does not mention any paper of this sort and even LÜTKEN's work on the limitation of the ganoids was apparently not very well known to him. It is consequently not so strange that he sticks to and even thinks that he has obtained additional proofs for the view put forward by HUXLEY as early as 1861.

¹) The order Ganoidei was divided by GÜNTHER into the following sub-orders: *Amioidei*, *Lepidosteidei*, *Polypteroidei* and *Dipnoi*.

HUXLEY (1861), ZITTEL (1887), GÜNTHER (1871; 1880) and later KOKEN (1911), SCHLOSSER (1918) and ABEL (1919) gave the different Crossopterygian families without any attempt to range them in groups according to their mutual affinity. LÜTKEN, on the other hand, as early as 1868, grouped them in two sub-divisions, «*Cycliferi*», and «*Rhombiferi*» and assigned the Coelacanthids to the former. COPE, in connection with his outline of a new classification of fishes, published in 1871 (pp. 450—451), suggests, among other things, the foundation of certain «orders» within the Crossopterygians. He then puts the Coelacanthids as the type and the single family in the «order» that he called *Actinistia*. In a few later papers he has also discussed the classification of the *Crossopterygii*.

TRAQUAIR 1875 (1875a, p. 394) divides the Crossopterygians in two sub-divisions, one of which contained the Polypterids, the other all the fossil forms. The latter sub-division was still further divided by him into three groups, the first of which comprised the Coelacanthids, the second the Rhombodipterids and Cyclodipterids, and the third Holoptychids and Phaneropleurids.

In 1891 WOODWARD (1891b) partly accepted the views put forward by COPE but, supported by a large amount of material, he was able to go farther. He divides the *Crossopterygii* into four equivalent sub-divisions, *Haplistia*, *Rhipidistia*, *Actinistia* and *Cladistia*, of which *Actinistia*, in accordance with COPE's suggestion, contained only the Coelacanthids. To *Haplistia* he referred the family *Tarassidae*, to *Rhipidistia* the families *Holothychidae*, *Rhizodontidae*, *Osteolepidae* and *Onychodontidae*, and to *Cladistia* the family *Polypteridae*. He looks upon the Coelacanthids as a group that has been very much specialized by degeneration (1898a, pp. 78—80).

In 1904 BRIDGE (pp. 476—485) seems to have been influenced to some extent by TRAQUAIR's view, as, like this author, he divides the *Crossopterygii* into two sub-orders, one of which comprised the Polypterids alone and the other all the fossil forms. For the former he adopted the name *Cladistia*; the other he called *Osteolepida* and to it he assigned the families *Osteolepidae*, *Rhizodontidae*, *Holoptychidae* and *Coelacanthidae*. GREGORY (1907, pp. 437—458), on the other hand, retains *Rhipidistia* and *Actinistia* as defined by WOODWARD, but places them together in one order, for which he chooses the name *Osteolepida*. He then sets up this order as of equal rank to the orders *Haplistia* and *Cladistia*, which he too retains with the same definition as WOODWARD.

GOODRICH in 1909 (pp. 280—302) represents a view that differs rather essentially from all the preceding ones. In his «Division I» of the Teleostomes is included only the order *Osteolepidoti*, which in its turn comprises the sub-orders *Haplistia* and *Rhipidistia* with the same signification as in the case of WOODWARD. To «Division II» he assigns the order «Coelacanthini», to «Division III» «Polypterini», and as «Division IV» he gives the *Actinopterygii*. As will be seen, he avoids the term *Crossopterygii*, and one is also struck by the unusually independent position which he assigns to the Coelacanthids as opposed to other forms with which they are usually more or less intimately grouped together, a view that was also to some extent taken by WATSON in 1912 (1912a, p. 5).

Finally POMERAI (1913, pp. 1136—1138) lays stress on the fact that our views about the Crossopterygii are still very incomplete. He looks upon them only as a provisional order. He considers COPE's, WOODWARD's and GOODRICH's classification of them not very successful and instead of these he suggests the foundation of the four sub-orders,

Holoptychii, *Osteolepidi*, *Coelacanthi* and *Polypteri*. To *Holoptychii* he then assigns the families *Holoptychidae* and *Rhizodontidae* and, with reservation, *Onychodontidae*; to *Osteolepidi* he refers the families *Glyptopomidae* and *Osteolepidae* and eventually also *Tarrassiidae*.

The geological range and geographical distribution of the Coelacanthids.

The Coelacanthids appeared as early as in the upper Devonian and persisted to the upper Cretaceous. Thus, as HUXLEY (1861) and WOODWARD (1898a) have pointed out, they seem to have existed for a longer time than any other known family among the extinct fishes and, as these investigators also emphasized, they have probably remained pretty well unchanged at least from the Carboniferous period.

They were rare in Devonian and, as far as one can ascertain, they also had a rather limited geographical distribution in this formation. The only species so far described, provisionally assigned by WOODWARD (1898b) to the genus *Coelacanthus*, is obtained from the neighbourhood of Gerolstein in Germany. According to JAEKEL (1906b) however, an additional form is found at Wildungen, and in a letter in 1917 JAEKEL tells me that this form is certainly closely connected with the earlier known one from Gerolstein, but that it undoubtedly must be considered as belonging to a new genus.

During the Carboniferous period the Coelacanthids were represented both in Europe and North America by a number of species. A Carboniferous or Permian species is also known from Madagascar (WOODWARD, 1910b, pp. 5—6)¹⁾.

We may very well take it as probable that Coelacanthids were fairly common even in Permian time, although at present we only know a little about this, since, apart from the above-mentioned species from Madagascar, the geological age of which is not quite certain, we only find one or perhaps a few European species (WOODWARD, 1891b, pp. 399—408). All the Carboniferous and Permian species are described by practically every investigator under the generic name *Coelacanthus*. As has been pointed out in the preceding chapter, it is only REIS (1888; 1900) who has suggested the generic name *Rhabdoderma* for the great majority of the Carboniferous forms, while, in his opinion, *Coelacanthus* ought to be restricted to the Permian ones.

While the Coelacanthids so far found in the Carboniferous and the Permian seem to be rather uniform in their development, those in the Triassic appear, on the other hand, to exhibit a little more variation. Besides *Coelacanthus* the genera *Diplurus* (NEWBERRY, 1888, pp. 70—76; WOODWARD, 1891b, p. 409; EASTMAN, 1911, pp. 42—45), *Graphiurus* (WOODWARD, 1891b, p. 409), *Heptanema* (DE ALESSANDRI, 1910, pp. 36—42) and *Undina* (ANDERSSON, 1916, pp. 14—16) are described from the Triassic. It is, however, probable that at least some of, or even all, the Triassic species included under the name *Coelacanthus* will actually turn out to belong to other, and perhaps in several cases even new, genera.

To the five Triassic genera given a number of new ones are now to be added, of which not less than five, described below, *Wimania*, *Sassenia*, *Axelia*, *Myracanthus* and

¹⁾ According to later views (cf. LENOIRE, 1911, pp. 5—6) this species comes from deposits of lower Triassic age. Stensio, Triassic Fishes from Spitzbergen.

Scleracanthus, come from Spitzbergen. A sixth new genus is probably represented in Redakteur KÖNIG's collection from the Muschelkalk at Heidelberg, and in this connection it is worthy of mention that the Coelacanthids apparently played a greater part in the Central European continental Triassic than was earlier thought to be the case. AGASSIZ (1844, vol. II, part 2, p. 173) has given *Coelacanthus minor* for the Muschelkalk and *C. gracilis* may also possibly come from the same formation. BERGER (1832) describes as pointed out above in the historical chapter, a Coelacanthid fish from the Keuper in the neighbourhood of Coburg, and REIS mentions (1888, p. 6) a number of Coelacanthid fragments from different horizons of the German Triassic. In various German museums which I had the opportunity of visiting I also found a number of more or less fragmentarily preserved remains of Coelacanthids from this formation. Thus the Stuttgart museum has a piece of a ceratohyoid ossification labelled *Ceratodus* sp. from the Keuper; the Senckenberg museum in Frankfurt am Main has an isolated urohyal from the Muschelkalk at Bayreuth and the Berlin museum two jugular plates from the Muschelkalk. Besides these specimens there are in the possession of Redakteur KÖNIG remains of a couple of pieces from the Muschelkalk at Heidelberg and two more, from this locality, belong to the Palaeontological Institute at Upsala. As to the specimens in Redakteur KÖNIG's collection it is obvious that they have been of considerable size, as is also certainly the case with one of the Upsala specimens.

As I shall show below it is also of great interest to find how the three genera *Axelia*, *Myliacanthus* and *Scleracanthus* appear to be more specialized in certain respects than other known Coelacanthid forms.

In Europe Triassic Coelacanthids are found in Germany, France, Austria (REIS, 1900), Hungary (JAEKEL, 1911b, pp. 20—21), Switzerland (ANDERSSON, 1916a, loc. cit.), Italy (DE ALESSANDRI, 1910, loc. cit.). At Spitzbergen they are also found and seem there to be especially common. Furthermore a species is known from the east of the United States (EASTMAN, 1911, loc. cit.), another from South Africa (BROOM, 1909b, p. 253) and a third is described from Canada (LAMBE, 1916, pp. 38—39) from deposits whose Triassic age can, however, be scarcely considered as having been clearly shown.

In the Jurassic too the Coelacanthids seem to have been somewhat common. In this formation there appear the genera *Undina* (REIS, 1888; WOODWARD, 1890b; 1891b; EASTMAN, 1914b, p. 358), *Heptanema* (REIS, 1888; WOODWARD, 1891b), *Libys* (REIS, 1888; WOODWARD, 1891b) and *Coccoderma* (REIS, 1888; WOODWARD, 1891b) with altogether more than ten species. With the exception of *Undina gulo* (EGERTON) and *U. barroviensis* A.S. WOODWARD, which both occur in the English Lias, and *Coccoderma substriolatum* (HUXLEY) which is described from the Kimmeridge clay, also from England, they are limited to the lithographic stone of South Germany, France and Spain (VIDAL, 1915, p. 33). In addition WOODWARD (1895a, pp. 3—4) has described remains of an undeterminable form from Australia, and from material belonging to the Palaeontological Museum of Christiania it is evident that the Coelacanthids were also present in the Jurassic of Spitzbergen. It is even probable that in the latter case we are concerned with a previously unknown genus.

From the Cretaceous there are described only the two genera *Macropoma* (REIS, 1888; WOODWARD, 1891b) and *Mawsonia* (WOODWARD, 1907a; 1908b), the former from England and Bohemia, the latter from the district of Bahia in Brazil. A fragment of

a Coelacanthid from King's Bay in Spitzbergen, found, according to the label, somewhat below the Tertiary coal-bed, also seems, if this statement is correct, to be of Cretaceous age¹⁾.

From what has been said it would appear that, as far as we know at present, the Coelacanthids had obtained a considerably greater distribution in the Carboniferous than during the Devonian, and that they had also become much more common. They seem to have attained their greatest flourishing in the Triassic. They are also represented by a number of genera in the Jurassic, while in the Cretaceous they become more rare and finally disappear.

Description of the Spitzbergen forms.

Genus *Wimania* n. g.

Syn. *Leioderma* STENSJÖ, 1918.

The genus in question is previously mentioned under the name of *Leioderma* in my description of *Dictyonostus* 1918 (STENSJÖ, 1918 c, p. 121), but as it turned out later on that the name *Leioderma* was already used, I have suggested instead of it *Wimania* after Professor C. WIMAN, my respected teacher and friend.

The type species of the genus *Wimania*, *W. sinuosa* described below, is partly very incompletely known, as apart from the head there are present only certain parts of the shoulder-girdle and a number of scales. Under these circumstances it is of course very difficult to decide whether one or two other species, which are represented practically exclusively by scales and parts of the axial and fin skeleton, belong to the genus in question. As a criterion of relationship one would in this case have to rely merely on certain common features in the sculpture of the scales, but anyone who has studied the Coelacanthids will realize that this cannot afford sufficiently certain evidence for deciding this question. It appears too that although the two doubtful species in question agree with each other pretty well with regard to the sculpture of the scales, they differ fairly considerably with regard to the development of the lepidotrichs and it seems to be most probable that we have in them representatives of different genera. But, as it appears from the above, it is impossible to decide which species should in this case with most justice be assigned to the genus *Wimania* and so for the present I have provisionally retained both in this genus.

On the other hand one cannot also quite help feeling that one of the two species mentioned, the one described below as *Wimania*? sp., might possibly really turn out to be identical with *W. sinuosa*, which it resembles, at least with regard to the sculpture of the scales.

Under these circumstances it is evident that a definition of the genus in question ought for the present to be based exclusively on the type species. A summary of the most distinctive characters of the genus will therefore appear as follows: Fairly large

¹⁾ This fragment belongs to the Riksmuseum in Stockholm.

fishes. The skull without or with very delicate ornament. The frontals long; the supra-orbitals probably narrow. The cheek plates not joined by sutures but fairly free from one another, partly even separated by wide interspaces; the jugal articulating with the middle post-orbital plate, but not reaching the dorsal one. The parasphenoid broad. The pterygoid with a broad posterior limb and a long anterior one. The coronoid triangular. The ossification in the ceratohyal long; the opercular very large. The dentition consisting of rather large conically pointed teeth on the margins of the jaws; otherwise the jaws, the parasphenoid and the membrane bones on the copula with small bluntly conical ones; the gill-arches with teeth of the same shape as on the

Text fig. 19. *Wimania sinuosa* n. sp.

The neurocranium from the left side with the cheek bones removed. The cartilaginous parts (dotted) of the orbito-temporal region restored chiefly after *Diclyonosteus*. The bones from *P.* 257. ¹¹.

Bp. h., basisphenoid; *Fr. dph.*, fronto-dermosphenotic; *Pa. it.*, parieto-intertemporal; *Peth. m.*, preethmoid; *Pro. o.*, prootico-opisthotic; *Pp. h.*, parasphenoid; *Stemp. ext.*, supratemporo-extrascapular; *al.*, forward pointing lamella from the basisphenoid-corpus; *c.*, posterior process from the prootico-opisthotic; *e.*, basipterygoid process; *f.*, anterior end of the prootico-opisthotic; *f_1*, dorsal process from the prootico-opisthotic; *fen.*, fenestration in the interorbital wall, probably corresponding to the entrance of the supposed myodome; *h.*, ventral process from the supratemporo-extrascapular; *v.*, ventral process from the basisphenoid-corpus; *II.*, for. opticum; *III.*, for. u. oculomotorii; *IV.*, for. u. trochlearis; *V_e*, outer opening of the canal for n. ophthalmicus profundus; *V_{23}*, sinus transmitting ramus maxillaris trigemini, n. mandibularis trigemini, n. buccalis lateralis and n. ophthalmicus superficialis; *n.*, ophthalmicus lateralis had its exit a little above these nerves through the same sinus; *VII.*, for. facialis; *IX?*, supposed position of the inner opening of the canal for n. glossopharyngeus.

margins of the jaws but much smaller and finer. The sensory canals well developed. The scales oval with ornament consisting of a rather large number of fine and rather short striae, generally running horizontally.

In many respects *Wimania* resembles the Carboniferous and Permian Coelacanthid type more than the Jurassic and Cretaceous ones, at least if we are to judge from the type specimen. The most striking common characters in this respect are the shape of the parasphenoid and the pterygoid, the relation between the latter bone and the metapterygoid, the general arrangements of the cheek plates and the considerable size of the opercular. On the other hand the relation between *Wimania* and the Triassic forms previously described is still very uncertain, as these are on the whole exceedingly incompletely known as far as the osteology of the skull is concerned. Of the Spitzbergen genera described below it is really only *Sassenia* that reminds us of *Wimania*; as has already been pointed out, the others are more specialized forms.

Wimania sinuosa n. sp.

(Pls. 4, 5, 6, 7 and Pl. 8, fig. 1.)

Synonym: *Leioderma sinuata*, STÉSSÖ, ERIK A. SON, Upsala, Geol. Inst., Bull. vol. 10, p. 121, 1918.

So far as can be seen, *Wimania sinuosa* is with certainty represented only by three incomplete specimens (*P. 257*, *P. 255*, *P. 677*). The best preserved one of these (*P. 257*) consists of a head with some scattered scales. Of the two other specimens only some remains of scales and a few fragmentary lepidotrichs (dermal fin-rays) are preserved. The head mentioned (*P. 257*) measures about 20 cm in length, with the opercular apparatus included, and its greatest height is about 10 cm. The following description of the cranial skeleton is based entirely on this specimen.

The primordial neurocranium and its ossifications.

The primordial neurocranium is on the whole (text figs. 19, 20, 21) rather high and relatively narrow in comparison with its length. The ethmoidal region is wide and low and of average length. The orbitotemporal region, on the other hand, is specially distinguished by its great length. In its anterior and middle parts it has been narrower than both the ethmoidal and the labyrinth region. Its middle part at least formed ventrally a rather thin interorbital wall and it is strongly open to question whether at one place this was not even fenestrated, as I shall try to explain later on. In the most posterior part the orbitotemporal region is wide and passes without any very decided boundary into the labyrinth region, which is of moderate length. The latter region increases rapidly in width posteriorly and probably passes in its turn rapidly into the occipital region, which, as far as one can judge, must have been rather short (text fig. 21).

In profile the dorsal contour line of the primordial neurocranium probably corresponded approximately to that of the dermal bones. In the labyrinth region and the posterior part of the orbitotemporal region it has consequently been fairly horizontal. Along by far the greater part of the orbitotemporal and the whole of the ethmoidal region, on the other hand, it slopes forward. The snout has probably been fairly low

Text fig. 20. *Wimania sinuosa* n. sp.

The neurocranium from the dorsal side with the cranial roof removed above the occipital region, the labyrinth region, and the posterior part of the orbitotemporal region. From specimen *P. 257*, $\frac{1}{4}$.

Alaph, alisphenoid, joined to and forming a ventrocaudal process from the fronto-dermo-sphenotic; *Baph*, basisphenoid; *Fr. diph*, fronto-dermo-sphenotic; *Na. ant.*, nasalo-anterior; *Pro. o.*, prootic-opisthotic; *Pypb*, parasphenoid; *Ptc*, posttemporal; *So*, supraorbital; *al*, forward pointing lamella from the basisphenoid-corpus; *c*, posterior process from the prootic-opisthotic; *v*, basipterygoid process; *V₂₅₇*, dorsal process from the corpus of the prootic-opisthotic; *lab. cau.*, cavity in the posterior part of the prootic-opisthotic, probably enclosing an anterior portion of the labyrinth; *m*, the opening of the myelome; *s₁*, sulcus for n. facialis; *v*, ventral process from the basisphenoid; *V₂₅₇*, see the explanation of the preceding figure.

and rather pointed in profile, but, when looked at from the dorsal or the ventral side, it is bluntly rounded, as is usual in Coelacanthids. The basis cranii is straight, at least from the snout and as far back as the anterior part of the labyrinth region.

The primordial neurocranium has consisted of cartilage to a considerable extent. The nerve exits have in most cases been situated in the cartilaginous parts, and as of course all the cartilage has disappeared in the present state of the skull under consideration it is not easy to make any exact division of the different regions from each other. This is especially the case with regard to the boundary between the occipital and the labyrinth region.

By far the greatest part of the occipital region has certainly been cartilaginous, and the chorda dorsalis has extended into it and perhaps still farther forward. Whether there were any ossifications present, as is the case in *Undina*, where a basioccipital was found (HEINEKE, 1907, p. 8), cannot be decided (cf. the chapter «Remarks on previously described Coelacanthids»). It is also very uncertain where the foramen vagi was situated.

In the labyrinth region of the Coelacanthids two ossifications have previously been described, an anterior one, interpreted by earlier investigators as the prootic, and a posterior one, taken by HUXLEY (1866, p. 35) to be the opisthotic + the lateral occipital and by REIS (1888, p. 26, p. 63; 1892, p. 23) as the opisthotic. It now appears in *Wimania sinuosa* that only the latter of these ossifications really quite falls within the labyrinth region, and that, as we shall see from the subsequent description, it has such a position and such an extension that it ought probably to be taken as the prootic fused with the opisthotic (cf. my exposition of *Birgeria mougeoti* below). It may thus conveniently

be termed the prootico-opisthotic. It must be noted, however, in this connection that the opisthotic component seems to be rather small.

The prootico-opisthotic (*Pro. o.*, text figs. 19, 20, 21, 23; Pl. 7, figs. 1, 2; Pl. 8, fig. 1) forms a rather considerable part of the lateral wall of the labyrinth region, which is

Text fig. 21. *Wimania sinuosa* n. sp.

A. The neurocranium from the dorsal side. The cartilaginous parts of the occipital and labyrinth region restored. The cartilage dotted. The bones from specimen P. 257. $\frac{1}{10}$.

Fr. dph., fronto-dermosphenotic; Na. ant., nasalo-antorbital; Pa. it., parieto-intertemporal; Pro. o., prootico-opisthotic; Pr., postrostral; So., supraorbital; Stemp. ext., supratemporo-extra, scapular; f. temp., temporal fossa; h., antero-ventrally pointing process from the supratemporo-extrascapular, joining the prootico-opisthotic.

B. Cross-section through the left supratemporo-extrascapular in its posterior part. $\frac{1}{4}$. lc, sensory canal.

otherwise composed of cartilage. Similarly the roof and floor of the same region seem to have been principally cartilaginous.

On the prootico-opisthotic there can be distinguished a corpus and two processes, a dorsal one (f_1) and a caudal one (c). The corpus is situated in the anterior basal half of the labyrinth region and is shaped like a four-sided pyramid, with the bluntly rounded point directed forward and somewhat medially, and the basal surface latero-caudally. Of its side-surfaces one is turned medially, one ventrally, one antero-laterally and one dorsally. Its anterior half consists of compact bone, its posterior part, on the other hand, is developed with a large cavity (*lab. cav.*, text fig. 20), which is open both dorsally and caudally.

The side-surfaces are really not very sharply marked off from one another, as the edges between them are rather rounded; this is chiefly the case with regard to antero-lateral and ventral ones. The medial one has an almost vertical position and is rather high posteriorly¹⁾. Its posterior margin has a small sinus in its ventral part near the angle between itself and the posterior process (c) and it is conceivable that this sinus might have some connection with the exit for the nervus glossopharyngeus (IX? text fig. 19). The ventral side-surface (text fig. 23; Pl. 7, fig. 2) is triangular, and its posterior margin has, besides the process c , a couple of smaller convex bends. Its medial margin is weakly and its lateral one rather strongly concave and the anterior corner is blunted. The antero-lateral side-surface (text figs. 19, 20) has an anterior part that is vertical and faces directly laterally and a posterior part that faces rostrally but at the same time somewhat dorsally as well. Its lower margin is concave, its posterior one convex, and its anterior corner is blunted. The upper one is convex in front of the process f_1 , concave behind it, and the posterior upper corner projects upwards in the shape of a broad triangular part, which is covered by a process (h) from the dermal cranial roof.

The cavity of the corpus of the prootico-opisthotic has the ossified walls (lateral, medial and ventral) thick and strong. Immediately in front of the cavity there issues on the dorsal side-surface of the corpus the process f_1 (text figs. 19, 20; Pl. 4, fig. 1; Pl. 5, fig. 1; Pl. 8, fig. 1) which in the species under discussion is wide and powerful and almost or quite reaches the cranial roof. Close to its base there runs on the medial side a distinctly marked longitudinal furrow (s_1 , text fig. 20). The part of the dorsal side-surface of the corpus situated in front of the same process f_1 is convex from side to side and bluntly rounded at the front.

The posterior process (c , text figs. 19, 20, 23; Pl. 7, fig. 2) is sent out from the corpus at about the angle between the medial and ventral sides and is thus situated close to the supposed cranial base. As will be seen from the figures already given, it is fairly long and its breadth is also fairly considerable, whereas its height, on the other hand, is small. In *Undina*, as is clearly shown by a specimen in the *British Museum* (B. M. P. 9130), by the original of REIS's (1888) figs. 21 and 22, Pl. 1, and also by HEINEKE's (1907) type specimen of his fig. 1, Pl. 6 and text fig. 1, the process in question is joined to the lateral surface of the basioccipital, which in this way becomes attached

¹⁾ Its characters are well displayed by the detached prootico-opisthotic figured on Pl. 7, fig. 4.

between the processes of the two sides. As we know, the basioccipital both in fishes and in other vertebrates extends as a rule a considerable distance forward in the basis cranii, and the fact mentioned need not therefore indicate in any way that the lateral occipital, as HUXLEY thought, includes the bone interpreted by me as the prootico-opisthotic. In addition it seems also probable that the basioccipital in *Undina* represents only the most anterior part of the bone that in the Teleostomes we call under ordinary circumstances the basioccipital.

The bone in the Coelacanthids that was taken by previous authors (HUXLEY, 1866, p. 35; REIS, 1888, pp. 25, 62—63; 1892, p. 21; HEINEKE, 1907, p. 12) to be the prootic is unpaired and, as I have said in a previous work (STENSIÖ, 1918 c, p. 120), corresponds to a basisphenoid. In *Dictyonosteus* its homologue forms an integral part of the large unpaired bone which extends there through the whole orbitotemporal region and which now, in accordance with the conditions in *Polypterus*, I consider ought to be termed a sphenoid (TRAQUAIR, 1871). Besides the basisphenoid there is also in the Coelacanthids a paired bone homologous to the dorso-caudal part of the sphenoid of *Dictyonosteus* and this bone in Coelacanthids is apparently most closely comparable with an alisphenoid although, as we shall see, it is coalesced secondarily with a bone in the dermal cranial roof.

By far the greater part of the basisphenoid in *W. sinuosa* is situated (*Bsph*, text figs. 19, 20; Pl. 4, figs. 1—2; Pl. 5, fig. 1; Pl. 6, figs. 3, 4; Pl. 7, fig. 5; Pl. 8, fig. 1) in the caudal part of the orbitotemporal region, but at the same time it reaches a short distance into the most anterior part of the labyrinth region, as we shall see from the nerve exits and the configuration of the cranial cavity. The anterior end of the prootico-opisthotic reaches a short distance forward along the lower part of its lateral surface on each side and in this way forms a decidedly projecting part (*f*), which was described by HUXLEY, 1866, in *Macropoma*, although in his opinion it belonged to the prootic,¹⁾ i. e. the bone termed by me the basisphenoid.

The basisphenoid in *Wimania sinuosa* is, seen from the side (*Bsph*, text fig. 19), rather short and high. It rests ventrally against the parasphenoid (*Psph*); dorsally it reaches up to and probably even partly comes into contact with the membrane bones of the cranial roof. Seen from above (text fig. 20) it appears short and wide. On it can be distinguished a corpus, and lamellae and processes issuing from the corpus.

The corpus is composed of a cancellous, the processes of a distinctly radiate, bony substance. The latter substance continues from all the processes into the corpus to a centre situated in the dorsal part of the latter. In shape the corpus is most comparable to a triangular plate, fairly thick at the top, thinner below. Its bluntly rounded point is directed ventrally, but does not reach down to the parasphenoid bone (text fig. 22). Otherwise it is placed in such a position that it slopes backwards (text fig. 19). The large posterior surface consequently faces downwards to some extent, the anterior surface, which is narrower and hollowed out into a dorsi-ventrally directed groove, in the same degree upwards. The upper surface (fig. 20) is situated strikingly high, at about the same level as the upper part of the process *f*₁ on the prootico-opisthotic, and has about the shape of a rectangle with the margins somewhat concave. It is

¹⁾ The same opinion was still held by REIS in 1892.

also deepened into a groove in the longitudinal direction of the skull. The two lateral surfaces are high and narrow and are hidden in their lower part by the anterior ends of the prootico-opisthotics, as has already been pointed out.

At the anterior corner of the upper surface, on the right and left sides of the corpus, there issues in a forward, upward and somewhat lateral direction a powerful process *e* (text figs. 19, 20, 22; Pl. 4, figs. 1, 2; Pl. 5, fig. 1; Pl. 6, figs. 3, 4; Pl. 7, fig. 5; Pl. 8, fig. 1) which increases in width and thickness distally and is rather abruptly truncated at its end. The ventral processes (*v*, text figs. 19, 20, 22) are sent out from the corpus near its ventral corner. They exhibit a slight divergence in the ventral direction and like the dorsal ones they also increase both in width and thickness distally. Their ventral ends rest on the parasphenoid bone, and since, as has already been pointed out, the corpus does not reach so far down, there arises between them a rather high but fairly short square longitudinal canal (*m*, text figs. 20, 22), which is bounded dorsally by the corpus of the basisphenoid and ventrally by the parasphenoid. The anterior surface of the ventral processes is smooth, like the lateral one, which is bounded from the former by a sharp vertical edge.

The anterior face of the corpus of the basisphenoid is free only in its median part. Its right and left borders form a fastening for a lamella which points forward and at the same time somewhat laterally (*al*, text figs. 19, 20, 22; Pl. 4, fig. 1; Pl. 5, fig. 1; Pl. 8, fig. 1). From the lateral sides and partly ventrally as well the two lamellae together bound a large fossa that is open at the front and upwards (text figs. 20, 22). The lamellae are rather thick at their postero-dorsal parts and form there a support for the proximal end of the process *e* on its ventral side. Their antero-dorsal parts are situated against the antero-medial border of the same process and attain the same height as the dorsal surface of the latter. Seen from above, they themselves are consequently visible on each side as a long narrow process, situated close to the antero-medial border of the process *e* (text fig. 20). The ventro-caudal process, from the dermal cranial roof, which corresponds to the alisphenoid (*Alsph*, text fig. 20; Pl. 4, fig. 1; Pl. 5, fig. 1; Pl. 8, fig. 1) joins their upper anterior corner on each side. Anterior to and at a level just below the process *e* on the lateral surface of the lamellae in question, where these are thickest, there is a little cavity in which a rather fine canal opens (*V_{le}*, text figs. 19, 22). The inner opening of this canal (*V_{li}*, text fig. 22) is found on the medial side of each lamella in its postero-dorsal part.

From the description and the figures given it is thus shown beyond all doubt that the basisphenoid is an unpaired bone, which cannot in any way be considered to enclose or surround the labyrinth. On the contrary it seems certain that the labyrinth stood in relation to the prootico-opisthotic and under these conditions it is most probable that its anterior part was situated in the backward and upward opening cavity in this bone. Behind the corpus of the prootico-opisthotic the capsula auditiva has been cartilaginous, probably to the extent shown by text fig. 21, and the posterior part of the labyrinth has apparently been situated in this cartilage.

Text fig. 22.

Wimania sinuosa n. sp.
The basisphenoid in anterior aspect. From P. 257. ¹/₄.
Bsph. basisphenoid; *Psph.* parasphenoid (in cross-section); *al*, forward pointing lamella from the basisphenoid corpus; *e*, basipterygoid process; *m*, the anterior opening of the myodome; *v*, ventral process from the basisphenoid corpus; *V_{le}*, outer opening of the canal for n. ophthalmicus profundus; *V_{li}*, inner opening of the canal for n. ophthalmicus profundus.

As we have seen, the basisphenoid corpus is considerably high. The floor of the cranial cavity is situated above it on a level with the dorsal part of the process f_n on the prootico-opisthotic (text figs. 19, 20, 22). Immediately in front of the basisphenoid corpus there then follows the deep fossa, open at the front and dorsally, that has just been described, and behind the same corpus the floor of the cranial cavity seems also to have sloped downwards, though not so rapidly. According to HEINEKE's view (1907, p. 8) the fossa hypophyseos followed in front of the basioccipital, and the unossified gap in the cranial base in front of this bone is termed by him the hypophyseal fenestra. With the interpretation I have given above of the different bones in the species described here, the fossa hypophyseos should, if HEINEKE's view were correct, be bounded by the basisphenoid anteriorly, the prootico-opisthotic laterally and the basioccipital posteriorly when the latter bone is developed. It is clear, however, without further discussion that this view is not tenable. The forward opening fossa on the basisphenoid seems instead to have such a special shape and otherwise to be in such a position that it has undoubtedly had some relation to the hypophysis and the ventral parts of the diencephalon in general. Thus the corpus of the basisphenoid would be situated behind the hypophysis in the same way as the corpus of the corresponding bone in Stegocephalians and reptiles. In other words the basisphenoid corpus probably belongs to the chordal part of the neurocranium.

Apart from the basisphenoid and the above-mentioned process (*Alsph*) from the dermal cranial roof, by far the greater part of the rest of the orbitotemporal region in *Wimania* might have consisted, as in other Mesozoic Coelacanthids, principally of cartilage (text fig. 19), which was attached to the corpus and the lamellae of the basisphenoid. The ventral processes (ν) on the same bone are so even and smooth at the bottom on the anterior side that it looks as if the cartilage had not joined them at this surface, but that a fenestration had been present under the fossa hypophyseos of about the same extent as I have tried to indicate in text fig. 19 (*fen*). The cranial cavity has certainly extended a considerable distance in front of the basisphenoid, probably as far as to the ethmoidal region, which was also the case in *Dictyonosteus* (STENSJÖ, 1918 c).

Judging from the size of the eye, the optic nerve (II) must have been strong. It has penetrated into the orbit probably fairly far forward, in about the way I have hypothetically marked in text fig. 19. In the same figure I have also hypothetically drawn the foramina for n. trochlearis (IV) and n. oculomotorius (III), which nerves must both have emerged into the orbit in front of the basisphenoid.

The above mentioned paired canal, which passes from the postero-dorsal part of the fossa hypophyseos (V_{Ti}) through the lamellae of the basisphenoid in an antero-lateral direction and whose outer opening (V_{Te}) is situated somewhat ventrally and antero-medially of the process e , has its exact equivalent in *Dictyonosteus* in the canal that I have there indicated by the letters fo (STENSJÖ, 1918 c, Pl. VI). Latero-caudally of this foramen there follows in *Dictyonosteus* the process Bp , which probably corresponds to e in *Wimania* and other Coelacanthids, although it is situated lower than in these.

The relation of the canal to the fossa hypophyseos is also similar in both cases. It seems rather probable that the canal in question both in *Dictyonosteus* and in the Coelacanthids was traversed by the trigeminus nerve or, more correctly speaking, by

some of its branches. That there can be no question of the nerve as a whole (cf. HUXLEY, 1866, p. 35; REIS, 1892, p. 21), seems to be shown partly by the rather slight width of the canal and partly by its position in relation to the fossa hypophyseos, as it is difficult to imagine the ramus maxillaris and mandibularis or the nervus ophthalmicus lateralis with a course of this sort. On the other hand the ramus profundus or a branch that is somewhat equivalent to this can often have its exit far forward, in front of the other trigeminal branches, sometimes together with or immediately behind the oculomotorius (ALLIS, 1897a, pp. 532—534; 1909a, pp. 80—83; GAUPP, 1911, p. 419; VEIT, 1907, p. 162, fig. 2, p. 187; 1911, p. 203; LEHN, 1918, figs. 2—4, pp. 353—355, pp. 391—393; PINKUS, 1895, pp. 296—299; BRIDGE, 1898, pp. 347—348; VAN WIJHE, 1882, p. 299). Consequently in my opinion it seems rather probable that in this case we are concerned with the canal for the r. ophthalmicus profundus.

Immediately behind the proximal part of the process *e* there now follows in *Wimania sinuosa* a broad but distinct sinus in the latero-dorsal edge of the basisphenoid corpus (*V₃*, s text figs. 19, 20; Pl. 4, fig. 1; Pl. 5, fig. 1). If my explanation of the cranium is correct in other respects this sinus has formed the ventral boundary of the foramen, through which the ramus maxillaris, r. mandibularis and the ophthalmicus trigemini as well as the n. ophthalmicus lateralis had their exits. In any case this foramen, or, if two or three foramina were present, these foramina, ought to have been situated in the cartilaginous part immediately above this incisure (cf. BRIDGE and PINKUS). It is certain that a comparison with other Teleostomes and with Tetrapods as well would also support this view with regard to the relations of the branches of the trigeminus.

Thus in *Polypterus* (LEHN, 1918, loc. cit.; VAN WIJHE, 1882, Pl. XV, fig. 6) the foramen of the ramus maxillaris and mandibularis trigemini lies immediately behind the sphenoid, and a special foramen for the ophthalmicus lateralis is situated a little above and somewhat in front of the former, but in the sphenoid. In *Amia* (ALLIS, 1897a, pp. 591—614) the foramen for the truncus maxillo-mandibularis is found considerably in front of the prootic anteriorly bounded by the alisphenoid and posteriorly by cartilage. The ophthalmicus lateralis in *Amia* has its exit by a special foramen in the alisphenoid above that of the truncus maxillo-mandibularis. In *Lepidosteus* (VEIT, loc. cit.) there is a single foramen developed for all the branches of the trigeminus with the exception of the profundus. The foramen for the latter is surrounded by the anterior part of the prootic and this is also, as a rule, the case in the *Teleostei*. As we shall find below in the description of the Palaeoniscids, the exit of the trigeminal branches is bounded, at least in certain forms, to a considerable extent by a large sphenoid. In the Stegocephalians (HUENE, 1913, pp. 320—322; WATSON, 1916, pp. 612—618; 1919; pp. 22—29; ABEL, 1919, pp. 239—243) and among reptiles, at least in Lacertilians and Rhynchocephalians, the ramus maxillaris and mandibularis trigemini have their exits in front of or above the anterior part of the prootic in close relation to or in contact with the upper portion of the basisphenoid (cf. GAUPP, 1911). In *Mammalia* these trigeminal branches penetrate the ala magna.

As I shall show in more detail later, the palatoquadrate of *W. sinuosa* and other Coelacanthids articulates with the process *e* on the basisphenoid. This process thus corresponds, at least functionally, to a basipterygoid process. In relation to the cranial cavity itself it occupies a somewhat normal position, but is situated, on the other hand,

considerably dorsally of the basis cranii. The explanation of this seems to be that the basal parts of the cranium have increased greatly in height at this place, a fact that may possibly, at any rate to some extent, be connected with the development of the basal canal *m* described above, which, for reasons to be given later, perhaps ought to be interpreted as a myodome.

In *Dictyonosteus* there is also apparently a basiptyergoid process (STENSIÖ, 1918c, *Bp*, Pl. IV, fig. 3, Pl. V, fig. 1, Pl. VI). There, however, it seems to occupy a more primitive position, as it issues farther ventrally on the lateral side of the neurocranium than in the Coelacanthids, without, however, being situated at the cranial basis itself. Another primitive feature in *Dictyonosteus* is that the cranial cavity over the part of the sphenoid that corresponds to the basisphenoid corpus is considerably higher in a vertical direction than in Coelacanthids and that consequently the basal parts of the cranium in this region are comparatively lower.

While the ramus maxillaris and ramus mandibularis trigemini in *W. sinuosa*, after their exit from the cranial cavity, presumably passed behind the basiptyergoid process or over its posterior part in a lateral direction, the nervus ophthalmicus lateralis must have crossed over this process in a forward direction close to the lateral wall of the brain-case. If my interpretation of the process in question is correct, the jugular vein (*v. capitis lateralis*) should also have proceeded in a similar way to that of the last mentioned nerve (cf. ALLIS, 1909 a, p. 44, pp. 183—208; 1914 a, pp. 225—253; 1914 b, pp. 625—637). That the relations of the trigeminal branches in the Coelacanthids have agreed in the main with those in *Dictyonosteus* seems to be evident from my description of this form and the reproductions published in connection with it (STENSIÖ, 1918c, Pl. IV, V, VI). Ramus maxillaris and r. mandibularis must thus in *Dictyonosteus* have penetrated the cranial wall postero-dorsally of the basiptyergoid process at one part, which is not, however, preserved. The nervus ophthalmicus lateralis must have had its exit at about the same place and after that in its forward course been situated for some distance in a rather short canal in the lateral wall of the pars alisphenoidea of the sphenoid, not far below the posterior part of the frontals (cf. *Axelia*).

With regard to n. facialis it may possibly be thought that in *Wimania sinuosa* it was transmitted together with the trigeminal branches (cf. GAUPP, 1911, p. 421), but this view does not seem probable. On the other hand it might also possibly have had its exit behind the process *f*₁. The furrow *s*₃, described above on the prootico-opisthotic medially of the process just mentioned has, however, such a forward, downward and lateral direction that at least the ramus palatinus must probably have been in relation to it. A comparison with *Lepidosiren* (BRIDGE, 1898, pp. 348—349) and *Eryops* (ABEL, 1919, fig. 188; HUENE, 1913, pp. 320—322; WATSON, 1916, pp. 612—618; 1919, pp. 22—29) suggests that in these forms the nerve as a whole has had its exit at the corresponding place. If this is correct, it thus has in *W. sinuosa*, with the present state of preservation of the cranium, its foramen in such a position (VII, text figs. 19, 20) that it is bounded anteriorly by the basisphenoid corpus, posteriorly by the process *f*₁ on the prootico-opisthotic, and ventrally by the anterior part of the corpus of the latter bone.

The possible position of the foramen nervi glossopharyngei has already been mentioned. It must be expressly stated that in this case, however, we are only con-

cerned with the inner opening of the canal of the nerve. From this opening the canal probably had its course obliquely posteriorly and laterally through the cartilaginous part of the lateral wall of the labyrinth region, and the outer opening would consequently be situated more caudally than the inner one. On the other hand the foramen vagi cannot be localized with any degree of certainty, as I have also sufficiently shown above.

In the ethmoidal region we find poorly preserved remains of a paired bone (*Pethm*, text figs. 19, 23; Pl. 7, figs. 1, 3), which, as I think I can show in the description of *Axelia robusta*, represents the so-called preëthmoid (septomaxillary, ALLIS, 1897a, Pl. XXI, figs. 8—10; 1898, pp. 446—450; 1909a, pp. 17—22; SAGENHEIL, 1884, p. 204; SWINNERTON, 1902, pp. 530—532). It is impossible to say anything as to the shape of this bone in the species in question. It is partly covered on the ventral side by the parasphenoid and seems medially to reach the median line pretty closely or altogether; it has thus perhaps entered into connection with the corresponding bone on the other side (text fig. 23). Otherwise by far the greater part of the ethmoidal region has been composed of cartilage.

The membrane bones of the neurocranium.

The ventral side of the neurocranium is covered for a considerable part by a large, broad parasphenoid (*Psph*, text figs. 19, 20, 22, 23; Pl. 4, fig. 2, Pl. 7, figs. 1—3). This is situated chiefly under the orbitotemporal region, but reaches also to the front under the ethmoidal region and, although only to a trifling extent, backwards under the anterior part of the labyrinth region. At its anterior extremity it is obtusely pointed, at its posterior end it is truncated. It is broadest in the neighbourhood of the former end, from which it grows gradually narrower backwards, to about the place between the first and second quarter of its length measured from behind, to increase again somewhat in breadth in the hindmost quarter. The centre of ossification about corresponds in its position to the narrowest part of the bone.

A transverse section through the parasphenoid taken in front of the centre of ossification shows a horizontal, thick median part, and thinner dorsally inflected lateral parts (text fig. 24 A). The thickening of the median part appears exclusively upon the ventral side of the bone, and as this thickening is sharply bounded laterally and also carries small teeth it becomes a prominent feature of the bone. Behind the centre of ossification, on the contrary, a transverse section shows a somewhat different appearance (text fig. 24 B). In this part the bone is convex from side to side on the ventral surface and correspondingly concave on the dorsal surface. The median part is not thickened, or only slightly so in relation to the lateral parts.

Text fig. 23.

Wimania sinuosa n. sp.
Parasphenoid, prootic-opisthotic,
preëthmoid and autopalatine, in
ventral aspect. From Pl. 257. 1/4.

Aup, autopalatine; *Pethm*, pre-
ëthmoid; *Pro.o*, prootic-opisthotic;
Psph, parasphenoid; *c*, posterior
process from the corpus of the
prootic-opisthotic.

An especially noticeable fact is that in the species in question as well as in all the rest of the Coelacanthids the processus ascendentes of the parasphenoid are wholly missing, which is probably the case in *Dictyonosteus* too (STENSIÖ, 1918 c).

A little in front of the basisphenoid in *W. sinuosa* there appears on the dorsal side of the parasphenoid, a shallow, fairly broad, longitudinal furrow, that continues backwards in between the ventral processes of the basisphenoid (text fig. 22) and forms with its bottom the ventral boundary for the above-mentioned canal *m*. This furrow may suggest that we have here some special formation. One might perhaps at first sight feel inclined to accept the canal *m* and the furrow mentioned as having originated in relation to the hypophysis. If now one compares the facts just stated with those given above concerning an eventual fenestration of the interorbital wall immediately in front of the ventral processes of the basisphenoid, one cannot avoid suspecting that

Text fig. 24.

Wimania sinuosa n. sp.
Cross-section through the
parasphenoid. From Pl. 257, 2/4.

- A) Section anterior to the
centre of ossification.
B) Section posterior to the
centre of ossification.

in reality it might be a question of a myodome. This suspicion gains in probability if one takes into consideration the considerable size of the eyeball in all the Coelacanthids, a circumstance that makes it probable that the recti muscles of the eye were well developed and had extended backwards into the basis cranii. An additional support for this view seems to me to be found in the fact that the supposed myodome would occupy the same position as that of the Actinopterygians, for, as far as one dare judge, n. opticus ought to have emerged into the orbit anteriorly to the fenestration of the interorbital wall, and the fenestration itself has such a position ventrally of the fossa hypophyseos that it must be regarded as coinciding with the place where one would have the right to expect the homologue of the canalis transversus of the

Elasmobranchii (pituitary canal, ALLIS, 1909 a, pp. 183—208; 1914 a, pp. 225—253); and it is, as known, in relation to this canal, as GEGENBAUR (1872, pp. 75—79), SAGENEHL (1884, pp. 215—217; 1885, pp. 85—87; 1891, pp. 574—575) and ALLIS (1909 a, loc. cit.; 1914 a, loc. cit.; 1918 a, pp. 241—246) have shown, that the myodome has developed in the Actinopterygians. — It thus seems fairly plausible that a myodome should occur in the Coelacanthids, though of course not strongly developed.

Nothing is yet known about the vomeres of *W. sinuosa*.

The membrane bones of the cranial roof in this fish have on the whole been closely attached to the dorsal surface of the primordial neurocranium. As I have had an opportunity of showing above, the posterior part of this surface lies horizontally, and forms an angle with the anterior, longer, forward sloping part, as is usual in the Coelacanthids.

On the posterior horizontal part we can now observe in *W. sinuosa* two bones on each side of the median line (text figs. 19, 20, 21, 25; Pl. 4, fig. 1; Pl. 5, fig. 1; Pl. 6, figs. 3, 4; Pl. 7, fig. 5; Pl. 8, fig. 1) as in other Coelacanthids. Of these bones the larger anterior one (*Pa. it*) has been considered by previous authors (HUXLEY, 1866; REIS, 1888; WOODWARD, 1891 b; o. a.)¹⁾ as a parietal, the smaller posterior one as a squamosal

¹⁾ In 1892 REIS on the contrary was of the opinion that the «parietal» and «squamosal» are usually fused (p. 20).

or, according to HUXLEY's view (1866, p. 34) as the squamosal + the post-temporal. I myself must, on grounds which I shall give later on, propose new terms for the two bones under consideration. The longer anterior one I shall call in the continuation the parieto-intertemporal, the posterior one the supratemporo-extrascapular.

In *W. sinuosa* the parieto-intertemporal bones are only imperfectly preserved, as their median and posterior parts are totally missing. Under such conditions one cannot define their precise extension backwards but an eventual deviation in this respect from my restoration in text fig. 21 may not be very important. The parieto-intertemporals ought to have been of a rectangular shape, and in breadth were probably rather more than half the length. At the postero-lateral corner each of them has a large sinus into which the supratemporo-extrascapular (*Stemp. ext*) fits. The centre of ossification of each parieto-intertemporal bone lies near the antero-lateral corner.

A perpendicular longitudinal lamella, which covers a stretch of the upper cartilaginous part of the labyrinth region on the lateral surface, issues on the ventral side a little medially of the lateral margin of the anterior part of the parieto-intertemporal (text fig. 19). With its ventral border this lamella anteriorly comes very near to, or even in touch with the process *f*₁ on the prootico-opisthotic and the dorsal parts of the basisphenoid. The horizontal part of the bone, which lies laterally of the line along which the perpendicular longitudinal lamella issues, is always in the Coelacanthids pierced by a sensory canal, but this canal has not been preserved in the species here under consideration.

On each postero-lateral corner of the dermal cranial roof the supratemporo-extrascapular bone forms a powerfully projecting process (*Stemp. ext*, text figs. 19, 20, 21, 25; Pl. 4, fig. 1; Pl. 5, fig. 1; Pl. 6, fig. 4; Pl. 8, fig. 1). Seen from the lateral side the supratemporo-extrascapular (text fig. 19) is shaped like a triangle with the apex pointing backwards and the base partly in connection with the parieto-intertemporal bone. The antero-ventral corner is extended to a long antero-ventrally and at the same time somewhat medially pointing process (*h*), which covers the postero-dorsal corner of the antero-lateral side surface of the prootico-opisthotic. In dorsal aspect the supratemporo-extrascapular bone appears to have a somewhat more complicated form (text fig. 21 A). One can observe, as before, its lateral surface, but it is now clearly understood that the direction of this surface is not purely lateral, but is also somewhat dorsal and even partially rostral; the process *h* can also be observed from the dorsal side, and the relation it bears to the prootico-opisthotic. Furthermore one finds a dorso-medial surface, which is only developed in the posterior part of the bone and of course is a good deal smaller than the lateral or, as it ought perhaps to be called, the dorso-lateral one. While the anterior part of the bone laterally occupies such a position that it forms nearly a direct posterior continuation of the perpendicular longitudinal lamella of the parieto-intertemporal bone and also, like that lamella, covers a dorsal and anterior part of the cartilaginous side wall of the labyrinth region, on its lateral surface this relation is changed posteriorly in such a way that the posterior half of the bone rests instead totally upon the dorsal surface of the same region. A transverse section of this posterior part, which shows plainly the relation between the dorso-medial and the dorso-lateral surface and at the same time makes it evident that the thickness

of the bone substance was not particularly great, is given in text fig. 21b. The bone is pierced throughout its length by a sensory canal and has the centre of ossification situated in the posterior half, rather near the posterior end.

The presence of a dorso-medial surface on the supratemporo-extrascapular bone, taken in connection with the shape of the bone otherwise, speaks strongly in favour, it seems to me, of a paired muscle fossa (fossa temporalis, ALLIS, 1897a, Pl. XXI, fig. 8; 1909a, pp. 8—12) having been developed on the posterior part of the labyrinth region. Text fig. 21a shows how one can imagine such a muscle fossa (*f. temp.*) would appear. Of course this figure can make no claim to be accepted as fully correct, as one has no point from which to judge of the extension of the fossa either forwards or medially. It is also clear from the same figure that the dorsal surface of the primordial neurocranium in this region was not directly covered by the dermal bones, but that these bones — the extrascapular bones — were situated loosely in the skin above the muscles, which reached into the two fossae described to take their insertion in them. Nothing is, however, preserved of the extrascapular bones referred to here.

In the labyrinth region too, but on its side wall, one finds certain hints of the presence of another fossa, which certainly must have been shallow, but in other respects of considerably larger dimensions than the dorsal one just described. This lateral fossa has been bounded dorsally by that part of the parieto-intertemporal bone which lies laterally of the line along which the perpendicular longitudinal lamella issues, and further by the most anterior part of the supratemporo-extrascapular bone; posteriorly by the process *h* and also by the posterior part of the corpus of the prootico-opisthotic. Its ventral and anterior boundaries are, on the contrary, very vague. In connection with my description of the visceral skeleton below, I shall return to this fossa and what it may mean.

As we have seen, in the part now dealt with of the dermal roof of the cranium in *W. sinuosa* and other Coelacanthids the number of bones is limited to two on each side of the median line, if one excepts the bones of the extrascapular (supratemporal) row. The *Rhipidistidia* are in this respect more primitive, as the investigations of TRAUQUAIR (1875a, 1881, 1896), WATSON and DAY (1916), and also GOODRICH (1919) have proved. The number of membrane bones in the corresponding part of the cranial roof of these fishes is, as a rule, three on each side median line, which have been called by WATSON, DAY and GOODRICH the parietal, the intertemporal and the supratemporal respectively. Of these the intertemporal has such an extension and is pierced by a sensory canal in such a way that its homologue in the Coelacanthids cannot be an independent bone (cf. the description of *Axelia robusta* below) but may be fused with the parietal and in consequence the term parieto-intertemporal bone, as I have proposed, must be quite justified.

The supra-temporal of the *Rhipidistidia* corresponds to the anterior part only of the supratemporo-extrascapular bone of the Coelacanthids. The posterior part of the supratemporo-extrascapular of Coelacanthids belongs, as ought already to be understood from the name, to the extra-scapular series, and has its nearest homologue, as I can show below in the description of a species belonging to the genus *Axelia*, in the lateral extrascapular bone of the Actinopterygians, or in a lateral part of that bone in the *Rhipidistids*, which WATSON and DAY, and after them GOODRICH, have called the tabular bone.

It cannot be proper to retain the earlier name squamosal for such a compound bone as that now under consideration in Coelacanthids, as the so-called squamosal or dermopterotic in the *Actinopterygii* may according to our present knowledge correspond to the supratemporal and intertemporal of the *Rhipidistia* fused into one bone. The name supratemporo-extrascapular proposed by me thus seems to be the only one justifiable. I shall have further reason to return to the question of the homologues of the supratemporo-extrascapular later on in this work.

Fusions of a kind similar to those now described between the membrane bones of the posterior part of the cranial roof of Coelacanthids have also taken place in the anterior part. Thus the «frontal» bone according to the terminology of earlier palaeontologists seems first and foremost to comprise the dermosphenotic (dermal postfrontal), which is normally found in the *Rhipidistia* as an independent bone, though among them it may also sometimes fuse with the frontal, as is found to be the case in *Rhizodopsis* (ALLIS, 1919b, p. 76). The course of the sensory canal shews plainly, as can be seen from the description of *Axelia robusta* given later, that in Coelacanthids the homologue of the dermosphenotic of the *Rhipidistia* forms the postero-lateral corner of the so-called «frontal». It is also plain that this so-called «frontal» has become fused ventrally with a part of cartilage bone, the above-mentioned alisphenoid, which belongs to the postero-dorsal part of the orbitotemporal region. The compound bone which has thus been formed through the fusion of the three bones mentioned, I shall call in the continuation, for the sake of shortness, the fronto-dermosphenotic, although it ought properly to be called the fronto-dermosphenotico-alisphenoid.

In *W. sinuosa* the two fronto-dermosphenotic bones (*Fr. dsph*, text figs. 19, 20, 21, 25; Pl. 4, figs. 1, 2; Pl. 5, figs. 1, 2; Pl. 8, fig. 1), are long and separated from each other by a straight median suture. At their posterior end they are considerably broader than the parieto-intertemporal bones; they are narrowest at their middle part, where they are of about the same width as the last-mentioned bones. They are situated for the most part over the orbitotemporal region and even stretch forward to some extent over the ethmoidal region, but reach no farther backwards than over the anterior part of the basisphenoid, where they meet the parieto-intertemporal bones in a straight transverse suture, which, to be more exact, lies over the anterior end of the basispterygoid processes (text figs. 19, 20). The centre of ossification in each fronto-dermosphenotic bone (text fig. 21) lies very far back and rather nearer to the lateral border than to the medial one. From this centre on the ventral side of the bone, in a ventro-caudal and somewhat medial direction, there issues a process (*Alsph*, text fig. 20; Pl. 4, figs. 1, 2; Pl. 5, fig. 1; Pl. 8, fig. 1), which meets the upper anterior corner of the lamella *al* of the basisphenoid. The topographical position as well as the structure of the process in question seem to me to indicate that it is the homologue of that part of the sphenoid of *Dictyonosteus* which corresponds to the alisphenoid in the higher *Actinopterygii*. Further proofs of the correctness of this view will be given later in the description of *Axelia robusta*.

The anterior greater part of the lateral margin of the fronto-dermosphenotic is concave. In front of the somewhat projecting postero-lateral corner, which, as I have demonstrated, represents the dermosphenotic, there are placed along the lateral margin

a number of supraorbitals, the so-called «Parafrontalia» according to the terminology adopted by REIS (1888). As the state of preservation of these supraorbitals is not very good it is impossible to determine their exact number, but it was probably not less than four or more than six. As far as one can make out they are rather narrow, and have been attached lengthways to the fronto-dermosphenotic with their medial margins. To what extent they have overlapped the lateral part of the fronto-dermosphenotic is uncertain.

The supraorbital row of bones is continued in front over the ethmoidal region by a large plate of bone (*Na. ant.*, text figs. 20, 21, 25; Pl. 5, fig. 1), which to some extent covers the antero-lateral corner of the fronto-dermosphenotic. The relation which the bone-plate has to the sensory canal and the external nasal opening in this species is not yet clear, but a comparison with other, better preserved forms, which are described later on, seems to point to the fact that it may correspond to the nasal elements and a great part of the antorbital bone (adnasal) of the primitive *Crossopterygii* and *Actinopterygii* (cf. the description of *Axelia* and at the same time my description of the *Palaeoniscidae*, *Catopteridae* and *Saurichthyidae* in this work). I have consequently called it the nasalo-antorbital.

Between the nasalo-antorbital of both sides there is found anterior to the fronto-dermosphenotics and partly covering their anterior ends, a paired rather large plate of bone (*Ptr.*, text figs. 20, 21, 25; Pl. 4, fig. 1; Pl. 5, fig. 1; Pl. 8, fig. 1), which I have called the postrostral. The two postrostral plates meet medially in a rather long suture which forms a direct anterior continuation of the suture between the fronto-dermosphenotic bones. With regard to the homologues of the postrostral plates and the rest of the membrane bones on the dorsal side of the ethmoidal region, I shall return to this question in my description of *Axelia robusta* and in the chapter headed, «Coelacanthids compared with some other fishes, and certain Tetrapods».

As all the membrane bones of the cranial roof are preserved as impressions of the medial side or else are found in a much weathered condition nothing can be decided in respect to their ornament.

Although not belonging directly to what has preceded in this part, it ought to be mentioned that a sclerotic-ring is found developed in *W. sinuosa*, and consists of about twenty quadrangular bone-plates (*Scr.*, text fig. 25; Pl. 5, fig. 4; Pl. 6, fig. 2).

The membrane bones of the cheek.

The dermal bones of the cheek in *W. sinuosa* are partly well preserved and lie pretty well in situ. One finds the three boneplates, which in general are a distinguishing feature in the Coelacanthids, lying in a vertical row postorbitally, and anterior to them the long bow-shaped bone, called in the current terminology of palaeontologists the suborbital, as indicated by the name, below the orbital opening. As it is more convenient to put off giving an account of the homologues of the four bones mentioned until it can be done in connection with a description of the sensory canals of the head, I shall only remark here that in the subsequent description I shall confine the term postorbital to the dorsal of the three postorbital plates and that I shall introduce for the middle one the term squamoso-preopercular and for the ventral one the term preoperculo-quadratojugal. The suborbital I shall call the lacrymo-jugal.

In *W. sinuosa* the postorbital (*Po*, text fig. 25; Pl. 5, figs. 2, 4; Pl. 6, figs. 1, 2) has a somewhat rounded quadrangular shape and is a little broader than it is high. Its posterior margin is convex, its anterior margin is concave; its lower margin is straight or very slightly convex and so is also its dorsal one with the exception of the part farthest forward, where there is a well marked sinus. The antero-dorsal corner is extended to a broad, obtuse process. The antero-ventral corner forms a pronounced angle while the postero-dorsal as well as the postero-ventral ones are well rounded off. Near the antero-ventral corner the anterior margin has a blunt little process and one or a pair of

Text fig. 25. *Wimania sinuosa* n. sp.

The head from the left side. The shape of the lower jaw rather uncertain. The course of the sensory canals indicated by dotted lines and shading. From *P.* 257. 1/2.

Co, coronoid; *De*, dental; *Fr. dsph*, fronto-dermosphenotic; *G*, jugular plate; *Lo. ju*, lacrymo-jugal; *Mx*, maxillary; *Na. ant*, nasalo-anterorbital; *Op*, operculum; *Pa. it*, parieto-intertemporal; *Po*, postorbital; *Pop. gul*, preoperculo-quadratojugal; *Ptr*, postrostral; *Sang. ang*, supraangulo-angular; *Scl*, sclerotic plates; *So*, supraorbital; *Spl*, splenial; *Sq. pop*, squamoso-preopercular; *Stemp. ext*, supratemporo-extrascapular; *X*, dermal bone-plate, probably corresponding to the dorsal part of the posterior end of the jugal of the *Rhipidistia*.

similar processes are discernible at the bottom of the sinus in the dorsal margin, just behind the base of the antero-dorsal process. — A sensory canal (*ifc*) traverses the postorbital from the dorsal to the ventral margin in the way shown by text fig. 25 and Pl. 5, fig. 2.

The squamoso-preopercular (*Sq. pop*, text fig. 25; Pl. 5, figs. 2, 4; Pl. 6, figs. 1, 2) is larger than both the preoperculo-quadratojugal and the postorbital. Its area is probably about three times as great as that of the latter bone. In shape it is somewhat irregularly four-sided. One can distinguish a posterior, an anterior, a dorsal and a ventral margin. The antero-ventral corner is much rounded and in other respects only slightly marked, the remaining corners are also rounded but are at the same time more pronounced, which is especially the case in reference to the postero-ventral one. The posterior margin is vertical, has a considerable height, and is slightly convex. Both the upper and lower margins are straight and converge towards the front, which makes the anterior margin

much shorter than the posterior one. The anterior margin is characterised also by two narrow, deep sinus with an anteriorly projecting process lying between them. At the obtuse end of this process a sensory canal enters the squamoso-preopercular, where it continues in an arch backwards and downwards (*jc*, Pl. 5, fig. 4) to the lower margin, which it reaches not far in front of the postero-ventral corner.

The preoperculo-quadratojugal (*Pop. quj*, text fig. 25; Pl. 5, figs. 2, 4; Pl. 6, figs. 1, 2, 3, 4; Pl. 7, fig. 5) is situated externally of the ventral part of the palatoquadrate. Its breadth is probably about twice as great as its height. Its shape, in respect to the lines of the contour, is not fully known with certainty. From the squamoso-preopercular a sensory canal has continued in a ventral direction and ought, according to what one can judge, to have also entered the preoperculo-quadratojugal in its posterior part. Concerning this bone it is further to be remarked that it is of a considerable thickness, and has a well discernible centre of ossification in the postero-ventral half.

The lacrymo-jugal (*La. ju*, text fig. 25; Pl. 5, figs. 2, 4; Pl. 6, fig. 2) is a long and on the whole narrow bone arched in such a way that it has the concavity dorsally and the convexity ventrally. It is highest (broadest) in its posterior part for about a third of its length. In front of this there follows a lower middle part, lying under the orbital opening, and yet again still more forward there is a somewhat higher but shorter part lying preorbitally, after which the remaining anterior part rather slowly decreases in height to the end, which becomes pointed. The posterior end, which is turned dorsally, is, on the contrary, blunt. In its posterior part the bone probably came into contact with, or in any case has lain very near to the process of the anterior margin of the squamoso-preopercular. Dorsally, on the other hand, it does not by a long way reach to the postorbital, but is connected with the latter, as far as one can understand, by a little four-sided plate (*X*, text fig. 25, Pl. 6, fig. 2), situated in a sinus open in front, which is bounded dorsally by the postorbital bone, caudally by the squamoso-preopercular, and ventrally partly by the latter and partly by the upper end of the lacrymo-jugal. The anterior end of the lacrymo-jugal has probably extended a good bit forward along the lateral surface of the ethmoidal region, as text fig. 25 shows. A part of a sensory canal pierces the plate *X* as well as the lacrymo-jugal.

All the cheek plates are, as far one can see, quite without ornament of ganoine. The postorbital and the squamoso-preopercular show plainly concentric lines of growth, while the preoperculo-quadratojugal, on the contrary, as already mentioned, has a well developed radiate bone structure.

The cheek plates of the species under consideration have not fitted with their margins towards each other so as to form a continuous covering of bone, but must have lain loosely in the corium in about the same way as they are found in the fossil. Partly they are even separated from each other by considerable interspaces. A specially large interspace seems to have existed behind the postorbital plate, as the squamoso-preopercular does not reach so high upwards as in *Coelacanthus* (WELLBURN, 1902, p. 475, fig. pag. 483) and no independent smaller plate seems to have existed here, which is the case in the species *Sassenia tuberculata*, described later on. Another large interspace seems to have been developed between the squamoso-preopercular, the preoperculo-quadratojugal, and the posterior part of the lacrymo-jugal bone.

It is very probable that in respect of the membrane bones of the cheek, some of the previously known Coelacanthids may show the same tendency to reduction as *W. sinuosa*, although nothing is yet known with certainty in this matter. The fact that the bones in question often are very poorly preserved or even quite missing in most Coelacanthids seems to me to speak in favour of such a suspicion being correct.

The visceral skeleton.

The cartilage of the palatoquadrate persisted presumably to a rather considerable extent, although one cannot prove that such was the case as plainly as in certain of the forms I shall describe below. The three replacing bones in the palatoquadrate cartilage, the autopalatine the quadrate and the metapterygoid are all well developed and preserved in situ.

The autopalatine (*Aup*, text figs. 23, 26; Pl. 4, figs. 1, 2; Pl. 6, figs. 1, 4; Pl. 7, figs. 1, 5; Pl. 8, fig. 1) is a rather small, solid bone, shaped something like a three-sided pyramid, with the point lying forwards and the basal surface straight caudally. It has a dorso-lateral, a dorso-medial, and a ventro-medial side surface, of which the two last-mentioned ones pass into each other without any distinct boundary. A rather thick but short process issues from the ventral part of the caudal surface backwards. The ventro-medial side-surface lies against the anterior end of the pterygoid, the dorso-medial one has articulated, as far as one can judge, with the ethmoidal region. — It ought to be mentioned in connection with this that HUXLEY (1866, p. 37, Pl. 8, fig. 3) has already described an autopalatine in *Macropoma*, calling it the palatine, and that REIS (1888, pp. 85—87) has described the same bone in Jurassic genera, though he uses the term «propterygoid» for it.

The quadrate (*Qu*, text figs. 26 A, B, Pl. 4, fig. 2) is of rather considerable size. It is broadest in its dorsal part, and narrowest a little above the ventral end, which is developed as a condyle for the articulation with the mandibula. In the species in question it is imperfectly preserved and its contours in text fig. 26 A and B are therefore partly restored according to what is known in other species. That its appearance did not differ essentially from my restoration is, however, tolerably certain. The dorsal part of the medial surface of the quadrate lies against the ventro-caudal corner of the pterygoid, but stretches at the same time a little behind the posterior margin of that bone.

The metapterygoid (*Mptg*, text figs. 26 A, B; Pl. 4, figs. 1, 2; Pl. 5, fig. 2; Pl. 6, figs. 1, 3, 4; Pl. 7, fig. 5; Pl. 8, fig. 1) lies at the dorsal end of the palatoquadrate. It is a rather thick plate, rhomboidal in shape, situated on the lateral side of the pterygoid bone, but united firmly with that bone only with its anterior margin. Besides this margin, which is slightly concave, a dorsal one can also be distinguished, which is likewise concave, as well as a posterior and a ventral margin, which are both convex and merge into each other in a postero-ventral corner that is much rounded off and thus is not distinct. The antero-dorsal corner is extended to a point, while the postero-dorsal one is rather rounded. The anterior lower corner forms almost a right angle. The centre of ossification lies near the dorsal margin of the bone, a little in front of the middle of that margin. The bone substance is clearly radiate.

With its dorsal, rather broad surface the metapterygoid articulates with the basi-ptyergoid process (*e*) and because of this articulation between the palatoquadrate and neurocranium most authors (HUXLEY 1866, pp. 35—37; WOODWARD, 1891 b, p. 395; 1898 a, p. 79;

1909, p. 175; WELLBURN, 1902, pp. 476—477; GOODRICH, 1909, p. 289; POMPECKJ, 1913, p. 1138;) have been of the opinion that the hyomandibula might have fused with the pterygoid. That is to say the suspension of the mandibula would, if this be true, be hyostylic and closely resemble that of the *Teleostei*. REIS (1888, p. 41) seems to have come nearest the

truth, in considering the mode of suspension of the mandibula as an auto-stylic one, and at the same time emphasizing the fact that the palatoquadrate was not coalesced with the neurocranium.

That the bone in *Wimania sinuosa* interpreted by me as the metapterygoid cannot belong to the hyoid arch, is shown by the following facts. As we have seen, it articulates with the basiptyergoid process situated on the basisphenoid, while the hyomandibular always articulates with or is attached to the capsula auditiva. The ramus maxillaris and the ramus mandibularis trigemini seem either to have passed along the posterior border of the basiptyergoid process and then across the dorsal margin of the basiptyergoid bone or to have crossed the dorsal surface of the basiptyergoid process obliquely in an antero-lateral direction

and then to have passed downwards and forwards along the lateral surface of the metapterygoid bone. The nervus facialis has had its exit from the neurocranium postero-medially of the metapterygoid, and the position of this bone in relation to the pterygoid bone is such that it cannot possibly be imagined to have been connected by ligaments

Text fig. 26. *Wimania sinuosa* n. sp.

A. The bones of the palatoquadrate in lateral view. From P. 257. $\frac{3}{4}$.

Aup, autopalatine; Mptg, metapterygoid; Pt, pterygoid; Qu, quadrate.

B. The bones of the palatoquadrate in relation to the mandibula. The figure also shows the relation between the substitution bones of the palatoquadrate and the pterygoid. From P. 257. $\frac{3}{4}$.

Co, coronoid; Md, mandibula; Otherwise the lettering as in figure A.

with the ventral elements of the hyoid arch. In some Spitzbergen species described below I think I can also show with full certainty that the metapterygoid and the quadrate were connected with each other by a thick cartilage.

It ought thus to be considered as pretty certain that the palatoquadrate of Coelacanthids articulated with the neurocranium in the posterior part of the orbitotemporal region at

about the corresponding place as in *Megalichthys* (cf. WATSON, 1912 a, pp. 9—10). I consider it very probable too that the palatoquadrate of *Dictyonosteus* articulated with or was in some way attached to the basipterygoid process. A connection of this sort between the palatoquadrate and the neurocranium thus seems to have been developed in several forms among the Crossopterygians and there may be every reason to ask whether this was not a character common to all of them.

Although the palato-basal articulation of the *Elasmobranchii* is rather variable in its position (GEGENBAUR, 1872, pp. 186—192; LUTHER, 1909, pp. 105—113) it seems, however, in essentials to correspond to that between the methapterygoid and the orbitotemporal region in the Coelacanthids and other Crossopterygians. It seems also to be probable that in both cases we are concerned with the primary articulation of the mandibular arch against the neurocranium, a view that has already been put forward by WATSON (1912 a) in the case of *Megalichthys* and primitive Tetrapods. Moreover in the more recent literature there is a fair degree of unanimity as to the palato-basal articulation, even in sharks, being an old formation that seems to represent the primary connection of the mandibular arch with the neurocranium, or that this articulation in any case was situated near the present palato-basal articulation (ALLIS, 1915; HUXLEY, 1876, pp. 43—45; GOODRICH, 1909, p. 98; LUTHER, 1909, pp. 112—113; SEWERTZOFF, 1899, pp. 299—300; VEIT, 1911, pp. 217—218);¹ SWINNERTON, (1902, pp. 568—573) also believes that he has found that the palatoquadrate in the ancestors of the *Actinopterygii* must have articulated against the posterior part of the trabecular section of the neurocranium between the exits of the optic and the trigeminus nerves.

To return now to *W. sinuosa*, the medial side of the palatoquadrate is covered in this species in the way characteristic for the Coelacanthids, by a large pterygoid (*P*), text figs. 26 A, B; Pl. 4, figs. 1, 2; Pl. 6, figs. 1, 3, 4; Pl. 7, figs. 2, 5; Pl. 8, fig. 1). On this bone one can distinguish a posterior vertical and an anterior horizontal limb, which are so connected that an angle, open antero-dorsally, is formed between them.

The posterior limb is strikingly broad and reminds one in this respect of the corresponding limb of the Palaeozoic Coelacanthids. It is broadest at its dorsal part. At the ventral part the breadth decreases considerably. The ventral corner is bluntly rounded off. The posterior margin is high and very convex, the dorsal one on the other hand slightly concave. The antero-dorsal corner is acutely pointed, the postero-dorsal one forms an obtuse angle and is not very conspicuous. From the antero-dorsal corner there extends downwards and somewhat backwards on the lateral surface a rounded ridge, which is strongest in its dorsal parts, from where it becomes gradually lower ventrally and finally disappears near the upper end of the quadrate. Posteriorly it is not sharply marked off from the other lateral surface of the bone, whereas its anterior border is, along the greater part of its length; it is accordingly convenient to take the latter border as the boundary between the posterior and anterior limbs.

¹) GEGENBAUR (1872, p. 186), as we know, was of an opposite view; he maintained that the primary articulation of the mandibular arch against the neurocranium was to be seen in the postorbital articulation between the palatoquadrate and the auditory capsule in Notidanids. JAEKEL (1899 a, pp. 249—258; 1899 b, pp. 56—60) also came to a similar conclusion.

The metapterygoid is attached dorsally for a rather considerable distance to the posterior border of the above-mentioned ridge and otherwise the position of the metapterygoid in relation to the posterior pterygoid limb is seen from text figure 26 and Pl. 4, fig. 2; Pl. 6, figs. 3, 4. Text fig. 26 B shows in addition to what extent the ventral part of the posterior pterygoid limb was covered by the quadrate.

The anterior limb of the pterygoid issues along the anterior border of the posterior limb and is at the posterior end nearly as high as the latter, which consequently has the anterior border free only farthest dorsally for about a fourth of the height.

As is the case in Carboniferous and Permian Coelacanthids the anterior limb is in the species under consideration long and, on the whole, low; only quite close to the posterior one does it, as has already been said, attain a more considerable height. Its lower margin is concave and rises gently anteriorly. Its dorsal margin is, on the whole, also concave but its course is in detail decidedly more complicated than that of the ventral one. Farthest back from the place where it meets the anterior margin of the posterior limb it slopes rapidly forwards and downwards for a rather short distance, after which it turns in a more postero-ventral direction and forms a marked sinus, open dorso-rostrally; in front of this sinus it slopes down again fairly rapidly for a short distance, to continue its subsequent course forward with only a very slight slope downwards.

The posterior limb occupies such a position that its lateral side faces somewhat dorsally and forward, its medial side in the same degree somewhat ventrally and backwards. The anterior limb is so twisted that its lateral surface is turned a good deal upwards and its medial surface correspondingly downwards, a condition that is more marked anteriorly than towards the posterior limb. The pterygoid as a whole is concave on the lateral side and convex on the medial one both in the direction from the anterior end to the posterior margin and from the dorsal to the ventral margin. The medial surface, apart from the teeth, is smooth. There are no formations corresponding to such ridges as are described by REIS (1888) in certain Jurassic Coelacanthids. The centre of ossification is situated near the postero-ventral corner of the boundary between the two limbs and is covered from the outside by the quadrate. — It seems not improbable that the pterygoid of the Coelacanthids corresponds both to the large high entopterygoid and to the smaller ectopterygoid of Rhipidistids (*Glyptopomus* WATSON and DAY, 1916, p. 11).

It is really very uncertain whether a dermopalatine has been present as an independent bone in *W. sinuosa* or whether it is fused with the pterygoid. The narrow bone with large teeth that is situated beneath the anterior part of the lacrymo-jugal, laterally of the anterior pterygoid limb (*Mx*, text fig. 25; Pl. 5, fig. 4), could perhaps be taken as the dermopalatine but on the other hand it cannot be denied either that this bone can equally well be taken as a maxillary, as I have provisionally interpreted it here, supported chiefly in this view by WELLSBURN'S (1902, pp. 475—476) statements with regard to *Coelacanthus* and the exposition of ALLIS, 1919 (1919a, pp. 379—382). The *Macropoma* specimens described by HUXLEY (1866) and WOODWARD (1909) give in this case, as I have had an opportunity of becoming convinced, no positive proof for one view or the other. The material described by REIS (1888, 1892) shows that an independent dermopalatine was undoubtedly present in certain forms, but that it was always very closely connected with the pterygoid, so that it might easily coalesce with it; indications of a maxillary

are on the contrary not to be observed. Besides, even if a dermopalatine occurs in certain Coelacanthids, this fact has not yet enabled us to prove that the presumed maxillary in *Macropoma* and *Wimania* is really identical with the dermopalatine.

With regard to the mandibula of the Coelacanthids it has been necessary, as in the case of the bones of the cranial roof and the cheek, to introduce other terms than those previously used. In doing this I have followed chiefly the results gained from BRANSON'S (1905, pp. 601—603), BROOM'S (1913 d, pp. 73—78; 1913 e, pp. 563—595), GREGORY'S (1915, pp. 325—334), WATSON'S (1912 a, pp. 10—12; 1912 b, pp. 573—587), WILLS (1916) and WOODWARD'S (1898 a, pp. 123—140; 1907 b, pp. 298—300) works on the homologues of the bones of the mandibula in primitive fishes and Tetrapods, but at the same time I have also gone farther in the direction opened up by these investigators, for reasons that will be given below. I now give the infradental of the Coelacanthids as the splenial, the large post-splenial plate as the intercoronoideo-prearticular, and the anterior splenial plates as the precoronoids; further I consider it probable that the bone formerly described as the angular (sometimes as the articulo-angular) may be composed at least of the supra-angular, the angular, and possibly also the pre-angular, so that it ought to be called the supraangulo-angular.¹⁾ The coronoid is situated quite on the medial side of the mandibula and ought thus to be only partly homologous with the bone termed in the same way in Tetrapods. For the present, however, I thought I ought to retain this name, especially as, according to WATSON'S (1912 a, pp. 11—12) statement, the coronoid in certain primitive Stegocephalians (*Loxomma*) was developed in a similar way.

In *W. sinuosa* the mandibula is very incompletely preserved and it is therefore not possible to ascertain its shape with certainty to any great extent. The reconstruction of it in text figs. 25 and 26 B is consequently given with the reservation that many details may really be different. It seems possible, however, to make one certain statement, namely that the mandibula as a whole has been rather large and powerful. Of its bones the dental (*De*, text fig. 25; Pl. 5, fig. 2; Pl. 6, figs. 1, 4), the supraangulo-angular (*Sang. ang.*, text fig. 25), the intercoronoideo-prearticular (*Icor. pra.*, Pl. 4, fig. 2; Pl. 6, figs. 1, 2, 3; Pl. 7, fig. 3) and possibly the autangular (*A. ang.*, Pl. 4, fig. 2; Pl. 7, fig. 4) as well are represented only by fragments. The coronoid (*Co*, text figs. 25, 26 B; Pl. 6, figs. 1, 2, 3, 4; Pl. 7, fig. 5), on the other hand, is completely preserved and lies fairly well in situ in relation to the intercoronoideo-prearticular, with which it has been closely connected. Its shape is triangular with a somewhat rounded upper and anterior corner. Two precoronoids (*Pco*, Pl. 5, fig. 2; Pl. 6, figs. 1, 4) are also fairly well preserved.

The large mandibula presupposes a powerful adductor muscle. This has certainly had its origin partly on the palatoquadrate, but it is probable that it has also arisen on the neurocranium, in the shallow fossa on the lateral wall of the labyrinth region, which has been described above. If this is correct, the arrangement of the musculature would thus in this respect have resembled that of the recent *Dipnoi* (LUTHER, 1913, pp. 33—45; ADAMS, 1919, pp. 80—83), although specialization has gone considerably farther in the latter than in the Coelacanthids (cf. REIS, 1892, pp. 21—22).

¹⁾ The bone *m* of WOODWARD'S description of 1907 (1907 a, p. 136, Pl. VIII, figs. 2, 8) and *x* of his description 1909 (p. 176, Pl. XXXV, fig. 9; Pl. XXXVII, fig. 5), may, I suppose, be the homologue of the autangular.

Stensjö, Triassic Fishes from Spitzbergen.

In the hyoid arch we find in *W. sinuosa* the two elements characteristic of Coelacanthids well developed and apparently in their original position in relation to each other. Of these the ossification in the ceratohyal (*Chy*, text fig. 27; Pl. 4, fig. 2; Pl. 7, fig. 3) is unusually long and powerful, and, as usual, slightly arched in such a way that it is convex on the ventral side and concave on the dorsal one. The ends, which in their present condition are truncated, have been furnished with cartilaginous epiphyses. The lower margin has a broadly rounded projection somewhat behind the middle. The posterior end of the bone reaches a good distance behind the pterygoid; the opposite end extends almost as far forward as the anterior limb of the latter bone.

The second ossified element of the hyoid arch (*Eph*, text fig. 27), which is usually called the stylohyal in the current terminology, I have here interpreted as the epihyal. It is short and fairly thick and truncated at the ends. In its interior it was cartilaginous — the ossification forms only a thin perichondral covering — and this cartilage was undoubtedly continuous with the epiphyses of the bone, which were also cartilaginous.

Text fig. 27. *Wimania sinuosa*, n. sp.
The two ossifications of the hyoid arch. From P. 257, 1/4.
Eph, epihyal ossification; *Chy*, ceratohyal ossification.

The epihyal ossification is widest at its dorsal end, from which it narrows fairly gently in ventral direction, increasing again in width in the neighbourhood of the ventral end. Its narrowest part is consequently situated near the latter end. Its dorsal end lies close to the basis cranii, postero-medially of the pterygoid bone, but in such a relation to the latter bone that, as has been pointed out above, it cannot have been connected with the metaptery-

goid. It must thus have joined the neurocranium, but it is impossible to decide whether this took place directly or whether another cartilaginous dorsal element corresponding to a pharyngobranchial was developed.¹⁾ As is clearly shown by this exposition, the skeleton of the hyoid arch in the Coelacanthids thus presents striking resemblances with that of the *Dipnoi*, both by the reduction in its dorsal part and with regard to the shape of the ceratohyal ossification (cf. GAUPP, 1904, pp. 920—931; VAN WIJHE, 1882, pp. 295—297; RUGE, 1897, pp. 257—284; FÜRBRINGER, 1904, pp. 490—495).

In the species in question the operculum is particularly high and broad. Its contours are, however, to a great extent badly preserved, so that the shape cannot be established with certainty. Similarly it is impossible to decide whether there was sculpture or not.

There are five pairs of gill-arches, which are ossified in two segments. The ventral of these segments, which I take to be a ceratobranchial (text figs. 28 A, B; Pl. 4, fig. 1; Pl. 7, fig. 3) is particularly long and arched in such a way that it has the convexity backwards and downwards and the concavity upwards and forwards. Its ventral end is

¹⁾ On the left side of the head in question (P. 257) there is a detached bone (γ , Pl. 4, fig. 2) laterally of the posterior end of the ceratohyal ossification. This bone probably belongs to the pectoral girdle or the endoskeleton of the pectoral fin.

truncated, its dorsal one has posteriorly a rather strong and pointed process. Interiorly all the ceratobranchials were partly cartilaginous (text fig. 26 B) and their two ends also undoubtedly had cartilaginous epiphyses. Their posterior surface is grooved longitudinally. The anterior edge, on the other hand, is rounded.

The dorsal ossified segment (text fig. 28 C) is small and bifurcate. It is uncertain how it was attached to the ceratobranchial and similarly it is not clear how it is to be oriented in other respects. It is still difficult to take any definite view as to its interpretation. But if one starts out from the conditions found in *Polypterus* and if the ventral element really represents a ceratobranchial, as I have assumed, it does not seem improbable that the dorsal element corresponds to a pharyngo-branchial or possibly this element together with a strongly reduced epibranchial (VAN WIJHE, 1882, pp. 257—258; GAUPP, 1904, pp. 907—913; ALLIS, 1918 b, pp. 258—261).

The gill-arches of the two sides were joined ventrally by means of a cartilaginous copula, but as nothing is preserved of this it is impossible to decide whether it formed a single piece or was sub-divided into several segments. It was covered dorsally by one or a few tooth-bearing dermal plates, which are thin and consequently much crushed. The bone hitherto generally interpreted as a copula is, as pointed out by REIS already in 1892 (pp. 26—27), a dermal bone that has been situated ventrally of the real copula and in other respects shows a complete corres-

Text fig. 28. *Wimania sinuosa* n. sp.
The ossifications of the gill-arches. From P. 257, 1/2.
A. Ceratobranchial. B. Cross-section through a ceratobranchial.
C. Pharyngo or epipharyngo-branchial.

spondence with the urohyal of the *Teleostei* (cf. GOODRICH, 1909, p. 350). In the species in question it is very large and long, and has, from the ventral side, the shape shown in text fig. 29 and Pl. 4, fig. 2 and Pl. 7, fig. 3. It consists, like other plates of membrane bone, of a very compact substance. The centre of ossification is at about the middle, and corresponds to the narrowest part of the bone. A cross-section at this place (text fig. 29 B) shows that the lateral margins were turned somewhat upwards, so that the upper surface became grooved longitudinally and moreover it is clear that there was developed on this surface a median longitudinal crista in the same way as on the corresponding bone in a number of the *Teleosts*. Just as in these the anterior end is bipartite in certain of the *Coelacanthids* studied by me, e. g. *Coelacanthus elegans* NEWBERRY and *Undina penicillata* MÜNSTER, but it is impossible to decide with certainty if this was the case in *W. sinuosa* too, as the anterior part of the bone in this species is incompletely preserved.

Dentition.

Larger, acutely conical teeth, bent slightly backwards, are found on the precoronoids and the supposed maxillary bone; smaller ones of the same shape occur partly on

the bones mentioned, partly on the gill-arches. Small or even very small teeth, usually blunt, are characteristic of the parasphenoid, pterygoid, coronoid, coronoideo-prearticular and the plates covering the copula.

The ventral surface of the parasphenoid has, in front of the centre of ossification, as I have shown above, a thickened median part, to which the teeth are limited. Behind the centre of ossification its teeth are very sparse and the thickened part is, as we have seen, quite absent.

The pterygoid has the medial surface of the anterior limb finished with teeth practically all over. The posterior limb of the same bone also bears teeth to a considerable extent, but the teeth do not extend quite as far as to the posterior margin and they are also absent farthest dorsally on a surface which corresponds in height to a third of the limb itself.

It is impossible to make out whether the teeth of the branchial arches are free or coalesced at their bases into small plates, as is usual in the Coelacanthids.

Text fig. 29.

Wimania sinuosa n. sp.

Urohyal. From Pl. 257. ¹/₄ in.

A. In ventral aspect.

B. Cross-section at about its narrowest part. Note the crista on the dorsal surface.

The sensory canals of the head.

The sensory canals of the head are well developed and enclosed as usual in membrane bones, which they consequently penetrate as tubes. The pores have presumably been small.

Nothing is preserved of the sensory canals of the cranial roof and mandibula. On the other hand, as has been partly shown above, we find the sensory canals rather well preserved on the cheek in the postorbital, lacrymo-jugal and the squamoso-preopercular.

In the fronto-dermosphenotic the infraorbital canal (text fig. 25) has probably turned laterally and with this course it has presumably left this bone and entered the antero-dorsal corner of the postorbital. In the latter bone (text fig. 25; Pl. 5, fig. 2; Pl. 6, fig. 1) it runs first for a short distance in a postero-ventral direction after which it takes a directly ventral course and reaches the lower margin of the bone not far behind the antero-ventral corner. Ventrally of the postorbital it has passed for a short distance through a membranous interspace, then penetrated the plate *x*, and afterwards continued through another short membranous interspace, finally entering the lacrymo-jugal, which it traverses to the anterior end.

From the postorbital part of the infraorbital canal there issues posteriorly between the lacrymo-jugal and plate *x* a sensory canal (text fig. 25; *jc* Pl. 5, fig. 4) which immediately enters the process on the anterior margin of the squamoso-preopercular and then runs downwards and backwards through this bone to the lower margin, just in front of the postero-ventral corner. In its continuation ventrally it seems first to have passed a membranous interspace and after that to have transversed the posterior part of the preoperculo-quadratojugal. It may possibly have also anastomosed with the mandibular canal.

It can scarcely be doubted that this last-mentioned sensory canal is homologous with the similarly situated one in *Osteolepsis* (GOODRICH, 1919). It seems also probable

that it may correspond, at least partly, to the hyomandibular canal and partly to the mandibular line of pit organs of the *Selachii* (cf. EWART, 1892, pp. 71—72; ALLIS, 1902, p. 108; JOHNSON, 1917, pp. 20—21). In *Amia* (cf. ALLIS, 1889, p. 506, Pl. XLII; 1905, pp. 406—407) and *Polypterus* (ALLIS, 1900a, p. 445) it seems to be represented by the horizontal cheek line of «pit organs» together with the ventral part of the preopercular canal and in the Stegocephalians by the «jugal canal» of MODIE's description (MODIE, 1908, p. 515; 1915a, p. 320).

As far as is known its agreement with the latter canal is very great and on this ground I have in the subsequent exposition used the term jugal canal for it (cf. WIMAN, 1914b, Pl. III, fig. 3; Pl. V, fig. 2).

While in *W. sinuosa* the jugal canal has, as we have seen, anastomosed with the infraorbital canal between the lacrimo-jugal and plate *x*, in *Osteolepis* (GOODRICH, 1919) this anastomosis on the contrary takes place in the jugal bone. Consequently, as far as one can judge, the lacrimo-jugal in *W. sinuosa* extends not so far dorsally in its postorbital part as the jugal in *Osteolepis*, and the part that is lacking corresponds to the plate *x*. If, however, the restorations of *Coelacanthus* (WELLBURN, 1902, p. 483), *Diplurus* (DEAN, 1895, p. 154, fig. 156), *Undina* (REIS, 1888, Pl. V, fig. 12; WOODWARD, 1898a, p. 80, fig. 60)¹⁾ and *Macropoma* (WOODWARD, 1909, p. 173) are correct, the jugal part of the lacrimo-jugal ought in these forms to reach the postorbital and thus in this respect to agree with the jugal of the *Rhipidistia*, i. e. the plate *x* ought to be comprised in the posterior part of the lacrimo-jugal, of which it has probably been originally an integral part.

As I have shown, the lacrimo-jugal extends in *W. sinuosa* a good way in front of the orbita along the lateral surface of the ethmoidal region and this is also the case in other *Coelacanthids*. This makes it probable that the lacrymal bone of the *Rhipidistids* (WATSON and DAY, 1916; GOODRICH, 1919), which is normally situated under the anterior part of the orbital opening, is contained in the lacrimo-jugal of the *Coelacanthids* in general together with the jugal, as I wished to indicate in my terminology here used.

The postorbital of *W. sinuosa* seems, on account of the course of the supraorbital canal and also because of its extent, to be undoubtedly the homologue at least of the postorbital of the *Rhipidistids* (WATSON and DAY, 1916), which also may be the case with the postorbital in the carboniferous *Coelacanthus*-species, if WELLBURN's (1902) view is correct, while, on the other hand, in *Diplurus* (DEAN, 1895), *Undina* and other Jurassic forms (REIS, 1888, 1892, WOODWARD, 1898b) and *Macropoma* (WOODWARD, 1909) the same plate would extend backwards right to the preopercular. In this connection it is interesting to find how the upper part of the squamoso-preopercular in the Carboniferous forms projects upwards between the postorbital and the opercular and thus shows exactly the same conditions as the dorsal part of the squamosal sometimes does in the *Rhipidistids*. On the other hand it is also noteworthy when one finds, for instance in *Sassenia tuberculata* described below, remains of a small independent plate situated behind the postorbital, and the squamoso-preopercular at the same time does not reach up dorsally between the latter and the opercular. It is also remarkable that this independent plate

¹⁾ In 1892 REIS gives another restoration of *Undina* (Pl. I, fig. 1; Pl. II, fig. 14) that differs rather considerably in this respect from that published by him in 1888. If this new restoration were correct the homologue of the plate *x* would probably be included in the squamoso-preopercular.

may sometimes be reduced to a certain extent or be quite absent as is the case in *W. sinuosa*, so that there is a large interspace between the postorbital and the opercular. To judge from what has been mentioned, this whole state of affairs seems to support the idea that the dorsal portion of the squamoso-preopercular, which in primitive Coelacanthids projects upwards dorsally behind the postorbitale, has in Mesozoic ones become detached from its connection with the other parts of the bone. It may then either have persisted as an independent element (*Sassenia*) or have coalesced with the postorbital (*Diplurus*, *Undina*, *Macropoma*, etc.) or else have been reduced (*Wimania*).

Besides the jugal and the postorbital the cheek in the Rhipidistids in general is covered with a fairly varying number of bones. Thus *Holoptychius* is said to have five, *Glyptopomus*, *Tristichopterus*, *Rhizodopsis* and *Megalichthys* to have three, and *Osteolepis* to have two, while in *Diplopterus*, *Gyroptychius* and *Eusthenopteron* only one large plate seems to occur (TRAQUAIR, 1875a, Pl. XXXII, figs. 1, 11; 1881, p. 172, fig. 2, pp. 176—177; 1896; WATSON and DAY, 1916, pp. 1—27; GOODRICH, 1919; WOODWARD, 1891b, pp. 319—320; 1898a, pp. 70, 72, 75—77; WELLBURN, 1900, pp. 62—63; Pls. XIII, XV; BIRKS, 1916, pp. 307—327). It is pretty clear, as WATSON and DAY (1916) have shown, that we are here concerned with various more or less advanced stages of fusion in the different forms and that forms with a larger number of these bones ought in this respect to be taken as more primitive than those with a smaller number. In *Holoptychius*, *Glyptopomus*, *Tristichopterus* and *Rhizodopsis* one can regularly identify the preoperculum, quadrato-jugal and squamosal; in *Holoptychius*, however, if WATSON and DAY's observations are correct, the last-mentioned bone consists of three independent plates; in *Osteolepis*, according to GOODRICH, a small independent preoperculum seems to be present besides the large postorbital plate, whereas this small plate was not observed by WATSON and DAY (1916).

If now we examine the Rhipidistids that have a preoperculum, quadrato-jugal and a squamosal, we may state the following facts about these bones: the preoperculum is situated close to the anterior margin of the operculum, along which it projects more or less far upwards in different forms; usually it is high and narrow. In front of it follows the squamosal, which is attached anteriorly to the jugal and the postorbital, ventrally to the maxillary and the quadrato-jugal, posteriorly to the preoperculum and to a little plate following in front of the anterior upper end of the operculum, or, if this is united with the operculum, to the antero-dorsal part of the latter. It reaches upwards right to the cranial roof, and seems to be pierced by the jugal canal, which enters it from the jugal and subsequently passes backwards and downwards towards the postero-ventral corner. The quadrato-jugal forms the postero-ventral part of the cheek and is attached dorsally to the squamosal and the preoperculum, anteriorly to the maxillary, and posteriorly with its upper part to the preoperculum. The remaining part of its posterior margin, like its whole ventral one, is free. In *Osteolepis* the postero-ventral part of the jugal canal pierces the preoperculum (GOODRICH, 1919); in other forms we do not know for certain the relation of this canal either to the preoperculum or to the quadrato-jugal, but it seems most probable that the last-mentioned bone has been situated in front of this canal.

If now we try to apply the experience gained by our examination of the region of the cheek in the Rhipidistids to the conditions found in the Coelacanthids it is evident that both the squamoso-preoperculum and the preoperculo-quadrato-jugal would comprise

the components indicated by their names, i. e. of the bones covering the cheek of primitive Rhipidistids the dorsal part of the preoperculum would be fused with the squamosal and the ventral part of the preoperculum with the quadrato-jugal to the squamoso-preopercular and preoperculo-quadratojugal respectively. In Mesozoic Coelacanthids we find, as I have pointed out above, that a dorsal part of the squamoso-preopercular has become detached secondarily from the other parts of the bone, to be then reduced more or less or perhaps in certain cases to fuse with the postorbital.

There still remains to be made a comparison between the cheek plates of the Coelacanthids on the one hand and certain of the bones in the cranial roof of Stegocephalians on the other, but I have found it more convenient to put this off till later on in the chapter «Coelacanthids compared with some other fishes and certain Tetrapods».

The shoulder girdle.

Together with the head of *W. sinuosa* described above (*P. 257*) there also occur incompletely preserved remains of the dermal bones of the shoulder girdle. Of these the cleithral (*Cl*, Pl. 7, fig. 3) was, as usual, long and large, but nothing else can be said in detail with regard to its shape. The clavicle (*Cl*, Pl. 7, fig. 3) on the other hand, is somewhat better preserved. It has a long slender dorsal limb, with which it joins the cleithral, and a ventral one which is developed as a rather large plate, lying horizontally and attached to the corresponding plate on the opposite side by a median suture. In shape the clavicle thus bears a considerable resemblance to that of *Rhizodus* (WOODWARD, 1891 b, Pl. XII, figs. 4, 7).

Text fig. 30.
Wimania sinuosa.
Scale from *P. 257*, $\frac{1}{10}$.

Squamation.

The squamation in *W. sinuosa* is very incompletely known. All that is preserved of it is some detached scales on the specimens *P. 257* and *P. 255*.

In shape the scales (text fig. 30) are oval with the anterior margin rounded and the posterior one somewhat pointed. The covered area is considerably larger than the exposed one. The latter has a sculpture (text fig. 30; Pl. 5, fig. 3) of numerous rather short and at the same time fine longitudinal striae, the middle ones of which are as a rule somewhat longer than those situated dorsally and ventrally.

* * *

Remarks: — As, from a linguistic point of view, the earlier name of this species, *sinuata*, is incorrect, I have altered it here to *sinuosa*. This name refers to the characteristic sinus on the upper margin of the anterior limb of the pterygoid bone.

Geological occurrence and localities. — *W. sinuosa* is only known from the fish horizon. Identifiable remains of it have so far been found at Mount Congress and Mount Andersson.

Wimania? sp.
(Pl. 9, figs. 2, 3.)

As *Wimania?* sp. I have grouped here a few remains that come from the caudal region of a fairly large Coelacanthid fish (*P. 253*, *P. 256*).

As is shown by Pl. 9, fig. 2, the neural and haemal arches are of the usual Coelacanthid type. The neural and haemal spines are long and narrow, and are attached to the lepidotrichia of the caudal fin in the usual way (SCHMALHAUSEN, 1913a, pp. 47—59). While in the anterior caudal region these spines form, both dorsally and ventrally, a somewhat big angle with the chorda, they are so inclined backwards that this angle gradually becomes more acute. The most posterior of them consequently take up a position almost parallel to the longitudinal axis of the fish. Their distal free segment about corresponds in length to the proximal one, which was continuously connected with the arch. Both in the neighbourhood of and at the place where the two segments are connected with each other they are somewhat thickened. The bone substance in them only forms a thin perichondral layer. The interior undoubtedly consisted of cartilage and both the distal end of the proximal segment and the two ends of the distal segment were furnished with a cartilaginous epiphysis.

The caudal fin is not completely preserved at its posterior part and it is thus uncertain if the so-called supplementary fin («Pinselflosse») has been developed. In the other parts the lepidotrichia are long and fairly robust but not expanded distally. Their number is about the same dorsally and ventrally — as far as one can judge about twenty. On one side — it is not possible to say if it is the dorsal or the ventral one — they are distinctly more robust than on the other, and, except for the three or four most anterior ones, they are jointed, although the proximal joints are of considerable length.¹⁾ Even the distal joints are fairly long, which is also the case in the lepidotrichia on the opposite side, but the latter lepidotrichia, on the other hand, have long unjointed proximal parts. With the exception of a piece of the proximal part all the lepidotrichia of the caudal fin have on their lateral sides a row of fine, short striae, or, if the expression is preferred, a row of somewhat lengthened tubercles.

The scales (Pl. 9, fig. 3) seem most closely to resemble those of *W. sinuosa* in their sculpture. As in this species, the sculpture consists of a rather large number of fine, but not specially long, striae. A few of the middle striae on each scale run, as in *W. sinuosa*, fairly horizontally in the longitudinal direction of the scale, the rest, situated dorsally and ventrally of these, show a certain concentric arrangement along the posterior margin and consequently their posterior ends are directed towards the longitudinal axis of the scale. — Nothing is known in detail as to the shape of the scales.

* *

Remarks: With regard to the sculpture of the scales the two Coelacanthid remains just described resemble, as has already been pointed out, *W. sinuosa* more closely than any of the other Spitzbergen species so far known. At the same time the deviations are very obvious, and as in other respects we are without any points of departure for a comparison, it is impossible at present to decide whether these two fragments really belong to *W. sinuosa* or the genus *Wimania* at all. Under these circumstances I have only hesitatingly included them in this genus.

Geological occurrence and localities. — The fish horizon at Mt Milne Edwards and Mt Trident.

¹⁾ The material at hand does not show whether these rays too have been longer than those on the opposite side.

Wimania? multistriata n. sp.

(Pl. 8, figs. 2—7; Pl. 9, fig. 1.)

Under the name of *W. multistriata* I have grouped together a number of pieces, mostly fragmentary, of a large Coelacanthid (*P. 238*, *P. 244—250*, *P. 252*, *P. 254*, *P. 674*, *P. 691*). I have also provisionally included under this name a detached bone-plate (*P. 203*), for reasons given below. Besides these, all of which belong to the Geological Institute of Upsala, there were found in the material investigated by HULKE, 1873, which is kept in the Natural History State Museum, Stockholm, several fragments of a huge Coelacanthid, probably belonging to the species in question.

W. ? multistriata has attained a very considerable size and in this respect it seems to be about equivalent to *Mawsonia gigas* WOODWARD (1907a). One jugular plate, for instance, measures 12 cm in width, and may have been about 40 cm long. A number of other remains of the bones of the head, fins etc. are correspondingly large, although in most cases the state of preservation makes it impossible to give any figures of measurements. Nothing is known with regard to the shape of the body, but if this did not differ to any very great extent from the usual type, one might venture to estimate the total length of the larger specimens as about a couple of meters or perhaps even more.

Membrane bones of the neurocranium and cheek-plates.

The substitution bones of the primordial neurocranium are not preserved. Of the membrane bones there are the parieto-intertemporals in a small specimen (*P. 252*) together with the supratemporo-extrascapulars and a number of fragments of other indeterminate plates.

The two parieto-intertemporals (text fig. 31 A; *Pa. it*, Pl. 8, fig. 2) are relatively long and narrow. Their greatest width is little more than half their length. They meet medially in a straight median suture, and the lateral margin has posteriorly a marked sinus, into which the antero-medial part of the supratemporo-extrascapular is inserted. The ventral longitudinal lamella issuing from the ventral surface is well developed (text fig. 31 B) though it is not vertical as in *W. sinuosa*, but is directed more ventro-laterally. I cannot say at present whether this is primary or is to be considered as having arisen through the effect of pressure during or after fossilization.

The supratemporo-extrascapular bones (Pl. 8, fig. 2) do not seem to show any essential deviation from those in *W. sinuosa* with regard to shape, but they are not well enough preserved for a detailed description to be possible.

Both the parieto-intertemporals and the supratemporo-extrascapulars and probably also the other bones of the cranial roof are without ornament. On the other hand the cheek-plates (*P. 252*, *P. 674*) are furnished with fine tubercles, which may be rounded or somewhat lengthened, sometimes, too, bent into the shape of a kidney or an S. On certain bone-plates, especially in larger specimens, the tubercles seem to be present rather densely and the character of the sculpture consequently agrees pretty well with that of the scales, which I shall describe below. On other bones, on the contrary, the tubercles are distinctly sparse.

Stensiö, Triassic Fishes from Spitzbergen.

Text fig. 31.

Wimania? multistriata n. sp.

Parieto-intertemporals.

From *P. 252*, 94.

A. From the dorsal side.

B. Cross-section through the anterior half.

Visceral skeleton.

Of the visceral skeleton only the quadrate is completely preserved. In addition there are fragments of the pterygoid, supraangulo-angular, dental, splenial, opercular, jugular plates, and a number of fragmentary gill-arches.

The quadrate (*P. 252*, *P. 238*) has about the same shape as in *W. sinuosa* and the same is true, to a certain extent, of the postero-ventral part of the pterygoid as well (text fig. 32). — The other parts of the pterygoid are not preserved. — It seems, however, as if the posterior limb has been comparatively narrower than in *W. sinuosa*. The supraangulo-angular (*P. 674*) had a rounded corner dorsally and seems to have been rather high. Anteriorly it projects with a point a short distance in between the dental and the splenial; these two bones have only their posterior parts preserved. Both these and the supraangulo-angular are without sculpture.

Text fig. 32. *Wimania multistriata* n. sp.
The postero-ventral part of the pterygoid. From *P. 238*, $\frac{1}{2}$.

The opercular (*P. 252*) is very incompletely preserved. It is quite clear, however, that it was large and probably of a rounded triangular shape. The jugular plates too are incompletely known. As far as one can judge they were without sculpture, while on the other hand the opercular had a sculpture of the same kind as that of the cheek-plates.

The conditions of the gill-arches are as in *W. sinuosa*. The ceratobranchials have a very deep furrow posteriorly and were partly cartilaginous interiorly (text fig. 33 A). The pharyngo or perhaps more correctly the epi-pharyngobranchials have about the same bifurcate shape as I have described in *W. sinuosa*.

Dentition.

The dentition on the pterygoid does not differ, as far as one can judge from the material at hand, very noticeably from that of *W. sinuosa*. The teeth in the presumed precoronoids are large, conically pointed (text fig. 33 B; Pl. 8, fig. 3), but, unlike those of *W. sinuosa*, probably straight.

Sensory canals of the head.

The sensory canals of the head were considerably stronger in this species than in *W. sinuosa*. The pores too are rather large and distinct. I found three of them on the supratemporo-extrascapular, one on the parieto-intertemporal (*P. 252*).

Axial skeleton.

With the exception of an unimportant part of the caudal region (*P. 254*) nothing is known with regard to the axial skeleton. This part shows, however, that the distal segments of the neural and haemal spines have been considerably thickened at their proximal ends.

Girdles and fins.

The fins are still extremely incompletely known in this species, as they are mostly represented only by detached lepidotrichia or parts that cannot be exactly defined. The lepidotrichia are often long and always taper gradually distally. They are unjointed for a fairly long distance proximally, but it is uncertain how great a part of their total length this distance represented. The joints (Pl. 9, fig. 1) are mostly rather short and wide, sometimes even very short. I have not found any tuberculation or striation on them, nor on the proximal unjointed part. The latter part often has, however, on each lateral side a longitudinal furrow with small rounded pits lying close together, and these pits possibly indicate that we have had free spines here articulating against the lepidotrichia in the same way as, for instance, in *Macropoma*. — A loose pelvic plate (P. 203) may also belong to *W.?* *multistriata*. This has, as shown in Pl. 8, fig. 7, a shape that resembles that of *Coelacanthus granulatus* (REIS, 1888, Pl. IV, fig. 7) very closely, and since, as I pointed out in the general description above, the type species of the genus *Wimania* at least resembles in several respects the typical *Coelacanthus* species, it is also most probable that the bone-plate in question belongs to some *Wimania* species, and, to judge from its size, it could in this case scarcely be any other than *W.?* *multistriata*.

Squamation.

Together with the other remains of this species there are often found scales which sometimes attain a length of close upon 5 cm. A distinguishing feature of the scales is the posterior margin, which has a definite though rounded corner (text figs. 34 A, B, Pl. 8, figs. 4—6; Pl. 9, fig. 1). In other respects their appearance is pretty variable. In some of them (e. g. those figured in text fig. 34 A and Pl. 7, fig. 4), the exposed part of the lateral surface is rather small compared with the covered part, and at the same time the upper and lower margins run in a continuous arch backwards to the corner mentioned. Other scales, on the contrary, have the exposed part of the lateral surface strikingly larger in comparison with the covered part and at the same time the appearance of the dorsal and ventral margin is also different, as is clearly shown in text fig. 34 B and Pl. 8, fig. 5. Transitional forms between the two extreme types just described are common. The sculpture consists of a very large number of fine striae, lying close together, which generally run parallel to the longitudinal axis of the scales. Not infrequently the striae may, however, be so long that they reach across the whole exposed surface. They are all, as a rule, somewhat undulating.

* * *

Remarks. — *W.?* *multistriata* is well characterized as an independent species by the nature of the ornament of its superficial head-bones and scales, the development of its lepidotrichia, and lastly also by its considerable size. It certainly reminds us, as we have seen, of the type species of the genus *Wimania* in a great many respects, but, on account of the deficient character of the material at our disposal, it is impossible as

Text fig. 33.

Wimania? *multistriata* n. sp.

From P. 238.

A. Cross-section through a gill arch.

B. Tooth, probably from a preopercle.

yet to decide with certainty whether it really belongs to the same genus as this. It is also worthy of mention that the lepidotrichia of *W.?* *multistriata* and those of the *Wimania?* sp. described above are rather different, a fact that seems to suggest that one of these two species really does not belong to the genus *Wimania*.

Geological occurrence and localities. — *W.?* *multistriata* occurs fairly commonly in the fish horizon. It is found at Mt Congress, Mt Rotunda (Student Valley), Sticky Keep, Mt Trident and Mt Milne Edwards.

Genus *Sassenia* n. g.

The genus *Sassenia* is still incompletely known and the diagnosis can consequently not lay claim to any completeness. The characteristics so far known can be summarized as follows: Fishes probably of average size or fairly small. The head with a sculpture of flattened tubercles situated more or less closely together. The parasphenoid wide. The postorbitally situated cheek-plates three in number with a small accessory one behind the dorsal one. Infraorbital long and arched. Pterygoid thin; its anterior limb with a

Text fig. 34. *Wimania?* *multistriata* n. sp.
A. Scales from P. 244. $\frac{1}{10}$. B. Scales from P. 247. $\frac{1}{10}$.

high and at the same time relatively broad caudal part. Coronoid probably triangular in shape. The ceratohyal ossification long; the opercular large, triangular, with rounded corners. The labial margins of the jaws probably with conically pointed rather large teeth; the gill-arches with

smaller ones, of a similar shape; otherwise the teeth small, bluntly conical or nearly spheroidal, often furnished with a small point set off as a verruca. The sensory canals developed normally. The scales oval with a rounded posterior margin and sculpture of rounded or somewhat lengthened tubercles, sometimes partly also of striae and tubercles together.

Like *Wimania*, *Sassenia* too shows in certain respects striking resemblances to the Carboniferous and Permian Coelacanthids, as, for instance, in the shape and size of the parasphenoid, the opercular, and to a certain extent in the development of the pterygoid as well, further, in the general arrangement of the cheek-plates and partly also with regard to the sculpture of the scales and the cranial bones. *Sassenia* is easily distinguished from *Wimania* by the shape of the opercular and the pterygoid. An additional important difference between them is that the sculpture of the head is, as we have seen, absent or weak in *Wimania*, while in *Sassenia* it is well developed.

A circumstance that deserves special mention in this connection is that one of the two *Sassenia* species described below, namely *S. tuberculata*, agrees closely with regard to the sculpture of its scales with the species from the Cava Trefontane in Tessin described by me under the name of *Undina* sp. (ANDERSSON, 1916a, pp. 14—16). An obvious resemblance of the same sort can also be observed bet-

ween *S. tuberculata* and *Undina gulo*. In other words, with regard to the sculpture of the scales and also the cranial sculpture *Sassenia* resembles in certain respects at the same time both the *Coelacanthus* and the *Undina-Macropoma* type, and it seems also to occupy a similar intermediate position with regard to the shape of the posterior pterygoid limb.

The resemblance between *Sassenia tuberculata* and the *Undina* species from the Cava Trefontane referred to is so great that one may even feel doubtful whether we have not really two species of the same genus present here, i. e. that the supposed *Undina* species from the Cava Trefontane would really belong to *Sassenia*. As at least one Actinopterygian genus, *Perleidus*, seems to be common to the Triassic of both Spitzbergen and Lombardy, this may to a certain extent indicate that with a complete knowledge of the two faunae we may expect to find still more common forms. But the fact that, if we judge merely from the sculpture of the scales, we have pretty much the same right to group together *Undina gulo* in the same genus with *S. tuberculata* shows us how careful we must be in deciding a case of this sort. The question as to whether *Sassenia* also includes the species from the Cava Trefontane described as *Undina* sp. must therefore be left undecided.

The name *Sassenia* for this genus is derived from the Sassen Valley.

***Sassenia tuberculata* n. sp.**

(Pl. 10).

Sassenia tuberculata is represented only by three incompletely preserved specimens (P. 224—P. 226) with portions of the head and the squamation. These three specimens all come from individuals of rather average size. The maximum height of the head — the only measurement at all reliable that can be obtained — may thus be probably estimated at about 6—7.5 cm.

The ossifications of the primordial neurocranium.

Of the ossifications of the primordial neurocranium the prootico-opisthotic (*Pro. o.*, text fig. 37) and the basisphenoid (*Bsph.*, text fig. 37) are only preserved fragmentarily. As far as can be seen, they have both been developed essentially as in *W. sinuosa*, but the nature of the material does not permit of any detailed comparison.

The membrane bones of the neurocranium.

Posteriorly beneath the labyrinth region the parasphenoid (*Psph.*, text fig. 37) has had the same slight extension as in *W. sinuosa*. In its anterior parts it is incomplete, but all the same it is obvious that it had lateral parts that were bent upwards and between these a somewhat thickened horizontal portion with teeth; just as in *W. sinuosa*, this thickened portion is not developed behind the centre of ossification.

The membrane bones of the cranial roof are not known, except for the supratemporo-extrascapular (*Stemp. ext.*, text fig. 35; Pl. 10, fig. 1) and the parieto-intertemporal (*Pa. it.*, text fig. 35, Pl. 10, fig. 1). These two bones, though partly deformed by pressure and incomplete in other respects, seem to have been in the main similar to those in *W. sinuosa*.

The membrane bones of the cheek.

Of the cheek-plates the following are present in a more or less fragmentary condition: the lacrimo-jugal (text fig. 38 A; *La. ju.*, Pl. 10, fig. 3), postorbital (*Po*, text fig. 35; Pl. 10, figs. 1, 3) squamoso-preopercular (*Sq. pop*, text fig. 35; Pl. 10, figs. 1, 3), a smaller plate (*a*, text fig. 35; Pl. 10, fig. 1) situated behind the postorbital, and probably also the preoperculo-quadratojugal *Pop. quj?*, text fig. 35; Pl. 10, figs. 1, 3). Their mutual relationship with regard to position and size seems to be essentially the same as in *W. sinuosa*, and this seems broadly to be true of their shape as well. It is also evident that they have been situated fairly loosely in relation to each other, but whether to the same extent as in *W. sinuosa*, is, however, uncertain. With regard to the plate *a* situated behind the postorbital I have already shown above (cf. *Wimania sinuosa* p. 77) that it seems to correspond to a dorsal part of the squamoso-preopercular. It is triangular in shape. — All the cheek-plates have a characteristic sculpture of flat, rounded tubercles situated exceedingly close together and sometimes arranged concentrically (Pl. 10, figs. 1, 3, 6).

Text fig. 35.

Sasania tuberculata n. sp.Portions of the cranial roof, cheek plates and visceral skeleton. The sculpture not drawn. From *P. 225*. $\frac{1}{2}$.

Mptg., metapterygoid; *Op.*, opercular; *Pa. it.*, parieto-intertemporal; *Po.*, postorbital; *Pop. quj?*, possibly a part of the preoperculo-quadratojugal; *Pt.*, pterygoid; *Sq. pop.*, squamoso-preopercular; *Stemp. ext.*, supratempero-extrascapular; *a.*, accessory plate originally belonging to the squamoso-preopercular; *Jc.*, jugal canal.

Visceral skeleton.

Of the metapterygoid (*Mptg.*, text fig. 35; Pl. 10, fig. 1) only a posterior part is preserved. The shape is accordingly rather uncertain, on the whole, nor can its position relative to the pterygoid be decided exactly, whether it extended posteriorly in a caudal direction a little behind that bone in the way seen in the type specimen of text fig. 35, and Pl. 10, fig. 1 or whether the conditions were the same as in *W. sinuosa*.

The pterygoid (*Pt.* text figs. 35, 36; Pl. 10, figs. 1, 4) is so preserved that a part of its posterior limb is present in the specimen *P. 225*, and practically the whole of the anterior limb in the one *P. 226*. In text fig. 36 I have tried to reconstruct the appearance of the bone as a whole with the help of the remains mentioned, but it must be pointed out that the

width of the posterior limb, like its height too, is rather uncertain in relation to that of the anterior one. The posterior margin of the posterior limb is slightly convex. The dorsal margin is on the contrary slightly concave and slopes rather rapidly backwards, i. e. it faces dorso-caudally. The postero-dorsal corner is obtuse-angled; the ventral corner is probably well rounded off. The posterior part of the anterior limb is very high, and this high part is also strikingly broad. The upper margin of this limb has a very characteristic course. Farthest posteriorly it is fairly horizontal for a short distance, then it bends round downwards and forwards, continuing in this direction for a considerable distance, then rather suddenly taking a direction almost straight forward and, with this direction, then continuing to the anterior end of the limb. The lower margin runs in a slightly concave arch from the lower corner of the posterior limb in an upward and forward direction. Otherwise, as far as one can see, the pterygoid is distinguished by the thin nature of its bone substance. (text fig. 37)

In the lower jaw are found remains of the supraangulo-angular (*sang. ang.*, Pl. 10, fig. 3), coronoid (text fig. 38 B; *Co.*, Pl. 10, figs. 3, 4) intercoronoideo-prearticular (*Icor. pra.*, text fig. 37; Pl. 10, fig. 4) and one precoronoid plate (*Pco.*, Pl. 10, fig. 4). The intercoronoideo-prearticular extends in the usual way far forward on the medial side of the mandible and at least the most posterior precoronoid-plate is joined to its upper margin; this latter plate was comparatively long and low.

The ossification in the ceratohyal (text fig. 38 C) is considerably more powerful than in *W. sinuosa*, to judge from the parts of it that are present. In addition the part that is situated behind the large ventral projection is shorter than in the latter species. The epihyal (text fig. 38 D), on the other hand, is longer and narrower than in this.

The opercular (*Op.*, text fig. 35; Pl. 10, fig. 1) is large and triangular in shape with one side at the front, one dorsally and one postero-ventrally. Of these the anterior and the dorsal ones, the latter of which is also the shortest of the three, are fairly straight, while the postero-ventral one, on the other hand, is convex. All the corners are well rounded, the antero-dorsal one, however, least. As on the cheek-plates the sculpture consists of small tubercles situated close together.

The jugular plates (*G.*, text fig. 37) are incompletely known, as they are only partly present as impressions. Their position in relation to the lower jaws, gill-arches and the urohyal is seen pretty well in text fig. 37, which is drawn directly from nature.

The exact number of gill-arches is still unknown. On a section through specimen *P. 226* (text fig. 37) only seven are found, but as this section was taken rather far forward and also obliquely it is quite possible that one or two have not been included. The ceratobranchials of course resemble the same bones in *W. sinuosa* and *W. ? multistriata* very considerably, but differ, however, distinctly from these by having a perichondral layer of bone that is as a rule considerably thinner, and a distinct endochondral ossification in the form of a spongy mass. Their position relative to the urohyal (*Uhy*) is illustrated by text fig. 37, and in the same figure is also clearly seen the crista on the dorsal side of the latter bone, which both in this respect and in its development otherwise resembles most closely that of *W. sinuosa*. The suprascapulars are thin and weak.

Dentition.

The dentition has in the main the same character as in the *Wimania* species, i. e. the parasphenoid, pterygoid, coronoid, coronoideo-prearticular, and the membrane bones on the copula have small bluntly conical or somewhat rounded teeth placed close together; the labial margins of the jaws, on the contrary, are furnished with rather large and conical teeth; those of the gill-arches are small, fine and conically pointed, and are grown together into small plates at their bases.

The postero-dorsal corner of the anterior pterygoid limb is without teeth over a rather considerable surface, and this toothless surface, though gradually becoming narrower,

Text fig. 36.

Sassenia tuberculata n. sp.
Metapterygoid (*Mptg*) and pterygoid (*Pt*) reconstructed from *P. 225* and *P. 226*. $\frac{1}{2}$. (The unbroken line according to *P. 226*.)

continues forward and downward for a good way. On the posterior limb the relation between the tooth-bearing and toothless parts is about the same as in *W. sinuosa*. In addition it is noteworthy that in the more blunted teeth on the pterygoid I found an indication of a small, verruciform apex, which causes these teeth to resemble rather closely certain of those in *Mawsonia gigas* (WOODWARD, 1907 a, p. 135; Pl. 8, fig. 4 b).

Text fig. 37.

Sassenia tuberculata n. sp.
Cross-section through the head at about the boundary between the labyrinth and orbitotemporal regions. From P. 226. *Bph*, basisphenoid; *B*, brachial plate; *Jor. pra.*, intercoronoideo-prearticular; *Br*, ceratobranchials; *Chy.*, ceratohyal ossification; *Pro. o.*, prootic-opisthotic; *Pspk*, parasphenoid; *Pt*, pterygoid; *Uhy.*, urohyal.

Text fig. 38. *Sassenia tuberculata* n. sp.

- A. lacrymo-jugal from P. 226;
B. Coronoid from P. 226;
C. Ceratohyal ossification from P. 226.
D. Epithyal ossification from P. 226.
All the figures in the size $\frac{1}{10}$.

Geological occurrence and localities. — *S. tuberculata* occurs rather infrequently in the fish horizon and has so far been found only at Sticky Keep, Mt Trident and Mt Andersson.

Sassenia? guttata (A. S. WOODWARD).

Synonym: *Coelacanthus guttatus* WOODWARD, A. S., Upsala Geol. Inst. Bull. 11, 1912.

The species is represented only by the type specimen (P. 219).

I have only the following facts to add to the description given by WOODWARD, 1912 (pp. 291—292). The pterygoid has the posterior limb rather narrow; otherwise its shape

Sensory canals of the head.

The sensory canals seem to be well developed, but our knowledge of them is still very incomplete. Only the part of the infra-orbital canal that lies in the posterior and middle part of the lacrymo-jugal (*jfc*, Pl. 10, fig. 3) and a postero-ventral part of the jugal canal (text fig. 35; *jc* Pl. 10, fig. 1) near to the lower margin of the squamoso-preopercular are present. No pores are observed.

Squamation.

The scales are strikingly large in relation to the animals' dimensions. Their shape is purely oval and both the anterior and the posterior margins are well rounded. The covered part seems as a rule to be large compared with the exposed part. The sculpture consists of small tubercles situated close together and small, fairly parallel, longitudinal striae (Pl. 10, figs. 2, 5). Generally there are striae dorsally, ventrally and anteriorly on the exposed surface, while the tubercles are more or less restricted to the middle and posterior part of the same surface. Irregularities in this respect are, however, not infrequent. As I have already pointed out in the general description of the genus *Sassenia*, the sculpture of the scales in this species resembles in character that of the species from the Cava Trefontane at Tessin described by me as *Undina* sp. As I have also mentioned above, it shows in the same respect considerable similarities to *Undina gulo* too.

* * *

is much the same as in *S. tuberculata*; the anterior limb is very high posteriorly, and this high part is, as far as one can see, broad. The lower jaw was relatively low. Of its elements the supraangulo-angular appears to be fairly well preserved and it seems as if it was elongated with a rounded but not especially decided dorsal corner. The dentition is of about the same type as in the species described above. With regard to it, however, it is worthy of special mention that there are distinct, rather strong, conically pointed teeth on the pre-coronoids. The pores of the sensory canals are, at least in the lower jaw, rather small and rounded. Nothing certain can be said as to their number.

* * *

Remarks. — This species was founded and described by WOODWARD 1912 (loc. cit.) under the name of *Coelacanthus guttatus* and it cannot be denied that in many respects it agrees with *Coelacanthus*. On the other hand I have been able to observe distinct agreement between it and *Sassenia tuberculata* and because of this I have, though with hesitation, considered it proper to refer it to the genus *Sassenia*.

Geological occurrence and locality. — *S. guttata* is found in the fish horizon. The single specimen known comes from the cliff on the shore of the south side of Sassen Bay between Flower Valley and De Geer Valley.

Genus *Axelia* n. g.

The most distinctive characters of this genus may be summarized as follows. Fishes of average size or rather large. The head as a whole robustly built and fairly broad, with a sculpture of tubercles and striae. The fronto-dermosphenotics rather short. The supraorbitals four in number, quadrangular. Cheek plates much reduced, represented only by a number of very small scale-like plates. The parasphenoid broad and thick. The pterygoid with a broad posterior and a long anterior limb, for the most part low; the dorsal margin of the posterior limb with a deep angular sinus. The supraangulo-angular high and triangular. The ossification in the ceratohyal short but strong. The opercular large. Nothing known about the dentition on the labial margin of the jaws; otherwise the dentition strong and adapted for crushing with closely arranged teeth. The sensory canals strongly developed and opening to the exterior by large pores. The paired fins rather small. The most anterior dorsal fin very high but short-based. The caudal fin also high, though its dorsal and ventral lobes are at the same time long. The lepidotrichia of all the fins narrow and unjointed for a long distance proximally; those of the first dorsal and caudal fin furnished with two rows of small tubercles on the lateral sides. The sculpture of the scales consisting of rather coarse striae, the median ones of which are often the most developed.

Axelia, like the two genera *Myrlacanthus* and *Scleracanthus* described below, is especially distinguished from other Coelacanthids so far known in detail by its dentition. Otherwise it differs from the ordinary Coelacanthid type only in some rather unimportant morpho-

The primordial neurocranium and its ossifications.

The primordial neurocranium is on the whole wider and more powerfully built than in *W. sinuosa* and relatively to its length it is not inconsiderably higher than in this species (text figs. 39, 40, 43, 44). The snout has probably been rather blunt and so resembles in profile to a certain extent that of the Palaeoniscids.

Nothing is preserved of the occipital region.

The labyrinth region is fairly long and at the same time considerably wide. It seems to have consisted of cartilage to about the same extent as in *W. sinuosa* and presumably had, as in this species, a paired muscle groove («temporal fossa») on the posterior part of the dorsal surface. A number of remains of the prootico-opisthotic (*Pro. o.*, Pls. 11, 12, 13); indicate that this bone has been well developed, but nothing more can be said as to its shape. A posterior smaller part of the basisphenoid also belongs to the labyrinth region.

The orbitotemporal region is somewhat shorter and broader than in *W. sinuosa*. The breadth especially is greater, if one pays attention to the ventral parts (text figs. 40, 41, 42; Pl. 14, fig. 5; Pl. 16, fig. 1). The basisphenoid is situated, as usual, in the posterior end of the region in question but is rather low and, contrary to the case in *W. sinuosa*, by no means reaches to the cranial roof dorsally. A considerable part of the lateral wall of the neurocranium above it has been cartilaginous. The anterior and by far the greater part of the orbitotemporal region, which forms the real interorbital wall, has probably been composed entirely of cartilage. With regard to the supposed fenestration which is situated immediately in front of the ventral part of the basisphenoid and which is supposed to correspond to the orbital opening of the myodome, according to what I have tried to show in *W. sinuosa*, nothing particular can be added to what has already been said in the

Text fig. 40. *Axelia robusta* n. sp.

Neurocranium from the dorsal side with the roof removed above the occipital region, the labyrinth region, and the posterior part of the orbitotemporal region. From *P. 195*, 24. (The prootico-opisthotic incompletely preserved in this specimen and therefore not drawn.)

Alsph, alisphenoid, joined to and forming a ventro-caudal process from the fronto-dermosphenotic; *Bsph*, basisphenoid; *Fr. dsph*, fronto-dermosphenotic; *Jr*, interrostrals; *Na. ant.*, nasalo-antorbital; *Paph*, parasphenoid; *Pir*, postrostrals; *R*, rostrals; *So*, supraorbitals; *al*, anterior lamella from the basisphenoid corpus; *e*, basitergoid process; *na₁*, anterior nasal aperture; *na₂*, posterior nasal aperture; *p*, pores of the sensory canal; furrow on the lateral side of the alisphenoid, indicating the course of the n. ophthalmicus lateralis; *s*, vertical furrow leading down to the entrance of the supposed myodome; *V₂₃*, sinus in the basisphenoid corpus situated under or in relation to the foramen or foramina transmitting r. maxillaris trigemini, r. mandibularis trigemini, n. ophthalmicus trigemini and n. ophthalmicus lateralis.

The basisphenoid (*Bsph*, text figs. 39, 40, 41; Pls. 11–13; Pl. 14, figs. 2, 3, 5) consists partly of cancellous, and partly of radiate, bone substance. The latter sort, however, is

limited to the ventral processes and a part of their dorsal extension. In addition to these processes the bone has, as in *W. sinuosa*, basiptyergoid processes and anterior lamellae, all of which are joined to a powerful corpus.

The corpus forms, in the same way as I have described in *W. sinuosa*, a triangular plate with its rounded point ventrally and its base dorsally. From side to side, however, it is wider and in an antero-caudal direction it is thicker than in the species just mentioned and it also takes up a more vertical position than in that species. On the corpus can be distinguished one anterior, one posterior and two lateral surfaces. Of these the dorsal one (text fig. 40; Pl. 14, fig. 3) has almost a rectangular shape, with its anterior and posterior margins long and the lateral ones short. All the margins are concave, the

Text fig. 41. *Axelia robusta*. Basisphenoid in anterior aspect. From P. 195. $\frac{1}{16}$.

BspH, basisphenoid; *PspH*, parasphenoid (cross-section); *al*, forward pointing lamella from the basisphenoid corpus; *e*, basiptyergoid process; *m*, the entrance of the supposed myodome; *r*, longitudinal ridge on the medial side of the forward pointing lamellae; *s*, unpaired vertical furrow leading down from the fossa hypophyseus to the myodome; ventral process from the basisphenoid corpus; *V1e*, outer opening of the canal for n. ophthalmicus profundus; *V1i*, inner opening of the canal for n. ophthalmicus profundus.

posterior ones least, the lateral ones most. The postero-lateral corners are comparatively slightly pronounced; the basiptyergoid processes (*e*) issue in the antero-lateral corners. The median part of the dorsal surface is somewhat deepened in the longitudinal direction of the animal. The two lateral surfaces (text fig. 39, Pl. 13) are relatively wide and low and pass into those of the anterior lamella and ventral processes without any boundary. The posterior surface is large and has the shape of a triangle with the well rounded point ventrally. It faces not only backwards but at the same time somewhat ventrally as well. The anterior surface (text fig. 41; Pl. 14, fig. 5) is freely visible only on a very small portion of its dorso-median part. Otherwise the anterior lamellae *al* issue with a broad base from its lateral and ventral parts. Finally it is noteworthy that the surface in question also faces somewhat dorsally.

The two basiptyergoid processes (*e* text figs. 39, 40, 41; Pls. 11—13; Pl. 14, figs. 2, 3, 5) agree fairly well in shape with the corresponding ones in *W. sinuosa*, but are stouter. They project from the antero-lateral parts of the dorsal surface of the basisphenoid corpus in an antero-latero-dorsal direction, so that they diverge from each other considerably more than in the *Wimania* species mentioned. In other respects it is worthy of special mention with regard to this that in the species in question they issue strikingly low on the lateral wall of the neurocranium (text fig. 39), in which respect they thus somewhat resemble these of *Dictyonosteus*.

The ventral processes (*v*) of the basisphenoid are, seen from the lateral side (text fig. 39; Pl. 13), short and broad. Seen from in front (text fig. 41; Pl. 14, fig. 5), they appear to be far apart and do not pass straight downwards but somewhat laterally as well, and in addition appear comparatively thick also in a transverse section. The ventral ends of these processes are attached to the parasphenoid.

Finally, with regard to the lamellae (*al*) of the basisphenoid these are distinguished, first, by a rather considerable thickness, especially in their posterior parts attached to the corpus (text fig. 41; Pl. 14, fig. 5). Their ventral parts bend towards and meet each other in the median line. Their dorsal parts are posteriorly connected with the antero-medial border of the basiptyergoid processes and so form a strong support for

the proximal parts of these. While in *W. sinuosa* they reach anteriorly as high as the dorsal surface of these processes, here in *A. robusta*, on the other hand, they only extend to the ventral one.

The posterior part of the fossa hypophyseos, bounded by the basisphenoid corpus and the anterior lamellae, is strikingly broad (text figs. 40, 41; Pl. 14, figs. 3, 5). From its base there passes vertically downwards to the supposed myodome (*m*) a median furrow (*s*) which has obviously formed the posterior part of an unpaired canal, whose anterior part has been surrounded by cartilage. This canal seems to have been in relation with the hypophysis. On the medial surface of the anterior lamellae we notice a rounded torus (*r*) running anteriorly and somewhat downwards and immediately above it a furrow, also running anteriorly and downwards, which becomes deeper as it continues anteriorly and leads into the canal for n. ophthalmicus profundus (*V₁₆*, text fig. 41), which canal penetrates the dorsal part of the lamella in an outward and somewhat downward direction and has its external opening *V₁₆*, (text figs. 39, 41; Pl. 14, fig. 5) about ventro-medially of the anterior end of the basiptyergoid process.

The cranial cavity in this species seems in the main to have been similar to that of *W. sinuosa*, except that it was broader and higher. The exits of the nerves, at least in the orbito-temporal region, have also had a similar position in both species. The canal for n. ophthalmicus profundus has, as we have seen, about the same position as in *W. sinuosa* and the same is true of the other trigeminal branches and the r. ophthalmicus lateralis, all of which have their exits (*V_{2,3}*, text figs. 39, 40) in *A. robusta* above the lateral margin of the dorsal surface of the basisphenoid corpus either in relation to this margin or a short distance dorsally of it, totally in cartilage. The n. ophthalmicus lateralis (and possibly n. ophthalmicus trigemini as well) has probably had its exit through a separate foramen somewhat dorsally of the other or else it has been transmitted through the dorsal part of the same foramen with these. After its exit it has in all probability had its course anteriorly along the lateral wall of the neurocranium above the basiptyergoid process and in this course it has crossed the ventro-caudal process (*Alsp*) of the fronto-dermosphenotic. Its course is indicated in the fossil by a well marked groove (*r. ophth*, text figs. 39, 40; Pl. 11, Pl. 14, figs. 2, 3). Other nerve foramina in the cartilaginous parts are hypothetically drawn in text fig. 39 in accordance with *Dictyonosteus*, as in the case of *W. sinuosa*.

The ethmoidal region of the species in question is high and rather broad (text figs. 39, 44; Pls. 11—13; Pl. 14, figs. 1, 4) and has consisted mainly of cartilage. Only a paired bone (*Pethm*, text figs. 39, 42; Pls. 12, 13; Pl. 16, fig. 1) is developed. The nasal capsule has probably been situated in the cartilage above the posterior and medial part of this bone, but, as will be seen, without having any direct relation to it so as to

Text fig. 42.

Axelia robusta n. sp.
Parasphenoid and prethmoid in ventral aspect. The parasphenoid with teeth. From *P. 165*, $\frac{1}{4}$.
Pethm, prethmoid; *Psp*, parasphenoid; *f. pal.* foramen for the dorsal branch of n. palatinus anterior; *lat. for.* foramen for the most anterior branches of n. buccalis and r. maxillaris trigemini; *ms*, furrow along the lateral side of the prethmoid for n. buccalis lateralis and r. maxillaris trigemini.

modify its form in any way. The bone in question is only half as high as the part of the region in which it is situated. It is shaped almost like a three-sided prism with a ventral horizontal surface, a lateral one that is vertical, and a dorso-medial one that has been attached to the cartilage. The posterior and anterior ends have also been joined to cartilage, as text fig. 39 shows. The bone is considerably broad and it is open to question whether it has not met that of the opposite side in a median suture. The lateral side has throughout its length, close to the ventral margin, a distinct, rather broad and deep groove (*ms*, text figs. 39, 42; Pls. 12, 13; Pl. 16, fig. 1), which towards the anterior end of the bone, leads into a canal (*lat. for*) which in its turn continues in an antero-medial direction.

The ventral side has in its anterior part towards the medial margin a small foramen (*f. pal*, text fig. 42; Pls. 12, 13; Pl. 16, fig. 1) which leads into a fine, vertically ascending, canal. The ventral side of the bone is in its median parts covered by the parasphenoid as shown in text fig. 42, and Pl. 16, fig. 1. The relation between the bone and the cartilaginous parts of the ethmoidal region is easy to understand from text fig. 39. It may, however, be specially emphasized that it by no means reaches backwards to the orbit.

It thus seems probable that this bone bears a close resemblance to the preëthmoid in *Amia*, although it is considerably more powerfully developed than in this form (SAGEMEHL 1884, p. 204; ALLIS 1897 a, Pl. XXI, figs. 8—10; 1898, pp. 446—450; 1909 a, pp. 17—22; SWINNERTON 1902, pp. 530—531). In the groove on the lateral side branches of ramus maxillaris superior trigemini and buccalis lateralis have apparently had their course, the latter for the innervation of the most anterior sensory organs of the infraorbital canal. The fine vertical canal ascending from the ventral side seems to have a dorsal branch of the nervus palatinus anterior running through it. In *Amia* this nerve does not penetrate the preëthmoid but is situated close to its medial margin. Thus it might easily be enclosed in this bone if there were a medial growth of this (cf. ALLIS 1897 a, Pl. XXI, figs. 8, 10).

The membrane bones of the neurocranium.

The parasphenoid *Psph*, text fig. 39, 40, 41, 42; Pl. 13; Pl. 14, fig. 5; Pl. 16, fig. 1) has the same extension as in *W. sinuosa*, i. e. it covers the whole basal surface of the orbitotemporal region and also stretches anteriorly under the ethmoidal region and posteriorly, although only to a slight extent, under the most anterior part of the labyrinth region. Its anterior end does not reach forward under the ethmoidal region quite so far as to the anterior end of the preëthmoid (text figs. 39, 42, Pl. 16, fig. 1), and it covers only the posterior medial part of the latter bone (cf. *W. sinuosa* text fig. 23). It is much thicker and stouter than in *W. sinuosa* and is also of a different shape. Its most distinguishing feature is, on the whole, its great breadth. The anterior end forms an obtuse angle, the posterior end is truncated and slightly concave. The greatest breadth lies near the anterior end and behind that comes a somewhat narrower part, while about and just behind the middle it becomes broader again, but not so broad as in the anterior part, after which it gradually grows narrower towards the posterior end, immediately in front of which lies the narrowest part. The centre of ossification is so situated that it corresponds to the posterior of the two broadest parts.

The parasphenoid in its anterior halves is flat and lacks the upward-curving lateral parts, which otherwise are so usual in the Coelacanthids. Such upward-curving lateral parts are, on the contrary, to be found in its posterior half (text figs. 39, 41; Pl. 13; Pl. 14, fig. 5), where most posteriorly they are considerably high. A transverse section through the parasphenoid posteriorly (text fig. 41; Pl. 14, fig. 5) shows plainly that these upward-curving parts have likewise been thick and strong and were formed of typical radiate bone substance of the same appearance as in the ventral processes (ν) of the basisphenoid. The horizontal part lying between them also has a similar structure in its dorsal half. The upward-curving parts, together with the ventral processes of the basisphenoid which rest against their dorsal surface, form lateral boundaries of the anteriorly open canal (m) which, as I have tried to show before, should correspond to a myodome. Dorsally this canal is bounded anteriorly by the ventro-lateral parts of the basisphenoid lamellae and behind them by the basisphenoid corpus; ventrally by the median horizontal part of the parasphenoid. Anteriorly the canal in question is broad and rather high and has a typical six-sided transverse section, posteriorly it diminishes rapidly in height so that at last only a low cavity remains. That the canal has not had its present circumference in reality, but has been partly filled by cartilage, is seen from the appearance of the surrounding bones.

While the parasphenoid in *W. sinuosa* was a dermal bone in the whole of its extension, there is much that suggests that in *A. robusta* it was partly developed as a primary bone in the posterior part. This view is favoured in the first place by the characteristic radiate structure of the bone in the upward-curving parts and partly also in the horizontal part lying between them, further by the way in which these upward-curving parts unite with the basisphenoid, and lastly by the relatively important extension in the way of height in the upward-curving parts at the expense of the ventral processes of the basisphenoid.

It is uncertain whether vomeres were to be found. If such was the case they ought, however, to have partly covered the anterior end of the parasphenoid bone with their posterior parts, and for the rest have borne the same relation to the prethmoidea as in *Amia* (ALLIS).

If we now turn to the cranial roof we naturally find in *A. robusta*, in respect to its membrane bones, that taken on the whole it is in agreement with that in *W. sinuosa*.

Text fig. 43. *Axelia robusta* n. sp.

Dermal cranial roof from the dorsal side. The sculpture is not drawn. Sensory canals with dotted lines and shading. From P. 195 v1.

Ext, Extrascapulars; Fr. dspb, Fronto-dermosphenotic; Jr, interrostral; Na. ant, nasalo-antorbital; Pa. it, parieto-intertemporal; Pitr, postrostral; R, rostrals; So, supraorbitals; Sscap, suprascapulars; Stemp. ex, supratermporo-extrascapular; na1, anterior nasal aperture; na2, posterior nasal aperture; p, pores of the sensory canal (belonging to the supraorbital canal).

Over the posterior part of the labyrinth region, behind the parieto-intertemporals and bounded laterally on each side by the dorsal edge of the supratemporo-extrascapular, there is a transverse row of six, scale-like, rounded, extrascapular plates («supratemporals») (*Ext*, text figs. 43, 44; Pls. 11-13; Pl. 14, fig. 1) which did not lie in contact with the primordial neurocranium but formed a roof over the muscle fossae on the dorsal side of the labyrinth region, i. e. over the so-called temporal fossae. At the same time it is clear that they have not been closely united with the neighbouring bones, nor with each other either.

The fronto-dermosphenotics (*Fr. dsph*, text figs. 39, 40, 43, 44; Pls. 11-13; Pl. 14, figs. 1-4) are situated in the usual way over the anterior and middle parts of the orbitotemporal region. They slope, as usual, downwards and forwards and posteriorly they meet with the parieto-intertemporals in an obtuse angle. The suture between them and the latter bones falls at a vertical plane somewhat in front of the basisphenoid (text fig. 39) and is obviously straight. They are shorter in length than in *W. sinuosa* and only slightly longer than the parieto-intertemporals. In their posterior third they are a little broader than the latter; otherwise, on the contrary, they are a little narrower. The medial and posterior margins are straight; the lateral margin has a posterior convex part corresponding to the broader third of the bone and an anterior slightly concave part, which in its turn shows two or three smaller concavities and convexities of the second rank; the appearance of the anterior margin is unknown at present. The centre of ossification is found in the same position as in *W. sinuosa* and from it there issues on the ventral side the large process, especially long here (*Alsph*, text figs. 39, 40; Pls. 11-13; Pl. 14, figs. 2, 3) which represents the alisphenoid. The process in question is, for the rest, broad and powerful. It is directed postero-ventrally and has been joined to the cartilaginous parts over the anterior lamella of the basisphenoid, as well as to the dorsal surface of the basiptyergoid process. On its lateral side it is, as already pointed out above, crossed by a distinct furrow which must be considered to indicate with the greatest probability the course of *r. ophthalmicus lateralis* and possibly even *r. ophthalmicus trigemini*, if the latter has been united with it.

Along the lateral margin of each fronto-dermosphenotic for about two thirds of its anterior part lie a row of four comparatively large, broad, four-sided supraorbitals (*So*, text figs. 39, 40, 43, 44; Pl. 14, figs. 1-4), which all have straight lateral and rather irregularly, curving medial margins, and are mutually united by somewhat undulating sutures.

Anterior of the supraorbital row there follows a rather large bone (*Na. ant*, text figs. 39, 40, 43, 44; Pls. 11-13; Pl. 14, figs. 1-4) which I have called the nasalo-antorbital. In lateral view (text figs. 39, 44) its shape seems to be almost that of an equilateral triangle with the apex lying rostrally and a little dorsally, the base lying caudally and a little ventrally. Its dorso-medial part rests upon the dorsal side of the ethmoidal region and thus covers the nasal capsule from above. All the other parts belong entirely to the lateral surface of the same region and surround the nasal aperture rostrally, ventrally and caudally, forming at the same time a septum that divides this aperture into an anterior (*na₁*) and posterior (*na₂*) foramen, of which the first lies a little lower than the last. Both seem to have a rather rounded shape. The slightly concave posterior margin of the bone in question has probably formed part of the anterior boundary of

the orbital opening; its antero-ventral and dorso-medial margins bound the bones that I shall describe immediately below. The centre of ossification lies dorso-medially of the anterior nasal aperture.

The ethmoidal region is covered between the nasalo-antorbital of both sides by a rather large paired plate which, as I have already mentioned in describing *W. sinuosa*, I propose to call the postrostral (*Ptr*, text figs. 39, 40, 43, 44; Pl. 11-13; Pl. 14, figs. 1-4). The two postrostrals are oval in shape and their maximum breadth is about half their length. With their longitudinal axis they converge a little in anterior direction and with their medial margins they meet in a rather short median suture that forms the direct anterior continuation of the median suture between the fronto-dermosphenotics. They rest with their posterior portions on the anterior ends of the last-mentioned bones and with their lateral margin each of them meets the nasalo-antorbital of its side and the anterior supra-orbital plate. The centre of ossification is situated a little in front of the middle. Otherwise there is nothing else to remark about these bones, except that they lie in a plane that forms the direct continuation of the fronto-dermosphenotics and consequently face dorsally and somewhat anteriorly.

In the angle between the anterior ends of the postrostrals there has been, as far as one can judge, a little double or single bone plate (*Ir*, text figs. 40, 43; Pl. 14, figs. 1-4) which I have called the inter-rostral.

In front of the nasalo-antorbitals, postrostrals and interrostrals is found a transverse row of four-sided bone-plates (*R*, text figs. 39, 40, 43, 44, Pls. 12, 13; Pl. 14, figs. 1-4) which might properly be called rostrals. The middle ones in their posterior part reach up to the dorsal surface of the ethmoidal region, while their anterior part covers the forward pointing surface of the same region and thus faces straight forward or even a little ventrally. The lateral rostral plates on the other hand belong more to the sides of the ethmoidal region. The total number of the rostrals cannot yet be fixed but there were probably not less than four or more than six of them. The centre of ossification is plainly marked in most of them.

It is evident merely from their topographical position that the bone-plates which I have mentioned respectively as the rostrals, the interrostrals and the postrostrals correspond to a large extent to a number of bone-plates found in the same position in the *Rhipidistia* (WATSON and DAY 1916) and the so-called «supraethmoid» of the Teleosts. I shall not, however, in this connection deal with the question of their homologues.

All the bones in the cranial roof of *A. robusta* have a very characteristic sculpture (Pl. 16, fig. 4), consisting of fine, close, transversal striae and tubercles. A similar transversal also distinguishes the four middle extra-scapulars, while each lateral one is striated longitudinally in the same way as the scales.

As far as one can judge from the sclerotic ring (*Scr*, text fig. 44; Pls. 11-13; Pl. 15, figs. 1, 5), the eye was larger than in *W. sinuosa*. The sclerotic ring was probably formed by about twenty plates of the usual four-sided shape.

The membrane bones of the cheek.

The membrane bones of the cheek must have been much reduced and are subdivided in a great number of small scale-like plates (Pl. 15, figs. 1, 2). The sculpture on these

plates consists of longitudinally placed striae, which in size and length correspond most closely to those of the scales.

The visceral skeleton.

The autopalatine is incompletely preserved and it is not impossible that this is due to a slight development of the bone itself, but one cannot form a definite conclusion from the material at hand.

The quadrate (*Qu*, text fig. 45 A, B; Pl. 11; Pl. 15, figs. 1, 2) covers, as usual, the ventrocaudal corner of the pterygoid on the lateral side. It has a very thick posterior part that can conveniently be called the corpus and a lamella that issues from the anterior border of the corpus. The centre of ossification lies in the ventral part of the corpus.

The corpus (Pl. 15, fig. 2) is rather high, but its longest axis does not stand vertically but slopes a little backwards. Its greatest breadth, which is about the same as half its

Text fig. 45. *Axelia robusta* n. sp.

A) The bones of the palatoquadrate with the exception of the autopalatine. Seen from the lateral side. From P. 187, P. 189 and P. 193, fig. 4.

Mptg, metapterygoid; *Pt*, pterygoid; *Qu*, quadrate.

B) The bones of the palatoquadrate with the cartilage connecting the metapterygoid and the quadrate restored. Lettering as in fig. A.

height, is at its upper end. From here it gradually grows narrower in the ventral direction, while at the same time it decreases a little in thickness up to the vicinity of the ventral end, where it swells out to a condyle for the articulation with the mandibula. This end is somewhat rounded, but otherwise it is too imperfectly preserved to make a closer study of the shape of the articulating surface possible. The dorsal end is, on the contrary, abruptly truncated, and extends posteriorly a little beyond the caudal margin of the pterygoid as in *W. sinuosa* and the majority of the Coelacanthids. While the part of the corpus lying on the ventral side of the centre of ossification, i. e. the condyle, is formed of compact bone, the remaining part dorsally of the centre of ossification has, on the contrary, been partly cartilaginous in its interior and united dorsally to cartilage. The anterior lamella, the shape and position of which are quite clear from text fig. 45, is united to the corpus for pretty nearly the whole of its height.

The metapterygoid (*Mptg*, text figs. 45, A, B; Pls. 11, 12; Pl. 15, figs. 1, 2) is a rather large and thick bone, which, as in the case of *W. sinuosa* and *S. tuberculata*, covers

the dorsal part of the posterior pterygoid limb from the lateral side. One can distinguish a dorsal, an anterior, a ventral, and a caudal margin, of which the two first named are slightly concave, the two last-mentioned being, on the contrary, greatly convex. The antero-dorsal corner is pointed and rather drawn out, although not so much as in *W. sinuosa*; the antero-ventral and the postero-dorsal ones, on the contrary, are both sharp and almost right-angled, and the postero-ventral one is well rounded off, so that the caudal and ventral margins merge into each other without any distinct boundary. The centre of ossification is plainly seen and is situated in the vicinity of the dorsal margin towards the antero-dorsal corner. As is the case in *W. sinuosa*, the bone in question has been united firmly to the pterygoid by means of its anterior margin; we shall find the same relation existing in the majority of the Coelacanthids.

It is plain that the posterior and ventral margin of the metapterygoid were joined to cartilage, and, as I have emphasized above, this was also the case with the dorsal end of the quadrate. It is an obvious supposition that the bones in question were mutually joined by a continuous piece of cartilage and this supposition is strengthened by the fact that the quadrate must have been connected dorsally with an especially thick cartilage, which undoubtedly was of considerable extent in a dorsal direction. The metapterygoid too, by reason of its function, requires a more fixed union ventrally than the suture with the pterygoid affords it. In other words, a firm connection ventrally is a necessity if the metapterygoid is to be the means by which the palatoquadrate articulates with the neurocranium, and such a connection is in this case only conceivable by means of cartilage continuously joining the metapterygoid and the quadrate. As far as one can judge, the palato-quadrate cartilage has thus persisted in its posterior part to a rather large extent. Whether this was also the case with its anterior parts cannot, on the contrary, be decided. In text fig. 45 B I have tried to make clear how the cartilage in question may have appeared.

The pterygoid (*Pt*, text figs. 45 A, B; Pls. 11—13; Pl. 15, figs. 1, 2) is large and considerably thicker and stronger than in any of the species known before. The centre of ossification lies, as usual, on the boundary between the two limbs but considerably higher than in *W. sinuosa*, and is not covered, as in that species, by the quadrate, but can be seen plainly anteriorly of the dorsal part of that bone. The limbs occupy the usual position in relation to each other.

The posterior limb is strikingly broad. Its posterior margin is slightly convex, partly even rather straight. Its dorsal margin has a deep and broad acute-angled sinus, that stretches downwards almost so far that it corresponds to the antero-ventral corner of the metapterygoid (text fig. 47). The antero-dorsal as well as the postero-dorsal corner is acute-angled, although it is more so in the latter, and on account of the deep sinus lying between them, they appear to some extent as dorsally directed processes, of which the posterior one is broader and also somewhat higher than the other. Towards the ventral end the limb in question narrows a little and its ventral corner is rounded off. A decided ridge runs from its antero-dorsal corner, downwards and somewhat backwards across its lateral surface; the metapterygoid is connected with this ridge in the same way as in *W. sinuosa*.

The anterior limb is rather long and for the most part very low. It is high only in the immediate neighbourhood of the posterior limb, with which it is connected along the anterior margin of the ridge just mentioned. Still it does not reach the same height as the posterior one, but farthest dorsally a small extent of the anterior margin of the ridge is free. The dorsal margin of the limb, as well as its ventral one, is concave. From its connecting place with the posterior limb the former margin runs first in a sharp concave arch downwards and somewhat forwards, but afterwards in the larger anterior part it takes a more straight direction; the latter margin rises throughout its length rather gradually forwards and upwards.

The mandible in *A. robusta* is preserved in a much more complete condition than in *W. sinuosa*, and it is plain that its posterior part was distinguished by a considerable height, while anteriorly it was comparatively low (text fig. 44).

The supraangulo-angular (*Sang. ang.*, text fig. 44; Pl. 11; Pl. 15, figs. 1, 2) is remarkably high, and has a nearly triangular shape. The ventral margin is fairly straight, the antero-dorsal one is slightly concave, and the postero-dorsal one is slightly convex. The anterior and posterior corners are acute-angled, the dorsal corner also forms an angle and projects rather decidedly, but yet it is more rounded than the other two. The lateral side of the bone, dorsally of the pores of the sensory canal, is sculptured with fine striae, running lengthways.

The dental (*De*, text fig. 44; Pl. 11; Pl. 15, figs. 1, 2) and splenial (*Spl*, text fig. 44; Pl. 15, figs. 1, 2) are only preserved in fragments; it can be plainly seen, however, that they were comparatively low, and without sculpture. Between their posterior ends the supraangulo-angular projects anteriorly to a slight extent. The intercoronoideo-prearticular (*Icor. pra*, text fig. 44; Pls. 11—13; Pl. 15, figs. 1—2) is large and probably had about the same shape as the supraangulo-angular.

The coronoid is fragmentarily preserved and the precoronoids are unknown.

The ossification in the ceratohyal (text fig. 46; *Chy*, Pls. 12, 13, 15) is short in comparison with that of *Wimania sinuosa* and *Sassenia tuberculata*. On the ventral margin it has the usual broad, rounded projection. The epihyal is still unknown.

The opercular (*Op*, text, fig. 44; Pls. 11—13; Pl. 15) is a large, triangular bone-plate, which has an anterior, an upper and a postero-ventral margin; its antero-dorsal corner is rather markedly angular, its postero-dorsal and ventral corners, on the contrary, are well rounded off. The anterior margin is concave in the upper part, but convex in the lower; the dorsal margin is, on the whole, slightly concave; the postero-ventral margin is markedly convex in the dorsal two thirds; in the remaining ventral third it is concave. The maximum breadth of the opercular is about two thirds of its height. The sculpture consists of rather short, horizontal, mutually parallel striae.

The branchial arches are, as far as their shape is concerned, in the main like those found in *W. sinuosa*, although they are more robust. Their number is as yet uncertain. The membrane bones on the dorsal side of the copula are most essentially stronger and thicker than in any of the Coelacanthids before known, a condition which is obviously due to the character of the dentition.

Text fig. 46.
Axelia robusta n. sp.
Ceratohyal ossification.
From P. 195. 74.

Dentition.

The dentition in *A. robusta* is, in its general character, typically adapted for crushing. The parasphenoid, the pterygoid, the intercoronoideo-prearticular, the coronoid and the membrane bones on the copula are furnished with spheroidal flat teeth which are largest and strongest on the parasphenoid and the membrane bones on the copula, smallest on the intercoronoideo-prearticular. On the last-mentioned bone they are also mainly confined to the dorsal parts. Their distribution on the parasphenoid is seen in text fig. 42 and Pl. 16, fig. 1 and on the pterygoid in text fig. 47.

The dentition of the precoronoids, maxillary and premaxillary is unknown.

The branchial arches were, as far as one can judge, furnished with small teeth-bearing plates. Large numbers of such plates are often seen, scattered among the different parts of the visceral skeleton. The teeth on these plates, the majority of which are small, are sometimes conically pointed, sometimes, and that is probably most general, they are blunt or spheroidal. The small plates which REIS (1888, pp. 47, 51; Pl. II, fig. 2)

has described in the Jurassic forms as «Sclerotical-pflaster» were probably tooth-bearing plates belonging to the branchial arches.

As far as one can see, the pointed conical teeth are smooth. The spheroidal ones, on the contrary, have a fine striation radiating from a centrally placed, wart-shaped little protuberance (Pl. 16, fig. 2); in this way they strongly remind one of the typical spheroidal *Colobodus*-teeth. Their agreement with the latter, as I have pointed out in an earlier work (ANDERSSON, 1916 a, pp. 27—28) is so great that if one met with them detached one would consider them undoubtedly as pertaining to *Colobodus*.

Text fig. 47. *Axelia robusta* n. sp.
Pterygoid with dentition.
From P. 187, P. 189 and P. 195. $\frac{1}{4}$.

The sensory canals of the head.

The sensory canals of the head were strongly developed and opened outward with large, generally oval pores. In the cranial roof and the mandibula they are preserved almost completely. In the cheek they are found in a more fragmentary condition, but their course is also there partly well shown.

The anterior end of the supraorbital canal (text figs. 43, 44) is situated in the most lateral one of the rostral plates, a little antero-ventrally of the anterior nasal aperture. From here it rises in an arch upwards and backwards, enters the nasalo-antorbital dorsally of the nasal capsule, runs through the whole length of that bone and then between the supraorbitals and the fronto-dermosphenotic, till at last in the postero-lateral part of the latter bone it anastomoses with the infraorbital canal. If this anastomosis was formed with its posterior end or whether this end continued in a posterior direction medially of the infraorbital canal as an anterior head line of pit organs it is not possible to say. In the part of the canal situated between the supraorbitals and the fronto-dermosphenotic three large oval pores are found (p. text figs. 39, 40, 43, 44; Pl. 14, figs. 1—2.) It is also evident that one or more pores of a similar kind must have been developed

on the anterior parts of the canal above the ethmoidal region, although the state of preservation makes it impossible to give a more detailed account of the conditions there.

With regard to the extent of the infraorbital canal I have here given it in the definition of EWART (1892), EWART and MITCHELL (1892) and COLE (1896; 1898), i. e. I restrict it to the parts which are innervated by the r. oticus lateralis and n. buccalis lateralis. The canal in the supratemporal part of the supratemporo-extrascapular, which was probably innervated by the r. dorsalis glossopharyngei, comes in this way to be assigned to the cranial section of the main lateral line of the body.

The most anterior part of the infraorbital canal is incompletely preserved in this species. There are, however, remains that indicate that an ethmoidal commissure was present, situated in the rostrals. From this commissure the canal has certainly continued backwards through the membrane bones on the lateral surface of the ethmoidal region ventrally of the nasal capsule, but in the material present there is nothing now preserved of this part. The sub- and postorbital parts, on the other hand, are preserved; and it is clearly seen (cf. Pl. 15, fig. 1) that they were enclosed in a tube of bone. When leaving the cheek the infraorbital canal enters the fronto-dermosphenotic at about the posterior margin of the most posterior supraorbital plate. From here the canal passes off medially and backwards in the dermosphenotic component of the fronto-dermosphenotic, then turning straight backwards. Just at the point where it takes the last-mentioned direction it anastomoses with the supraorbital canal. Continuing in a caudal direction, it reaches the suture between the fronto-dermosphenotic and the parieto-intertemporal. In its further course backward it was first quite surrounded by membranous tissue on the ventral side of the lateral part of the parieto-intertemporal, then entered the lateral part of the bone, finally passing over into the ventral lamella furthest backwards. Guided chiefly by the exits of the cranial nerves I place its posterior end at the suture between the parieto-intertemporal and the supratemporo-extrascapular.

The foramen trigemini, as we have seen above, is so situated that the r. oticus lateralis must have been sent off from n. buccalis lateralis beneath about the median part of the parieto-intertemporal; on the other hand, the n. glossopharyngeus ought to have had its exit in such a position that its ramus dorsalis may be supposed to have met the anterior half of the supratemporo-extrascapular, if it ascended somewhat vertically. As far as one can see from this, the region of innervation for r. oticus lateralis would thus be restricted to a part of the sensory canal in the parieto-intertemporal, while r. dorsalis glossopharyngei would innervate the anterior part of the canal in the supratemporo-extrascapular (cf. ALLIS, 1889, p. 516, Pl. XLII; 1900 a, p. 449; 1905, pp. 405, 482; 1919, p. 73; HERRICK, 1901, p. 207; POLLARD 1892 a, p. 397; 1892 b, pp. 529, 532, 535, 536, 538).

The number and position of the pores of the infraorbital canal are not yet known.

The jugal canal (*jc*, Pl. 15, fig. 1) has the same course as in *Wimania sinuosa*. As we have seen, the cheek plates in this region are reduced to small scale-like plates and the canal is preserved only because it was enclosed in a tube of bone.

The mandibular canal (*mc*, Pl. 15, figs. 1, 2) passes through the whole length of the supraangulo-angular and then continues forward in the splenial. In its passage through the former bone it has opened outwards with five large pores (*p*¹), which are

situated some distance ventrally of the canal itself. The tubes are wide and unbranched. There seem to be at least two pores in the splenial.

According to the definition of the infraorbital canal above, the cranial section of the main lateral line of the body extends in the Coelacanthids up to the suture between the parieto-intertemporal and the supratemporo-extrascapular. From this suture, where it forms a continuous junction with the infraorbital canal, the cranial section of the main lateral line first passes through the supratemporo-extrascapular, which it leaves on the medial edge near to the posterior end. Afterwards, as far as one can see, it traversed a small membranous interspace. Here it has a supra-temporal branch, which continues through the extrascapulars towards the median line and there presumably joins that of the opposite side, forming a continuous supratemporal commissure (text figs. 43, 44, s. com, Pls. 11—13; Pl. 14, fig. 1). Immediately behind this commissure the section in question of the lateral line has turned in a more purely caudal direction, being in its course just for a short distance situated close to the medial edge of the supratemporo-extrascapular. Near the posterior end of this bone it leaves the membranous interspace and enters a small rounded scale-like plate probably representing the suprascapular (*Sscap*, text figs. 43, 44; Pls. 11, 12, 13; Pl. 15, fig. 1). — Nothing is known with regard to pores in this part of the lateral line.

Neither on the cranial roof nor on the cheek have I been able to observe «pit-lines» or anything corresponding to these.

If we now examine the *Rhipidistia* as regards the sensory canals, we shall find in them, at least to judge from *Osteolepis* (GOODRICH 1919), *Eusthenopteron* (text fig. 57) and *Dictyonosteus* (text fig. 58), a very great resemblance to *A. robusta*, *W. sinuosa* and other Coelacanthids. A comparison between the same forms with regard to the relation between the sensory canals and the dermal bones, on the other hand, also clearly shows that several of the elements that are found separate in the Rhipidistids must in the Coelacanthids, on the contrary, be united to one another in about the way I have tried to indicate by the nomenclature used in this work. From the relations of the infraorbital canal it is thus easily understood that the homologues of the parietal and the intertemporal of the Rhipidistids have coalesced to form the parieto-intertemporal of the Coelacanthids, and that in the same way the homologues of the dermosphenotic and frontal of the Rhipidistids together have formed the fronto-dermosphenotic of the Coelacanthids. The conditions of the supraorbital canal also show clearly that the homologue of the nasal of the Rhipidistids and that of their antorbital may be united to the nasalo-antorbital of the Coelacanthids, and finally the cranial section of the lateral line together with its supratemporal commissure shows that in the Coelacanthids the homologue of the supratemporal of the Rhipidistids has incorporated with itself certain parts of the lateral-extrascapular («tabular»), so that it may quite correctly be called the supratemporo-extrascapular.

The course of the mandibular canal indicates that the row of independent elements that, at least in a number of Rhipidistids, usually follow in front of the angular («infradentals», of TRAQUIR's descriptions) is divided in Coelacanthids among the splenial and supraangulo-angular. It is, however, impossible to establish more closely which of these in this case forms part of the one or the other bone mentioned. On account of its considerable extension dorsally it is probable, as I have already pointed out, that

the supraangulo-angular comprises, besides possible infradental components, both the homologues of the angular and the supraangular of the *Rhipidistia*.

The homologues of the cheek-bones have already been dealt with in connection with the description of *W. sinuosa*.

The axial and fin skeleton.

The neural and haemal arches with their spines are, as usual, only ossified perichondrally. Otherwise the spines are narrow and fairly long. Only in the caudal region at the transition between the proximal and distal segments are they somewhat thickened in the same way as in *Wimania*? sp. described above.

The caudal fin has apparently been large (Pl. 16, fig. 3), but apart from this nothing is known in detail about its shape or whether a supplementary fin had been developed. The number of its lepidotrichia seems to have been about twenty both dorsally and ventrally and all were long, narrow, and not expanded distally. On their lateral surface the lepidotrichia are furnished with a distinct longitudinal furrow, and both anterior and posterior to this furrow there are to be found small tubercles. At least on one lobe of the fin — it cannot be decided whether it is the dorsal or ventral one — the ten to twelve anterior lepidotrichia are undivided in their proximal parts for a long distance, while the posterior eight to ten show a few long joints at the corresponding parts.

Some of the proximal ends of the lepidotrichia of the anterior dorsal fin are preserved in connection with a supporting bone-plate, which seems to have had about the same shape as in *Coelacanthus granulatus* (cf. WILLEMOES-SUHM, 1869, Pl. 11, fig. 1).

The shoulder girdle is badly preserved. It is true that remains of the cleithral and the clavicle can be distinguished, but little can be said as to their shape and their relations in general.

The pectoral fin consisted of several fine, long lepidotrichia, which were jointed and branched dichotomically only in their distal parts. The joints seem in most cases to be fairly short.

Squamation.

In *A. robusta* the scales are comparatively large and are oval in shape with a rounded posterior margin. The exposed surface certainly varies fairly considerably in size in scales from different regions, but all the same it may be considered, on the whole, to be rather small.

The sculpture (Pl. 16, figs. 3, 5) consists of a number of fairly coarse striae, running horizontally; some of these are long and even stretch right across the exposed surface, others, again, are short, not infrequently almost tubercle-shaped. Sometimes some of the middle striae are thicker than the others situated dorsally and ventrally of them, and very often all or a number of these middle striae, too, are coarser and higher posteriorly than anteriorly. As far as one can see, the sculpture of the scales also varies somewhat according to their position. Thus it seems to be coarse on the middle and upper part of the sides of the body, while ventrally it is finer and weaker.

* * *

Geological occurrence and localities. — *A. robusta* is only known from the fish horizon. It is undoubtedly more common in Sassen Valley than any of the other Coelacanthids, while, on the other hand, it is found more sparsely in Dickson Land and on the west side of Ekman Bay. The finds are divided among the following places: Mt Congress, the cliffs of the shore south of Sassen Bay, Mt Marmier, Mt Hamilton, Mt Trident, Mt Milne Edwards and Mt Andersson.

Axelia elegans n. sp.

(Pl. 16, figs. 6, 7; Pl. 17, figs. 1, 2.)

Besides *A. robusta*, described above, there are remains of another *Axelia* species, for which I have proposed the species name *elegans*. The species in question is at present represented only by three incontestable specimens (*P. 220, 221, 223*), which are all very incompletely preserved. Thus of the bones of the head only a few are present and of the rest of the body only remains of some fins and a number of scales.

With regard to size at least the specimens so far discovered are smaller than *A. robusta*. Thus the length of the head in the specimen *P. 223* cannot be estimated as more than about 10 cm.

Text fig. 48.

Axelia elegans n. sp.

Remains of the cranial roof and the visceral skeleton. Sculpture not drawn. Sensory canals with dotted lines and shading. From *P. 223*, 1/2.

Fr. dph., fronto-dermosphenotic; *Op.*, opercular; *Pa. it.*, parieto-intertemporal; *Pt.*, pterygoid; *Qu.*, quadrate; *So.*, supraorbital; *Stemp. ext.*, supratemporo-extrascapular.

The membrane bones of the neurocranium and the visceral skeleton.

The membrane bones of the cranial roof show in most respects close agreement with those of *A. robusta* (text fig. 48; Pl. 17, figs. 1, 2). The supratemporo-extrascapular (*Stemp. ext.*) differs, however, inasmuch as it also includes the lateral end of the supratemporal commissure of the cranial section of the lateral line, while in *A. robusta*, as we have seen, the whole of this commissure is situated medially of the supratemporo-extrascapular. The sculpture on all the superficial bones is relatively coarser than in *A. robusta* and consists of rather sparse, edged, sometimes somewhat lengthened tubercles. Unlike what is the case in *A. robusta*, the tubercles have, however, no special orientation but are generally scattered in an irregular manner.

With regard to the parasphenoid (*Psph.* Pl. 17, fig. 1), pterygoid (*Pt.* text fig. 48; Pl. 17, fig. 1) and quadrate (*Qu.* text fig. 48; Pl. 17, fig. 1) there is nothing to add beyond what has been said about *A. robusta*. The opercular (*Op.* text fig. 48; Pl. 16, fig. 6; Pl. 17, fig. 1), on the other hand, is higher than in this species and has also a considerably stronger concave part on the dorsal portion of the anterior margin. Its sculpture (Pl. 16, fig. 6) consists of somewhat coarse striation. The striae are fairly short and run, chiefly horizontally, on the greater part of the dorsal portion of the bone from the anterior to the posterior margin. Towards the ventral end of the bone on the other hand, they are arranged, unlike in *A. robusta*, in a characteristic way in curved lines, the convexities of which are turned dorsally. The arrangement of the striae is in other respects more irregular than in *A. robusta*.

Skeleton of the fins.

The caudal fin has probably been similar to that of the preceding species. The anterior dorsal fin (*D₁*, Pl. 17, fig. 1) has a short base and was very high in relation to the size of the fish. Several of its lepidotrichia are in their present condition not less than 9 cm in length and seem when complete to have been considerably longer (text fig. 49). Their exact number cannot be established with certainty, but in the present condition of the fin they amount to nine or ten. They are all slender and not expanded distally. At least in the distal parts their lateral sides had a weak tuberculation. The proximal parts are unjointed for a fairly long distance. The joints are short and almost square. The pectoral fins were probably rather weakly developed. Their lepidotrichia are all fine, and are jointed in about the distal two thirds (*Pc*, Pl. 17, fig. 2).

Squamation.

The sculpture of the scales bears a fairly considerable resemblance to that of *A. robusta* (Pl. 16, fig. 7) but there are fewer striae, their number generally not exceeding eight and fairly often being only four or five. As a rule the striae are not so long that they reach across the free surface, but, on the other hand, short and more tubercle-like striae are also infrequent. Another difference from *A. robusta* is that the striae often show a slight divergence posteriorly.

* *

Remarks. — *A. elegans* is undoubtedly closely related to *A. robusta* but is also clearly distinguished from this species by the sculpture on the cranial roof and the opercular. Other minor differences can also be observed between the two species, e. g. in the extent and shape of certain elements in the cranial roof and the opercular apparatus.

Geological occurrence and locality. — *A. elegans* occurs sparsely in the fish horizon. All the specimens come from Mt Congress.

Text fig. 49.

Axelia elegans n. sp.
Lepidotrich from the
anterior dorsal fin. From

P. 22.5, 1/16.

Note the height in
relation to the head in
text fig. 48.

Genus *Mylicanthus* n. g.

The genus *Mylicanthus* is very incompletely known with regard to the skeleton of both the head and the body. Its most important peculiarities, so far known, are as follows: Rather large fishes. The skeleton of the head robustly built. Sculpture of the head consisting of somewhat elongated strong tubercles or short striae, arranged longitudinally and fairly parallel to each other. The posterior pterygoid limb is high and rather narrow; its upper margin has a deep angular sinus; the anterior limb, on the other hand, is comparatively low. The metapterygoid and the quadrate are high; the latter also particularly strong. The angular is high and triangular. The opercular large with a spiny or lobed postero-ventral margin. The dentition is strong and adapted for crushing. The sensory canals are much developed, with large pores. The scales are oval, with a sculpture consisting of short striae, diverging somewhat posteriorly.

With regard to dentition and the strong development of the sensory canals this genus resembles *Axelia*, as has already been pointed out above. The pterygoid also has many features in common in the two genera, though at the same time it shows rather great differences. The chief characteristics of *Myllacanthus*, as far as we know, are the lobed or spiny postero-ventral margin of the opercular and the high shape of the metapterygoid, quadrate and posterior pterygoid limb. With regard to the scale sculpture *Myllacanthus* resembles *Libys* to some extent.

Myllacanthus lobatus n. sp.

(Pl. 18, figs. 1, 4).

There are only three incomplete specimens of this species (*P.* 216—218), with remains of the visceral skeleton and a number of scales. To judge from the specimens present, *M. lobatus* seems, with regard to size, to correspond approximately to *W. sinuosa* or it has perhaps been somewhat larger than this species.

Text fig. 50.

Myllacanthus lobatus n. sp.

The bones of the palato-quadrate, with the exception of the autopalatine, in lateral view.

From *P.* 217 and *P.* 218. $\frac{1}{2}$.

Mptg, metapterygoid; *Pt*, pterygoid; *Qu*, quadrate.

Visceral skeleton.

The pterygoid (*Pt*, text fig. 50; Pl. 18, fig. 4) most closely resembles that of *Axelia* in its general configuration, but the posterior limb is strikingly narrower and higher, the anterior one, on the contrary, considerably lower or — to express it in another way — the anterior limb does not reach so far upwards along the anterior border of the posterior limb as in the *Axelia* species. The upper margin of the posterior limb is characterized by having a very deep sinus, which at its lower part even comes ventrally of the antero-ventral corner of the metapterygoid bone.

The quadrate (*Qu*, text fig. 50; Pl. 18, fig. 4) is exceedingly powerful and thick and also high. Its dorsal part covers in the usual way the postero-ventral corner of the pterygoid from the lateral side. It reaches considerably farther ventrally than was the case, for instance, in *Axelia*. In addition the corpus and the anterior lamella on it are distinguished in the usual way, as has been described in *A. robusta*. The corpus does not consist of compact bone in its dorsal half, but it has undoubtedly been cartilaginous in its interior. Farthest dorsally only a fairly thin perichondral layer of bone seems to have been present.

The metapterygoid (*Mptg*, text fig. 50) is rather higher than broad. In other respects it has the usual shape, with a concave dorsal and almost straight, anterior margin. The caudal and ventral margins are strongly convex and pass into each other without any very distinct boundary. The anterior upper corner is less drawn out than in both *A. robusta* and *W. sinuosa*.

Of the substitution bones of the Meckelian cartilage only one, the autangular (*Aang*, Pl. 18, fig. 4) is present, though poorly preserved. It forms the most posterior corner of the lower jaw and is undoubtedly identical with the bone denoted by WOODWARD

1907 (1907a, p. 136, Pl. VIII, figs. 2, 8) with the letter *m* in *Macropoma* and *Mawsonia* and 1909 with the letter *x* in *Macropoma* (p. 176; Pl. XXXV, fig. 9, Pl. XXXVII, fig. 5).

The supraangulo-angular (*Sang. ang.*, Pl. 18, fig. 4) is, as in *A. robusta*, triangular in shape and its height is fairly great. The base is straight, the antero-dorsal margin perhaps concave and the postero-dorsal one convex. Unlike that of *A. robusta*, however, the latter has a broad and rather large process. Both the dental (*De*, Pl. 18, fig. 4) and splenial (*Spl.*, Pl. 18, fig. 4) are poorly preserved.

The sculpture of the mandibula is restricted to the supraangulo-angular and on this, as in *A. robusta*, to the part dorsally of the pores of the mandibular sensory canal. It consists of strong and somewhat elongated tubercles, which are situated fairly close to one another and are as a rule arranged parallel to the longitudinal axis of the mandibula.

As in other Spitzbergen Coelacanthids the opercular is of considerable size. It is only preserved, however, in its ventral half but even this fully shows that it had a very characteristic shape, distinctly different from that of all other known species (*Op.*, Pl. 18, fig. 4). At least the ventral half of the anterior margin is weakly convex or almost straight. The postero-ventral margin has a broad, fairly deep acute-angled sinus in its ventral part; on account of it the ventral part of the bone appears as a broad and rounded but fairly well defined process. Dorsally of this larger sinus there follow on the postero-ventral margin a number of smaller sinus, which decrease, however, rather rapidly in depth and size upwards. By means of these sinus the postero-ventral margin is divided into lobes, which in their turn are split up by other smaller sinus into lobes of the second order. Along the anterior margin of the bone there extends a rather broad zone without sculpture. The other part of the lateral surface has a sculpture which, as on the supraangulo-angular, consists of somewhat elongated strong tubercles with a horizontal arrangement.

Nothing is preserved of the branchial arches. On the other hand remains of strong and thick plates, which have probably covered the copula, are found. A part, possibly of a jugular plate (*G?* Pl. 18, fig. 4), has the tubercular sculpture characteristic of the species, but the tubercles are arranged so that they show a certain radiation from a point, which was probably the centre of ossification.

Dentition.

The dentition is adapted for crushing and agrees very closely on the whole with that of *A. robusta*. (Pl. 18, fig. 4 shows a number of scattered remains of the supracopular plates and smaller plates from the branchial arches.)

Sensory canals of the head.

The sensory canals have apparently been strongly developed, but only the mandibular canal (Pl. 18, fig. 4), is partly preserved. This has pierced the supraangulo-angular and the splenial in the usual way and, as in *A. robusta*, it was developed with large oval pores (*p.*, Pl. 18, fig. 4), four or five of which were situated on the supraangulo-angular and at least two on the splenial.

Squamation.

As far as one can judge from the few scales present, these were oval and rather low (Pl. 18, fig. 1). Both their anterior and posterior margins are well rounded, the upper and lower ones, on the other hand, are fairly straight or at any rate only weakly convex. The exposed part of the lateral surface is somewhat large. The sculpture consists of a rather large number of sharp, short striae, which are situated close together on the anterior middle part of the exposed surface and run in an antero-caudal direction, fairly parallel to each other. In a zone along the dorsal, posterior and ventral margins they are sparse and are so arranged that they diverge posteriorly in about the same way as in *Libys*.

* * *

Geological occurrence and localities. — *M. lobatus* occurs rather infrequently at the fish horizon. So far it has only been found at Mt Andersson and Mt Wallenberg.

***Mylacanthus spinosus*, n. sp.**

(Pl. 19, fig. 3; Pl. 20, fig. 2)

There are two opercula (*P. 687*, *P. 703*) of a second species, called by me *M. spinosus*. A specimen with remains of a jugular plate and some of the bones of the mandibula (*P. 215*) probably belongs to this species as well.

This species has certainly been at least about as large as *M. lobatus*.

The two opercula are large. The best preserved one (*P. 703*) is about 9 cm high and almost 6 cm broad (Pl. 20, fig. 2). In general shape it resembles that of *A. robusta* very closely. Thus one can distinguish an anterior, a postero-ventral and a dorsal margin. The last-mentioned of these is, however, not preserved. The anterior margin is slightly concave in its upper part, slightly convex at the lower part; the postero-ventral margin, on the other hand, is quite the reverse, so that its upper part is convex and its lower part chiefly concave. It is also noteworthy about this margin that all the large sinus of the sort described in *M. lobatus* are quite absent. Instead, however, it is furnished with a large number of fine, pointed spines in the way shown in Pl. 20, fig. 2. The antero-dorsal corner seems to have been fairly distinctly developed and almost right-angled; the ventral one is rounded, but has a more prominent angle than in the *Axelia* species and *M. lobatus*. The sculpture resembles in all essentials that of the latter species, but has perhaps been somewhat finer.

The specimen *P. 215* (Pl. 19, fig. 3), on which parts of the supraangulo-angular (*Sang. ang.*), dental (*De*), splenial (*Spl*) and jugular plates (*G*) are to be seen, differs from *M. lobatus* chiefly by having a weaker and finer sculpture on the supraangulo-angular, and a considerably stronger development of the pores of the mandibular sensory canal.

* * *

Remarks. — It is not yet possible to decide with certainty whether the specimen *P. 215* belong to *M. spinosus*. Accordingly this species can be considered as distinguished only by the spiny postero-ventral margin of the opercular, a character which is sufficient, however, to keep it apart from *M. lobatus*, to which it is rather closely related otherwise with regard to sculpture and probably also in other respects.

Geological occurrence and localities. — *M. spinosus* is only known from the fish horizon, where it occurs sparsely. Of the three specimens here referred to *P. 215* is from Mt Andersson and the other two from Mt Congress.

Genus *Scleracanthus* n. g.

The genus for which I have chosen the name *Scleracanthus* is, like the preceding one, still very incompletely known. Its most typical characters may be summarized as follows: Large fishes. The neurocranium probably robustly built on the whole. Its sculpture is strong, consisting of long, sharp striae. The pterygoid is thick and robust, probably with a high posterior and a low anterior limb; the anterior limb with a deep sinus on the dorsal margin. The dentition is strong, adapted for crushing; the tooth-bearing parts of the medial surface of the anterior pterygoid limb are raised in relation to the toothless parts. The sensory canals are strongly developed and have large pores. The anterior dorsal fin is large, consisting of about 15 broad lepidotrichia, unjointed for a long way proximally; each of the lepidotrichia has two rows of sharp tubercles on the lateral surfaces. The scales are rather triangular in shape with a high, pretty straight or weakly convex anterior and a pointed posterior margin. The sculpture of the scales consists of strong, fairly long longitudinal striae, somewhat parallel or sometimes slightly converging posteriorly.

As far as one can judge from the facts so far known, *Scleracanthus* seems in several respects to be related to *Myliacanthus* in the same way as the latter in its turn appeared to be closely allied to *Axelia*. But it is well distinguished from *Myliacanthus* by having a stronger pterygoid, stronger dentition, a very different shape of the scales and also a different sculpture. Of course it also offers certain clear resemblances to *Axelia*, but the differences from this genus are, however, rather marked. In this case the development of the fins is especially different.

In addition it may be pointed out that the sculpture of the scales in *Scleracanthus* partly resembles that of certain Carboniferous *Coelacanthus* species (cf. HUXLEY, 1866, Pl. II, figs. 3, 4; Pl. III, figs. 1 a, 3 a), as is also the case with the shape of the scales, though this has also certain similarities with the shape described above for *Wimania? multistriata*.

Scleracanthus asper n. sp.

(Pl. 17, fig. 3; Pl. 18, fig. 2; Pl. 19, figs. 1, 2; Pl. 20, fig. 1.)

S. asper is represented by a few incomplete specimens (*P. 239—242*, *P. 709*) with remains of the visceral skeleton, axial skeleton, fin skeleton and squamation.

With regard to size this species certainly immediately followed *W.? multistriata* among the Spitzbergen species. But it is not possible to obtain any reliable measurements which can give us an exact idea of its proportions.

Visceral skeleton.

The pterygoid (*Pr*, Pl. 18, fig. 2), which is incompletely preserved, is very thick and strong, especially at the anterior limb. The posterior limb was apparently high, with a deep sinus in its dorsal margin. This sinus was, however, broader than in *Myliacanthus*

and in this respect rather resembled *Axelia*. The upper part of the anterior margin of the posterior limb is free for a considerable way, about as in *Myllacanthus*, or perhaps still more, and the anterior limb seems thus to have been comparatively low even at the most posterior part.

Like the pterygoid the metapterygoid (*Mptg*, Pl. 18, fig. 2) is also very thick and strong. Only its anterior part, however, is preserved, so that no details can be obtained as to its shape. In relation to the pterygoid it has occupied the same independent position as in Spitzbergen species, i. e. it is connected with this bone only by its anterior border.

The autangular (*Aang*, Pl. 19, fig. 1) is about the same as in *Myllacanthus*, but is more in situ.

A part of the articular (*Art?*, Pl. 19, fig. 1) is also possibly present. The curious shape of this bone in its present state of preservation does not, however, at first sight seem to support this view. In a Carboniferous *Coelacanthus* species in which I have observed the articular in a very good state of preservation its articulating fossa is, however, divided into a lateral and a medial part by a ridge and both parts are relatively deep. As the supposed articular in *S. asper* is only accessible in cross-section its curious shape may easily be explained in connection with my observations on the above-mentioned *Coelacanthus* species. For it is conceivable that the part that is present forms a section just through the articulating fossa and that consequently what appear here to be process-like parts really constitute the lateral boundaries and parts of the medial ridge mentioned.

The supraangulo-angular (*Sang. ang*, Pl. 19, fig. 1) was probably large but it is impossible to establish whether it had a high and triangular shape similar to that of *Axelia* and *Myllacanthus*, or if it was long and low. Its sculpture consists of numerous long and fairly coarse striae, some also sharp. All these striae are situated close together and run horizontally in the longitudinal direction of the bone. As is the case in *Axelia* and *Myllacanthus*, they are limited to the part above the pores of the mandibular sensory canal and here it is more obvious than in these other genera that the part that has been situated ventrally of these pores has partly been directed downwards, i. e. has belonged to the ventral side of the mandible.

A couple of fragments of some larger bone, possibly the opercular, are furnished with exceedingly powerful sculpture of the same type as on the supraangulo-angular (Pl. 20, fig. 1).

The jugular plates (*G*, Pl. 19, fig. 1) are narrowly oval, with the lateral and medial margins weakly convex. Their anterior ends are rounded off; their posterior ones are not preserved. The sculpture consists of longitudinal striae as on the supraangulo-angular, but seems to be somewhat weaker than on this bone.

Dentition.

The dentition is of the same type as in *Axelia* and *Myllacanthus*. The teeth are generally, however, larger and stronger, while at the same time tooth-bearing bones are thicker and more powerful to a corresponding degree. On the pterygoid the teeth are obviously restricted in the main to the anterior limb and the antero-ventral part of

the posterior limb. The tooth-bearing parts of the medial surface of the bone do not lie in the same plane as the toothless ones but are somewhat raised in relation to these. The bone-plates on the copula have strong, spheroid teeth and the tooth-plates of the branchial arches have smaller and blunt ones or partly spheroid ones. — The shape of the teeth on the whole closely resembles that of *Colobodus*.

Sensory canals of the head.

The sensory canals were strongly developed. The mandibular canal (*mc*, Pl. 19, fig. 1) on the supraangulo-angular has four or five large pores (*p*) as in *Axelia* and *Myliacanthus*.

Axial- and fin skeleton.

To judge from a small specimen (*P. 23g*, Pl. 17, fig. 3) the neural arches with their spinal processes are weak and fine, at least in the abdominal region. The same specimen also shows the first dorsal fin fairly well preserved and also remains of the supporting bone of the posterior dorsal fin.

The most anterior dorsal fin (*D₁*, Pl. 17, fig. 3) is exceedingly large and strong compared with what is usually the case in the Coelacanthids previously known. The number of lepidotrichia is about 15, all, except the most anterior one or possibly the two most anterior ones, long, broad and powerful. But they are not preserved in their original length. Their proximal part is unjointed for a long distance. The remaining distal part is closely jointed and the joints are short and broad. On the lateral surface the lepidotrichia had a characteristic sculpture in the form of pointed, fixed small tubercles or spines, which may sometimes be scattered irregularly, sometimes more or less distinctly arranged in two longitudinal rows. Especially towards the distal parts of the lepidotrichia this arrangement of the tubercles in two rows becomes more distinct. At the proximal end all the lepidotrichia are forked so as to articulate against the supporting plate (*Sp₁*). The dorsal end of this plate (Pl. 17, fig. 3) is broad and comparatively thick, the ventral end, on the other hand, is thinner, considerably narrower, and divided by a dorsally ascending sinus into two processes.

The supporting plate for the posterior dorsal fin (*Sp₂*, Pl. 17, fig. 3) resembles most closely in shape that of *Undina* and *Macropoma*, i. e. its distal part is fairly small, while its proximal part consists of two long, narrow processes, the anterior one of which is directed fairly horizontally, the posterior one antero-ventrally.

A number of detached lepidotrichia or, more correctly, fragments of these, show the same sort of sculpture on the lateral surfaces as is seen on the anterior dorsal fin. Others, on the other hand, have no such sculpture at all and, as far as one can understand, have belonged to some of the paired fins or the posterior dorsal fin.

The clavicularae had their ventral limb developed as a rather broad horizontally situated plate (*Cl*, Pl. 19, fig. 1) as in *Wimania sinuosa*.

Squamation.

The scales (Pl. 19, fig. 2) have a very characteristic shape. For the most part their height and breadth is fairly similar, less often the breadth is greater. The greatest

height is situated only slightly caudally of the high and weakly convex anterior margin. From this the upper and lower margins converge fairly strongly backwards and meet in a fairly prominent, but still somewhat rounded angle. The shape of the scales can therefore be conveniently compared to an isosceles triangle, with its angles rounded off and its base directed forward. On most of the scales there is strong sculpture consisting of sharp striae, mostly fairly long and situated close together; the striae may sometimes run horizontally and fairly parallel to each other, sometimes, on the other hand, they converge backwards. They are never quite straight, however, but are more less undulating, nor are they situated in a line one after the other, but alternate in a fairly irregular way. The middle ones are not infrequently somewhat stronger than those situated dorsally and ventrally of them, being about as strong as in *Axelia*. The exposed part of the lateral surface of the scales is rather considerable compared with the size of the scales.

Text fig. 51.

Mylacanthus or *Scleracanthus*? sp.

The anterior part of the cranial roof.

From P. 198, 11.

Fr. dsph. fronto-dermosphenotic; *Jr.* interrostral; *Pa. it.* parieto-intertemporal; *Ptr1*, anterior postrostral plate; *Ptr2*, posterior postrostral plate; *R.* rostrals.

* * *

Geological occurrence and localities. — *Scleracanthus asper* occurs in the fish horizon, where it is rather rare. It has been found at Mt Congress, Mt Milne Edwards and Mt Andersson.

Mylacanthus? or *Scleracanthus*? sp.

(Pl. 18, fig. 3).

Under this heading I place provisionally a part of a cranial roof (P. 198) that originates from a rather large Coelacanthid. This part comprises the fronto-dermosphenotic and a number of the dermal plates on the dorsal side of the ethmoidal region.

As far as can be judged from the specimen present, the head has been strikingly broad and short, at least in its orbitotemporal and ethmoidal regions (text fig. 51).

The fronto-dermosphenotics (*Fr. dsph*, text fig. 51; Pl. 18, fig. 3) were short and broad. The postrostrals are divided

into two independent bone-plates, a smaller anterior one (*Ptr1*, text fig. 51; Pl. 18, fig. 3), triangular in shape, and a considerably larger posterior one (*Ptr2*, text fig. 51; Pl. 18, fig. 3), pentagonal, which is attached to the posterior plate of the opposite side by a short median suture. The interrostral (*Ir*) is, as far as can be seen, paired and is almost quite wedged in by the anterior and posterior postrostral plate on each side. The two interrostrals meet in the median line in a straight suture and are attached anteriorly for a short distance to the rostrals (*R*, text fig. 51). The latter are four-sided, arranged bilaterally symmetrically, and were probably represented by four plates on each side of the median line. Of these the most lateral one, which has been situated antero-laterally of the nasalo-antorbital, is the next largest one. The largest one is situated nearest to the median line. The latter one is attached posteriorly partly to the interrostral, partly to the anterior postrostral plate; the two rostral plates situated between the lateral and

median one on each side are also joined posteriorly to the most anterior postrostral plate. The centres of ossification are clearly discernible in all the bone-plates now described with the exception of the interrostrals.

Nothing is preserved of the sculpture of the bones or of the sensory canals.

* * *

Remarks. — At present it is impossible to decide with certainty whether this specimen belongs to any of the genera that have been described above or whether it represents a new one, but as, in spite of considerable deviations from the *Axelia* type, it still seems to be most closely connected with this, it is most probable that it will turn out to belong to some *Myliacanthus* or *Scleracanthus* species.

Geological occurrence and locality. — Fish horizon, Mt Trident.

Some remarks on previously described Coelacanthids.

With the help of the experience gained from the material now described from the Spitzbergen Triassic it may be of use also to discuss briefly some questions of detail with regard to the previously described Coelacanthids. This seems to be all the more justified because I have had an opportunity to study the more important type specimens of Coelacanthids preserved in European museums. At the same time as I briefly mention in this connection some new observations I must, however, show to a considerable extent the mistakes in certain older views, and the following short exposition accordingly not only forms an addition to previously known facts but also partly takes the form of a criticism.

The primordial neurocranium and its ossifications. — HEINEKE in 1907 (p. 8) described a basioccipital in *Undina* and the correctness of his interpretation of this bone seems to me obvious, partly from his own type specimen and partly from another specimen belonging to the British Museum (*B. M. P. 9130*). Other occipital bones are not developed, as far as I could find out. It is true that in 1888 REIS (pp. 24–25) also described a supraoccipital and a paired exoccipital (lateral occipital) in *Undina*, but an investigation of the specimen on which he based his description shows, however, quite evidently that his supraoccipital is really identical with the basioccipital and his exoccipital with the posterior parts of the very much flattened prootico-opisthotic, seen from beneath. The detached fragments of bones that lie between the basioccipital and the prootico-opisthotics and which REIS takes to be vertebral arches, cannot be exactly defined (cf. REIS, 1888, p. 25, Pl. I, fig. 22). With regard to the bone or the part of that bone of *Macropoma* that HUXLEY interpreted in 1866 (p. 36) as a possible «vertebra», which, in his opinion, corresponded to one of the «vertebrae» that are coalesced with the occipital region in the recent ganoids, it is impossible to pronounce any quite definite opinion. But it does not seem improbable that this bone, as HEINEKE (1907, p. 8) has also pointed out, might be the basioccipital, which in this case has come loose from its original position.

The prootico-opisthotic and the basisphenoid seem apparently, at least in the majority of Coelacanthids, to have been developed as in the Spitzbergen forms described above. Besides in these, the bones in question are partly or entirely preserved in *Macropoma*

(HUXLEY, 1866, pp. 35—36; REIS, 1888, pp. 62—63; WOODWARD, 1909, p. 172), *Coccoderma* (HEINEKE, 1907, pp. 12—13), *Undina* (REIS, 1888, pp. 24—26; 1892, pp. 22—23), *Libys* (REIS, 1888, Pl. II, fig. 1), *Coelacanthus* (a couple of specimens from the Carboniferous) and *Mawsonia* (WOODWARD, 1907 a, p. 134). In *Mawsonia*, however, there are only remains of the basisphenoid (*B. M. P. 10355*, *M. gigas*; one of the type specimens of WOODWARD's description 1907), which has strong basiptyergoid processes as usual and, with regard to the development of the anterior lamellae, closely resembles the corresponding bone in *Axelia*. WOODWARD'S (1907 a, p. 134) view that the parts of bone that are present belong to the otical region is thus only correct to a very slight extent, but it ought in justice

to be pointed out at the same time that the explanation of these strongly flattened and crushed remains must have been very difficult without a deep knowledge of material such as that obtained from Spitzbergen.

The interorbital wall, as WOODWARD (1891 b, p. 395; 1909, p. 172) and WELLBURN (1902, p. 476) have pointed out, was in forms so far known unossified. The orbitosphenoid of the descriptions of *Undina* by REIS (1888, Pl. I, fig. 22) and HEINEKE (1907, fig. 1, p. 8) is in fact only an upward-bending lateral part of the parasphenoid and this is also true in certain cases of the bone in *Macropoma* described by HUXLEY, 1866 as the prefrontal (cf. HUXLEY, 1866, Pl. VIII, fig. 1, *Pr. f*).

Text fig. 52.

Undinapencillata MÜNSTER.
 Sketched from the type specimen
 of REIS, Pl. I, fig. 9, 1888. *
Mptg., metapterygoid; *Pt.*, ptery-
 goid; *Qu.*, quadrata.

Text fig. 53.

Coccoderma suevicum
 QUENSTEDT.

Sketched from the type specimen
 of HEINEKE's text fig. 2 and
 Pl. VI, fig. 11, 1907.
Mptg., metapterygoid; *Pt.*, ptery-
 goid; *Qu.*, quadrata.

In other cases, on the contrary, I have found that HUXLEY's prefrontal in *Macropoma* corresponds to my preëthmoid, and, as far as one can judge from WOODWARD's description of *Macropoma* 1909, the latter author (1909, p. 174) also gives the preëthmoid of my nomenclature as the prefrontal. The material described by REIS (1888) from the white Jurassic is very incomplete as regards the ethmoidal region, so that his interpretations of the elements there is unreliable and in many respects undoubtedly incorrect. I myself have really little to add with regard to this material, as the state of preservation scarcely enables one to come to any certain conclusions as to how the different fragments of bone belonged together. What REIS (p. 48; Pl. II, fig. 1) has called the prefrontal is, however, contrary to the bone so called by HUXLEY and WOODWARD, the remains of a membrane bone belonging to the sensory canal category and may possibly correspond to my nasalo-antorbital or perhaps, more correctly, to the nasal component of this bone.¹⁾

The membrane bones of the neurocranium. — In all the nearer known Coelacanthids the membrane bones of the cranial roof seem, on the whole, to resemble those of the Spitzbergen forms, and in this connection I have nothing to add to what has been put forward above in the descriptions of these.

¹⁾ In this connection it may be pointed out that the view of ALLIS, 1919 (1919 a, pp. 379—382) with regard to the primordial neurocranium of *Macropoma* is erroneous, which, however, is due to the fact that he based his exposition on the old interpretations of the cartilage bones.

In the Jurassic and Cretaceous forms the parasphenoid is in most cases rather narrow between the orbits, while — at least in the majority of Palaeozoic forms and in the Triassic forms from Spitzbergen — it is distinguished on the whole by a considerable breadth.

The question of the vomeres ought at present to be considered an open one. The material so far available scarcely permits of any certain conclusions. The plates in *Undina* called vomeres by HEINEKE (1907) may very well be remains of detached tooth-bearing plates from the copula or the branchial arches. Such plates, as we have seen, are often found scattered about in great numbers everywhere among the head bones of Coelacanthids. The unpaired tooth-bearing bone found in the mouth of *Macropoma* and *Coelacanthus* (HUXLEY, 1866, p. 36; WELLBURN 1902, p. 477; WOODWARD 1909, p. 174, Pl. XXXVII, figs. 3, 3a) may, as HUXLEY pointed out, be interpreted either as an unpaired vomer or a premaxillary, with about the same degree of correctness in either case. A third possibility with regard to this unpaired bone also seems to me worthy of attention, namely that it might represent both vomeres and premaxillae fused into one bone. In any case the view put forward by GOODRICH 1909 in his text figure 261B is untenable, as he figures both vomeres and premaxillae in *Macropoma* as paired, independent elements. On the other hand nothing certain can be said about the parts of the skeleton that REIS (1888, pp. 6, 7, 13, 43, 44, 56, 59) has described as vomeres and premaxillae in certain Jurassic forms.

The membrane bones of the cheek. — In the majority of Coelacanthids the membrane bones of the cheek are incompletely preserved or quite unknown. *Coelacanthus*, *Undina*, *Libys* and *Macropoma* are, as we know, the forms that, from this point of view, are the best preserved. DEAN has also given a restoration of *Diphurus*, according to which the plates in question seem to bear the closest resemblance to those of the Jurassic forms (DEAN, 1895, text fig. 156). In the species *Coelacanthus welleri* from the Carboniferous, EASTMAN (1908, pp. 251—252) has described three postorbital cheek plates situated in a vertical row, the ventral one of which he considers to be the Huxleyan «postmaxillary» (coronoid, according to our modern opinion). As far as one can judge from his exposition there seems, however, not to be the slightest doubt that this plate is identical with my preoperculo-quadrato-jugal, and that in this respect *Coelacanthus welleri* closely agrees with the Carboniferous Coelacanthid type.

A number of peculiarities with regard to the shape and degree of development of the cheek plates in different forms have already been pointed out in connection with the descriptions of the Spitzbergen material above.

Visceral skeleton. — Both in the Carboniferous and Permian Coelacanthids the pterygoid is, as far as we know, developed in a fairly uniform way. It seems to be more variable in the Triassic, Jurassic and Cretaceous forms.

The metapterygoid, quadrate and autopalatine are not infrequently preserved and fairly often easy to observe. The metapterygoid has, for instance, been found by me

Text fig. 54.

Mawsonia gigas. A. S. WOODWARD.
 Sketched from Woodward's type specimen
 1907. About $\frac{1}{4}$. B. M. P. 10355.
 Mptg, metapterygoid; Pt, pterygoid.

more or less distinctly in the following species: *Coelacanthus elegans*, NEWBERRY, (B. M. P. 7912), *C. granulatus* AGASSIZ (cast at Greifswald from an original at Marburg), *Undina acutidens* REIS (original specimen of HEINEKE's text fig. I och Pl. VI, fig. I, 1907), *Undina penicillata* MÜNSTER (orig. spec. of REIS, Pl. I, fig. 9, in 1888), *Libys superbus* ZATTEL, *Coccoderma suevicum* (probably orig. spec. of QUENSTEDT, Pl. 100, fig. 14 in «Der Jura» 1852; and orig. spec. of HEINEKE's Pl. VI, fig. 11 in 1907), *Macropoma mantelli* (a number of specimens in the British Museum, as P. 36, P. 4219, P. 4247 and 4548), *M. speciosum* REUSS (orig. spec. of REIS, Pl. IV, fig. 1, 1888) and *Mawsonia gigas* (B. M. P. 10355, orig. spec. of WOODWARD, Pl. VII, fig. 1; 1907a).

It is interesting to find, as shown by text figs. 52, 53, 54, that at least in a number of the geologically younger Coelacanthids the metapterygoid was comparatively low and more also closely connected to the pterygoid than is the case in the Palaeozoic and older Mesozoic forms. Even the ventral margin of this bone, which, contrary to what was the case in the Spitzbergen forms, passes into the anterior margin without any real boundary, seems in these younger forms to have been closely connected with the pterygoid, and in certain forms, as, for instance, *Mawsonia* (text fig. 54) this connection may be very intimate.

Text fig. 55. *Coelacanthus* sp.

Sketch of a posterior part of the mandibula from the medial side. Original in Museum f. Naturkunde, Berlin. About $\frac{1}{16}$.

Art, articular; Icor. pra, intercoronoideo-prearticular; Sang. ang, supraangulo-angular.

Text fig. 56.

Coccoderma suevicum QUENSTEDT.

Sketch of the lower jaw from the medial side. Original in Naturalienkabinett, Stuttgart. About $\frac{1}{16}$.

Art, articular; Icor. pra, intercoronoideo-prearticular; Sang. ang, supraangulo-angular.

There seems to be no doubt, as REIS's figures also show, that in certain forms a dermopalatine has been developed. I have observed it especially distinctly in *Coccoderma nudum* (orig. spec. of REIS, 1888, Pl. III, fig. 16) and in *Libys superbus* it is also found, though closely connected with the autopalatine (REIS, 1888, Pl. II, fig. 1).

With regard to the maxillary I refer to what has been said about it above in the description of *W. sinuosa* pp. 72-72.

In the mandibula of *Mawsonia* the articular has been shown by WOODWARD as an independent bone. In *Macropoma*, on the other hand, the same bone is said by him (1909, p. 176) to be fused with the supraangulo-angular; in spite of a careful examination of his material I can neither confirm nor deny this. Both in *Coelacanthus* (one specimen in the Berlin Museum labelled *Coelacanthus* sp. from Linton, Ohio) and in *Coccoderma* I have found it as a clearly independent ossification (text figs. 55, 56).

What REIS called the hyomandibular in *Libys polypterus* (REIS, 1888, p. 41; Pl. III, fig. 1) really consists of remains belonging to the neurocranium, either the prootico-

opisthotic or the basisphenoid. — In 1888 (pp. 46, 55—57) REIS took the epihyal to be the metapterygoid.

In all the Coelacanthids in question the urohyal seems to have resembled that of *Wimania* and *Sassenia*. In the majority of Jurassic and Cretaceous forms, however, it is considerably narrower than in the two Spitzbergen genera just mentioned and in the Palaeozoic *Coelacanthus* species. I have been unable to come to any conclusion as to what is really represented by the cruriform bone that HUXLEY (1866, p. 19, Pl. IV, fig. 1) has described and figured in a specimen¹ of *Coelacanthus lepturus* AGASSIZ. On the other hand the ossified mass which DAVIS (1884, p. 430; Pl. 47, fig. 1) compares in a specimen (*B. M. P.* 7734) of *C. tingleyensis* DAVIS with the above-mentioned cruriform of *C. lepturus* consists exclusively of ossifications belonging to the primordial neurocranium, which have been strongly compressed. Immediately to the left of the anterior end on the urohyal I can thus identify the lower surface of the prootico-opisthotic, and farther forward between the two jugular plates there is a part representing the compressed basisphenoid.

The sensory canals of the head. — The sensory canals of the head are, as we know, developed to a different degree in different Coelacanthid forms and the pores too may show considerable variations both in size and number. In *Coelacanthus Undina* and *Macropoma* the pores often seem to be rather small and numerous. Thus, for instance, on the supraangulo-angulare of *Coelacanthus elegans* NEWBERRY I have found no less than twelve and on the same bone of *Undina gulo* the number is probably still greater.

In *Macropoma speciosum* REIS has taken the sensory canal in the supratemporo-extrascapular and the parieto-intertemporal as a fossa temporalis (REIS 1888, p. 62, Pl. IV, fig. 2).

* * *

Some remarks on the different genera of the Coelacanthids.

The present state of our knowledge of the Coelacanthids seems to indicate that these fishes show a rather greater variability than we have been inclined to think, and also that their generic characters as a rule are somewhat more strongly marked than was thought to be the case by a number of authors (LÜTKEN, 1868, p. 61; NEWBERRY, 1888, p. 71; REIS, 1900, p. 191). In my opinion it is therefore necessary to maintain the majority of the species described earlier, in spite of the fact that in a number of cases we cannot yet fully define them. On the whole I agree on this question most closely with WOODWARD's view, as put forward in his «Catalogue» of 1891.

Although I do not think it improbable that with more extensive knowledge of the Carboniferous and Permian Coelacanthids it may be necessary to divide them into two genera, as REIS (1888) has suggested, still a present a division of this sort cannot be conveniently carried out, as our knowledge of the differences between them is very incomplete. On the other hand, even under present conditions it seems to be necessary to exclude at least certain of the Triassic species from the genus *Coelacanthus*, as for instance *C. lutzensis* REIS (cf. SCHLOSSER, 1918, p. 87).

¹ I have not had an opportunity to study this specimen.

Of the Jurassic forms *Coccoderma gigas* cannot, as REIS (1900, p. 191) has pointed out, be taken any longer as a *Coccoderma* species. According to the conclusions I have been able to draw, it certainly represents a new genus.

The organization of the Coelacanthids. Summary.

The primordial neurocranium and its ossifications. — Looked at as a whole the primordial neurocranium of the Coelacanthids is high and often relatively narrow. Its basis is straight from the snout and backwards at least as far as the anterior part of the labyrinth region, while its roof, on the other hand, is developed with an angle that is in most cases prominent, as the posterior part is horizontal and the anterior part slopes more or less forward. The angle between the two parts is situated above the posterior part of the orbitotemporal region.

In most cases the ethmoidal region is broad and moderately long and, seen from above, bluntly rounded. In profile, on the other hand, it is either relatively high and blunt anteriorly (*Coelacanthus*, *Axelia*) or else relatively lower and more pointed (*Macropoma*, *Undina*, *Wimania*).

The orbitotemporal region is characterized in most cases by a considerable length and is also always high. It is only in certain forms of the *Axelia* type that it seems to have been more distinctly shortened. It was narrowest (thinnest) at the ventro-medial part, at which farthest posteriorly beneath the fossa hypophyscos it probably had a fenestration immediately above the parasphenoid. While in such forms as *Coelacanthus*, *Sassenia*, *Axelia* its ventral parts seem to have been comparatively wide, in others (e. g. *Undina* and *Macropoma*), on the contrary, these parts must have been considerably narrower.

Posteriorly the orbitotemporal region has passed without any sharp boundary into the labyrinth region. This latter region forms the broadest part of the neurocranium, is well developed in other respects, and seems to have had a fairly normal length. On its dorsal side a paired muscle fossa («fossa temporalis») was apparently developed in the posterior half.

The occipital region is very incompletely known but was most probably short.

It is true that a large number of ossifications appear in the primordial neurocranium, but the main part of these undoubtedly consisted of cartilage in the forms nearer known.

In *Undina* (HEINEKE, 1907) and possibly in *Macropoma* (HUNLEY, 1866; HEINEKE, 1907) too we only know one basioccipital in the occipital region. In these forms no other ossifications seem to exist in this region. At present it is impossible to ascertain whether the other Coelacanthids also showed the same conditions or whether there were also forms that had a quite cartilaginous occipital region. In all the Coelacanthids the chorda dorsalis extended into the occipital region and possibly still farther forward.

The lateral walls of the labyrinth region are formed to a rather considerable extent by a paired prootico-opisthotic, which seems to have surrounded an anterior part of the labyrinth. The main part of the bone is really situated in the anterior, ventral part of the labyrinth region and from this main part, which can conveniently be called the corpus, there issues a strong process dorsally and, as a rule, a long one in

a caudal direction as well. The latter process runs horizontally near the base of the neurocranium and its posterior end joins the lateral side of the basioccipital when this is developed.

As the corpora of the prootico-opisthotics are situated far apart, there is thus at the basis cranii between them an unossified interspace which in its continuation backwards is bounded on the lateral sides by their posterior processes, posteriorly by the basioccipital, when there is one, and anteriorly by the basisphenoid. In this interspace, which was at least partly filled with cartilage, the chorda dorsalis has extended.

Behind the corpus of the prootico-opisthotic of either side the lateral wall of the labyrinth region was cartilaginous, apart from the small part consisting of the posterior process of the bone mentioned. Dorsally of the corpus of this bone on both sides of its dorsal process there have certainly been cartilaginous parts. The whole roof of the region has also consisted of cartilage, except for possible fontanelles.

The anterior and larger part of the orbitotemporel region, the part that forms the real interorbital wall, was unossified throughout and apparently cartilaginous; the posterior part of this region, on the other hand, is occupied to a rather considerable extent by an unpaired ossification, which can be called the basisphenoid. This bone also reaches, however, somewhat backwards into the most anterior part of the labyrinth region, but for practical reasons I prefer to describe it as if it was entirely within the orbitotemporal region. In extent it really corresponds fairly closely to the basisphenoid in Stegocephalians (WATSON, 1912a; 1916; 1919; HUENE, 1913; etc.) and Reptiles. As comparisons with *Dictyonosteus* (STENSIÖ, 1918c) and *Polypterus* (TRAQUAIR, 1871) indicate, one is probably justified in considering it as the postero-ventral part of a large sphenoid, which originally extended forward to the ethmoidal region. While an additional component of this sphenoid, situated postero-dorsally and corresponding about to an alisphenoid is still present in Coelacanthids, although it is fused with a dermal element of the cranial roof, the homologue of the orbitosphenoid component of the sphenoid, on the other hand, is quite reduced.

The corpus of the basisphenoid is situated behind the fossa hypophyseos and ought thus to belong to the chordal part of the cranium. Strong basipterygoid processes, situated high up, against which the metapterygoid of either side articulates, are developed, and besides these there issues from the corpus anteriorly on each side a lamella which bounds the posterior part of the fossa hypophyseos laterally and partly also ventrally, and, in addition, a paired process issues in a ventral direction and is attached to the parasphenoid.

Between the last-mentioned processes from the basisphenoid corpus and the parasphenoid there is found a more or less strongly developed, forward open canal, so situated that it may have had its exit through the supposed fenestration in the interorbital wall. Both on account of this position and because of the strong development of the eye bulbs in all Coelacanthids, this canal ought, it seems, to be interpreted as a myodome.

In the ethmoidal region we only find one paired ossification, which, as far as can be judged, constitutes a preëthmoid (septomaxillary in the same meaning as in *Amia*), while homologues of the exethmoids were not developed. Each preëthmoid bone is situated in the ventral part of the region in question and extends so far medially

that it seems to meet that of the opposite side in the median line or at any rate to come very near this. Otherwise the ethmoidal region was cartilaginous throughout, both anteriorly, posteriorly and dorsally of the præthmoids.

In the posterior part of the orbitotemporal region and the anterior part of the labyrinth region, i. e. above the basisphenoid corpus, the cranial cavity is situated very high above the basis cranii. In front of the basisphenoid corpus it sinks rapidly, forming a deep and long fossa hypophyseos, and even at the back, towards the occipital region, it seems to have sunk down, though more slowly. Thus behind the fossa hypophyseos one has a large dorsum sellae, formed by the basisphenoid corpus. In an anterior direction the cranial cavity has probably, as in *Dictyonosteus*, extended through the whole orbitotemporal region.

It is impossible at present to localize exactly the place of exit of the vagus nerve and this is also the case to a certain extent with the n. glossopharyngeus, although this cannot, however, in any case have had its exit far behind the corpus of the prootico-opisthotic. Finally the relations of the n. acusticus to the cranial wall are also rather uncertain. On the other hand n. facialis seems to have penetrated the cranial wall between the basisphenoid corpus and the dorsal process of the prootico-opisthotic. Of the trigeminal branches probably r. maxillaris, r. mandibularis and with them r. ophthalmicus superficialis have emerged through a foramen above the basisphenoid corpus immediately behind the basiptyergoid process. Either together with these or immediately dorsally of them n. ophthalmicus lateralis has left the cranial cavity and in certain forms, e. g. *Axelia*, the course of this nerve can be clearly traced in a fine horizontal sulcus across the lateral surface of the alisphenoid (the ventro-caudal process from the fronto-dermosphenotic). R. ophthalmicus profundus or a partly corresponding nerve may have issued in the orbit in front of the basiptyergoid process through the upper part of the forward pointing lamella of the basisphenoid. The places of exit for n. trochlearis, n. oculomotorius and n. opticus have, as far as can be understood, been situated in the cartilaginous part of the interorbital wall. Nothing certain is known with regard to n. abducens. It is conceivable that this nerve had its exit together with r. maxillaris and mandibularis trigemini, which may sometimes be the case in a number of recent fishes.

The nasal capsule was situated above the posterior part of the præthmoid and opened outwards with two foramina situated close together, an anterior and a posterior one. The præthmoid has on its lateral side at the base a distinct longitudinal furrow, which continues anteriorly in a somewhat medially and upward directed canal. The furrow and the canal have certainly been related to the anterior branches of the n. buccalis lateralis and the r. maxillaris trigemini, both of which, as is usual in fishes, continued along to the most anterior part of the nose. The præthmoid is penetrated from the ventral side by a dorsally ascending fine canal, probably for a branch of r. palatinus anterior.

The eye-bulbs were large, as already mentioned, and a bony sclerotic ring is always developed.

The membrane bones of the neurocranium. The parasphenoid is large and in the majority of Carboniferous Permian and Triassic forms it is wide, while in a large number of Jurassic forms and at least in *Macropoma* among the Cretaceous ones it is

strikingly narrow at one place between the orbitae. A special characteristic of it is the absence of processus ascendentes and the fact that its extension backwards is exceedingly slight, as its posterior end is situated beneath the most anterior part of the labyrinth region. Sometimes it has on its anterior half upward-bending lateral parts, which have covered the lateral surfaces of the interorbital wall ventrally. Sometimes, on the other hand, as in e. g. *Axelia* and probably also other of the forms related to this, the posterior part of the bone in question is instead powerful and thick under the basisphenoid and has there on each side a similarly thick dorsally directed lamella, which is connected with the ventral processes from the basisphenoid corpus. These lamellae and the dorsal portion of the part of the parasphenoid situated between them may perhaps, to judge from their structure, be developed in cartilage.

Nothing certain is yet known about the vomeres.

A characteristic feature of the dermal cranial roof in Coelacanthids is the fact that fusions have taken place between the homologues of certain bone elements that are independent in more primitive Crossopterygian forms (*Rhipidistia*; WATSON DAY, 1916; GOODRICH, 1919; ALLIS, 1919b). Thus the following bones of the *Rhipidistia* may in Coelacanthids be fused: the supratemporal with a part of the lateral extrascapular plate (tabular), the parietal with the intertemporal, the frontal with the alisphenoid and the dermosphenotic, and the nasal elements with the antorbital. According to the elements fused I have called the compound bones formed in this way in the Coelacanthids by the double names of supratemporo-extrascapular, parieto-intertemporal, fronto-dermosphenotic and nasalo-antorbital.

On each side of the median line the supratemporo-extrascapular forms the postero-lateral, usually strongly projecting corner of the dermal cranial roof. By a generally well developed forward and downward pointing process it is connected with the posterior upper part of the corpus of the prootico-opisthotic of its side. Its posterior part forms the lateral boundary of the paired muscle fossa («fossa temporalis») on the posterior part of the roof of the labyrinth region.

The parieto-intertemporals are generally large, somewhat rectangular bones, meeting in a median suture. They always occupy an almost horizontal position, while the bones in front of them all belong to the part of the cranial roof that slopes forward. The angle of the cranial roof is thus always between them and the fronto-dermosphenotic bones. In a number of forms they are somewhat narrower at their anterior end than at the posterior (*Wimania*, *Axelia*), in others, on the contrary, they seem to be of nearly equal width throughout their length. From their ventral surface they send out in the neighbourhood of the lateral margin a ventrally pointing rather low lamella, which covers a dorsal part of the lateral wall of the labyrinth region from the outside.

Behind the parieto-intertemporals and bounded at the sides by the supratemporo-extrascapulars a transversal row of extrascapular plates has been situated. These plates are only preserved, however, in *Axelia*, where they are six in number and have a rounded scale-like shape. They have been loosely situated in the corium above the muscles that had their insertion into the so called «fossae temporales».

The anterior ends of the fronto-dermosphenotics seem as a rule to reach to the ethmoidal region, while the posterior ends are situated above or just in front of the

basisphenoid. Only *Macropoma* seems, as far as is known, to be different, inasmuch as in this species the fronto-dermosphenotics are possibly subdivided into two parts, an anterior and a posterior one, the former of which is the longer. The fronto-dermosphenotics come into contact with each other medially and posteriorly as already pointed out, they meet the parieto-intertemporals. Anteriorly they have been covered to some extent by bone-plates belonging to the ethmoidal region. Their greatest width is situated towards the posterior end, where the dermosphenotic component is included. In this posterior part there issues from their ventral side in a downward and backward direction a powerful process which, as far as one can see, represents the alisphenoid. The process of each side joins either the anterior lamella of the basisphenoid (*Wimania*), or the upper surface of the proximal part of the basiptyergoid process (*Axelia*). In the latter case it has also been closely joined to the cartilage that followed immediately dorsally of the anterior lamella.

The fronto-dermosphenotics differ rather considerably in their extension in different forms. Thus while in *Wimania*, *Coelacanthus* and possibly *Undina* too they are longer than the parieto-intertemporals, in *Axelia* and closely related forms they are more or less shortened, which is also the case to a certain extent in *Macropoma*, where in addition they are strikingly small.

A row of supraorbitals follows along the lateral margin of each fronto-dermosphenotic in front of the part that represents the dermosphenotic component. As far as is hitherto known this row of supraorbitals seems to be confined to the orbitotemporal region. The number of these as well as their shape seems to be subject to considerable variations. The smallest number observed was four (*Axelia*).

The ethmoidal region is covered with a number of plates, arranged, as in *Wimania*, *Axelia* and other genera, according on a common basis, even though deviations in detail have been considerable between the different genera. It is not yet possible to establish whether *Macropoma* can also be included on the same basis with regard to this. If this is not the case then, however, it seems to be certain that in this fish we are concerned with a secondary condition.

Anteriorly of the fronto-dermosphenotics but covering to some extent the anterior ends of them there follows on the ethmoidal region a paired, fairly large bone-plate, the postrostral (*Axelia*, *Wimania*), which in certain forms is subdivided into a posterior and an anterior part by a transversal suture (*Myrlacanthus*? or *Scleracanthus*? sp.). The two postrostrals meet on a comparatively short stretch in a median suture. Between their anterior ends there is a small paired or unpaired interrostral, and in front of both them and the interrostrals there is a transversal row of several small bone-plates, which have been pierced by the ethmoidal commissure of the infraorbital canal. These plates, called by me rostrals, may have been bounded anteriorly by the premaxillae if these were developed.

The nasal capsule is covered both dorsally and laterally by the nasalo-antorbital, which also forms a septum between the two external nasal apertures (*Axelia*).¹⁾ Posteriorly the dorsal corner of this bone is connected to the most anterior supraorbital plate, while

¹⁾ There is no internal nasal aperture.

otherwise its posterior margin has to a considerable extent formed the anterior boundary for the orbital opening. Medially, where the bone reaches up on the dorsal surface of the ethmoidal region, it joins the postrostral and is attached anteriorly to the lateral rostral plate, which seems as a rule to be larger than other rostral plates.

The membrane bones of the cheek. — With regard to the membrane bones of the cheek in the *Coelacanthids* it is possible to observe, as in the case of the cranial roof, certain fusions of elements that were independent in the *Rhipidistia*. The homologues of the lacrymal and the jugal of the *Rhipidistids* both probably form together the lacrymo-jugal of the *Coelacanthids* and the homologue of the preopercular of the former is probably so divided in the latter that the dorsal part of it has been fused with the squamosal and the ventral part with the quadratojugal. The two last-mentioned complex bones have for these reasons been called by me the squamoso-preopercular and the preoperculo-quadrato-jugal respectively.

The lacrymo-jugal is an arched bone, whose anterior part reaches forward on the lateral surface of the ethmoidal region, while its posterior portion partly forms the posterior boundary of the entrance to the orbit. It is generally attached posteriorly both to the squamoso-preopercular and to the dorsal one, called by me the postorbital, of the three postorbitally situated cheek plates. In *Wimania* and possibly in *Sassenia* too, its conditions are somewhat different, as in these species it is joined only to the squamoso-preopercular, while its connection with the postorbital is made by means of a small independent plate.

The postorbital, squamoso-preopercular and preoperculo-quadrato-jugal are situated in a vertical row behind the orbit.

The anterior margin of the postorbital forms the upper part of the posterior boundary of the orbital entrance. In *Coelacanthus*, *Wimania* and *Sassenia* it does not reach backwards to the opercular, but the space between it and the last-mentioned bone is filled either by a dorsal part of the squamoso-preopercular (*Coelacanthus*, WELBURN 1902) or by an independent bone-plate (*Sassenia*), which in its turn may also sometimes be strongly reduced or be absent (*Wimania*). On the other hand in *Macropoma* (WOODWARD 1909) and if REIS (1888; 1892) and WOODWARD's (1898a) view is correct, in Jurassic forms as well, the postorbital comes into direct contact with the opercular, and thus in all these latter forms it seems not quite equivalent to the bone that is denoted by the same name in the older ones.

The squamoso-preopercular is the largest of the three postorbitally situated cheek plates and in the oldest forms (*Coelacanthus*) it has a more primitive character than in the younger ones on account of its extension behind the postorbital. *Wimania* and *Sassenia* occupy in this respect a typical intermediate position.

The preoperculo-quadratojugal is so situated that it corresponds to the lower part of the palatoquadrate and the articulation between this and the mandibula.

While in *Coelacanthus* and, as far as we know up to now, in the Jurassic and Cretaceous forms too, the cheek plates have, at least to some extent, had their margins closely joined together and have fitted rather well together with one another, in others, as e. g. *Wimania* and *Sassenia*, they have been separated from each other by more or less large interspaces, which means that they were more or less in a process

of reduction. In at least certain species of *Axelia* they are still more reduced, and are represented merely by a number of small scale-like plates.

Visceral skeleton. — The palatoquadrate cartilage was present to a rather considerable extent. In its anterior end an autopalatine is developed. In its ventro-caudal corner we always find a powerful quadrate, and in its dorso-caudal end a metapterygoid, generally also powerful.

The autopalatine is a rather small bone, which, at least in a number of forms, has articulated against the preëthmoid (*Macropoma*). The quadrate is always large and powerful and generally also thick, with a well developed condyle in the ventral end. The metapterygoid usually consists of a fairly large bone-plate, which has without doubt been continuously attached ventrally to the quadrate by a persisting part of the palatoquadrate cartilage. While the metapterygoid is large and well developed, especially in the earlier forms (*Coelacanthus*, *Wimania*, *Axelia*, *Mylacanthus*, *Scleracanthus*), it seems in a number of younger ones to be more or less reduced and more intimately connected with the pterygoid (*Undina*, *Mawsonia*).

The palatoquadrate articulates against the basiptyergoid process of the basisphenoid by means of the dorsal border of the metapterygoid and we have here apparently a correspondence to the so called palato-basal articulation of the sharks. This articulation must certainly be looked upon as a very old formation, since, as far as can be discovered, it is also present in other fossil Crossopterygians (*Megalichthys*, WATSON, 1912 a; *Dictyonosteus*, STENSIÖ 1918) besides the Coelacanthids. We probably have in this the primitive connection of the mandibular arch with the neurocranium.

The palatoquadrate has on the medial side a very large pterygoid which probably corresponds both to the ecto- and the entopterygoid of the *Rhipidistia* (WATSON and DAY 1916) and probably sometimes also to the dermopalatine of those fishes. In shape it is an angular bone with a posterior limb situated vertically and an anterior horizontal one issuing from this. They both show in detail in different genera and species considerable variation with regard to width, height, the course of the margins, etc.

The dorsal part of the posterior limb is covered externally by the metapterygoid, which, as pointed out, is more or less intimately connected to it. The usual conditions of this connection are that the anterior border of the metapterygoid is firmly attached to only the dorsal part of a ridge along the anterior margin of the posterior limb (*Coelacanthus*, *Wimania*, *Axelia*, *Mylacanthus*, *Scleracanthus*, etc.). It seems to be more rare for the firm connection to be extended to the ventral border of the metapterygoid as well, or for a fusion between the two bones in question to have begun (*Undina*, *Mawsonia*). — The lower corner of the posterior limb is covered from the lateral side by the dorsal part of the quadrate, but no firmer connection between the two has existed. The anterior limb, which is always turned so that its medial surface faces somewhat downwards and its lateral one somewhat upwards, is anteriorly in connection with the lower surface of the autopalatine.

In certain forms the dermopalatine is present as an independent narrow bone along the lateral margin of the anterior pterygoid limb in the anterior part of the latter (*Coccodeima*, *Libys*, *Undina*). In other forms, on the contrary, it may perhaps, as already mentioned, have been fused with the pterygoid (*Wimania*, *Axelia*, etc.) or be reduced.

Only two ossifications are known in the Meckelian cartilage, namely the articular and the autangular, both comparatively small. The membrane bones of the mandibula consist of a supraangulo-angular, dental, splenial, coronoid, intercoronoideo-prearticular and two or three precoronoids.

The supraangulo-angular is a large bone, apparently arisen by fusion of the homologues of the angular and supraangular of the Rhipidistids and possibly one or more of their so-called infradentals as well. Sometimes it has a fairly high, triangular shape (*Axelia*, *Myliacanthus*), sometimes, on the other hand, it is low and long. The dental and the splenial are both fairly short and low. The coronoid is fairly large and often triangular. The intercoronoideo-prearticular covers the inside of the mandible from the symphyse almost to the posterior end. To its upper margin the coronoid is joined posteriorly and the precoronoids anteriorly.

The conditions of the maxillary and premaxillary are still rather uncertain. As a maxillary I have, however, provisionally interpreted a narrow bone in *Wimania sinuosa*, which lies loose in relation both to the pterygoid and the lacrymo-jugal. It is also possibly present in *Coelacanthus* (WELLBURN 1902).

In the hyoid arch there appear two ossifications, a long and powerful one in the ceratohyal and a smaller vertical one in a segment situated dorsally of this, which may probably be considered to correspond to the epihyal. If a hyomandibular was developed, it must have been cartilaginous, relatively small and probably only corresponded to a pharyngobranchial (cf. ALLIS 1915). The ceratohyal ossification always has a typical rounded projection on the ventral margin.

The opercular apparatus consists only of a large plate called the opercular. This plate is especially large in the Palaeozoic and Triassic forms. Its postero-ventral margin may sometimes show a spiny or lobed shape (*Myliacanthus*).

Between the mandibles there are always two large, well developed jugular plates, more or less elongated in shape.

Five pairs of branchial arches are usually present. In *Macropoma*, however, there are said to be only four. In them there constantly appears a long ventral ossification, probably corresponding to a ceratobranchial and a dorsal one, possibly representing both the epi- and the pharyngobranchial. Both ossifications have generally had cartilaginous epiphyses. The ceratobranchialia are characterized by a deep longitudinal furrow on their posterior side.

The ventral ends of the branchial arches have been connected by a cartilaginous copula. It is of course impossible to decide whether this in its turn consisted of a uniform piece of cartilage or was divided into segments. It was covered by a number of tooth bearing plates, sometimes very thick and strong as is the case in *Axelia*, *Myliacanthus* and *Scleracanthus*.

As in the *Actinopterygii* a large and strong urohyal is found developed.

Dentition. — The precoronoids and the bone interpreted as a maxillary has, at least in the majority of Coelacanthids, rather large conically pointed teeth. The parasphenoid, the plates on the copula, the pterygoid, the dermopalatine, the intercoronoideo-prearticular and the coronoid generally have small teeth more bluntly conical or sometimes even rounded. The dentition of the branchial arches consists of small plates furnished with small and more or less pointed conical teeth.

The three genera *Axelia*, *Myrlacanthus* and *Scleracanthus* differ from the usual type and are distinguished by a dentition adapted for crushing. In these forms the parasphenoid, the plates on the copula, the pterygoid, the coronoid and the intercoronoideo-prearticular are furnished with low, often even flattened, spheroidal teeth, which greatly resemble those of *Colobodus* in their shape and sculpture. Those on the parasphenoid and the supracopular plates are largest and most strongly developed. The conditions of the maxillary and the precoronoids with regard to dentition are not yet known. The teeth of the branchial arches are, as usual, small and fused with their bases into plates as in the other forms. In most cases they are spheroid in shape.

The sensory canals of the head. — The infraorbital canal, as I have taken it in agreement with the definition of EWART (1892), EWART and MITCHELL (1892) and COLE (1896, 1898) etc. may have its posterior end on the boundary between the supratemporo-extrascapular and the parieto-intertemporal. It passes in a forward direction through the latter bone, reaches the fronto-dermosphenotic, which it pierces in the dermosphenotic component. There it turns off laterally and then enters the postorbital on the cheek. It penetrates this bone near the anterior margin, after which it passes off downwards and forwards in the lacryma-jugal under the entrance to the orbit. Anterior of the lacrymo-jugal it has continued ventrally of the nasal apertures, forward to the snout, where, situated in the rostrals, it has formed a commissure with the corresponding canal of the opposite side. In the fronto-dermosphenotic it anastomoses with the supraorbital canal.

The supraorbital canal continues from this anastomosis with the infraorbital canal in the dermosphenotic component of the fronto-dermosphenotic fairly straight forward and after a short distance arrives between the supraorbitals and the lateral margin of the frontal component of the fronto-dermosphenotic. In this position it continues along to the ethmoidal region, where it passes through the nasal part of the nasalo-antorbital dorsally (medially) of the nasal apertures. In front of this last-mentioned bone it enters into the lateral rostral plate, bending at the same time first downwards and then backwards. It is uncertain whether it anastomosed there with the infraorbital canal.

In the posterior part of the lacrymo-jugal (*Undina*, *Libys*, *Macropoma*, etc.) or immediately dorsally of this (*Wimania*, *Sassenia*) a canal issues in a backward and downward arch from the postorbital section of the infraorbital canal. This, for which I have adopted the term jugal canal of MOODIE (1908, 1915a), and which seems to correspond in all essentials to the similiary situated one in the *Stegocephali*, runs first through the squamoso-preopercular to the lower margin not far from the posterior corner, after which it presumably continued in a ventral direction through the posterior part of the preoperculo-quadratojugal. It is impossible to decide whether it anastomosed with the mandibular canal.

The mandibular canal penetrates the supraangulo-angular and the splenial and extends almost to the symphyse between the two mandibulae.

The most anterior part of the main lateral line on the head extends, according to the definition I have followed for the boundaries of the infraorbital canal, along through the supratemporo-extrascapular. Close to or in this bone there issues from it the supra-temporal commissure that pierces the extrascapular row of plates.

It has not yet been possible to observe «pit lines» either on the cranial roof or the cheek.

In *Libys*, *Axelia*, *Myrlacanthus* and *Scleracanthus* the sensory canals are strikingly powerfully developed and the pores are large. Little is known of the number and position of the pores in many of the forms. It is clear, however, that there is much variation in this respect in different genera. In *Coelacanthus*, *Undina* and *Cocoderma*, for instance, the pores are probably very numerous; in the forms that have the sensory canals strongly developed they are on the other hand, relatively few and much enlarged.

Axial skeleton. — As I have nothing fresh to add to our knowledge with regard to the axial skeleton I merely refer to earlier accounts of it (REIS, 1888, 1892; SCHMALHAUSEN, 1913 a). As to the caudal region I mention below, in connection with the description of the caudal fin, the views that have recently been put forward by SCHMALHAUSEN (1913).

Skeleton of girdles and fins. — The primordial skeleton of the shoulder girdle was, at least partly, ossified (REIS, 1892). Parts of its ossifications are known in *Undina*, *Libys*, *Macropoma*. The dermal skeleton consists of the clavicle («infraclavicular»), cleithral, supracleithral and suprascapular («posttemporal»). It is uncertain whether a postcleithral was developed.

The clavicle was probably on the whole rather high and narrow. In certain genera, however, as shown by *Wimania*, it was fairly wide in the ventral horizontal limb and connected to that of the opposite side in a median suture. The cleithral is higher than the clavicle and generally narrower too. The supracleithral is short and seems to exhibit a rather great variety in shape. Finally the suprascapular is known in detail only in *Axelia*, where it is represented by a little scale-like plate.

The pectoral fins are bluntly lobed and the inner skeleton in each (WOODWARD, 1895 a, pp. 3—4; WELLBURN, 1901, pp. 71—72) consists, at least in certain genera (*Coelacanthus*, etc.) of a number of ossified endoskeletal radials arranged radially in relation to a centre situated in the primary girdle skeleton, with which as a matter of fact they articulated. The lepidotrichia are usually unjointed for a longer or shorter distance proximally.

The pelvic girdle is represented by a paired bone-plate, closely resembling in shape the so-called basale metapterygii of the *Teleostei*. This plate is generally loosely attached to the one on the opposite side and is sometimes, as, e. g. in *Coelacanthus*, developed with spines on the medial margin. At the postero-caudal part it has on the lateral side a wide postero-lateral projection with which the inner skeleton of the ventral fin has articulated. The homologues of the plate are of course not yet quite clear, but, as far as one can venture to judge, it seems on the whole to correspond well to the pelvis in *Eusthenopteron* (cf. GOODRICH, 1901).

The ventral fins, like the pectoral ones, are bluntly lobed. Their inner skeleton was cartilaginous throughout and nothing is known about it so far. The lepidotrichia show the same conditions as in the pectoral fins, but they are generally somewhat weaker and shorter than in these.

As in the Rhipidistids so in the Coelacanthids one finds an ossified supporting plate both in the two dorsal fins and the anal fin. In the anterior dorsal fin the lepidotrichia are in direct articulation with the plate, while in the posterior dorsal and anal fin the articulation must have been by means of cartilaginous elements.¹⁾ The supporting plates

¹⁾ According to DEAN the lepidotrichia of the second dorsal fin of *Diplurus* were directly attached to the supporting plate (DEAN, 1895, fig. 156, p. 154), but this must certainly be a mistake, as is also confirmed by NEWBERRY's figure 1, pl. 20, in his monograph on the Triassic fishes from New Jersey and Connecticut Valley 1888.

of the two last-mentioned fins are also characterized by being always more or less strongly bifurcated in their proximal part, while that of the anterior dorsal fin is generally rounded and triangular. In exceptional cases, however (*Scleracanthus*), it is bifurcated in about the same way as the other two but not so much. It has generally been considered that the plates in question have been formed by fusion of the proximal segments of the endoskeletal radials, and it is probably pretty certain that this is true of those of the posterior dorsal fin and the anal fin. With regard to that of the anterior dorsal fin, on the other hand, it seems most probable that this comprises not only the proximal but also the middle segments of the endoskeletal radials.

Both the posterior dorsal fin and the anal fin are weakly lobed. The anterior dorsal fin, on the contrary, is not lobed and in consequence has a straight basal line. In all three fins the lepidotrichia usually grow narrower, in most cases continuously, towards the distal ends. In certain Mesozoic forms, however, they expand first in distal direction, decreasing then towards the ends. A longer or shorter proximal part is most often unjointed. All the lepidotrichia of the anterior dorsal fin are furnished in Mesozoic forms with tuberculation or spines on the lateral surfaces.

The caudal fin generally consists of three lobes, a dorsal one, a middle one and a ventral one, and has nearly a diphycercal shape. It is however practically never quite symmetrical, but the ventral lobe has generally a few more lepidotrichia than the dorsal one. The middle lobe, the so-called supplementary caudal fin (called «Pinselflosse» in German works), is developed nearly as a small independent fin, reaching more or less far backwards caudally of the two other lobes. It may, however, also be quite reduced as is the case in *Macropoma* and *Heptanema*.

The lepidotrichs of the caudal fin show the same conditions as to shape, joints, etc., as the ones of the other unpaired fins. Like those of the anterior dorsal fin they are furnished in the Mesozoic forms with spines or tubercles on the lateral surfaces. The only exceptions in this case are, as I have hitherto found, the so-called *Coelacanthus africanus* BROOM and *C. gracilis* AGASSIZ, where instead of tuberculations they have some fine longitudinal striae of a shining ganoine-like substance.¹⁾

For our views on the inner skeleton of the caudal fin SCHMALHAUSEN's investigations, published a few years ago (1913a) are of great importance and I may consequently be allowed in this connection to give some of his most important results.

After SCHMALHAUSEN by means of embryological investigations (1912) came to the conclusion that the supporting endoskeleton of the unpaired fins had arisen phylogenetically without connection with the axial skeleton he set to work to study the Dipnoans, Coelacanthids and Cyclostomes, all of which had previously been considered as presenting evidence in favour of the view of the endoskeleton of the unpaired fins having originally been developed from the axial skeleton.

The endoskeleton of the caudal fin in *Dipnoi* has its «Anlage», as SCHMALHAUSEN has verified, in connection with the axial skeleton, and because of this he looks upon it as only being distal parts of the neural and hemal spines. The anatomy etc. of the muscle shows moreover that the caudal fin is progressively developed forward

¹⁾ This is clearly shown by the specimens in British Museum.

on both the dorsal and the ventral side with a simultaneous reduction of the unpaired fins. Like REIS (1892) and DOLLO (1895), he considers the diphyercy in the recent *Ceratodus* to be secondary, and he finds evidence for this view of his in the fossil forms, in *Ctenodus* among others.

While in the primitive *Dipnoi* and the *Crossopterygii* the caudal fin was of a heterocercal shape, we find, as he also points out, in the somewhat more spezialized representatives of these fishes a number of types in which it is rather symmetrically developed. Among the *Crossopterygii* he pays the closest attention to *Eusthenopteron* in this respect, and he considers, like DOLLO (1895), that the caudal fin of the Coelacanthids is developed from a type of this sort. He then continues as follows (pp. 55—56):

«Die Schwanzflosse der *Coelacanthidae* ist derselben der *Rhizodontidae* sehr ähnlich, wir können sie nur als ein weiteres Umbildungsprodukt in derselben Richtung ansehen. — Ausbildung einer vollkommenen Symmetrie und progressives Wachstum der Dornfortsätze, welche auch dorsal eine Abgliederung erworben haben, zeichnen das Skelett dieser Flosse aus. — Was die Bedeutung der Pinselflosse anbelangt, so scheint es mir, daß sie vollkommen dem mittleren Schwanzlappen des *Eusthenopteron* entspricht und daß folglich die sekundäre Symmetrie genau in derselben Weise ausgebildet wurde.»

The diphyercal shape of the caudal fin in the Coelacanthids should thus be secondary and the endoskeletal supporting elements connected with the axial skeleton are to be considered as distal segments of the neural and haemal spines.

Air-bladder. — With regard to the air-bladder I have only to remark that it has been impossible so far to trace it in any of the Triassic forms from Spitzbergen.

Squamation. — The most important characters of the scales are well known from a number of earlier works and as I have nothing of importance to add here I shall simply refer to these (HUXLEY, 1866; REIS, 1888, 1892; ZITTEL, 1887; WILLIAMSON, 1849; WOODWARD, 1891b; 1909).

Coelacanthids compared with a number of other fishes and certain tetrapods.

Coelacanthids and other Crossopterygians.

Coelacanthids and Rhipidistids. — In the Rhipidistids the ossifications of the primordial neurocranium are very seldom preserved. It is really only in *Dictyonosteus* (STENSTÖ, 1918c) and *Megalichthys* (YOUNG, 1866; COPE, 1883; WATSON, 1912a; BIRKS, 1916) and to some extent in *Dendrodus* and *Cricodus* (ROHON, 1889) that we know a number of them more or less incompletely.¹⁾

In the occipital region in *Megalichthys*, according to YOUNG's description (1866, p. 605), only a basioccipital seems to be developed in the same way as in Coelacanthids.

¹⁾ PANDER (1860, pp. 15—16) described fragments of substitution bones from the anterior portions of the head of *Osteolepis*.

The primordial neurocranium of *Rhizodopsis* is said by WATSON and DAY, 1916 (pp. 13—14) to have consisted of cartilage. I do not feel convinced, however, that this is really the case, but consider it more probable that the «cartilage» was bone of a similar structure as in *Dictyonosteus*.

The chorda dorsalis also in both cases probably continued into the neurocranium and at any rate pierced the occipital region. COPE (1883, p. 628) described — also in *Megalichthys* — «ossified parachordals» occupying the basal parts of the neurocranium and, if I interpret his brief description correctly, these parachordal ossifications should correspond most closely to the paired prootico-opisthotic in the Coelacanthids. The autosphehotic is absent in Coelacanthids and probably in Rhipidistids as well. In *Megalichthys* WATSON (1912a, pp. 9—10) mentions a basisphenoid which seems to agree in all essentials with that of the Coelacanthids. As in these, it consequently corresponds to the postero-caudal part of the large sphenoid in *Dictyonosteus*. It does not seem improbable that in addition a large sphenoid similar to the one in this form was developed in a number of Devonian forms as well. The conditions in *Dendrodus*, if ROHON's figures (Pl. 1, figs. 1, 9) are correct, would, inter alia, support this view. It is also noteworthy that in *Dictyonosteus* the homologues of the alisphenoid of the Coelacanthids forms an integral part of the sphenoid without any signs of fusion with the membrane bones in the cranial roof.

Both in *Dictyonosteus* and in *Megalichthys* the basisphenoid has distinct basiptyergoid processes with which the palatoquadrate probably articulated (*Dictyonosteus*) or was fixed (*Megalichthys* according to what is indicated by WATSON's statement 1912a, p. 9). The basiptyergoid processes in *Dictyonosteus* are situated, as I have pointed out, not close to the basis cranii but somewhat higher up and thus show in this respect a certain resemblance to those in the *Coelacanthids* (specially those in *Axelia*). As far as one thus can see, the Coelacanthids and the Rhipidistids agree, inter alia, in having an articulation or a connection developed between the palatoquadrate and the posterior part of the orbito-temporal region, a fact that is of great importance for our judgement of the relations of these fishes.

The ethmoidal region is certainly preserved in both *Dendrodus* and *Cricodus*, but, as ROHON's (1889) interpretation of it is incorrect throughout (cf. TRAQUAIR 1889), no great reliance can be placed in his figures either. In *Dictyonosteus* we find this region practically entirely occupied by a large paired ossification, which to judge from its extent, ought to comprise the homologues of both the preethmoid and the exethmoid.

The shape and extent of the cranial cavity and the position of the nerve foramina seem to show strikingly great agreements in Coelacanthids and *Dictyonosteus*, as I have had occasion to point out in detail above and as is shown in my previously published work on *Dictyonosteus* (1918c).

The parasphenoid agrees in *Dictyonosteus*, *Sauripterus* (EASTMAN, 1917, Pl. 7, fig. 8, and possibly *Glyptopomus* too with the same bone in the Coelacanthids. On the other hand it seems, if we can believe the figures published by ROHON 1889, that it was strikingly narrow in *Dendrodus*.

With regard to the membrane bones of the cranial roof the Coelacanthids can, as we have already seen above, be derived from a Rhipidistid-like type. Their supratemporo-extrascapular has arisen by fusion of the homologues of the supratemporal and a part of the lateral extrascapular plate of the Rhipidistids, and in a similar way their parieto-intertemporal is formed by the fusion of the homologues of the parietal and the intertemporal, and their fronto-dermosphenotic by the fusion of the homologues of the

frontal and the dermosphenotic. And the following facts show that the Coelacanthids also, with regard to the arrangement of the bone-plates on the dorsal side of the ethmoidal region, have in the main several features in common with the Rhipidistids.

In *Eusthenopteron* (text fig. 57) we find, as I have been able to show after careful investigations of a well-preserved specimen in the museum here, the rostrals (*R*), interrostrals (*Ir*)¹⁾ and the postrostrals (*Ptr*) with about the same conditions as in the above described Coelacanthids from the Triassic of Spitzbergen. On the other hand the antorbital (*Ant*) is an independent bone, situated in the normal way between the entrance to the orbit (*orb*) and the external nasal aperture (*na*), and the nasal bone (*Na*) is, as in Teleosts, a narrow bone, pierced by the supraorbital canal and situated on the dorsal side of the nasal capsule along the lateral margin of the postrostral. The supraorbitals (*So*) are probably represented by one long, narrow bone on the lateral side of each frontal (*Fr*).

According to WATSON and DAY's (1916) reconstructions *Glyptopomus* and *Osteolepis* show on the whole an arrangement very similar to *Eusthenopteron* and Coelacanthids in this respect. But what these two investigators have interpreted as the prefrontal (WATSON and DAY's text fig. 2) is presumably a posterior nasal element, and their nasal corresponds to my postrostral. Further, the lacrymal of their interpretation seems to represent both the real lacrymal and the antorbital of *Eusthenopteron*. In *Osteolepis* (cf. WATSON and DAY's text figs. 5, 9), on the other hand, the nasal may be correctly determined, but probably the plate situated in front of it belongs to it as well. The postrostrals seem to be represented by at least two separate elements on each side of the median line, which, as we have seen, may also be the case in certain Coelacanthid forms.

In *Megalichthys*, as far as one can judge from the figures given by BIRKS' (1916), there are also probably conditions corresponding to what we have just described in the three preceding Rhipidistids. The nasal + ethmoid of BIRKS' description (cf. his Pl. 14, fig. 2) corresponds in any case at least to the postrostral, while, if his figures are correct, the rostrals probably form part of his premaxillaris. The nasal may be an independent bone situated laterally of the postrostral as in *Eusthenopteron*. WELLBURN's exposition of *Megalichthys* (1900) seems in many respects to be unreliable.

By a new investigation of *Dictyonosteus* I was able to verify, as seen in text fig. 58, that this form too shows in all essentials the same conditions as the other fossil Crossopterygians here considered with regard to the membrane bones on the dorsal side of the ethmoidal region. We can thus discover without difficulty the postrostrals (*Ptr*), an unpaired interrostral (*Ir*), the rostrals (*R*), nasal (*Na*) and antorbitals (*Ant*). It is noteworthy,

Text fig. 57.

Eusthenopteron fordii
WHITEAVES.

Cranial roof from a specimen belonging to the Palaeontological Institution Upsala. η_1 .

Ant, antorbital; *Dsph*, dermosphenotic; *Ext*, lateral extrascapular plate; *Ext. m*, median extrascapular plate; *Fr*, frontal; *Ir*, interrostral; *It*, intertemporal; *La*, lacrymal; *Mx*, maxillary; *Na*, nasal; *Pa*, parietal; *Pmx*, premaxillary; *Ptr*, postrostral; *R*, rostrals; *So*, supraorbital; *Stemp*, supratergital; *na*, nasal aperture; *orb*, orbit.

¹⁾ The interrostrale has probably been developed here as a paired bone.

however, that the postrostral of each side of the median line is represented by two plates, an anterior one (*Ptr*₁) and a posterior one (*Ptr*₂), and the nasal by three plates (*Na*₁-*Na*₃), all pierced by the anterior section of the supraorbital canal. The antorbital is probably represented by two plates, of which the anterior one (*Ant*₁) is situated immediately behind the external nasal aperture (*na*), while the posterior one (*Ant*₂) which also seems to be the larger one, forms part of the boundary of the aditus orbitae. — I am practically certain that the considerable number of independent elements in the dermal cranial roof of the ethmoidal region is a primitive feature (cf. WATSON and DAY 1916, pp. 21—23).

Text fig. 58. *Dictionosteus arcticus* STENSIÖ. The anterior part of the cranial roof. Sensory canals with dotted lines and shading. From P. 355. $\frac{1}{2}$. *Ant*₁, anterior antorbital element; *Ant*₂, posterior antorbital element; *Dph*, dermosphenotic (dermal post-frontal); *Fr*, frontal; *Ix*, interrostral; *Na*₁-*Na*₃, nasal elements; *Pmx*, premaxillary; *Ptr*₁, anterior postrostral element; *Ptr*₂, posterior postrostral element; *R*, rostrals; *So*, supraorbitals; *na*, external nasal aperture; *orb*, orbita; *y*, accessory bone-plate.

We can thus, in the present state of our knowledge, refer all the Rhipidistids and Coelacanthids with regard to the cranial roof to a common type, which they still rather closely resemble. The same is also true of the bone-plates of the cheek, as I have been able to show above in the description of *W. sinuosa*.

In at least *Tristichopterus*, *Rhizodopsis* and *Glyptomus* among the Rhipidistids we find a large pterygoid element, which probably corresponds most closely to an entopterygoid. An ectopterygoid is also shown to exist at least in certain forms (cf. TRAQUAIR, 1875 a, pp. 387—388; 1881, p. 171; WATSON and DAY, 1916, pp. 11, 14, 23). The strong development of the entopterygoid posteriorly in *Rhizodopsis* is especially noteworthy, as the bone almost comes into contact with the cranial roof (cf. WATSON and DAY, p. 14). A similar state of affairs is also seen in the Coelacanthids, where, as I have shown above, the posterior limb of the pterygoid is in most cases high and strongly developed. On the other hand, as I have also pointed out, the Coelacanthids have no independent ectopterygoid.

We have seen that in the Coelacanthids the hyoid arch is weakly developed in its dorsal part and it is even uncertain whether a hyomandibular was present. Among the Rhipidistids, on the other hand, according to TRAQUAIR's 1881, p. 171) and WATSON and DAY's (1916, p. 16) investigations, there seems to have been a rather powerful hyomandibular, at least in certain forms. Like the hyoid arch, the opercular apparatus of the Coelacanthids, unlike that of the Rhipidistids, is also somewhat reduced, since, as we know, only one large opercular plate is preserved in the former.

The teeth show, as far as we know, a simpler structure in the Coelacanthids than in the Rhipidistids, but it seems at present difficult to decide whether this difference is to be considered as a primary or a secondary one. In this case it would be of interest to undertake a microscopical investigation of the teeth of the Devonian Coelacanthids.

With regard to the course of the sensory canals *Osteolepis* (GOODRICH, 1919) and *Eusthenopteron* (cf. text fig. 57) agree completely with the Coelacanthids and probably this is also the case with the majority of the other Rhipidistids as well.

Finally, as has already been known for a long time, the Coelacanthids are most closely related to the Rhipidistids with regard to the fin skeleton as well. This is especially true of the dorsal fins and the anal fin, and to some extent of the paired fins too, while the caudal fin apparently differs considerably. But SCHMALHAUSEN'S investigations (1913a), as mentioned above, seem to show that this fin too is probably more closely related to that of the Rhipidistids than has been known.

As the result of this comparison we thus find that the Coelacanthids and the Rhipidistids are really closely related. It is true that there are a number of differences between them, but these cannot be regarded as being of a profound nature and in any case are of little significance in comparison with the series of obvious agreements that are observed in other respects. Accordingly, as far as we can decide from the facts now known, the Coelacanthids ought to be taken as a highly specialized group, the ancestors of which are to be sought for among the primitive Rhipidistids.

Coelacanthids and Tarassids. — *Tarassius* in still too incompletely known for anything in detail to be discovered as to its relationship with the Coelacanthids. As far as we know at present, the only common feature are the bluntly lobed form of the pectoral fins.

Coelacanthids and Polypterids. — The account given above ought to show that neither the Coelacanthids nor the Rhipidistids are so closely related to the Polypterids as has been believed previously. The Polypterids represent rather, as GOODRICH (1909, pp. 298—300) has pointed out, a type that is more closely allied to the *Actinopterygii*, although in my opinion they cannot be grouped with these either.

Coelacanthids and Dipnoans.

As has already been pointed out several times before in this work, the Coelacanthids present several similarities to the Dipnoans. This fact was observed early, as we have seen from the historical introduction, and the Coelacanthids have even for a long time been considered as being closely related to forms which we now definitely place among the *Dipnoi*.

The most important resemblances between the *Coelacanthidae* and *Dipnoi* are briefly the following: the general shape of the mandible and the development of its membrane bones (cf. HUXLEY 1861, p. 20), the reductions in the hyoid arch and in the opercular apparatus, the development of the axial skeleton and the diphycercal shape of the caudal fin as well as the character of the endoskeleton of this fin. — In addition it has been considered that in Coelacanthids as in Dipnoans the air bladder has had a respiratory function (REIS 1888, p. 33) and finally the branchial arches of the Coelacanthids also show in their segmentation similarities to those of the Dipnoans (cf. GAUFF, 1904, p. 920—931; FÜRBRINGER, 1904, pp. 483—488; VAN WUJHE, 1882, pp. 295—297). As, however, we do not know the conditions of the other Crossopterygians with regard to the last-mentioned character, it is still uncertain whether this peculiarity is not also characteristic for them.

In the first place with regard to the mandible the agreement between the Coelacanthids and the Dipnoans is not as great as was originally thought probable, but is limited almost to the general shape. The bones described in the mandible of the *Dipnoi* certainly show at first sight fairly similar conditions to certain bones in the Coelacanthids, but a closer examination shows immediately that they are fewer and have probably been formed by fusion of other elements than in Coelacanthids. Besides as a matter of fact the bones in question show rather different conditions in different *Dipnoi*, e. g. in *Dipterus* and *Ceratodus*.

In *Dipterus* the bone called «angular» by TRAQUAIR (1878, p. 7, Pl. III) has probably its nearest equivalent in the supraangulo-angular of the Coelacanthids, while his «dental» certainly also includes the homologues of the splenial of the Coelacanthids (the most anterior or some of the most anterior infradental elements of the *Rhipidistia*), a fact which is clearly shown by the course of the mandibular canal. Conditions different from those in Coelacanthids are found also in the bones of the coronoid series, which, as we know, is represented both in *Dipterus* and other Dipnoans by a single large bone, usually called the «splenial». In addition TRAQUAIR describes an articular in *Dipterus*.

In the recent *Ceratodus* (cf. GÜNTHER, 1871, pp. 521—526; HUXLEY, 1876, pp. 33—34; VAN WIJHE, 1882, pp. 295—297, Pl. XVI, fig. 14; TELLER, 1891, pp. 18, 22, Pl. III) the «angular» of HUXLEY's description in 1876 may possibly include both the homologue of the dental and supraangulo-angular of the Coelacanthids, while the «dental» of the same description seems in fact to represent one or more of the most anterior infradentals of the Rhipidistids. Thus the latter bone may in my terminology used here be provisionally called the splenial.¹⁾ It seems as if the reduction both in the hyoid arch and opercular apparatus has taken place independently in Coelacanthids and Dipnoans, as the primitive *Rhipidistia* generally may have been normally developed in this respect.

In a number of Rhipidistids too the axial skeleton was developed in somewhat the same way as in Dipnoans and Coelacanthids, which in this case thus do not occupy any special separate position. As is shown by the investigations of SCHMALHAUSEN (1913a) summarized above, the diphycceral caudal fin of the Coelacanthids is probably developed secondarily from a Rhipidistid fin of the type found in *Eusthenopteron* and thus need not imply any direct relationship with the Dipnoans.

Finally it ought also to be mentioned that in the Coelacanthids an internal nasal aperture situated similarly to that of the *Dipnoi* is quite absent, while on the other hand such an aperture is found in the Rhipidistids (STENSIÖ, 1918 c, p. 120; DOLLO, 1895, p. 109; WATSON and DAY, 1916, p. 24), e. g. *Dictyonosteus*, *Osteolepis*, *Diplopterus*, *Rhizodopsis* and *Megalichthys*. The nasal apertures of the Coelacanthids show instead almost the same conditions as those of the Actinopterygians, a fact that thus does not seem to support the view that their air bladder had a respiratory function.

The facts mentioned here and what has been said of the caudal fin above (p. 131) ought to show sufficiently clearly that characters indicating a very close affinity between Coelacanthids and Dipnoans really do not exist. Several of the resemblances between them are, as can clearly be seen, parallelisms.

¹⁾ As will, be seen from the works cited above and from K. FÜRBRINGER's exposition in 1904 (pp. 442—444), there has been much discussion in the literature on the homologues of the membrane bones of the mandibula in *Ceratodus*.

Before leaving the Dipnoans there is, however, one more matter that is worthy of attention. As now it seems to be practically proved that not only Coelacanthids but also certain of the Rhipidistids had an articulation between the palatoquadrate and the posterior part of the orbitotemporal region, this fact removes, in my opinion, one of the most important differences between the *Dipnoi* on the one hand and the Rhipidistids and Coelacanthids on the other. We have in these Crossopterygian forms simply the original type from which the autostyle of the *Dipnoi* must have arisen, and not only is this true, but, if WATSON's statement 1912 (1912 a, p. 9) with regard to *Megalichthys* proves to be correct there are also forms among the Crossopterygians which bear a considerable resemblance to the *Dipnoi* inasmuch as they have a rather firm connection between the palatoquadrate and the neurocranium.

The study of the Coelacanthids thus seems also to be of help in throwing fresh light on the relationship of the *Dipnoi* to the Crossopterygians. According to our present knowledge (cf. DOLLO, 1895, pp. 105—110; WATSON and DAY, 1916, pp. 41—45) the latter or forms very nearly allied to them must be considered as the ancestors of Dipnoans, and must consequently be grouped closely together with them from a systematic point of view (cf. DEAN, 1900, p. 29). There is thus no justification at all for separating the *Dipnoi* from the other Teleostomes, as has hitherto often been done (cf. DOLLO, 1895, p. 113).

Coelacanthids and Actinopterygians.

In the primordial neurocranium of primitive Actinopterygians we find, as will be seen from the description of *Birgeria mougeoti* (AGASSIZ) given below in this work, at least the following bones: a basioccipital, a paired prootico-opisthotic, comprising also the homologue of the epiotic, a paired autosphenotic and an unpaired sphenoid.

Of these the two prootico-opisthotics are certainly on the whole considerably larger and stronger than is the case in the Coelacanthids, but as in these, they only extend forwards to the posterior boundary of the exit for nervus facialis.¹⁾ The sphenoid is also large and corresponds in its extension rather closely to the similarly termed bone in *Dictyonosteus* (STENSJÖ, 1918 c) having, as in this form, its pars basisphenoidea extending into the labyrinth region behind the fossa hyphophyseos and thus belonging with this part to the chordal region of the cranium. Basipterygoid processes are present, but are situated low, and there is no connection between them and the palatoquadrates. As far as one can see from the facts mentioned, the primitive *Actinopterygii* thus show, in spite of great differences, a decided approach to the Crossopterygian type.

As I have tried to show, the Coelacanthids, like the higher Actinopterygians, seem to have had a myodome developed, and, if my opinion is correct, this, although it has arisen quite independently of that in the Actinopterygians, has still been developed in close relation to the so-called canalis transversus, which is pierced by v. pituitaria (GEGENBAUER, 1872, pp. 75—79; SAGEMEHL, 1884, pp. 215—217; 1885, pp. 85—87; 1891, pp. 574—575; ALLIS 1909 a, pp. 183—208; 1914 a, pp. 225—253; 1918 a, pp. 241—246).

¹⁾ In higher Actinopterygians the prootic generally extends, as is known, forward to the exit of the trigeminus and often surrounds the foramen prooticum.

Stensjö, Triassic Fishes from Spitzbergen.

In primitive Actinopterygians we still find, as we shall see, the myodome in a very primitive stage of development.

The parasphenoid of the primitive *Actinopterygii*, unlike that of the Coelacanthids and the Rhipidistids, is characterized by the strong and high processus ascendentes.

Several of the membrane bones that were independent in the Rhipidistids are found fused with one another in the Actinopterygians. These fusion have, however, taken place partly in another way than in the Coelacanthids. Thus while the membrane bone-plates on the dorsal side of the ethmoidal region in the Coelacanthids have comparatively well preserved their primitive arrangement and to a certain extent their mutual independence as well, they exhibit in Actinopterygians in general a stronger degree of specialisation. It is however, not convenient in this connection to give a detailed account of the homologues of the elements on the ethmoidal region of the *Actinopterygii*, but I refer the reader to the description of Palaeoniscids, Catopterids and Saurichthyids given below in this work, where the recent forms are also dealt with.

Further it seems to be evident that the so-called dermopterotic («squamosal») of the *Actinopterygii* or its equivalent (the dermal component in the so-called pterotic of the Teleosteans) corresponds both to the supratemporal and the intertemporal of the Rhipidistids (cf. REGAN, 1904, p. 339; ALLIS, 1919 b, pp. 73—77). On the other hand it is more difficult to be quite certain as to the homologues of the cheek-plates of the Actinopterygians as the course of the sensory canals and the so-called «pit-lines» in the primitive forms among them is inadequately known. It seems, however, to be certain that at least the posterior part of the large «preopercular» in the Palaeoniscids, Platysomids and Catopterids (cf. my description of these forms below, and GREGORY, 1915, p. 332) and the whole of the bone that is termed the preopercular in higher Ganoids and Teleosts are homologueous to the similarly termed bone in the Rhipidistids. In addition we also find, as will be seen from the account given below in this work, in Saurichthyids, Chondrosteids and Acipenserids an independent element probably corresponding to the quadratojugal of the Rhipidistids. It seems probable too that this element is contained in the posterior part of the maxillary in Palaeoniscids, Platysomids and Catopterids, while in other Actinopterygians it may either be reduced (certain higher Ganoids and at least the majority of Teleosts) or represented by one or more of the ventral postorbital- (suborbital-) plates (Semionotids, Eugnathids and other higher Ganoids).

In higher Ganoids the post- and suborbital sections of the infraorbital canal may generally run through the so-called «circumorbitals», which to judge at least from the conditions in Semionotids and *Lepidosteus* (ALLIS, 1905, pp. 407—417), seems to me most probable.¹⁾ Then the circumorbital plates situated behind, beneath and in front of the orbit should together correspond to the postorbital, jugal and lacrymal of the Rhipidistids. For the same reason the bones in the infraorbital chain of the Teleostei ought together to correspond to some extent to the bones mentioned in the Rhipidistids.

¹⁾ According to COLLINGE (1894 a. Pl. I, fig. 4) the sections in question of the infraorbital canal in *Dapedius* pass off through the postorbitals (suborbitals) and the maxillary. This view does not, however, seem to be supported by the knowledge we now possess of the course of this canal, e. g. in *Lepidosteus* (ALLIS, 1905). The course of the anterior part of the supraorbital canal in *Dapedius* as given by COLLINGE seems also very doubtful.

As we know, there is no cheek-plate* in the Actinopterygians that can be directly compared with the squamosal of the Rhipidistids. WATSON and DAY (1916) have shown, as has been pointed out above, that in primitive forms among the Rhipidistids the squamosal consists of several independent elements, and I now think that this fact can guide us in judging of the conditions in the Actinopterygians. Thus one may venture the supposition that all the homologues of the elements forming the squamosal in the Rhipidistids have never been fused with one another into one bone-plate in the Actinopterygians, but that they were either distributed among the surrounding bones or with partial transformation had been fused into certain larger units which afterwards preserved their mutual independence or else were finally more and more reduced. In the Palaeoniscids, Platysomids and Catopterids it is conceivable that the original squamosal elements were divided up between the maxillary and the preopercular and that they have even possibly provided material for the so-called postorbitals; in certain Protospondyli, such as the Semionitids and Eugnathids, they all probably provided material for the majority of the so-called postorbitals (suborbitals); — the ventral one, or some of them, can probably, as we have seen, be considered as corresponding to the quadratojugal; in the Teleosts the homologues of the squamosal elements usually seem to be reduced. Sometimes, however, it is possible that parts of them may persist in the plates of the infraorbital chain, in the cases when these plates are much developed and cover the cheek between the orbit and the preopercular to any great extent.

The large pterygoid of the Coelacanthids together with the quadrate and the metapterygoid usually resemble the suspensory apparatus in the Teleosts. Owing to this fact it has hitherto been thought that the hyomandibular was intimately fused with the palatoquadrate, a view that I have been able entirely to refuse in this work.

In the presence of a strong urohyal the Coelacanthids resemble the teleosts (GOODRICH, 1909, p. 350) and, as I shall show below, also certain Palaeoniscids (*Acro-rhaddus*).

As far as can be judged at present from the skeleton of the head, the fossil Crossopterygians have undoubtedly a more primitive appearance than the *Actinopterygii* (ABEL, 1919, p. 155).¹⁾ These latter appeared as early as in the middle Devonian well differentiated from the Crossopterygians and so far no Crossopterygian form is known from which the Actinopterygians could have arisen. Since, however, as we have seen, it is evident that the more primitive forms among the Actinopterygians resemble the Crossopterygians in certain respects with regard to the skeleton of the head, and in a number of other respects can from a theoretical point of view easily be derived from a Crossopterygian-like type, it seems not improbable that they originate from some early Devonian or Upper Silurian form, from which the Crossopterygians have also been developed (cf. ABEL, 1919, p. 184; STROMER, 1920).

It seems fairly certain that this common ancestral form resembled the Crossopterygian type with regard to the cranial skeleton, and several authors (ABEL, 1919, pp. 185—186; BRAUS, 1901, p. 287; GEGENBAUR, 1873, 1876, 1894, 1898; GOODRICH, 1909, pp. 106—109; STROMER, 1920, p. 17; JAEKEL, 1909a, b; SIMROTH, 1891, pp. 342—351) have

¹⁾ An opposite view is maintained by REGAN (1904, p. 347) and several other authors.

maintained that this is true of the development of the paired fins as well. The reductions which according to a view of this sort have taken place in the skeleton of these fins are caused, according to ABEL (1919, p. 185) by the adaption of the Actinopterygians for rapid swimming at a very early phylogenetic stage.

The pectoral fins of the Coelacanthids have a certain interest in this connection, as their skeletons, as WOODWARD (1895a, pp. 3—4) and WELLBURN (1901, pp. 71—72) have emphasized, resemble that of the Actinopterygians to a certain extent, a fact that seems to support the view that a developing of the paired fins of the Crossopterygians in the direction towards the Actinopterygian type could probably take place fairly easily.

In the continuation of this work I shall have a further opportunity to enter on a number of theoretical questions with regard to the skeleton of the paired fins and so I confine myself here to what has been said (cf. my description below of the skeleton of the ventral fins in *Birgeria mougeoti* and *Saurichthys ornatus*).

Coelacanthids and Tetrapods.

According to the view now prevailing the Tetrapods are supposed as we know, to descend more or less directly from some Crossopterygian forms or at any rate forms that were closely allied to the Crossopterygians (BAUR, 1896; BIRKS, 1916; BROOM, 1913c, d; DOLLO, 1895; GREGORY, 1913, 1915; MODIE, 1908; POLLARD, 1892; SMITH, 1912; THEVENIN, 1910; WATSON, 1912a; 1913b; WOODWARD, 1898a, pp. 123—125, etc.). Among the known *Crossopterygii* the Rhipidistids are justly considered to show the closest relationship to the Tetrapods. We have seen above that the Coelacanthids, on account of their specializations, have been thought to differ greatly from the Rhipidistids and thus from the ancestral forms of the Tetrapods as well. The Spitzbergen Coelacanthids described above have, however, helped in this case to give us to some extent another view; it is certain that in spite of their specialization the Coelacanthids have preserved a number of primitive characters and that because of this they show obvious resemblances to the primitive Tetrapods.

It is not my intention within the limits of this work to embark on an exhaustive account of the relations between Coelacanthids and Tetrapods and I have accordingly confined the following exposition merely to certain details with regard to the structure of the head. I have taken the Stegocephalians as types of the Tetrapods and among them especially the two sub-orders *Temnospondyli* and *Stereospondyli*.

The Coelacanthids and also the Rhipidistids have, with regard to the general shape of the primordial neurocranium, resembled the Tetrapod type more closely than other known fishes. This is due, in the first place, to absence of a real postorbital process, but in addition a number of other common features, although less prominent and at the same time less important, can also be traced with regard to the mutual relations and the shape of the different regions. Further there is often a certain habitual agreement between the Coelacanthids on the one hand and certain *Temnospondyli* and *Stereospondyli* on the other with regard to the distribution of the ossified and cartilaginous (possibly also membranous) parts of the primordial neurocranium. But in this case it is, at least to some extent, not a question of any primary resemblance, but a secondary one, due to

a reduction of originally stronger ossifications. In the case of the Stegocephalian orders mentioned a reduction of this sort has been clearly shown by WATSON (1919) and with regard to the Coelacanthids I have myself already pointed out in this work that the same thing can be observed, at least in the orbitotemporal region.

In the Temnospondylous and the Stereospondylous Stegocephalians and especially in the more primitive forms among them, the occipital region is well ossified. As WATSON (1919, pp. 62—63) has pointed out, everything indicates that this was also the case in their ancestors too. On the other hand, in the Mesozoic Coelacanthids, as we have seen, the same region has, to a very great extent, been cartilaginous. A basioccipital is known with certainty only in one genus, *Undina*, and it is impossible to decide whether a slight degree of ossification like this is to be regarded as primary or secondary, as we do not know the conditions either in the more primitive Palaeozoic representatives of the Coelacanthids or in the Rhipidistids.

With regard to the occipital region it is thus impossible to decide with certainty whether it offers any common features of a more special nature in fossil Crossopterygians and primitive Tetrapods.

If, on the other hand, we pass to the labyrinth region, we undoubtedly find better agreement. In the more primitive *Temnospondyli* and *Stereospondyli* both the prootic and the opisthotic are as a rule developed, but in more specialized, younger forms, on the contrary, these bones are reduced (WATSON 1919, pp. 62—63; BROOM 1913 e, pp. 573—574, 583—588). The opisthotic, when present is, however, often found fused with the lateral occipital or in exceptional cases (*Pteroplax*) with the prootic (WATSON, 1912 a, p. 7; 1916, pp. 612—618, 630—632; 1919, pp. 14, 26, 50—59, 62—63; BROOM 1913 e, pp. 573, 574, 583, 584, figs 6 B).¹⁾ The prootic of primitive forms (HUENE, 1913, pp. 318—322, 378; BROOM, 1913 e, pp. 574, 587; WATSON, 1912 a, p. 7; 1916, pp. 615—616, fig. 1; 1919, pp. 19, 23, 26, 52, 55, figs. 11, 12, 14, 16; WIMAN, 1914 b, pp. 13, 19; Pl. II, fig. 5, 6; Pl. V, fig. 4)²⁾ extends in a dorsal direction up towards the cranial roof in such a way that its uppermost part bears a considerable resemblance both in shape and position to the dorsal process (*fi*), from the prootico-opisthotic of the Coelacanthids. The lower part of the same bone, on the other hand, may even in the primitive forms not infrequently be thin and weakly developed but it seems from WATSON's exposition 1919 (pp. 51—59) that it originally in the earliest Stegocephalians ought to have been strong and to have at least to some extent resembled its homologue in Coelacanthids. Finally it is especially noteworthy that the autosphenotic («postorbital ossification», «postfrontal» in the sense of substitution bone), which is otherwise so distinctive a feature for the majority of the *Teleostomi*, is lacking both in the Coelacanthids and Rhipidistids just as in the Tetrapods.

¹⁾ The opisthotic of WIMAN's descriptions (1914 b; 1916 b, 1917) may after all be only a ventral process from the tabular. At least in *Platystega* and *Lyrocephalus* I have found the opisthotic as an independent bone, lying immediately anterior to the exoccipital. In *Lyrocephalus* (Pl. 20, fig. 4) however, it is very small.

²⁾ In Pl. 20 fig. I have figured the prootic of *Lyrocephalus euri*. In the specimen figured it is undoubtedly an independent rather thin and short plate of bone pierced by a foramen probably for the facialis nerv. After all this plate has had no direct relation to the labyrinth and might correspond to a dorsal part of the same bone in *Eryops*. The prootic and sphenotic of WIMAN's description 1916 (1916 b, pp. 217—218; Pl. XVI, fig. 4) are only parts of the otic process of the epipterygoid, as can clearly be seen from the figure published by me on Pl. 20, fig. 3 (cf. WATSON, 1919, pp. 28, 52, 58, figs. 12, 14).

The most striking resemblance between the Coelacanthids and the Temnospondylous and Stereospondylous Stegocephalians with regard to the ossifications of the primordial neurocranium is seen in the orbito-temporal region. If we first examine the basisphenoid we find that in such forms as *Loxomma*, *Eryops*, *Laccocephalus*, *Capitosaurus*¹⁾ etc. (HUENE, 1913, pp. 319—322, fig. 6; BROOM, 1913 e, p. 587, fig. 14; BROILI, 1917, pp. 572—574; 1918, p. 173; WATSON, 1912 a, pp. 2—3, 7—9; 1916, pp. 612—618, 631—632; 1919, pp. 10, 19, 27, 51—59, figs. 11, 12) it showed the same conditions as in the Coelacanthids. Thus it is situated with its corpus behind the fossa hypophyseos and as the corpus is often rather high it forms a high dorsum sellae. To judge from this position it seems probable that the corpus belongs to the chordal position of the cranium. Basipterygoid processes are often developed in primitive forms such as *Loxomma*, *Pteroplax*, *Eryops*, *Actinodon*, *Archegosaurus*, *Cacops*, *Broiliellus*, etc., but are generally lacking in younger and more specialized forms. — WATSON (1912 a, pp. 9—10) has shown in *Megalichthys* that with regard to the basisphenoid the Rhipidistids are developed in about the same way as the Coelacanthids and thus present a good resemblance to the Stegocephalians. I have myself pointed out above (p. 60) that this was also true in *Dictyonosteus*, although in this species the basisphenoid is not, however, an independent bone but forms a part of the large sphenoid.

The ossified part of the interorbital wall which constitutes the alisphenoid in the Coelacanthids is part of the so-called sphenethmoid in *Eryops* (BROOM, 1913 e, pp. 587 588, figs. 14—17; WATSON, 1919, fig. 11 A, B; BROILI, 1917, pp. 572—574), *Pteroplax* (WATSON 1912 a, p. 7), *Lyrocephalus* (WIMAN, 1916 b, pp. 216—219, Pl. XVI, fig. 4) and probably other allied forms (cf. BROILI, 1918, p. 173) in exactly the same way as the pars alisphenoidea in *Dictyonosteus* is part of the sphenoid. It seems also probable that in certain primitive Stegocephalians the basisphenoid too was an integral part of the so-called sphenethmoid (*Pteroplax*, WATSON 1912 a, p. 7; 1917 p. 981), and, if this be true, we consequently have also in this respect a remarkable agreement between them and *Dictyonosteus*. Finally it is also worthy of mention that both in primitive Stegocephalians and in *Dictyonosteus* the middle and anterior parts of the so-called sphenethmoid and sphenoid respectively seem to correspond most closely to the orbitosphenoid.

With regard to the skeleton of the ethmoidal region it is of interest in this connection to find how in such forms among the Stegocephalians as *Eryops*, *Trimerochachis* and *Zatrachys* the septomaxillaries seem to occupy almost the same position in relation to the nasal capsules as the preëthmoids in the Coelacanthids (cf. BROOM, 1913 e, figs. 11, 19, 21; ABEL, 1919, p. 237, figs. 185, 202, 211). According to the prevalent view, however, the septomaxillaries are supposed to belong to the category of membrane bones, while the preëthmoid, as we have seen, forms an ossification in the ventral and middle part of the cartilage of the ethmoidal region. GAUFF (1905, pp. 617, 746, 756, 773) also states very definitely with regard to the recent *Amphibia* and *Reptilia* that the septomaxillaries are not to be homologized with the preëthmoids.

HUENE'S (1913), BROOM'S (1913 e) and WATSON'S (1916; 1919) descriptions and figures of *Eryops* and *Capitosaurus* (cf. also BROILI, 1917; ABEL, 1919) show very clearly

¹⁾ According to WATSON (1919, p. 27) the basisphenoid is paired in *Capitosaurus*.

that there were considerable resemblances in many respects between the shape of the cranial cavity in Temnospondylous and Stereospondylous Stegocephalians on the one hand and Coelacanthids and Rhipidistids on the other. Thus in both cases we find, *inter alia*, a deep fossa hypophyseos with a well-developed dorsum, which is formed by the basisphenoid corpus. In addition there follows in the cranial base, caudally of the basisphenoid corpus, another deeper fossa, which was presumably filled with cartilage to a great extent or even entirely, and the farthest posteriorly, the basioccipital. Finally it is also interesting to find that the portion of orbitotemporal region that is situated between the canalis transversus and the foramen opticum is rather long.

The nerve exits in the Crossopterygians and Stegocephalians in question, at least in the orbito-temporal region and the anterior part of the labyrinth region, have also shown rather similar conditions. In this connection it is of special importance that the exits of the trigeminal branches were situated immediately above the basisphenoid corpus in front of the prootic. While all the trigeminal branches were probably transmitted at this place in the Stegocephalians, this does not seem to have been the case in the Rhipidistids and the Coelacanthids. For in these the ramus ophthalmicus profundus, as far profundus as we can judge, has pierced the cranial wall considerably farther forward and has emerged into the orbit antero-medially of the basiptyergoid process.

In several Rhipidistids there is undoubtedly an inner nasal aperture developed as in the Tetrapods, while this is lacking, as we have seen, in the Coelacanthids.

A characteristic common feature of the parasphenoid of Stegocephalians, Rhipidistids and Coelacanthids is the absence of processus ascendentes, while as we shall see, such processus are, on the contrary, strongly developed in the primitive Actinopterygians.

One of the grounds for considering the Rhipidistids as ancestral forms of the Stegocephalians is, as is known the resemblances of their membrane bones above the labyrinth and orbitotemporal regions. As is clear from my exposition in this work the *Coelacanthids* are in this respect rather specialized and thus cannot be directly compared with the Stegocephalians.

The parietal, supratemporal, intertemporal, tabular, postparietal, frontal and postfrontal (dermosphenotic) of Rhipidistids usually seem to have been taken as homologues or approximate homologues of the similarly denoted bones in Rhipidistids (cf. ALLIS, 1899, pp. 58, 67—70; 1919b, pp. 82—86; BAUR, 1896, pp. 658—662; GOODRICH, 1919, pp. 186—187; GREGORY, 1915, pp. 325—338; MOODIE, 1908, pp. 511—538; POLLARD, 1892a, pp. 408—412; WATSON and DAY, 1916, text fig. 9; WOODWARD, 1898a, pp. 123—125, fig. 81).

Among the Stegocephalians the intertemporal occurs, however, as an independent element only in certain primitive forms; as a rule in the other forms it seems most commonly to form part of the bone that is called according to the current terminology the supratemporal, which, under these circumstances, would be a supratemporo-intertemporal as in the *Actinopterygii* (cf. ALLIS, 1919b, loc. cit.). In certain forms, however, it may have fused with some other of the bones situated close to it. The postparietal is paired in the Stegocephalians, unpaired, on the other hand, in the Rhipidistids. Finally the postfrontal of the Stegocephalians has practically always a considerable extension above the orbit. As anteriorly it is attached to the bone that is sometimes called the lacrymal, sometimes the prefrontal and independent supraorbital elements are lacking,

it looks as if it comprises both the homologue of the dermosphenotic of the Rhipidistids (the postfrontale in the sense of a membrane bone) and the homologues of one or more of the posterior supraorbitals of these fishes.

Neither in Coelacanthids nor in Rhipidistids have we previously had sufficient knowledge of the membrane bones on the ethmoidal region to enable us even approximately to compare them with those of the Stegocephalians. It is true that WATSON and DAY's observations on the *Osteolepis* and *Glyptopomus* published in 1916 and BIRKS' paper on *Megalichthys* published the same year constitute a great advance in this respect, but it is only on the basis of the results given above, arrived at by my investigations of *Eusthenopteron*, *Dictyonosteus* and the Coelacanthids, that we are able to attain to some extent a real understanding of the arrangement and morphological value of the bone elements in question. — It is especially noteworthy in this connection, as we have seen, that the Coelacanthids too have preserved a rather primitive character, in this respect.

As far as we know (cf. text figs. 43, 44, 51, 57, 58) the membrane bones on the dorsal surface of the ethmoidal region both in Rhipidistids and Coelacanthids are arranged in the following way. 1) Farthest laterally we find on each side a number of rather small nasal elements or one larger nasal plate, apparently formed by fusion of a number of originally independent elements. In *Dictyonosteus* there are three nasal elements on each side; in *Eusthenopteron*, on the other hand, they seem to be fused into one plate and in the Coelacanthids not only in this case but the nasal elements may also have fused with the antorbital elements as well. As the original number of nasal plates on each side seems to have been at least three, I shall speak of a nasal series of elements in the continuation. This series is pierced by the supraorbital canal and is also characterized by its position on the dorsal side of the nasal capsule and by the fact that it always forms the dorso-medial boundary of the external nasal aperture(s). 2) Medially of the nasal series there is usually one paired, fairly large bone-plate, the postrostral, which meets that of the opposite side in a median suture. In *Dictyonosteus* and certain Coelacanthids the postrostral is represented on each side by an anterior and a posterior plate, in *Eusthenopteron* and a number of Coelacanthids, on the contrary, only one larger plate is present. It is probable, however, that the original number on each side was at least two, a view that seems to be also supported by WATSON and DAY's restorations of *Osteolepis*, provided that these are correct. 3) A paired or unpaired bone-plate, generally rather small, is always wedged in between the anterior ends of the postrostrals (or their most anterior elements). I have chosen the name of interrostral for this. 4) A series usually consisting of a number of rather small elements which I have termed rostrals, extends across the anterior end of the snout immediately in front of the nasal series, the postrostrals and the interrostral (possibly interrostrals, if it was paired). Anteriorly the rostrals are bounded by the premaxillae and an additional characteristic of them is that they are pierced by the ethmoidal commissure between the infraorbital sensory canals.

It is of special importance to note in this connection too that the premaxillae in both *Dictyonosteus* and *Eusthenopteron* do not extend on to the dorsal surface of the ethmoidal region or do so to only a very slight extent; they are very low and give the impression of having arisen by fusion of bases of teeth (cf. ALLIS 1919a).

In certain Stegocephalians we find a distinctly developed ethmoidal commissure between the infraorbital canals (*Tertrema*, WIMAN, 1914b, Pl. VII; *Loxomma*, EMBLETON and ATTHEY, 1874, Pl. IV). This commissure is situated there on the premaxillae. In a number of forms the supraorbital canal also extends into the premaxillary on each side and may anastomose there with the ethmoidal commissure as in *Tertrema* (WIMAN, loc. cit.). Now since, as we know, the premaxillae of the Stegocephalians often have a rather considerable extension backwards over the dorsal surface of the ethmoidal region, and also always form part of the dorso-medial boundary of the nasal apertures, it can of course scarcely be doubted that these bones are not homologous with the similarly termed bones in *Dictyonosteus* and *Eusthenopteron*. For, as far as one can see, they seem in the first place to correspond not only to the premaxillae of the Rhipidistids but also to the rostrals of these fishes (cf. ALLIS, 1898, pp. 450—456), and it is also very probable that in their posterior part, medially of the external nasal apertures, the most anterior elements of the nasal series are included. In certain Stegocephalians, as e. g. *Keraterpeton* (FRITSCH, 1883, vol. I, p. 139, fig. 83), it seems, at least to judge from their extension backwards, that even the homologues of the interrostrals might occasionally be fused with the premaxillae. On the other hand the homologues of the postrostral elements on each side, by fusion with the homologues of the middle element of the nasal series of its side and often probably with the homologues of the interrostral as well, has given rise to the large paired bone-plate, called «nasal» in the Stegocephalians. The most posterior nasal plate in Stegocephalians is, to judge from the course of the supraorbital canal, probably fused with the bone that is sometimes called the adlacrymal, sometimes the lacrymal.

The conditions just described also seem to explain the appearance of certain unpaired elements in the cranial roof of Stegocephalians. Thus WATSON's internasal (cf. WIMAN, 1917, pp. 232—236; BROILI, 1917, pp. 571—576; WATSON, 1913a, p. 340; GREGORY, 1917, pp. 977, 979, 980) seems apparently to correspond to a rostral element, and the so-called interfrontal might eventually correspond to a pair of fused postrostral plates. It is more probable, however, that the interfrontal is homologous with a bone of *Dipterus valenciennesi* lettered by PANDER 1858 in his Pl. 3, fig. 1 with the figure 3.

With regard to the membrane bones of the cheek I must first of all strongly controvert the view of BAUR (1896) and a number of succeeding authors (MOODIE, 1908; ALLIS, 1898, pp. 439—445; 1919b, pp. 81—86) that the squamosal (paraquadrate, GAUPP, 1895) of the Stegocephalians corresponds to a preopercular and their quadratojugal to a subopercular or preopercular.¹⁾ The knowledge we now possess of the skeletal elements in the cheek of Rhipidistids and Coelacanthids and the course of the sensory canals, shows us that BAUR's homologization cannot be correct. Similarly it is evident that the quadratojugal of the Stegocephalians cannot correspond to an interopercular, as GREGORY (1915, p. 335) has maintained. It seems instead to be fairly certain that the bone termed the squamosal in the Stegocephalians is a squamoso-preopercular and the quadratojugal a preoperculo-quadratojugal in the same sense as in the Coelacanthids. It is also probable that in the same way as in the Coelacanthids the jugal of Stegocephalians includes both the homo-

¹⁾ That POLLARD's view 1892 (1892a, p. 410) in this case is still more wrong is easy to understand from the facts put forward above.

logues of the jugal and the lacrymal of the Rhipidistids, according to the terminology used by WATSON and DAY (1916) and GOODRICH (1919). Finally with regard to the postorbital of the Stegocephalians it is not possible to establish whether it corresponds to that of the Rhipidistids alone or whether it has other components as well.

As is seen, the cheek plates of the Coelacanthids thus practically all show a similar composition to those in the Stegocephalians. It appears most probable, however, that this is not a primary agreement but a secondary one, originating in both cases from a Rhipidistid-like type.

We have found that the palatoquadrate of the Coelacanthids and probably of the Rhipidistids is attached to the posterior part of the orbitotemporal region in about the same way as in the primitive Stegocephalians. In addition it is also striking that in the majority of Coelacanthids and at least in certain Rhipidistids the entopterygoid has been exceedingly high and wide at its posterior part, owing to which it has a considerable resemblance to that of the Stegocephalians.

The mandible of the Coelacanthids is, as we have seen, more specialized than that of the Rhipidistids and therefore different from that of the Stegocephalians in various respects. It still preserves certain primitive features, however, and such bones as the coronoid and the compound splenial (infradental) show relations somewhat like those of the similarly termed bones in the Stegocephalians.

With regard to the hyoid arch the Coelacanthids and the primitive Tetrapods show at least a superficial resemblance, inasmuch as its dorsal part is considerably reduced. In Rhipidistids, on the other hand, according to TRAQUAIR'S (1881, p. 171) and WATSON and DAY'S (1916, p. 16) statements, a hyomandibula which, if not strongly ossified, is still somewhat large is developed, and it seems very probable that under such circumstances the reduction of the hyoid arch in the Coelacanthids ought to be considered as an independent specialization not implying any relationship with the Tetrapods.

Finally the sensory canals in Stegocephalians shows in their course considerable resemblances in several respects with those both of Coelacanthids and Rhipidistids, as is clearly shown by GOODRICH'S (1919) figures of *Osteolepis* and my own figures in this work of *Dictyonosteus*, *Eusthenopteron*, *Wimania* and *Axelia*.

* * *

The facts mentioned above ought to show that the Coelacanthids too have contributed essentially to a correct understanding of the fossil *Crossopterygii* and of the affinities of the latter with the Tetrapods. We can now see more clearly than before that the Stegocephalians most closely resemble in several respects the fossil *Crossopterygii* and among them specially the Rhipidistids. I consider it improbable, however, that the Tetrapods originate from Rhipidistids of any known type. It is true that among the primitive Teleostomi the ancestral form of the Stegocephalians has apparently resembled most closely the Rhipidistian type, but it must, however, have been still more primitive than this. We must suppose, for instance after what we have seen with regard to the relations of the membrane bones in the roof of the ethmoidal region, that this primitive ancestral form had the dermal skeleton of the cranial roof over the labyrinth and orbitotemporal region developed somewhat as is found in *Dipterus valenciennesi*, and

over the ethmoidal region according to the pattern still seen more or less distinctly persistent in *Dictyonosteus*, *Eusthenopteron* and Coelacanthids. Moreover, the bone-plates of the cheek must also have consisted of a larger number of independent elements than is found in, e. g., *Holophychius* (cf. WATSON and DAY, 1916, pp. 2-7, 22, fig. 1). — In other words, in this theoretical ancestral form of Tetrapods and Crossopterygians the dermal skeleton in the cranial roof and cheek would have consisted of a rather large number of fairly small plates, arranged in a certain regular way. The majority or perhaps all of the elements for which we now use the same names in Tetrapods and fossil Crossopterygii would not be inherited as such from a common ancestral form, but might have arisen independently in both cases.

If my view with regard to the common ancestral form of the Rhipidistids and Tetrapods is correct, it also implies that the Tetrapods were developed very early probably in lower Devonian or even in upper Silurian (cf. SROMER, 1920; BROILI, 1918, p. 165).

Concluding remarks on the systematic position of the Coelacanthids.

I have been able to show in this work the untenability of the view maintained by GOODRICH 1909 and to some extent by WATSON (1912) as to the mutual relations of the Coelacanthids and the Rhipidistids. On the other hand GOODRICH's assumption as to the relationship of the Polypterids has partly received additional support, and because of this I have considered that I ought to separate these from the fossil *Crossopterygii* and place them as an independent order between the latter and the *Actinopterygii*. My suggestion for a provisional classification will therefore appear as follows:

Order Crossopterygii

Sub-order *Haplistia*

Fam. Tarassiidae

Sub-order *Rhipidistia*¹⁾

Fam. Holophychidae

» Rhizodontidae

» Osteolepidae

» Onychodontidae

Sub-order *Actinistia*

Fam. Coelacanthidae

Order Brachiopterygii

Sub-order *Cladistia*

Fam. Polypteridae

Order Actinopterygii.

¹⁾ WATSON and DAY (1916, p. 26) point out the great difficulty now present with regard to the subdivision of the Rhipidistids into families. The prevalent classification in this request has not turned out to correspond to the natural relationship between the different forms. Both these investigators consider it most convenient at present to refrain provisionally from any attempt at a classification into families. BIRKS (1916, p. 327) also came to the conclusion that the subdivision of the Rhipidistids hitherto used is unsatisfactory.

Order Actinopterygii.

Family Palaeoniscidae.

Historical remarks.

In 1873 MARTIN (723—734) had grouped the genera *Palaeoniscus* BLAINVILLE, *Acrolepis*, AGASSIZ, *Amblypterus* AGASSIZ, *Pygopterus* AGASSIZ, *Saurichthys* AGASSIZ and *Cheirolepis* AGASSIZ in one family to which he gave the name of *Palaeoniscidae*. But the family obtained its present definition by TRAQUAIR's works and it is TRAQUAIR's great merit that he has elucidated in detail its systematic position in connection with a thorough study of the osteology of the forms belonging to it. TRAQUAIR's numerous works on this subject (cf. DEAN, 1917, Bibliography of fishes, pp. 551—557) and especially his large monograph on the Palaeoniscids of the British Carboniferous formations (1877—1914) constitute a great advance in our knowledge of the anatomy of the more primitive *Actinopterygii* in general.

In the work just mentioned TRAQUAIR dealt also with the earlier history of the Palaeoniscids, and so I merely refer to his account (1877 a, pp. 1—13, 34—42) for information about this.

In addition to TRAQUAIR it is especially WOODWARD (1889 b, c, d; 1890 a; 1891 b; 1893 a; 1895 a; 1898 a; 1903; 1906 a, b; 1908 a; 1910 a; 1912 etc., cf. DEAN 1917, Bibliography of fishes, pp. 645—653), who has devoted his attention to the study of the Palaeoniscids during the last few decades. Among other investigators who have also been occupied with them recently may be mentioned ABEL (1919, pp. 183—190), BRIDGE (1878, pp. 719—724), BROOM (1909 a; 1913 a, b), DAMES (1888), EASTMAN (1907, pp. 256—274), FRITSCH (1895, vol. 3, pp. 76—80, 83—126), GOODRICH (1909, pp. 210—223; 302—321), LAMBE (1910; 1916), MODIE (1915) and TORNQUIST (1904).

The majority of the investigators who have worked at the Palaeoniscids have in the main treated their material from the point of view of its classification and stratigraphical distribution. Besides TRAQUAIR, WOODWARD and BRIDGE it is thus really only ABEL, BROOM, FRITSCH and MODIE who have made contributions of any great importance to our knowledge of the anatomy. It is true that in many cases the state of preservation of the material present has not been suitable for a more detailed investigation, but sometimes at least better results could surely have been attained; this is my experience from the study of the Palaeoniscids from the Triassic of Spitzbergen.

Some remarks on the geological appearance and the geographical distribution of the Palaeoniscids, with special reference to the Triassic forms.

The Palaeoniscids appeared, as has already been mentioned, already in the middle Devonian with *Cheirolepis* (WOODWARD, 1891 b, pp. 451—457) and *Rhadinichthys* (TRAQUAIR, 1910, pp. 126—127; EASTMAN, 1907, pp. 258—260, 282; STENSJÖ, 1918 a, p. 71) and perhaps

also other genera.¹⁾ In the Carboniferous they soon flourished exceedingly and became wide-spread and during the Permian they were also represented by many forms. They are still not unusual in the Triassic, but become rare in the Jurassic and extinct in the Lower Cretaceous (WEALDEN) with *Coccolepis* AGASSIZ (WOODWARD, 1898 a, pp. 84—86; 1915, p. 23; TRAQUAIR, 1911 b, pp. 9—15).

From the Triassic, which is of special interest to us in this connection, the following genera are described: *Acrolepis* AGASSIZ (WOODWARD, 1912, pp. 292—293; LAMBE, 1916, pp. 42—44).²⁾ *Apatheolepis* A. S. WOODWARD (WOODWARD, 1890 a, pp. 12—15), *Atherstonia* A. S. WOODWARD (WOODWARD, 1889 d; 1893 a, pp. 393—397, BROOM, 1913 a, p. 3), *Helichthys* BROOM (1909 a, pp. 254—258), *Gyrolepis* AGASSIZ (STOLLEY, 1920, pp. 25—29, 75, 79, 83), *Myriolepis* EGERTON (WOODWARD, 1890 a, pp. 7—11; 1891 b, p. 515)³⁾, *Oxygnathus* EGERTON (BROOM, 1909 a, pp. 259—262), *Palaeoniscus* BLAINVILLE (WOODWARD, 1908 a, p. 22),⁴⁾ *Pygopterus* AGASSIZ (STOLLEY, 1920, p. 81) and *Urolepis* BELOTTI (DE ALESSANDRI, 1910, pp. 42—49). From strata which might possibly be Triassic but whose age is not quite certain we have in addition the genera *Elonichthys* GIEBEL (LAMBE, 1916, pp. 39—42), *Psilichthys* HALL (HALL, 1900), and a supposed Palaeoniscid fish *Turseoos* LEIDY (cf. WOODWARD, 1891 b, p. 527) really not determinable.⁵⁾

In the Triassic rocks of Spitzbergen are found several genera of Palaeoniscids and it is evident that the Palaeoniscids there constitute an important part of the fish fauna. In 1912 WOODWARD described a number of Palaeoniscid remains in the material collected by B. HÖGBOM. The new material now present contains a number of additional forms and at present we know no less than five genera, *Birgeria* STENSIÖ (1919, pp. 177—181), *Glaucolepis* n. g., *Pygopterus* AGASSIZ, *Boreosomus* n. g. and *Acrorhabdus* n. g.

Birgeria is, as we shall see, established for a species that is identical with or at any rate very closely related to the species *Saurichthys mougeoti* AGASSIZ. As far as one can judge at present, *Glaucolepis* seems to resemble *Gyrolepis*. The species mentioned by WOODWARD 1912 (p. 293) under the name of *Myriolepis*? sp. has with the more complete material now present, turned out to belong to the genus *Pygopterus*, while the forms that he referred to to the genus *Acrolepis* on the same occasion have revealed themselves as

¹⁾ Cf. WOODWARD, A. S., 1916, Quart. Journal, Geol. Soc. vol. 72 p. LXXX.

²⁾ The species described by LAMBE as *Acrolepis laetus* from deposits of probable lower Triassic age in the district of Alberta, Canada presumably does not belong to the genus *Acrolepis*. The *Acrolepis* species described from Spitzbergen undoubtedly represent a new genus as we shall see.

I cannot say anything as to the conditions of the two Tasmanian species *A. hamiltonii* JOHNSTONE and MORTON and *A. tasmanicus* JOHNSTONE and MORTON as the literature about these was not accessible to me (cf. CHAPMAN, 1914).

³⁾ The doubtful *Myriolepis* from Spitzbergen, noticed by WOODWARD in 1912 (p. 293), seems in fact to belong to *Pygopterus* AGASSIZ.

⁴⁾ WOODWARD is doubtful (1908 a, p. 22) and probably with justice, whether the species from the Triassic described as *Palaeoniscus* really belong to this genus.

⁵⁾ CHAPMAN in 1914 (p. 264) put *Psilichthys* among the Jurassic fishes. On the other hand in the same work (p. 263) he considers that all the fish genera described from the Hawkesbury series at St. Peter's (WOODWARD, 1908 a) are of upper Triassic age. Thus he even includes the species that WOODWARD expressly states to be of Perno-Carboniferous age. With regard to the Palaeoniscids this means that, besides the genera mentioned above, *Elpisopholis* A. S. WOODWARD ought also to occur in the Triassic. In this case, however, CHAPMAN's view does not seem probable.

representatives of a new genus, *Boreosomus*. The species noticed by myself in 1918 (1918b, p. 77) as *Gyrolepis*? sp. also undoubtedly seems to pertain to the new genus for which I have suggested the name *Glaucolepis*.

The Triassic of Spitzbergen has thus at least two genera of Palaeoniscids, *Birgeria* and *Pygopterus*, in common with the continental European Triassic formations (cf. STOLLEY, 1920, pp. 75—83).

Genus *Birgeria* STENSIÖ.

Synonym: *Saurichthys* (in part) AGASSIZ, Poissons fossiles, 1844, Vol. II, part II, p. 85.

As I have had occasion to mention in an earlier notice (STENSIÖ, 1919, pp. 177—178) we find in the Triassic of Spitzbergen remains of a large fish which is apparently identical with or at any rate very closely related to AGASSIZ's *Saurichthys mougeoti* (WOODWARD, 1895b, pp. 20—21). A closer study of these remains clearly showed, as I had also mentioned, that the so-called *S. mougeoti* is distinguished from the typical *Saurichthys* species, and that it is impossible to refer it to the same genus as these, but it must be set up as the type of a new genus, for which I have suggested the name *Birgeria* after Dr. BIRGER SJÖSTRÖM my friend and companion during the Spitzbergen expedition of 1915. It has appeared, in addition, as is also pointed out in my notice, that the relationship between *Birgeria* and *Saurichthys* cannot be particularly close, and that the former apparently cannot be referred to the Saurichthyids, but must belong to the Palaeoniscids.

The Rhaetic species *S. acuminatus* AGASSIZ (cf. WOODWARD 1895b, pp. 21—22) ought also to be incorporated provisionally with the genus *Birgeria*, and with much hesitation I include in it another species, the so-called *Saurichthys annulatus* WINKLER (WINKLER, 1880, pp. 132—135). For the reasons for this I refer to my critical revision of the genus *Saurichthys* below in this work (Part 2).

AGASSIZ's description of *B. mougeoti* was published in 1844 (vol. II, part 2, pp. 85—86). Already in 1837, however, the species in question was mentioned by HOGARD (p. 405). Afterwards a large number of investigators, e.g. GIEBEL (1848, p. 257), V. MEYER (1849a, p. 203; 1849b, p. 235), QUENSTEDT (1852, p. 231), SCHMID (1861, pp. 21—22, erroneously called *S. apicalis*), ECK (1865, p. 120), MARTIN (1873, pp. 723—735), REIS (1891, pp. 153—154) and WOODWARD (1895b, p. 20) have given more or less detailed descriptions of it. All the authors mentioned have, however, only been able to extend our knowledge of it very slightly, because of the very incomplete nature of the material available for them.

The most important characters distinguishing the genus *Birgeria* can be summarized as follows: Large fishes. The head low and broad. Ossifications in the primordial neurocranium and the visceral skeleton strongly developed. Myodome in a primitive stage of development. Mouth large; suspensorium oblique. Maxilla of the usual Palaeoniscid-type with a sculpture of tooth-like tubercles. Dentition well developed; teeth pointed and conical with a vertically striated, two-edged enamel cap; basally of this sometimes only a vertical very fine striation; sometimes in addition rather coarse vertical ridges, which then in their turn have the fine striae; no plicid-dentine is developed. Along the lateral margin of the maxillary and the dental there is a row of rather small teeth; medially of them is found another row of much higher and stronger teeth. The pterygoid and

the mixicoronoid have small teeth. The axial skeleton has a well-developed chorda, and, at least in the caudal region, ossified neural and haemal arches. From the latter ossified parts extend dorsally on both side of the ventral half of the chorda forming a sort of hypocentra. The unpaired fins are strong. The caudal fin is strongly heterocercal, deeply forked and nearly equilobate. The dorsal and the anal fin with numerous (more than 50) lepidotrichia. The endoskeletal radials of the dorsal fin with ossifications in the proximal and middle segments; those of the ventral fin have, only posteriorly, separate ossifications in the proximal and middle segments; otherwise only a single long ossification in each endoskeletal radial, extending from the haemal spines to the lepidotrichia. The anal fin opposite at least the posterior half of the dorsal fins. The ventral fins large with a rather long base and consisting of a large number (about 50) of lepidotrichia. In all the fins the lepidotrichia are unjointed for a short distance proximally; the other parts are closely jointed. The ganoine ornament is totally lacking on all of them. The rige scales are very powerful on the upper lobe of the caudal fin; fulcra are not known. The squamation is reduced except for the dorsal lobe of the caudal fin, where the scales are narrow and high and without ganoine. The lateral line of the body was surrounded by fine bone-tubes.

Little has as yet been ascertained as to the relationship between *Birgeria* and other known genera of Palaeoniscids. It is, however, presumable that, at least in certain respects, *Birgeria* was more specialized than several of the earlier Palaeozoic Palaeoniscids.

Birgeria mougeoti AGASSIZ.

(Pl. 20, fig. 6; Pl. 21; Pl. 22, figs. 1-3; Pl. 23, figs. 1-3; Pl. 24, figs. 1, 2.)

Synonyms; *Saurichthys mougeoti*, AGASSIZ, 1844, vol. II, part 2, p. 85; for extensive list of synonyms see WOODWARD A. S. Catalogue of Fossil fishes in the British Mus., part III, 1895, p. 20.

Detached teeth of this or possibly of a couple of closely related species as well are found in several horizons within the Triassic rocks of Spitzbergen (*P.* 1-5, 11, 15, 31, 48, 52, 603, 623-624, 626-628, 633-634, 795, 878; some detached teeth in the possession of Prof. SALOMON of Heidelberg). At the fish horizon there occur not infrequently, together with such teeth, more or less well preserved parts of heads (*P.* 165, 169, 171, 340-342, 345, 348-349). In addition there were fairly often found in this horizon remains from the abdominal and caudal regions of a large Palaeoniscid fish, which I am unable to refer to any species other than *B. mougeoti*. It is true that I have never found these remains (*P.* 143, 144, 150-158, 160-164) in connection with teeth or crania of *B. mougeoti*, but the other circumstances of the finds and the size suggest very decidedly that they belong to this species. Confirmation of this is afforded to some extent by a large Palaeoniscid-like maxilla with typical teeth described by me in an earlier paper from the German Muschelkalk (STENSJÖ, 1919).

B. mougeoti attained a very considerable size. The greatest height of the body between the dorsal and the anal fin in specimen *P.* 155*d* was thus no less than 25 cm., and a couple of caudal fins (*P.* 153, 155*c*) were probably more than 40 cm high from the extremity of the dorsal lobe to that of the ventral one. The smallest caudal fin so far found is more than 20 cm high. The maxilla from the German Muschelkalk is, I have already stated in my earlier description of this, over 18 cm long. Assuming that *B. mougeoti* did not differ essentially from other Palaeoniscids in the shape of the body, we

may, according to our present knowledge, venture to estimate its length in large specimens at between 1 and 2 m.

The primordial neurocranium and its ossifications.

The best and most completely preserved neurocranium (*P. 165*; text fig. 61; Pl. 20, fig. 6; Pl. 22, figs. 1, 3; Pl. 24, fig. 2) was probably about 11–12 cm wide at its widest part. Its length in its present state of preservation is only about 11 cm, but has undoubtedly been much greater, as both the occipital and the ethmoidal are lacking. When nothing to the contrary is stated the following description is based on specimen *P. 165*.

The greatest width of the neurocranium was about between the well developed postorbital processes or was at least not far behind these (text fig. 61). The conditions of the anterior orbital boundary are impossible to state, but it is evident, however, that the orbits had a rather considerable size. The interorbital wall is in the whole thick and strong. The labyrinth region is wide in its anterior part; the posterior part grows fairly rapidly narrower and in this way passes, very much narrowed, into the occipital region. The greatest height of the neurocranium seems to be relatively slight, only 3.5 cm., which is probably partly due to the state of preservation of the cranium in question, as this is somewhat compressed in a dorso-ventral direction. The maximum height (text fig. 62) is situated in the posterior part of the labyrinth region; then there follows a somewhat lower part at about the boundary between the labyrinth and the orbitotemporal regions, and then once more a somewhat higher portion in the middle part of the last-mentioned region, after which the height continuously decreases anteriorly. The dorsal side of the neurocranium slopes gently and uniformly forward and the variations in height present here are due, as text fig. 62 and Pl. 20, fig. 6 show, to situations in the basal surface.

The lateral surfaces of the labyrinth region face strongly downwards in the anterior part. Backwards, on the other hand, this state of affairs gradually changes, so that they first turn directly laterally and then, towards the boundary of the occipital region, somewhat backwards as well owing to the rapid narrowing that, as already pointed out, takes place here. The lateral surfaces of the orbito-temporal region are directed in the same way as the anterior part of those of the labyrinth region.

The primordial neurocranium is to an unexpectedly great extent occupied by substitution bones. These are often considerably thick and massive and in several places they have undoubtedly corresponded to the entire thickness of the cranial wall. The smooth periosteal lamellae that characterize the exposed surfaces on the substitution bones in the majority of Teleosts are here in *B. mougeoti* (*P. 165*) very thin and usually weathered away, so that the other, cancellous substance appears and gives the bone a characteristic granulated surface. The centres of ossification, which in most cases are very distinct in the substitution bones of the Teleosts cannot be traced in this species.

The macroscopic appearance of the bone substance might possibly give the impression of calcified cartilage. A close investigation shows, however, immediately that this cannot be the case, but that we are concerned here with real bone substance. This bone substance is formed of thin lamellae, connected with each other and surrounding small cavities, which are filled with calcite, infiltrated during the process of fossilization. Afterwards, when the lamellae between these cavities are weathered, and the contents, which have

greater powers of resistance, remain, this gives the surface of the bones the granular appearance we have mentioned. I was able to observe cell spaces (lacunae) here and there in the lamellae.

Substitution bones of a similar structure are found in Saurichthyids, in *Dictyonosteus* among the Rhipidistids, and partly in the Coelacanthids as well. WOODWARD (1915, p. 39, p. 44) has found a bone substance with a similar structure in *Lepidotus* to. It is thus not improbable that this structure is characteristic both for lower *Actinopterygii* and *Crossopterygii*. On the other hand the conditions of the fossil *Dipnoi* (*Dipterus*) in this respect are uncertain. I myself have not had an opportunity to investigate any cranium of these, and no definite information on this matter is found in the literature at my disposal.

At least a basioccipital was present in the occipital region of *B. mougeoti*. The anterior end of this bone is still preserved, as it extended in anterior direction under the most posterior part of the labyrinth region (*Bo*, Pl. 20, fig. 6; Pl. 22, figs. 1, 3). In cross section (*Bo*, text fig. 59) this end of it is almost semicircularly curved with the concavity dorsally. In the concavity there probably rested the anterior part of the chorda dorsalis, which probably extended through the entire occipital region, from which it probably also continued some distance into the caudal part of the labyrinth region.

In the labyrinth region are found two paired substitution bones, one of which (*Ausph*, text figs. 61, 64 A, Pl. 22, figs. 1, 3) is situated in the postorbital process, while the other occupies the posterior and middle parts of the region (*Pro.o*, text figs. 59, 60, 61, 62; Pl. 20, fig. 6; Pl. 22, figs. 1, 3; Pl. 24, fig. 2).

In a caudal direction the latter bone extends farther than the present cranial part is preserved and it is therefore impossible to decide as to its conditions in its most posterior part. In a rostral direction it extends nearly to the exit of the facialis nerve, where it is separated by a cartilaginous interspace from another ossification situated in the orbitotemporal region (text fig. 62); this cartilaginous interspace forms the most anterior part of the labyrinth region. The height of the bone in question equals the whole lateral wall of the neurocranium. From its medial upper edge there issues dorsally of the cranial cavity a horizontal longitudinal list (*k*, text figs. 59, 60; Pl. 24, fig. 2) which towards the posterior end of the bone meets the corresponding list of bone of the opposite side in the median line, but it is impossible to decide whether a fusion has taken place there between them or whether a suture still exists. The dorsal surface of this list forms the upper surface of the roof of the primordial neurocranium and is covered directly by membrane bones. The ventral surface of the list on the other hand, has, as far as can be seen, been joined to cartilage, and this has also been the case with the rest of the medial surface of the whole bone in question. Consequently, as I have tried to show in text figs. 59 and 60, the cranial cavity was in this region mostly surrounded by cartilage.

To judge from its extension, the large bone just described corresponds not only to the opisthotic but also the epiotic and prootic. Below I shall give a more detailed account of its homologues. I shall only add here that in the following, for the sake of brevity, I shall call it the prootico-opisthotic, and that among the recent forms it seems most to resemble TRAQUAIR's, opisthotic + epiotic in *Polypterus* (TRAQUAIR, 1871, p. 168).

If we now examine this peculiar prootico-opisthotic of *B. mougeoti* in detail we find the following. The cranium *P. 165* is certainly split both along and across and can therefore be investigated in several different sections, but in spite of this there is not much to observe in the labyrinth region, as part of this is much affected by pressure, so that the cavity for the labyrinth and certain foramina can no longer be clearly distinguished. To this is to be added the fact, which has already been emphasized, that it consisted partly of cartilage, which is of course not preserved.

Farthest caudally the prootic-opisthotic (*Pro. o.*, text fig. 59) is rather thin and was situated with the ventral half of its medial surface apparently against a strong ascending lamella (*pl*) of the parasphenoid. In the present state of preservation of the cranium, it is true, the prootico-opisthotic does not show the same conditions, but is somewhat removed from the parasphenoid lamella, *pl*. Everything goes to indicate,

Text fig. 59.

Birgeria mougeoti AGASSIZ.
Cross-section through the posterior end of the labyrinth region. After *P. 165*. *ch*, Cartilaginous parts dotted.

Bo, basioccipital; *Pro. o.*, prootico-opisthotic; *Psp*, parasphenoid; *ch*, chorda canal; *cv*, cranial cavity; *k*, medial list from the prootico-opisthotic in the roof of the primordial neurocranium; *pl*, profound lamella of the parasphenoid; *sl*, superficial lamella of the parasphenoid.

however, that this is a secondary condition, due to the compression of the cranium. The parasphenoid lamella, *pl*, which is paired, is about half as high as the neurocranium. Dorsally and partly also medially of it cartilage was present around the cranial cavity and partly round the chorda as well. Under these circumstances it is impossible to obtain an exact idea of the extent of this cartilage and the size and shape of the cranial cavity. Text fig. 59 is only intended to give an approximate representation of the conditions with regard to this.

A transverse section somewhat farther forward than the one described is shown in text fig. 60. Contrary to what was the case in the preceding section, the medial list of each prootico-opisthotic (*k*) does not reach the median line and becomes rapidly thinner medially. The lateral surface of the prootico-opisthotic of either side is covered in a dorsal part by a ventral longitudinal lamella (*vl*) from the supratemporo-intertemporal («squamosal»). Anteriorly each prootico-opisthotic has joined the cartilage in the anterior part of the labyrinth region. On the medial surface of this bone cartilage has certainly been present, and the labyrinth recess (*lb*, text fig. 60) was partly contained in this cartilage but, as has already been said, nothing certain can be established as to the shape of this recess or its connection with the cranial cavity. The parasphenoid lamella *pl* is strongly developed, although it is here of another shape and not quite so high as in the cross-section further back just described. It is impossible to decide whether the space between it and the ventral part of the prootico-opisthotic was filled with cartilage or bone. As a matter of fact it is not improbable that the labyrinth recess extended a little way down between them.

On the right side of the cranium we find in the most posterior part of the prootico-opisthotic a partly exposed canal, running dorso ventrally, which cannot have contained anything but the canalis semicircularis posterior (*c. sem. post.*, Pl. 22, figs. 1, 3). The canal is situated with its ventral half laterally of the parasphenoid lamella, *pl*, which I shall call in the subsequent description the profound lamella. I have also been able to verify, beyond all doubt, that the can. semicircularis externus (*c. sem. ext.*, Pl. 22, fig. 3)

n. glossopharyngeus. The lateralis branch, that has its exit together with this nerve, runs quite close to the lateral surface of the opisthotic for some distance in a dorsal direction and finally pierces the opisthotic and extends in this way on to the dorsal surface of the neurocranium. The posterior semicircular canal, according to SAGEMEHL (1884, p. 206) almost always comes into immediate contact with the epiotic.

In young specimens of *Lepidosteus* VERT (1907, pp. 173—188) has only found the prootic in close connection with the labyrinth. In older specimens, I have found that this was also the case with the epiotic and the lateral occipital, both of which were pierced by the posterior semicircular canal. While in younger individuals of a long-nosed *Lepidosteus* species I found a rather large cartilaginous interspace between the lateral occipital and the prootic, in adult specimens of a short-nosed species of the same genus I observed that these bones meet in a suture on the lateral wall of the labyrinth region, and, according to AGASSIZ, the same bone seems to have had a similar extension in the large specimen of *Lepidosteus osseus* investigated by him (AGASSIZ 1843, vol. II, Pl. B', fig. 2). In the adult specimens mentioned both of the bones in question have grown until they meet each other, and it is noteworthy that in the short-nosed species — the only one I had an opportunity of testing with regard to this — n. glossopharyngeus pierces the posterior part of the prootic. In older specimens the foramen vagi is quite surrounded by the lateral occipital. PARKER (1882, p. 481) says that he found an independent opisthotic, but I was unable to find anything of this sort in the specimens investigated by me. In his explanation of fig. 321, in «Cyclostomes and fishes» (1909, p. 342) GOODRICH says that the opisthotic of *Lepidosteus* may possibly be fused with the lateral occipital, a view to which I shall return later on.

In *Polypterus* TRAQUIR describes (1871, p. 168), as is mentioned above, only one paired substitution bone in the labyrinth region, which he interprets as the opisthotic + epiotic. TRAQUIR also points out that this bone is pierced both by the posterior and the external semicircular canals, and that it is also closely related to the sacculus («aids in the support of the otholithic sac»). On the other hand WIJHE (1882, pp. 257—258, Pl. XV, fig. 6) states that besides this bone he observed a small independent prootic, which was intimately connected with the parasphenoid. GOODRICH (1909, p. 295) holds a similar view too and considers that the prootic might be fused to the parasphenoid. Both POLLARD (1892a) and LEHN (1918) seem, however, to have overlooked WIJHE's statement mentioned above; at any rate they accept TRAQUIR's view without any criticisms. Recently SUPINO (1914, p. 183) has mentioned the occurrence in *Calamoichthys calabricus* SMITH of a large prootic, an epiotic and a small opisthotic, so that WIJHE's observations obtain a certain importance.

With regard to the opisthotic in *Polypterus* ALLIS in 1899 (pp. 55—56), after describing TRAQUIR's view, makes the following remark, which is very interesting in this connection: «It seems to me that it must include not only those two elements, which are, respectively, the intercalar and exoccipital of my description of *Amia* but also the so-called primary part of the squamosal of teleosts». It is therefore of great importance to know in more detail the relations of the squamosal, the opisthotic and the prootic in *Calamoichthys*, but unfortunately I have not had any opportunity of investigating this form and SUPINO has almost confined himself merely to giving the

names of the different bones. On a large *Polypterus* cranium at my disposal I have seen that the part of the parasphenoid which according to VAN WIJHE and GOODRICH corresponds to the prootic has a greater extension backwards and upwards than in the specimen figured by TRAQUAIR (1871). For while in this the lateral wall of the neurocranium between the opisthotic, the lateral margin of the parasphenoid and the process running dorso-caudally from the parasphenoid which is pierced by n. facialis consisted only of cartilage, this is not the case in the specimen investigated by me. The part of the parasphenoid that occupies the place of the supposed prootic here covers the lateral side of the bulla acustica saccularis in its anterior half and only a small amount of cartilage is visible behind it. I was able to observe with certainty, however, that this part was not attached in any very intimate way to the capsula auditiva, i. e. it is not to be looked upon as a replacing bone, and there is consequently no prootic component in it. On the other hand I was able to observe a weak remains of a much reduced independent prootic in the wall of the primordial neurocranium (*Pro*, Pl. 20, fig. 5). More closely defined, this rudimentary prootic is situated in the anterior lower corner of the bulla acustica saccularis. But it does not come into direct contact with the labyrinth, as it is considerably thinner than the cranial wall.

The conditions of the substitution bones in the labyrinth region in fossil Ganoids have hitherto been somewhat well known in *Lepidotus* alone.¹⁾ According to WOODWARD (1893 b, p. 560; 1915, pp. 37—39) the prootic and epiotic are there joined together here by means of a suture. One or both of them must therefore have more than the usual extension. Consequently it does not seem improbable that their relations to the labyrinth can be different from what is otherwise the rule. In this case the most probable assumption would be that the external semicircular canal pierced one or both of them. If the epiotic had a considerable extension antero-ventrally and if this alone was pierced by the external semicircular canal, it would seem as if it contained the homologue of that part of the pterotic of the *Teleostei* that consists of cartilage bone. On the other hand this last-mentioned pterotic component would of course probably be fused with the prootic, if this bone had a greater extension in the dorso-caudal direction than usual and if at the same time it could be shown that it enclosed the main part of the external semicircular canal. If, finally, the epiotic and the prootic had grown together and both helped to surround the external semicircular canal the conditions would be more complicated and difficult to explain.

From the account given, without a more detailed analysis of the conditions one might perhaps be inclined to overestimate the differences with regard to the relation between the labyrinth and the substitution bones in the capsula auditiva in different Teleostomes. To some extent (SAGEMEHL 1884, p. 207) it seems to be fairly certain that these different relations are due to a different degree of development of the labyrinth itself. They seem, however, to be chiefly more apparent than real, as they are presumably due to an incorrect idea as to the homologues of the different bones or to unsuitable

¹⁾ That the primordial neurocranium was well ossified in both *Dapedius* and other fossil forms is certainly well known (WOODWARD 1893b, pp. 563—564; 1895 b, pp. 128, 190, 287, 330 etc.; FROST 1913, pp. 219—222), but it has not been possible to establish anything in detail about the extension and relations of the different ossifications in these forms.

terminology. That this is the case may already be clear to some extent from what has been said above. But in order to obtain a somewhat deeper insight into the question it is necessary to discuss here briefly the different views that have so far been put forward about certain homologues of the so-called pterotic («squamosal») and opisthotic (intercalar) of the *Teleostei*.

SCHMID-MONNARD (1883, pp. 109—111, 116—123, 127—134) is of the opinion that he found the «squamosal» (pterotic) of the *Teleostei*, to be composed of three or four components. These components are said to arise separately during the ontogenetical development and are as follows:

- 1) a sensory canal component, which arises round the sensory canal;
- 2) a component of cartilage bone, which is formed round the external semicircular canal and occurs regularly together with the former;
- 3) in addition a fibrous component, formed in connection with the tendons that are attached on the posterior part of the bone in question, and finally
- 4) a fibro-cartilaginous component appearing in relation to the articulating surface for the hyomandibula. — Components 3 and 4, however are said to be inconstant.

SCHMID-MONNARD's view is followed in essentials by ALLIS (1899). Thus the latter describes in *Scomber* three of the above-mentioned components. Only the fibro-cartilaginous one is stated not to be present. With regard to the relations of the components in the «squamosal» (pterotic) in fishes in general ALLIS speaks as follows in 1899 (p. 59): «We thus see that the squamosal of fishes is composed of a canal component and a deeper-lying component which may be either a so-called membrane bone, or such a bone fused with a so-called primary ossification. The primary ossification may be wholly wanting, and perhaps the canal component too. Furthermore the canal component may be found entirely separate from the underlying bone, may be found fused simply with an underlying membrane component or may be found fused with such a component and with a so-called primary ossification, which latter ossification, alone, is traversed by the external semicircular canal. The canal component apparently always united with the underlying dermal bone may as a so-called dermal bone be fused with other adjoining dermal bones; while the primary ossification may be fused with other primary ossifications (*Ctenodus*) or with such ossifications and the intercalar (*Polypterus*). It is the primary part of the bone and not its «Deckknochenteil» that gives articulation to the hyomandibula».

SAGEMEHL (1885, p. 59; 1891, p. 507) describes in the *Teleostei* two components in the «squamosal» (pterotic), a dermal and a primary one.

Turning to the opisthotic we find that HUXLEY (1864, 1871) saw in it an integral ossification in the capsula auditiva.

SAGEMEHL (1884, pp. 191—192; 1885, pp. 45—46; 1891, pp. 556—558) also followed HUXLEY inasmuch as he considered the opisthotic as a bone that was originally developed phylogenetically in the cartilage of the capsula auditiva. Afterwards, according to his view, a secondary component could in certain cases be added to it, a fibrous ossification, which had arisen in the ligament fastening the suprascapular process to it. Further, according to his view, a partial or total reduction of the primary part took place in the *Teleostei*, so that the fibrous component alone is present in these. The reduction

would according to SAGEMEHL be caused by the «squamosal» developing more and more as a substitution bone in the capsula auditiva, so that the primary part of the opisthotic would be thrust aside and could not be developed. As has been pointed out above, he took the opisthotic in *Amia* to be a substitution bone.

Several years before SAGEMEHL-VROLIK (1873) had already shown convincingly that the bone called the opisthotic in the *Teleostei* is only a membrane bone, and because of this he introduced the new name of intercalar of it. Later on ALLIS (1899) especially adopted this view, and he too, as has already been pointed out, definitely states that he found that the opisthotic of *Amia* belonged to the category of membrane bones. The embryological investigations so far carried out on some *Teleostei* seem to show that the so-called opisthotic (intercalar) in these is formed exclusively as a membrane bone¹⁾ SCHLEIP, 1904, pp. 379—380; GAUFF, 1905, pp. 677—678, BÖKER, 1913, p. 385).

It is clear from what has been stated that we ought to adopt the name intercalar in the sense of a membrane bone for the so-called opisthotic of the *Teleostei* and *Lepidotus*. If ALLIS's account is correct the same term ought also to be used for the so-called opisthotic in *Amia*. In *Polypterus*, according to ALLIS (1899), the intercalar seems to be fused to the cartilage bone that forms the caudal part of the labyrinth region. — Because of its nature as a fibrous ossification the intercalar cannot possibly be homologous with the opisthotic in the Tetrapods (cf. ALLIS, 1897 b, p. 21; 1899) which, as we know, is a cartilage bone that is developed in relation to the posterior part of the labyrinth.

Among the recent Teleostomes it is easiest in *Polypterus*²⁾ to find a homologue to the opisthotic of the Tetrapods, as we have seen from the above summary of the literature. In this fish the opisthotic seems, together with the epiotic and intercalar, to form part of the large ossification that occupies the labyrinth region and is pierced by n. glossopharyngeus.³⁾

In the *Teleostei* the conditions of the pterotic and lateral occipital are such that a component of the opisthotic seems to form part of each of these bones. The opisthotic component in the pterotic would then be represented by the part that consists of cartilage bone. In the lateral occipital the opisthotic component would have its correspondence in the part that extends forwards in the lateral wall of the labyrinth region. The opisthotic might thus be divided over two of the adjacent bones.

It seems rather probable that the dorsal part of the opisthotic is reduced in *Lepidosteus*. The ventral part, on the other hand, might perhaps be divided over the lateral occipital and the prootic.

In *Amia* the reduction of the opisthotic has proceeded much farther, and it is very uncertain whether anything is left of it. If this were the case the remaining part would perhaps have fused to the prootic.

Among the fossil Teleostomes we find in the Coelacanthids nothing developed of the dorsal part of the opisthotic. On the other hand the ventral part seems to have been present in these fishes, as has been shown above (p. 54—61) although fused to the prootic.

¹⁾ The bone described by WOODWARD (1915, p. 38) in *Lepidotus* under the name of opisthotic seems in all respects to show almost the same conditions as the intercalar (so-called opisthotic) in the majority of the *Teleostei*.

²⁾ I except here the conditions in *Calamoichthys*, which are still very incompletely known.

³⁾ This is evident in the large specimen investigated by me.

In *Lepidotus* the opisthotic might perhaps have been divided into a ventral and a dorsal part, of which the former would, as in the *Teleostei*, be fused to the lateral occipital, while the latter would have been distributed over both the prootic and the epiotic or eventually only over one of them.

Instead of the view now put forward it might also be maintained that in several of the fishes mentioned the opisthotic might have been reduced, and that its place might have been occupied secondarily by adjacent bones. In this way, for instance, one might suppose could be explained the extension of the lateral occipital and the prootic in *Lepidosteus*, the lateral occipital, the prootic and the epiotic in *Lepidotus*, the prootic in the Coelacanthids and the lateral occipital in the *Teleostei*. With regard to the pterotic of the *Teleostei* one is compelled to assume, if it is desired to carry these views through consistently, that the cartilage component of this bone is a new formation.

It is of course possible that objections of this sort are more or less justified, but it seems difficult to me at present to accept them for the following reasons:

1) Elements of bones equivalent to the opisthotic of the Tetrapods exist in lower Teleostomes, e. g. *Polypterus* and *Birgeria*. To assume, under these circumstances, that the cartilaginous bone component of the pterotic in the *Teleostei* would be a new formation, seems to be unjustified so long as no certain evidence of this is put forward.

2) The conditions in *Birgeria* which will be described below, seem to indicate the way in which fusion between the opisthotic and the membrane bones of the cranial roof would have taken place, and how after this the dorsal part of the opisthotic may be supposed to have become loosened from the ventral part by mechanical processes.

3) If in connection with the facts mentioned we remember that in Tetrapods (cf. GAUPP, 1905, pp. 711—712, 772, 780, 786 etc.; cf. also p. 141 above) the opisthotic is often fused with the lateral occipital, we ought not to find it especially curious that the ventral part of the opisthotic may be fused with the lateral occipital in certain of the Teleostome fishes. On the other hand there seems to be an example in the Tetrapods (cf. p. 141 above) to show that the opisthotic can be fused to the prootic, and so the conditions that I think I have found in the Coelacanthids do not seem to be so exceptional either as one might perhaps be inclined to think.

In order now to connect the description with *Birgeria mougeoti* we find that the opisthotic component of the prootico-opisthotic of this fish is presumably pierced by n. glossopharyngeus (IX, text fig. 61). It is obvious that this component in its entirety corresponds well to the similarly named component in *Polypterus*. This is also true in the main of the epiotic component in the two genera.

The prootic component in the prootico-opisthotic of *B. mougeoti* is not particularly strongly developed. Forwards it only extends to the facialis canal. Its most anterior part is pierced by a fine canal, which rises from the facialis canal and has its exit on the dorsal side of the primordial neurocranium under the supratemporo-intertemporal antero-medially of the ossification centre of this bone. In my opinion we are probably concerned here with the canal for r. oticus lateralis.

Whether the prootico-opisthotic of *B. mougeoti* also had any intercalary component incorporated with it cannot be established because of the deficient state of preservation of the present material. With regard to the very interesting relation between the prootico-

opisthotic and the supratemporo-intertemporal, of which something has been indicated above, I may refer to the description below of the membrane bones of the cranial roof.

The above-mentioned (p. 153) paired cartilage bone in the postorbital process of *B. mougeoti* apparently represents the autosphenotic (*Ausph.*, text figs. 61, 64 A, Pl. 22, figs. 1, 3). Its length is about $2\frac{1}{2}$ times as great as its minimum breadth and its two ends are blunt. The posterior end and the medial margin have been joined with cartilage in the way shown in text figs. 61 and 64 A.

The cartilaginous part in the anterior portion of the labyrinth region has been pierced by n. facialis (VII, text figs. 61, 62; Pl. 20, fig. 6; Pl. 22, figs. 1, 3), and probably by the spiracular canal as well, if this was developed. Farthest anteriorly this cartilage forms the posterior boundary of the foramen through which the trigeminus roots had their exit (V, text figs. 61, 62; Pl. 20, fig. 6; Pl. 21, fig. 3). Moreover the hyomandibula must apparently have articulated with the same cartilage at least to some extent. The places of exit for trigeminus and facialis are described in detail below.

The actual boundary between the orbitotemporal and the labyrinth regions is, as usual, not sharp. The autosphenotic extends dorsally a long way forward over the orbit and has been attached medially (text figs. 61, 64 A) to cartilage that passes over into the interorbital wall. This cartilage (*ca*, text fig. 61), which was situated immediately beneath the dermal bones of the cranial roof certainly grew thinner rostrally. While the boundary in the dorsal parts of the cranium is thus found far forward, in the middle and ventral parts, on the other hand, it is situated considerably more backwards. For reasons that will be given below most ventrally it ought really to be drawn through the postero-ventral parts of the large ossification that occurs in the orbito-temporal region, but for practical reasons I have here in my

Text fig. 61. *Birgeria mougeoti* AGASSIZ.

The neurocranium from the ventral side. After P. 163. $\frac{1}{2}$. The cartilaginous parts are dotted.

Ausph., autosphenotic; *Pro. o.*, prootic-opisthotic, including the opiotic as well; *Psph.*, parasphenoid; *Sph.*, sphenoid; *a.*, corner on the edge between the latero-dorsal and lateral (ventro-lateral) surfaces of the sphenoid; *ca.*, cartilage joining the autosphenotic with the latero-dorsal surface of the sphenoid; *my. trig.*, opening of the myotome and trigemino-facialis chamber; *ophth. lat.*, anterior opening of the canal for n. ophthalmicus lateralis; *pr. asc.*, processus ascendens of the parasphenoid; *t.*, nerve or blood vessel foramen; *vi*, ventral lamella from the supratemporo-intertemporal; *vp.*, ventral process from the supratemporo-intertemporal; *v.s.*, *v.g.*, foramina presumably for vessels and nerves to the cranial roof; *VII*, the posterior opening of the facialis canal; *IX*, foramen for n. glosso-pharyngeus.

description placed it at the line between this ossification and the cartilage following behind in the anterior part the labyrinth region.

As has already been mentioned, the orbito-temporal region is occupied chiefly by a powerful bone, which, curiously enough, is unpaired (*Sph*, text figs. 61, 62, 63, 64; Pl. 20, fig. 6; Pl. 21, figs. 1—3; Pl. 22, figs. 1, 3). From the place of exit of the trigeminal roots (V) this bone extends forwards to the ethmoidal region or ought at any rate to have reached fairly near this region with its anterior end. Apart from its anterior and posterior parts its height is equal to or only slightly less than that of the primordial neurocranium. In position and extension it thus seems to correspond most closely to a sphenoid in the same sense as in *Polypterus*, or *Dictyonosteus* (cf. pp. 56—60, 121, 142 above),

and the account given below will show that this view is correct. I have accordingly used the term sphenoid for this bone.

For a more exact description it is proper to distinguish on the sphenoid of *B. mougeoti* an unpaired pars basalis and two partes laterales, one issuing along the right and one along the left border of the dorsal surface of the pars basalis (text figs. 62, 63, 64; Pl. 20, figs. 6; Pl. 21, figs. 1—3; Pl. 22, figs. 1, 3).

The pars basalis (*d*, *bsph*, *pc*) extends caudally somewhat farther than the partes laterales; rostrally, on the other hand, it is considerably shorter than these (text figs. 62, 63 A, B, C; Pl. 20, fig. 6; Pl. 21, figs. 1—3; Pl. 22, figs. 1, 3). Its anterior end is

Text fig. 62. *Birgeria mougeoti* AGASSIZ.

A somewhat schematized sagittal section through the lateral wall of the neurocranium. After P. 165, 24. Section surfaces through cartilage bones marked with a fine reticulum. The restored cartilaginous parts are dotted:

Pro. o., prootico-ophthotic; *Psph.*, parasphenoid; *Sph.*, sphenoid; *al.*, anterior portion of the pars lateralis of the sphenoid; *a. opt.*, foramen for art. optica; *p.*, process on the posterior margin of the pars lateralis of the sphenoid; *b. sph.*, portion of the pars basalis of the sphenoid between the fenestra optica and canalis transversus; *c.*, process on the posterior margin of the pars lateralis of the sphenoid; *c. transv.*, canalis transversus (pituitary canal); *d.*, portion of the pars basalis of the sphenoid anterior to the fenestra optica; *fen. opt.*, fenestra optica; *my.*, fossa in which musc. rectus externus had its origin. The fossa corresponds to a part of the median section of the myodome in *Amia* and *Teleostei*; *ophth. lat.*, probable exit of the n. ophthalmicus lateralis; *pc.*, basal parachordal plate of the sphenoid; *pl.*, profound lamella of the parasphenoid; *v.*, foramen probably for vena cerebialis anterior; *II*, foramen opticum; *III*, foramen oculomotorii; *IV*, foramen trochlearis; *V*, place of exit for the trigeminal roots; *v.*, canal for n. ophthalmicus profundus or a somewhat equivalent nerv. (longitudinal section); *VII*, assumed position of the exit for n. facialis.

truncated. Its anterior half (*d*) is in the anterior portion much more narrow farthest ventrally than dorsally and a transverse section through it consequently shows the shape of a triangle with the point ventrally and the base dorsally. In the posterior portion of the same half (*d*), however, the appearance of the cross-section is somewhat complicated, owing to a fenestration (*fen. opt.*, text figs. 62, 63, 64 A; Pl. 20, fig. 6; Pl. 21, figs. 1—3) between the two orbits, and this fenestration, as we shall see, corresponds to a ventral part of the fenestra optica in the *Teleostei* and higher ganoids. Dorsally this fenestration is separated from the cranial cavity by a thick and fairly wide mass of bone (text figs. 63 C, 64 A), ventrally, on the other hand, it is bounded only by a narrow rib of bone lying against the dorsal surface of the parasphenoid (*Psph*). — As will be obvious from what has been said above, the ventral surface on the anterior half of the sphenoid is reduced nearly to an edge (text figs. 63 B, 64 A; Pl. 21, figs. 1—3; Pl. 22, figs. 1, 3).

The posterior half of the pars basalis of the sphenoid (*bsph*, *pc*), which begins immediately behind the fenestra optica, has quite a different shape from that of the anterior half. The width is about as great dorsally as ventrally. The transverse section has consequently a somewhat rectangular shape, and we can distinguish a dorsal and a ventral surface besides a right and a left lateral (text figs. 63, 64 B; Pl. 20, fig. 6; Pl. 21, figs. 1—3).

Text fig. 63. *Birgeria mougeoti* AGASSIZ.

The sphenoid. After P. 163, 1/2. The section surfaces shown by reticulation.

A) Sphenoid from the right side; B) from the ventral side; C) in a median sagittal section.

Psph, parasphenoid; *a. ap*, corners on the edge between the latero-dorsal and the lateral surfaces; *a. car. int.*, foramen for arteria carotis interna; *a. opt.*, foramen presumably for arteria optica; *al*, anterior portion of the pars lateralis of the sphenoid; *b. c.*, processes on the posterior margin of each pars lateralis of the sphenoid; *bp*, basipterygoid process; *bsph*, portion of the pars basalis of the sphenoid between fenestra optica and canalis transversus; *c. transv.*, canalis transversus (pituitary canal); *d.*, portion of the pars basalis of the sphenoid anterior to the fenestra optica; *dors. sell.*, dorsum sellae; *fen. bas. post.*, remains probably of fenestra basicranialis posterior; *fen. opt.*, fenestra optica; *fi*, incisus probably pierced by n. abducens; *f. hyp.*, fossa hypophyseos; *my*, fossa in which musculus rectus externus has originated. Corresponds to a part of the middle part of the myelome in *Ania* and Teleosts; *ophth. lat. prob.* place of exit for n. ophthalmicus lateralis, *ophth. lat. p.* posterior opening of the canal for ophthalmicus lateralis; *ophth. lat. a.* anterior opening of the same canal; *pc*, the basal parachordal plate of the sphenoid; *r.*, canal for vessel and nerve branches to the cranial roof; *v. p.*, *v. p.*, *v. p.*, *v. p.*, foramina for vessels and nerve-branches; *v. p.*, canal probably for vena cerebri anterior; *II*, for. opticum; *III*, for. oculomotorii; *IV*, for. trochlearis; *V*, incisus indicating the place of exit for the trigeminal roots; *V. p.*, outer opening of the canal for n. ophthalmicus profundus as a somewhat equivalent nerve; *V. p.*, inner opening of the same canal.

In the posterior half of the pars basalis of the sphenoid we can distinguish an anterior portion, *bsph*, comparatively high and massive, and a posterior one, *pc*, lower and more plate-like. On the dorsal side these portions pass into each other without any very distinct boundary, whereas this is not the case on the ventral side. For, corresponding to the anterior part of the plate-like region *pc*, we find on this side a rather deep and broad transverse furrow (*c. transv.*, text figs. 62, 63; Pl. 20, fig. 6; Pl. 21, figs. 1, 3),

which is bridged over by the parasphenoid ventrally so that a transversal canal arises. The diameter of this canal had, as is shown by text fig. 63 C, its greatest height immediately behind the region *bsph*, from which it follows that this region becomes very sharply cut off from the one following behind it.

Along the ventro-lateral margin of the region *bsph* there issues a paired, large but rather thin process (*bp*, text figs. 63 A, B, 64 B; Pl. 22, fig. 1, 2). The process extends in caudal direction past the transversal canal (*c. transv.*) in the basis cranii, forming the ventral boundary for the exit of this canal. Because of the development of the processes *bp* the posterior margin of the region *bsph* appears in ventral aspect very concave, while the anterior margin, in the same aspect, appears convex (text fig. 63 B; Pl. 21, fig. 1).

A median sagittal section through the sphenoid (text fig. 63 C) shows that the region *bsph* dorsally of the fenestra optica is closely attached to the regions of the pars basalis situated in front of it. As a similar section also shows, the floor of the cranial cavity has its highest point in the orbitotemporal region situated about over the posterior end of the fenestra optica and from this sinks more slowly forwards than backwards.

Immediately behind the region *bsph* there follows on the dorsal surface of the pars basalis of the sphenoid, i. e. on the floor of the cranial cavity, a deep and rather narrow fossa (*f. hyp*, text fig. 63 C; Pl. 21, fig. 2), which pierces the basis cranii and opens into the above described transversal canal (text fig. 63 B, C; Pl. 21, fig. 1; Pl. 22, fig. 3). Posteriorly this fossa is bounded by a fairly thin bony part (*dors. sell*, text fig. 63 C), which forms the most anterior end of the region *pc*. From this place this region sinks backwards until its ventral surface is at about the same level as the ventral surface of the region *bsph* and this sinking also affects the basal surface of the cranial cavity, which as a matter of fact is also hollowed out in the longitudinal direction of the cranium so that its median parts are situated more deeply than its lateral ones. With regard to the region *pc* of the pars basalis of the sphenoid it is noteworthy in this connection too that it is pierced by a large oval foramen (*fen. bas. post*, text fig. 63 B, C; Pl. 21, figs. 1, 2; Pl. 22; fig. 3), and that in its posterior part it is sharply cut off from the partes laterales of the same bone (here the processes *c*) by a paired, narrow but deep incisur (*fi*) penetrating from the back.

The fossa described above (*f. hyp*), which opens into the transversal canal, undoubtedly represents the fossa hypophyseos and the region of the pars basalis of the sphenoid situated in front has, as far as can be judged, a partial correspondence in *Amia* in the cartilage lying between the hypophysis and the fenestra optica, called the transversal «Wulst» (ALLIS, 1897 a, p. 493; Pl. XXI, figs. 9, 11, *w*) and in Teleosts in their so-called basisphenoid. At least the upper and the middle parts of the fossa have certainly been occupied by the infundibulum. The hypophysis would therefore have been situated in its ventral parts and probably extended also down into the basal transversal canal. It seems very probable that the saccus vasculosus too was situated with it in this canal. Under these circumstances it is clear that the anterior part of the region *pc* in the pars basalis of the sphenoid would correspond both in function and position to the roof of «cavum sacci vasculosi» in *Polypterus*¹⁾ (cf. LEHN, 1918, p. 364, fig. 4), and to the anterior

¹⁾ The name cavum sacci vasculosi for the space in question in *Polypterus* is incorrect, as both the hypophysis and the saccus vasculosus are situated in it (cf. LEHN 1918, p. 364, figs. 9—12; Tafel XVII).

part of the «prootical bridge» in *Amia* and Teleosts (cf. ALLIS, 1897, a, pp. 492—497; Pl. XXI, fig. 11; 1909 a, pp. 183—203). Nor does it seem impossible that the anterior part of the region *pc* should also have a corresponding part in *Lepidosteus* in the roof of the transversally situated cavity that is considered by SAGEMEHL (1885, p. 86) to be homologous with the canalis transversus of the Elasmobranchs (cf. ALLIS, 1909 a, pp. 188—189). With regard to this it is noteworthy that the roof of the cavum sacci vasculosi consists in *Polypterus* of a bone lamella belonging to the sphenoid as in *B. mougeoti*, while the «prootic bridge» in *Amia* and Teleosts and its equivalent, the roof of the mentioned transversal cavity, in *Lepidosteus*, are formed by a medial process from the prootic of each side.

While the cavum sacci vasculosi in *Polypterus* is, as we know, fairly large and has a rather great extension in the rostro-caudal direction and communicates with the cranial cavity by means of a wide opening, the fossa hypophyseos in *B. mougeoti* forms a fairly narrow, vertical pit in the floor of the cranial cavity and it is only this pit that, as we have seen, is, by means of a foramen in its floor, in communication with the transversal canal in the basis cranii.

In *Lepidosteus* the transversal cavity in the basis cranii is, as we know, closed at both ends, and the vena pituitaria (sinus transversus) pierces the cranial base rostrally of it (ALLIS 1909 a, pp. 183—190; 1914 a, pp. 241—243; VEIT 1907, p. 199; SAGEMEHL 1885, p. 86). In *Polypterus*, on the other hand, we find the wall of the «cavum sacci vasculosi» pierced on each side by a foramen that obviously transmits v. pituitaria (LEHN 1918, p. 364), and this vein seems to occupy a somewhat corresponding position in relation to the fossa hypophyseos in fishes in general (ALLIS 1909 a, pp. 183—208; 1911, p. 291; 1914 a, pp. 225—253; 1914 b, p. 627; ALLEN 1905, p. 81, Pl. II, fig. 15; GREIL 1913, p. 1260; O'DONOGHUE 1914, pp. 440—441). It is noteworthy that in Elasmobranchs it has been found to pierce the transversally running canal in the basis cranii for which GEGENBAUR (1872, pp. 75—79) introduced the term canalis transversus.¹⁾

If we now examine the conditions in the pars basalis of the sphenoid in *B. mougeoti* with reference to the course of v. pituitaria it is clear that this vein must have pierced the transversal canal (*c. transv.*) beneath the anterior end of the region *pc*. The transversal canal itself must certainly be homologized with the canalis transversus of the Elasmobranchs, and I shall accordingly refer to it by this term in the sequel. It is difficult to decide with certainty whether it was bridged over ventrally by the parasphenoid alone or whether its ventral boundary besides consisted to some extent of cartilage. It seems, however, beyond all doubt that at any rate there was a larger or smaller gap, probably corresponding to a fenestra basicranialis anterior, ventrally of the canalis transversus.

If my view referred to above of the position of the infundibulum and the hypophysis of *B. mougeoti* is correct, the mesencephalon and the anterior part of the medulla oblongata must have been situated above the region *pc* of the pars basalis of the sphenoid. The foramen (*fen. bas. post.*, text fig. 63 B, C; Pl. 21, fig. 1, 2; Pl. 22, fig. 3) which, as has been mentioned, pierces this region, can clearly not be placed in any

¹⁾ ALLIS (1914 a, b;) has tried later on to establish the name «pituitary canal» for this canal on account of its relations to v. pituitaria.

relation to the ventral parts of the diencephalon. Ventrally it is covered by the parasphenoid. Whether we are to see in it only a secondary fenestration or we are to take it as a remaining part of the fenestra basicranialis posterior between the anterior ends of the parachordals (cf. GAUFF 1905, p. 663) is of course difficult to establish, but the latter alternative seems most probable. It seems certain that the region *pc* of the pars basalis of the sphenoid, on account of its position in relation to the fossa hypophyseos, belongs to the parachordal section of the neurocranium, so that in the continuation I shall call it the basal parachordal plate of the sphenoid. In the Coelacanthids it seems to have its equivalent in the basisphenoid corpus and this is also the case in the Lacertilians, where the basisphenoid is formed in the crista sellaris (cf. GAUFF 1905, p. 759, fig. 382; ALLIS 1909 a, pp. 191—192).

In the most posterior part of the lateral surface of the pars basalis of the sphenoid there is in *B. mougeoti* a paired fossa (*my*, text figs. 62, 63 A, B; Pl. 20, fig. 60; Pl. 21, figs. 1, 3), which I have not mentioned above. As will be seen from the figures quoted, this fossa is low and oval in shape. In the anterior end of it the canalis transversus has its exit and the two fossae are thus in communication with each other here, while the parts situated posteriorly are separated by the median parts of the basal parachordal plate (*pc*). Dorsally each fossa is bounded by this plate and the process *c* (text figs. 62, 63 A, B, C; Pl. 20, fig. 60; Pl. 21, figs. 1, 3), rostrally by the posterior surface of the region *bsph* and ventrally by the parasphenoid. The posterior boundary was partly formed by the basal parachordal plate and partly by cartilage belonging to the most anterior part of the labyrinth region. Finally it is also noteworthy in this connection that the above-mentioned incisur *fi* (text fig. 63; Pl. 21, figs. 1—3; Pl. 22, fig. 3) is situated in the roof of the fossa (*my*) in question.

The ventral half of the caudal part of the sphenoid seems to have been narrower than the cartilaginous part following behind in the labyrinth region. Now as the parasphenoid has been situated close to the lateral surface of this cartilaginous parts and in its forward extension over the most posterior part of the orbitotemporal region has retained its position in the same plane as in the labyrinth region, there has arisen on either side between it and the basal half of the sphenoid an anteriorly open cavity which, as we shall see from my account given below, seems to include the homologues of the trigeminofacialis chamber and myodome. The fossa *my* described above now occupies such a position that it must have formed the posterior end of the myodome part in this cavity and, for reasons that will be given in more detail later in this description, ought to represent at least an antero-lateral part of the myodome of the *Teleostei*. In other words the myodome is in a very primitive phylogenetic stage of development. For here we seem to have a fossa merely for *m. rectus externus*, and this muscle would thus, in relation to the exit for the canalis transversus, have penetrated in to the basis cranii in a medial and posterior direction. The two fossae (*my*) formed in this way are, as we have seen, still widely separated, but, if extended more in a medial direction, would have met the fontanel in the cranial base, which I interpreted as the fenestra basicranialis posterior. The conditions present in the basal part of the orbitotemporal region in *B. mougeoti* thus seem well to support the view attained by comparative anatomy and embryology as to the phylogenetic origin of the myodome (cf. GEGENBAUR 1872,

pp. 75—79; SAGENEHL 1884, pp. 215—217; 1885, pp. 85—87; 1891, pp. 574—575; GAUFF 1905, pp. 667, 669; ALLIS 1909 a, pp. 183—208; 1914 a, b; 1918 a).

Having examined the *pars basalis* of the sphenoid rather completely let us turn to its *partes laterales*. These issue in a dorso-lateral direction from the *pars basalis*. Their ventral part is fairly thin, but their thickness increases dorsally and soon becomes rather considerable, still farther dorsally suddenly beginning to decrease again (text fig. 64 A, B). Towards their posterior ends the thickest part is situated half way between the base of the neurocranium and the dorsal surface, towards their anterior ends this part is displaced gradually upwards, and finally at their most anterior parts it is situated quite close to the cranial roof.

As has already been pointed out, the *partes laterales* of the sphenoid extend considerably farther forward than the *pars basalis*, while, on the other hand, they do not reach quite so far backwards as this. The anterior margin of either of them is almost vertical. The posterior one, on the other hand, passes off obliquely backwards and downwards in its upper part, becoming vertical in its lower part. By a marked and rather deep and wide sinus (V, text fig. 63 A, B, C; Pl. 20, fig. 6; Pl. 21, figs. 1—3; Pl. 22, figs. 1, 3) the posterior margin is divided into a dorsal (*b*) and a ventral (*c*) process, both of which are blunt and robust. The ventral process (*c*), as already mentioned above, is well marked off ventrally from the basal parachordal plate (*pc*) by the deep incisur *fi*, penetrating from behind.

In the *pars lateralis* of each side we can distinguish four surfaces, well marked off from each other, a medial, a dorsal, a latero-dorsal and a lateral one, of which the last in fact really faces ventro-laterally. The medial and the lateral ones are the largest, the dorso-lateral one the smallest.

The dorso-lateral surface (text fig. 63 A; Pl. 21, figs. 2, 3) is fairly wide at its caudal end and meets the medial surface here in a distinct edge. Anteriorly it grows continuously narrower. It is also separated from both the dorsal and the lateral surfaces by distinct longitudinal edges, the most prominent of which is the one between it and the lateral surface, which has two rounded corners (*a*, *a_l*) in its posterior half. This edge corresponds to the place where the *partes laterales* again begin to decrease in thickness upwards, and thus at each point of its extension it coincides with the position of their thickest place, as is shown by text figs. 64 A, B.

The dorsal surface is plane; the lateral one is concave both in the direction from front to back and from above to below, the medial one only in the latter direction. The latero-dorsal surface, apart from smaller and very shallow concavities, is convex from the anterior to the posterior end.

The dorsal surface was directly covered in its posterior half by the membrane bones of the cranial roof. Its anterior half, on the other hand, was separated from these by a very thin layer of cartilage. The latero-dorsal surface has been connected by cartilage throughout its extension and cartilage has also been attached to the medial one at its anterior and posterior ends and along a longitudinal zone close to the dorsal margin (text fig. 64). Further we find that cartilage must have been attached to the *partes laterales* along the posterior and anterior borders and along the ventral border, in the part situated in front of the *pars basalis*.¹⁾

¹⁾ The surfaces to which cartilage has been attached are very easy to identify by their appearance and there is consequently no doubt as to the relations of the sphenoid to surrounding cartilaginous parts.

From what has been said it thus seems evident that, apart from possibly existing fontanels, the roof of the primordial neurocranium between the two partes laterales consisted of cartilage. As we shall see, a fontanel is found in the Saurichthyids, in which it extends from the labyrinth region into the most posterior part of the orbito-temporal region (cf. Part II).

The cranial cavity continues forward through the whole sphenoid and even in the anterior part of this bone it still seems to have had a fairly considerable size. Text fig. 64 A, B

Text fig. 64. *Birgeria mougeoti* AGASSIZ.

Cross-section through the orbitotemporal region. After P. 165. 7.

The cartilaginous parts are dotted.

A) through the middle part of the orbitotemporal region.

B) through the posterior part of the same region.

Ausph. autosphenotic; *Dsph.* dermosphenotic; *Fr.* frontal; *Psph.* parasphenoid; *Sph.* sphenoid; *Stemp. int.* supratemporo-intertemporal; *bp.* basipterygoid process; *bosph.* portion of the pars basalis of the sphenoid between fenestra optica and canalis transversus; *cv.* cranial cavity; *fen. opt.* fenestra optica; *my.* myodome portion of the postorbital cavity; *ophth. lat.* canal for r. ophthalmicus lateralis; *pr. asc.* process on the medial side of the parasphenoid probably indicating the position of the homologue of the alisphenoid pedicle of *Amia*; *pr. asc.* processus ascendens of the parasphenoid; *trig. fac. ch.* portion of the postorbital cavity, corresponding to a trigemino-facialis chamber; *vl.* ventral lamella from the supratemporo-intertemporal.

shows the conditions in a transverse section in the middle and posterior part of this bone.

From the forward extension just described of the cranial cavity it ought to be evident that n. olfactorius had an intracranial course (right) until it reached the nasal capsule.

The foramen opticum (II, text figs. 62, 63 A, B, C; Pl. 20, fig. 6; Pl. 21, figs. 1—3; Pl. 22, figs. 1, 3) is situated not far above the posterior end of the fenestra optica (*fen. opt.*) and thus has its normal position. Immediately in front of it there is another smaller foramen, which has probably been, pierced by some vessel, the most probable one being arteria optica (a. retinalis,

DANFORTH, 1912, p. 443; cf. also ALLIS, 1897a, pp. 498—499; 1908a, p. 223; 1908b, pp. 258—262; 1909a, p. 186; 1911, p. 290; 1912, pp. 119—120; ALLEN 1905, pp. 56—57).

N. oculomotorius (III, text figs. 62, 63 A, B, C; Pl. 20, fig. 6; Pl. 21, figs. 2, 3; Pl. 22, fig. 3) apparently had its exit in the orbit through a foramen a short distance behind the for. opticum and slightly higher than this.

High up dorsally and somewhat rostrally of the latter foramen there are three foramina in a group (IV, v_2 , v_4 , text fig. 62, 63 A, B, C; Pl. 20, fig. 6; Pl. 21, figs. 1—3; Pl. 22, figs. 1, 3). The most posterior of them (v_2) does not lead into the cranial cavity but into a canal that pierces the pars lateralis of the sphenoid in a dorsal direction. The two others form the outer exit of two canals, situated close together, which pierce the pars lateralis in a postero-medial direction and consequently have their inner openings situated somewhat caudally of their outer ones. One of these two canals must have been

pierced by n. trochlearis, and as this nerve is always rather narrow, it does not seem improbable that it was the smaller one (IV). The anterior and larger one (ν_4) seems to have transmitted a vessel and its position seems to suggest that this vessel was v. cerebialis anterior.

In Elasmobranchs this vein is developed (REX 1891, Pl. 25, fig. 10; Pl. 26, fig. 21; BURCKHARDT 1907, Pl. 3, fig. 5; ALLIS 1902, Pl. 12, fig. 6; O'DONOGHUE 1914, pp. 439—440; T. J. PARKER 1887, p. 712). In *Amia* ALLIS (1897a, Pl. XXI, figs. 9, 10, 11; 1909a, p. 39) found it and, according to his statements (1909a, p. 187), it is also found in *Lepidosteus* and Teleosts (1909a, p. 39; p. 207).¹⁾ In *Polypterus* LEHN (1918, p. 380, figs. 3, 4) has found two vein foramina in the neighbourhood of for. trochlearis, one of which is situated caudally, the other dorsally of the nerve foramen mentioned. LEHN does not give any detailed description of the veins that passed through these foramina and it is therefore uncertain which of them transmitted the v. cerebialis anterior.

ALLIS (1909a, pp. 51—55) has described in certain Teleosts a fine arterial branch that pierces the alisphenoid, and, according to DENME (1860, p. 10) in *Accipenser ruthenus* a couple of small rami perforantes are sent off from art. carotis externa during its forward course «an der inneren Wand der Schläfen und Augenhöhle». I have been unable to establish whether any foramen for such a branch was present in the sphenoid of *B. mougeoti*. In any case it seems to me highly improbable, however, that the foramen (ν_4), should have transmitted such an arterial branch instead of the vena cerebialis anterior.

The place of exit for the trigeminal roots in *B. mougeoti* was, as already shown by my account above, situated on the boundary between the sphenoid and the anterior cartilaginous part of the labyrinth region. It appears accordingly, in the present state of preservation of the cranium, only as a considerable incisur (V) on the posterior margin of the sphenoid between the two processes *b* and *c* (text figs. 62, 63 A, B, C; Pl. 20, fig. 6; Pl. 21, figs. 1, 3; Pl. 22, figs. 1—3).

In the anterior boundary of the trigeminus incisur on the sphenoid we find the posterior opening (V_{10} , text fig. 63 C) of a fine canal (V_1 , text fig. 62) which passes off forwards and somewhat laterally. The anterior opening of this canal (V_{10} , text fig. 63 A, B; Pl. 21, figs. 1, 3) is situated about half way between the anterior boundary of the trigeminus incisur and the foramen oculomotorii (III) and is divided by an incomplete septum into a dorsal and a ventral part. As is shown by comparisons with recent Elasmobranchs, Ganoids and Teleosts, it cannot in this case be anything but the canal for r. ophthalmicus profundus or a nerve fairly equivalent to this. It is difficult to say with certainty what is the signification of the division of the external opening of the canal into two parts. It may of course be connected with a bifurcation of the ophthalmicus profundus itself into two branches and, on the other hand, it is not inconceivable that it may be caused by some vein corresponding to v. encephalica of the *Teleostei* (ALLIS 1909a, pp. 44, 48; ALLEN 1905, pp. 84—85; Pl. III, fig. 24), which has left the cranial cavity together with r. ophthalmicus profundus. I consider it impossible that n. oculomotorius should have had its exit this way as in *Polypterus* (TRAQUAIR 1871, p. 170; Pl. VI, fig. 3; POLLARD 1892a, pp. 394—395; Pl. 28, fig. 12; LEHN 1918, p. 380,

¹⁾ The same vein is also noticed in *Lepidosteus* by VEIT 1907, p. 193.

Stensiö, Triassic Fishes from Spitzbergen.

figs. 3, 4) and in certain Teleosts (ALLIS 1909a, pp. 82—83), as the canal in question is too narrow to be able to contain, in addition to *r. ophthalmicus profundus*, the presumably rather powerful oculomotorius nerve as well, and moreover, as we have seen in my account above, there is found a special foramen (III) which can only be related to this last-mentioned nerve.

From a small incisur (*ophth. lat.*, text fig. 62, 63 C; Pl. 21, fig. 2) on the posterior margin of the sphenoid dorsally of the trigeminus incisur a shallow furrow (*ophth. lat.* Pl. 22, fig. 3) extends in a rostral direction. Straight above the outer opening of the profundus canal, between it and the corner *a*, this furrow proceeds through the aperture *ophthal. lat.*, into a canal that continues in a rostro-dorsal direction to a position below and somewhat behind the corner *a*, where it has its anterior opening (*ophth. lat.*, text figs. 61, 63 A, B; Pl. 21, figs. 1, 3). The position of the canal in the sphenoid is shown in text fig. 64 B (*ophth. lat.*). In a dorsal direction there issues from this canal another one of finer calibre, which opens on the latero-dorsal surface of the pars lateralis (*r.*, text fig. 63 A; Pl. 21, figs. 2, 3) in the present state of preservation of the cranium. Originally, however, this finer canal has continued in a dorsal direction through the cartilage that was attached to this surface and has consequently had its exit on the dorsal surface of this cartilage, immediately beneath the membrane bones of the cranial roof.

The fairly coarse canal, *ophth. lat.*, now described has, as far as can be understood, been pierced by the *n. ophthalmicus lateralis* (perhaps by *ophthalmicus trigemini* as well) and the shallow furrow leading to the small incisur on the process *b* may also have been developed in relation to the same nerve (cf. GEGENBAUR 1872, pp. 67—69; VAN WIJHE 1882, pp. 229—230). The fine canal that proceeds in a dorsal direction from the *ophthalmicus lateralis* canal may have contained some nerve branch to the supraorbital canal, and it is not impossible that vessels have also passed through it. This seems to be supported by the fact that the foramen *v*₂ forms the ventral opening of a canal that proceeds dorsally and probably opens into the *ophthalmicus lateralis* canal about opposite the fine canal *r* just mentioned issuing from the dorsal side in an upward direction.

The abducens nerve was probably transmitted through the incisur *f* described above (text fig. 63 A, B, C; Pl. 21, figs. 1—3; Pl. 22, fig. 3). For this incisure seems to have been situated slightly in front of the place where *n. abducens* must have left *medulla oblongata*, and it is also in the right position in relation to the supposed place of origin of *m. rectus externus* (*fossa my*). *N. abducens* would thus have had a short straight course in a rostro-lateral direction as in Teleosts. That it cannot have had its exit together with or in close connection with the trigeminus branches as in certain other recent fish forms (GEGENBAUR 1872, p. 73; ALLIS 1902, pp. 132—133; VEIT 1907, p. 188; LEHN 1918, pp. 372, 391) seems to be shown by the fact that in such a case it would first have had to turn off in a dorsal direction to arrive at the trigeminus exit situated high above the floor of the cranial cavity and then to reach *m. rectus externus* in a ventral direction.

As has been pointed out above, the *n. facialis* has pierced the anterior cartilaginous part of the labyrinth region. In the description of the myodome and the trigemino-facialis chamber below I shall have an opportunity to enter in more detail upon the question of its course through the cranial wall, and in this connection I may therefore confine

myself to a brief orientation with regard to its main portion, the truncus hyoideo-mandibularis.

After having separated from the palatinus portion this truncus must have turned off in a caudal direction entering a latero-caudally running canal, which is bounded by the prootico-opisthotic, the cartilage anterior of this bone, the processus ascendens of the parasphenoid and a process (νp) from the supratemporo-intratemporal. The position of the posterior opening (VII) of this canal is seen in text fig. 61 and Pl. 22, figs. 1, 3.

On the sphenoid there occur a few additional foramina for vessels and nerves that have not so far been mentioned. The most important of these is the paired foramen (*a. car. int.*, text fig. 63 B; Pl. 20, fig. 6; Pl. 21, figs. 1, 2; Pl. 22, figs. 1, 3) found on the ventral surface of the portion *b sph* of the pars basalis. Each of these foramina forms the ventral opening for a vertically ascending canal, whose dorsal opening (*a. car. int.*, text fig. 63 C; Pl. 21, fig. 2) is situated rostro-laterally of the fossa hypophyseos just behind the foramen opticum of its side. As I shall show in more detail in part II of this work, this canal, which is also found in *Saurichthys*, has been pierced by arteria carotis interna (cf. ALLIS 1897a, pp. 497—498; 1908a, pp. 222—223; 1908b, pp. 257—258, 260—262; 1909a, pp. 54, 186; 1909b; 1911, p. 290; 1912, pp. 119—120; 1912a, p. 489; 1914a, pp. 228, 238, 247; DANFORTH 1912, pp. 442—445; DEMME 1860, pp. 11—14; ALLEN 1905, pp. 56—57; T. J. PARKER 1887, p. 694; VEIT 1907, p. 189, fig. 3; etc.). This artery has, as is clearly seen, occupied its usual position.

Through the foramina ν_3 and ν_5 (text fig. 63 A, B; Pl. 21, figs. 1—3) both of which are situated on the border between the latero-dorsal and the lateral surface of the pars lateralis of the sphenoid, vessel and nerve branches to the cranial roof may have had their course. Foramen ν_1 on the latero-dorsal surface forms the present dorsal opening for the canal of which ν_2 is the ventral one. From ν_1 the canal has undoubtedly continued a short distance through cartilage until it reached the cranial roof.

With regard to the distribution of bone and cartilage in the orbitotemporal region in *B. mougeoti* I refer to the text figs. 61, 62, 64, where I have tried to reconstruct the cartilaginous parts.

A comparison between the orbitotemporal region in *B. mougeoti* and a number of other Teleostome fishes shows the following features.

In the *Teleostei* (ALLIS 1909a; SAGEMEHL 1885; 1891; RIDWOOD 1904a; 1904b; etc.) the cranial cavity is in the interorbital wall somewhat displaced to the dorsal side as is usual in Actinopterygians, and the ventral part of the interorbital wall is thin. The cranial cavity is often reduced also in the anterior part of the interorbital wall, and this part is then also thin and continuous with the thin ventral part. Under such circumstances the anterior and basal parts of the interorbital wall are thus reduced to a more or less thin interorbital septum. A fenestra optica is always present. The myodome is a rule well developed. The portion of the basis cranii, situated between the fossa hypophyseos and the fenestra optica, is very thin and always considerably shortened.

The ossifications present in the orbito-temporal region of the *Teleostei* are, as we know, a paired alisphenoid, a paired or unpaired orbitosphenoid and an unpaired so-called basisphenoid. The anterior part of the prootic also undoubtedly falls within this region. Of these bones the orbitosphenoid is very inconstant. The so-called basisphenoid,

which is weak, may also sometimes be quite absent. The hypophysis is situated in a foramen that is bounded anteriorly by the basisphenoid, if this bone is present, posteriorly and laterally by a medial process from the prootic of each side.

When the orbitosphenoid is absent or is reduced, the side walls and the floor of the cranial cavity consist farthest anteriorly of membranous tissue connected ventrally with the membrane that occupies the fenestra optica and farther ventro-caudally sometimes also with the membrane that forms the floor of the fossa hypophyseos and in addition represents to some extent the roof of the myodome. Under the same circumstances by far the greater part of the interorbital septum below and anterior of the cranial cavity may consist either of cartilage or membranous tissue or of a combination of these two.

In those *Teleostei* in which the anterior part of the cranial cavity is reduced n. olfactorius has its course free through the orbit, afterwards entering the ethmoidal region through the foramen olfactorium advehens on the planum antorbitale (cf. GAUPP 1905, pp. 585—586). N. opticus has its exit into the orbit through the posterior part of the fenestra optica, and in certain forms n. oculomotorius has also emerged into the orbit through this fenestra. It seems however to be more common for this nerve to have pierced the antero-lateral part of the medial process of the prootic which forms the «prootic bridge» with that of the opposite side, or for it to have passed through the suture between the same medial process of the prootic and the basisphenoid. The n. trochlearis has its exit through or just in front of the alisphenoid, and the trigeminus either through the most anterior part of the prootic or on the boundary between this and the alisphenoid, or else so that its main portion passes through the prootic or on the boundary between this and the alisphenoid, while an anterior portion (cf. SÄGEMEHL 1891, pp. 568—599) pierces the alisphenoid.

In the *Teleostei* the arteriae carotides internae or their equivalents, art. encephalica, if they have been fused into one vessel, have their course immediately behind the so-called basisphenoid upwards to the cranial cavity.

From what has been mentioned it ought easily to be seen that in *Teleosts* the prootic has encroached upon certain of the parts of the neurocranium that are occupied by the sphenoid in *B. mougeoti*. The so-called basisphenoid of the *Teleosts* corresponds in *B. mougeoti* only to the part of the pars basalis of the sphenoid that is situated between the canals for the arteriae carotides internae and the fenestra optica. On the other hand it is evident that in *B. mougeoti* the fenestra optica forms only the ventral part of the fenestration with the same name in the *Teleosts*.

Amia (ALLIS, 1897a; SÄGEMEHL, 1884) is, as we know, related to the *Teleostei* in several respects with regard to the development of the orbitotemporal region, but it also shows some features that seem to resemble *Birgeria mougeoti*. Thus in *Amia* the prootic does not extend so far forward as in *Teleosts*, but the most anterior part of the labyrinth region consists of cartilage. Finally it is also noteworthy that r. maxillaris and r. mandibularis trigemini together with n. buccalis lateralis have left the trigemino-facialis chamber on the boundary between the alisphenoid and the anterior, cartilaginous part of the labyrinth region (cf. p. 164 above).

In *Lepidosteus* (ALLIS, 1909a, pp. 183—190; VEIT, 1907, pp. 188—193) the orbitotemporal region is, as we know, very much lengthened in its anterior part, and the

interorbital wall forms there only a thin septum. A myodome is lacking, while the fenestra optica is developed. Only two of the substitution bones of the primordial neurocranium fall exclusively within the orbitotemporal region, namely the orbitosphenoid and the alisphenoid. The anterior part of the prootic, however, as in the *Teleostei*, also extends into the orbitotemporal region and joins the alisphenoid by means of a suture. The ventero-lateral part of the prootic forms the greatest part of the basiptyergoid process of each side. ALLIS (1909a, p. 189) has described the conditions immediately round the fossa hypophyseos as follows: «Immediately anterior to the cross-canal there is, in the floor of the cranial cavity, the pit like and slightly oval pituitary fossa. The lateral and anterior walls of this fossa are of cartilage, the floor of the fossa is perforated by a nearly circular opening, the opening being closed ventrally by the parasphenoid.»

The foramen trochlearis is situated in *Lepidosteus* in the alisphenoid, the foramen trigemini in the anterior part of the prootic, the foramen oculomotorii in the suture between this bone and the alisphenoid, while the foramen for the profundus branch is situated immediately behind the foramen oculomotorii, also in the suture between the prootic and the alisphenoid. N. olfactorius has a free course for a long distance through the orbit. The carotis interna enters the cranial cavity through the cartilaginous floor in front of the fossa hypophyseos. The vena pituitaria traverses the fossa hypophyseos in a transversal direction, and in order to emerge into the orbit of each side pierces the cartilaginous part of the cranial wall that lies between the posterior boundary of the fenestra optica, the prootic and the alisphenoid.

The part of the floor of the orbitotemporal region in *Lepidosteus* that corresponds to the region *biph* in *B. mougeoti* is, as can easily be seen from the facts given above, preponderatingly cartilaginous. It is also noteworthy that it is fairly weakly developed. V. pituitaria seems in *Lepidosteus* to occupy pretty nearly the same position as in *B. mougeoti*, and I cannot see any special reason to assume that it should not occupy its normal position (cf. ALLIS, 1914a, p. 242). The part of the basiptyergoid process in *Lepidosteus* that is formed by the prootic seems to be homologous at least with the posterior part of the process *bp* in *B. mougeoti*.

In *Polypterus* (TRAQUAIR, 1871, pp. 169—171; LEHN, 1818, p. 384) an unpaired sphenoid extends, as we know, through the whole orbitotemporal region and forms, as has been pointed out above, the roof for the cavum sacci vasculosi. The sphenoid is pierced by the nervus opticus, n. oculomotorius, n. trochlearis, r. profundus trigemini, arteria carotis interna¹⁾ and a number of veins, inter alia v. pituitaria. The roots of trigeminus have their exit from the cranial cavity through a foramen situated on the boundary between the sphenoid and the anterior cartilaginous part of the labyrinth region. The lateralis fibres, with the exception of those destined to the preoperculo-mandibular sensory canal, all emerge behind the sphenoid through a special foramen quite surrounded by cartilage. (LEHN, 1918, pp. 394—395). N. abducens accompanies the trigeminus roots.

The sphenoid in *Polypterus* thus shows in many respects a striking agreement with the similarly termed bone in *Birgeria mougeoti*. In spite of this, however, it is evident

¹⁾ Arteria carotis interna in *Polypterus* enters the cranial cavity on each side through or close behind the foramen opticum, thus far anterior of the cavum sacci vasculosi.

that with regard to the development of the orbitotemporal region *Polypterus* represents a far less specialized type than *B. mougeoti*, which has evidently started to develop in the direction of *Lepidosteus*, *Amia* and Teleosts. For in *Polypterus* the cranial cavity not only extends through the whole orbitotemporal region but has also about the same width dorsally as ventrally. The floor of the cranial cavity in *Polypterus* is therefore comparatively wide and the cranium gets a certain platybasic character. Under these circumstances the interorbital wall is of course relatively thick. It is also noteworthy that both the myodome and the fenestra optica are absent. The distance between the foramen opticum and v. pituitaria is long and not shortened as in the *Teleostei* and in *Amia*, *Lepidosteus* and *Birgeria*. In this respect *Polypterus* thus resembles *Dictyonosteus* and the Elasmobranchs.¹⁾

It is also evident that with regard to the general characters of the orbitotemporal region *B. mougeoti* is considerably more specialized in the direction of the *Teleostei* than the sturgeons.

Among fossil ganoids only *Dapedius* and *Lepidotus* are so far known to any extent with regard to the development of the orbitotemporal region. As far as one can understand, the general characters of this region have in them been fairly like those in the *Teleostei*. Ossifications have been present but no details are known as to the boundaries of these (WOODWARD, 1893 b, pp. 560—565; 1915, p. 39; FROST, 1913, pp. 219—222). The fenestra optica is well developed.

Among the Crossopterygians *Dictyonosteus* (STENSIÖ, 1918 c) shows a striking resemblance to *B. mougeoti* by its large sphenoid, which extends into the most anterior part of the labyrinth region, and this is also the case to a certain extent which the Coelacanthids, where the basisphenoid corpus is situated in the labyrinth region in a similar way to the pars basisphenoidea of the sphenoid in *Dictyonosteus*. For further details with regard to this I refer to my description of the Coelacanthids in this work above (pp. 56—60, 91—92, 132). It is, however, evident that with regard to the development of the orbitotemporal region both *Dictyonosteus* and the Coelacanthids show in other respects rather different conditions from *B. mougeoti*, and that in this respects they probably resembled *Polypterus* in essentials.

We thus see that with regard to the development of the orbitotemporal region *Birgeria mougeoti* has started to develop in the direction of the *Teleostei*, but that it also has certain characters in common with *Polypterus* and Crossopterygians. It also seems to me fairly evident that these characters are primitive and indicate a close relationship between the primitive *Actinopterygii* and the *Crossopterygii* (cf. pp. 137—140 above).

It is also worth mentioning in this connection that our view of the relationship of the Polypterids to other Teleostomes has become rather clearer because of the more exact knowledge gained with regard to the development of the orbitotemporal region in *B. mougeoti* on the one hand and in *Dictyonosteus* and Coelacanthids on the other. It certainly seems evident that with regard to the orbitotemporal region the Polypterids resemble *Dictyonosteus* and the Coelacanthids very much, but there seems to be no reason to refer them to the *Crossopterygii* because of this, as, on account of the

¹⁾ In *Calamichthys* there are in the orbitotemporal region according to SUPINO (1914, p. 183) a paired basisphenoid, alisphenoid and orbitosphenoid, but no details are given as to their extension or relation.

conditions described in *B. mougeoti*, we may now expect the region in question of the primordial neurocranium to be like that of the *Crossopterygii* even in the most primitive *Actinopterygii* (cf. p. 139 above).

Finally the account given here ought to show that in primitive forms among the Teleostomes the prootic did not extend farther forward than to or at any rate a very little in front of the facialis foramen. The extension of the prootic in the majority of the *Teleostei* in front of this foramen ought, to judge from the facts so far known, to be looked upon as secondary. It seems to have taken place with a simultaneous reduction of the most posterior part of the sphenoid or of corresponding ossifications in case the sphenoid was divided into several bones.

The membrane bones of the primordial neurocranium.

Parasphenoid. The primordial neurocranium is covered ventrally by a wide, powerful parasphenoid (*Psph*, text figs. 61, 62, 64; Pl. 20, fig. 6; Pl. 22, figs. 1, 3; Pl. 23, fig. 2), the two end parts of which are not preserved. The anterior end has undoubtedly been situated under the ethmoidal region, the posterior one has at least reached as far as the anterior part of the occipital region. The greatest width is under the anterior, cartilaginous part of the labyrinth region and to some extent under the posterior end of the sphenoid. On the boundary between the orbitotemporal and the labyrinth region a large processus ascendens (*pr. asc*) text figs. 61, 64; Pl. 22, figs. 1, 3) is sent out on either lateral surface of the neurocranium. From the posterior end of the bone a deep median sinus, rounded anteriorly, has extended forward (*P. 171*, text fig. 65). A similar sinus is found in *Acipenser* (PARKER 1882, Pl. 16, fig. 3; WOODWARD, 1895 b, fig. 8, p. 36), *Scaphirhynchus* (IVANZOW, 1887, Pl. I, fig. 2), *Gyrosteus* (WOODWARD, 1895 b, fig. 7, p. 36) and the *Saurichthys* species described below. In the recent ones of these forms we find that the sinus in question contained the arteria dorsalis. It is therefore probably correct to conclude that this artery in *Birgeria*, *Gyrosteus* and *Saurichthys* also had a similar position.

A bifurcation of the posterior end of the parasphenoid by a sinus also occurs in *Polypterus* and a number of other forms. The anterior end of the sinus is, however, not rounded off but has an acute angle. In such cases the sinus is occupied by the basioccipital and has nothing direct to do with the arteria dorsalis.

As has already been pointed out above (p. 154) the parasphenoid in the labyrinth region shows very special conditions. From its dorsal surface there issues a paired longitudinal lamella (*pl*, text figs. 59, 60, 62; Pl. 20, fig. 6; Pl. 22, fig. 1, 2) in a dorsal direction. This lamella, called by me the profound lamella of the parasphenoid, is on either side situated between the prootic-opisthotic and the basioccipital in the posterior part of the labyrinth region (text fig. 59), but extends somewhat higher up than this last-mentioned bone, so that it has presumably come into direct contact with cartilage dorsally and medially. At about the middle part of the labyrinth region the profound lamella has in transverse section the appearance shown in text fig. 60. At this place it is also situated medially of the prootico-opisthotic but did not come into direct contact with this bone, probably being separated from it partly by the labyrinth recess, partly by cartilage. Its relations medially to possibly existing cartilage and to the cranial cavity cannot be made out. In the anterior part of the labyrinth region it

decreases rapidly in height and finally disappears entirely at the posterior end of the basal parachordal plate of the sphenoid. Its approximate height and extension through the whole labyrinth region are shown in text fig. 62 and Pl. 20, fig. 6.

The parasphenoid in the whole has its dorsal surface concave throughout its length and its ventral surface convex from one side to the other. This character is most prominent in the orbito-temporal region, where the ventral parts of the sphenoid are sunk as if in a groove (text figs. 64 A, B). Cross-sections through the parasphenoid on the one hand and the prootic-opisthotic and cartilaginous parts on the other are shown in text figs. 59 and 60.

The exit for n. glossopharyngeus has been situated so low that even the parasphenoid (IX, text fig. 61) helped to form the boundary of the outer opening for its canal on the ventral side.

The processus ascendens of the parasphenoid (*pr. asc.* text figs. 61, 64 B; Pl. 22, figs. 1, 3) is, as already mentioned, powerful and extends dorsally almost up to the cranial roof. Immediately behind this process there is in the lateral border of the parasphenoid a characteristic sinus, which indicates the position of the posterior opening for the canalis facialis (VII, text fig. 61; Pl. 22, figs. 1, 3).

The parasphenoid as a whole consists of a compact radiate bone substance than can be split up into thin lamellae; it also has a well developed ossification centre situated under the canalis transversus. In the profound lamella it has a very special character to which no parallel can be found in recent forms. Among fossil forms there are perhaps found indications of a lamella of this sort, as we shall see in *Saurichthys*. Whether this was also the case in other forms is not yet known (cf. DAY 1915, pp. 422—434; FRITSCH 1895, pp. 79, 91, 99, 116; JAEKEL 1903; pp. 46—50; TRAQUAIR 1877 a, p. 16).

Apart from the profound lamella the parasphenoid in *B. mougeoti* seems to be of a similar type to that of the recent Sturgeons. It would thus be rather considerably different from the corresponding bone in Palaeoniscids in general, which, as far as we know, would not have extended so far backwards as in the recent Ganoids and Teleosts and which, in addition, has the part that is situated behind the centre of ossification very wide. An additional characteristic, at least for certain Palaeoniscids that are so far known, is that the parasphenoid on the dorsal surface has a fossa developed at about the place of the centre of ossification, and also that the part behind this centre sends out on either side two processes in a latero-dorsal direction. JAEKEL and DAY are of the opinion that the hypophysis was situated in the fossa, and the latter investigator even says that because of this the basisphenoid may be fused with the posterior part of the parasphenoid. The anterior of the two processes is accordingly interpreted by him (DAY) as a basiptyergoid process, and he considers that he has found it developed with a facet for articulation with the palatoquadrate.

It ought however to be noted that DAY's view does not seem probable in the preceding case. The fossa present on the dorsal surface of the parasphenoid in Palaeoniscids might, it seems to me, very well have been related to the hypophyse without for that reason the basisphenoid forming part of the parasphenoid. As an instance we may mention that the fossa hypophyseos both in *Polypterus* and *Lepidosteus* was bounded ventrally by the parasphenoid and that, at least in young specimens of the former genus,

the hypophysis was in connection with the mucous membrane of the mouth cavity by a foramen in the parasphenoid (cf. LEHN 1918, figs. 9—12). In addition the ontogenetic development of the hypophysis also of course supports the idea that certain forms it may remain in more or less direct contact with the parasphenoid, or be partly surrounded by that bone. Nor do I consider that DAY's interpretation of the anterior process as a basipterygoid process can be maintained either. For a process with about the same position as this one in the Palaeoniscids also occurs in *Lepidosteus*, where it undoubtedly belongs to the parasphenoid, in spite of the fact that, together with an antero-ventral part of the prootic, it is developed with a facet for articulation with the metapterygoid (ALLIS, 1909 a, p. 184; VEIT, 1907, p. 186). It thus seems presumable that at least certain Palaeoniscids showed in this respect about the same conditions as *Lepidosteus*. Others, on the contrary, such as, e. g., *B. mougeoti* seem to have been without any articulation between the palatoquadrate and the neurocranium.

The trigemino-facialis chamber and the myodome. — I have already had an opportunity above (p. 166) to describe a paired, large, forward open cavity, situated behind the orbit. In connection with this I have also noted that this cavity presumably corresponds to a great extent both to the trigemino-facialis chamber and the myodome. Now that we have got to know the relation between the primordial neurocranium and the parasphenoid it may be convenient to look more closely at this postorbital cavity.

It has extended rather considerably rostro-caudally, reaching from the anterior part of the labyrinth region forward to about the boundary between the posterior and the middle third of the sphenoid. Its most posterior part, which falls within the labyrinth region, was probably surrounded on all sides by cartilage. Its anterior and incomparably much larger part, which belongs to the orbitotemporal region, is bounded in its present state of preservation entirely by bone (text fig. 64 B). The basal part, *bsph*, of the sphenoid and the basal parachordal plate (*pc*) form together the medial wall, and the parasphenoid with its processus ascendens forms the lateral (ventro-lateral) one. The dorsal (dorso-medial) wall consists of the pars lateralis of the sphenoid, and the ventral wall in the anterior part of the basipterygoid process (*bp*) and in the posterior one of the parasphenoid. It is, however, rather probable that a lamella of cartilage may have continued forward from the labyrinth region both along the lateral wall of the cavity and along its ventral wall to the posterior margin of the basipterygoid process, especially if we may judge from *Saurichthys*, as we shall see below (Part II). If this were the case the parasphenoid would in reality not at all or perhaps only slightly (farthest forward on the lateral side) have formed part of the boundary of the post-orbital cavity.

The postorbital cavity is low and wide in shape. The width in greatest anteriorly and decreases continuously posteriorly. In cross section the anterior part of the cavity (*myr*; *trig. fac. ch*, text fig. 64 B) has an irregularly quadrangular shape, while its posterior part is more oval.

At least from a functional point of view the postorbital cavity can be divided into a ventro-medial and a dorso-lateral half, the former of which functioned as a myodome, the latter presumably as a trigemino-facialis chamber (cf. ALLIS 1897 a, pp. 492—506;

1909 a, pp. 183—208; 1914 a, pp. 225—253; 1918 a, pp. 241—246). For it is evident that the musculus rectus externus must have extended throughout the entire ventro-medial half of the cavity to reach its supposed place of origin in the fossa *my*. Since, as far as can be judged, the other three muscoli recti of the eye may have originated principally on the lateral surface of the basal region (*bsph*) of the sphenoid and the dorsal surface of the basiptyergoid process, the posterior ends of these too have extend into the cavity and been situated in this medially and presumably also somewhat ventrally of the m. rectus externus. Further, n. oculomotorius and n. abducens had their exit in the same half of the cavity, the former nerve far forward, the latter far backward. Finally it is very probable (cf. *Saurichthys ornatus* part II) that v. jugularis in its backward course also entered this half, where, however, it would have turned fairly soon in a dorsal direction reaching the dorso-lateral half of the cavity.

At the posterior part of this dorso-lateral half of the cavity the trigeminus and lateralis roots have pierced the medial wall of the cavity, which was rather thick at this place. A part of the ganglionic complex that was formed by these roots must presumably have been situated in the medial wall (incisure V in my figures), another part, on the contrary, probably had its position laterally of this in the cavity itself. Of the branches sent out from the ganglionic complex at least r. maxillaris, r. mandibularis and n. buccalis lateralis have had an anterior course through the dorso-lateral half of the cavity throughout its length. R. ophthalmus profundus or (a somewhat corresponding nerve) has had its exit far forward rather in the dorso-lateral than in the ventro-medial half or at the boundary between the two. Whether, finally, the roots for n. facialis closely accompanied the trigeminus roots and thus entered the most posterior end of the cavity or whether they pierced the cranial wall behind the cavity, must still be considered an open question. The trigeminus incisure (V, text figs. 62, 63; Pl. 20, fig. 6; Pl. 21, figs. 1—3; Pl. 22, figs. 1, 3) on the posterior margin of the sphenoid certainly seems by its size to indicate that the trigeminus and facialis roots might have had their exit together or in close proximity, but there is no real proof of this.

As far as one can judge there has been at least no osseous or cartilaginous septum between the dorso-lateral and ventro-medial halves of the postorbital cavity, for on the lateral surface of the sphenoid there is no trace of a fastening for a septum of this sort. Whether, on the other hand, a membranous septum was present or not is very difficult to decide, except just at the very opening to the orbit. For at this opening we find on the medial side of the parasphenoid quite close to the lateral edge of the basiptyergoid process a small dorso-medially directed process *pd* (text fig. 64B) with about the same position as the ventral end of the process in *Amia* that ALLIS (1897 a, pp. 492—497; 1909 a, pp. 39—41, 48; 1914 a, pp. 246—248; 1918 a, 244—245) called the alisphenoid pedicle. In *Amia* this process has its ventral end in contact partly with the cartilage laterally of the orbital opening of the myodome, partly with the processus ascendens of the parasphenoid. In the *Teleostei* ALLIS (1909 a, pp. 39—41, 48) has shown that a correspondence to the alisphenoid pedicle is present, although it is often represented only by a ligament issuing from a process or a ridge-like swelling of the alisphenoid and extending to the processus ascendens of the parasphenoid. The ligament may be partly or entirely ossified by «invading growths» from the alisphenoid and the parasphenoid,

and I now imagine that the above-mentioned process *pd* in *B. mougeoti* indicates that a ligament homologous with the alisphenoid pedicle in *Amia* was present and that an «invading growth» of bone had taken place from the parasphenoid in the ventral end of the ligament. But I have not found any distinct traces of a fastening for such a ligament on the pars alisphenoidea of the sphenoid.

As has been pointed out above, it is rather probable that the parasphenoid in *B. mougeoti* did not form part of the direct boundary of the postorbital cavity or did so possibly only farthest forwards. As I mentioned, a cartilaginous lamella probably extended from the cartilage in the anterior part of the labyrinth region some distance in a rostral direction along the medial surface of the parasphenoid both on the lateral and the ventral sides of the cavity. Consequently, if this were correct, the cavity would have been to a considerable extent a space in the cranial wall itself or, to put it more briefly, an intramural space (ALLIS). The medial wall of the trigemino-facialis part of the cavity would then correspond to the ossified wall that, at least in several Teleosts, (cf. ALLIS, 1909a, pp. 45—47, 207—208; 1914a, pp. 243, 246—248; 1918a, pp. 244—246) separates the real trigemino-facialis chamber (or trigeminus chamber) from the trigemino-facialis recess. This recess would apparently have been present in *B. mougeoti* partly bounded by the large trigeminus incisur (*V*) in the posterior border of the sphenoid, partly by the cartilage following behind this bone and belonging to the labyrinth region. In *Amia* and probably in *Lepidosteus* as well, according to ALLIS (1909a, loc. cit.; 1914a, loc. cit.; 1918a, loc. cit.) the trigemino-facialis recess has probably fused with the trigemino-facialis chamber, and the wall between them has been resorbed. With this assumption the trigemino-facialis part of the postorbital cavity of *B. mougeoti*, leaving out of consideration the possible extra-cranial part, would thus be homologous with the trigemino-facialis chamber of Teleosts or at least with the trigeminal part of this chamber.¹⁾ If the trigemino-facialis part of the cavity were in addition separated from the myodomic part by a membranous septum, the agreement with the *Teleostei* would have been rather great; if, on the other hand, both parts had been in open communication with each other, the conditions would have formed an intermediate stage between those in *Amia* and in Teleosts.

If the postorbital cavity in *B. mougeoti* has to a great extent been an intramural space it is also evident that its myodome, apart from the extra-cranial, anterior part, would on either side be homologous with an antero-lateral part of the myodome in *Amia* and the *Teleostei*. It would presumably represent only a small part of the compartment of the myodome in the Teleosts that ALLIS (1918a, p. 243) called the dorsal one. If the basal part *bsph* of the sphenoid were to be somewhat reduced and the wall formed by the basal parachordal plate (*pc*) between the myodomes was broken through and partly resorbed, we should get a myodome that, at least in its essential parts, would be homologous with that in *Amia*. If the basal part *bsph* of the sphenoid were reduced to a thin septum too and the origin of the musculus rectus externus extended into the fenestration (*fen. bas. post.* text fig. 63 B; Pl. 21, figs. 1—3; Pl. 22, fig. 3) that might represent fenestra basicranialis posterior, and if this muscle

¹⁾ As we know, at least in several cases the trigeminus part alone of the trigemino-facialis chamber may be developed in many Teleosts (ALLIS, 1914a, p. 246).

continued to extend backwards between the parasphenoid and the basis of the primordial neurocranium, a myodome would arise that was in all respects homologous with that of the *Teleostei* (cf. GAUPP, 1905; pp. 667—669; ALLIS, 1909a, p. 195; 1918a).

Finally the possible extra-cranial part that would form the most posterior part of the postorbital cavity would be situated between the sphenoid on the one side and the parasphenoid and the anterior part of its processus ascendens on the other, as is evident from the account given by me above. An extra-cranial part of this sort would of course be added to the myodome and the trigemino-facialis chamber in *Amia*, if the parasphenoid of this fish were wider and its processus ascendens extended farther forward.

If we now start out instead from the alternative that the postorbital cavity in *B. mougeoti* was preponderatingly an extramural space, the trigemino-facialis part probably showed about the same conditions as in *Polypterus*, i. e. it would have corresponded to a trigemino-facialis chamber only functionally (cf. LEHN, 1918, pp. 403—404). With regard to the myodome it too could, under similar conditions, be termed a myodome chiefly from a functional point of view. This would also be true of its anterior and middle parts. The posterior part, on the other hand, seems, as we have found, on account of the development of the fossa *my* to present such conditions that it is difficult not to regard it as homologous to at least a small antero-lateral part of the myodome in *Amia* and the Teleosts.

The view that the postorbital cavity in *Birgeria mougeoti* is chiefly an extramural space does not, however, in my opinion, fit in well with the development of the orbito-temporal region as a whole. It is true that in *Birgeria mougeoti*, as we have seen, this region has a number of features in common with the corresponding region in Polypterids and Crossopterygians, but as a whole it can be unconditionally characterized as Actinopterygian-like. In several respects it even appears to be considerably more specialized than that of the sturgeons and approaches that of the higher Ganoids and Teleosts. It would consequently be rather strange if this specialisation had not appeared with regard to the postorbital cavity as well, so that not only functionally but also in reality it corresponded to more or less considerable parts of the myodome and trigemino-facialis chamber of the higher Ganoids and Teleosts.

A rather important support for the correctness of this view would be afforded by my interpretation, given above, of the small process *pd* on the medial side of the sphenoid, provided that this interpretation could be shown to be the right one.

As in any case I consider that I have proved that the progress leading to the development of myodome had already definitely begun in *B. mougeoti*, there is nothing surprising in this. For according to what we know of the myodome in primitive Teleosts (ALLIS, 1909 a, pp. 201—202) and Semionotids (ALLIS, 1909 a, p. 201; WOODWARD, 1893 b, p. 564; FROST, 1913, p. 221), we must expect it to occur in more primitive forms than the higher Ganoids, and in that case most probably already in Palaeoniscids, a view, which, according to the observations made on *B. mougeoti*, seems to be correct. But I do not mean to suggest by this that a myodome is found in all Palaeoniscids. As I have tried to show above in this work (pp. 62, 93, 121) a myodome was probably developed in Coelocanthids too.

The membrane bones of the cranial roof. — The cranial roof in *B. mougeoti* (Pl. 24, fig. 2) as far as it is preserved, seems to show on the whole Palaeoniscid-like conditions. One can identify the paired frontal (*Fr*, Pl. 24, fig. 2), dermosphenotic (dermal postfrontal, *Dsph*, Pl. 24, fig. 2), supratemporo-intertemporal («squamosal», *Stemp*, Pl. 24, fig. 2) and probably the parietal (*Pa*), and a supraorbital (*So*) as well. All these bones are, however, only fragmentarily preserved and their bone substance is to a great extent quite weathered away, so that in most cases only impressions of the lower side are left. Some of them are also partly much broken. It is not possible under these conditions to fix quite accurately in details the course of the sutures between them.

The frontals are long and relatively narrow. Their posterior end is situated above the anterior half of the labyrinth region. Their anterior one is not preserved but must have extended on to the ethmoidal region. The centres of ossification are above the posterior half of the partes laterales of the sphenoid. Medially they meet each other in the normal way, and the suture between them was probably fairly straight.

The dermosphenotic is a rather large bone, on either side of the cranial roof, with its centre of ossification over the anterior part of the autosphenotic. Its lateral and rostral extensions cannot be established.

The parietals, normally situated above the posterior part of the labyrinth region, are presumably represented merely by the anterior ends.

The supratemporo-intertemporal of either side seems to have been a large and rather wide bone extending forward as far as over the most posterior part of the orbit, where it meets the dermosphenotic in the usual way. Medially it was bounded by the frontal and parietal. A considerable posterior portion of it is not preserved, and its extension backwards cannot therefore be established. The centre of ossification is not preserved either, but, to judge from the radiation of the bone substance, it was probably above the lateral edge of the prootico-opisthotic, fairly far back. A line drawn between the ossification centres of the two supratemporo-intertemporals would in its middle part have almost coincided with the suture between the parietals and frontals.

Each supratemporo-intertemporal extended laterally out past the lateral edge of the primordial cranium, but it is impossible to ascertain how far. On the ventral side there issues from each of them a perpendicular, long, but not especially high lamella (*vl*, text figs. 60, 61, 64B) which is closely actual in its posterior part to the upper part of the lateral surface of the prootico-opisthotic. The anterior and larger part of this ventral lamella, however, has rested against cartilage and reaches forward nearly to the posterior end of the autosphenotic.

From the posterior part of this lamella there issues in a forward, downward and medial direction a long process (*vp*, Pl. 22, fig. 3) which in the present state of preservation is somewhat broken and squeezed in the gap between the prootico-opisthotic and the processus ascendens of the parasphenoid. It is evident, however, that this process cannot be much displaced from its original position, at its ventral end must, on account of its shape, have helped to form the dorsal boundary of the posterior exit of the facialis canal. It ought therefore to have been situated in about the way shown in text fig. 61 (*vp*). As it was rather thick it must of course have been sunk in cartilage to some extent. Its posterior edge was situated close against the anterior margin of the prootico-opisthotic.

In sturgeons the supratemporo-intertemporal has a lamella that closely resembles the one (*vp*) in *B. mougeoti*, though it has not the long forward, downward and medially directed process, and SAGEMEHL (1884, foot-note pp. 188—189) also describes a rather similar one in *Amia*. In Coelacanthids too, as is shown by my description in this work (pp. 63, 81, 96 above), I found a lamella in a similar position, issuing from the supratemporal part of the supratemporo-extrascapular and the intertemporal part of the parieto-intertemporal. In addition the Coelacanthids have on the supratemporo-extrascapular, as we have seen, a process (*h*) that, at least at a hasty inspection, appears to have about the same conditions as the process *vp* in *B. mougeoti*. If, however, *n. facialis* in Coelacanthids has had its exit from the cranial cavity in front of the process *f₁*, as I consider most probable at present (cf. p. 60), the process *h* in them would be situated somewhat caudally of the process *vp* in *B. mougeoti*. If, on the other hand, *n. facialis* in Coelacanthids has had its exit behind the process *f₁*, the two processes in question here might possibly be homologous.

As we shall see from the following description (part. II), in Saurichthyids too there seems to be a certain correspondence to the process *vp* in *B. mougeoti*.

The relation we found in *B. mougeoti* between the supratemporo-intertemporal and the prootico-opisthotic is noteworthy from another point of view as well. For the fixation between the supratemporo-intertemporal and the primordial neurocranium that has arisen in this case seems to afford us an idea as to how the pterotic was developed in Teleosts and of the homologue of the cartilaginous bone component in this bone (cf. pp. 154—161 above; cf. also SAGEMEHL 1884, foot-note pp. 188—189).

For if we assume that the prootico-opisthotic, for instance, extended farther forward on the dorsal side of the posterior exit of the facialis canal, it would, at least partly, have surrounded the process *vp*, so that the supratemporo-intertemporal would have obtained a very fixed connection with the primordial neurocranium. From a stage of this sort a fusion between the prootico-opisthotic and the supratemporo-intertemporal can easily be thought to have arisen, and if this is so, then finally, owing to the influence of *musculus constrictor superficialis 2* or muscles derived from this (cf. VETTER 1878; RUGE 1897), the supratemporo-intertemporal together with a dorsal part of the prootico-opisthotic would have been broken loose from the other parts of the prootico-opisthotic. This dorsal part of the prootico-opisthotic would form about the dorsal half of an opisthotic. The cartilaginous bone component in the pterotic would thus, as I have tried to show above, be homologous with the dorsal part of the opisthotic.

With regard to the membrane bones of the cranial roof in *B. mougeoti* it ought finally to be noted that, as far as one can judge, they rest close against the dorsal surface of the primordial neurocranium and that apparently no muscle fossae have been developed beneath them. Above the anterior part of the labyrinth region the frontals are broken off and somewhat pressed down into the cranial cavity (see Pl. 24, fig. 2), which may perhaps indicate that a fontanel had been situated at this place as in *Saurichthys ornatus* (cf. Part II).

Visceral skeleton.

Specimen *P. 171* has several elements of the visceral skeleton well preserved. The account given here is entirely based on this specimen.

The palatoquadrate and mandibula were very long. The mouth was consequently large and extended so far backwards that its posterior end was situated caudally of the orbital entrance, as in the Palaeoniscids in general.

It is impossible to ascertain to what extent cartilage was present in the palatoquadrate. Of its membrane bones two are preserved, one of which I interpret as an ectopterygoid (*Ecpt*), the other as an entopterygoid (*Enpt*).

The ectopterygoid (*Ecpt*, text fig. 65, Pl. 23, figs. 1, 2) is a long bone situated along the lateral margin of the palatoquadrate. In its present state of preservation it is defective medially, anteriorly, and to some extent also laterally, so that its width and its extension forwards cannot be ascertained with certainty. Backwards it extended to the quadrate. It occupies such a position that one of its surfaces is directed ventro-medially, the other dorso-laterally. The dorso-laterally directed one is weakly concave in a transversal direction the ventro-medially directed one correspondingly convex. The lateral margin is almost straight. The bone substance is strikingly thin. The centre of ossification is situated towards the posterior end of the bone rather near the lateral margin.

The entopterygoid (*Enpt*, text fig. 65; Pl. 23, fig. 2) is represented by a small portion, situated between the anterior end of the ectopterygoid and the parasphenoid (*Psph*). Medially it is in direct contact with the latter bone. The preserved part is rather narrow. It may possibly have had a considerable extension backwards as in other allied forms.

Along the lateral margin of the ectopterygoid are found slight remains of the maxilla (*Max*, text fig. 65; Pl. 23, fig. 2). It is evident that this bone was very long and that it presumably extended as far as the pars quadrata of the palatoquadrate, covering this on the outside. In its present state of preservation a posterior and longer part of it is situated close to the ectopterygoid without coming into connection with it. In the anterior part, on the other hand, its medial edge has been covered with a thin lamella from the ectopterygoid, and it also seems probable that this lamella existed farther posteriorly. That in this case we are not concerned with an accidental covering due to displacement of the two bones in question towards each, is shown by the fact that the lamella of the ectopterygoid that covers the maxilla is definitely distinguished from the rest of the ectopterygoid by the absence of teeth or any indication of them.

I have previously shown (STENSIÖ 1919) that the maxilla in *B. mougeoti* is typically Palaeoniscid-like in its general shape. I have further been able to show here that it was firmly attached medially to the ectopterygoid. TRAQUAIR (1877 a, p. 18) also surmised that a connection of this sort existed in Palaeoniscids. WOODWARD (1889 b, p. 301) has described in *Birgeria acuminata* on the medial side of the maxilla a «palatal plate» that seems apparently to have been covered by the ectopterygoid. In *Chondrosteus*, (TRAQUAIR, 1887, pp. 253—256) as in the recent Acipenserids and Polyodontids, the maxilla is also closely joined to the palatoquadrate and this is also the case in *Saurichthys*. In the last-mentioned form there occurs, as we shall see (cf. Part II), as in *B. acuminata*, a medial lamella or list that is covered dorsally by the ectopterygoid. Finally we also find, as is known, a firm connection between the palatoquadrate and the maxillary in *Polypterus*, a connection which is formed posteriorly in the same way as in *B. mougeoti* and *Saurichthys*, but is due farther anteriorly, on the other hand, to the so-called maxilla covering the anterior end of the so-called ectopterygoid.

Of the bones of the lower jaw only the mixicoronoid («splenial») (*Mco*, text fig. 66; Pl. 23, fig. 1) is preserved in the material of *B. mougeoti* so far found. This bone is very long and seems to have been strickingly low. It probably covered the medial side of the Meckelian cartilage throughout the whole length. Its most posterior part, which was situated about medially of the insertion of musculus adductor mandibulae, is somewhat lower than the incomparably longer part in front. The anterior part is otherwise very distinctly differentiated from the posterior part by its tooth-bearing labial margin.

Some large teeth embedded in stone just laterally of the mixicoronoid show that the dental had its normal position. The dental itself is, however, completely weathered away.

Nothing is preserved of the hyoid arch and the fifth branchial arch. The four remaining branchial arches (text figs. 65, 66; Pl. 23, figs. 1, 2), on the other hand, are fairly complete. They are all long and slender and are ossified to a considerable extend. Thus in the three most anterior pairs of them one finds the hypo-, cerato- and epibranchials occupied by ossifications, and in addition the second pair has an ossification in the infrapharyngobranchial. In the fourth pair only a ceratobranchial ossification is preserved, and it is uncertain whether an epibranchial ossification was also developed. The different ossifications in each arch were connected with one another by means of cartilaginous epiphyses.

The hypobranchials I—III (*Hbr*₁—*Hbr*₃ text fig. 66; Pl. 23, fig. 1) are embedded in the stone in such a way that they are only accessible for investigation from the ventral side. They grow narrow towards the ventral ends, which are distinctly bent in a medial direction towards the copulae. Towards the posterior end of its anterior third hypobranchial II has a small process (*pr. int.*, text fig. 66; Pl. 23, fig. 1), which may either have been developed in connection with the insertion for the ligamentum interarcuale ventrale (cf. ALLIS 1897a, Pl. XXXIII, figs. 49, 50) or may represent a broken ventro-medially pointing process which has been

attached to the copulae, i. e. the anterior end of the hypobranchial II would, if the latter alternative were correct, have been befurcated. It is impossible to decide whether hypobranchials I and III had similar processes. Hypobranchial IV must have been cartilaginous if it was present as in independent segment.

Ceratobranchials I—IV (*Cbr*₁—*Cbr*₄, text fig. 66) are long and slender, each with a rather deep longitudinal furrow on the posterior surface.

Epibranchials I—III (*Ebr*₁—*Ebr*₃, text fig. 65) are in the same way as the ceratobranchials long and slender and have on the posterior surface a relatively deep longitudinal furrow. The dorsal side of those of branchial arches I and II is divided by a

Text fig. 65.

Birgeria mougeoti AGASSIZ.

Parasphenoid and parts of the visceral skeleton, seen from the dorsal side.

After P. 171. ^{2/3}.

*Ebr*₁—*Ebr*₃, epibranchials of the gill-arches I—III; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Ifr*₂, infrapharyngobranchial belonging to gill-arch II; *Mx*, maxillary; *Psp*, parasphenoid, incompletely preserved.

sinus into an anterior and a posterior short truncate process. Whether that of branchial arch IV was ossified or consisted of cartilage is a question that cannot be answered from the present material.

At least in the second and probably also in the first pair of branchial arches the pharyngobranchials were divided into infra- and suprapharyngobranchial, all of which, except the infrapharyngobranchial II (*Ifrbr*₂, text fig. 65; Pl. 23, fig. 2), were probably cartilaginous. Infrapharyngobranchial II consists of a relatively large bone, shaped somewhat like in hour-glass, which had a cartilaginous epiphyse at either end. The pharyngobranchials of the third pair of branchial arches, and presumably also of the fourth pair as well, do not seem, at least if we judge from the dorsal end of epibranchial III, to have been divided into infra- and suprapharyngobranchials, and it is also probable that they had no ossification.

The gill filaments have had in their interior ossified or calcified supporting gill-rays, some of which are still preserved. As far as can be seen, the gill-rays are not comb-shaped.

The ventral ends of the branchial arches were joined in the usual way by a row of copulae. The material present does not show the conditions of this row in front of the first gill-arch pair. Behind this pair and between it and pair IV it was strong. In this part it was also strikingly well ossified, as we find there no fewer than three well developed ossifications (*Co*₁—*Co*₃, text fig. 66; Pl. 23, fig. 1). The most anterior of these, which is at the same time the shortest, is situated between the first and second pairs of branchial arches, the following one between pairs II and III, and finally the most posterior one, which is also the longest, between pairs III and IV. All the ossifications were separated from each other by short cartilaginous interspaces and caudally of the last one there was also certainly cartilage. It is of course impossible to decide the relations of these ossifications to the segmentation of the row of copulae¹⁾.

The investigations of TRAQUAIR (1877a, p. 22), FRITSCH (1895, vol. 3, p. 79) and others have already shown that the branchial skeleton in the Palaeoniscids was well ossified,

Text fig. 66. *Birgeria mougeoti* AGASSIZ.
Parts of the visceral skeleton from the ventral side.
After P. 171, 76.

*Cbr*₁—*Cbr*₄, ceratobranchials; *Co*₁—*Co*₃, ossifications in the copulae; *Ecp*, ectopterygoid; *Hbr*₁—*Hbr*₃, hypobranchials; *Mco*, mixicoroid; *pr. int.*, process possibly representing a fastening for ligamentum interarcuale ventrale.

¹⁾ As GAUPP (1904, pp. 910, 914) has pointed out, our knowledge of the copular skeleton of the Ganoïds and the Teleosts is very incomplete. Moreover the name copula or basibranchial has been used as a term both for each of the cartilaginous segments of the copular row and for each of the ossifications that appear in this, even if two or more of these ossifications corresponded to one cartilaginous segment. It is easy to understand that such a method of procedure has caused a great deal of confusion. In this work I have consequently followed GAUPP and avoided calling the copular ossifications copulae.

but hardly anything was known as to the conditions of its different elements. From the description given by me above we see, however, that the skeleton of the branchial arches can as a whole be looked upon as typically Actinopterygian-like. Among the recent *Actinopterygii*, *B. mougeoti* seems, at least with regard to the ossifications in the branchial arches and copulae, to approach most closely to *Amia* and the Teleosts.

Dentition.

All the teeth are more or less pointedly conical in shape.

The labial border of the maxillary and dental are furnished with two rows of teeth, a medial row of large powerful ones and a lateral row with considerably smaller ones. The teeth situated nearest to the lateral margin of the ectopterygoid and on the upper margin of the mixicoronoid are of about the same order of magnitude as those in the lateral row of the maxilla. The ectopterygoid and the mixicoronoid together with the entopterygoid are, in addition, densely provided on their medial surfaces with strikingly small teeth. The conditions of the dentition on the parasphenoid and the premaxilla are unknown. The branchial arches had numerous fine and relatively long teeth.

On the smallest teeth (e. g. the majority of those belonging to the pterygoid and the mixicoronoid) only few details can be observed. As a rule, however, it is possible to verify that the pulp cavity was present and the point was covered with a cap of enamel.

The largest teeth present (*P. 345*) are about 15 mm high with their distal part not infrequently bent a little like a thorn towards the medial side. They seem to resemble most the shape of tooth that MÜNSTER (1839, p. 119) and AGASSIZ (1844, vol. II, part 2, p. 87) have distinguished under the name of *Saurichthys semicostatus*, but which WOODWARD (1895b, p. 20) and previously v. MEYER (1849 b, p. 235) and ECK (1865, p. 120) adopted as a synonym of *Saurichthys mougeoti*, i. e. of *Birgeria mougeoti*. The enamel cap that covers the point is $\frac{1}{2}$ — $\frac{1}{4}$ of the total length of the teeth and is divided into a medial and a lateral half by a sharp edge placed sagittally. This cap is also furnished with a sculpture of some raised and fairly sharp striae (Pl. 21, figs. 5, 6), placed sparsely and generally developed in about the same way on both sides of the sagittal edge. If these are sometimes weaker on one side, then it always seems to be the medial side. They proceed from the basal edge of the enamel cap and extend distally to about the middle of its height or slightly farther. The remainder of the cap is therefore smooth. With regard to the striae it may further be added that they are often not quite straight but somewhat undulating, and that generally they are of rather different height on the same tooth.

A macroscopic investigation of the big teeth shows clearly that the enamel is not restricted to the cap alone but that it continues from there towards the bases of the teeth as a thin covering. This covering can be seen extending about to the boundary between the middle and proximal thirds of the total heights of teeth but is exceedingly thin nearest this place.

The larger teeth from the fish horizon (Pl. 21, fig. 5) all seem to have had the enamel-covered part furnished, basally of the real enamel cap, with a very fine vertical striation. The same conditions are also shown by a number of larger teeth (Pl. 21, fig. 6) found in the bone-bed 33 m above the fish horizon at Mt Viking, while others from

the latter bone-bed present a partially different appearance (Pl. 21, fig. 7). These deviating teeth have the enamel-covered part basally of the enamel cap developed with fairly coarse vertical ridges, and these ridges have then in their turn fine striae or fine folds in the longitudinal direction. There are, however, several transitional forms between this type of tooth and the others.

Of special interest are the teeth of the branchial arches that are preserved in situ on one specimen from the fish horizon (*P. 171*). These are of about the same height as those on the lateral part of the ectopterygoid and the dorsal edge of the mixicoronoid. Relatively to their length they are, however, more slender than other teeth and also have a longer and more pointed enamel cap than these. Their enamel caps is also characterized by the fact that, unlike that in the other teeth, it seems to be without striation.

We thus see that the teeth of the branchial arches differ considerably from the other teeth in the same species, and the difference is even so great that we should probably not have ventured to refer them to the same species as the others if they had not been found in the same individual as these. We thus get an idea of the difficulty of distinguishing different fish species from each other merely by means of detached teeth.

Nothing certain is known as to the arrangement of the teeth on the branchial arches.

All the teeth of the fish in question have a large pulp cavity that extends up into the enamel cap. This cavity is surrounded mostly by a layer of ortho-dentine, which is rather thin towards the base a fact that explains why detached teeth of *Birgeria* species practically never have their basal parts preserved. Outside the layer of ortho-dentine there follows in the distal part of the teeth the enamel cap, and this is continued basally, as I have mentioned above, by the thin enamel covering which seems to stop at the boundary between the middle and basal thirds of the teeth. At any rate it does not reach as far down as to the base. This enamel covering seems to have been overlooked by AGASSIZ (1844, vol. II, part II, p. 153).

The *Birgeria* teeth show, as we know, a great resemblance to the *Saurichthys* teeth, which has also caused *B. mougeoti* to be adopted as a *Saurichthys* species. We shall see, however (cf. part II), that a very characteristic quality of *Saurichthys* teeth is that they have the dentine somewhat folded (plicidentine) in their basal parts, which is not the case in *Birgeria*, and in addition that their enamel cap generally lacks striation. If striation is developed it is, however, extremely delicate and abundant.

Axial skeleton.

The axial skeleton in *B. mougeoti* is represented by a number of remains from the caudal region and the most posterior part of the abdominal region. The remains from the latter region are very incomplete and little suited for a more thorough investigation. I have therefore been compelled to confine myself almost entirely to a description of the axial skeleton in the caudal region. Where nothing else is stated the description is based on specimen *P. 155*.

It is evident that the chorda dorsalis has played an important part and has been well developed. A thin brownish layer (the brown colour due to the infiltration of

bitumen) found in the place occupied by the chorda may possibly constitute remains of its sheath.

The neural and haemal arches are preponderatingly ossified and are situated fairly well in situ both relative to each other and to the space occupied by the chorda (text fig. 67 A; Pl. 21, fig. 4).

The neural arches consist in each segment of two paired elements. One of these elements (*Id*) is trapezoidal in shape with the shortest margin directed dorsally and the longest, which rests against the chorda, ventrally, while the anterior and posterior margins are so situated that they converge upwards. In the segments belonging to the most anterior part of the caudal region the height of the elements *Id* is only slightly smaller than the length, and in these segments the antero-dorsal corner of each of these elements has also a rather deep sinus. Posteriorly, towards the middle and posterior parts of the caudal region the height of the elements *Id* decreases gradually with each segment, and the above-mentioned sinus becomes larger and more shallow, finally occupying nearly the whole of the dorsal margin.

The other element (*Bd*, text fig. 67, Pl. 21, fig. 4) in each neural arch is considerably more strongly ossified than the one just described and, unlike it, very much drawn out in height. It is not placed vertically but is inclined backwards and this inclination increases the closer one approaches to the caudal fin. With regard to function we may conveniently distinguish in this element a short, widened proximal part, which forms part of the boundary of the neural canal, and a distal part, which forms a long neural spine. Both these parts pass into each other without any distinct boundary, and the element as a whole has a shape that most closely resembles a rifle with the butt towards the chorda. The proximal part extends in between two adjacent elements *Id* and has presumably reached down to the chorda, though it can have come into direct contact with this only over a rather short stretch. Its relations to the elements *Id* are shown in text fig. 67 and in Pl. 21, fig. 4.

In the anterior part of the caudal region we find that the elements *Bd* have on their caudal (ventro-caudal) margin a weak, though distinct, sinus, situated opposite the sinus on the anterodorsal corner of each element *Id* following immediately behind. On the elements *Bd* that fall within the middle and posterior part of the caudal region the sinus gradually becomes indistinct and finally can no longer be distinguished. In the abdominal region, on the other hand (P. 157; text fig. 67 B; Pl. 22, fig. 2), the sinus is very strong and is bounded dorso-caudally by a narrow downward-pointing process (*p*₁).

On the anterior (antero-dorsal) margin too the proximal part of the element *Bd* has a sinus, bounded posteriorly and at the top by a small process (*p*). This sinus is found clearly developed both in the abdominal and the whole caudal region.

The sinus in the antero-dorsal corner of each element *Id* together with the sinus in the caudal margin of each element *Bd* situated in front, has obviously formed a foramen, which has apparently been pierced by the ventral spinal nerve root. The dorsal root may have been transmitted dorso-caudally of the ventral one presumably close to the anterior margin of each element *Bd*. It is not impossible that it may then have had some connection with the sinus on the anterior (antero-dorsal) margin of the proximal part on the element *Bd*.

The exit of the roots of the spinal nerve in each segment shows that in the elements *Id* we are concerned with inter dorsals (cranial neural elements) and in the elements *Bd* with basidorsals (caudal neural elements) in the signification given to these terms by SCHAUINSLAND (1905).

If we now turn to the haemal arches, we shall find these represented partly by robust four-sided skeletal elements (*Iv*, text fig. 67 A; Pl. 21, fig. 4) and partly by long ventro-caudally pointing elements, *Bv*. To each skeletal element *Iv* corresponds an element *Bv*. In the most anterior part of the caudal region each element *Bv* is in connection with the ventral margin of each element *Iv*. Towards the back, however, this state of affairs is altered, the connection being displaced first to the postero-ventral corner and then still farther backwards to the posterior margin of the elements *Iv*.

Each elements *Iv* has a dorsal part that extends upwards along the chorda (*pc*, text fig. 67 A; Pl. 21, fig. 4), and a ventral part situated entirely under this. The dorsal part, consisting of a spongy bone substance, is best developed in the anterior

Text fig. 67. *Birgeria mougeoti* AGASSIZ.

Parts of the axial skeleton. $\times 1/2$.

A) Part of the caudal region with the chorda reconstructed. After P. 155.

B) Neural arch element from the posterior part of the abdominal region. After P. 157.

Bd, basidorsal; *Bv*, haemal spine, representing the distal part of a basiventral; *Ch*, Chorda dorsalis; *Id*, interdorsal; *Iv*, interventral + a proximal part of the basiventral; *pc*, process on the posterior border of the basidorsal; *p*, process on the anterior border of the basidorsal; *pc*, dorsal part of the interventral, which together with the corresponding part on the other side forms a semicircle surrounding the ventral half of the chorda

part of the caudal region, where it has a characteristic four-sided shape, and a height corresponding to about half the diameter of the chorda. As one approaches the caudal fin it becomes gradually lower with each segment and consequently assumes a somewhat rectangular shape. The ventral part of each element *Iv* is also highest in the anterior end of the caudal region, and its shape is rectangular there, gradually becoming trapezoidal in the segments following backwards, because the anterior margin decreases in height. Contrary to the dorsal part the ventral one consists of a rather compact bone substance like the elements *Bv* and the elements of the neural arches. Both parts are incompletely

separated from each other by a horizontal sinus penetrating from the back. The sinus is most strongly developed towards the posterior part of the caudal region, as is seen in textfig. 67 A.

The elements $I\nu$ are not in contact with each other but are separated by fairly large gaps, through which the intersegmental vessels may have had their exit from the haemal canal. As far as can be discovered each element $I\nu$ is situated opposite an interdorsal and each element $B\nu$ opposite a basidorsal. From this one might conclude that the element $I\nu$ represented an interventral and the element $B\nu$ a basiventral, but the conditions are probably more complicated than this. For it seems to me probable that the element $I\nu$ in each segment also includes a proximal part of the basiventral, while the element $B\nu$ would, if this were correct, represent only the distal part of a basiventral, i. e. it would represent only a haemal spine. This view is, at least to a certain extent, supported by the relations stated above between the elements $B\nu$ and the elements $I\nu$ in the anterior part of the caudal region.

With regard to this last-mentioned element ($I\nu$) it ought finally to be remarked that I was unable to ascertain whether it was fused with that of the opposite side. In any case, however, it has formed with this a semicircle which has surrounded the ventral half of the chorda in each segment. We thus have the beginning of the formation of a vertebral body, a hypocentrum, but the chorda was certainly very little affected by this.

As will be seen from what has been mentioned, the vertebral column in *B. mougeoti* has retained its original segmentation as in the sturgeons. It is however somewhat more specialized than in these in the following respects: 1) a stronger degree of ossification; 2) indications of the formation of vertebral centra; 3) the beginning of reduction in the contact between the basidorsals and the chorda; 4) the assumed fusion between the interventral and the proximal part of the basiventral in each segment. In these respects *Birgeria* resembles most closely *Amia* and certain of the higher fossil Ganoids.

The skeleton of the unpaired fins.

The anal fin (*A*, Pl. 21, fig. 4) is only preserved in specimen *P. 155*. It was apparently well developed and had in this specimen at the base a length of at least 20 cm. The lepidotrichia were very numerous; their total number was probably about 70. Their distal parts are not preserved, and the shape of the fin cannot therefore be seen from the material present. They are, as is usual in Palaeoniscids, situated close together, but while in Palaeoniscids in general they are closely jointed throughout their length, in *B. mougeoti* they have here a short unjointed proximal part, which is also found in the dorsal and caudal fins. *Birgeria mougeoti* thus shows in this respect a certain specialization in the direction of the higher ganoids. The lepidotrichia of the anal fin were, however, as usual, far more numerous than the endoskeletal radials, and it is also noteworthy that they had no ganoine covering.

The endoskeleton of the anal fin may have consisted of about 25 radials, 22 of which are partly preserved. The anterior 16 ($Ps + Ms$, Pl. 21, fig. 4) are each practically occupied throughout their length by a single ossification, extending from the distal ends of the haemal spines to the basal ends of the lepidotrichia, while the remaining 5 have two ossifications, the proximal one (Ps , Pl. 21, fig. 4), which reaches close to the distal ends of the haemal spines, being the longest.

As we know the endoskeletal radials of the dorsal and anal fins are generally divided into three segments (cf. SCHMALHAUSSEN 1912, 1913a, 1913b), it now seems probable to me that the proximal ossifications in the five posterior endoskeletal radials of the anal fin in *B. mougeoti* were situated in the proximal segments, while the distal ossifications (*Ms*) belonged to the middle segments. The distal segments have been small and cartilaginous, as in the *Actinopterygii* in general. Thus we have in the posterior part of the anal fin both ossified axonosts and baseosts, to use COPE's (1887, p. 1016) and WOODWARD's (1891b) terminology.

The long ossifications in the 16 most anterior endoskeletal radials of the anal fin must either have been situated entirely in the proximal segments, which would then be very much lengthened at the expense of the middle ones, or have arisen by a fusion of the ossifications of the middle and proximal segments in each radial. If the former alternative is correct both the middle and the distal segments would of course have been small and cartilaginous.

In certain primitive Palaeoniscids, e. g. *Elpisopholis* (WOODWARD, 1908a, p. 20), both axonosts and baseosts are present, though the baseosts are short. On the other hand in *Coccolepis*, which is geologically the youngest representative of the Palaeoniscids, baseosts are absent, at least as independent bones (WOODWARD, 1895a, pp. 4—8; TRAQUAIR, 1911b, pp. 13—14). The modification of the endoskeleton of the unpaired fins thus seems in the Palaeoniscids to go in such a direction that the baseosts disappear either by being fused with the axonosts or being reduced. *Birgeria mougeoti* shows in this respect an intermediate stage between *Elpisopholis* and *Coccolepis*.

Another circumstance with regard to the endoskeletal radials in the anal fin of *B. mougeoti* ought also to be noted in this connection. It is evident that the endoskeletal radials correspond to some extent to the number of the haemal spines only in the anterior part of the anal fin. In the middle part of the fin we find two and in its posterior part two or three inner radials to each haemal spine.

Similar conditions have already been shown by TRAQUAIR for the dorsal fin of *Phaneroesteon* (1911a, p. 167) and seem also to occur in Palaeoniscids in general, both in dorsal and anal fins (*Psilichthys*, HALL, 1900, p. 147).

The dorsal fin (*D*, Pl. 21, fig. 4; Pl. 22, fig. 2) in *Birgeria mougeoti* was situated rather far caudally and had a large posterior part opposite the anal fin. It is very incompletely preserved, so that nothing is to be seen with regard to its shape. It is evident, however, that it was large and had a considerable number of lepidotrichs, which showed in all respects the same conditions as those of the anal fin. The endoskeleton consists, as is usual in Palaeoniscids, of axonosts and baseosts (TRAQUAIR, 1877a, p. 24; WOODWARD, 1891b, p. 427; 1898a, p. 84; 1908a, p. 20), which seem, as in *Phaneroesteon* (TRAQUAIR, 1911a, p. 167, fig. 9) to have been of about the same length. This would apparently mean that the proximal and middle segments of the endoskeletal radials were equally strongly developed, a condition that, according to SCHMALHAUSSEN's investigations (1912—1913), is to be considered as rather primitive. As in the anal fin, the number of the endoskeletal radials was greater than that of the neural spines.¹⁾

¹⁾ A fragment either of a dorsal or an anal fin, probably belonging to *B. mougeoti*, has a certain interest, as it shows that endoskeletal radials were also present in front of the fins in question (cf. TRAQUAIR, 1877a, p. 24).

The caudal fin is large and strongly heterocercal (Pl. 24, fig. 1), deeply cleft and nearly equilobate. The lepidotrichia are very numerous, situated close to each other and are ramified dichotomically in their distal parts. Apart from a shorter proximal part they are densely jointed throughout. The joints are always longer than broad and are often somewhat sinuated into the shape of an hour-glass at the middle. The dorsal lobe has a row of strong ridge-scales on its dorsal edge. All the lepidotrichia of the fin lack ganoine covering.

The haemal spines (*hsp*, Pl. 24, fig. 1) were long and strong in the most anterior part of the ventral lobe, but slightly flattened from the sides. Towards the middle and posterior part of the same lobe they decrease in size but seem to maintain the same shape as in the anterior part.

The skeleton of the girdles and the paired fins.

The pectoral fins in *B. mougeoti* are still unknown, as is also the case with the shoulder girdle.

The pelvic girdle and the ventral fins. Two ventral fins, found together in a nodule (*P. 154*) seem to have certainly belonged to the species in question. As these fins do not occur together with other parts of the skeleton it is impossible to decide their original position in relation to other fins. Nor is it possible to say which of them was originally the right and which the left one, and of course under such circumstances one cannot decide either which of their surfaces was situated dorsally and which ventrally. This state of affairs is, however, of no importance at all for the description and interpretation of the different skeletal elements.

The two fins are fairly well preserved, but one of them — the left one as they now lie — has both its lepidotrichia and inner skeletal elements turned 180° from its original position, in the way seen from text fig. 68 A and Pl. 23, fig. 3. They seem to have had a rather long base, a character that is also found in many other Palaeoniscids, e. g. *Cheirolepis* (WOODWARD, 1891 b, p. 451; 1898 a, p. 85, fig. 62; REGAN, 1904, p. 334), *Nematophrychi* (TRAQUAIR, 1909, p. 118—119, Pl. XXVI, fig. 1) *Cryphiolepis* (TRAQUAIR, 1907, p. 105, fig. 4, *Elpisopholis* (WOODWARD, 1908 a, pp. 17, 20, Pl. IV, fig. 2), *Atherstonia* (WOODWARD, 1891 b, p. 514), *Coccolepis* (TRAQUAIR, 1911 b, p. 13, fig. 2, Pl. I, fig. 1; WOODWARD, 1895 a, p. 7; Pl. I, fig. 16; 1898 a, p. 86; 1915, p. 33) etc. The lepidotrichia are very numerous. No less than about 50 are preserved, but it is probable that the total number has been somewhat larger. They are all incomplete at the distal ends and nothing certain can therefore be discovered as to the shape of the fins. They are also strikingly fine, are situated close together and are without ganoine covering. Apart from a proximal part they are fairly closely jointed and towards the distal ends they are also possibly dichotomically ramified. The joints are, it is true, not specially long, but their length is still considerably greater than the breadth.

The endoskeleton in each fin is represented in its present state of preservation by a large bone-plate (*Pv*) and ossified remains of radials (*po*, *do*, text fig. 68 A; Pl. 23, fig. 3).

The bone-plate *Pv* is represented in the present state of preservation only by an incompletely preserved impression. To judge from this it had a wide posterior and a narrow anterior part, which passed fairly rapidly into each other. It is impossible,

however, to establish with certainty whether this shape is the original one or whether certain lateral portions of the anterior part of the plate have been broken off. I call the plate in question preliminarily a pelvic plate. I shall return to its homologues below.

As far as one can judge, the endoskeletal radials were 16 or 17 in number, of which the most anterior 4 or 5 seem to have articulated with the pelvic plate, while the remainder were situated caudally of this plate.¹⁾ They were all divided into two segments, a proximal and a distal one, the latter being very short.

The proximal segments have had a small cartilage epiphysis on each end. Otherwise each of these segments is occupied by a compact, somewhat hour-glass shaped ossification (*po*, text figs. 68 A, B, Pl. 23, fig. 3), which, apart from a thin peripheral layer of lamellar character, consisted entirely of the same cancellous substance as the replacing

Text fig. 68. *Birgeria mougeoti* AGASSIZ.

Skeleton on the ventral fins. After P. 154, 3/4.

A) Skeletal elements as preserved in the fossil. B) Reconstruction of the endoskeleton. The cartilaginous parts dotted.

Mt, metapterygial elements; Pv, pelvic plate; do, ossification in the distal segments of the endoskeletal radials po, ossification in the proximal segments of the endoskeletal radials.

bones of the neurocranium, a fact that seems to show that we are here concerned mainly with endochondral bone. In *Polyodon* and possibly also in certain recent sturgeons, where a corresponding ossification is found in each proximal segment of the endoskeletal radials of the ventral fins, this ossification consists only of a rather thin perichondral bone layer (v. RAUTENFELD, 1882, p. 26, Pl. I, fig. 5; REGAN, 1904, Pl. VII, fig. 2).

The distal segments, unlike the proximal ones, practically all consist of cartilage. It is interesting, however, that some few of them, belonging to the middle radials, had a little ossification developed (*do*, text figs. 68 A, B; Pl. 23, fig. 3)

¹⁾ Similar radials have been observed in *Elpisopholis* and *Coccolepis*. In *Elpisopholis*, according to WOODWARD (1908 a, text fig. on p. 17), they are developed to about the same number as in *B. mougeoti*. In *Coccolepis macropterus* (TRAQUAIR, 1911 b, p. 14) there are only 9, in *C. australis* (WOODWARD 1895 a, Pl. I, fig. 1 b), on the other hand, about 25.

Together with the pelvic plate and the endoskeletal radials, now treated, a larger or several smaller cartilaginous elements must also have been present in the endoskeleton of the ventral fins. For the 10 or 12 radials that did not articulate against the pelvic plate occupy such a position that their proximal ends must have articulated with one or several cartilaginous elements situated behind this plate. In other words, there must have been one or, according to my view, most probably several cartilaginous metapterygial elements. In my reconstruction of the endoskeleton of the ventral fins in text fig. 68 B I have drawn a number of such elements (*Mt*) but of course in this respect I cannot claim to have hit on the correct number or shape. In such a case as this a reconstruction must always be more or less arbitrary.

Guided chiefly by the conditions in *Coccolepis*, REGAN (1904, p. 334) and to some extent WOODWARD (1895a, p. 7) have expressly stated that the Palaeoniscids must have been developed to some extent in the same way as the recent sturgeons with regard to the endoskeleton of the ventral fins. The conditions in *Birgeria mougeoti* now show that this view was partly correct. For it is easy to see that in the pelvic plate in this species we have an element that in certain respects resembles the plate in the sturgeons that v. RAUTENFELD (1882) calls the «Basalplatte» and WIEDERSHEIM (1892, p. 63, text fig. 11) «vorderes (proximales) Basale», and, further, that the metapterygoid elements in the same species had a position in relation to the surrounding elements corresponding to that of the so-called «basalsegmente» (v. RAUTENFELD, 1882) or «distalen basalia» (WIEDERSHEIM, 1892) in the sturgeons. Common to both *B. mougeoti* and the sturgeons is the subdivision of the inner radials into two segments, of which the proximal one may show an ossification in the sturgeons as well.

On the other hand the present material also seems to make clear that the endoskeleton of the ventral fins shows, at least in certain Palaeoniscids, several deviations from that of the sturgeons. Not only has *B. mougeoti*, for instance, ossifications in a greater number of elements than the sturgeons, but the ossifications in these elements are more strongly developed and mainly of an endochondral nature, and further, the pelvic plate is without any indications of subdivisions in the lateral parts, which, on the other hand, is often the case in the sturgeons in their so-called «Basalplatte».

As GOODRICH pointed out (1909, p. 303), the endoskeleton of the ventral fins of the recent sturgeon fishes resembles to some extent that of the Cladodontids. And the same may be said with equal justification about that of the Palaeoniscids, according to what we have seen in *B. mougeoti*. We can even say that the skeleton of the ventral fins possesses a certain, at least a habitual, agreement with that of the *Elasmobranchii* in general.

If from these general comparisons we now pass on to attempt to discover the homologues of the different elements in the endoskeleton of the ventral fins in *B. mougeoti*, we shall find considerable difficulties. In order to have a general view of the questions that emerge in connection with this attempt at homologization it is, however, first necessary to give a brief historical account of the different views that have been put forward with regard to the inner skeleton of the ventral fins in the *Actinopterygii* in general.

GEGENBAUR was really the first to start to make a comparative anatomical investigation of the skeletons of the extremities in the lower vertebrates — and especially in the sharks. In this he paid attention preferably to the phylogenetic points of view, and his

attempt to show a common plan of organisation in the skeleton of the extremities in all vertebrates resulted, as we know, in his very much debated Archipterygium theory. As early as 1865 then and later in several works he expresses, with regard to the skeleton of the paired fins in the ganoids and Teleosts, the view that it had probably originated by reduction of an Elasmobranchian-like one. GEGENBAUR's work in this department aroused general interest for the study of fish fins in general and the result of this soon became apparent in the literature.

In 1876 the fin-fold theory was clearly put forward for the first time by BALFOUR (1876, pp. 132—135) and was supported not long afterwards by THACHER (1877a, b) and MIVART (1879, pp. 458—482) as well. As the endoskeleton in the ventral fins of the sturgeons resembled in a number of respects that of the unpaired fins, this was interpreted by THACHER as an argument for the correctness of the fin-fold theory. The skeleton of the ventral fins of the sturgeons was considered to be very primitive, even more primitive than that of the Elasmobranchs.

Starting out from the views put forward by GEGENBAUR and putting before himself the question of what had become of the different elements in the abdominal fins of the Selachians, v. DAVIDOFF (1879, 1880, 1884) undertook an investigation of the ventral fins in the Teleostomes, in which he paid attention not only to the osteology, but also the myology and neurology. He then thought that he was able to show that the plate in *Amia*, *Lepidosteus*, *Polypterus* and Teleosts that preceding authors had interpreted as the pelvis, really corresponded most closely to the basale metapterygii of the Elasmobranchs, while the pelvis was reduced or rudimentary (*Polypterus*).¹⁾ According to v. DAVIDOFF the sturgeons, to judge from the development of their ventral fins, had entered on quite a different direction of development from that of the above-mentioned Teleostomes. For he considered that in the sturgeons the basale metapterygii was absent, but that the pelvis was present, although its caudal part in different genera and species showed a more or less strong subdivision into segments, a phenomenon that he considered to be secondary. In the last-mentioned point, however, he fairly soon modified his view, owing to a work published by v. RAUTENFELD in 1882.

In this work v. RAUTENFELD (1882, pp. 30—32, 44—45) came to the conclusion that the process of subdivision that v. DAVIDOFF considered he was able to verify in the pelvis of the sturgeons, was really the operation of a process of fusion of basal segments of the endoskeletal radials. Farthest anteriorly a number of basal segments had, according to his opinion, already fused to a single plate, which he calls the basal plate and homologizes with the basale propterygii of the Elasmobranchs. In general he considered the skeleton of the paired fins of the Ganoids Teleosts as reduced. The so-called pelvis of the Teleosts, which v. DAVIDOFF took to be the basale metapterygii, he considers as a basale propterygii arisen in the same way as in the sturgeons.

OLGA METSCHNIKOFF (1880, pp. 426—427) was of the opinion that the pelvis and metapterygial stem together formed the elements of a single branchial arch.

WIEDERSHEIM (1892, pp. 60—84) in his work «Das Gliedmaßenskelett der Wirbeltiere» appears as an eager partisan of the fin-fold theory. He maintained that the

¹⁾ v. DAVIDOFF took the little paired or unpaired piece of cartilage between the anterior ends of the basale metapterygii of either side in *Polypterus* as a rudiment of the pelvic girdle.

skeleton of the ventral fins in the sturgeons is primitive, even more primitive than in the Elasmobranchs. The skeletal element that v. RAUTENFELD called the «Basalplatte» is termed by him, as already mentioned above, the «vorderstes (proximales) Basale», and he believed that he had also discovered that this skeletal element not only corresponded to a basale propterygii but that it also comprised the pelvis and the most anterior part of the basale metapterygii. «Kurz», he writes (p. 71), «es handelt sich bei jener Knorpelplatte gleichsam noch um einen indifferenten, basiptyrgealen Mutterboden, in welchem in der Regel auch noch das Becken latent bleibt. In manchen Fällen aber gliedert sich dasselbe mehr oder weniger vollkommen ab, verbindet sich in Form einer primitiven Symphyse und unter mehr oder weniger vollkommener Verknöcherung, resp. Verkalkung mit seinem Gegenstück.» The cartilaginous elements (the free basal segments of v. RAUTENFELD's description) following behind this most anterior basale together form, according to WIEDERSHEIM's view, a polymereous metapterygeal axis.

In order to explain the skeleton the ventral fins in *Polypterus*, *Amia*, *Lepidosteus* and Teleosts WIEDERSHEIM starts out from the conditions in the sturgeons. The skeletal element of *Polypterus*, *Amia*, *Lepidosteus* and Teleosts termed by v. DAVIDOFF the basale metapterygii is taken by him to be homologous with the «vorderstes Basale» of the sturgeons, if the pelvic part of this «Basale» was excluded. In the Teleosts, however, the «Basale» is said to include also the complex of endoskeletal radials situated distally of it in sturgeons and other ganoids. In *Polypterus* he thought, like THOMPSON (1886, p. 534), he could discover an equivalent to the pelvis in the paired or unpaired little piece of cartilage between the anterior ends of the «vorderstes Basale» of either side. In *Amia*, *Lepidosteus* and Teleosts, on the other hand, a pelvic element or a pelvic part would be absent. The absence of the pelvis in these forms he was of course inclined to take to be most probably primary, i. e. the higher Ganoids and the Teleosts would originate from forms in which a pelvis was not yet developed. On the other hand he emphasizes, however, that the possibility must also be taken into consideration of the pelvis being reduced.

MOLLIER (1893, p. 121—128; 1897, pp. 53—60) has in his general considerations of the paired extremities of the vertebrates also dealt with the ventral fins of the sturgeons. He states that all the endoskeletal radials of either of the ventral fins in *Polyodon* sometimes articulate with a large plate, which, in accordance with the results that he considered he had attained with regard to the fin skeleton in general, he called the primary basal. This large primary basal he considers to comprise, if I interpret his account correctly, the homologues of the basale pro- and basale metapterygii and parts of the pelvic girdle as well. On the other hand in the cases when a skeletal plate towards which radials articulate is present only in the anterior part of the endoskeleton, he holds the posterior part of the primary basal to be partly reduced and this interpretation of the conditions is maintained by him for sturgeons in general, thus approaching rather near to WIEDERSHEIM's view with regard to the interpretation of the elements of the fin skeleton. Contrary to WIEDERSHEIM, however, he upholds the view that the inner skeleton in the ventral fins of the sturgeons must be considered to be strongly reduced, a conclusion to which GEGENBAUR, v. RAUTENFELD and EMERY (1894) also arrived. Like GEGENBAUR he too states, contrary to WIEDERSHEIM, that the same must be the case with the endoskeleton in the corresponding fins in *Polypterus*.

GEGENBAUR in his work «Vergleichende Anatomie der Wirbeltiere» (1898, p. 567—571) has adopted the interpretation given by v. RAUTENFELD for the skeleton of the ventral fins of the sturgeons, though he still continues to hold fast to his archipterygium theory. With regard to the pelvis in *Polypterus* he naturally follows, under these circumstances, v. DAYDOFF's view, i. e. he takes it to be rudimentary. He explains the loss of the pelvis in Ganoids and Teleosts as due to an alteration in the function of the ventral fins. «Sie (the ventral fin) hat», he says, «bei den Ganoiden den bei Selachiern so mächtigen Apparat des Mixipterygiums verloren, jedenfalls nicht ausgebildet, und damit schwand auch der Flossenstamm, und nur die Radien des Flossenskeletts erhielten sich. Das Schwinden des Stammes erklärt auch den Verlust des Beckens, an welches er gestützt war.»

BRAUS (1901, pp. 251—252) in connection with his extensive investigation of the paired fins in *Ceratodus* also entered upon the question of the skeleton of the ventral fins in fishes in general. According to his view both in sturgeons and higher Ganoids and Teleosts the pelvis and all the basals were completely reduced and replaced by new formations, which would have arisen by the fusion of proximal parts of the endoskeletal radials. These new formations would be homologous with the middle segments in the endoskeletal radials of the Elasmobranchs. The radials that had then taken part in this new formation of basal elements would only be those that had originally been situated in front of the basale metapterygii; the others would be quite reduced.

The view that the pelvis in Ganoids and Teleosts had been reduced has been opposed by GOODRICH (1902; 1909, pp. 276—277) especially among other writers; in this he supports his opinions chiefly by facts from the fossil forms. He believes he can show a pelvis in primitive fossil *Crossopterygii* and also believes it probable that the so-called basal of primitive fossil Elasmobranchs corresponds to one. Starting from this he comes to the conclusion that the pelvis is a very old element, which ought to have existed even in the ancestors of the Teleosts and Elasmobranchs. He enters further on the difficulties that arise when one tries to explain the processes that would have led to the reduction of the pelvis. In the main he tries to prove that so far no decisive proofs have been put forward to compel us to take the pelvic-like element in the recent Ganoid and Teleosts as being anything but a formation homologous to the pelvis of the Elasmobranchs, fossil *Crossopterygians* and *Dipnoans*.

A view similar to that of GOODRICH's was arrived at later on by DERJUGIN and ROZHDESTVENSKY on the basis of embryological investigations in Teleosts (1912, pp. 645—647).

The brief survey I have given shows how little agreement there has been and there still is with regard to the interpretation of the different elements in the endoskeleton of the ventral fins in the recent *Brachiopterygii* (Polypterids cf. p. 147 above) and *Actinopterygii*. It is true that after what has been seen from DERJUGIN's and ROZHDESTVENSKY's (1912) exposition we may hope that a careful study of the ontogenetic development of the ventral fins may afford us a number of new views on the present problems, but one can scarcely expect to arrive at a solution of these problems merely from the evidence of recent fish fins. As in so many other cases we must wait to see what the primitive fossil forms have to tell us.

In this connection I shall briefly give only certain of the views to which I have come myself. I do not intend to enter here on the arguments for these views but

have postponed these till below (Part II) in connection with the description of the Saurichthyids, in which the skeleton of the ventral fins is more completely preserved than in *B. mougeoti*.

As far as I can see the pelvis in different *Elasmobranchs* is not equivalent. We must presumably assume that to the primitive pelvic plate, as it appears e. g. in Cladodontids and Pleuracanthids, there was added during the phylogenetic development more or less of the proximal parts of the radials. To the primitive pelvic plate — called by various authors a basal — a secondary component would thus have been added. In other words, in the fishes in which this process took place we can discern in the pelvic plate a primary component representing the primitive pelvic plate and a secondary component, arisen from proximal segments of the endoskeletal radials.

A process of the same sort as this in the *Elasmobranchs* seems, to judge from the conditions in *Saurichthys* (cf. Part. II), to have taken place in primitive fossil *Actinopterygii* and even to have proceeded rather far. At the same time as this has happened the primary pelvic component has been more or less exposed to reduction. The metapterygoid elements seem entirely or partly to have fused with one another and with the secondary pelvic component, at the same time as they lost their importance and decreased in size. When the process continued later, the conditions have finally appeared that we find in higher Ganoids and Teleosts.

The skeleton of the ventral fins in *B. mougeoti* — to connect our description with this — has probably been developed in a somewhat similar way to that of *Saurichthys*, and the plate that I referred to preliminarily as the pelvis probably consists here too both of a primary and a secondary component, which is probably also the case with the corresponding formations in the sturgeons. It is impossible to decide what were the conditions of the metapterygoid elements in *B. mougeoti* — whether one or more of them were fused to the pelvic plate. It is noteworthy, however, that they form together a rather long row, and thus that they could not have been much reduced, a fact that gives the fin skeleton as a whole, as we found, an Elasmobranch-like character.

The occurrence of a long metapterygoid axis in the paired fins in primitive *Elasmobranchs* and *Actinopterygians* and a more or less centrally situated axis in the same fins in *Crossopterygians* and *Dipnoans* now seems, as has been put forward from several quarters (ABEL 1919, pp. 113, 185; 1920, pp. 335—336; STROMER 1920, pp. 17, 18; JAEKEL 1919a, pp. 27, 30; SIMROTH 1891, pp. 340—351), to indicate that the usual paired fish-fins are something secondary and have most probably originated from a transformation of supporting or crawling organs. This transformation is due according to ABEL (1919; 1920), to an adaptation from a benthonic to a nectonic mode of life. An additional argument in favour of the view mentioned here seems to be present in the curious pelvis of the *Cocosteids*, in which, as we know, this element was probably in connection with the vertebral column (STROMER 1920, p. 17).

As far as the fin-fold theory is concerned in this connection, it cannot of course, so well founded as it undoubtedly is, be considered as being essentially disturbed by the facts that have so far arisen from the palaeontological side. We must still remain of the opinion that it affords the best explanation of the origin of the paired extremities.

An attempt to modify somewhat the contradiction that has arisen between this theory and the more recent theory advocated by Palaeontology has been made by ABEL, as he points out that the theory of the lateral fold must perhaps be considered applicable to such forms as the *Acanthodes* (1919, pp. 113, 147, 148). But in my opinion it is open to question whether these, like the *Actinopterygii*, were not adapted to a nectonic mode of life and whether under such circumstances a transformation of their paired fins did not take place.

Squamation.

The squamation was almost entirely reduced. As in *Phanerosteon* (TRAQUAIR, 1911 a, pp. 165—166, text fig. 9; FRITSCH, 1895, pp. 93—94, text fig. 287), *Elpisopholis* (WOODWARD, 1908 a, p. 17) and *Psilichthys* (HALL 1900, p. 148), scales were present only on the dorsal lobe of the caudal fin. These scales (Pl. 24, fig. 1) are high and narrow and are arranged in the way that is characteristic for the Palaeoniscids. The evidence seems to show that they are without ganoine covering.

Main lateral line of the body.

The lateral line of the body (l, Pl. 21, fig. 4) was enclosed in small, narrow tubes of bone, arranged in a series one after the other. In the caudal fin the lateral line passes off, as in the sturgeons, along the lower margin of the dorsal lobe, quite close to the bases of the lepidotrichia.

* * *

Remarks. — I consider that I have established with certainty that the remains described here as *Birgeria mougeoti* belong to the same genus as the species adopted by AGASSIZ under the name of *Saurichthys mougeoti*.

The determination as to species, on the other hand, can only be regarded as provisional, as it is based almost exclusively on the teeth. Nor was it possible to decide with certainty whether the material present represents one or two closely related species.

Geological occurrence and localities. — Detached teeth of the *Birgeria mougeoti* type occur in the bone-bed found by SALOMON in the lower Triassic, in a bone-bed in the fish horizon and in the bone-bed 33 m above this horizon. The other remains all originate from the fish horizon.

The localities of the finds were as follows: Mt. Congress, Mt. Marmier, Mt. Viking, Sticky Keep, Mt. Trident, Mt. Milne Edwards and Mt. Andersson.

Birgeria sp.

(Pl. 24, fig. 3.)

Under this heading I have placed a number of detached teeth from a bone-bed in the upper Triassic (P. 712—P. 718). The teeth in question are all incompletely preserved, their basal parts being always more or less absent. In addition they often seem to be somewhat worn.

They are rather small and slender and generally have a rather long and strikingly pointed enamel cap (Pl. 24, fig. 3). In most cases this enamel cap has a sculpture of

vertical striae, and in many cases this striation extends quite to the point of the cap. The enamel-covered part basally of the enamel cap has a very fine striation, as on the typical teeth from the fish horizon.

* * *

Remarks. — The teeth described here in general show the closest resemblance in shape to the teeth of the gill-arches in *B. mougeoti*, but differ from these by having striation on the enamel cap. Since this striation, as has been mentioned, often extends right out to the point, it gives the teeth a character that clearly differentiates them from teeth belonging to *B. mougeoti*. For this reason I consider it probable that they may belong to a new species.

Geological occurrence and locality. — The teeth in question are only known from the upper Triassic, where they are found at Mt. Bertil in a bone-bed about 263 m above the fish horizon.

Genus *Glaucolepis* n. g.

Synonym: *Gyrolepis*? STENSIÖ, 1918.

The species referred to in my notice of the Triassic fish remains from Horn Sound as *Gyrolepis*? sp. (STENSIÖ, 1918b, p. 77) has with the present material turned out to belong to a previously unknown genus, for which I suggest the name *Glaucolepis*.

The most characteristic features so far known of this new genus can be summarized as follows: Small fishes with rather slender bodies. Pectoral fins unknown. Other fins weak with closely jointed and bifurcated lepidotrichia. The anal and dorsal fins with a short base and small fulcra. The dorsal fin has its posterior half opposite the anterior half of the anal fin. The caudal fin is deeply cleft with both lobes somewhat similarly developed, or possibly the ventral one somewhat stronger than the dorsal one; the dorsal one has rather large ridge-scales, the ventral one small fulcra. The scales on the anterior part of the lateral surfaces of the body are somewhat longer than wide; farther back they are rhombic, and towards the ventral side, especially in the abdominal region and the anterior part of the caudal region, they are low. Dorsal ridge-scales presumably small and not prominent. All scales have the anterior covered area narrow; the exposed one is totally covered by a layer of shining ganoiné. This ganoiné layer has raised ridges, mostly running more or less diagonally.

With regard to the sculpture of certain of the scales *Glaucolepis* is confusingly like *Gyrolepis*. The similarity is even so great that it would be very difficult or impossible to distinguish the two genera from each other only with the help of detached scales. Another resemblance between them is found in the absence of enlarged ridge-scales in the abdominal region and the anterior part of the caudal region. *Glaucolepis* is distinguished clearly, however, from *Gyrolepis* by the shape of the unpaired fins and their weak development (cf. DAMES, 1888, pp. 5–23, Tafel I, Tafel III, fig. 1a, b; STOLLEY, 1920, pp. 25–28, Tafel X, fig. 1).

The small height of the scales on the ventral side is a peculiarity that *Glaucolepis* shares with, inter alia, *Platysiagum* (WOODWARD, 1895b, 533–534), *Oxygnathus* (WOODWARD, 1891b, pp. 516–520), *Urolepis* (ALESSANDRI, 1910, p. 48), *Acrolepis* (WOODWARD, 1891b, pp. 501–509).

***Glaucolepis gyrolepidoides* n. sp.**

(Pl. 25, figs. 1, 2).

Synonym: *Gyrolepis*? sp. STENSIÖ, ERIK A:SON, Norsk Geol. Tidskr. vol. V., p. 77, 1918.

The present material of *G. gyrolepidoides* is rather poor and incomplete. The Palaeontological Institute of Upsala has in its possession three incomplete specimens (*P. 166*, *P. 671 a, b*) and a number of detached scales (*P. 5*, *P. 7*, *P. 9*, *P. 27*, *P. 650*, *P. 652*, *P. 656*, *P. 657*, *P. 665*, *P. 667*). The Palaeontological Institute of the University of Christiania has in its collection, as I have already had occasion to mention (1918 b, p. 77), an incomplete specimen from the Ice Fjord and some detached scales from Horn Sound.

The species in question was probably of medium or fairly small size. To judge from specimens *P. 671 a* and *b* it has a rather slender body (Pl. 25, fig. 1).

Nothing is preserved of the head and the most anterior part of the abdominal region.

The skeleton of the unpaired fins.

The anal fin (*A*, Pl. 25, fig. 1) is small, with a short base and triangular in shape. Its lepidotrichia, which are about 20 in number, decrease rather rapidly in height backwards and are situated close together. They are jointed throughout their length, and are probably also ramified dichotomically in their distal parts. Their lateral sides are covered with ganoine. Fulcra are not observed with certainty.

The dorsal fin (*D*, Pl. 25, fig. 1) is of about the same size and shape as the anal fin and its exoskeleton shows in all respects the same conditions as in this fin. It is so situated that its posterior half is about opposite the anterior half of the anal fin. The fulcra are small but distinct.

The caudal fin (Pl. 25, fig. 1) is fairly weakly developed, deeply cleft, with both lobes of about equal strength. If either of these was stronger than the other it was the ventral one. The numerous ganoine covered lepidotrichia are dichotomically ramified in their distal parts and are closely jointed right to the base. Both here and in the other fins the length of the joints is greater than their width. The dorsal lobe has a number of enlarged ridge-scales. The anterior margin of the ventral lobe is furnished with numerous small fulcra.

The skeleton of the paired fins.

The pectoral fins are quite unknown.

The ventral fins are poorly preserved. They were apparently small and weak (*V*, Pl. 25, fig. 1). Their lepidotrichia, the number of which cannot be established, were closely jointed throughout their length and presumably dichotomically ramified in their distal parts.

Squamation.

The lateral surfaces of the body nearest to the head must have had scales that were somewhat higher than broad. Otherwise the scales of the whole lateral surface are more or less typically rhombic, like those of the back as well. Those of the ventral side, on the other hand, especially in the abdominal region and the most anterior part of the caudal region, are characterized by their very low shape. Those of the dorsal

caudal lobe gradually become higher and narrower towards the extremity of the lobe. No large or prominent ridge-scales have been developed either above the abdominal or the caudal region apart from those over the dorsal lobe of the caudal fin. As far as can be seen the anterior covered area of the scales is narrow. Their upper margin has a distinct articulatory spine and the medial surface, as usual, a vertical ridge. The posterior margin is distinctly serrate.¹⁾ The exposed part of the lateral surface is quite covered with ganoine.

The sculpture consists of obliquely placed folds or striae, issuing from or in the neighbourhood of the anterior and dorsal margins of the exposed surface of each scale and running fairly parallel to one another backwards and downwards towards the lower and posterior margins.

On the scales that have belonged to the anterior and middle parts of the body this sculpture is present over all the exposed surface, and the striae there are broad, comparatively strong and sharp. One or two of them, situated farthest ventrally on each of these scales, are often also bent in the way that their posterior half is parallel to the ventral margin of the scale and the anterior half to the anterior margin. Otherwise the striae on the scales in question are often somewhat irregular and the middle ones on each scale do not reach continuously across the whole of the exposed surface, but two or three shorter striae follow one another or alternate with each other there.

Towards the posterior part of the abdominal region the sculpture is gradually weakened on the postero-ventral half of the scales, in the caudal region being restricted mainly to the antero-dorsal half (Pl. 25, fig. 2). Most of the scales covering the dorsal lobe of the caudal fin entirely lack sculpture, only the most anterior ones having traces of it. It is also noteworthy that the sculpture on the scales of the posterior parts of the body consists only of diagonal striae. In connection with this partial reduction of the sculpture the remaining parts of the striae also decrease in strength and become more rounded.

* * *

Remarks. — *Glaucolepis gyrolepidoides* comprises in its present definition material from different horizons, and it must therefore be considered possible that the species name suggested here may turn out to be a collective name for a couple of species.

In the sculpture of the scales *Glaucolepis gyrolepidoides* is confusingly like certain *Gyrolepis* species, e. g. *Gyrolepis alberti*, and it is this fact that I have indicated by the species name *gyrolepidoides*.

Geological occurrence and localities. — Detached scales of this species are found within the Ice Fjord district in the bone-bed 33 m above the fish horizon, at Mt Viking, and in a bone-bed about 50 m above the fish horizon on Corrie Down, and in the material from the bone-bed found by SALOMON in the lower Triassic of Mt. Congress. In addition, as I have shown, detached scales occur in the Triassic strata at Horn Sound (STENSIÖ, 1918 b, loc. cit.).

Specimens *P. 166*, *P. 671 a*, *P. 671 b* and the specimen in the possession of the Palaeontological Collection of the University of Christiania previously noticed by me

¹⁾ In *Gyrolepis* too I have found serration on the posterior margin of the scales, e. g. in *G. alberti* and *G. agassizi* (cf. DAMES, 1888, Tafel I, fig. 1 a, b; Tafel III, fig. 1 c, d; Tafel V, fig. 2 a, b).

(1918 b, loc. cit.) were all four found at the fish horizon. The three first-mentioned specimens come from Mt. Congress; the Christiania specimen was found in the steep shore below the Swedish station at Cape Thordsen.

Genus *Pygopterus* AGASSIZ.

Synonym: *Myrrolepis*? WOODWARD, A. S. Upsala, Geol. Inst., Bull. vol. XI, p. 293, 1912.

The genus *Pygopterus* was founded in 1833 by AGASSIZ (1833, vol. II, part 1, p. 10; 1844, vol. II, part 2, p. 74), and after him several authors have studied it more or less in detail. Among these we may specially mention EGERTON, who published fine figures of his material (1850, pp. 232—234; Pls. 23, 24), TRAQUAIR, who undertook a thorough revision of the species of the genus described up to 1877 (1877 b, pp. 572—578), and WOODWARD, who in 1891 (1891 b, pp. 470—475) gave a short description of the material of the British Museum and at the same time gave a detailed list of synonyms and a list of the earlier literature.

TRAQUAIR's revision caused the genus *Pygopterus* to be restricted to the Permian formation. For a long time it was really only known from the upper part of this formation in England, Russia (KROTOV 1904, pp. 30—31) and Germany.¹⁾ Now, however, according to DEECKE (1913, p. 77) it has also been found in the upper part of the bunter Sandstone of Germany (cf. STOLLEY 1920, p. 81) and, according to the material at my disposal, it seems also to occur in the lower part of the Triassic at Spitzbergen, where, as far as is known, it is represented by a single species. An incomplete and very much crushed specimen of this species is mentioned by WOODWARD 1912 (p. 293) and put by him, though with much hesitation, under the generic name *Myrrolepis*.

My fresh material from Spitzbergen can scarcely increase our knowledge of this genus to any great extent, and I am therefore unable to give any more complete definition of it than that formulated by WOODWARD 1891 (1891 b, p. 470), which I consider it superfluous to repeat here.

Pygopterus de geeri n. sp.

(Pl. 25, fig. 3; Pl. 26, figs. 1, 2; Pl. 27, fig. 1.)

Synonym: *Myrrolepis*? sp. WOODWARD, A. S., Upsala, Geol. Inst. Bull., vol. XI, p. 293, 1912.

The material on which I have based the species *Pygopterus de geeri* consists of six incomplete specimens (*P. 106*, *P. 109—112*, *P. 671 c*).

That this species attained a comparatively large size is shown by the specimen investigated by WOODWARD in 1912 (*P. 111*), in which the height of the body just behind the head was about 11 cm. A couple of other specimens (*P. 109*, *P. 112*) seem to have attained the same or almost the same size. The smallest specimen present (*P. 671 c*) has its body 4 cm high just behind the head.

The shape of the body seems apparently to have been fairly elongated and the head relatively short, its length being probably little more than about a fifth of the total length of the animal.

¹⁾ The type-specimen for the so-called *Pygopterus bonardii* AGASSIZ (AGASSIZ 1833, vol. II, part. 2, p. 11) from the lower Permian of Autun was in 1890 described and figured by SAUVAGE (1890, pp. 25—26; Pl. IV, fig. 1). According to SAUVAGE this species undoubtedly would belong to *Pygopterus*. Neither his description nor his figure, however, give any definite proof for the correctness of his opinion.

The general shape of the head is the typical one for the Palaeoniscids, with the large orbital opening far forward. Nothing is known about the substitution bones of the primordial neurocranium.

Membrane bones of the neurocranium.

Nothing is preserved of the parasphenoid. The membrane bones of the cranial roof, on the other hand, are partly present on one specimen (*P. 671 c*, Pl. 26, fig. 2), but they are so much broken that it is impossible to establish their extension and mutual relations. Their sculpture consists of somewhat lengthened ganoine tubercles which run principally in the longitudinal direction of the head. They are placed transversally only over the middle part of the labyrinth region.

Visceral skeleton.

Nothing is known as yet with regard to the palatoquadrate and its bones.

The maxillary (*Mx*, text fig. 69; Pl. 25, fig. 3; Pl. 26, figs. 1, 2) is of the ordinary Palaeoniscid type with a low suborbital and a high and long postorbital part. Its postero-ventral corner is somewhat produced downwards, covering from the lateral side the posterior upper corner of the mandible.

The mandible (*Md*, text fig. 69; Pl. 25, fig. 3; Pl. 26, fig. 2) is well though not particularly strongly developed. Its anterior end is pointed. The coronoid process is lacking, as is usual in the Palaeoniscids.

Of the bones of the opercular skeleton the preoperculum, operculum, suboperculum and a number of radii branchiostegi are present.

The preoperculum (*Po*, text fig. 69, Pl. 26, fig. 1; Pl. 27, fig. 1) is incompletely preserved, but it is evident, however, that it has been an angular bone, whose ventral and narrower shank extended downwards in the usual way between the maxilla on the one side and the operculum, suboperculum and most dorsal branchiostegal ray on the other.¹⁾ Its dorsal and wider shank extended far forward over the cheek towards the orbit. From the whole position and shape of the bone we can certainly conclude that the hyomandibular was situated very obliquely, in the way that is characteristic of many Palaeoniscids.

The operculum (*Op*, text fig. 69; Pl. 26, figs. 1, 2; Pl. 27, fig. 1) is a fairly large bone-plate, whose height is about double its width. From its position we can distinguish on it an anterior, a lower, a posterior and an upper margin. Of these the anterior one faces not only forward but also somewhat downward, the posterior one not only backward but also somewhat upwards, and finally the lower one not only downward but also somewhat backward. The anterior margin is fairly straight or weakly concave and meets the lower one in a somewhat round and bluntly angular corner. The lower margin is undulating in such a way that it is convex at the anterior and concave at the posterior part. The posterior margin, which is weakly convex, meets the lower one in an acute-angled corner. From the dorsal margin, which has also been weakly convex, it is not sharply marked off, as the corner between them is much rounded. The

¹⁾ Here as otherwise in the *Actinopterygii* I have described the preoperculum in connection with the visceral skeleton.

corner between the dorsal and the anterior margins must have been rather acute-angled but it is not preserved in any of the specimens present.

The suboperculum (*Sop*, text fig. 69; Pl. 26, figs. 1, 2; Pl. 27, fig. 1) is fairly small relatively to the operculum, probably scarcely more than a third of this. It is pentagonal in shape and its width is almost twice its height. One margin faces backward, one upward, one downward and two backward. When the bone is in situ the anterior margin, however, is turned so that it faces somewhat downward, the upper one so that it faces somewhat forward, the lower one so that it faces somewhat backward, and the upper of the two posterior ones so that it faces somewhat upwards. The anterior margin is weakly concave or almost straight and is separated from both the upper and the lower one by a right-angled corner. The lower margin is rather strongly concave and meets the lower of the two posterior ones in a somewhat rounded corner. The two posterior margins are fairly straight and meet each other in a backward pointing rather blunt corner. Finally the upper margin is sometimes almost straight, sometimes, on the other hand, it is concave at its anterior and convex at its posterior part. It meets the upper of the two posterior margins in an angular corner.

The radii branchiostegi (*Rbr*, text fig. 69; Pl. 26, fig. 1; Pl. 27, fig. 1) were numerous, but their exact number cannot be established. They decrease gradually in length forwards. Farthest forwards at the angle between the two halves of the mandible there was presumably a small unpaired jugular plate (*P. 110*).

The sculpture on the bones of the visceral skeleton described agrees closely with that on the membrane bones of the cranial roof, i. e. it consists as a rule of somewhat lengthened and rather dense tubercles, mostly arranged somewhat parallel to the longitudinal axis of the animal. On the mandible the tubercles may become rather long, so that a longitudinal striation arises. Pl. 27, fig. 1, gives a detailed view of their arrangement on the operculum, suboperculum and radii branchiostegi.

The branchial arches were ossified, but no details can be given about the different elements in them.

Dentition.

The dentition is known only on the maxillary and the dental. It consists as usual of a medial longitudinal row of larger and a lateral one of smaller teeth. All the teeth are conically pointed.

The sensory canals of the head.

The sensory canals of the head are comparatively fine and are, apart from possibly occurring «pit lines», entirely enclosed in the membrane bones. They open outwards with a large number of fine pores, situated close together and directly laterally of the canals themselves, thus showing exactly the position of the latter.

The most anterior part of the supraorbital canal, anterior to the frontal, is not known. From the anterior end of either frontal the canal (*ifc*, Pl. 26, fig. 2) has had its course backwards and somewhat medially, continuing to the anterior part of the parietal.

The infraorbital canal is only partly preserved in its posterior part (*soc*, Pl. 26, fig. 2). Its position is the usual one, and it has, at least posteriorly, not communicated with the supraorbital canal.

The cranial section of the main lateral line of the body has, as usual, constituted the direct posterior continuation of the infraorbital canal.

Nothing is preserved of the other sensory canals.

Axial skeleton.

As the scales are rather small and thin it is evident that the ossifications of the axial skeleton are more easily accessible for investigation than in the majority of Palaeoniscids. Remains of the axial skeleton are found preserved in *P. 111* and *P. 671 c*.

The chorda seemed apparently well developed, as in Palaeoniscids in general.

The basidorsals (*Bd*, Pl. 26, fig. 2) are represented in the abdominal region by comparatively short and robust bones. In the anterior part of the caudal region basidorsals are also found preserved, but it is obvious, however, that they increase in height towards this region, their distal part becoming narrow at the same time.

Interdorsals cannot be shown with complete certainty, but one may undoubtedly conclude that they were small and mainly cartilaginous. It is noteworthy that they perhaps extended in a basal direction so that they covered a dorsal part of the chorda on the lateral sides. This seems to be the case, at least to judge from certain fragments of bone on *P. 671 c*.

The unpaired neural spines (*Nsp*, Pl. 26, fig. 2) consist as usual of a row of free ossified elements, corresponding in number to the basidorsals. Similar neural spines are developed in the whole abdominal region and at least in the anterior part of the caudal region, where, however, they begin to decrease in length and to be replaced by the lengthened basidorsals themselves.

Text fig. 69. *Pygopterus de geeri* n. sp.
Parts of visceral skeleton and shoulder girdle. After *P. 111* $\frac{1}{2}$.
Cl, cleithral; *Jcl*, clavicle; *Md*, mandibula;
Mx, maxillary; *Op*, operculum; *Po*, preoperculum; *Rbr*, branchiostegal ray; *ScI*, supracleithral; *Sop*, suboperculum; *Scap*, suprascapular.

It is very noteworthy that these unpaired neural spines are not situated so as to form a direct continuation of the basidorsals in a distal direction but so that they really come into contact with the anterior margin of these. Each of the unpaired neural spines thus corresponds most closely to the gap between two successive basidorsals.

The unpaired neural spines seem generally to have had a similar position also in other Palaeoniscids (cf. *Coccolepis*, WOODWARD 1895a, Pl. 1, fig. 1; *Phanerosteon* TRAQUAIR, 1911a, p. 166, text fig. 9; etc.), higher ganoids (*Caturus*, *Hypsocormus*, WOODWARD 1898a, text figs. 76, 78; *Ania*, GOODRICH 1909, text fig. 311B) and many primitive Teleosts (*Leptolepis*, etc. WOODWARD 1898a, text fig. 80 etc.). In a number of other Teleosts they are also shown to exist, though there they are rudimentary (SCHAUINSLAND 1905, p. 468, text fig. 261). According to ZITTEL's figure of *Dorypterus* (ZITTEL, 1887—1890, text fig. 264) they also occur in Platyosmids.

What has already been put forward strongly supports the view that the unpaired neural spines are not to be considered as distal segments of the basidorsals. They may instead of that represent a distal part of the interdorsals, a view that has been maintained

by SCHAUINSLAND (1905, p. 261) for *Amia*, *Lepidosteus* and Teleosts. We shall see that we have an additional support for this view in the fact that in certain fossil *Actinopterygii* both the inter- and basidorsals are probably developed similarly and produced into a long spine (cf. *Saurichthys*, Part II). Under these circumstances unpaired neural spines are of course lacking (cf. in addition SCHMALHAUSEN 1913a, pp. 1-7).

The elements of the haemal arches (*Hb*, Pl. 26, fig. 2) are poorly preserved, so that nothing can be established about them in detail.

That there is to a certain extent a commencement of the formation of vertebral centra in this species is not impossible, according to what I have found with regard to the interdorsals. It is evident, however, that, under any circumstances, these centra were weak and that the chorda cannot have been much influenced by them.

TRAQUAIR (1877a, p. 23) is of the opinion that he found indications of vertebral centra in *P. humboldti* AGASSIZ. His statement is as follows: «Only in *Pygopterus* I have seen anything resembling a vertebral body. In this genus, in which partly owing to the comparative thinness and smallness of the scales, the internal skeleton is more completely seen than in any other, a series of nodular-looking ossifications may generally be observed, though much crushed and obscured, extending backwards from the head along the abdominal region of the body in the position of the vertebral axis, and which certainly do remind us of vertebral centra, as which they were considered by AGASSIZ. That these were completely developed osseous vertebrae like those of Teleostei and certain Ganoids is not probable from their general appearance; it is more likely that they had only attained the stage of «hemi-vertebrae» or at most of «ring-vertebrae», and that in any case the notochord passed on uninterruptedly through them».

LATER SAUVAGE too (1890, p. 26, Pl. IV, fig. 1) thought that he had found in the so-called *P. bonnardi* the beginning of formations of vertebral bodies, which he describes as «renflements nodulaires à la base des apophyses épineuses». To judge from his figure, however, it is only the proximal and somewhat widened part of the basidorsals that he interprets in this way. He does not show that the elements of the neural arches are lengthened in a ventral direction (cf. also p. 203 above).

With regard to *P. de geeri* we may mention finally that ossified ribs were not developed.

The skeleton of the unpaired fins.

The anal fin (*A*, Pl. 25, fig. 3) has the shape characteristic of *Pygopterus* rather distinctly developed. It thus has a rather long base and is in the anterior part relatively high, while its posterior one is low and weak. The lepidotrichia are about 50 in number, are situated close together and are all jointed throughout their length. They are also probably dichotomically ramified at their distal parts. Only a few fragments of the endoskeletal radials of the anal fin are preserved (*Ra*, Pl. 26, fig. 2).

The dorsal fin has, as far as one can judge, had at least its posterior half opposite the anal fin. It is very incompletely preserved and its position is only indicated by a few fragments of the endoskeletal radials (*Rd*, Pl. 26, fig. 2).

The caudal fin (Pl. 25, fig. 3) is large and robust and deeply cleft. It cannot be decided with certainty whether it was equilobate as the dorsal lobe is not completely

preserved. Its numerous lepidotrichia are situated close together and are closely jointed practically right down to the base. Their distal parts are dichotomically ramified. The dorsal lobe has strong and large ridge scales; the ventral lobe has very small fulcra.

Beneath the ridge-scales of the dorsal lobe there follows a series of endoskeletal radials (*Icr*, Pl. 25, fig. 3) in the usual way (cf. SCHMALHAUSEN, 1913a, pp. 20—35). The haemal spines (*hsp*, Pl. 25, fig. 3) that belong to the anterior part of the fin and form a support for the lepidotrichia of the ventral lobe, are long and strong but not flattened. The other haemal spines following behind those mentioned are weaker and of course decrease in size posteriorly to the same extent as the dorsal lobe grows narrower.—All the lepidotrichia in the unpaired fins probably lacked a covering of ganoiné.

The skeleton of the girdles and the paired fins.

Nothing is preserved of the primordial shoulder girdle or its ossifications. Its membrane bones show the same conditions as in Palaeoniscids in general (text fig. 69; Pl. 26, figs. 1, 2; Pl. 27, fig. 1). We can distinguish the suprascapular (*Scap*), supracleithral (*Scl*), cleithral (*Cl*), and clavicle (*Clv*).

The sculpture on all these bones consists as a rule of short, dense striae or somewhat lengthened tubercles. The suprascapular and a dorsal and larger part of the supracleithral has its striation mainly oriented so that it is parallel with the longitudinal axis of the fish. Towards the ventral end of the supracleithral the striation becomes oblique, the striae taking a somewhat ventral direction. On the cleithral and clavicle the striae run principally in a dorsi-ventral direction, though here and there deviations and irregularities occur in their arrangement.

The pectoral fins (*Pc*, Pl. 25, fig. 3; Pl. 26, fig. 1; Pl. 27, fig. 1) are well developed and triangular in shape. The lepidotrichia are numerous—about 30—and generally unjointed in the proximal two-thirds of their length. Only some of the most posterior and smaller ones might possibly have been jointed to any greater extent. All the lepidotrichia are dichotomically ramified at their distal ends and seem to lack ganoiné covering. Fulcra are present, though not particularly large. Of the endoskeleton of the pectoral fin only few radials (*R*, Pl. 26, fig. 1) are preserved.

The ventral fins (*V*, Pl. 25, fig. 3; Pl. 26, fig. 1) are very incompletely preserved. With regard to their position relative to the other fins no certain statement can be given. Their lepidotrichia were presumably densely jointed throughout their length, and in addition were probably without any ganoiné covering.

Squamation.

The scales are on the whole very small and thin. Only immediately behind the cleithral do we find a couple of vertical rows with obviously enlarged scales (Pl. 26, fig. 1; Pl. 27, fig. 1).

In shape the scales in the rows immediately behind the shoulder girdle are somewhat higher than wide. Otherwise the scales of the abdominal region seem to have been fairly rhombical, apart from those of the ventral side, which were probably somewhat wider than high. Nothing is known in detail as to the shape of the scales in the caudal region.

On the most anterior scales the anterior covered area is comparatively wide. Its conditions on the scales following farther posteriorly are not known with certainty, but it is most probable that it was not so wide as on the anterior ones. A strong and rather broad articulatory spine is developed on the dorsal margin of most of the scales. It is impossible to discover whether the antero-dorsal corner was also produced upwards to form a sort of accessory articulatory spine as in *P. humboldti*. The vertical ridge on the medial side has either been absent or weakly developed. It was impossible to decide whether the posterior margin was serrated.

The sculpture on all the scales consists of striation and, apart from the enlarged scales behind the cleithral, is rather fine. The striae in their turn are generally somewhat coarser at the anterior than the posterior ends, and are often ramified or somewhat situated. Some of them are long and extend over the whole exposed surface of the scales; others, on the contrary, are short and are wedged in here and there among the longer ones.

On the anterior higher scales the striae are rather numerous and are all arranged so that they run more or less obliquely from the anterior and upper margins to the posterior and lower ones. Farther posteriorly this oblique striation is restricted to the antero-ventral half of the scales, while the dorso-caudal half is gradually occupied by striae arranged parallel to the ventral and dorsal margins. The latter striae, of which the ventral ones are, of course, the shortest, meet with their posterior ends the striae of the ventral half to form acute angles. The character of the sculpture on the scales close behind the shoulder girdle is shown by Pl. 27, fig. 1.

* * *

Remarks. — As has already been mentioned, WOODWARD (1912) hesitatingly gave the above described species under the name of *Myriolepis*? sp. That there can be no question of a *Myriolepis* species is, however, obvious, especially from the shape and development of the fins (cf. TRAQUAIR 1893, pp. 54—56; 1911 a, pp. 162—164; WOODWARD 1891 b, p. 515; 1906 b, pp. 416—419; 1908 a, pp. 14—17; BOLTON 1894, pp. 1—4). It is also certain that the Spitzbergen species in question cannot belong to the genus *Oxygnathus*¹⁾ either, and it seems improbable that it should be closely connected with *Urolepis* (DE ALLESSANDRI 1910, pp. 42—49) or *Platysiagum* WOODWARD (1895 b, p. 533).

On the other hand, it is not difficult to see that we are able to verify in it certain obvious points of agreement with *Pygopterus*, in the development both of the fins and the scales and the cranial skeleton, and consequently I have considered that I ought to refer it to this genus.

Pygopterus de geeri is, on account of the sculpture of the head, the shoulder girdle and the scales, and the shape of the anal fin, a well characterized species, which I have named after Professor G. DE GEER of Stockholm, whose works have contributed so much to our knowledge of the geology and geography of Spitzbergen, and to whom I am much indebted for many valuable informations about Spitzbergen.

Geological occurrence and localities. — *P. de geeri* is only known from the fish horizon, where it occurs rather sparsely.

¹⁾ The species from the upper Karoo formation described by BROOM (1909 a, pp. 259—262; Pl. XIII, fig. 8) as *Oxygnathus brownii* really belongs probably not to the genus *Oxygnathus* but would seem to represent a new genus.

The specimens so far found are from the following localities: Mt Congress, the South side of Sassen Bay, Mt Trident, Mt Milne Edwards and Mt Andersson.

Genus *Boreosomus* n. g.

Synonym: *Acrolepis* (in part) WOODWARD, A. S. Upsala Geol. Inst. vol. XI, 1912.

The new genus for which I have suggested the name *Boreosomus* is characterized by the following features: Small or medium-sized fusiform fishes. The head with a sculpture of generally rather coarse longitudinal striae or somewhat lengthened tubercles. Mouth large. Hyomandibular oblique with a large processus opercularis. Branchiostegal rays few. Median jugular plate very large. Dentition probably rather weak, consisting on the margins of the jaws of fairly small acutely conical teeth, otherwise, at least partly, of small bluntly conical or almost spheroid teeth. Shoulder girdle sculptured in the same way as the head. The dorsal fin fairly weak, situated far forward, probably above or in front of the ventral fins. The caudal fin deeply cleft. The pectoral fins not especially strong. The ventral fins small and short-based. The lepidotrichia of the pectoral fins unjointed, at least in their proximal half; the lepidotrichia of the other fins densely jointed throughout their length and situated close together. All the lepidotrichia are presumably more or less covered with ganoine. Fulcra are present, at least on the pectoral fin, but are small. The scales on the most anterior part of the lateral surfaces of the abdominal region are higher than broad, gradually decreasing in height backwards, upwards and downwards, so that finally their width becomes greater than their height. Dorsally in each vertical row a number of the scales (10—20) are very low. On the ventral side there are also low scales, but scarcely to the same extent as dorsally. Between the two ventral fins there are a few enlarged scales. Dorsal ridge-scales, at least in front of the dorsal fin, slightly enlarged, but not prominent. All the scales are strong and thick, with the anterior covered area relatively wide. The antero-dorsal corner sometimes produced upwards. The dorsal margin with an articulatory spine, the posterior one serrated. The sculpture of the scales immediately behind the shoulder girdle fine, otherwise consisting of a number of coarse, wide, densely placed ganoine striae, mainly running obliquely downward and backwards from in front and above. These striae, of which the ventral ones in certain species have their anterior ends bent upwards parallel to the anterior margin, are sometimes anastomosed and extend as a rule quite over the exposed surface of the scales, ending with the posterior ends in the serrations of the posterior margin. Between their posterior ends short striae are inserted only on the most anterior flank scales, but these short striae are never numerous and are always of the same or almost the same coarseness as the longer ones.

Boreosomus closely resembles *Acrolepis*, especially in the development of the ornament of the scales, and WOODWARD's view (1912, pp. 292—293) that the latter genus was represented in the Triassic of Spitzbergen is thus easily explainable. It is not yet possible to decide how close the relationship really is between them. It is evident, however, that *Boreosomus* differs from *Acrolepis* in the more forward position of the dorsal fin and the low shape of the scales towards the dorsum, and the small size of the dorsal ridge-scales.

Of the genera so far known *Boreosomus* is undoubtedly most closely allied to the new genus *Acrorhabdus* found in the Triassic of Spitzbergen and described below.

***Boreosomus arcticus* (A. S. WOODWARD).**

(Pl. 27, fig. 2).

Synonyms: *Acrolepis arctica*, WOODWARD A. S., Upsala Geol. Inst., Bull., vol. XI, pp. 292—923, 1912.

Acrolepis arctica? STENSÖ, E. A.: SON, Norske Geol. Tidsskrift, vol. V, p. 77, 1918.

Of this species, there are in the collections of the Palaeontological Institution of Upsala remains of six specimens (*P. 132*, *P. 136*, *P. 137*, *P. 139*, *P. 695*, *P. 800*) and in the Palaeontological Collection of the University of Christiania a number of detached scales. Perhaps a specimen in the British Museum (*B. M. P. 10729*) may also be referred to this species.

All the known specimens are fragmentarily preserved, and very little can be stated as to their general proportions. The length may however be estimated to about 35—40 cm.

Visceral skeleton.

The palatoquadrate is a triangular plate, which has its suborbital part low and its post-orbital one, on the contrary, high. One of its margins is directed ventrally, one antero-dorsally and one postero-dorsally. The antero-dorsal one is principally concave, the two others weakly convex. The anterior corner has presumably been rather pointed, but is not completely preserved. The posterior corner is prolonged downwards and the upper corner is truncated.

The larger middle part of the palatoquadrate is situated rather sagittally. The anterior part is somewhat horizontal and the posterior part, corresponding about to the pars quadrata, is bent in a lateral direction.

In the palatoquadrate there are two substitution bones, the autopalatine and the quadrato-metapterygoid.

The autopalatine (*Aup*, text fig. 70) is a small flat bone situated, as usual, near the anterior end of the palatoquadrate. It consists of a cancellous bone substance.

The quadrato-metapterygoid (*Mptg. Qu*, text fig. 70) is a large and high bone. It occupies the most posterior part of the palatoquadrate cartilage and there is no doubt that it contains the homologues both of the quadrate and the metapterygoid, as is indicated by the name I have suggested for it. No suture at all or any indication of a suture between the two components can be discovered, and it is certain that none has existed. The bone consists as a whole of cancellous substance. It is exceedingly noteworthy that the metapterygoid component has on its anterior margin an antero-dorsally directed truncated process (*pr*), which may possibly have articulated with the basal part of the neurocranium in the caudal end of the orbitotemporal region. The position

Text fig. 70. *Boreosomus arcticus* (A. S. WOODWARD). Palatoquadrate, mandibula and hyomandibular.

After *P. 137* 1/4.

Aup, autopalatine; *Eapt*, ectopterygoid; *Eapt*, entopterygoid; *Hm*, hyomandibular; *Mk*, ossification in the Meckelian cartilage; *Mptg. Qu*, quadrato-metapterygoid; *mg*, fossa for musculus adductor mandibulae; *pr*, process from the metapterygoid component of the quadrato-metapterygoid, possibly articulating with the neurocranium; *pr.op*, processus opercularis.

of this process resembles that of the one found in *Lepidotus* (WOODWARD, 1893b, p. 561, fig. 6) and *Amia* (ALLIS, 1897a, Pl. XX, fig. 2).¹

Of the membrane bones of the palatoquadrate only the ecto- and entopterygoid are preserved.

The ectopterygoid (*Ecpt*, text fig. 70) is a narrow bone situated along the lateral border of the palatoquadrate and extending backwards right to the quadrate component of the quadrato-metapterygoid. It consists of a radiate bone substance and its centre of ossification is situated far forward.

The entopterygoid (*Enpt*, text fig. 70) is rather high and large. It extends so far dorsally that it partly covers the metapterygoid component of the quadrato-metapterygoid on its medial surface. Like the ectopterygoid it is built up of a radiate bone substance. The ossification centre is near its ventral margin rather far backwards.

Up to now the palatoquadrate in Palaeoniscids has been very incompletely known. TRAQUAIR (1877a, p. 18; 1901, p. 84; 1909, p. 118) described remains of it in a couple of forms (*Nematoptychius* and *Elonichthys*), and said that in these forms it consisted of several ossifications, although in most cases it was impossible to establish their shape and extent. His statement in this connection that the quadrate and metapterygoid were independent and not fused as in *Boreosomus* is of special interest.

As TRAQUAIR is known for his accuracy and as he has, in addition, described and figured the quadrate and the metapterygoid as mutually independent elements in a Platysmoid (*Cheirodus*, 1879, pp. 366—367; Pl. V, fig. 10), one is not yet justified in doubting to any extent the correctness of his observations. Consequently, as far as we know at present, there probably occurred in the Palaeoniscids both forms in which the quadrate and the metapterygoid were independent and forms in which these two bones were fused with each other, as in *Boreosomus*. I shall have an opportunity to show below (Part II) that the latter conditions are found in another form (*Saurichthys*) among the lower Ganoids.

The mandible (text fig. 70) is relatively robust and has the shape usual in Palaeoniscids, i. e. it is quite without a coronoid process and its labial margin is straight. Its lower margin is weakly convex. Its postero-ventral corner is well rounded.

Only one substitution bone is found in the mandible (*Mk*, text fig. 70), reaching throughout the whole length of this from the symphyse to the posterior end. In the anterior two-thirds this bone is only a narrow rod, but increases considerably in height in its posterior third. From the lateral to the medial side it is rather thick, and it can be clearly seen that it consists of a cancellous bone substance. It is principally situated in the dorsal half of the mandible. Only its posterior part reaches somewhat down into the ventral half. The anterior and middle thirds of its upper surface are directly covered with the medial tooth-bearing lamella that issues from the upper margin of the dentalsplenial. Its posterior third, on the other hand, is freely visible on the dorsal surface of the mandible and has an articulatory fossa for the quadrato-metapterygoid not far from the posterior end. In front of the articulatory fossa there follows on the lateral side of the bone a fairly long and rather deep niche (*mg*, text fig. 70), closed laterally by the membrane

¹ In *Amia*, however, this process does not articulate with the neurocranium, and it is uncertain whether it did so in *Lepidotus*. In *Lepidotus*, on the other hand, an articulation is, as we know, developed between the metapterygoid and the neurocranium.

bones. We thus have here a dorsally open fossa, which undoubtedly has been developed in connection with the insertion of the musculus adductor mandibulae.

The bone now described must, as can easily be seen, represent a considerable part of the Meckelian cartilage and nothing like it is known so far in any Teleostome fish. It is evident, however, that the bone in question has such an extension that it must presumably comprise not only the homologues of the articular and the autangular but also that of the mentomandibular. One might possibly suspect that the autocoronal may also form part of it.

Of the membrane bones of the mandible the dentalo-splénial, angular and supra-angular («articular» TRAQUAIR, 1877 a, p. 19) are incompletely preserved. The dentalo-splénial has, as already mentioned, along its dorsal margin a medial tooth-bearing lamella that covers the long substitution bone in the Meckelian cartilage. The supra-angular was as usual a small bone forming together with the dentalo-splénial the lateral wall of the fossa for the insertion the musculus adductor mandibula described just above. No further details are known as to the boundaries or shape of the three bones in question.

The hyomandibular is a large and powerful bone whose shape is seen in text fig. 70 (*Hm*). Its middle part, which is relatively thin, consists of compact bone. The dorsal and ventral parts, both of which are rather thick, have consisted of cartilage interiorly, and this cartilage has formed a continuation of the cartilaginous epiphysse which has certainly been present at either end of the bone. The bone substance is radiate, and a distinct centre of ossification is discernible, situated in the middle part of the bone. From the posterior margin of this part there issues a long processus opercularis (*pr. op*) whose distal end was evidently covered with cartilage. As we shall see, a similar process is also found in the Palaeoniscid genus *Acrorhabdus* described below.

The occurrence of this process shows beyond all doubt that with regard to the development of the musculature of the gill-cover both *Boreosomus* and *Acrorhabdus* have been specialized in the same direction as the higher Ganoids and Teleosts. A musculus dilatator operculi would consequently have been developed from the musculus constrictor superficialis I, at the same time as musculus constrictor superficialis II was probably weakened and subdivided into more sharply localized independent muscles (cf. VETTER, 1878; RUGE, 1897; SAGEMEHL, 1885, p. 62; LUTHER, 1909, 1913).

This state of affairs is especially noteworthy as the hyomandibular in Palaeoniscids which have hitherto been known, has shown more primitive conditions. According to TRAQUAIR's exposition (1877 a, p. 17, p. 39; Pl. I, fig. 3; Pl. II, fig. 2) the processus opercularis is thus not developed or at any rate not distinct in the genera *Palaeoniscus*, *Nematoptychius*, *Oxygnathus*, *Elonichthys*, *Cycloptychius* and *Amblypterus*, to which may also be added *Gyrolepis*, which I have had an opportunity to investigate myself. Finally by TRAQUAIR's investigations (1879, p. 366) it was also shown that a distinct processus opercularis was not present either in *Cheirodus* among the Platysomids.

The morphological importance of these facts was obviously quite clear to TRAQUAIR, as he says with regard to the relation between *Polyodon* and *Palaeoniscus* (1877 a, p. 39): «In neither is the operculum attached to the hyomandibular by a joint, but secured in its place only by skin and muscles.» In other words, no musculus dilatator operculi

would have been developed, and the movements of the opercular apparatus would have proceeded in the same way as in the recent sturgeons, i. e. by contraction of the *musculus constrictor superficialis II*, which on the whole would have been rather slightly specialized.

It does not seem impossible, however, that TRAQUAIR has gone a little too far in this. It certainly seems to be settled that there is no real *processus opercularis* present in the genera mentioned, but, according to what is shown by his description of the hyomandibular in *Palaeoniscus* (1877 a, p. 17) and *Cheirodus* (1879, p. 366; Pl. V, fig. 10), this bone has at its posterior margin a more or less marked corner, which might be imagined to be a process of this sort in a primitive stage of development. In *Palaeoniscus* this corner is so situated that, according to TRAQUAIR's statement, it would correspond to the boundary between the operculum and the suboperculum. In *Cheirodus*, on the other hand, it is found farther dorsally, so that it corresponds to the upper part of the medial surface of the operculum. I have myself observed in *Gyrolepis* too a corner, situated about as in *Cheirodus*.

Whatever may be the case about this corner, it is obvious that in the *Palaeoniscids* we find both forms in which the musculature of the operculum has been comparatively primitive and forms in which it was rather highly specialized in the direction of the higher *Ganoids* and *Teleosts*.

It may be added with regard to the hyomandibular in *Boreosomus arcticus* that it was probably not pierced by the *truncus hyoideomandibularis facialis* or any of its branches.¹⁾

Of the opercular skeleton in *Boreosomus arcticus* nothing is present except what has been described and figured by WOODWARD (1912, pp. 292–293, Pl. XIV, fig. 2).

The skeleton of the unpaired fins.

Of the unpaired fins there are only some lepidotrichia, probably belonging to the dorsal fin, which all are densely jointed throughout their length and divided dichotomically in their distal parts.

The skeleton of the paired fins.

I have nothing to add to WOODWARD's description of the membrane bones of the shoulder girdle.

The pectoral fins were fairly small and their lepidotrichia, at least in the *Upsala* specimen *P. 132*, were jointed only in their distal third (orig. spec. of WOODWARD's description 1912, and his Pl. XIV, fig. 2). The endoskeletal radials of these fins were, at least partly, rather long.

The ventral fins were probably small. Their lepidotrichia, a few of which are present, are fine and probably jointed throughout their length.

¹⁾ It is of interest to note that in the hyomandibular of *Gyrolepis alberti* (specimen belonging to the Palaeontological Institute of Upsala) I have found a rather coarse canal which was probably pierced by the *truncus hyoideomandibularis facialis*. The canal, which is situated near the posterior margin of the hyomandibular, passes off in a ventro-lateral direction and has its exit immediately antero-ventrally of the corner of the posterior margin.

Squamation.

The shape and sculpture of the scales were described earlier by WOODWARD (1912). In order to be able to show more precisely the difference between this and the species described below it is, however, necessary to state some additional details as to the sculpture. I have all the more reason to do so as one of the specimens found after 1912 has its scales partly in a fine state of preservation (*P. 695*, Pl. 27, fig. 2).

One always finds immediately behind the covered anterior area on each scale one or a couple, sometimes even three or more, ganoine ridges mainly running parallel to the anterior margin of the scales. Sometimes one or more of these ridges may be divided into shorter, mutually independent pieces. The most anterior ridge, or sometimes the two most anterior ones, usually have their lower ends finishing directly at the ventral margin of the scales. It may also happen, however, that they are both bent backwards in their ventral parts, so that they run for a bit along the ventral margin, but this is more often the case with the second one counting from in front. When a third one, or possibly still another is present, these two are always bent and pass over into the broad and flat ridges, running obliquely backward and downward, that occur on the remaining and far greater part of the exposed surface on each scale. The ridges of this latter category often anastomose at their posterior parts and sometimes also along the ventral margin of the scales in the way shown in Pl. 27, fig. 2.

All the ridges, both those running parallel to the anterior margin of the scales and the others, are smooth and level. The fine corrugation or a similar appearance that often occurs in the species described below is entirely lacking here. Finally it is worth mentioning that the ridges are as a rule very flat and considerably wider than the furrows between them.

* * *

Remarks. — *Boreosomus arcticus* is well characterized as an independent species by its scale sculpture. Especially characteristic are the frequent anastomosings of the ridges towards the posterior and lower margins of the scales. Another important character consist in the direction of the ridges that follow along the anterior margin of the exposed surface of the scales.

Geological occurrence and localities. — *B. arcticus* is known from SALOMON'S bone-bed at Mt. Congress, from the fish horizon at the south shore of Sassan Bay at Mt Marmier, and from the Triassic strata at Horn Sound.

***Boreosomus reuterskiöldi* n. sp.**

(Pl. 22, fig. 4; Pl. 27, fig. 3; Pl. 28, fig. 1).

To this species I assign remains of five specimens (*P. 115*—*P. 117*; *P. 119*; *P. 678*). It is possible that a number of head bones (*P. 676*), not determinable in detail, and a number of detached scales (*P. 118*; *P. 777*; *P. 798*) also belong here.

The material present is not adapted to give any exact idea of the general shape and proportions of the species. One can, however, conclude that the shape of the body was fusiform and that the total length of the best preserved specimens (*P. 117* and *P. 119*) amounted to 20—25 cm. If, however, one of the two doubtful specimens (*P. 676*)

turns out to belong here, then it would show that the species had a rather considerable size.

The membrane bones of the neurocranium.

Nothing is preserved of the substitution bones of the primordial neurocranium and of the membrane bones there are only certain ones belonging to the cranial roof (Pl. 27, fig. 3), namely the frontal (*Fr*), dermosphenotic, parietal (*Pa*) supratemporo-intertemporal (*Stemp. ii*) and a large extrascapular (*Ext*).¹⁾ Nothing further can be established as to the shapes of and relations between these bones. Their sculpture consists of longitudinal striae, which are somewhat long and fairly coarse on the anterior parts of the frontals, becoming rather short and fine further backwards on the parietals, supratemporo-intertemporals and extrascapulars, where they may be replaced by tubercles at several places.

Text fig. 71.

Borcosomus reuteri n. sp.

Parts of the visceral skeleton.

After E. 119. 1/4.

Md, mandible; *Mg*, median jugular plate; *Mx*, maxillary; *Op*, operculum; *Po*, preoperculum; *Rbr*, radii branchiostegi; *Sop*, suboperculum.

Visceral skeleton.

The palatoquadrate is not preserved on the present material of this species.

The maxillary (*Mx*, text fig. 71; Pl. 28, fig. 1) is incompletely preserved and partly broken, but one can certainly see that its shape cannot as a whole have differed very essentially from the usual one in the Palaeoniscids.

The mandible (*Md*, text fig. 71; Pl. 28, fig. 1) is long and robust and almost the same height throughout its length, as the lower margin is straight for a considerable stretch and runs parallel to the upper one. As is usual in the Palaeoniscids it has no coronoid process.

The preoperculum (*Po*, text fig. 71; Pl. 28, fig. 1) is an angular bone, extending forward towards the orbital opening in the usual way.

The hyomandibular must have been oblique as in the majority of Palaeoniscids.

The operculum (*Op*, text fig. 71; Pl. 25, fig. 1) is partly incomplete. It is obvious, however, that it was both large and wide, with the anterior margin concave, the posterior one convex and the lower one fairly straight.

The suboperculum (*Sop*, text fig. 71; Pl. 28, fig. 1) is very fragmentarily preserved and nothing can be established with certainty as to its shape or size.

The radii branchiostegi (*Rbr*, text fig. 71; Pl. 28, fig. 1) must have been few in number. Only four are present, and it is improbable that the total number exceeded five. They are long and rather uniformly wide.

In front of the radii branchiostegi there follows between the two mandibulae an unpaired and very large median jugular plate (*Mg*, text fig. 71; Pl. 28, fig. 1).

¹⁾ The extrascapulars must obviously be only two in number, one on either side of the median line. At least in certain Palaeoniscids they are, on the contrary, represented by a number of small plates (TRAQUAIR, 1877a, p. 21; 1901, p. 83; Pl. XIV, fig. 1.

The sculpture on the opercular bones and the radii branchiostegi is comparatively fine and consists of numerous tubercles, which are somewhat prolonged in the longitudinal direction of the fish. The posterior part of the maxillary also has a similar sculpture. On the anterior part of the same bone, on the contrary, the tubercles become longer and coarser so that they might really be called short striae, and in addition it is to be noted that they are not situated quite horizontally, but are directed somewhat forwards and downwards. The jugular plate has at its anterior part a rather well developed longitudinal striation, while farther backward sculpture is lacking except on a median part which has a weak tuberculation. The mandible is relatively coarsely ornamented with numerous, densely placed striae and tubercles, the latter forming a row along the labial margin; the striae, on the other hand, apart from the rather long ones situated farthest posteriorly, are often somewhat undulating and arranged so that as a rule, they run not quite horizontally but with a slope downwards and backwards.

The sensory canals of the head.

The sensory canals of the head are incompletely preserved. They are fine and, as far as can be judged, seem to show the usual conditions. Apart from possible «pit-lines» they are quite enclosed in bone.

The supraorbital canal (*soc*, Pl. 27, fig. 3) may have had its course backwards and somewhat medially through the frontal, continuing farther backwards into the parietal, where it extended almost close to the posterior margin.

The infraorbital canal (*ifc*, Pl. 27, fig. 3) forms, as usual, a direct anterior continuation of the cranial division of the lateral canal. Passing off in a forward direction it pierces the intertemporal component of the supratemporo-intertemporal and from there enters the dermosphenotic. In the latter bone it turns laterally and downwards, leaving the cranial roof and passing over to the cheek. As far as can be seen there was no anastomosis between its posterior portion and the supraorbital canal.

The preopercular canal (*poc*, Pl. 27, fig. 3) enters with its dorsal end into the supratemporo-intertemporal and there communicates with the infraorbital canal and the cranial division of the lateral canal at about the place where these pass into each other. Further details of its course are not known.

The cranial section of the main lateral line of the body (*l*, Pl. 27, fig. 3) is only preserved in its anterior part; which is situated in the supratemporal component of the supratemporo-intertemporal. It is obvious, however, that, in spite of this, it must have pierced the lateral part of the large extrascapular, then continuing through the suprascapular. The supratemporal commissure can be distinctly shown (*s. com*, Pl. 27, fig. 3) and is, as usual, situated in the extrascapulars.

On the lower wall of that part of the cranial division of the lateral canal that is situated in the supratemporal component of the supratemporo-intertemporal there are two small foramina, each of which probably transmitted a nerve branch for a sensory organ (cf. ALLIS 1889, Pl. XLII; 1900a, b; 1905; COLE 1898, Pl. 22 etc.). Each of the foramina in question has a tubulus corresponding to it and this tubulus issues in a lateral direction and opens on the dorsal surface of the supratemporo-intertemporal near the lateral margin.

On each of the parietals there is a short transversally placed furrow (*mp*, Pl. 27, fig. 3), which apparently represents a «pit-line» of sensory organs. It probably corresponds to the middle one of the three lines of this sort that are found on the posterior part of the cranial roof in *Amia* and other Teleostomes (cf. ALLIS 1889, pp. 502—509, Pl. XLII; 1903a, p. 187; 1905, pp. 406, 410, 418, 440, 452, 465, 469, 474, 484; HERRICK 1901, pp. 222—223; Pl. XIV, etc.).

The skeleton of the unpaired fins.

The dorsal fin (*D*, Pl. 27, fig. 3) is rather weakly developed. It is situated strikingly far forward and seems to have been opposite the ventral fins. Its shape cannot be established with certainty as the lepidotrichia are not preserved in their total length. The lepidotrichia, which are somewhat over 25 in number, are situated close together and are closely jointed. The fulcra are small and weak.

The caudal fin is incompletely preserved and nothing can be established as to its shape. The ridge-scales on its dorsal lobe were probably rather small or at least not enlarged to any great extent.

The skeleton of the shoulder girdle and the paired fins.

Of the membrane bones of the shoulder girdle the little suprascapular and the supracleithral (*ScI*, Pl. 27, fig. 3) are partly preserved. Both these bones are pierced by the lateral canal and show the same conditions as to shape as are usual in the Palaeoniscids. The sculpture consists of short and rather fine striae, parallel to the axis of length of the fish.

The pectoral fins (*Pc*, Pl. 28, fig. 1) are fragmentarily preserved. It can, however, clearly be seen that their lepidotrichia were unjoined in a long proximal part.

The ventral fins (*V*, Pl. 28, fig. 1) are small and short-based. The lepidotrichia, which seem to have been present to a number of 14 or 16, are closely jointed throughout their length.

Squamation.

Only on the most anterior part of the abdominal region immediately behind the supracleithral and the cleithral were there scales whose height was greater than their width (Pl. 27, fig. 3; Pl. 28, fig. 1). On the middle part of the sides of the abdominal region the scales are fairly rhombic or their width is somewhat greater than their height, farther posteriorly towards the caudal region their height decreases still more. This is also the case both towards the ventral side and the dorsum in the abdominal and the caudal regions. It is especially noteworthy that, as is shown in Pl. 37, fig. 3 a large number of the scales situated towards the dorsum in each vertical row are even very low, which gives the whole squamation a very characteristic appearance. Some of the scales close to the base of the dorsal fin are even so low that their height is only $\frac{1}{5}$ — $\frac{1}{6}$ of their width. The dorsal ridge-scales, which are somewhat larger than the scales at their sides, do not seem to have been prominent. Some enlarged scales are found on the ventral side between the bases of the ventral fins (Pl. 28, fig. 1).

The majority of scales probably have the covered anterior area wide (Pl. 22, fig. 4). In addition they have a well developed articulatory spine and a serrated posterior margin.

The sculpture on the great majority of the high scales consists of numerous fine and rather short striae running rather obliquely in the directions backwards and downwards. The other scales have a coarser sculpture, which consists to a great extent of a relatively small number (the number decreases with the height of the scales) of wide, densely arranged striae (Pl. 22, fig. 4), running somewhat parallel to the upper and lower margins. These striae are generally so long that they extend right across the exposed surface of the scales, each of them ending in one of the small spines on the posterior margin. Shorter striae, however, often occur inserted between these longer ones. Anastomosis between the striae are rare, and occur only on the scales of the most posterior part of the caudal region.

Especially on the scales belonging to the ventral side and the anterior part of the sides of the abdominal region the striae are finely rugose, in about the same way as is figured by TRAQUAIR (1901, Pl. 13, fig. 5) in *Elonichthys pectinatus*.

A further characteristic of the sculpture on the great majority of scales is that the striae never bend off in a dorsal direction along in the anterior margin as in *B. arcticus*, and that between their anterior ends (Pl. 22, fig. 4) there are practically always small tubercles or shorter striae. Finally it ought to be noted that the striae on the scales of the caudal region tend, according as one approaches the caudal fin, to take a direction parallel to the diagonal of each scale that can be drawn from the antero-dorsal to the postero-ventral corner.

* * *

Remarks. — *Boreosomus reuterskiöldi* is well separated from *B. arcticus* by its scale sculpture, but bears instead a striking resemblance to certain *Acrolepis* species, e. g. *Acrolepis hopkinsi* M'COY (TRAQUAIR, 1909, p. 109—112; Pl. 24, Pl. 25, fig. 6).

It is named after Cand. ADAM REUTERSKIÖLD, my friend and my companion during the expedition to Spitzbergen in 1917.

Geological occurrence and localities. — *Boreosomus reuterskiöldi* is hitherto known only from the fish horizon at the following localities: Mt. Congress, Mt. Sture, Mt. Marmier, Mt. Trident and Mt. Andersson.

Boreosomus sp.

(Pl. 29, figs. 1—3).

Under the heading *Boreosomus* sp. I have grouped some mostly very fragmentary fish remains (*P. 114*, *P. 120—131*), all of which seem to have belonged to rather large individuals. The best preserved specimen (*P. 120*) is about 12 cm high just behind the head. The body has been fusiform, but no other details can be given as to its length or its general proportions.

Visceral skeleton.

Among the elements of the visceral skeleton there are only very badly preserved remains of the maxillary (*Mx*, Pl. 29, fig. 1), the mandible (*Md*, Pl. 29, fig. 1), the preoperculum (*Po*, Pl. 29, fig. 1) and possibly also of the operculum and the radii branchiostegi. The sculpture on these bones has consisted of fine tubercles, somewhat

lengthened in the longitudinal direction of the fish. It is noteworthy that in this case the sculpture on the whole maxillary is developed in the same way and is not, as in *B. reuterskiöldi*, stronger on the anterior part.

Dentition.

The dentition is fairly weak. The teeth are of two kinds: pointedly conical and very bluntly conical, almost spheroid. The former variety is found on the maxillary and the dentalo-splénial, where they are arranged in two longitudinal rows, a lateral and a medial one. As usual the teeth of the medial row are considerably longer and more robust than those of the lateral one. On these stronger teeth can be observed a bright little enamel cap.

The bluntly conical teeth are almost *Colobodus*-like in appearance, as, like those of *Colobodus*, they possess the little verruca that obviously corresponds to the enamel point on the pointedly conical ones. They have, however, no striation radiating from the verruca, as is the case in *Golobodus*. Teeth of this type are only found on a loose fragment of bone which may probably have formed part of a pterygoid, or of the parasphenoid.

The sensory canals of the head.

Only some smaller parts of the mandibular canal are preserved and show that the sensory canals were fairly fine, and that they opened outwards with long simple tubules. The number of these cannot be established.

The skeleton of the unpaired fins.

The dorsal fin (*D*, Pl. 29, fig. 1) is preserved in specimen *P. 120* and is situated there far forward, its distance from the head being only about 10 cm, while the height of the body in the most anterior part of the abdominal region is, as has been mentioned, about 12 cm. It is fairly well developed, is triangular in shape with height and length about equal and consists of about 30 rather coarse, closely situated lepidotrichia, jointed throughout; each of these has on the posterior half of the lateral sides a number of fine, often confluent, longitudinal striae of ganoine. The anterior half of the lateral sides, on the other hand, is without ganoine and is smooth. Nothing is preserved of the fulcra,

Of the caudal fin there is only a fragment of the dorsal lobe present (*P. 122*), which has already been noticed by WOODWARD 1912 (p. 293). This fragment is interesting inasmuch as it shows undoubtedly that we are concerned with a heterocercal fish. Otherwise it gives us no further idea as to the exact form or size of the fin. The lepidotrichia are on the whole densely jointed and coated with a smooth layer of ganoine.

The skeleton of the paired fins.

The shoulder girdle is represented, in its present state of preservation, only by very indistinct remains of the supracleithral and the cleithral, both of which have a very fine sculpture, consisting of short, horizontally running striae, or, if the term is preferred, somewhat lengthened tubercles, oriented in the longitudinal direction of the fish.

The pectoral fin (*Pc*, Pl. 29, fig. 1) is very incompletely preserved. It is only represented by some proximal parts of lepidotrichia, which appear to be unjointed.

Squamation.

The scales are of about the same shape and arranged in the same way as in *B. reuterskiöldi*. Most of them are consequently wider than high, and this is especially the case towards the dorsum and on the ventral side. Their anterior covered area is in general wide and their antero-dorsal corner is not infrequently somewhat produced upwards. Their dorsal margin has a well developed or in certain cases even a long articular spine, and their medial surface is furnished with a broad vertical ridge, at least on the scales of the abdominal region. Their posterior margin is serrate.

The scale sculpture resembles also on the whole that of *B. reuterskiöldi*. The striae pass off as in this species and anastomoses between them are similarly unusual. Finally, tubercles or shorter striae occur in both species between the anterior ends of the longer striae, and, in addition, the fine folds on all the striae. The only difference that can be shown seems to consist in the fact that the striae are relatively coarser in *B. reuterskiöldi* than is the case here.

The number of striae is rather great on the highest, anterior scales, but decreases according as the scales diminish in height. The character of the striation on some scales from the anterior part of the lateral surfaces of the abdominal region is shown in Pl. 29, fig. 2 and it is noteworthy that the striae on these scales grow very fine as they approach the posterior margin, and that a number of equally fine shorter ones are inserted between their posterior ends. The striae of the latter category are, however, only to be found on the scales in the most anterior vertical rows. The shape and the sculpture on the scales of the ventral side is shown as a negative in Pl. 29, fig. 3.

* * *

Remarks. — It is evident from the description just given that the differences that can be observed between the specimens described in this connection and *B. reuterskiöldi* are of rather slight importance. It is probable, however, that a number of additional differentiating characters would be found if we had a more complete material at our disposal.

As it is thus impossible at present to decide whether in the remains described here we are concerned with a variety of *B. reuterskiöldi* or a new and independent species closely related to this, I have merely placed them under the heading *Boreosomus* sp.

Geological occurrence and localities. — All the specimens included under the heading *Boreosomus* sp. come from the upper Saurian horizon. The localities of the finds are as follows: Cape Svea, Mt Congress, Mt Tschermak, Mt Marnier and Mt Viking.

***Boreosomus? scaber* n. sp.**

(Pl. 24, fig. 4; Pl. 26, fig. 3; Pl. 35, fig. 4).

Under this name I include a fragment of a smaller fish, *P. 877*, and a large number of detached scales.

I shall begin my description with specimen *P. 877* and afterwards pass on to the detached scales.

Specimen *P. 877* consists only of a portion with connected scales from the caudal region or the transition between this and the abdominal region (Pl. 24, fig. 4). The

scales are all somewhat broader than high and have the anterior, covered area fairly wide, although scarcely so wide as in the typical *Boreosomus* species described above. The sculpture consists partly of striae, partly of tubercles. The striae, which pass off obliquely backwards and downwards, are long with sharp backs, and often wide; they are also situated close together. Those that are situated nearest to the lower margin on each scale may not infrequently have their anterior ends bent upwards parallel to the anterior margin, but they never run any long distance in this way, as is the case in *B. arcticus*. All the striae have the very fine folds previously described by me in *Boreosomus* sp. and *Boreosomus reuterskiöldi*.

The tubercles on each scale are situated in front of the anterior ends of the striae, where they are arranged in a couple of rows parallel to the anterior margin of the scale. The tubercles themselves are somewhat lengthened in a dorsi-ventral direction. The sculpture of the scales obtains through the arrangement of the tubercles a feature that recalls *Boreosomus arcticus* to some extent.

If we now turn to the detached scales (Pl. 26, fig. 3; Pl. 35, fig. 4) we are able to distinguish different types according to the position they have occupied. We find some that are higher than wide, having evidently been situated rather close behind the shoulder girdle, some in which the height is slightly less than the width, having belonged to the middle part of the lateral sides of the abdominal region, and finally those in which the width is considerably greater than the height. These last-mentioned scales are probably from the ventral side and the back.

These scales are closely related in all respects to those just described above in specimen *P. 877*, but differ from these by having the vertical rows of tubercles in front of the striae in most cases more numerous, usually three and sometimes even four or five.

* * *

Remarks. — The scales described here show such agreement in their characters in several respects that I consider myself able provisionally to group them under one species name. They resemble somewhat those in *Boreosomus arcticus*.

Finally it must be pointed out that the generic determination of these scales must be looked upon as rather uncertain.

Geological occurrence and localities. — Specimen *P. 877* comes from the fish horizon at Mt Bertil.

The detached scales occur in the bone-bed of the lower Saurian horizon, and in bone-beds between this and the fish horizon. In the bone-bed of the lower Saurian horizon they sometimes appear in such great numbers that they really form the rock. The localities of the finds are as follows: The mountain between De Geer Valley and Flower Valley (Corrie Down) on the south side of Sassen Bay, Mt Marmier and Mt Viking.

Genus *Acrorhabdus* n. g.

As far as is known up to the present, the new genus that I call *Acrorhabdus* is characterized by the following features: Small to medium fusiform fishes. The primordial neurocranium like the primordial visceral skeleton strongly ossified. The posterior part of the entopterygoid is, at least in certain species, represented by a number of

mutually independent, small tooth-bearing plates. Hyomandibular situated obliquely with a large processus opercularis. Mouth large. Preoperculum wide of a rather triangular shape; operculum large, high. Suboperculum small, low. Branchiostegal rays few or at least not very numerous. Median jugular plate very large. All the external membrane bones of the visceral skeleton with a sculpture of fine, fairly short, longitudinally arranged striae. Dentition probably somewhat robust with both pointedly conical and bluntly conical teeth. The sculpture of the shoulder girdle like that of the opercular bones. Dorsal fin probably opposite the ventral fins. Anal fin small, situated far backward. Caudal fin deeply cleft. Pectoral and ventral fins weakly developed, the latter probably situated about half way between the pectoral fins and the anal fin. Lepidotrichia of all fins, apart from the two or three most anterior ones in the pectoral fins, closely jointed. Fulcra present, at least on the pectoral fins, but small. Scales higher than wide only on the very anterior part of the lateral surfaces of the abdominal region, decreasing in height in a caudal, dorsal and ventral direction, so that the width becomes predominant. Towards the dorsum a number of scales in each vertical row are very low, and even ventrally there are low scales. The scales often rather thin. At least the scales of the abdominal region have their covered area wide and the antero-dorsal corner somewhat produced upwards. On the dorsal margin an articular spine is developed. The sculpture on all the scales consists partly of longer, partly of shorter striae. The longer ones cross the whole exposed surface of the scales from the anterior to the posterior margin, in most cases sloping somewhat downwards and backwards. The shorter ones are always fine, numerous, and developed exclusively in the immediate neighbourhood of the posterior margin between the posterior ends of the longer ones.

It is easy to see that the genus *Acrorhabdus* has most of its characters in common with *Boreosomus*, to which it is undoubtedly closely related. It is, however, clearly distinguished from *Boreosomus*, especially by the sculpture of the head and the scales, and by the fact that almost all the lepidotrichia in the pectoral fins are jointed throughout their length. We shall see that differences between the two genera can also be observed with regard to the development of a number of bones in the head.

Like *Boreosomus*, *Acrorhabdus* shows, at least with regard to the shape and sculpture of the scales, certain agreements with *Acrolepis*.

It is beyond all doubt that both *Boreosomus* and *Acrorhabdus* represent among the Palaeoniscids a special group, characterized by the position of the dorsal fin and certain specializations in the visceral skeleton. As I have already been able to show to some extent (pp. 213—214), this specialization has, at least partly, proceeded in the same direction as in higher Ganoids and Teleosts. According to what I am able to show below, the gap between *Boreosomus* and *Acrorhabdus* on the one hand the Catopterids on the other must really have been rather slight.

Acrorhabdus bertili n. sp.

(Pl. 31; Pl. 32, figs. 2—5.)

The determinable material of this species at my disposal consists of only two incomplete specimens (*P. 172*, *P. 174*). Besides these I include here too, though with hesitation, a couple of fragments with scales (*P. 113*, *P. 175*) and the remains of a caudal fin (*P. 135*).

One may venture to put the total length of the two specimens (*P. 172* and *P. 174*) at about 35 to 45 cm. The shape of the body was probably fusiform, but no details can be established about it.

The primordial neurocranium and its ossifications.

As in *Birgeria mougeoti* the primordial neurocranium is composed to a considerable extent of replacing bones, but is very much crushed and compressed from the sides, so that only a few details can be observed.

In the labyrinth region are found remains of a large prootico-opisthotic (*Pro. o*, Pl. 31, figs. 1, 2; Pl. 32, fig. 3), evidently homologous to the similarly termed bone in *Birgeria mougeoti*, to which it also seems to correspond in its extension (cf. pp. 153—161 above).

As in *Birgeria mougeoti* the wall of the neurocranium was cartilaginous immediately in front of the prootico-opisthotic (Pl. 31, figs. 1, 2; Pl. 32, fig. 3). Anteriorly of this cartilage quite as in *Birgeria mougeoti* (cf. pp. 161—175 above), there follows the posterior part of the large sphenoid (*Sph*, Pl. 31, figs. 1, 2; Pl. 32, fig. 3) which, in my description of *Birgeria mougeoti*, I have shown reaches with its basal parts into the most anterior part of the labyrinth region, while its main part falls within the orbitotemporal region. An incisure (V) on the posterior margin of the sphenoid indicating the exit of the second and third branches of the trigeminus can be observed, but it is somewhat more completely enclosed by bone than in *Birgeria mougeoti*. It does not even seem impossible that it was bounded caudally by a thin bridge of bone and that the trigeminus would thus pierce the sphenoid in the immediate proximity of the posterior margin. Nothing is preserved of the anterior parts of the sphenoid.

Both the substitution bones described in the neurocranium have no radiation and consist exclusively of a cancellous bone substance as in *Birgeria mougeoti* (cf. pp. 152—153).

What has been shown here is certainly not much in itself, but it is all the same of great importance as it supports the view that the ossifications of the primordial neurocranium in Palaeoniscids in general were on the whole developed as in *Birgeria mougeoti*.

The membrane bones of the neurocranium.

The parasphenoid (*Psph*, Pl. 31, figs. 1, 2; Pl. 32, fig. 3) was wide and presumably rather strong beneath the orbitotemporal region. Under the labyrinth region it is only represented by fragments. Nothing else is known as to its shape and relations.

Nothing is preserved of the membrane bones of the cranial roof in the material present.

Visceral skeleton.

The palatoquadrate seems apparently to have been triangular as in *Boreosomus arcticus*, but no further details as to its shape can be established. Of its substitution bones the metapterygoid (*Mptg*, Pl. 31, fig. 3) and the quadrate (*Qu*, text fig. 72, Pl. 31, fig. 1) are present in a very fragmentary condition, and it is uncertain whether they were separate bones or fused as in *Boreosomus arcticus*. Of the membrane bones the ecto- and entopterygoid are present, except for their most anterior parts.

The ectopterygoid (*Ecpt*, text fig. 72, Pl. 31, figs. 1, 3; Pl. 32, fig. 5) extends along the lateral border of the palatoquadrate right to the quadrate, as in *Boreosomus arcticus*, but it is considerably higher than in this latter species.

The entopterygoid (*Enpt*, text fig. 72; Pl. 31, figs. 1, 3; Pl. 32, fig. 5) is in its anterior part of about the same height as the ectopterygoid, becoming rapidly higher posteriorly. Its posterior part, which covers the medial surface of the whole metapterygoid and that of almost the whole quadrate, shows, however, very curious conditions, at it is subdivided into a number of oval or rounded tooth-bearing plates. The transition between this posterior part and the anterior part takes place gradually.

It seems at first sight rather natural that in this condition of the entopterygoid we should see a good proof of the theory of the phylogenetic origin of certain membrane bones through the concrescence of teeth (cf. GAUPP, 1905, pp. 613—615), i. e. that we should have the posterior part of the entopterygoid at a primitive phylogenetic stage of development here. Close reflection will show us, however, that an opposite interpretation of the facts in question is possible and even more probable than the first-mentioned one.

As we now know (cf. pp. 126, 134, 146) a large, high entopterygoid, reaching in a caudal direction right to the posterior margin of the palatoquadrate, is developed in Stegocephalians and at least in several Rhipidistids. It has also been possible to show in this work that the entopterygoid component of the pterygoid of the Coelacanthids is large and high and has about the same extension as in Rhipidistids and Stegocephalians and we have found that a rather Rhipidistid-like entopterygoid was developed in certain Paleoniscids (*Boreosomus*) too.

The facts mentioned support, in my opinion, the view that a Rhipidistid-like entopterygoid is a very old formation, which was not acquired independently by primitive Tetrapods, Crossopterygians and Actinopterygians but was inherited from an ancestral form common to them all.

The strong development of the entopterygoid in *Boreosomus* would thus be primitive, if this argument is correct, while the conditions found in *Acrorhabdus bertili* would indicate the beginning of a reduction process, whose continuation would lead to total disappearance of the caudal, larger part of the bone. The remaining anterior part would then correspond to the bone that is called the entopterygoid in recent higher ganoids and Teleosts, and *Acrorhabdus bertili* would thus, with regard to the entopterygoid, have entered upon a direction of development leading to the Teleostean type.¹⁾

¹⁾ It is noteworthy in this connection that both in *Amia* (VAN WIJHE, 1882, p. 280) and *Polypterus* (VAN WIJHE, 1882, p. 253; POLLARD, 1892, p. 412) we find teeth developed on the medial side of the metapterygoid and quadrate (*Amia*). These teeth indicate that certain remains of the posterior part of the entopterygoid exist, though they were fused to the metapterygoid.

Stens16, Triassic Fishes from Spitzbergen.

Text fig. 72. *Acrorhabdus bertili* n. sp.

Parts of the visceral skeleton. After P. 174, 1/4.

Art, articular, or possibly articular portion of a single large ossification through the whole Meckelian cartilage; Chy, ossification in the ceratohyal; Ecpt, ectopterygoid; Enpt, entopterygoid; Hm, hyomandibular; Mco, mixicoronoid; Qu, quadrate; Sthyl? possibly stylohyal; Sympl, symplectic; ohy, indication of ossification in the posterior end of the ceratohyal; pr.op., processus opercularis.

The lower jaw is represented only by two fragments of bone. One of them is a part of the articular (*Art*, text fig. 72; Pl. 31, figs. 1, 3) or of the articular component if a large and long bone of the same sort as in *Boreosomus arcticus* was developed in the Meckelian cartilage. The other fragment is a dorsal part of the mixicoronoid (*Mco*, text fig. 72; Pl. 31, figs. 1, 3; Pl. 32, fig. 5). As far as can be seen, no coronoid process or indications of one are present, the labial margin of the mandible being straight right to the posterior end. The articulatory fossa on the articular (or possibly the articular component) is clearly visible in profile (Pl. 31, fig. 1).

The mouth is large and extended far back as in the majority of Palaeoniscids.

The hyomandibular (*Hm*, text fig. 72; Pl. 31, figs. 1, 3), which is situated immediately behind the palatoquadrate, occupies its usual oblique position, i. e. it is directed backwards and downwards. It is a large bone, bent somewhat above the middle in such a way that the anterior border is concave and the posterior one, on the whole, convex. The centre of ossification lies just at the bend, and on the posterior border opposite this centre issues the robust processus opercularis (*pr. op*). From the ossification centre the bone gets wider towards both ends, especially towards the dorsal one. Both the ends are in their present state abruptly truncated, and there was evidently a cartilaginous epiphysse on each of them. The processus opercularis has also probably been provided with a similar epiphysse. With regard to the signification of this process I refer to my account on pp. 213—514 above. No canal or foramen for truncus hyoideo-mandibularis facialis is present. — The bone substance is radiate as in the corresponding bone in other Palaeoniscids.

Connected with the ventral end of the hyomandibular we find on specimen *P. 174*, both on the right and left sides, a small but rather thick spongy bone (*Sympl*, text fig. 72; Pl. 31, figs. 1, 3) which was probably surrounded by cartilage. The bone is situated immediately behind the articulation between the quadrate and the lower jaw and probably corresponds to a part of the symplectic, which, as we know, occupies a similar position in sturgeons, in which it may also sometimes be ossified (PARKER 1873, p. 257, Pl. XX; VAN WIJHE 1882, p. 224; GAUPE 1904, p. 901). In addition BROOM (1909 a, p. 260) states that he observed an ossified symplectic in the so-called *Oxygnathus browni* (cf. p. 209 above).

The conditions of the stylohyal are still uncertain. On the left side of specimen *P. 174* there is certainly an impress of a badly preserved bone that might be the stylohyal (*Stly*? text fig. 72; Pl. 31, fig. 3), but on the other hand the possibility cannot be denied that it may really be an impress of a scale or something that has no connection at all with the hyoid arch.

Medially and somewhat ventrally of each half of the mandible we find on specimen *P. 174* a large hour-glass shaped ossification in the ceratohyal (*Chy*, text fig. 72; Pl. 31, figs. 1, 3; Pl. 32, fig. 5). This ossification is truncated at both ends and probably forms entirely or at least preponderatingly a perichondral diaphysse. That an ossificatory process had also begun in the part of the ceratohyal situated behind this ossification is also seen from specimen *P. 174*, where we find an impress of a thin bone lamella (*ohy*, text fig. 72; Pl. 31, figs. 1, 3; Pl. 32, fig. 5) behind and adjacent to the ceratohyoid ossification. Here we evidently have the beginning of an ossification on the part of the ceratohyal that

is occupied in *Amia*, *Lepidosteus* and Teleosts by the so-called epihyal, according to the rather inconsistent but most usual terminology (cf. GAUFF, 1904, pp. 902—904).

The operculum (*Op*, Pl. 31, fig. 1; Pl. 32, fig. 4) is a wide and high bone-plate. Its ventral margin is straight and meets the posterior one almost at a right angle. The posterior margin has a weak concavity immediately dorsally of the postero-ventral corner; otherwise it is convex.

The suboperculum (*Sop*, Pl. 31, fig. 1; Pl. 32, fig. 4) is incomplete, but it is obvious, however, that it was wide and rather low. Its upper margin is straight, its posterior one convex.

A couple of radii branchiostegi are partly preserved, but no details can be ascertained as to their shape.

The sculpture on the operculum, suboperculum and radii branchiostegi consists of short and rather dense striae, mainly arranged parallel to the axis of length of the body. On the lower part of the operculum, however, they deviate somewhat from this arrangement as they run obliquely backwards and downwards.

The branchial arches (Pl. 31, fig. 2; Pl. 32, fig. 3, 5) are strongly ossified and apparently subdivided into the usual segments. Thus I can distinguish, at least in the three anterior arches, a hypo- (*Hbr*), cerato- (*Cbr*), and an epibranchial (*Ebr*), of which the two latter are long and have a rather deep longitudinal furrow on the posterior side. The basibranchials (*Bbr*) are also strongly ossified but no details can be established either as to the shape or number of the ossifications. On the dorsal side they are covered with tooth-bearing bone-plates. Both the branchial arches and the basibranchials consist of the same sort of bone substance as the substitution bones in the neurocranium.

Along the posterior surface of each of the gill-arches present there is, mostly in situ, as is seen in several of my figures, a double row of long slender comb-shaped supporting gill-rays (GOODRICH 1909, p. 94, fig. 57; filamentary cartilages DANFORTH 1912, p. 422; fig. 9; gill filaments WOODWARD 1895 b, pp. 80, 219; Kiemenstäbchen GAUFF 1904, p. 909). These supporting gill-rays may attain a length of as much as 15 mm, and are almost always somewhat arched, the processes that cause the comb-like shape issuing on the concave side (Pl. 31, fig. 4). Shorter processes may sometimes also occur on the convex side, so that under these circumstances we may speak of a double-sided comb-shape, but this is not general. The supporting gill-rays are all somewhat thickened at their proximal ends and bent towards the concave side, forming a condyle for the articulation with the branchial arches. In each double row they have been so situated that they had the convex sides turned towards each other, i. e. towards the septum.¹⁾ A single row of supporting gill-rays occupies such a position in relation to the hyoid arch (Pl. 31, figs. 1, 3) that it decidedly indicates the presence of a large hyoid gill, which has extended from the dorsal end of the operculum downwards and forwards on to the radii branchiostegi. The most ventral of these supporting gill-rays are situated, to put it more exactly, behind the posterior end of the ceratohyal ossification and like those situated farthest dorsally, they are weak and short.

¹⁾ Comb-shaped supporting gill-rays are not uncommon among the Teleostomes. WOODWARD (1895 b, pp. 80, 219) has described them in *Lepidotus* and *Mesturus*, RIESS (1881, p. 522) in *Salmo* and *Cyprinus*, and I have myself observed that they are also developed in this way in *Clupea*. According to GOETE (1901, p. 557) and STANNIUS (1846, pp. 114—115) this is also the case in *Acipenser* (cf. also *Polyodon* DANFORTH 1912, p. 421, fig. 9).

Finally with regard to the tissue in the supporting gill-rays I have been unable to undertake a microscopical investigation of this in the species in question, but it seems certain that we have here either calcified cartilage or bone. In many recent Teleostomes the supporting gill-rays sometimes consist exclusively of cartilage (e. g. in the sturgeons), while in other they are to a greater or less extent built up of hard tissue, which may be either bone or calcified cartilage (STANNIUS 1846, pp. 114—115; RIESS 1881, pp. 531—524; WOODWARD 1985 b, pp. 80, 219).

Dentition.

The dentition evidently consisted of both bluntly conical and pointedly conical teeth, but is not specially powerful.

The teeth in the maxillary, premaxillary and dentalo-splénial are not preserved, but the evidence seems to show that they were pointedly conical. Similar though rather small teeth probably occurred on the labial margin of the mixicoronoid as well, while the medial side of this bone is quite without teeth.

The ecto- and entopterygoid have over the whole medial surface closely situated small teeth of a bluntly conical shape, and similarly dense, though somewhat larger teeth are also found on the parasphenoid and the membrane bone-plates above the basibranchials.

Text fig. 73.

Acororhabdus

bertili n. sp.

Gill-rakers.

After P. 174: 1/4.

The dentition of the gill-arches is very characteristic. On the medial side (from a morphological point of view the caudal side) of each arch it consists of small plates with dense, fine pointedly conical teeth, while on the lateral side it is represented by club-shaped gill-rakers of the appearance shown in text fig. 73. The distal widened part on each of these gill-rakers has a number of closely set, fine spines. All the gill-rakers are filled inside with white calcite.

The skeleton of the unpaired fins.

The anal fin (*P. 172*) was apparently small and inserted rather near to the caudal fin. It consists, as is usual in the Palaeoniscids, of dense, closely jointed lepidotrichia, whose number cannot be stated with certainty.

The dorsal fin (*P. 172*) is badly preserved. It is situated far forward, its posterior part being opposite the ventral fins. The lepidotrichia, whose number cannot be exactly established, are densely jointed throughout.

The caudal fin (*P. 134*) is distinctly heterocercal and deeply cleft but otherwise nothing can be said as to its shape or its relative strength. Its numerous lepidotrichia show the same conditions as those of the dorsal and anal fins.

The skeleton of the shoulder girdle and paired fins.

The shoulder girdle is rather completely preserved, both with regard to the primary skeleton and the membrane bones. For practical reasons I shall first give here an account of the latter bones.

The suprascapular (*Sxcap*, Pl. 31, figs. 1, 2, 3; Pl. 32, figs. 3, 4, 5) is found in situ, but is very incomplete. The surracleithral (*Scl*, Pl. 31, figs. 1—3; Pl. 32, figs. 3—5) and the cleithral (*Cl*, text fig. 74; Pl. 31, figs. 1—3; Pl. 32, figs. 3—5) are both high and large

and typically Palaeoniscid-like (cf. TRAQUAIR, 1877a, Pl. 1, fig. 5). With regard to the cleithral it is specially noteworthy that its anterior part, which is bent in a medial direction and helps to form the posterior boundary of the gill-chamber, is well preserved (text fig. 74 A, D, E, F). It is also noteworthy that the concavity in the lower part of its posterior margin is weak. The two cleithrals meet ventrally in the median line or at least come very close to each other.

The two clavicularae (*Icl*, text fig. 74; Pl. 31, figs. 2, 3; Pl. 32, figs. 3, 5) are relatively strong and large. Posteriorly they surround together the anterior ends of the cleithrals, ventrally they meet in a median longitudinal suture (text fig. 74 B), and dorsally too they have come into contact with each other,

at least by means of the process *prc*. Their dorso-lateral surfaces have helped to form the lower boundary of the gill-chamber. Seen in profile on the lateral side, each of the bones (text fig. 74 C) is triangular, with one ventral, one caudal and one antero-dorsal margin, of which the ventral one is almost straight and the caudal one concave. The antero-dorsal margin is weakly concave or almost straight in its posterior half; anterior to this there comes a small but very marked sinus (*sin. cor. post*), which is bounded anteriorly by the process *prc*, and finally in front of this process another sinus which reaches to the anterior corner of the bone. This corner is truncate, while the other two more rounded. The postero-dorsal one is somewhat produced. Seen from the ventral side (text fig. 74 B) the two bones in question have somewhat convex lateral margins, and the suture between their medial margins appears to be rather straight. On each bone the anterior end is blunt and concave in such a way that with that of the other bone it forms a rather large sinus.

A specimen of *Acipenser ruthenus* that I had an opportunity to investigate shows that in this species the clavicle is developed in nearly the same way as in *Acrorhabdus bertili*, not only in the general features but also in many details. Thus on the dorso-

Text fig. 74. *Acrorhabdus bertili* n. sp.

Parts of the shoulder girdle. After P. 174. $\frac{1}{2}$.

A. Cleithral, clavicle and primary girdle plate of the right side.

B. Clavicles in ventral aspect.

C. Left clavicle in lateral aspect.

D. Primary girdle plate in its relation to the cleithral and clavicle.

E. Section through shoulder girdle along line Z-Y.

F. Section through shoulder girdle along line X-U.

Cl, cleithral; Icl, clavicle; Scc, ossified primary girdle plate; d, g, processes on the posterior margin of the ossified primary girdle plate; m. cor. arc. ant., anterior portion of musculus coraco-arcualis; m. cor. arc. post., posterior portion of musculus coraco-arcualis; n, nerve canal; prc, process on the dorso-medial margin of the clavicle; sin. cor. post, sinus for the posterior portion of the coraco-arcualis muscle; v, process on the ventral part of the posterior margin of the primary girdle plate.

medial margin of each clavicle of *Acipenser ruthenus* one can distinguish a process (*prc*, text fig. 75), which has a marked sinus both in front and behind. As in *Acrorhabdus bertili* the process also comes into contact with the one on the opposite side. To judge from the figures given by GEGENBAUR (1865, Pl. 6, fig. 2) and PARKER (1868, Pl. 1, figs. 6, 7) the same process would also be present in *Acipenser sturio*, although there it is wider and not so strongly developed.

In my specimen of *Acipenser ruthenus*, as text fig. 75 shows, one portion of VETTER'S (1878, pp. 480—482) musculus coraco-arcualis has its exit on the anterior side (*m. cor. arc. ant*) and one on the posterior side (*m. cor. arc. post*) of the process *prc* on the dorso-medial margin. The anterior portion, which is the stronger, passes off forwards and is related to the sinus situated in front of the process *prc*, while the posterior portion, which has principally a dorsal course, passes upwards through the sinus behind the same process.

Text fig. 75. *Acipenser ruthenus*.
Left half of shoulder girdle from the
lateral side. *Sccl*,
Sccl, supracleithral Lettering otherwise as
in text fig. 74.

From what has been mentioned it seems very probable that the musculus coraco-arcualis in *Acrorhabdus bertili* was subdivided into two portions in the same way as in *Acipenser ruthenus*. It is also very noteworthy in this connection that in *Acrorhabdus bertili* (P. 174) we find a large, well developed urohyal (*Uhy*, Pl. 31, fig. 2; Pl. 32, fig. 3) situated in the same way as in the Teleosts. I have already shown in this work (pp. 75, 87) that there is a urohyal in the Coelacanthids as well, and this bone can thus no longer be looked upon as being characteristic for the Teleosts alone, as GOODRICH especially (1909, p. 350) maintained.¹⁾

The sculpture on the supra-cleithral and the cleithral has the same character as that of the opercular, i. e. it consists of striation with the same direction as the axis of the animal (Pl. 32, fig. 4).

The primary shoulder girdle in *Acrorhabdus bertili* is represented by a somewhat high, quadrangular bone-plate (*Sccl*, text fig. 74, Pl. 31, figs. 1—3; Pl. 32, figs. 3, 5) which is rather thin on the whole. Of its margins one is directed forward, one downward, one backwards and one upwards and backwards. The one directed forward is concave and joins the transversal lamella of the cleithrum, which helps to form the posterior boundary of the gill-chamber of its side. The one directed backward, which is also concave and has somewhat above the middle a small, rounded, blunt process (*g*, text fig. 74 A, D), is visible behind the posterior margin of the cleithral. The one directed downwards is almost straight or weakly concave and has its anterior part against the ventral end of the cleithral, which there is arched towards the median line and has a nearly horizontal position. The one directed upwards and backwards is the shortest of the four margins and weakly concave. The anterior lower corner is pointed and produced forwards; the anterior upper one is rounded, the posterior upper one prolonged in a rather considerable process (*d*) in a backward and downward direction, and the posterior lower one (*V*) is blunt and rounded.

¹⁾ In *Polypterus*, however, formations have long been known (MÜLLER, 1844, pp. 149—150; Pl. 1, fig. 3) that may be looked upon as partly corresponding to the urohyal.

In a dorsal direction the primary shoulder girdle plate has not by far the same height as the cleithral (text fig. 74 D). Ventrally the two primary shoulder girdle plates come near each other, and this is especially the case with their anterior lower corners, which were probably connected by ligaments.

Only the dorsal half of the primary shoulder girdle plate is in contact with the sagittally placed lamella of the cleithral. For between the ventral half of the shoulder girdle plate and the ventral part of the cleithral a fossa is developed which opens backwards and downwards. This fossa, into which the ventral musculature of the pectoral fin extended and had its origin, is rather deep in the direction from front to back, but narrow in the transversal direction. In its roof a wide, short nerve canal (*n*) has its opening. This canal pierces the primary girdle plate in an upward and medial direction, then continuing on its medial side as a wide, ascending furrow. A section through the primary shoulder girdle plate near the lower end of the nerve canal (along the line X—U in text fig. 74 D) is shown in text 74 F. Another similar section, taken farther dorsally (along the line Z—Y in text fig. 74 D) is figured in text 74 E. In the latter section one finds that the canal is continued by a deep sulcus, which is bounded anteriorly by the transversal lamella of the cleithral, posteriorly by a vertical torus on the medial side of the primary girdle plate (this torus is shown in the cross section as a medially directed process).

The pectoral fin must have articulated with the primary shoulder girdle plate in neighbourhood of the little process *g*. No canal for the dorsal fin musculature is developed.

Finally with regard to the primary shoulder girdle plate it is noteworthy that it consists throughout of the same sort of cancellous bone substance as the replacing bones of the neurocranium.

The account and figures given here ought easily to make it clear that the primary shoulder girdle in *Acrorhabdus bertili* is not closely related either to that of the sturgeons or of *Amia* and the Teleosts. While a wide canal for the dorsal musculature is already found in the sturgeons and the development of this has proceeded farther in *Amia* and the Teleosts (GEGENBAUR 1865, pp. 95—135) a canal of this sort is lacking, as we have seen, in *Acrorhabdus bertili*, which in this respect seems to have remained at a primitive Selachian-like stage of development.

The pectoral fins (*Pe*, Pl. 32, fig. 4) are incompletely preserved and consequently no details can be given either as to their shape or size. All their lepidotrichia, except the two or three most anterior ones, are densely jointed right to the base and are furnished with a fine ganoine striation in a longitudinal direction.

The judge from *P. 172* the small ventral fins are situated about half-way between the pectoral fins and the anal fin. They are poorly preserved, and it is only possible to establish that their lepidotrichia were jointed throughout their length.

Squamation.

The squales in *Acrorhabdus bertili* are mostly wider than high, and this is specially strongly marked on the ventral side and towards the dorsum, where their height is sometimes only $\frac{1}{5}$ — $\frac{1}{6}$ of their width. Only immediately behind the posterior part of the supracleithral and the upper part of the cleithral do we find in a couple of vertical

rows some scales whose height exceeds their width (Pl. 32, fig. 2), and ventrally of them there then follow some enlarged scales, which gradually, as they approach the ventral side, become low. In the most posterior part of the caudal region the scales gradually become smaller and almost rhombic.

The scales generally appear to have been fairly thin. Their anterior covered area is relatively wide, at least in the abdominal region. Their dorsal margin has in this region a distinct articulatory spine, apart from the lowest scales farthest dorsally and ventrally. The medial surface on each scale is furnished with a vertical ridge and has, in the usual way, close to the ventral margin, a fossa for articulation with the spine on the nearest ventral scale of the same vertical row. It is impossible to establish with certainty whether the posterior margin was entire or serrated.

The sculpture of the scales consists of striation and is obviously stronger and coarser on the ventral parts of the fish than on the other. On the scales belonging to the ventral side several of the striae are wider than the intervals between them, or at least of the same width. Higher up on the scales of the lateral surfaces of the body the striae gradually become narrower, while the intervals between them increase in proportion. On the scales towards the dorsum, where the striation is finest, the width of the striae is only half to a third that of the intervals, or perhaps even less.

On the majority of the scales the striae can be subdivided into three categories, of which those belonging to the most striking one (Pl. 31, fig. 5; Pl. 32, fig. 2) run across a large part of the exposed surface obliquely backwards and downwards to the lower and posterior margins, gradually becoming narrower as they approach to these margins. On the ventral scales there are only two or three of these striae. On the scales of the lateral surfaces of the abdominal region their number gradually increases to the same degree as the scales themselves increase in height, finally decreasing again towards the dorsum. On the higher anterior scales immediately behind the shoulder girdle they number 16—20 (Pl. 32, fig. 2); somewhat farther posteriorly, on the middle part of the abdominal region, they are 10—12, growing gradually fewer towards the caudal region. On the ventral scales the most ventral of them is bent upwards at the anterior end in front of the others, so that it becomes nearly parallel to the anterior margin. On the scales where the striae of the category in question are more numerous, except on those situated immediately behind the shoulder girdle, the two, sometimes even the three or four ventral striae (Pl. 31, fig. 5) are often bent round in a dorsal direction in the same way, but not infrequently their upward bent parts are not continuous with the other ones but subdivided into a row of somewhat lengthened tubercles. Finally it is noteworthy that the long striae running across the scales never anastomose and that they show a fine corrugation especially on the scales of the ventral side.

The striae belonging to the next category occur only along the posterior margin of the scales between the posterior ends of the previously described ones, and are very short and fine; their number is most often rather great.

Finally the striae belonging to the third category occur farthest anteriorly on the exposed surface of the scales in front of all the rest and pass off downwards from above, parallel to the anterior margin. They are lacking on the scales in a couple of the rows following closest to the shoulder girdle and are also probably not developed

on the scales towards the dorsum either. On the scales of the ventral side they number two or three, on the other scales probably only one, and sometimes at least this single stria may be subdivided into a row of somewhat lengthened tubercles.

As is clearly seen the scale sculpture in the present species has many features in common with that of the *Boreosomus* species and among them specially with *B. arcticus*.

* * *

Remarks. — *Acrorhabdus bertili* is, as we shall see, distinctly separated from the two other species belonging to the same genus by the scale sculpture.

The species name *bertili* is given to the present species after DR. BERTIL HÖGBOM, who, as has been partly mentioned above, has published a number of valuable geological works on Spitzbergen and has brought back fine collections of fossils, among which the vertebrates from the Triassic occupy a very prominent place.

Geological occurrence and localities. *Acrorhabdus bertili* is known only from the fish horizon. The two type specimens *P. 172* and *P. 174* come from the shore south of Sassen Bay and from Mt. Trident respectively. The doubtful specimens were found at Mt. Andersson.

Acrorhabdus asplundi n. sp.

(Pl. 30, figs. 1, 2.)

Only one specimen (*P. 173*) of this species has been found so far, and this is incompletely preserved in many respects. The specimen has been of about the same shape and size as the type specimen of *Acrorhabdus bertili* or perhaps somewhat larger. The state of preservation does not enable us to establish anything as to the general shape of the body.

Visceral skeleton.

The mouth is large, extending, as in the majority of Palaeoniscids, backwards far behind the orbit.

The maxillary (*Mx*, text fig. 76; Pl. 30, fig. 1) is large and long and widened to a plate behind the orbit. In shape this postorbital part is fairly low and triangular, with one margin turned ventrally, one antero-dorsally, and one postero-dorsally; of these margins the last-mentioned one is on the whole weakly convex, while the two others are weakly concave.

The mandible (text fig. 76; Pl. 30, fig. 1) seems to have been rather strong and high, at least in its posterior part, which alone is preserved. Its upper margin is straight and is without any coronoid process. Of the bones there are only fragments of the dentalo-splénial (*De*) and angular (*Ang*).

The preoperculum (*Po*, text fig. 76; Pl. 30, fig. 1) is a strikingly wide, triangular plate and not, as is most often the case, a narrow, arched bone, consisting of two limbs. Of its margins the shortest, which was probably weakly concave, is turned towards the orbit, while the longest one, which is convex, faces dorsally and backwards and comes into contact with the operculum, the suboperculum, and the nearest following branchiostegal radius ventrally of the suboperculum. The remaining margin, which is weakly

concave, joins the postero-dorsal margin of the maxillary. The shape of the preoperculum in the whole bears a striking resemblance, as we shall see below, to that of the Catopterids.

The operculum (*Op*, text fig. 76; Pl. 30, fig. 1) is large and quadrangular in shape, with its shorter margins upwards (antero-dorsally) and downwards (postero-ventrally) and the longer ones forwards (antero-ventrally) and backwards (postero-dorsally) respectively. The upper, posterior and lower ones are weakly convex, the anterior one, on the other hand, is weakly concave. The posterior upper corner is well rounded, while the other corners are more or less well marked.

The suboperculum (*Sop*, text fig. 76; Pl. 30, fig. 1) is low but wide, the area of its surface being only about a third of that of the operculum. It has quadrangular shape but is especially low at its anterior end. Its anterior and upper margins are weakly concave and the posterior and lower ones are weakly convex. The posterior lower corner is rounded; the other corners are well developed.

The radii branchiostegi (*Rbr*, text fig. 76; Pl. 30, fig. 1) are poorly preserved, and it is therefore impossible to establish their number with certainty.

All the bones of the visceral skeleton described have a sculpture of fine striae, most often not particularly long, usually running parallel to the axis of length of the animal. More important deviations from this arrangement are only found on the ventral part of the operculum, where the striae run obliquely backwards and downwards. Other minor irregularities in the course of the striae do not disturb to any extent the impression of the horizontal arrangement of the sculpture.

Text fig. 76. *Acrorhabdus asplundi* n. sp.

Parts of visceral skeleton. After P. 173. $\frac{1}{2}$.
Ang, angular; De, dento-splenic; Mx, maxillary; Op, operculum; Po, preoperculum; Rbr, radii branchiostegi; Sop, suboperculum; orb, orbit.

Dentition.

The maxillary and dental are furnished on the labial margins with small pointedly conical teeth. Nothing else is known as to the character of the dentition.

Skeleton of the shoulder girdle and the paired fins.

Among the membrane bones belonging to the shoulder girdle we find remains of a high supracleithral (*ScI*, Pl. 30, fig. 1) and a fragment of the cleithral (*Cl*, Pl. 30, fig. 1), both of which have a sculpture of the same character as that of the opercular bones and the jaw-bones.

The pectoral fins (*Pc*, Pl. 31, fig. 1) are incompletely preserved. One can see, however, that some of their anterior lepidotrichia, probably as many as 7–8, were unjointed for some distance in their proximal part, and that the anterior margin of the

fins had a row of fulcra. The unjointed lepidotrichia have a sculpture of fine longitudinal striae of ganoine, while the other were probably without any ganoine covering. — Finally it ought also to be added that the joints of the lepidotrichia preserved are considerably longer than broad.

Squamation.

The squamation is very incompletely known, only the middle scales in the 18—20 vertical rows behind the shoulder girdle being preserved (Pl. 30, fig. 1). The scales in general seem to have been rather thin.

As far as can be decided, in a few vertical rows immediately behind the shoulder girdle there were scales that were higher than wide. The majority of the scales present, however, show the opposite condition, i. e. their width is greater than the height.

The sculpture consists of fine striation. The striae are of two sorts: partly such as traverse the exposed surface of the scales right from the anterior to the posterior margin, and partly such as are short and fine, only occurring along the posterior margin. The former kind of striae, which are relatively fine and rather uniformly narrow, occur in small numbers on each scale, and the intervals between them are consequently very wide (Pl. 30, fig. 2). Another characteristic of them is that they pass off nearly parallel to the upper and lower margins and are not situated more or less diagonally or with their anterior parts bent upward as in *Acrorhabdus bertili*. The other type of striae, which is found along the posterior margin, occurs on all the scales present. As shown by Pl. 30, fig. 2, they are short and fine.

* * *

Remarks. — *Acrorhabdus asplundi* is well separated from *A. bertili* especially by the different development of the scale sculpture. Additional differences between them consist in the shape of the operculum, the number of the basally unjointed lepidotrichia in the pectoral fins and the conditions of the sculpture on the lepidotrichia of these fins.

This species is named after my friend Docent DR. ERIK ASPLUND, who took part in the Spitzbergen expeditions of 1913 and 1915.

Geological occurrence and locality. — *Acrorhabdus asplundi* was found in the fish horizon at Mt Andersson.

Acrorhabdus latistriatus, n. sp.

(Pl. 29, fig. 4; Pl. 30, figs. 3—5).

The material present of this species consists only of an incomplete specimen (*P. 170*), considerably smaller than the previously described specimens of *Acrorhabdus bertili* and *Acrorhabdus asplundi*. Apart from this fact no details can be established as to the general shape and proportions of the species.

Visceral skeleton.

The maxillary (*Mx*, Pl. 29, fig. 4) and mandible (*Md*, Pl. 29, fig. 4) are both very incompletely preserved, and it is therefore impossible to observe much about their shape. The mouth was large and extended far back, as in the two preceding species.

The preoperculum (*Po*, text fig. 77; Pl. 29, fig. 4) is, as in *Acrorhabdus asplundi*, a large triangular plate, but is wider than in this species. Its posterior margin is convex, the two other margins are probably concave.

The operculum (*Op*, text fig. 77; Pl. 29, fig. 4) apparently had a similar shape to the one in *Acrorhabdus asplundi*, but it is strikingly higher and has a more vertical position than in this species. Its anterior margin is strongly concave, while the three others are weakly convex. Of the latter the dorsal and caudal ones pass over into each other without any definitive boundary, as the postero-dorsal corner is well rounded. The other corners are well pronounced, and especially noteworthy is that the anterior lower one is here obtuse-angled, while in *Acrorhabdus asplundi*, on the other hand, it is almost right-angled.

The suboperculum (*Sop*, text. fig. 77; Pl. 29, fig. 4) is low and very small compared with the operculum. It is only a little larger than the branchiostegal radii following ventrally of it. Its shape is quadrangular, being somewhat higher posteriorly than anteriorly, but not so much as in *Acrorhabdus asplundi*. As in this species, its anterior and upper margins are weakly concave and its posterior and lower ones weakly convex. All four corners are rounded and the postero-dorsal one is considerably more blunt than in *Acrorhabdus asplundi*.

The branchiostegal radii (*Rbr*, Pl. 29, fig. 4) are very few; their number was probably not above five. Except for the dorsal one they are all incompletely preserved.

The median jugular plate (*Mg*, Pl. 29, fig. 4) is also certainly incomplete too, but it is undoubtedly clear that it was of about the same size as in *Boreosomus reuterskiöldi* (cf. text. fig. 71; Pl. 28, fig. 1).

The sculpture on the above-described bones consists mostly of fine, rather short, sparse striae, principally running in the longitudinal direction of the animal. Along the labial margin of the maxillary and dentalo-splénial the striae are replaced by comparatively small, round tubercles, lying close together. On the median jugular plate a number of median striae pass off in the usual way in a longitudinal direction, but on each side of these on the lateral parts of the plate the striae are arranged so that they run in a postero-lateral direction, and the striae directed so are on the whole more weakly developed than the longitudinal ones.

The skeleton of the shoulder girdle and the paired fins.

Of the shoulder girdle we know with certainty only a part of the supracleithral, which is high as usual (*ScI*, Pl. 29, fig. 4). A fragment of the suprascapular is possibly present as well. Both these bones have been sculptured in the same way as the opercular bones.

The pectoral fins (*Pc*, Pl. 29, fig. 4) are small and triangular. Their lepidotrichia are about 25 in number and are all ramified distally in the usual way. The two or three most anterior ones are unjointed for a short distance proximally; the others, on

Text fig. 77.

Acrorhabdus latistriatus n. sp.

Parts of visceral skeleton after

P. 170, 1/2.

Op, operculum; *Po*, preoperculum;

Sop, suboperculum.

the contrary, are jointed throughout their length, the joints being longer than wide. Ganoine sculpture in the form of fine longitudinal striae occurs on all the lepidotrichia. No fulcra are preserved.

Nothing is known with regard to the ventral fins and the unpaired fins.

Squamation.

As far as is known, the scales (Pl. 29, fig. 4) are mostly wider than high. As in the two other *Acrorhabdus* species, specially low scales are found on the ventral side and towards the back. Only in about the 5 or 6 most anterior vertical rows do we find behind the supracleithral and the dorsal part of the cleithral a number of scales with their height exceeding their width. Backwards, upwards and downwards on the body these scales gradually become lower. A few enlarged scales are found in front of the base of the pectoral fins.

The anterior covered area of the scales was probably fairly wide, at least on those of the abdominal region. The conditions of the upper margin are not known, nor we know whether their posterior margin was entire or serrated.

The sculpture on the present scales is on the whole rather strong. Immediately behind the shoulder girdle and at least on the anterior part of the back, however, it is considerably weaker than on the other known parts of the abdominal region. It consists of striation, and the striae are of two kinds, long ones traversing the exposed part of the lateral surface of each scale from the anterior to the posterior margin, and very short, always fine, ones occurring only along the posterior margin between the posterior ends of the former ones (Pl. 30, figs. 3—5). On the scales of the anterior vertical rows the long striae run rather obliquely in a backward and downward direction, then on the scales following backwards taking up such a position that they become nearly parallel to the upper and lower margins. On the scales present from the dorsum both the short and the long striae are fine (Pl. 30, fig. 5) and, although the latter occur in comparatively great numbers, the interstices between them are large. A similar fine sculpture is also present on those of the scales from the lateral surface of the abdominal region that follow in a couple of the vertical rows nearest to the shoulder girdle. On other scales belonging to the lateral surface of the abdominal region the sculpture is exceedingly characteristic owing to a special development of the long striae (Pl. 30, fig. 3). These, which are present to a number of from 4—8 according to the height of the scales, are rather narrow at the anterior ends but increase rather much in width backwards, finally at their posterior parts beginning to grow narrow again and becoming very much pointed close to their posterior ends. This narrowing towards the posterior ends always takes place rather suddenly, and the posterior fourths of the striae are consequently always separated from one another by rather large interstices, in which are found farthest posteriorly striae of the second kind. With regard to the long striae on the scales in question it is also noteworthy that they are flat and even, and that sometimes two or three of the ventral ones on each scale may have their anterior ends bent upwards more or less parallel to the anterior margins of the scales.

Towards the ventral side of the fish (Pl. 30, fig. 4) the sculpture gradually changes so that all the longer striae become more uniformly narrow, the interstices between their

posterior ends being decreased in width but at the same time extended more forward. The scales on the ventral side seem, with regard to their sculpture, scarcely to differ from the correspondingly situated ones in *Acrorhabdus bertili*. A difference may, however, possibly exist in the number of the longer striae being somewhat greater in *A. bertili* than in the species in question here.

* * *

Remarks. — *Acrorhabdus latistriatus* is characterized especially by its partly unique scale sculpture and is clearly separated by this both from *Acrorhabdus bertili* and *Acrorhabdus asplundi*. As has also been shown by the account given above, it further differs from these two species by a somewhat different shape in certain of the bones of the head.

The scales on the ventral parts in the species under discussion and those in *Acrorhabdus bertili* are so similar that it is impossible to distinguish them with certainty when they occur detached.

The species name *latistriatus* refers to the character of the striation of the scales belonging to the lateral surfaces of the abdominal region.

Geological occurrence and locality. — *Acrorhabdus latistriatus* is so far only known from the fish horizon at Mt Andersson.

The organisation of the Palaeoniscids. Summary.

It is not my intention in this connection to give a complete account of the organisation of the Palaeoniscids, but I shall confine myself chiefly to a summary of the most important results afforded by the Spitzbergen material. In connection with this, however, it has also been necessary to give a summary of a number of scattered observations published during recent years with regard to the osteology or the Palaeoniscids.

The primordial neurocranium and its ossifications.

The primordial neurocranium in *Birgeria* is, as we have seen, low and broad. In the great majority of the Palaeoniscids, on the other hand, to judge from the general form of the head, it cannot have shown the same conditions, but must have been higher and narrower. The snout is always prolonged to some extent and forms a short rostrum. The dorsal surface slopes down rather gently and uniformly forward. The basal surface is only known in any detail in *Birgeria*, where, seen in profile, it is somewhat convex under the anterior part of the orbitotemporal region, becoming concave posteriorly under the posterior part of this region and the anterior part of the labyrinth region. The greatest height of the primordial neurocranium is in *Birgeria* in the middle or posterior part of the labyrinth region.

In the majority of Palaeoniscids the ethmoidal region is high and, in spite of the rostral prolongation, short. No further details are known about it. The orbitotemporal region forms a wide interorbital wall between the large orbits and the cranial cavity has continued through the whole length of this region. Posteriorly the orbitotemporal region passes without any sharp boundary into the labyrinth region and at least in certain forms (*Birgeria*) its ventral part may be pierced by a small fenestration so situated that it partly corresponds to the fenestra optica of the Teleosts. As is usual in fishes,

the labyrinth region forms the widest part of the neurocranium. In *Birgeria* it grows rapidly narrower in its posterior part and in this way passed over into the occipital region, of whose shape and extension nothing is known.

In the primordial neurocranium ossifications are generally found developed (TRAQUAIR, 1877a, p. 16; FRITSCH, 1895, p. 123), but details as to these are only known in *Birgeria* and *Acerorhabdus*.

In both these genera the ossifications, at least in the orbitotemporal and labyrinth region, are considerable and the cartilaginous parts in these regions were therefore relatively small. The ossifications are strong and thick, consisting of cancellous bone substance throughout. No traces of ossificatory centres can be found, nor radiation either. Their periostal lamellae are very weak and thin.

In the occipital region a basioccipital is developed which with its anterior end extended into the posterior part of the labyrinth region. If any other occipital bones were present is not known. The chorda may have extended through the whole occipital region and may also have continued a good bit into the labyrinth region.

In the labyrinth region there are two paired ossifications, the autosphenotic and the prootico-opisthotic, the latter of which probably corresponding not only to the components indicated by its name¹⁾ but to the epiotic as well.

The autosphenotic is a somewhat elongated bone in the postorbital process.

The prootico-opisthotic occupies a considerable part of the lateral wall of the labyrinth region. It extends forward to the canalis facialis, backwards presumably right to the boundary towards the occipital region. Its dorsal parts extend medially into the tectum synoticum, where farthest back they are even so developed that they meet the corresponding ones of the bone on the opposite side in the median line. Otherwise the bone surrounds more or less directly the greater part of the labyrinth and is presumably pierced by n. glossopharyngeus.

The most anterior part of the labyrinth region in front of the prootico-opisthotic has been cartilaginous in the roof, lateral walls and floor, and through this cartilage the roots of n. facialis have their exit from the cranial cavity. From the ganglionic complex of these roots the truncus hyoideomandibularis was given off and took its course for a short distance postero-laterally through the rather wide facialis canal, through whose posterior opening it definitely left the cranial wall. The roots of n. trigeminus, n. ophthalmicus lateralis and n. buccalis lateralis left the cranial cavity just in front of the facialis roots, at the posterior margin of the large unpaired ossification that occupies practically the whole orbitotemporal region. A trigemino-facialis chamber has probably been present, but it is uncertain whether the ganglionic complex of the facialis roots was situated in this together with that of the trigeminus roots.

The large unpaired ossification mentioned in the orbitotemporal region has been called by me the sphenoid according to the terminology of TRAQUAIR 1871, in his description of *Polypterus*. Forward it reaches quite or at least almost to the ethmoidal region and backward right to the cartilage in the anterior part of the labyrinth region. Basally a

¹⁾ It is very noteworthy that in the Coelacanthids too a large paired prootico-opisthotic is present in the labyrinth region. This prootico-opisthotic, however, does not include any epiotic component. It would of course be of great theoretical interest to know the conditions of *Dictyonosteus* in this respect.

part of it, situated behind the fossa hypophyseos, has even extended into the labyrinth region for a short distance, i. e. it belongs to the chordal region of the cranium. In height it reaches from the basis cranii quite or almost up to the cranial roof. It has evidently alone the same extension as, in usual cases, the orbitosphenoid (or orbitosphenoids if they are paired), the alisphenoids, the basisphenoid and an anterior part of the prootic of the Teleosts together, and thus in this respects bears an striking resemblance to the similarly termed bone in *Polypterus* and *Diclyonosteus* (cf. p. 53—61, 120—140 above), but is on the whole considerably more specialized than this, at least in *Birgeria*, in which the conditions are as follows.

The part situated between the orbits grows somewhat thin basally of the cranial cavity, even causing at one place a fenestration, which, as is pointed out above, partly corresponds to the fenestra optica of Teleosts. Just postero-dorsally of this fenestration is situated the foramen opticum and a short distance behind the latter the foramen oculomotorii. The nervus trochlearis has had its exit straight above the fenestration but so high up that its foramen is found about half-way between the basis cranii and the cranial roof. The exit of the trigeminal roots is marked by a large incisure in the posterior margin of the sphenoid (in *Acorrhodus* it is presumably quite enclosed in the sphenoid) and from the anterior wall of this incisure a canal probably for n. ophthalmicus profundus passes off into the lateral wall of the sphenoid for a short distance and has its exit about half-way between the trigeminus incisure and for. oculomotorius. Just in front of and somewhat dorsally of the trigeminus incisure on the lateral surface of the sphenoid there is found the posterior opening of a somewhat coarse canal running in an antero-dorsal direction. This canal is apparently pierced at least by n. ophthalmicus lateralis, which probably had its exit from the cranial cavity just above the trigeminus incisure. Either of the two carotides internae penetrated upwards into its special canal, opening into the cranial cavity just behind and somewhat medially of the foramen opticum on its side. A canalis transversus homologous with that of the *Elasmobranchii* is found strongly developed and situated in the postero-ventral part of the sphenoid, somewhat posterior to the place where this is pierced by the canals for the carotides interna. The aperture of the transversal canal has on each side clearly begun to be affected by the musculus rectus externus, so that we have here a myodome that is as yet in so primitive a stage that it is paired. In the roof of the myodome of each side n. abducens probably had its exit.

The distance between the foramen opticum and the canalis transversus is very much shortened, a condition that has also strongly affected the fossa hypophyseos, so that this has formed a narrow vertical pit in the floor of the sphenoid. Ventrally the fossa hypophyseos opens into the canalis transversus, which indicates that the hypophysis extended into the transversal canal, and that probably the saccus vasculosus may also have been situated there. On the part between the foramen opticum and the transversal canal there issues from the basal edge of the sphenoid towards each side a thin and rather large process, probably representing a basiptyergoid process. Behind the transversal canal the bottom of the sphenoid consisted only of rather thin bone-plate, the basal parachordal plate, with a median oval foramen, possibly representing the remains of the fenestra basicranialis posterior.

The development of the sphenoid clearly shows that the orbitotemporal region in *Birgeria* had definitely entered upon a development in the direction of the higher ganoids and Teleosts, although at the same time it preserved certain primitiva Crossopterygian-like characters. The latter characters consist especially in the presence of a single large ossification and the extension of this ossification basally behind the hypophysis.

We do not know yet whether there were ossifications in the ethmoidal region.

The membrane bones of the neurocranium.

The parasphenoid seems in Palaeoniscids generally to have been large and well developed, and especially the part situated behind the ossification centre is sometimes characterized by a considerable width (TRAQUAIR 1877 a; FRITSCH 1895; JAEKEL 1903; DAY 1915). This part is also at the same time rather short and probably did not as a rule extend backwards as far as to the posterior end of the neurocranium, while the anterior part reaches beneath the ethmoidal region. In the posterior part of the bone there issue on either lateral margin two processes, the anterior one of which is said to be furnished with a facet, against which the palatoquadrate would have articulated (DAY 1915). The posterior process, which is always the most strongly developed, clearly corresponds to the processus ascendens in other ganoids. On the dorsal side of the bone there is sometimes described (JAEKEL 1903; DAY 1915) a fossa or a foramen that seems to have been related the hypophysis.

In *Birgeria* the parasphenoid seems to be of a somewhat different type, a type resembling to some extent the usual actinopterygian one as it is found developed, for instance, in the sturgeons. It has extended posteriorly at least to the anterior part of the occipital region and is on the whole very wide and large. It has only the one processus developed on either lateral margin, and this which is very broad and issues far from the posterior end in such a way as to cover the basiptyergoid processes of its side from the outside. This fact is especially noteworthy as it shows that no articulation can have taken place between the basiptyergoid process and the palatoquadrate. In the posterior end of the parasphenoid we find a deep longitudinal sinus, in which, according to the evidence of comparisons with the sturgeons, the arteria dorsalis was situated. No foramen or fossa related to the hypophysis is developed on the dorsal surface of the bone. On the other hand there issues from this surface on the part situated behind the ossification centre a paired ascending lamella, called by me the profound lamella, which projects into the lateral wall of the primordial neurocranium, where it reaches high up posteriorly.

The posterior portion of this lamella lies between the basioccipital and the prootico-episthotic and is so situated that the labyrinth recess presumably reached to some extent in between it and the prootico-episthotic, probably without coming into direct contact with the latter bone; except perhaps most ventrally the relations between the profound lamella and the cranial cavity cannot be established.

In the profound lamella the parasphenoid has in *Birgeria* a very special character. It is possible that a similar lamella also exists in other Palaeoniscids, although so far it has not been found preserved. Nothing can as yet be said as to its morphological significance.

The processus ascendentes of the parasphenoid in *Birgeria* cover from the lateral sides that part of the wall of the primordial cranium where the trigemino-facialis chamber and the myodome are situated. Perhaps they extended somewhat farther forward, and, if so was the case, an extracranial space would of course be added both to the myodome and the trigemino-facialis chamber, which otherwise seem to be intramural spaces. On the medial side of the process there is a small spine-like formation, whose position and direction suggest that in it we perhaps have the partial homologue of the alisphenoid pedicle of *Amia*, although this may preponderatingly have been of a membranous nature.

With regard to the membrane bones on the cranial roof I have little that is new to add to what has already been shown by TRAQUAIR's investigations, and in order not to repeat previously familiar facts with regard to the configuration of the different bones and their mutual relations I refer to TRAQUAIR's excellent account of 1877 (1877a, pp. 15—16) and WOODWARD's of 1891 (1891b, pp. 423—527). The only fact that needs perhaps be pointed out is that the extrascapulars («supratemporals» TRAQUAIR) are in several cases represented by a single large plate on each side of the median line (*Cheirolepis*, *Boreosomus*).

According to what has been shown by my investigations of the membrane bones of the cranial roof in Crossopterygians (cf. pp. 62—66, 94—98, 102—105, 133—134, 138, text figs. 43, 51, 57, 58) it seems, however, as if a number of alterations ought to be made in the nomenclature used by TRAQUAIR and previous authors. Thus TRAQUAIR's squamosal should correctly be called the supratemporo-intertemporal, a term already introduced by me in my description above. His prefrontal ought to be termed antorbital (ALLIS 1905, p. 491), while his large ethmoid presumably comprises several different elements, among which there are especially the homologues of the nasals, postrostrals and interrostral elements of both sides of the Crossopterygians (cf. GOODRICH 1909, p. 309 and my description of the sensory canals of the cranium below). For the sake of brevity I have called it after its most important components the nasalo-postrostral. According to TRAQUAIR (1877a, Pl. I, fig. 8) no independent rostral elements seem to be present. They may as far as one can understand have fused with neighbouring bones, but as the position of the ethmoidal commissure between the infraorbital canals and the anterior portions of these canals are not known, it is impossible to decide with certainty how the fusions have taken place. It does not seem improbable, however, that a couple of the most medially situated rostral elements from part of the nasalo-postrostral. With regard to the homologues of the lateral rostral plates of the Crossopterygii, it seems as if in the Palaeoniscids, if TRAQUAIR's view is correct, they form part either of the premaxillary or the antorbital of each side, most probably, however, the former.

The labyrinth, as we have seen, has been principally situated in the prootico-episthotic. I have clearly observed the cavities both for canalis semicircularis externus and canalis semicircularis posterior. Otoliths are described in *Palaeoniscus* (HENNIG 1915, p. 52—55), *Amblypterus* (FRITSCH 1895, p. 126; Pl. 122, figs. 1, 3, 4, 5) and *Rhadinichthys* (TRAQUAIR, 1910, p. 127).

Visceral skeleton.

The palato-quadrate seems as a rule to have been triangular in shape. In the anterior part it has a small autopalatine, in the posterior one the metapterygoid and

quadrate are well developed and seem, at least in some cases, to be fused with each other to a single large bone (*Boreosomus*). The metapterygoid has also, at least in certain forms (*Boreosomus*), a blunt antero-dorsally directed process, so directed that it may possibly have articulated with the neurocranium in the posterior basal part of the orbitotemporal region. The autopalatine, metapterygoid and quadrate consist all three, at least in *Boreosomus* and *Acrorhabdus*, of the same cancellous bone substance as the substitution bones of the neurocranium.

Of the membrane bones of the palatoquadrate only the ento- and ectopterygoid are so far known. Of these the entopterygoid often shows the same conditions as in Crossopterygians, its postorbital part being high and covering the whole metapterygoid and a large part of the quadrate on their medial surfaces (*Boreosomus*). The postorbital part of the entopterygoid may sometimes, however, be represented by a number of mutually independent plates (*Acrorhabdus*), and then the transition between this part and the anterior part takes place gradually. In my opinion we are concerned in the latter case with a secondary phenomenon, the posterior part of the bone being reduced. If this reduction process were continued so that the posterior part disappeared, the remaining anterior part would correspond fairly well to the metapterygoid in Teleosts and higher ganoids.

The ectopterygoid is in most cases a long and narrow bone reaching backwards in a caudal direction to and covering the medial side of the ventral part of the quadrate. In *Birgeria* it has had, at least in its anterior part, a lateral lamella covering another lamella from the medial side of the maxillary, a character that possibly occurs in Palaeoniscids in general (TRAQUAIR, 1877a, p. 18). The maxillary is always high behind and low beneath the orbital entrance. As I have pointed out above (p. 139), and as I shall show still further below (see my account of the Saurichthyids in Part II), it probably comprises not only the homologue of the maxillary of the Rhipidistids but at least also the homologue of their quadratojugal, so that it ought really to be called the maxillo-quadratojugal. It is also conceivable that the homologues of certain of the squamosal elements of the Rhipidistids have been fused with it, which could naturally be decided with a somewhat great degree of probability if one knew the position of the «pit-lines» of sensory canal organs that were presumably developed on the cheek (cf. also ALLIS, 1919a, pp. 374—382, 385—386).

The mandible is always long and has a straight upper margin. Its cartilage may, at least in certain forms (*Boreosomus*), have been occupied by a single long ossification of a cancellous structure. This ossification, which extends from the anterior to the posterior end of the mandible, has on its dorsal surface the articulatory fossa for the quadrate, and on the lateral side in front of this another fossa in which the musculus adductor mandibulae was inserted; according to its extension and relations it thus seems to comprise the homologues of the articular, autangular, mentomandibular and possibly the autocoronal as well.

The bone described by TRAQUAIR (1877a) as the articular is apparently a supraangular according to the prevalent terminology.

Besides this supraangular the lateral side of the mandible is covered by an angular and a large dentalo-splénial. The latter, as indicated by its name, is, as far as can be judged, a complex bone (cf. also SCHLEIP, 1904, pp. 398—399). It is pierced ven-

trally by the mandibular canal and should therefore comprise not only the homologue of the dental of the Rhipidistids but also that of the splenial, and possibly also those of certain of the elements following between this and the angular.

The medial side of the mandible is covered with a single large and long coronoid element, for which I have suggested the name mixicoronoid, as it presumably includes homologues of several of the elements that are found independent in Tetrapods and Rhipidistids.

The hyomandibular is always large and well developed, but at least generally it is ossified mainly perichondrally. Like other cartilage bones of the hyoid arch it too has had cartilaginous epiphyses. As a rule it is somewhat angular, in such a way that its angle is directed backwards and enters more or less closely into contact with the operculum or the operculum and the suboperculum (TRAQUAIR, 1877a). While the majority of forms seem to show these primitive conditions, we find in *Boreosomus* and *Acrorhaddus* a large, well developed processus opercularis issuing from the angle on the posterior margin, which must of course mean that the musculature of the gill-cover was developed in this two genera in about the same direction as in the higher ganoids and Teleosts. Neither in *Boreosomus* nor in *Acrorhaddus* have I found the hyomandibular pierced by any canal for the truncus hyoideomandibularis facialis. On the other hand I found a canal of this sort in *Gyrolepis*. The hyomandibular is in most cases situated very obliquely in such a way that the axis of length through it runs from above and from in front downwards and backwards; it is less frequently vertical or almost vertical.

An ossified little symplectic is found in *Acrorhaddus* and in the so-called *Oxygnathus brownii* (BROOM, 1909a). On the other hand no stylohyal is shown as yet with certainty.

In the middle part of the ceratohyal there always occurs a large hour-glass-shaped perichondral diaphysis of bone. There are indications, however, that the cartilaginous epiphysis situated caudally of this had also begun to be ossified, i. e. we have here presumably the earliest known homologue to the bone in higher ganoids and Teleosts that has been incorrectly called the epihyal (cf. GAUFF, 1904, pp. 902—904).

The preoperculum is generally a curved bone consisting of two shanks, a vertical narrow one, situated behind the maxillary, and a more or less horizontal and wider one lying dorsally of the maxillary and reaching far along towards the entrance of the orbit, thus covering a rather considerable portion of the postorbital part of the cheek. The bone under discussion may, however, be also developed in the form of a large, wide triangular plate (*Acrorhaddus*), by which, as we shall see, it bears a great resemblance to that of the Catopterids.¹⁾

In certain species, as, for instance, in *Cheirolepis trailli* AGASSITZ (TRAQUAIR, 1875 b, Pl. 17, fig. 7, bone y), *Elonichthys pectinatus* TRAQUAIR (TRAQUAIR, 1901, pp. 83, 84, fig. 1, bone x) and the so-called *Oxygnathus brownii* (BROOM, 1909a, p. 259), there occurs between the forward directed shank of the preoperculum and the operculum a long and narrow bone, element, which occupies such a position that it may perhaps have been pierced

¹⁾ In *Rhadinichthys argentinicus* TORNQUIST the reconstruction given by TORNQUIST (1904, pp. 346—351) seems to be incorrect, at least as regards the shape of the preoperculum. For as far as can be seen from TORNQUIST's own figure of the type specimen (Pl. 36), the preoperculum had two shanks, although the vertical one seems to be poorly preserved.

by the preopercular sensory canal in a longitudinal direction. If this were the case, it would, in the species in which it is not present as an independent element, be fused with the bone elements lying in front of it on the cheek, as in such forms the preoperculum, according to what we now know, should have been pierced by the preopercular canal along the posterior margin.

Assuming that the above-mentioned narrow skeletal element was pierced by the preopercular canal, we should also have a very strong argument in favour of the view that a part of the forward directed shank in the bone previously called the preoperculum should correspond to certain of the squamosal elements of the primitive Rhipidistids (cf. pp. 76—79, 139).

The operculum and the suboperculum vary a great deal in shape and size in different genera, as TRAQUAIR pointed out in detail already in 1877 (1877 a). Sometimes (*Boreosomus*, *Acrorhabdus*) the suboperculum may be so low that it shows almost the same conditions as a branchiostegal ray.

The radii branchiostegi vary in number and are sometimes (*Boreosomus*, *Acrorhabdus*) very few, probably not more than 5. Anterior to them between the two mandibulæ there is, at least in most forms, a median jugular plate, which, curiously enough, in certain forms is very large (*Boreosomus*, *Acrorhabdus*).

The gill-arches are at least in several forms strongly ossified (TRAQUAIR, 1877 a, p. 22; FRITSCH, 1895, vol. 3, p. 79). Four pairs have so far been observed, but it is probable the a fifth existed too. At least in *Birgeria* and *Acrorhabdus* the hypo-, cerato- and epibranchial are found ossified in the first three pairs. In *Birgeria* pharyngobranchials have also been found to exist in the two anterior pairs of arches, although with the exception of infrapharyngobranchial II, which is represented by a comparatively large ossified element, they were cartilaginous. In the fourth pair of arches only a ceratobranchial is known so far. All the cerato- and epibranchials have a comparatively deep longitudinal furrow on their posterior surface.

The basibranchials have formed a long row between the ventral ends of the gill-arches in the usual way and are occupied partly by ossifications (cf. FRITSCH, 1895, vol. 3, p. 79). In *Birgeria* three of these ossifications are shown to exist, but it is not impossible that an additional one may have been present. On the dorsal surface the basibranchials are covered with tooth-bearing bone plates of membranous origin.

Supporting gill-rays are sometimes calcified or ossified and could therefore be preserved (*Acrorhabdus*, *Birgeria*). In *Acrorhabdus* a number of them situated in a single row occupy such a position in relation to the opercular bones and the hyoid arch that they must have belonged to a hyoid gill, which has been large.

Dentition.

With regard to this I have very little here to add to our knowledge, and I can therefore merely refer to TRAQUAIR's description of 1877 (1877 a, pp. 32—33; cf. ALLIS, 1919 a, pp. 374—377).

The sensory canals of the head.

The sensory canals of the head are fine and, apart from the lines of the pit organs, situated within the bones. They open outwards with a large number of fine tubuli, which seem in most cases to be straight and unramified.

The supraorbital canal has its posterior end situated in the middle or posterior part of the parietal, from which it passes off anteriorly, entering the frontal, which it pierces in a longitudinal direction. Anteriorly of this bone it looks as if it should enter the antorbital, but the part of the sensory canal situated in the latter bone continues forward laterally of the nasal aperture, and should most probably belong to the infraorbital canal and correspond to the upper end of the infraorbital section of this canal (ALLIS 1905, p. 491; cf. also ALLIS 1919 a, p. 375). This view is also supported by the fact that this part of the sensory canal presumably communicated with the infraorbital canal, as is the case in the closely related Catopterids (cf. text figs. 80, 81, 85, 86). If this is correct, the most anterior part of each supraorbital canal must of course be reduced or else have a pit-line on the nasalo-postrostral corresponding to it.

The infraorbital canal forms, as usual, a direct anterior continuation of the cranial section of the main lateral canal. It runs forward through the anterior part of the supratemporo-intertemporal and from this bone enters the dermosphenotic with a gradual bend to the lateral side. From the dermosphenotic it probably entered the infraorbitals, in which it continued first downwards and then forwards. No further details of its course in these bones are, however, known. No anastomosis is developed between its posterior part and the supraorbital canal, as in Teleosts, recent higher ganoids, and sturgeons.

Of the preopercular canal only the dorsal end has been observed so far (*Boreosomus*), and this end is situated in the supratemporo-intertemporal, where it anastomoses with the infraorbital canal and the cranial section of the main lateral canal at the place where these two pass over into each other. In its downward course it may have entered the preoperculum, where, as far as we can judge from the conditions in the closely allied Catopterids, it ought to have been situated fairly close to the posterior margin. It is not known whether it anastomosed with the mandibular canal.

I have distinctly observed the mandibular canal in a number of forms. It is situated rather near the posterior and ventral margins of the mandible and pierces both the angular and the dentalo-splénial.

The cranial section of the main lateral canal of the body extends through the lateral extrascapular or the lateral part of the extrascapular plate (if only a large paired plate is present on each side of the median line) into the supratemporo-intertemporal, where, as has been mentioned, it is continued without interruption by the infraorbital canal. Between the cranial sections of the right and left sides there is a distinctly developed supratemporal commissure, situated in the usual way in the extrascapulars (*Boreosomus*; *Elonichthys*, TRAQUAIR 1901, p. 83).

Only one head line of pit organs could be observed (*Boreosomus*). This one, which is situated on the parietal, is rather short and is situated transversally in relation to the axis of length of the head and seems to correspond to the middle one of the three lines of pit organs found in *Amia* and many recent Teleosts. Nothing is known as yet with regard to cheek lines of pit organs.

AXIAL SKELETON.

The chorda dorsalis has been well developed and does not seem to have been affected to any noticeable extent by the formation of vertebral bodies.

In each neural arch are found two paired skeletal elements, a small and weak interdorsal, and behind this a large and high basidorsal, both of which were ossified in *Birgeria*. In other forms the basidorsals alone seem as a rule to be ossified. The slender unpaired neural spines are always ossified and seem as a rule to be developed in the whole abdominal region, so that the most anterior of them are often found under the anterior part of the dorsal fin. It is true that they enter into contact with the distal parts of the basidorsals, but they are so situated in relation to these that they seem to represent the distal parts of the interdorsals, or perhaps, to express it better, they belong, like the interdorsals, to the anterior halves of the sclerotomes.

Ventrally of the chorda we find, at least in the caudal region of *Birgeria*, a large paired bone-plate for each segment. This bone-plate has probably arisen from a fusion of the interventral and a proximal part of the basiventral. The distal part of the basiventral, on the other hand, is probably represented by the long haemal spine.

It is very noteworthy that from each of the large haemal bone-plates of *Birgeria* a broad structure of very cancellous bone issues in a dorsal direction, forming with that of the opposite side a semicircle around the ventral half of the chorda. The formation of vertebral bodies is thus begun and, like TRAQUAIR (1877 a), I consider it probable that this is the case in *Pygopterus*, but it does not seem impossible that we have there instead the interdorsals extended downwards. Finally vertebral body structures are also described by FRITSCH (1895, pp. 92, 94) in *Sceletophorus* FRITSCH and *Phanerosteon* TRAQUAIR, but at least in the case of the latter genus it seems as if FRITSCH has made a mistake, as TRAQUAIR (1911 a, p. 166) states that he did not find any traces of them there.

In the majority of forms indications of vertebral bodies seem to be quite lacking as in *Palaeoniscus* (TRAQUAIR 1877 a, p. 23), *Phanerosteon* (TRAQUAIR 1911 a, p. 166), *Psilichthys* (HALL 1900, p. 147), *Coccolepis* (WOODWARD 1891 b, p. 426; 1895 a, p. 6, Pl. 1, fig. 1; Pl. 2, fig. 4; 1915, p. 24; TRAQUAIR 1911 b, p. 13), *Apateolepis* (WOODWARD 1890 a, pp. 13—14) and *Elpisopholis* (WOODWARD 1908 a, p. 19).

Ribs have not been ossified in any of the forms so far known.

The skeleton of the unpaired fins.

The skeleton of the unpaired fins is well known on the whole (TRAQUAIR, 1877 a, pp. 24, 26—28; WOODWARD, 1891 b, pp. 426, 427; 1895 a, pp. 6, 7; 1908 a, pp. 19, 20; HALL, 1900, pp. 146, 147; ABEL, 1919, pp. 184, 185; etc.) and in this connection I need only point out a few details.

In most Palaeoniscids the dorsal fin is situated far back. In *Boreosomus* and *Acro-rhabdus*, however, we have also become acquainted with forms in which it is opposite the ventral fins or even has its anterior half extended in front of these. Its endoskeletal radials are represented as a rule by two longitudinal rows of ossifications, of which the proximal ones are known as axonosts, the distal ones as baseosts. As far as we know, the only exception to this is *Coccolepis*, in which so far it has not been possible to show any baseosts with certainty.¹⁾

¹⁾ In a specimen of *Coccolepis bucklandi* AGASSIZ belonging to the Alte Akademie of Munich I think, however, I was able to find traces of baseosts as well.

The axonosts probably correspond to the proximal and the baseosts to the middle segments of the endoskeletal radials. The distal segments must evidently have been small and cartilaginous.

In *Phanerosteon* (TRAQUAIR, 1911a, p. 167) and *Birgeria* the axonosts and baseosts of the dorsal fin are of about the same length, which seems to mean that the proximal and distal segments of the endoskeletal radials were equally long, a condition that, according to SCHMALHAUSEN's investigations (1912; 1913a; 1913b), ought to be considered as rather primitive. In other forms, on the contrary, the axonosts are more or less longer than the baseosts (*Psilichthys* HALL, 1900; *Elpisopholis* WOODWARD, 1908a, etc.), i. e. the proximal and the distal segments in the endoskeletal radials show conditions more like those in higher ganoids and Teleosts.

In the endoskeletal radials of the anal fin as a rule only one long ossification seems to be present in each radial. In *Elpisopholis*, however, WOODWARD (1908a) has shown both axonosts and baseosts in all the radials of the fin in question and in *Birgeria* too I found both these elements, though only in a number of the most caudal radials. The remaining endoskeletal radials of this fin have a single long ossification in the usual way.

Both in *Elpisopholis* and *Birgeria* the baseosts of the anal fin are rather short compared with the axonosts. Whether the baseosts have fused with the axonosts to the single long element of bone usually found in the endoskeleton of the fin or whether they are more or less reduced and cartilaginous, it is of course not easy to say with certainty. It appears to me, however, at present most conceivable that the former alternative is the more probable one.

The ventral lobe of the caudal fin is always supported by a number of haemal spines. Under the large fulcra of the dorsal lobe is regularly found a series of endoskeletal radials (SCHMALHAUSEN, 1912, 1913a, 1913b), which are in an unusually distinct state of preservation in *Coccolepis australis* WOODWARD (WOODWARD, 1895a, Pl. 2, fig. 4).

The lepidotrichia in all the unpaired fins are always densely placed and are generally jointed throughout their length, except in *Birgeria*, in which a proximal, shorter part is unjointed.

The skeleton of the girdles and the paired fins.

The skeleton of the primary shoulder girdle is only known in *Acrorhabdus*, in which it is represented by a plate, ossified in one piece. This plate in pierced in a dorsi-ventral direction by a nerve canal. No canal for the dorsal musculature of the pectoral fin has been developed and the plate as a whole seems in this respect to show the closest resemblance to the girdle in the Selachians. As in the substitution bones of the primordial neurocranium the bone substance is cancellous throughout.

The membrane bones of the shoulder girdle are developed in the usual way. With regard to the clavicolae (infraclavicolae, TRAQUAIR, WOODWARD and other palaeoichthylogues) it is, however, noteworthy that they may be developed almost in the same way as in *Acipenser ruthenus* and *Acipenser sturio*. We find, inter alia, in *Acrorhabdus*, a sinus on their dorso-medial margin situated at exactly the same place as in the two sturgeon species mentioned, in which, according to VETTER (1878), the sinus is related to a posterior

portion of the musculus coraco-arcualis. By analogy we may thus be justified in concluding that a similar portion of this muscle occurs in *Acrorhabdus*.

It is also noteworthy that between the anterior portion of the musculus coraco-arcualis of the right and left sides in *Acrorhabdus* there was a well developed urohyal (basibranchiostegal), as in Teleosts and Coelacanthids.

I have nothing important to add about the development of the pectoral fins.

The pelvic girdle is known so far only in *Birgeria*, where it consists of a fairly large bone, expanded in the postero-distal part. This bone shows no indications at all of division into segments, as in the sturgeons. It probably comprises not only a component homologous to the pelvis of the Cladodontids and Pleuracanthids but also a component that in these forms is represented by the proximal segments of the anterior endoskeletal radials.

Behind the pelvic plate and following immediately upon it there must have been either a single long metapterygeal element or a series of several small ones, which were cartilaginous. The endoskeletal radials, which were probably about 16 in number, articulated against the pelvic plate and the metapterygeal elements just mentioned. Only the 4—5 most anterior ones, however, articulated against the pelvic plate. The all consist of a long proximal and a short distal segment, the former of which is always ossified, while the latter only shows ossification in some of the middle endoskeletal radials. A row of ossified proximal segments of endoskeletal radials is known in addition in *Coccolepis* (WOODWARD, 1895a, 1898a; TRAQUAIR, 1911b) and *Elpisopholis* (WOODWARD 1908a).

The lepidotrichia of the ventral fins are generally jointed right to their bases. An exception to this is seen, however, in *Birgeria*, where at least a large number of the anterior ones are unjointed in their proximal parts.

Squamation.

As we now know, the Palaeoniscids show considerable variation with regard to the development of the squamation. Thus in *Chryphirolepis* (TRAQUAIR, 1907, p. 104—106) and *Coccolepis* (TRAQUAIR, 1911b, p. 11—15) the scales are cycloid apart from those covering the dorsal lobe of the caudal fin, and in *Birgeria*, *Psilichthys*, *Elpisopholis* and *Phanerosteon* the scales are quite reduced except for the dorsal lobe of the caudal fin, where they are constantly retained.

Main lateral canal of the body.

In *Birgeria* we find the lateral line of the body enclosed in small tubular bones lying in a continuous longitudinal row. In *Elpisopholis* (WOODWARD, 1908a, p. 20) it is situated in a row of <-shaped small shields. On the upper lobe of the caudal fin it passes off along the ventral margin of the axis, i. e. close to the bases of the lepidotrichia, as in the sturgeons.

* * *

Some general remarks.

As we see, the Palaeoniscids include forms that have attained rather different degrees of specialization. Such genera as, e. g. *Acrorhabdus* and *Boreosomus* much

resemble the Catopterids, to which they appear to be transitional forms, while others, on the contrary, such as *Cheirolepis*, *Rhadinichthys* were probably more primitive.

WOODWARD (1891 b, p. 425), and FRITSCH (1895, p. 126) have supposed that the family *Palaeoniscidae*, when better known, ought to be subdivided, and GREGORY (1907, p. 463) considered later on that he ought also to emphasize its heterogeneous nature. «It is noteworthy», he says, «that the early Heterocerchi, commonly grouped together in the family *Palaeoniscidae*, include forms (e. g. *Cheirolepis*, *Holurus*, *Coccolepis*) which are so different in several important respects that they might almost be regarded as types of different families».

Against this it must, however, be pointed out (cf. TRAQUAIR, 1911 b, p. 8) that, according to what we now know, the *Palaeoniscids* show on the whole a rather uniform type of organization. In spite of the fact that they comprise certain forms that appear to be specialized in some respects, yet a subdivision of them into two or more separate families would mean the breaking of strong phylogenetic bonds or at any rate cause difficulties in denoting the close relationship that undoubtedly exists between them. On the other hand, however, we can scarcely be justified in going so far as ABEL (1919, pp. 186—190), who includes the Catopterids among the *Palaeoniscids*. We should then be justified with about the same right in adding to the family *Palaeoniscidae* in the definition given to it by ABEL, the *Platysomids* as well, since these, as we know (TRAQUAIR, 1879, pp. 379—389), must be considered as originating from the *Palaeoniscids*, to which in any case they seem to be very closely related.

The relation between the *Palaeoniscids* on the one hand and the *Saurichthyids* (*Belonorhynchids*), *Chondrosteids*, *Acipenserids* and *Polyodontids* on the other cannot be discussed until later on in connection with my description of the Catopterids and the *Saurichthyids* (Part II). Here, however, I may point out that, with regard to the development of the membrane bones on the dorsal side of the ethmoidal region and of the supraorbital sensory canal, the *Palaeoniscids* show special conditions which are without parallel among the *Actinopterygii* except for the *Platysomids* and Catopterids. These facts are of special interest as they seem to controvert the view upheld especially by WOODWARD (1889 c, pp. 42—43; 1895 b, pp. V—VIII; 1898 a, pp. 82—95; 1915 a, p. LXXII—LXXIV) and after him by GOODRICH (1909, pp. 307—321) that *Chondrosteids* and recent sturgeon fishes are directly descended from the *Palaeoniscids*.

Finally for a large number of other conditions with regard to the *Palaeoniscids* I may refer to my account given below.

Family *Platysomidae*.

General remarks.

Right up to quite a recent date the *Platysomids* were known exclusively from the Carboniferous and Permian formations (TRAQUAIR 1879; ZITTEL 1887—1889; WOODWARD 1891 b: 1898 a; KROTOV 1904). In 1913, however, BROOM (1913 a) was able to show the existence of a species in the Lower Triassic of South Africa and the following year LAMBE (1914)

described a species from Canada in deposits that might also possibly be of Lower Triassic age. Finally a *Platysomid* form, described by WOODWARD 1910 (1910 b) from Madagascar, may be of Lower Triassic age as well (cf. LEMOINE 1911, pp. 5—6).

To these I have now to add at least two species of *Platysomids* found in the Lower Triassic of Spitzbergen. As far as can be judged from the fragmentary material present, they both resemble *Platysomus*, so that provisionally I have referred them to this genus.

It is noteworthy in this connection that both one of the species from the Triassic of Spitzbergen, *Platysomus nathorsti*, and the Canadian species that LAMBE took to be a *Platysomus* and called *Platysomus canadensis*, have attained an exceedingly large size.

Genus *Platysomus* AGASSIZ.

The genus *Platysomus* occurs both in the Carboniferous and the Permian. In Europe it appears in the latter formation together with *Globulodus* (WOODWARD 1891 b, p. 534) and *Dorypterus* (ZITTEL 1887—1889, pp. 250—252; REIS 1891, pp. 167—170). From the possibly Lower Triassic strata in Madagascar WOODWARD (1910 b, pp. 2—5) has described the new genus, *Ecrinesomus*, which, at least with regard to squamation, closely resembled *Platysomus* (cf. ANDERSSON 1916 b, pp. 227—229).

The supposed Triassic species *Platysomus canadensis* seems, according to the description given by LAMBE (1914) to differ rather essentially from the usual type of the genus *Platysomus*. The most important differences are (1) the general shape of the body, (2) the position of the pectoral fins high up on the sides of the body, (3) the close agreement in the number of the lepidotrichia and the endoskeletal radials of the dorsal and anal fins, (4) the sculpture of the scale, which is said to consist of «pustules». LAMBE considers, it is true, that the characters enumerated here only have a specific value, but I do not feel convinced that this is the case, but think it more probable that we are concerned with a representative of a new genus.

The two *Platysomus* species from the Triassic of Spitzbergen are still very incompletely known and, as already pointed out, I have only included them provisionally in the genus *Platysomus*. The smaller of them, which I shall describe below as *Platysomus* sp., seems to some extent to resemble *Ecrinesomus*.

Platysomus nathorsti n. sp.

(Pl. 27, fig. 4; Pl. 28, fig. 2; Pl. 32, fig. 1).

This species is so far only represented with certainty by some fragments with scales, remains of fins and basidorsals (P. 141, P. 142). A number of detached scales of rather varying size also possibly belong to it (P. 203 b, P. 692, P. 693, P. 879).

The species has attained a very considerable size. Certain of the larger scales are thus 85—90 mm high and 18—25 mm wide. By way of comparison we may mention that the larger scales in *Platysomus canadensis*, which is more than a metre in length, are only 65 mm high and 22 mm wide.

The basidorsals, of which only the proximal ends are preserved, seem to have resembled most closely those in *Birgeria*.

As far as can be judged the lepidotrichia are without ganoine covering and are unjointed for a short distance at their proximal ends. Otherwise they seem to have been densely jointed. The joints vary somewhat in shape. Thus sometimes they are wider than long, sometimes, on the other hand, they are somewhat longer than wide.

The scales (Pl. 27, fig. 4; Pl. 28, fig. 2; Pl. 32, fig. 1) are of the usual type characteristic of the *Platysomids*. The dorsal margin has close to the anterior end a well developed, sharply marked off articulatory spine. The anterior covered area of the lateral surface is fairly narrow, as it ought to be in *Platysomus*. On the medial side there is close to the anterior margin a well marked rounded ridge, whose upper end extends into the above mentioned articulatory process on the dorsal margin (Pl. 28, fig. 2). It is noteworthy that the ridge is widest and most robust at its middle parts. Just behind the ventral part of this ridge we find, at least on certain scales, the usual articulatory fossa. The posterior lower corner on all the scales has an obtuse angle. The anterior lower and posterior upper ones are most often acute-angled, but may also in certain cases be almost right-angled. The posterior margin is straight and not denticulated.

The sculpture of the scales (Pl. 32, fig. 1) consists of a number of extremely fine striae lying close together and running from above downwards and somewhat forwards. As a rule they are weakly undulating but may also at a number of places make more abrupt curves and exhibit some irregularities in the arrangement. On certain scales a few striae are also found directed along the upper and lower margins, while the great majority are in the normal position.

* * *

Remarks. — This species is well characterized both by its considerable size and the sculpture of its scales. I have named it after the late Professor A. G. NATHORST, whose contributions to the investigation of the geology of Spitzbergen are too well known to make it necessary for me to give any detailed reasons for this step.

Geological occurrence and localities. — Specimens *P. 141* and *P. 142* come from the fish horizon at Mt Trident. The detached scales (*P. 203*, *P. 692*, *P. 693*, *P. 879*), that I have hesitatingly included here, come partly from the fish horizon, partly from strata immediately below that. The localities were Mt Trident, Sticky Keep and Mt Marmier.

Platysomus sp.

Under this heading I place only one specimen (*P. 140*), which is poorly preserved and incomplete on the whole. In its present state of preservation it measures about 16 cm in length without head and caudal fin. One might venture to estimate the total length at close on 25 cm. As far as can be seen the greatest height is about 11 cm and the fish has thus the general shape characteristic of the *Platysomids*.

The dorsal fin is very long and consists of a large number of lepidotrichia, but no details as to the nature of these can be given. Some of the ossified middle segments (baseots) of the endoskeletal radials are preserved. They are rather short and somewhat hour-glass-shaped. Nothing can be established as to their number in relation to the lepidotrichia.

Of the pectoral fins — presumably rather well developed — only a few lepidotrichia and endoskeletal cordials are present; as will be seen, the lepidotrichia are unjointed, at least in their proximal and middle thirds. It is also noteworthy in this connection that the pectoral fins possibly had a rather high position.

The scales are partly poorly preserved, partly weathered, so that nothing certain can be discovered as to their shape. Along the anterior margin, however, their medial surface had a relatively robust ridge. The sculpture consists of dense striae running as usual downwards and somewhat forwards. The striae are, however, thicker, fewer, and the whole considerably straighter than in *Platysomus nathorsti*, to which it may be added that none of them has been found parallel to the lower or upper margin of the scales as in this species.

* * *

Remarks. — The specimen *P. 140* just described is clearly distinguished from *Platysomus nathorsti* by its scale sculpture. It presumably represents a new species. But until more material is available I have only placed it under the heading *Platysomus* sp.

The species seems to differ from *Platysomus* in the high position of the pectoral fins, and by the development of the lepidotrichia of these fins, and because of this it may probably with better preserved material turn out to be a representative of a new genus. With regard to the high position of the pectorals the fish resembles to some extent *Ecrinosomus*.

Geological occurrence and locality. — Fish horizon, Mt Trident.

Family Catopteridae.

Historical remarks.

The family *Catopteridae* was established by WOODWARD 1890 (1890a, pp. 15–16) for the Triassic genera *Catopterus* J. H. REDFIELD and *Dictyopyge* EGERTON. While these genera were at that time generally placed together with *Acentrophorus* and *Semionotus* among the so-called «Lepidosteids» (cf. TRAQUAIR 1877 b, p. 565–567; ZITTEL 1887, p. 203; NEWBERRY 1888, pp. 50–65; etc.), WOODWARD was now able to show convincingly that their characters, although incompletely known, indicated instead a close relationship to the Palaeoniscids. For these reasons WOODWARD maintained that the family *Catopteridae* ought to «be assigned to whatever great subdivision of the «Ganoids» is made to include the Palaeoniscids and their allies». In 1895 (1895b, pp. V–VIII and pp. 1–9) he grouped the families *Palaeoniscidae*, *Platysomidae*, *Catopteridae*, *Acipenseridae* and *Polyontidae* in the sub-order *Chondrostei*.

In 1901 SCHELLWIEN (pp. 17–28) put forward the view that the species described as *Semionotus letticus* O. FRAAS and *Semionotus altolepis* DEECKE really showed a number of peculiarities that were incompatible not only with the genus *Semionotus* but also with the family *Semionotidae* and the *Protospondyli* in general. SCHELLWIEN also expressed the view that the two species most probably ought to be referred to the Catopterids. In accordance with this DE ALLESSANDRI (1910, pp. 49–51) in his monograph on Triassic

fishes of Lombardy placed his new genus *Perleidus*, based on the so-called *Semionotus altolepis*, in the family *Catopteridae*.

The majority of the modern authors, such as SCHELLWIEN (1901, loc. cit.), EASTMAN (1904, pp. 95—100; 1911, pp. 46—57; 1914 a, pp. 139—146; 1917, pp. 279—280), GREGORY (1907, p. 448), GOODRICH (1909, p. 313), DE ALESSANDRI (1910, loc. cit.), KOKEN (1911, p. 102), SCHLOSSER (1918, p. 100), etc. have, like WOODWARD, looked upon the *Catopterids* as an independent family. Recently, however, ABEL in his large work «Die Stämme der Wirbeltiere» (1919, pp. 187, 189) has grouped them with the *Palaeoniscids*.

In the definition that the family *Catopteridae* has had up to now, it has only comprised, as has been shown, the genera *Catopterus*, *Dictyopyge* and *Perleidus*.

In 1916 I was able myself to observe a considerable agreement between the genus *Colobodus* AGASSIZ on the one hand and *Palaeoniscids* and *Platysomids* on the other (ANDERSSON 1916 a, pp. 17—25). I accordingly assigned to *Colobodus* a close relationship with the *Catopterids*, although under the conditions then present I did not consider that I could refer it to these, but established a new family *Colobodontidae* for it. With this family I then incorporated provisionally the new genus *Meridensia*.

In a work on the Ganoids of the German Muschelkalk, published in 1920, STOLLEY (pp. 25—86) has grouped the genera *Colobodus* s. str., *Nephrotus* H. v. MEYER, *Crenilepis* DAMES and *Dollopterus* ABEL into one family, which he also calls *Colobodontidae*.¹⁾ This family, according to his opinion, would form (p. 45) «einen zusammengehörigen Formenkreis, der ganz vorwiegend den germanischen Muschelkalk charakterisiert und in keine der bisher unterschiedenen Familien hineinpaßt. Durch die Ausbildung der Kopfknochen einerseits an *Palaeonisciden* und *Platysomiden* erinnernd, zeigt er andererseits auch vorgeschrittenen, den *Orthoganoiden* ähnlichen Charakter und verdient zu einer besonderen Familie zusammengefaßt zu werden, die füglich den Namen der *Colobodontidae* zu tragen hat. Diese Familie kann im geltenden System nicht mehr den *Heterocerci* als jüngste und vorgeschrittenste Familie eingefügt werden, da sie eben keine heterozerke Schwanzflosse mehr besitzt, sondern muß den *Orthoganoiden* als erste und primitivste, die Verknüpfung mit den *Heterocerci* herstellende Familie eingereiht werden, gefolgt von den *Semionotiden* und den älteren wie jüngeren *Lepidotiden* im hier präzisierten Sinne dieser letzteren Familie (pp. 76—79).»

He feels very doubtful as to whether the genus *Perleidus* really belongs to the family *Catopteridae* or *Colobodontidae* and in this connection writes as follows on the relations between these two families (p. 65): «Wenn *Catopterus* und *Dictyopyge* in der Ausbildung der maßgebenden Kopfknochen entsprechend beschaffen sein sollten, wie *Perleidus altolepis* und ?*P. letticus*, so dürfte für alle diese Formen der Familienname *Catopteriden* berechtigt sein und die Stellung dieser Familie würde dann entfernt von den *Semionotiden* und *Lepidotiden* in der Nähe der *Colobodontiden* zu wählen sein, zwischen diesen und den altertümlicheren *Palaeonisciden* der *Heterocerci*.»

I have dealt here in detail with STOLLEY's views because I shall have to criticize it below on the basis of new facts. As we shall see, it seems as if we are no longer justified in maintaining the family *Colobodontidae*, but *Colobodus*¹⁾ s. str. and *Dollopterus* and

¹⁾ At least for the present *Crenilepis* ought, according to my opinion, to be regarded as a synonym of *Colobodus* (cf. STOLLEY 1920, p. 44).

Perleidus as well ought probably to be included among the Catopterids. Provisionally one might also possibly incorporate *Meridensia* with them. On the other hand I do not think it probable that *Nephrotus* belongs here.

The geological occurrence and geographical distribution of the Catopterids.

The family *Catopteridae*, even in the more extensive definition given to it by me, is known exclusively from the Triassic.

In spite of this rather short life from a geological point of view its representatives attained a very extensive geographical distribution. The genus *Catopterus* is thus known from the east of the United States (WOODWARD, 1895b, pp. 1—3; EASTMAN, 1904, p. 95; 1911, p. 47; 1914a, p. 139; 1917, pp. 279—281), *Dictyopyge* from the east of the United States, Ireland, England, Germany, Switzerland, Eastern Australia and South Africa (cf. WOODWARD, 1895b, pp. 4—9; EASTMAN, 1904, p. 95; 1911, p. 47; 1914a, p. 139; BROOM, 1909a, pp. 257—258 and p. 262), *Perleidus* from Northern Italy (DE ALLESSANDRI, 1910, pp. 49—51) and now as far as one can judge from Spitzbergen as well, *Colobodus* s. str. from France, Germany, Northern Italy, Switzerland¹⁾ (WOODWARD, 1895b, pp. 68—77; ANDERSSON, 1916a, pp. 18—25; STOLLEY, 1920, pp. 38—45, 75—86), *Dollopterus* from Germany (STOLLEY, 1920, pp. 45—68) and finally *Meridensia* from Northern Italy (ANDERSSON, 1916a, pp. 25—29).

The occurrence of *Perleidus* in the Triassic of Spitzbergen is of great interest as showing that, as I pointed out above (p. 85) we may expect to find additional forms that are related to those from the Alpine Triassic.

Description of the Spitzbergen material.

Genus *Perleids* DE ALLESSANDRI.

Synonyms: *Semionotus* (in part), DEECKE, 1889, *Colobodus* (in part), WOODWARD, A. S. 1912.

As already mentioned above, DE ALLESSANDRI in 1910 established the genus *Perleidus* for a fish described by DEECKE in 1888 (pp. 120—121) under the name of *Semionotus altolepis*. The type specimen, which belongs to the Senckenbergian Museum at Frankfurt am Main, was until recently the only specimen known. During a visit to the Senckenbergian Museum in the autumn of 1919, I was able to discover, however, that a second specimen of the same species was present in the material of Lombard Triassic fishes described by DEECKE, although up to that time this specimen had been looked upon as belonging to *Heterolepidotus pectoralis* BELOTTI (Senckenberg Museum, P. 1258).²⁾ In addition a critical examination of the figures in DE ALLESSANDRI's monograph (1910) on the Triassic fishes of Lombardy suggests that it is not impossible that two more spe-

¹⁾ A doubtful species, *C. sibiricus*, is described from Siberia and another similar one, *C. africanus*, from Africa (WOODWARD, 1895b, p. 76; TRAQUAIR, Quart. Journal. Geol. Soc. vol. 66. London 1910, pp. 249—251).

²⁾ According to a note on the label of this fish already DE ALLESSANDRI has had a suspicion that this specimen might be identical with *Perleidus altolepis*.

cimens of *Perleidus altolepis* or a species closely related to this may be present, although their state of preservation makes a proper identification of them difficult. A supposition of this sort is possible both in the case of the specimen figured by him in Pl. VI, fig. 3 as *Heterolepidotus serratus* BELLOTTI and the one that in his Pl. IX, fig. 6 he calls *Pholidophorus barazzati* BASSANI. In any case it seems to be clear that the former specimen cannot be referred to *Heterolepidotus*.

The type specimen of *Perleidus altolepis* is in certain respects incompletely and incorrectly described in the previous literature (DEECKE, 1888, pp. 120—121; DE ALLESSANDRI, 1910, pp. 49—51), and as the second newly-discovered specimen in the Senckenberg

Museum helps considerably to increase our knowledge of the genus *Perleidus* as a whole, I consider it necessary to communicate some of my own observations.

The relation and the appearance of the membrane bones of the cranial roof is partly shown in text fig. 78 A, which cannot lay claim to any very great degree of accuracy with regard to the finer details, but still reproduces what can be distinctly observed. Text fig. 78 B is a similar sketch showing the skeleton of the jaws and opercular apparatus. Of special interest is the large palaeoniscid-like preoperculum (*Po*) that is clearly preserved on both the specimens in the Senckenberg Museum (cf. DE ALLESSANDRI, 1910, p. 50; STOLLEY, 1920, p. 65). The scales (text fig. 79) are only partly serrated on the posterior margin, the upper part of this margin being entire. The ridge-scales are very indistinctly preserved, so that nothing certain can be said as to their shape, in spite of express statements to the contrary both by DEECKE and DE ALLESSANDRI. Besides the main lateral line of the body we can distinguish also a shorter dorsal body line running dorsally of the former from the region of the neck backwards towards the anterior margin of the dorsal fin.

In connection with his revision of the genus *Colobodus* 1920 STOLLEY (pp. 38, 40—41, 84—85) arrived at the view that the species described by WOODWARD (1912, pp. 296—297) from Spitzbergen under the name of *Colobodus altilepis* does not really belong to the genus *Colobodus* in the restricted sense that this genus ought now to have according to my own (ANDERSSON 1916a) and his (1920) investigations. STOLLEY is in addition of the opinion that *Colobodus altilepis* A. S. WOODWARD ought either to be put in connection with the species *Colobodus ornatus* (AGASSIZ) and *Colobodus latus* (AGASSIZ), for which he suggests the new generic name *Parolepidotus*, or with *Heterolepidotus dorsalis* KNER.

The new material of *Colobodus altilepis* A. S. WOODWARD now at my disposal shows undoubtedly that STOLLEY's view is correct inasmuch as this species cannot belong to the genus *Colobodus* s. str. On the other hand it is, however, equally clear, as we shall see, that STOLLEY is wrong in his considerations as to the affinities of this species.

With regard to the head skeleton *Colobodus altilepis* A. S. WOODWARD belongs to the Palaeoniscid type and seems, as far as is known, to be very closely connected on the

Text fig. 78.

Perleidus altolepis DEECKE.

After P. 1258 in the Senckenberg museum in Frankfurt am Main.

A) Sketch of the membrane bones of the cranial roof.

B) Sketch of the opercular skeleton.

Exr, extrascapular; Fr, frontal;

So, row of supraorbital bones;

Md, mandibular; Mx, maxillary;

Op, operculum; Pa, parietal;

Rbr, branchiostegal radius;

Sop, supraorbital; Sop, suboperculum; orb, orbit.

whole with *Perleidus altilepis*. The only character of any importance that separates the two species is the position of the dorsal fin. For in *Colobodus altilepis* WOODWARD the dorsal fin has its posterior part opposite the anal fin, while in *Perleidus altilepis* the same fin is situated instead so much farther forward, that its anterior part is opposite the ventral fins. On the basis of this character alone, however, I did not think I ought to set up a new genus for *Colobodus altilepis* A. S. WOODWARD, but placed it, at least provisionally, under *Perleidus*.¹⁾

The most important characters known for the genus *Perleidus* in its present definition may be summarized as follows. Small or medium sized fusiform or rather high fishes. The external membrane bones of the head with well developed ganoine sculpture of tubercles or striae or both. The nasalo-postrostral including not only the interrostrals but also certain of the middle rostral elements. Lateral rostral elements forming a paired independent plate. Maxillary and mandibula robust. Preoperculum large and wide. Suboperculum high. Branchiostegal radii not specially numerous. Teeth partly pointed, partly adapted for crushing; the former variety limited to the premaxillae and the anterior parts of the maxillary and dentalo-splénial. All the teeth have as a rule a point which on a the teeth adapted for crushing is marked off as a verruca, but there are no striae radiating from this. Fins relatively weak. All the lepidotrichia, except those of the caudal fin, unjointed for a long stretch proximally. The fulcra are fairly robust. The dorsal fin situated either far forward and partly opposite the anal fin or somewhat farther backward, so that its posterior part is opposite the anal fin. Ventral fins situated considerably nearer the anal fin than the pectoral fins. The ventral fins with few lepidotrichia. The scales on the ventral side fairly low; those on the anterior part of the lateral surfaces of the abdominal region, considerably higher than broad, decreasing in height towards the dorsum and backwards toward the posterior parts of the abdominal region so that they gradually become rhombical in shape. The anterior covered area of all the scales narrow or fairly narrow; the exposed surface with an almost smooth ganoine covering. The upper margin with an articulatory spine, the posterior margin serrated but always more or less entire in its dorsal part. The ridge-scales wide, blunt posteriorly. Besides the main lateral line of the body on either side a second shorter lateral line extending from the neck to about the basis of the dorsal fin.

Text fig. 79.

Perleidus altilepis (DEECKE).
Scales from different parts of the body. After the specimens in the Senckenberg Museum in Frankfurt am Main.

- A) From the anterior part of the abdominal region.
- B) From the posterior part of the abdominal region.
- C) From the caudal region.

Perleidus woodwardi nom. nov.

(Pl. 28, fig. 3; Pls. 33; 34; Pl. 35, figs. 1—3).

Synonyms: *Colobodus altilepis* WOODWARD A. S. Upsala Geol. Inst. Bull. vol. XI, pp. 296—297, 1912.

ANDERSSON, E. Upsala Geol. Inst. vol. XV, 1916.

Perleidus woodwardi is one of the most common species among the Triassic fishes of Spitzbergen. The present material comprises no less than 14 specimens (P. 166b,

¹⁾ STOLLEY has in 1920 (p. 65) also with much hesitation placed the so-called *Semionotus letticus* O. FRAAS in the genus *Perleidus*, but this species, as I have found, may instead probably belong to the genus *Dollopterus* (cf. foot-note on p. 267).

P. 176—P. 186, P. 697, P. 881), of which some are even so well preserved that they afford us a fairly good idea of the appearance and general proportions of the animal, which, as we have already partly seen, is not often the case with the fishes from the Triassic of Spitzbergen.

The largest specimens known attained a length of 25–30 cm, the smallest about 7 cm. Compared with the length the height is rather considerable; in specimens *P. 185* (Pl. 33) and *P. 176* (Pl. 35, fig. 1) it is, however, larger than it was in reality, because of the state of preservation. The greatest height is situated considerably in front of the dorsal fin about half-way between this and the head and is apparently from about a third to a quarter of the total length. Posteriorly towards the tail the height decreases rather rapidly both dorsally and ventrally, and both the dorsal and the ventral outlines seem therefore fairly strongly convex, the former, however, more than the latter. The length of the head seems to be from a quarter to a fifth that of the whole fish.

The membrane bones of the neurocranium.

There were undoubtedly ossifications in the primordial neurocranium, but no details are known as to these. The membrane bones, on the other hand, are partly well preserved.

The parietals (*Pa*, text figs. 80, 81; Pl. 34, figs. 1, 2) are, as WOODWARD has already mentioned, developed symmetrically and have an almost square shape. They seem to have met in a fairly straight median suture. The frontals (*Fr*, text figs. 80, 81; Pl. 33; Pl. 34, figs. 1, 2) also seem to have been fairly symmetrical. Their width is rather great and, at its greatest point, is about half the length. The medial margin is rather straight. The lateral one, on the other hand, has a projecting corner, by which it is divided into an anterior and a posterior part, both of which are concave. Against the posterior part, which is the shortest, is situated the anterior part of the supratemporo-intertemporal (*Stemp.it.*, text figs. 80, 81; Pl. 34, figs. 1, 2), which is long and narrow. (For its homologues see pp. 138, 242 above). The extrascapulars are represented only by a single rather large plate (*Ext*, text figs. 80, 81; Pl. 34, figs. 1, 2) on either side of the median line. In front of the supratemporo-intertemporal, along the anterior part of the lateral margin of the frontal, there are some supraorbitals (*So*, text figs. 80, 81; Pl. 33), which are, however, crushed and poorly preserved, so that their number cannot be established with certainty. The most posterior of them seems, as we shall see from the course of the infraorbital canal, to correspond most closely to the dermosphenotic.

The ethmoidal region is preserved only in two specimens (*P. 166* and *P. 477*), but is partly crushed in both. Its anterior end has been blunt with an indication of a rostrum as in the Palaeoniscids, but it is impossible to decide whether the profile was exactly as I have shown it in my reconstruction in text fig. 81 or still more blunt.

In the roof of the ethmoidal region anterior to the frontals there is a rather long and relatively narrow unpaired bone-plate (*Na. ptr.*, text fig. 80, 81; Pl. 34, figs. 1, 2), which is bent in a characteristic way, indicating that it not only covered a part of the dorsal surface of the region but also a considerable part of the anterior one below the anterior extremity of the rostrum in the way shown in text fig. 81. The anterior part of this bone-plate is pierced by the ethmoidal commissure of the infraorbital canals and

each lateral margin forms together with the medial margin of the antorbital (*Ant*) the boundary for the two nasal apertures of each side. As we thus see from its extension and relation to the sensory canals and the nasal apertures this bone-plate probably includes not only the homologues of the postrostrals, nasals and interrostrals of the primitive Rhipidistids, but also one or more of the homologues of the medial rostral elements (cf. pp. 124, 133—134, 242 above) of these fishes.

On both sides of this so composed nasalo-postrostral, as for the sake of brevity I shall call the bone just described, there is, as in the Palaeoniscids, a large antorbital (*Ant*, text fig. 80, 81; Pl. 34, figs. 1, 2), which comes into contact with the most anterior element of the supraorbital series, with a rostral (*R*) and the most anterior element among the infraorbitals. It has helped to some extent to form the anterior boundary of the entrance to the orbit and has, in addition, as has been mentioned, taken part in the boundary of the nasal apertures. Laterally of the nasal apertures it is penetrated longitudinally by a sensory canal in the same way as in the Palaeoniscids (cf. my account of the Palaeoniscids p. 246, and ALLIS, 1889, pp. 471, 475; Pls. XLI, XLII; 1898, pp. 436—438; 1900 a, p. 438; 1905, p. 491; TRAQUAIR, 1877 a, p. 16, Pl. 1, figs. 2, 3, 7, 8, 11; 1879, Pl. 4, fig. 9; Pl. 5, fig. 1; Pl. 6, figs. 5, 6, 12; STOLLEY, 1920, the so-called «Antefrontale», pp. 31, 36, 48, 84).

In front of the antiorbital on each side there follows, as has already been mentioned, a bone-plate (*R*, text figs. 80, 81; Pl. 34, figs. 1, 2), which is pierced by the infraorbital canal and obviously must be a rostral (cf. my account on pp. 98, 103, 133—134, 242 above). This plate does not meet that of the opposite side, but is separated from this by the anterior part of the nasalo-postrostral, a part which for reasons given above, ought to be homologous with one or a couple of medial rostral elements.

The orbital entrance (*orb*, text fig. 81; Pl. 33; Pl. 34, figs. 1, 2; Pl. 35, fig. 1) is large and situated far forward as in Palaeoniscids and Platyosmids. Posteriorly and ventrally it is bounded by a row of infraorbital bones (*Ifo*, text fig. 81; Pl. 33; Pl. 34, figs. 1, 2), which are, however, crushed and incompletely preserved, so that their number cannot be established with full certainty. A couple of so-called suborbitals (*x₁*, *x₂*) were also possibly present.

Text fig. 80.
Perleidus woodwardi
nom. nov.

The membrane bones of the cranial roof, after P. 177, 178, 179. *Ant*, antorbital; *Ext*, extrascapular; *Fr*, frontal; *Na.pir*, nasalo-postrostral + interrostrals + one or a couple of medial rostral elements; *Pa*, parietal; *R*, rostral; *Stemp.it*, supratemporo-intertemporal; *na₁*, *na₂*, nasal apertures.

Text fig. 81. *Perleidus woodwardi* nom. nov.
Head from the side. Mainly after P. 185, to a smaller extent after P. 177 and P. 166, 171.

Ant, antorbital; *Cl*, cleithral; *Dsph*, dermosphenotic; *Ext*, extrascapular; *Fr*, frontal; *Jcl*, jugal; *Ifo*, infraorbital plates; *Md*, mandible; *Mx*, maxillary; *Na.pir*, nasalo-postrostral + interrostrals + a couple of medial rostral elements; *Op*, operculum; *Pa*, parietal; *Pmx*, premaxillary; *Po*, preoperculum; *R*, rostral; *Rbr*, branchiostegal rays; *ScI*, supracleithral; *So*, supraorbital; *Sop*, suboperculum; *Scsup*, suprascapular; *Stemp.it*, supratemporo-intertemporal; *na₁*, *na₂*, anterior and posterior nasal aperture; *orb*, orbit; *x₁*, *x₂*, probably so-called suborbitals.

All the membrane bones described here are ornamented with rather coarse and flat ganoine tubercles, in most cases closely arranged (Pl. 33; Pl. 35, fig. 1).

Visceral skeleton.

The quadrate is well ossified and consists of cancellous bone substance as in the Palaeoniscids. No details are known as to its extension and shape. Nothing is preserved of the metapterygoid and the autopalatine.

The ecto- and entopterygoid both seem to have been present, but are incomplete.

The maxillary (*Mx*, text fig. 81; Pl. 33; Pl. 33; Pl. 34, figs. 1, 2; Pl. 35, fig. 1) is of the Palaeoniscid type, i. e. its suborbital part is low, while its postorbital part forms a large, rather high plate on the cheek. The postorbital part seems to have been relatively longer than in *Colobodus* (STOLLEY 1920; ANDERSSON 1916a).

The mandible is robust and, as far as can be seen, had a straight labial margin without any coronoid process. Among its bones only the large high dentalo-splenic can be clearly distinguished, and this is pierced by the mandibular canal as in the Palaeoniscids and other Actinopterygians, so that it probably comprises equivalents not only to the dental of the primitive *Crossopterygii* but also to a number of their splenic elements, as I have indicated by the name I have chosen for it.

Text fig. 82.
Perleidus woodwardi nom. nov.
Left hyomandibular
from the lateral side.
After *P.* 185, 1/4.
Can. tr. fac., canal for
the truncus hyoideomandibularis facialis; *pr. op.*, processus opercularis.

The hyomandibular (text fig. 82) is an angular bone as in the Palaeoniscids. The angle is situated at about the same height as the upper part of the operculum and at this place there issues on the posterior margin a short and wide processus opercularis (*pr. op.*), so that the musculature of the opercular apparatus must have shown somewhat analogous conditions to those in *Amia* and the Teleosts (cf. pp. 213—214, 226 above). The dorsal part of the bone is considerably wider than the ventral one. Both the dorsal and the ventral ends and the processus opercularis have been furnished with cartilaginous epiphyses. A canal for truncus hyoideomandibularis facialis (*can. tr. fac.*) can be distinctly observed¹⁾.

It is evident that the hyomandibular was oblique in the same way as in the Palaeoniscids, although not so much as in the majority of these. The corresponding bone certainly occupied a similar position in *Colobodus* and *Dollopterus* too.

The preoperculum (*Po*, text fig. 81; Pl. 33; Pl. 34, figs. 1, 2; Pl. 35, fig. 1) is a large and wide triangular plate of about the same type as in *Perleidus altolapids* (cf. text fig. 78). Its long posterior margin, which meets the operculum (*Op*) and the suboperculum (*Sop*), is convex, its anterior margin concave, and its forward and downward pointing margin, which is in contact with the postero-dorsal margin of the maxillary, is also concave. The anterior corner forms a little point, which projects in a characteristic way forward and downward for a short distance along the antero-dorsal margin of the maxillary. The ventral corner is pointed, the dorsal one, on the other hand, probably

¹⁾ It is of interest to note that the hyomandibular in *P. woodwardi* greatly resembles in shape that of *Colobodus bassani* (cf. ANDERSSON, 1916a, *Hm*, Pl. II). In this latter species too it is pierced by a canal for truncus hyoideomandibularis facialis.

abruptly truncated. Finally it may be mentioned that the bone in question is pierced by the preopercular sensory canal.

In this connection it ought to be noted that a preoperculum of a similar form has also been found in *Colobodus* (ANDERSSON 1916a *Po*, text fig. 2; Pl. I, figs. 1, 2; Pl. II; STOLLEY 1920, Pl. X, fig. 2; Pl. XI, fig. 3; cf. also text figs. 85, 87 below).

The operculum (*Op*, text fig. 81; Pl. 33; Pl. 34, figs. 1, 2; Pl. 35, fig. 1) is a relatively small quadrangular plate with its width almost the same as its height. Its dorsal and posterior margins are nearly straight, or weakly convex, passing over into each other by a rounded corner. The anterior margin is concave and the lower one convex. It is impossible to decide whether the anterior upper corner was produced into a point extending forward into the angle between the posterior margin of the preoperculum and the supratemporo-intertemporal or whether this part forms an independent little bone-plate. The postero-ventral and antero-ventral corners are both angular but rather blunt and rounded off.

The suboperculum (*Sop*, text fig. 81; Pl. 33; Pl. 34, figs. 1, 2; Pl. 35, fig. 1) is somewhat larger than the operculum. It is quadrangular in shape with its height considerably greater than its width. Of its margins the anterior one is weakly and the upper one strongly concave, while the lower and the posterior ones are both weakly convex. The anterior lower corner is almost right-angled, and the posterior lower one well rounded. The anterior upper and posterior upper ones are acute-angled.

Both the operculum and the suboperculum thus show almost the same conditions as in *Perleidus altolepis* (cf. this work text fig. 78 B; DEECKE 1888, Pl. 6, fig. 10; DE ALESSANDRI 1910, Pl. II, fig. 2).

The radii branchiostegi (*Rbr*, text fig. 81; Pl. 33; Pl. 34, figs. 1, 2), of which those following immediately below the suboperculum were rather wide, seem to have been less numerous than in *Colobodus*. Their exact number could not be established.

The external membrane bones of the jaws and the opercular bones are ornamented as a rule with densely arranged flattened tubercles in the same way as the membrane bones of the cranial roof.

Dentition.

The dentition is rather robust compared with the size of the fish and consists partly of pointed teeth and partly of teeth adapted for crushing.

The premaxillary seems to have had only one row of large pointed teeth and similar teeth are also present in the anterior parts of the dentalo-splénial and maxillary. In a posterior direction, however, the teeth in these two latter bones soon become more blunt and more or less distinctly clubshaped (text figs. 81, 83), at the same time decreasing in height and increasing in thickness. Finally those farthest posteriorly which are situated close together get in profile the appearance shown in text fig. 83B, Pl. 35, fig. 2, and in that shown in text fig. 83C.

Small teeth, probably mostly rather pointed, are found in a row laterally of the larger ones just described on the maxillary and dentalo-splénial.

Text fig. 83.

Perleidus woodwardi
nom. nov.

Teeth from the
maxillary and
dentalo-splénial.
All magnified $\frac{1}{10}$.

A) From the
anterior part of
the dentalo-
splénial; After
P. 185.

B) From the
posterior part of
the maxillary in
profile. After
P. 186.

C) From the
posterior part of
the maxillary in
coronal aspect.
After *P. 186*.
The arrow in
this figure
points forwards.

The dentition of the pterygoid consists of robust, densely situated crushing teeth, most frequently rather irregular in shape. The masticatory surface on these teeth often show facets, probably due to wearing.

With regard to the dentition on the mixicoronoid («splenial» according to the earlier terminology, cf. p. 244 above), parasphenoid and gill-arches nothing is known.

All the teeth have a pulp cavity of rather considerable dimensions and often a milky white point, about as in *Colobodius*. On the blunt teeth this point has generally an unsymmetrical position and is marked off as a verruca; on the pointed ones, on the other hand, this condition is less distinct. No striation is present contrary to what is the case in typical *Colobodius* teeth.

The sensory canals of the head.

The sensory canals of the head are fine and open outwards with numerous short tubuli, which seem to be simple. In most cases the outer opening of the tubuli is difficult to observe and can be easily overlooked, especially on bones on which the sculpture is developed more strongly. It is of course impossible to decide with certainty whether the number of sensory organs corresponded to the large number of tubuli, but it does not seem probable that this should be the case, as the entrance foramina for the nerves and vessels in the sensory canals are fewer than the tubuli (cf. ALLIS, 1889, Pl. XLII; COLE, 1898, Pl. 22; HERRICK, 1899, Pl. XVII; 1901, Pl. XIV; etc.).

As far as can be judged, the sensory canals run in the same way as in the Palaeoniscids. They are partly well preserved and it was possible to follow them all throughout practically their entire extension. For the reasons in favour of the terminology used here see my account above (pp. 102—105, 245—246).

The supraorbital canal (*soc*, Pl. 34, fig. 1, text figs. 80, 81) of either side has its posterior end situated in the parietal and is developed there for a short distance as a furrow, i. e. towards its posterior end it passes over into a «head-line of pit organs» (*ap*, Pl. 34, fig. 1), which is undoubtedly homologous with the anterior one in *Amia* (ALLIS, 1889, pp. 505—506), *Polypterus* (ALLIS, 1900a, p. 445), and Teleosts (HERRICK, 1901, p. 222, Pl. XIV; ALLIS, 1905). From the parietal the supraorbital canal continues through the frontal, where it does not, however, run straight forward but somewhat laterally as well. At the anterior end of the frontal it passes over continuously, as in the Palaeoniscids, into a part of a canal piercing the antorbital.

This part of canal, which is thus situated laterally of the nasal apertures, continues anteriorly and enters the rostral, where it anastomoses with the infraorbital canal of its side. As I have pointed out above (p. 246), I agree with ALLIS (1905, p. 491) that this part of the canal does not belong to the supraorbital canal, but that we are here concerned with the upper anterior end of the suborbital part of the infraorbital canal. The anterior end of the supraorbital canal would thus either be absent or else only developed as a «pit-line». If a «pit-line» were present, this would have had its course forwards over the frontal in such a way that it reached the nasalo-postrostral, on which it would probably have continued for a short way anteriorly.

There is no anastomosis developed between the posterior parts of the supra- and infraorbital canals.

The infraorbital canal of either side (*ifc*, text figs. 80, 81; Pl. 34, fig. 1) is, as usual, connected posteriorly with the anterior end of the cranial section of the lateral canal in the supratemporo-intratemporal. It passes off forward through this bone with a gradual bend to the lateral side and has then presumably entered the dermosphenotic, where it is not, however, preserved. In its further course downwards and forwards it first pierces the infraorbitals behind and beneath the orbital entrance, then entering the rostral. In this bone it has, if the view just put forward by me above is correct, been so ramified that one branch passed off upward and backward through the antorbital, while the other continued forward and medially, entering the nasalo-postrostral, where it formed an ethmoidal commissure with that of the opposite side. This commissure forms a deep sinus backwards within the nasalo-postrostral (*ethm. com*, text fig. 80; Pl. 34, figs. 1, 2).

On the commissural section of the infraorbital canal from the place of communication with the suborbital section in the rostral plate to the place where it meets that of the opposite side in the median line, 5-6 foramina for nerve branches to the sensory organs could be observed. On the canal portion in the antorbital there are about number of these foramina.

The preopercular canal (*poc*, text fig. 81; Pl. 34, fig. 1) is situated quite close to the posterior margin of the preoperculum and on this margin numerous exceedingly small tubuli have their openings. It was impossible to observe whether it communicated with the mandibular canal and the canal in the supratemporo-intertemporal.

The mandibular canal (text fig. 81) runs as usual through the mandible in the same neighbourhood of its posterior and lower margins.

The cranial section of the main lateral canal (text figs. 80, 81; Pl. 34, fig. 1) had its course from its anterior end in the supratemporo-intertemporal backwards through that bone, then piercing the lateral part of the extrascapular. Between this section of the sensory canal on the right and left sides there is a supratemporal commissure, situated in the extrascapulars (*s. com*, Pl. 34, fig. 1).

An anterior «head-line of pit-organs» (*ap*, Pl. 34, fig. 1) is described above in connection with the description of the supraorbital canal, of which it formed a direct posterior continuation. In addition, however, a middle and a posterior head-line are found, each represented by a rather short furrow on the parietal. The posterior head-line (*pp*, Pl. 34, fig. 1), which issues from the posterior margin of the parietal, runs first anteriorly for a short way and then bends off antero-medially. The middle head-line (*mp*, Pl. 34, fig. 1), which begins between the posterior and the anterior one, passes off laterally and somewhat anteriorly (cf. text figs. 80, 81).

It cannot be established with certainty whether «check lines» of pit-organs were present or not.

The skeleton of the unpaired fins.

The anal fin (4, Pl. 28, fig. 3; Pl. 33; Pl. 35, figs. 1, 3) is rather small and is situated fairly far back. It is triangular in shape with its base and height almost of equal size. The ganoine-covered lepidotrichia number about 10, all of which are unjointed for a comparatively long distance proximally. Otherwise they are closely jointed and even dichotomically ramified distally. The fulcra are numerous and strong.

The dorsal fin (*D*, Pl. 28, fig. 3; Pl. 33; Pl. 34, fig. 2; Pl. 35, figs. 1, 3) is somewhat larger than the anal fin, but has about the same shape as this. Its anterior margin corresponds on the ventral side to a point situated about half-way between the ventral fins and the anal fin; its posterior part is opposite the latter fin. The lepidotrichia are 14—15 in number. They decrease uniformly in length posteriorly and are also developed in other respects in the same way as those of the anal fin. The fulcra are strong and numerous.

The endoskeletal radials of the dorsal fin are represented by a row of long bone elements (*Rd*, Pl. 28, fig. 3), which follow about 2—3 mm proximally of the bases of the lepidotrichia. These elements may correspond to at least the proximal segments of the radials and perhaps also to the middle ones (cf. SCHMALHAUSEN, 1912, 1913 a, 1913 b). On the other hand the distal ones were undoubtedly cartilaginous and, as usual, small.

It is specially noteworthy that the endoskeletal radials correspond exactly or almost exactly in number to the lepidotrichia, a condition which we shall see is also the case in the other forms included by me among the Catopterids. This agreement in the number of lepidotrichia and endoskeletal radials is of morphological importance inasmuch as it shows that a specialization of the musculature has taken place in the direction of the conditions in higher ganoid forms and Teleosts (cf. SCHMALHAUSEN, 1912, 1913 a, 1913 b). Palaeoniscids, Platysomids,¹⁾ Chondrosteids, Acipenserids, Polyodontids and Saurichthyids in general show, as we know, primitive conditions in this respect (cf. TRAQUAIR, 1877 a, p. 27; 1879, p. 386; WOODWARD, 1890 a, pp. 15, 16; 1891 b, p. 427, 1895 b, pp. 11, 27; 1898 a, pp. 84, 89—90, 92, 93; GOODRICH, 1909, pp. 211—212, 308—309, 321; etc.).

The caudal fin is incompletely preserved in all the present specimens. It is, however, distinctly observable that it was abbreviate-heterocercal or fairly homocercal. Its lepidotrichia are relatively fine and closely jointed right down to the base. Fulcra can be observed, at least on the ventral lobe.

All the lepidotrichia, both in the paired and unpaired fins, were covered with ganoiné.

The skeleton of the shoulder girdle and the paired fins.

Of the shoulder girdle only the membrane bones are known. Of these the cleithral (*Cl*, Pl. 34, figs. 1, 2) was developed about as in the Palaeoniscids with a high posterior shank, situated vertically and a shorter anterior one which is fairly horizontal. The supracleithral (*ScL*, Pl. 34, figs. 1, 2; Pl. 35, fig. 1) is high. The suprascapular seems to be represented by a comparatively large oval plate (*Sscap*, Pl. 33). The clavicularae were probably present, although they were of course small; only insignificant remains of them are preserved (*Icl*, Pl. 34, figs. 1, 2) in one specimen (*P. 177*).²⁾ Immediately behind the posterior shank of the cleithrum we find, as in certain *Protospondyli* (*Lepidotus*,

¹⁾ An exception from this is found in the so-called *Platysomus canadensis* LAMBE (1914, pp. 17—23) where the lepidotrichia and endoskeletal radials are said to be present in equal numbers.

²⁾ In *Colobodus maximus* I have found clavicularae, and STOLLEY (1920, p. 36) considers that he too observed them in *C. kōnigi*, but I am not convinced that his view is correct, at least to judge from his figure 5 on Pl. XI. — In this connection it is worth adding that I found rudiments of clavicularae in *Lepidosteus* too, where they seem to occur rather often.

Dapedius), two very much enlarged scales (*Pcl*, Pl. 33; Pl. 34, figs. 1, 2), the upper one of which is about twice as high as the lower one.

The membrane bones of the shoulder girdle have the same sort of sculpture as the external ones of the head.

The pectoral fins (*Pc*, Pl. 33; Pl. 34, figs. 1, 2; Pl. 35, fig. 1) are relatively more strongly developed than the other fins. They are incompletely preserved and their shape cannot therefore be established with certainty. Their lepidotrichia number about 12—14 and have a rather long proximal part unjointed. Otherwise they are closely jointed and dichotomically ramified. The most anterior of them has numerous *A* but not specially strong fulcra.

The ventral fins (*V*, Pl. 33; Pl. 34, fig. 1; Pl. 35, figs. 1, 3), which are situated considerably nearer the anal fin than the pectoral fins, are strikingly short-based and consist only of 8—9 comparatively long lepidotrichia, which are jointed and dichotomically ramified only in their distal halves. Fulcra are clearly discernible.

Squamation.

The scales are thick and strong and because of this they are well preserved. Altogether one can probably count about 40 vertical rows of scales on a level with the main lateral line. In the rows immediately behind the shoulder girdle there are on the lateral surfaces of the body as shown in Pl. 34, figs. 1, 2 a number of scales that are higher than wide. Except for the scales on the ventral side, which are wider than high, the other scales have a rhombic or almost rhombic shape. The transition between the higher scales and the others takes place gradually. As Woodward (1912, p. 296) states, the dorsal ridge scales are certainly somewhat rhombic in shape, but at the same time they have a posterior margin developed which is finely serrated. While the height of the highest anterior lateral scales is about twice as great as the width or sometimes even more, the relation in the scales of the ventral side is quite the opposite, the width often being more than double the height.

The anterior covered area of the scales is rather narrow but distinctly somewhat wider on the anterior scales than on the posterior ones (text fig. 84, A, B, C, D.). The dorsal margin has a well developed articulatory spine and the medial surface has a corresponding articulatory fossa at its lower margin. The antero-dorsal corner is also often somewhat produced in the shape of a spine, as is clearly shown in text fig. 84 A, B and C. The ridge of the medial surface is weakly developed or is absent. The antero-ventral corner is always somewhat rounded, the postero-ventral one acute-angled, and the postero-dorsal one obtuse-angled. The posterior margin is serrated on all the scales, though not entirely, its dorsal part being always to some extent entire (text fig. 84). The small backward and downward directed serrations on this margin occur in great numbers only on the high anterior scales* (text fig. 84 A). Both on the scales situated upwards towards the dorsum, backwards and downwards they become less in number. Towards the posterior end of the caudal region there are scales of the type figured in text fig. 84 D.

*Stensiö, Triassic Fishes from Spitzbergen.

Text fig. 84.

Perleidus woodwardi.
Scales from different parts of the body. After P. 185, 1/2.

A) From the anterior part of the lateral surfaces of the abdominal region.

B) From the anterior part of the lateral surfaces of the caudal region.

C) From the ventral side.

D) From the posterior part of the lateral surfaces of the caudal region.

which have only one serration farthest ventrally and on the tail even this one seems to be absent. The ventral scales also generally have only one or two serrations.

The exposed surface of the scales is covered by a layer of shining ganoine, which is smooth on the whole. Small furrows are visible on this really only close to the posterior margin, where they are arranged so that each of them reaches this margin in the small sinus between two neighbouring serrations. This character is most striking in the abdominal region (text fig. 84 A), and is gradually lost backwards. The scales on the neck immediately behind the extrascapulars sometimes show a tubercular sculpture of the same type as that on the membrane bones of the cranial roof. As can easily be seen, *P. woodwardi* shows a great resemblance to *P. altolepis* (DEECKE) with regard to the development of the scales.

The lateral canals of the body.

The main lateral canal of the body can be followed in *P. woodwardi* for a considerable distance. It pierces the supracleithral as usual and then runs backwards and somewhat downwards, first penetrating the uppermost high scales of the anterior vertical rows (I, Pl. 34, figs. 1, 2). It opens with narrow vertical pores, which are found on every third or fourth, sometimes on every fifth scale.

Another shorter lateral line runs on either side higher up from behind the extrascapulars backwards towards the dorsal fin. It has thus the same position and extension as in *P. altolepis* (cf. p. 256 above) and *Lepidotus* (WOODWARD 1895 b, p. 95, fig. 22).

* * *

Remarks. — *Perleidus woodwardi* was described for the first time (1912) by WOODWARD under the name of *Colobodus altilepis* and I myself later on (ANDERSSON 1916a) placed it under this name. Recently STOLLEY (1920, pp. 38–43; 84–85) has emphasized that it cannot belong to the genus *Colobodus*, but that, like the so-called *Colobodus ornatus* (AGASSIZ), and *Colobodus latus* (AGASSIZ), it is most closely related to *Lepidotus* instead. He is doubtful, however, whether to group it with these two Alpine species in the genus *Paralepidotus* established by him, or whether to place it in closer relation to *Heterolepidotus dorsalis*. According to his opinion, *Perleidus woodwardi* would thus even belong to quite another family than *Colobodus*.

The present material has, however, completely proved that the so-called *Colobodus altilepis* A. S. WOODWARD shows the closest resemblance to the Palaeoniscids with regard to the skeleton of the head and the development of the sensory canals, and that it must undoubtedly belong to the same large group as *Dollopterus*, *Perleidus* and *Collobodus* s. str. The evidence seems also to show that among these genera it is most closely related to *Perleidus*, and, as pointed out above, I considered that I ought, at least for the present, to include it in this genus.

As under these conditions there would be in the genus *Perleidus* two species with practically identical names, I considered it necessary to suggest the new name *woodwardi* for the Spitzbergen species, after the eminent palaeontologist Dr. A. S. WOODWARD, especially as he was the first to describe the species.

P. woodvardi is well separated from *P. altolepis* by the position of the dorsal fin and the development of the cranial sculpture and by its larger size.

Geological occurrence and localities. — *Perleius woodvardi* occurs rather commonly in the fish horizon. It seems to be most common in Dickson Land, where no less than 10 of the present 14 specimens were collected. The finds are distributed over the following localities: Mt Congress, Mt Sture, Mt Tschermak, Mt Rotunda (Student Valley), the south shore of Sassen Bay, Sticky Keep and Mt Andersson.

Some remarks on the genera *Catopterus*, *Dictyopyge*, *Colobodus* s. str., *Perleius*, *Dollopterus* and *Meridensia*.

Skeleton of the head. — In *Catopterus* and *Dictyopyge* the osteology of the head is still little known. EASTMAN (1911, p. 53) mentions, however, in *Catopterus* an unpaired «ethmoid», so situated in relation to the frontals, that in my opinion it corresponds at least to the fused nasals and postrostrals, i. e. the membrane bones of the ethmoidal region would show fairly Palaeoniscid-like conditions (cf. p. 242 above). The maxillary is said (p. 54) also to have a Palaeoniscid-like shape. Further it may be pointed out that the outlines of the head seem to be very Palaeoniscid-like (cf. WOODWARD, 1890a, Pl. IV, figs. 5, 6, 7, 8).

That with regard to the skeleton of the head *Colobodus* s. str. belonged to the Palaeoniscid type was shown by me already in 1916 (ANDERSSON 1916a, pp. 22–23), and in 1920 STOLLEY (pp. 30–32, 35–36, 38–45) gave further proof of this. As in 1919 I had an opportunity to study a part of STOLLEY's original material¹⁾ and as the Institution at Upsala possesses a quantity of fine *Colobodus* material both from German Muschelkalk and Alpine Triassic, I am now in a position to supplement rather essentially our former knowledge of the membrane bones of the head in the genus *Colobodus*.

In the first place it is obvious that a large unpaired nasalo-postrostral (*Na. ptr*, text figs. 85, 86) is present, which probably includes in itself the interrostrals as well. The antorbital (*Ant*, text figs. 85, 86) is a triangular plate, situated, as usual, laterally of the nasalo-postrostral, together with which it forms the boundary of the nasal opening. In front of the antorbitals and the nasalo-postrostrals there are three rostrals situated in a transversal row (*R*, text figs. 85, 86). Otherwise the bones show the conditions seen in text figs. 85, 86 and 87.²⁾

As STOLLEY (1920, pp. 45–65) has shown, the head in *Dollopterus*³⁾ shows similar conditions to that of *Colobodus*.

¹⁾ The private collection of Redacteur KÖNIG of Heidelberg and the collection of the Geological Institute of Heidelberg.

²⁾ In ought perhaps also to be pointed out that the parietals both in *C. bassanii* and *C. maximus* are small and square, and that in both these forms the head skeleton is very similar. It is therefore impossible, at least at present, to follow STOLLEY (1920, p. 44) in separating *C. bassanii* from the genus *Colobodus* s. str. (cf. p. 254 above).

³⁾ STOLLEY (1920, pp. 64, 65) points out the agreement between the so-called *Senionotus letticus* O. FRAAS and *Dollopterus*. I have myself had an opportunity during a visit to Stuttgart to make sure that the type specimen of this species really seems to belong to *Dollopterus*. Among other specimens in the Stuttgart Museum labelled *S. letticus* there were also a number that turned out to belong to *Gyrolepis*. STOLLEY (1920, p. 65) considered, however, that the ought provisionally to incorporate *S. letticus* with the genus *Perleius*.

The new genus from Tessin, *Meridensia*, established by me in 1916 (ANDERSSON 1916 a, pp. 25–29) also shows a number of primitive Palaeoniscid-like features with regard to the head skeleton.

The sensory canals of the head. In *Colobodus maximus* and *C. bassanii* I was able to trace the sensory canals of the head practically throughout their extension. In *C. königi*, on the other hand, I have only found them preserved in the ethmoidal region.

As is seen in text figs. 85, 86 and 87, they run in the same way as in *Perleidus woodwardi* and *Palaeoniscids*.

Fin skeleton. — While all the genera and especially *Catopterus*, *Dictyopyge*, *Colobodus s. str.* and *Perleidus* thus seem to show rather similar conditions with regard to the skeleton of the head, the same thing cannot be said about most of their fins. All the genera are, however, characterized by the abbreviate-heterocercal caudal fin. *Catopterus* and *Dictyopyge* have all the lepidotrichia of the anal and dorsal fins close together and jointed to the base, as is the case in Palaeoniscids and Platsysomids. In *Dictyopyge* it is certain, at least as far as the anal fin is concerned, that the lepidotrichia and the endoskeletal radials corresponded to each other in number, indicating a fin musculature specialized in the direction of the higher Ganoids and Teleosts (cf. SCHMALHAUSSEN 1912, 1913a, 1913b). Little is known about the ventral fin. To judge from *Dictyopyge macrura* its lepidotrichia ought on the whole to be jointed.

The unpaired fins show an essentially different type in *Perleidus* (DE ALLESANDRI 1910, Pl. II, fig. 2). The lepidotrichia of the dorsal and anal fins of this genus are not situated so close together as in the Palaeoniscids and are unjointed and unramified for a long distance proximally. The number of the endoskeletal radials is, at least in the dorsal fin, the same as that of the lepidotrichia. Both the exoand endoskeleton thus show in this case complete agreement with the higher Ganoids and Teleosts. The lepidotrichia of the ventral fins are, as in these forms, unjointed and unramified for a long distance proximally. *Dollopterus* and *Meridensia* resemble *Perleidus* at least with regard to the exoskeleton of their fins.

In *Colobodus*¹⁾ the lepidotrichia in the dorsal and anal fins are situated rather close together and the vast majority of them are also densely jointed. It is easy, however, to observe that a rather short proximal part is unjointed, that one or more joints immediately distally of this part are often longer than those following still more distally, or else that instead of the proximal unjointed part there are two or more strikingly long joints. It is also often possible to trace a tendency for the joints to fuse with one another

Text fig. 85. *Colobodus bassanii* DE ALLESANDRI.
After a specimen belonging to the Palaeontological Institute
at Upsala P. 725. 7/2. Sensory canals shown by shading.
Mx, maxillary; Op, operculum; Po, preoperculum; other terms
as in text fig. 86.

¹⁾ Observations made on specimens belonging to the Palaeontological Institute of Upsala.

in the proximal parts of the lepidotrichia. Both on the dorsal and anal fin the number of endoskeletal radials corresponds almost or exactly to that of the lepidotrichia. The epidotrichia of the ventral fins are unjointed, at least to a rather great extent. We find here, as is shown by these facts, a process undoubtedly going on towards the development of the type of fin described in *Perleidus*, which is, already pointed out, characteristic of the higher ganoids and Teleosts. *Colobodus* s. str. thus forms a natural link between the more primitive genera *Catopterus* and *Dictyopyge* on the one hand and *Pleidus*, with possibly *Dollopterus* and *Meridensia*, on the other. Under these circumstances there seem to be no arguments at all in favour of separating *Perleidus* and the forms that agree with it and establishing a special family for them, as one might at first feel called upon to do.

Some observations on the family Catopteridae; a summary.

From the account given above it ought to be obvious that the genera *Catopterus*, *Dictyopyge*, *Colobodus* s. str., *Perleidus* and *Dollopterus* are on the whole closely related to one another and that they form together, as far as we can judge at present, a rather uniform group. Because of this I see no reason to maintain a family *Colobodontidae* any longer, but consider it most convenient to group all the mentioned genera in the family *Catopteridae*. Whether *Meridensia* also belongs to this family is a question that cannot yet be answered. Provisionally, however, it seems as if we might include this genus as well among the Catopterids (cf. STOLLEY, 1920, pp. 83, 84).

The distinguishing features of the family *Catopteridae* may under these circumstances be summarized as follows. The shapes of the fishes vary rather considerably; sometimes they are rather slender, sometimes more deep-bodied. The head has a blunt snout with a weak indication of a rostrum. The eye far forward. Mouth large, extended far back. External membrane bones of the head ornamented with ganoine. On the ethmoidal region there lies posterior to the premaxillae a transverse series of rostrals, and behind them there follows a median unpaired rather large nasalo-postrostral, and on the right and left side of this an antorbital bone. The latter bone and the nasalo-postrostral surround the nasal apertures of either side. The nasalo-postrostral includes the nasal elements and the interrostrals of both sides, and sometimes also one or a couple of median rostral elements. The maxillary is low beneath and high behind

Text fig. 86. *Colobodus maximus* DAMES.

After a specimen belonging to the Palaeontological Institute at Upsala $\frac{1}{1}$. Sensory canals shaded.

Ant, antorbital; Dph, dermosphenotic; Ext, extrascapular; Fr, frontal; Na.pr, nasalo-postrostral; Pa, parietal; R, rostrals; So, supraorbital; Stemp.it, supratemporo-intertemporal; na, external nasal aperture.

Text fig. 87. *Colobodus maximus* DAMES.

Sketch after a specimen belonging to Redakteur Köstle of Heidelberg. $\frac{1}{1}$. Sensory canals shaded. Md, mandible; Mx, maxillary; Op, operculum; Po, preoperculum; Rbr, radii branchiostegi; Sop, suboperculum.

the orbital entrance. The mandibles lack coronoid processes. The hyomandibular is more or less oblique and has a processus opercularis. The preoperculum is a large triangular plate, extending far in front over the cheek. The operculum and the suboperculum both well developed, the latter often high. Interoperculum lacking. A median jugular plate is present. Dentition often adapted for crushing. The supraorbital canal has its posterior end in the parietal; posteriorly it does not anastomose with the infraorbital canal; anteriorly, on the other hand, there is an anastomosis through the antorbital, laterally of the nasal opening, between the two. The infraorbital canals have an ethmoidal commissure anteriorly through the rostrals. The preopercular canal runs along the posterior margin of the preoperculum. The cranial section of the lateral canal has a supratemporal commissure. On the parietal, the anterior, middle and posterior head-lines of pit organs are to be found at least in certain forms. The chorda dorsalis persistent and the ossifications of the neural and haemal arches probably rather weak. The caudal fin abbreviate-heterocercal or almost homocercal, always with its lepidotrichia jointed throughout. In both the anal and dorsal fin the lepidotrichia are present in nearly or quite the same number as the endoskeletal radials; in these fins each endoskeletal radial with only one long ossification; the lepidotrichia sometimes quite jointed, sometimes more or less unjointed proximally. The shoulder girdle has a large cleithral and a small clavicle (infraclavícula). The lepidotrichia of the pectoral fins are usually unjointed for a long distance proximally. The ventral fins are short-based; their lepidotrichs are jointed throughout or else unjointed for a bit in their proximal part. Fulcra are often rather powerfully developed on all the fins. Scales thick and robust with a covering of ganoine. In some forms an accessorial lateral line dorsally of the main one is found, extending from the neck towards the basis of the dorsal fin.

It is certain that, especially with regard to the development of the head and the shoulder girdle, the Catopterids are closely related to the Palaeoniscids, while, on the other hand, with regard to the development of the fins, they have attained a higher specialization than these. Although, as we have seen, the degree of specialization differs in this respect in different forms, still they all have, unlike the Palaeoniscids, an abbreviate-heterocercal caudal fin and about the same or practically the same number of lepidotrichia as endoskeletal radials in both the dorsal and anal fins. To this may be added that the ventral fins are, presumably as a rule, considerably more short-based than in the Palaeoniscids.

When these characters thus occur together it becomes necessary to separate the Palaeoniscids and Catopterids from a systematic point of view, even although it seems to be quite clear that the latter are descended directly from the former. I must therefore differ decidedly from ABEL, who (1919, pp. 186—189) did not recognize the Catopterids as an independent family, but grouped it with the Palaeoniscids (cf. p. 250 above).

I have already pointed out above (pp. 249—250) that such forms as *Boreosomus* and *Acrorhabdus* among the Palaeoniscids appear with regard to the anatomy of the head to be specialized in the same direction as the Catopterids, while the fins exhibit the conditions typical for Palaeoniscids. On the other hand it is also of interest to find that such genera among the Catopterids as *Catopterus* and *Dictyopyge* show typical Palaeoniscid-like conditions in the lepidotrichia, while *Perleidus* and *Dollopterus* are in this respect developed like genuine *Protospondyli*.

In any case it is clear from my account above that the Catopterids with the definition I have given to them, are closely connected phylogenetically with the Palaeoniscids. They must therefore be assigned from a systematic point of view to the sub-order *Chondrostei*, in which, as we shall see from my account below (Part II), they form together with Palaeoniscids and Platysomids a group that is well defined both from the Saurichthyids and the sturgeons.

It is of course impossible to decide with certainty whether the Catopterids form an intermediate link between the *Chondrostei* and the higher ganoids, but this does not seem probable. As we have found and as will be shown still further below, even the Palaeoniscids appear to be more specialized in certain respects than we should expect of forms from which, for instance, *Protospondyli* and Teleosts could be supposed to have descended, and it seems as if the same thing is true of the Catopterids. It is, above all, the development of the membrane bones of the cheek and the ethmoidal region and the course of the supraorbital canal that form arguments against the suppositions that Catopterids or the Palaeoniscid-like forms in general could have been the ancestors of the *Protospondyli* and other higher Ganoids and Teleost.

It ought also to be noted here that it seems as if a specialization of the skeleton of the unpaired fins in the direction of the Teleosts had taken place independently in Palaeoniscids (*Coccolepis*), Platysomids (LAMBE, 1914, p. 21), and Catopterids. We thus see that this specialization can take place rather easily among Chondrosteans, and that it must not be considered to be such an important morphological feature as has hitherto been thought.

Palaeoniscids, Platysomids and Catopterids compared with recent Ganoids and Teleost.

Palaeoniscids, Platysomids and Catopterids compared with sturgeons.

TRAQUAIR (1877 a, pp. 34-42; 1879, pp. 377-389; 1887, pp. 248-257) and WOODWARD, (1889 c, pp. 24-44; 1890 a, pp. 6-7, 15-16; 1895 b, pp. V-VIII; 1898a, pp. 81-94) have clearly shown that Palaeoniscids, Platysomids and Catopterids offer many resemblances to the sturgeons, and that they ought to be placed together with these in a common larger group. In the description given above I have been able to state some additional common features, as e. g., with regard to the extension of the chorda far forward in the basis cranii, the relations and shape of the inter- and basidorsals, the endoskeleton of the ventral fins, the pelvic girdle, and the membrane bones of the shoulder girdle.

On the other hand my investigations above also show the existence of considerable differences between the fossil forms under discussion under the sturgeons, and I intend here to pay attention to these differences so as to try to show their morphological importance.

A character that strikingly separates the Palaeoniscids and the allied families among the fossil forms from the sturgeons is the considerably greater degree of ossification in the primordial skeleton of the former. There is, however, a good deal of evidence to

support the view that in this respect the sturgeons are regressively specialized, as WOODWARD especially (loc. cit.) and after him GOODRICH (1909, p. 316) have maintained in opposition to BRIDGE (1878, pp. 717—731) and others, who saw in this a primitive character instead. Thus, as we have seen above, the primordial skeleton is very much ossified even in the Rhipidistids, Coelacanthids and Palaeoniscids, and below (Part II) we shall see how this is even more true in the case of the Saurichthyids, which are rather closely related to the sturgeons. In primitive fossil *Dipnoi*, according to TRAQUAIR (1878, p. 5), at least the primordial neurocranium is strongly ossified, while in the recent forms it is cartilaginous practically throughout. Even in certain Teleosts (GIERSE, 1904, p. 605—615; HANDRICK, 1901, p. 3—5) the ossifications in the primordial skeleton may be reduced, and we thus see that similar reductions may occur in the most different forms among the Teleostomes. An additional support for the view of WOODWARD and GOODRICH seems to me to be present in the fact that several ossifications actually exist in the primordial neurocranium of the sturgeons (BRIDGE, 1878, p. 698; PARKER, 1882a, pp. 175, 176) although they have lost their importance and therefore develop so late that they are as a rule only found in old specimens.

As far as can be judged, however, these ossifications seem, according to BRIDGE'S (1878) and PARKER'S (1882a) account, to show conditions that are on the whole rather Teleostean-like, while according to what we have seen in this work, the Palaeoniscids appear in this respect to be developed more in agreement with Polypterids and Crossopterygians. It is impossible to decide with certainty the position of the Saurichthyids in this respect, as the primordial neurocranium in them — at least in fully-grown specimens — is ossified in a single piece.

As we have seen from my account above, certain Palaeoniscids, e. g. *Birgeria*, are rather specialized in the direction of *Amia* and the Teleosts with regard to the orbito-temporal region. In *Birgeria* the ventral part of the interorbital wall has thus become thin and at one place fenestrated, and there is also a myodome, though in a very primitive stage of development. To this it may also be added that in this fish the distance between the foramen opticum and the canalis transversus is much shortened and that the fossa hypophyseos is very small, only forming a narrow vertical pit in the basis cranii. I do not, however, consider it probable that all the Palaeoniscids showed the same conditions, but that a number of them had a thick interorbital wall and had the orbito-temporal region developed on the whole as in the recent sturgeons.

The Palaeoniscids and even certain of the Catopterids have, as we have seen, indications of a rostrum, and we thus find conditions here that, as it were, predisposed to the development of the frequently very long rostrum of the sturgeons. It is noteworthy in this connection that in the Saurichthyids the lengthening process affected not only the rostrum but the mandibula as well.

In the sturgeons the parasphenoid is developed almost as in the higher ganoids, while at least in certain Palaeoniscids, as we have found, it shows a very curious specialization.

In the sturgeons the rostrum is covered, as we know, by a rather large number of bone-plates, and that we are not concerned here with primary conditions, but with secondary ones, is already evident from the differences present in this respect in different

species (cf. ALLIS, 1905, Pls. XVIII, XX; BERG, 1911, Pls. IV—VIII); a further support for this consists in the fact that neither the Palaeoniscids, Platysomids, Catopterids nor Saurichthyids (cf. Part II) show any indication at all of anything similar.

For similar reasons I also consider it obvious that the cheek and opercular skeleton is also reduced in the sturgeons. We have as a matter of fact found a fine example of a similar phenomenon in *Axelia* among the Coelacanthids, as we have seen above (pp. 98—99).

The connection between the palatoquadrates anteriorly under the rostrum is, as we know, a very remarkable character in the sturgeons, while by BRIDGE (1878, pp. 723, 724), and others has been interpreted as a primitive selachoid one. The Palaeoniscids and the closely allied forms show, on the contrary, the ordinary conditions, the palatoquadrates in them being separated anteriorly and each of them having articulated with the ethmoidal region by means of an autopalatine or perhaps sometimes by cartilage; this is also the case with the Saurichthyids, which, as we shall see, have in several respects sturgeon-like characters. It thus seems very probable that we are concerned here with a secondary character, a selachoid adaptation, in the sturgeons.

The absence of premaxillaries in the sturgeons must of course also be looked upon as secondary, as these bones are found in Saurichthyids, Palaeoniscids, Catopterids and Platysomids. That the premaxillaries could be reduced is seen in other Teleostomes as well such as Dipnoi and possibly the Coelacanthids too.

In the mandible of *Acipenser* we generally find, as is known, a couple of investigating bones. In old specimens, on the other hand, PARKER (1873, p. 256) says he has found an angular, dental, mixicoronoid («splenial») and mentomandibular. In the Liassic *Chondrosteus*, which can already be considered to be a sturgeon, TRAQUAIR (1887, p. 256) states that he has observed a dental and two other bones, one of which he takes to be the angular, the other as the articular. According to what we can assume, however, the dental both of *Acipenser* and *Chondrosteus* is a dentalo-splenial and the articular is probably the same bone as the one we called the supraangular in the Palaeoniscids above, and other bones too, as well as the development of the mandible as a whole, seem to have been Palaeoniscid-like. The evidence seems thus to show that the small number of bone elements in the mandible of the sturgeons is secondary and is probably due chiefly to reduction. In the Saurichthyids too we find, as we shall see, the same number of bones in the mandible as in the Palaeoniscids.

With regard to the development of the sensory canals the sturgeons certainly show a rather great resemblance to Palaeoniscids, Platysomids and Catopterids, but at the same time great differences can be observed. Thus in the sturgeons the supraorbital sensory canal anastomoses at its posterior end with infraorbital canal, then continuing in the normal way forward on to the ethmoidal region, where it runs forwards and downwards through the septum between the two nasal apertures of either side. In Palaeoniscids and the forms closely related to them the supraorbital canal has no connection posteriorly with the infraorbital canal and always extends into the parietal, to which is to be added the specially important fact that it never continues along in the ethmoidal region medially of the nasal aperture. It extends forward to the upper corner of the antorbital instead, where it is connected uninterruptedly with a portion of the infraorbital

canal running downwards and forwards laterally of the nasal aperture. Whether the continuation of the supraorbital canal forwards and medially of the nasal aperture is totally lacking or was developed as a «pit-line» is unknown. If we could verify the absence of this anterior part of the supraorbital canal, this would mean that Palaeoniscids, Platsomids and Catopterids belonged to a special type, from which neither the sturgeons nor the higher Ganoids could be thought to descend. With regard to the anterior end of the supraorbital canal the Saurichthyids show the conditions of typical sturgeons, while, on the other hand, with regard to the posterior end of this canal they resemble the Palaeoniscids.

At least in certain Palaeoniscids (*Acrorhabdus*) the primary skeleton of the shoulder girdle is, apart from its strong degree of ossification, considerably more primitive than in the recent sturgeons, as the canal for the dorsal musculature of the pectoral fin is quite absent. On the other hand, however, it appears to a certain extent to be specialized by the strong development of the nerve canal.

As ought to be clearly seen, most of the characters in which the sturgeons differ from the Palaeoniscid type are to be considered as regressive specializations. The sturgeons are closely related to the Palaeoniscids and forms nearest to them, but the idea that they should be directly descended from the Palaeoniscids, as WOODWARD (1889 c, pp. 42, 43; 1895 b, pp. V—VIII; 1898 a, pp. 82—94; 1915 a, p. LXXII) especially and GOODRICH (1909, pp. 307—321) have tried to show, seems, however, to be contradicted both by the condition of the ossifications of the primordial neurocranium, the extension and course of the supraorbital canal, and possibly also by the development of the shoulder girdle. Many of the better known Palaeoniscid forms are otherwise too strongly specialized for us to be able to imagine that the sturgeons had arisen directly from any of them.

Palaeoniscids, Platsomids and Catopterids compared with *Amia*.

On pp. 152—182 above I have been able to make detailed comparisons between the neurocranium of *Birgeria* among the Palaeoniscids and that of *Amia* among higher ganoids. I merely refer here to this account, but must, however, emphasize, as I have done just previously, the fact that a number of Palaeoniscids may possibly in certain respects, e. g. the fenestration of the orbitotemporal region, have shown more primitive conditions than *Birgeria*.

Apart from this I shall only in this connection enter upon some questions concerning the homologues of the membrane bones on the dorsal side of the ethmoidal region.

First with regard to the bone in *Amia* previously known as the ethmoid (ALLIS 1889, Pl. XLI; 1898, pp. 433—436; 1909 a, pp. 13—14, 17—22, 23—28), this apparently corresponds to the middle rostral in *Colobodus* and a couple of median rostrals in primitive Rhipidistids. The homologue of the paired lateral rostral in *Colobodus* is in *Amia* probably fused with the antorbital. Whether the middle rostral in *Amia* — a term that I now introduce instead of «ethmoid» — also includes within itself elements corresponding to the interrostrals of the Crossopterygians, is of course impossible to decide with certainty. To judge from the extension of the bone backwards between the nasals, this does not, however, seem improbable.

The antorbital in *Amia*, apart from its anterior end, which we have just dealt with, seems to be homologues with at least an anterior part of the antorbital of Palaeoniscids, Platsomids and Catopterids.

The nasal in *Amia* is pierced, as we know (ALLIS 1889, Pl. XLI), in a longitudinal direction by the most anterior part of the supraorbital canal and, in spite of its considerable width and extension in a medial direction, probably corresponds as a whole only to the nasal elements in the primitive Crossopterygians (cf. p. 98, 102—105, 114, 133—135 above). In Palaeoniscids, Platsomids and Catopterids, as we have seen, all the homologues of the nasal and postrostral elements of the Crossopterygians are probably fused into a single large plate, which also seems to include the interrostrals and sometimes one or more rostral elements (*Perleidus*).

In order to understand in *Amia* what has become of the homologues of the postrostrals of the primitive Crossopterygians we must first examine the conditions in *Polypterus*.

In this last-mentioned fish (TRAQUAIR, 1871; ALLIS, 1900 a, fig. 2, pp. 435—437; 1900 b, p. 262; 1905, pp. 417—420; 1917, pp. 111, 112) we find an unpaired so-called ethmoid, which is long and relatively narrow. Backwards it extends between the nasal elements of the right and left sides to the anterior end of the frontals and its posterior longer part is covered from the sides to a rather considerable extent by the nasal elements. In its anterior end, which is somewhat expanded, it is pierced by the ethmoidal commissure between the two infraorbital sensory canals. It thus corresponds (cf. ALLIS, 1900 b, p. 262) with its anterior part to a median or a couple of medial rostral elements, while its posterior parts probably include the homologues of the inter- and postrostrals.

I may now be supposed that in *Amia* the homologues of the post- and interrostral elements gradually became overgrown with nasal elements in the same way as has begun in *Polypterus*, at the same time becoming fused with premaxillaries anteriorly. This view seems, at least as far as can be now seen, to be far more probable than the one that ALLIS (1898, pp. 433—436; 450—456; 1909 a, p. 28) tried to maintain, namely that the posterior processes from the maxillaries of *Amia* should be the homologues of the articulatory processes of Teleosts (cf. ALLIS 1919 a).

Palaeoniscids, Platsomids and Catopterids compared with *Lepidosteus*.

With regard to the primordial neurocranium I have nothing to add to what I have said in my description of *Birgeria nougeoti* (cf. pp. 152—180 above). Here I shall confine myself to some remarks about the bones on the dorsal side of the ethmoidal region. The homologue of the middle rostral of *Colobodus* is represented in *Lepidosteus*, as in *Amia*, by the bone that was formerly called the ethmoid (ALLIS, 1905, pp. 407—417), and the homologue of the paired lateral rostral of *Colobodus* may have fused in *Lepidosteus*, in the same way as in *Amia*, with the antorbital, representing a considerable part of that bone.

The specimens of *Lepidosteus* investigated by me (belonging both to *L. platystomus* and to a smaller long-snouted species) show that, as ALLIS pointed out in 1905, pp. 415—416, the so-called ethmo-nasal of each side is connected anteriorly under the nasals uninterruptedly with the premaxillary on its side and that, in addition, its

anterior part has the same relation to the nasal capsule as the so-called posterior process from the maxillary in *Amia*, which has been dealt with above. ALLIS states further that this bone is pierced by n. olfactorius. I have observed myself that it extends ventrally so far downwards that it comes into contact with the vomer, and that the most anterior end of the palatoquadrate is attached to its ventral part. In these respects its ventral part thus shows conditions that make it probable that it is homologous with the preëthmoid of *Amia* (ALLIS 1897a, Pl. XXI, figs. 8—10; 1898, pp. 446—450; 1909a, pp. 17—22; SWINNERTON 1902, pp. 530—533). The anterior dorsal part of the bone, which is covered by the nasals, seems at least to some extent to be homologous to the correspondingly situated part in *Amia*, i. e., according to what we can discover from the fossil forms, it should comprise at least the homologue of the anterior postrostral elements of the Rhipidistids.

It is impossible at present to answer the questions as to whether the homologue of the posterior postrostral element of the Rhipidistids is also included in the part of the nasalo-ethmoid, which is covered by the nasals, or whether, together with the homologues of some posterior nasal elements, it formed the posterior part of the «nasalo-ethmoid», which is exposed behind the nasals, or finally, whether the posterior part of the «nasalo-ethmoid» is only to be taken as an anterior portion of the frontals, secondarily fused with the postrostrals.

Finally, with regard to the nasals in *Lepidosteus*, it seems as if they were homologous with the corresponding ones in *Amia*, but, as will be clear from what has just been said, it is also possible that they correspond only to certain of the anterior nasal elements of the Rhipidistids.

Palaeoniscids, Platyosomids and Catopterids compared with Teleosts.

With regard to the development of the neurocranium in Teleosts on the one hand and Palaeoniscids as represented by *Birgeria* on the other, I may refer to my account above (pp. 152—180). In addition, as in the case of *Amia* and *Lepidosteus*, I shall confine myself here as well to dealing with the homologues of the membrane bones on the dorsal side of the ethmoidal region. It may, however, be pointed out in this connection that our knowledge of the Teleosts is still very incomplete in this respect, and that there is still much to be learned before any far-reaching conclusions are possible.

In Teleosts there is a paired, frequently rather narrow nasal bone, situated dorsally of the nasal capsule and pierced longitudinally by the most anterior part of the supraorbital canal. It may sometimes happen that the nasals (*Arapaima*, *Heterotis*, *Osteoglossum*, *Notopterus*, *Petrocephalus*; RIDGEWOOD 1904a, pp. 69, 70) are developed in width in a medial direction so that they come more or less into contact with one another in the median line, as in *Amia* and *Lepidosteus*, covering, as RIDGEWOOD expressed it, the «mesethmoid.» In any case it will be clear that the nasals of the Teleosts are homologous with the similarly termed bones in the Rhipidistids, or more correctly speaking that they have been formed by fusion of the homologues of the nasal elements of these fishes.

The so-called «mesethmoid» is developed rather differently in different Teleosts. It is generally unpaired and extends between the nasals of the two side backward to the anterior ends of the frontals. It may also, however, as in *Esox* (HUXLEY 1864, fig. 69;

ALLIS 1898, pp. 434—436; 1905, Pl. 14, fig. 22; 1909 a, pp. 27, 28) be paired or show a certain indication of having had a paired origin, as in *Megalops* (RIDEWOOD 1904 a, p. 43), *Chatoësus* and *Dussumieria* (RIDEWOOD 1904 b, pp. 464, 469). As far as is known, it is only in *Elopsaurus* that it is pierced by an ethmoidal commissure between the infraorbital sensory canals. In certain cases a pit-line corresponding to the ethmoidal commissure may be situated above its anterior part, as in *Salmo*, *Esox*, *Silurus* etc. (cf. ALLIS 1905; 1909 a). Usually, however, this pit-line or indications of it are quite absent, and in at least the majority of the forms investigated the premaxillaries seem, as ALLIS has pointed out, to have such conditions that the anterior parts of the mesethmoid, which was related to the ethmoidal commissure, should be incorporated with them and form their processus ascendentes (ALLIS 1898, pp. 450—456; 1909 a, pp. 23—28).¹⁾

My observations in the fossil forms dealt with in this work seem to render possible a closer homologization of the so-called mesethmoid, at the same time also affording an argument in favour of the view maintained by ALLIS. It thus seems very probable that at least in such a form as *Elops* and possibly even in *Salmo*, *Silurus* and *Esox*, the anterior part of the so-called mesethmoid is homologous to the middle rostral in *Colobodus* or one or more of the medial rostral elements of the Rhipidistids, while its posterior part includes the homologues of the inter- and postrostrals of the latter.²⁾ It would thus be most closely homologous to the so-called ethmoid of *Polypterus*.

Under these circumstances it is not difficult to imagine either that in certain Teleosts the homologues of certain of the medial rostral elements of the Rhipidistids might, together with the interrostrals, fuse with the corresponding premaxillaries and form a processus ascendens, as ALLIS considered to be the case. As we have seen (pp. 144—145) an analogous phenomenon may be observed in Tetrapods.

In certain Teleosts the mesethmoid has, as we know, entered into the cartilage situated beneath it and is thus partly developed as cartilaginous bone.

The homologue of the antorbital (cf. ALLIS 1898, pp. 436—438) seems in Teleosts generally either to be reduced or to form part of the so-called lacrimal or possibly the ect-ethmoid as well. Only in certain Siluroids may an anterior part of it perhaps be represented (cf. JUGE 1898, Pl. 1; Mc MURRICH, 1884, p. 278; Pl. 2, fig. 1; Pl. 3, figs. 1, 2).

As ALLIS (1909 a, pp. 17—22) has shown, the preëthmoids seem to be fused with the vomere(s) in several Teleosts.

¹⁾ In 1917, however, ALLIS (1917 a, pp. 111—112) came to the conclusion that he must relinquish this view.

²⁾ In *Esox*, however, it is uncertain whether some of the middle rostrale elements are not absent, as in his form the two so-called ethmoids have their anterior ends separated.

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EXPLANATION OF PLATES.

Where nothing special is stated, the type specimens of the figures given here belong to the Palaeontological Institute of Upsala. The great majority of the photographs were taken by Miss AINA LAURELL of Upsala.

There were many great difficulties in the photographing and, in spite of great efforts, it was not possible to obtain as good figures as was desirable. This was due in the first place to the state of preservation of the material. The specimens were often very much broken and large pieces were missing here and there. The bone substance was sometimes dark-coloured, little differentiated from the rock, while sometimes, on the other hand, it was partly or entirely blue in colour because of transformation into vivianite.

Another reason why the figures given here do not satisfy all the demands one is entitled to make on them is that the photographic-apparatus at my disposal was partly of a very primitive and deficient nature.

When nothing is said to the contrary the figures show the natural size.

Plate I.

- Fig. 1. *Hybodus rapax* n. sp., tooth (*P. 41 b*); *a*, in medial aspect; *b*, in lateral aspect. $\frac{1}{1}$.
 » 2. » » » » » (*P. 41 a*); *a*, » » » » *b*, » » » » $\frac{1}{1}$.
 » 3. *Hybodus sasseniensis* n. sp., tooth (*P. 39 a*); *a*, in medial aspect; *b*, in lateral aspect. $\frac{2}{1}$.
 » 4. » » » » » (*P. 39 b*); *a*, » » » » *b*, » » » » $\frac{2}{1}$.
 » 5. » » » » » (*P. 39 c*); *a*, » » » » *b*, » » » » $\frac{2}{1}$.
 » 6. » » » » » (*P. 39 d*); *a*, » » » » *b*, » » » » $\frac{2}{1}$.
 » 7. » » » » » (*P. 39 e*); *a*, » » » » *b*, » » » » $\frac{2}{1}$.
 » 8. » » » » » (*P. 38*); *a*, » » » » *b*, » » » » $\frac{2}{1}$.
 » 9. » » » » » (*P. 633*); in lateral aspect. $\frac{4}{1}$. Below the tooth there is seen a dermal denticle.
 » 10. » » » » » (*P. 40*); in lateral aspect. $\frac{1}{1}$.
 » 11. Hybodontid selachian; basal plate of cephalic spine (*P. 351*); *a*, seen from the external surface; *b*, seen from the basal surface. $\frac{1}{1}$.
 » 12. Generically indeterminable selachian; basal portion of fin-spine (*P. 44*) in lateral aspect. $\frac{2}{1}$.
 » 13. » » » » » (the same species as in the preceding figure); anterior portion of fin-spine (*P. 43*) in lateral aspect. $\frac{2}{1}$.
 » 14. Detached dermal denticle (*P. 884*), probably from a hybodont selachian. $\frac{3}{2}$.
 » 15. Hybodont selachian; portion of fin-spine (*P. 102*) in lateral aspect. $\frac{1}{1}$.
 » 16. » » » » » (*P. 883*) » » » » $\frac{1}{1}$.
 » 17. » » » » fin-spine (*P. 282*) in lateral aspect. $\frac{1}{1}$.
 » 18. Probably hybodont selachian; portion of fin-spine (*P. 42*). *a*, in posterior aspect; *b*, in lateral aspect. $\frac{1}{1}$.
 » 19. Generically indeterminable selachian; fin-spine (*P. 35*); *a*, in posterior aspect; *b*, in lateral aspect. $\frac{2}{1}$.

- Fig. 20. *Acrodus scaber* n. sp., tooth (belonging to Prof. Dr. W. SALOMON at Heidelberg) in lateral aspect. $\frac{2}{1}$.
- » 21. *Polyacrodus pyramidalis* n. sp., tooth (*P. 717a*). $\frac{2}{1}$.
- » 22. » » » » » (*P. 714a*). $\frac{2}{1}$.
- » 23. » » » » » (*P. 715a*); **a**, in coronal aspect; **b**, in medial aspect; **c**, in lateral aspect. $\frac{3}{1}$.
- » 24. » » » » » tooth (*P. 716*). $\frac{2}{1}$.
- » 25. » » » » » (*P. 712b*). $\frac{2}{1}$.
- » 26. » » » » » (*P. 715a*). $\frac{2}{1}$.
- » 27. *Polyacrodus angulatus* » » » (belonging to Prof. Dr. W. SALOMON at Heidelberg). $\frac{2}{1}$.
- » 28. *Palaeobates* sp., tooth (*P. 97*). $\frac{2}{1}$.
- » 29. » » » » » (belonging to the Palaeontological Collection of the University of Christiania). $\frac{2}{1}$.

Plate 2.

- Figs. 1—19. *Acrodus spitzbergensis* Hulke; teeth. Figures 1, 7—17 and 19 after specimens *P. 98a-m* respectively, figures 2—6 after specimens *P. 99a-e* respectively and figure 18 after specimen *P. 100*. All the teeth are figured in coronal (**a**), medial (**b**), and lateral (**c**) aspects and with magnification $\frac{2}{1}$.
- » 20—21. *Acrodus vermiformis* n. sp., two teeth (*P. 98n* and *P. 101* respectively); **a** in coronal, **b** in medial and **c** in lateral aspect. Both figures with magnification $\frac{2}{1}$.

Plate 3.

- Fig. 1. *Acrodus oppenheimeri* n. sp., tooth probably from the unpaired symphyseal transverse row (from specimen *P. 105*); somewhat magnified.
- » 2. » » » » » tooth probably from some of the most anterior transverse rows; in medial aspect. From specimen *P. 105*. $\frac{4}{3}$.
- » 3. » » » » » same tooth as in the preceding figure in lateral aspect. $\frac{3}{2}$.
- » 4—5. » » » » » teeth in shape intermediate between those of the anterior and middle transverse rows (from *P. 105*). $\frac{4}{3}$ and $\frac{7}{3}$ respectively.
- » 6. » » » » » tooth from some of the middle transverse rows, in lateral aspect. (*P. 105*). $\frac{4}{3}$.
- » 7. » » » » » tooth from some of the posterior transversal rows (*P. 105*). $\frac{5}{4}$.
- » 8. » » » » » tooth of the same type as that in figure 6; **a**, in coronal, **b**, in medial, and **c** in lateral aspect. Original belongs to the Royal State Museum at Stockholm. $\frac{4}{3}$.
- » 9. » » » » » tooth of about the same type as that in the preceding figure in lateral aspect (*P. 105*). $\frac{4}{3}$.
- » 10. » » » » » two teeth, the right one of which is a transitional type between those of the middle and posterior transverse rows (*P. 105*). $\frac{3}{2}$.
- » 11. » » » » » Tooth from the most posterior transverse row (*P. 105*). $\frac{5}{2}$.
- » 12. *Palaeobates polaris* n. sp., tooth probably from the unpaired symphyseal row (*P. 107*). $\frac{3}{2}$.
- » 13. » » » » » two teeth from rows **b** and **c** (cf. fig. 16) in coronal aspect (*P. 107*). $\frac{2}{1}$.
- » 14. » » » » » tooth from row **b** showing the relations between the real masticatory and the lateral surfaces of the crown (*P. 107*). $\frac{2}{1}$.

Fig. 15. *Palaeobates polaris* n. sp., tooth, possibly from row *b*, in medial aspect (*P. 107*). Showing the relations between the masticatory surface and the baso-medially directed surface of the crown. $\frac{2}{1}$.

» 16. » » » left mandible (*b*) and counterpart (*a*) with the left ceratohyal (*chy*) and five transversal rows of teeth (*a—c*) in situ (*P. 107*). $\frac{1}{1}$.

Figs. 17—18. *Palaeobates polaris* n. sp. Teeth in transverse section (*P. 107*) *p*, pulp cavity. Enamel not visible in the sections. $\frac{3}{1}$.

Fig. 19 *a—d*. *Ceratodus* sp. right mandibular tooth in section (*a*) in medial (*b*) in dorsal (*c*) and in ventral (*d*) aspects (*P. 350*). *k*, contact surface by which the tooth has met that of the opposite side (referred to in the text as surface *a*). $\frac{1}{1}$.

Plate 4.

Fig. 1. *Wimania sinuosa* n. sp., head from the right side with the cheek plates and parts of the cranial roof removed (*P. 257*).

» 2. *Wimania sinuosa* n. sp., the same head seen from the left side.

Explanation of index letters.

Aang, autangular; *Alsph*, alisphenoid fused with and forming a ventral process from the fronto-dermosphenotic; *Aup*, autopalatine; *Br*, ceratobranchial; *Bsph*, basisphenoid; *Chy*, ceratohyal; *Fr. dsph*, fronto-dermosphenotic; *Icor. pra*, intercoronoideo-prearticular; *Mptg*, metapterygoid; *Op*, operculum; *Pa. it*, parieto-intertemporal (represented by the posterior part of the ventral longitudinal lamella); *Psph*, parasphenoid (anterior end); *Pt*, pterygoid; *Ptr*, postrostral; *Qu*, quadrate; *Stemp. ext*, supratemporo-extrascapular; *Uhy*, urohyal; *al*, paired forward-pointing lamella from the basisphenoid corpus; *e*, basiptyergoid process; *f*, anterior end of the prootico-opisthotic; *f₁*, dorsal process from the prootico-opisthotic (dorsal end); *h*, antero-ventral process from the supratemporo-extrascapular; *j*, loose bone probably from the shoulder girdle; *V_{2, 3}*, sinus in the dorso-lateral edge of the basisphenoid indicating the exists of the roots for the r. maxillaris trigemini, r. mandibularis trigemini, ramus ophthalmicus trigemini, n. buccalis lateralis and n. ophthalmicus lateralis.

Plate 5.

Fig. 1. *Wimania sinuosa* n. sp., the same head (*P. 257*) as in the preceding plate, seen from above. The cranial roof partly imperfectly preserved (posteriorly and on the left side).

» 2. » » » » cheek plates and certain bones from the visceral skeleton of the right side. The same specimen as in Pl. 4 (*P. 257*).

» 3. » » » » Some remains of scales (*P. 255*). $\frac{3}{2}$.

» 4. » » » » cheek plates and some bones from the visceral skeleton of the left side. The same specimen as in Pl. 4 (*P. 257*).

Explanation of index letters.

Alsph, alisphenoid fused with and forming a ventral process from the fronto-dermosphenotic; *Aup*, autopalatine; *Bsph*, basisphenoid; *Co*, coronoid; *De*, dental; *Fr. dsph*, fronto-dermosphenotic; *Icor. pra*, intercoronoideo-prearticular; *La. ju*, lacrimo-jugal; *Mptg*, metapterygoid (posterior part); *Mx*, maxillary; *Na. ant*, nasalo-antorbital; *Op*, operculum; *Pa. it*, parieto-intertemporal (ventral longitudinal lamella); *Pco*, precoronoid plates; *Po*, postorbital; *Pop. quj*, preoperculo-quadratojugal; *Ptr*, postrostral; *Scl*, sclerotic plates; *So*, supraorbitals (boundaries between the various elements indistinct); *Sq. pop*, squamoso-preopercular; *Stemp. ext*, supratemporo-extrascapular; *al*, paired for-

ward-pointing lamella from the basisphenoid corpus; *e*, basiptyergoid process; *f₁*, dorsal process from the prootico-opisthotic (in this plate only the dorsal extremity); *ifc*, infraorbital sensory canal (in this plate only a part of it preserved in the postorbital); *jc*, jugal sensory canal (in this plate only preserved in the squamoso-preopercular); *V_{1, 2, 3}*, sinus in the dorso-lateral edge of the basisphenoid indicating the place of exit for the roots of the r. maxillaris trigemini, r. mandibularis trigemini, r. ophthalmicus trigemini, n. buccalis lateralis and n. ophthalmicus lateralis.

Plate 6.

Fig. 1. *Wimania sinuosa* n. sp., postorbital cheek plates and certain remains of the visceral skeleton of the right side (cf. Pl. 5, fig. 2). The same specimen as in Pl. 4 (P. 257).

- » 2. » » » » cheek plates and certain bones of the visceral skeleton of the left side. Counter part to the piece in Pl. 5 fig. 4. (P. 257).
- » 3. » » » » parts of the visceral skeleton of the right side showing the metapterygoid in its relation to the pterygoid and the basiptyergoid process. A dorsal part of the posterior limb of the pterygoid removed in such a way that the metapterygoid is visible in its total extension. Anteriorly the metapterygoid is partly preserved as an impression of the lateral surface as is also the case with the greater part of the pterygoid. The same specimen as in Pl. 4 (P. 257).
- » 4. » » » » parts of the visceral skeleton of the right side (partly the same as in figures 1 and 3). In this figure the dorsal end of the posterior limb of the pterygoid (*Pt*) in situ showing that the metapterygoid (*Mptg*) is situated laterally of it. (P. 257).

Explanation of index letters.

Aup, autopalatine (impression of the outer side); *Bsph*, basisphenoid (here represented only by an end of the basiptyergoid process *e*); *C*, coronoid; *De*, dental; *Icor, pra*, intercoronoideo-prearticular; *La. ju*, lacrymo-jugal (posterior part only in this plate); *Mptg*, metapterygoid (in fig. 1 only the posterior end); *Op*, fragment of the operculum; *Pa. it*, parieto-intertemporal; *Pco*, precoronoid plates; *Po*, Postorbital; *Pop. quj*, preoperculo-quadratojugal; *Pt*, pterygoid (preserved as impression of the external surface); *Ser*, sclerotic plates; *Sg. pop*, squamoso-preopercular; *Stemp. ext*, supra-temporo-extrascapular; *e*, basiptyergoid process (distal part); *ifc*, infraorbital sensory canal (here only preserved in the postorbital and plate X); *x*, plate of bone pierced by the infraorbital canal. The plate has been situated between the postorbital and the upper (posterior) end of the lacrymo-jugal.

Plate 7.

Fig. 1. *Wimania sinuosa* n. sp., parasphenoid and preethmoid together with parts of autopalatine and prootico-opisthotic in ventral aspect. From the same specimen as Pl. 4 (P. 257).

- » 2. » » » » part of the ventral surface of the prootico-opisthotic and the posterior part of the parasphenoid as impressions in the stone. To the right of both a part of the pterygoid of the right side. From the same specimens as the preceding figure (P. 257).
- » 3. » » » » head in ventral aspect. The same head is in Pl. 4 (P. 257).
- » 4. indet. genus et spec. Detached prootico-opisthotic (right) in medial aspect; the posterior end with the process. Original of the figure belongs to the Royal State Museum at Stockholm.

- » 5. *Wimania sinuosa* n. sp., metapterygoid, pterygoid, basiptyergoid process, and some fragments of other bones of the right side; in lateral aspect. Cast of the piece reproduced in plate 6, figs. 1, 3, 4 (P. 257).

Explanation of index letters.

Aang, autangular; *Aup*, autopalatine; *Br*, ceratobranchial (only ventral ends visible); *Bsph*, basisphenoid (basiptyergoid process *e*); *Chy*, ceratohyal; *Cl*, cleithral; *Co*, coronoid; *Icl*, clavicle; *Icor*, *pra*, intercoronoideo-prearticular; *Mptg*, metapterygoid; *Pa. it*, parieto-intertemporal; *Pethm*, preethmoid in ventral aspect; *Pop. quj*, preoperculo-quadratojugal; *Pro. o*, prootico-opisthotic; *Psph*, parasphenoid; *Pt*, pterygoid; *Uhy*, urohyal; *e*, basiptyergoid process; *c*, posterior process from the corpus of the prootico-opisthotic.

Plate 8.

Fig. 1. *Wimania sinuosa* n. sp., the same head as in Pl. 4. (P. 257) with a dorsal part of the posterior limb of the pterygoid removed to show the shape and position of the prootico-opisthotic (*Pro. o*).

- » 2. *Wimania? multistriata* n. sp., supratemporo-extrascapular (*Stemp. ext*) and parieto-intertemporal (*Pa. it*) of a small specimen (P. 252) seen from the ventral surface.
 » 3. » » » tooth (P. 238).
 Figs. 4-6. » » » » scales (P. 247 and P. 248).
 Fig. 7. » » » » pelvic bone (P. 203).

Explanation of index letters.

Alsph, alisphenoid fused with and forming a process from the fronto-dermosphenotic; *Aup*, autopalatine; *Br*, ceratobranchial anterior part; *Bsph*, basisphenoid; *Fr. dsph*, fronto-dermosphenotic; *Mptg*, metapterygoid (antero-dorsal part); *Op*, operculum; *Pa. it*, parieto-intertemporal (in fig. 1, only posterior parts of the ventral lamella); *Pelh*, pelvic plate; *Pro. o*, prootico-opisthotic; *Pt*, pterygoid; *Ptr*, postrostrals; *Stemp. ext*, supratemporo-extrascapular; *al*, part of the anteriorly pointing lamella of the basisphenoid; *e*, basiptyergoid process; *f*, anterior end of the prootico-opisthotic; *fj*, dorsal process from the prootico-opisthotic; *h*, process from the supratemporo-extrascapular reaching downwards and forwards to the prootico-opisthotic.

Plate 9.

Fig. 1. *Wimania? multistriata* n. sp., scales and lepidotrichia (P. 246).

- » 2. » sp., portion from the caudal region with the dorsal and ventral lobes of the caudal fin (P. 253).
 » 3. » » scale from the specimen in preceding figure (P. 253). $\frac{2}{1}$.

Plate 10.

Fig. 1. *Sassenia tuberculata* n. sp., parts of the cranial roof and visceral skeleton (P. 225). The bones mainly preserved as impressions of the inner surface.

- » 2. » » » » scales (P. 224).
 » 3. » » » » bones of the cheek and bones of the visceral skeleton (P. 226) partly preserved as impressions of the lateral surface.
 » 4. » » » » parts of the visceral skeleton (P. 226).

Fig. 5. *Sassenia tuberculata* n. sp., scales (P. 226). Exposed area of lateral surface. $\frac{2}{1}$.
 » 6. » » » » Ornament of a cheek plate (*Pop, quj?* on fig. 3) preserved as
 an impression in the stone (P. 226). $\frac{2}{1}$.

Explanation of index letters.

Co, coronoid (anterior and ventral part); *Mptg*, metapterygoid (posterior part); *Icor. pra*, intercoronoideo-prearticular (dorsal part); *La. ju*, lacrymo-jugal; *Op*, operculum; *Pa. it*, parieto-inter-temporal; *Pco*, precoronoid; *Po*, postorbital; *Pop. quj?* probably preoperculo-quadratojugal; *Pt*, pterygoid; *Sang. ang*, supraangulo-angular, fragment; *Sq. pop*, squamoso-preopercular; *Stemp. ext*, supratemporo-extrascapular; *a*, bone-plate situated in the interspace between the postorbital and operculum dorsally of the squamoso-preopercular; *jc*, jugal canal (in the squamoso-preopercular); *jfc*, infraorbital canal (in the lacrymojugal, where its posterior part is weathered away and marked by a shallow furrow).

Plate II.

Axelia robusta n. sp., head (P. 195) seen from the right side. The external bones partly preserved as impressions of the outer surface, counterpart figured in plates 12 and 13.

Explanation of index letters.

Alsph, alisphenoid fused with and forming a long ventral process from the fronto-dermosphenotic; *Br*, ceratobranchial (in this figure represented by a fragment only); *Chy*, ceratohyal (in this figure only the posterior end is seen); *De*, dental (fragment); *Ext*, extrascapular plates; *Fr. dsph*, fronto-dermosphenotic; *Icl*, clavicle (part of the ventral limb in this figure); *Icor. pra*, intercoronoideo-prearticular (in this figure only a dorsal part of the bone visible); *Mptg*, metapterygoid; *Na. ant*, nasalo-antorbital; *Op*, operculum; *Pa. it*, parieto-inter-temporal; *Pro. o*, prootico-opisthotic (in this figure only a postero-lateral part of the bone preserved); *Pt*, pterygoid; *Ptr*, postrostral; *Qu*, quadrate; *Sang. ang*, supraangulo-angular; *Scl*, supracleithral; *Scl*, sclerotic ring; *Stemp. ext*, supratemporo-extrascapular; *e*, basipterygoid process of the basisphenoid (here only a part of the distal end is seen); *lc*, the cranial section of the lateral line in the supratemporo-extrascapular; *na₁* and *na₂*, nasal apertures; *r. ophth*, furrow crossing the lateral side of the alisphenoid and indicating the course of the n. ophthalmicus lateralis; *s. com*, supratemporal commissure between the cranial sections of the lateral line of the right and left sides.

Plate 12.

Axelia robusta n. sp., head (P. 195) from the right side. Counter part figured in Pl. 11. The external bones mainly preserved as impressions of the inner side.

Explanation of index letters.

Aang, autangular; *Alsph*, alisphenoid fused with and forming a long process from the fronto-dermosphenotic; *Br*, ceratobranchial; *Chy*, ceratohyal; *Co*, coronoid (fragment); *Ext*, extrascapular plates; *Fr. dsph*, fronto-dermosphenotic; *Icl*, clavicle (ventral part); *Icor. pra*, intercoronoideo-prearticular; *Mptg*, metapterygoid; *Na. ant*, nasalo-antorbital; *Op*, operculum (impression of inner side); *Pa. it*, parieto-inter-temporal; *Pethm*, preëthmoid; *Pro. o*, prootico-opisthotic (only a small part visible); *Pt*, pterygoid; *Ptr*, postrostral; *R*, rostral-plates; *Scl*, supracleithral; *Scl*, sclerotic ring; *Sscap*, suprascapular; *Stemp. ext*, supratemporo-extrascapular; *e*, basipterygoid process of the basisphenoid; *lat. for*, foramen on the preëthmoid for vessels and nerve branches to the extremity of the snout (branches of r. maxillaris trigemini and n. buccalis lateralis); *Ms*, furrow along the ventral border of the lateral surface of the preëthmoid for vessels and nerves (r. maxillaris trigemini and n. buccalis lateralis); *na₁*, anterior nasal aperture; *s. com*, supratemporal cross-commissure between the cranial sections of the lateral lines.

Plate 13.

Axelia robusta n. sp., the same parts of the head (P. 195) as in the preceding plate but with the metapterygoid and a dorsal part of the posterior limb of the pterygoid removed to show better the ossifications in the primordial neurocranium. The prootico-opisthotic (*Pro. o*) in this figure is represented by an imperfect impression of the medial side.

Explanation of index letters.

Bsph, basisphenoid (in lateral aspect); *Psph*, parasphenoid (here only the posterior part seen); *al*, paired forward pointing lamella from the basisphenoid corpus; *v*, paired ventral process from the basisphenoid corpus.

Other index letters the same as in plates 11 and 12.

Plate 14.

Fig. 1. *Axelia robusta* n. sp., head seen from above. The same head as in plates 11, 12, 13 (P. 195). The external surface of the bones of the dermal cranial roof not preserved.

Figs. 2-3. " " " " The anterior part of the cranial roof and its relations to the basisphenoid. Same specimen as in the preceding figure (P. 195). The posterior end for the furrow of the n. ophthalmicus lateralis (*r. ophth.*) clearly seen on the alisphenoid.

Fig. 4. " " " " The membrane bones on the upper side of the ethmoidal region seen from in front. The same specimen as in the figures above (P. 195).

" 5 " " " " basisphenoid seen from in front.

After the same specimen as the other figures on this plate and plates 11-13 (P. 195)

Bsph, basisphenoid with the anterior ends of the basiptyergoid processes (*e*) and the anterior parts of the anteriorly pointing lamella (*al*) lacking. The fossa bounded by the corpus and the anterior pointing lamellae is clearly shown. Parasphenoid in transversal section.

Explanation of index letters.

Alsph, alisphenoid fused with and forming a long process from the fronto-dermosphenotic; *Bsph*, basisphenoid; *Ext*, extrascapular plates; *Fr. dsph*, fronto-dermosphenotic; *Ir*, interrostral; *Na. ant*, nasalo-antorbital; *Pa. it*, parieto-intertemporal (the part laterally of the ventral lamella not preserved); *Psph*, parasphenoid (in transverse section); *Ptr*, postrostral; *R*, rostrals; *So*, supraorbitals; *Sscop*, suprascapular; *Stemp. ext*, supratemporo-extrascapular; *al*, paired anteriorly pointing lamella of the basisphenoid; *e*, basiptyergoid process; *ife*, infraorbital canal (in the dermosphenotic component of the fronto-dermosphenotic); *m*, myodome; *na1* and *na2*, nasal apertures; *p*, pores of the supraorbital sensory canal; *r*, torus on the medial side of each anterior lamella of the sphenoid; *r. ophth*, furrow for the n. ophthalmicus lateralis (posterior end) on the alisphenoid; *s*, furrow developed in relation to the hypophysis. Together with cartilage it has formed a vertical canal opening in the myodome; *v*, paired ventral process from the basisphenoid corpus; *V_L*, longitudinal section through the canal for the n. ophthalmicus profundus or a somewhat equivalent nerve.

Plate 15.

Figs. 1, 2. *Axelia robusta* n. sp., parts of the visceral skeleton of the right side (P. 169). The bones to some extent preserved as impressions of the lateral surface. In fig. 2 a part of the pterygoid (*Pt*), ceratohyal (*Chy*) and

the intercoronoideo-prearticular (*Icor. pra*) removed to show the supraangulo-angular (*Sang. ang*) and the corpus of the quadrate (*Qu*). In figure 1 there are seen behind the sclerotic ring (*Scr*) a number of loose very small bone-plates which cover the cheek, and besides there are two tubes of bone, one of which surrounds a part of the infraorbital canal (*jfc*) and the other a part of the jugal canal (*jc*). A well developed mandibular sensory canal (*mc*) is clearly shown in figure 2.

Explanation of index letters.

Chy, ceratohyal; *De*, dental; *Icor. pra*, intercoronoideo-prearticular; *Mptg*, metapterygoid; *Na. ant.*, nasalo-antorbital (fragment); *Op*, operculum; *Pt*, pterygoid; *Qu*, quadrate; *Sang. ang.*, supraangulo-angular; *Scr*, sclerotic ring; *Spl*, splenial; *jc*, tube of bone surrounding a part of the jugal sensory canal; *jfc*, tube of bone surrounding a part of the infraorbital sensory canal; *mc*, mandibular sensory canal; *p*, pores of the mandibular sensory canal; *t*, tubuli of the mandibular sensory canal.

Plate 16.

Fig. 1. *Axelia robusta* n. sp., parasphenoid (*Psph*) and preëthmoid (*Pethm*) in ventral aspect. The same specimen as the one figured in plates 11—14 (*P. 195*). On the ventral surface of the parasphenoid a number of rather large spheroid teeth preserved.

- » 2. » » » » tooth from the parasphenoid reproduced in fig. 1 (*P. 195*). $\frac{5}{2}$.
- » 3. » » » » Part of the caudal fin and a part of the squamation (*P. 222*) preserved as impression.
- » 4. » » » » part of the parietointertemporal of the same specimen as in plates 11—14 (*P. 195*) magnified to show the character of the ornament. $\frac{3}{2}$.
- » 5. » » » » part of the squamation (*P. 230*).
- » 6. » *elegans* » » operculum preserved as impression of the lateral surface (*P. 223*).
- » 7. » » » » part of the squamation (*P. 221*). $\frac{2}{1}$.

Explanation of index letters.

Pethm, preëthmoid; *Psph*, parasphenoid; *f. pal*, foramen probably for a dorsal branch of the r. palatinus anterior; *lat. for.*, foramen for vessels and nerve branches (branches of r. maxillaris trigemini and n. buccalis lateralis) to the foremost parts of the snout; *ms*, furrow along the ventral border of the lateral surface of the preëthmoid for vessels and for r. maxillaris trigemini and n. buccalis lateralis.

Plate 17.

Fig. 1. *Axelia elegans* n. sp., parts of the head skeletons together with the anterior dorsal fin (*D1*) and one of the pectoral fins (*P. 223*).

- » 2. » » » » magnified detail of the same specimen (*P. 223*) as in figure 1 showing some of the membrane bones of the cranial roof and some scales. Especially noteworthy are the conditions of the cranial section (*lc*) of the lateral line, as the supratemporal cross-commissure (*s. com*) is given off from it within the supratemporo-extrascapular (*Stemp. ext*). $\frac{3}{2}$.
- » 3. *Scleracanthus asper* n. sp., anterior dorsal fin (*D1*) with its supporting endoskeletal bone (*Sp1*), the endoskeletal supporting bone of the posterior dorsal fin (*Sp2*), and parts of the axial skeleton (*P. 239*).

Explanation of index letters.

Alsph, alisphenoid fused with and forming a process from the fronto-dermosphenotic; *D₁*, anterior dorsal fin; *Fr. dsph*, fronto-dermosphenotic; *Op*, operculum; *Pa. it*, parieto-intertemporal; *Pc*, pectoral fin; *Psph*, parasphenoid (posterior half); *Pt*, pterygoid (upper part of the posterior limb); *Qu*, quadrate; *So*, supraorbitals; *Sp₁*, supporting bone for the anterior dorsal fin; *Sp₂*, supporting bone for the posterior dorsal fin; *Stemp. ext*, supratemporo-extrascapular; *lc*, cranial section of the lateral canal; *s. com*, supratemporal cross-commissure given off already within the supratemporo-extrascapular.

Plate 18.

- Fig. 1. *Myrlacanthus lobatus* n. sp., some scales from the specimen (*P. 218*) in figure 4 of this plate. $\frac{2}{1}$.
 » 2. *Scleracanthus asper* » » parts of metapterygoid (*Mptg*) und pterygoid (*Pt*) in medial aspect; from specimen *P. 211a*.
 » 3. *Myrlacanthus?* or *Scleracanthus?* sp., membrane bones on the anterior part of the cranial roof (*P. 198*). The specimen with the postrostral subdivided into one anterior (*Ptr₁*) and one posterior (*Ptr₂*) plate. The interrostral (*Ir*) probably paired and the rostrals (*R*) more numerous than in *Axelia*. For the explanations of designations cf. further Pls. 11—14.
 » 4 » *lobatus* n. sp., parts of the visceral skeleton of the right side with fragments of the shoulder girdle (*Cl* and *Icl*) of specimen *P. 218*. The bones partly preserved as impressions in the stones. Among the other bones there are seen several of various sizes (*Dp*), which have covered the copula and the gill-arches and which are provided with more or less large spheroid teeth.

Explanation of index letters.

Aang, autangular; *Cl*, cleithral; *De*, dental; *Dp*, tooth-bearing plates from the copulae and the gill-arches; *Fr. dsph*, fronto-dermosphenotic; *G?* jugular plate?; *Icl*, clavicle; *Ir*, interrostral; *Mptg*, metapterygoid; *Na. ant*, nasalo-antorbital; *Op*, operculum; *Pt*, pterygoid; *Ptr₁*, anterior postrostral plate; *Ptr₂*, posterior postrostral plate; *Qu*, quadrate; *R*, rostrals; *Sang. ang*, supraangulo-angular; *Spl*, splenial; *p*, pores of the mandibular sensory canal.

Plate 19.

- Fig. 1. *Scleracanthus asper* n. sp., parts of the visceral skeleton of the right side together with the ventral limbs of the clavicles (*Icl*) of specimen *P. 240*. The bones partly as impressions of the external side. *Aang*, autangular; *Art?* possibly articular in section; *G*, jugular plate; *Sang. ang*, supraangulo-angular; *Scrp*, sclerotic plate; *mc*, posterior portion of the mandibular sensory canal and *p*, a number of pores of this canal.
 » 2. » » » » scale (*P. 242a*). $\frac{2}{1}$.
 » 3. *Myrlacanthus spinosus?* n. sp., parts of the visceral skeleton and a fragment of the parasphenoid (*Psph*) of specimen *P. 215*.

Explanation of index letters.

Aang, autangular; *Art?* possibly articular; *De*, dental; *Dp*, tooth-bearing plate, probably one of those which have covered the copular series; *G*, jugular plate; *Icl*, clavicle (in fig. 1, only the ventral limb preserved); *Psph*, parasphenoid; *Sang. ang*, supraangulo-angular; *Scrp*, sclerotic plate; *Spl*, splenial; *mc*, mandibular sensory canal; *p*, pores of the mandibular sensory canal.

Plate 20.

Fig. 1. *Scleracanthus asper* n. sp., part of an external bone of the head from impression in the stone.

The character of the ornament clearly shown. After specimen *P. 242 c*.

- » 2. *Myliacanthus spinosus* n. sp., operculum preserved as impression of the inner surface (*P. 703*).
- » 3. *Lyrocephalus euri* WIDMAN, parts of the neurocranium and visceral skeleton of the right side (orig. of WIDMAN 1916).
- » 4. " " " parts of the neurocranium and visceral skeleton of the left side with the prootic and opisthotic in situ.
- » 5. *Polypterus* sp., part of neurocranium seen from the left side showing the prootic (*Pro*) at the anterior end of the bulla acustica saccularis (*b. a.*).
- » 6. *Birgeria mougeoti* (AGASSIZ) neurocranium (*P. 165*) seen from the right side. In the posterior half certain lateral parts both of the sphenoid (*Sph*) and the prootico-opisthotic (*Pro. o*) removed.

Explanation of index letters

Alsph, autosphehotic (in fig. 5); *Bo*, basioccipital; *Co. a.*, columella auris; *Epo*, epiotico-opisthotic; *Ept*, epipterygoid; *O*, opisthotic; *Pp*, postparietal (ventral process); *Pro*, prootic; *Pro. o*, prootico-opisthotic; *Psph*, parasphenoid; *Pt*, pterygoid; *Qu*, quadrate; *Sph*, sphenoid; *al*, anterior portion of the pars laterales of the sphenoid; *a. car. int.*, paired foramen for arteria carotis interna; *a. opt.*, foramen probably for the arteria optica; *b.*, process on the posterior margin of the pars lateralis of the sphenoid; *b. a.*, bulla acustica saccularis; *bsph*, part of the pars basalis of the sphenoid between the fenestra optica and the canalis transversus; *c.*, processus on the posterior margin of the pars lateralis of the sphenoid; *d.*, portion of the pars basalis of the sphenoid anterior to the fenestra optica; *fc*, canalis facialis (posterior opening); *fen. opt.*, fenestra optica; *my*, fossa in which the musculus rectus externus had its origin. At the anterior end of this fossa lies the opening of the canalis transversus. The fossa corresponds partly to the myodome of *Amia* and Teleosts; *n. olf.*, canal for the nn. olfactorii through the sphenoid; *pl*, profound lamella of the parasphenoid; *pr. asc.*, processus ascendens of the epipterygoid; *pr. ot.*, processus oticus of the epipterygoid; *v.*, foramen probably for the vena cerebialis anterior; *II*, for opticum; *III*, foramen oculomotorii; *IV*, foramen trochlearis; *V*, place of exit for the trigeminal except r. ophthalmicus profundus. The n. buccalis lateralis was also transmitted at this place; *VI*, canal for r. ophthalmicus profundus in section; *X*, incisure on the opisthotic indicating the course of the vagus nerve through the cranial wall backwards.

Plate 21.

Fig. 1—3. *Birgeria mougeoti* (AGASSIZ), sphenoid after a model made in accordance with my observations in specimen *P. 165*. The model is reproduced in ventral (fig. 1), dorsal (fig. 2) and lateral (fig. 2) aspects.

- » 4. " " " anterior part of the caudal region (*P. 165*) with dorsal and anal fins.
- » 5—7. " " " teeth *P. 626*, *P. 628*, *P. 884* respectively. The teeth *P. 626* and *P. 628* with magnification $\frac{5}{2}$, and tooth *P. 884* with magnification $\frac{3}{2}$.

Explanation of index letters.

A, anal fin; *Bd*, basidorsal; *Bv*, basiventral (probably only distal part); *Ch*, chorda-space; *D*, dorsal fin; *Id*, interdorsal; *Iv*, interventral (— probably a proximal part of the basiventral); *Ms*, baseost; *Ps*, axonost; *Ps+Ms*, long ossifications in the majority of the endoskeletal radials of the anal fin, perhaps formed by the fusion of originally independent axonosts and baseosts; *a*, *a*₁, corners on the edge between the latero-dorsal and the lateral surface of the sphenoid; *a. car.*,

int., foramen from the arteria corotis interna; *al.*, anterior portion of the pars lateralis of either side of the sphenoid; *a. opt.*, foramen probably for the arteria optica; *bp.*, basiptyergoid process; *basp.*, portion of the pars basalis of the sphenoid between the fenestra optica and the canalis transversus; *b.*, *c.*, processes on the posterior margin of the pars lateralis of either side of the sphenoid; *c. transv.*, canalis transversus; *d.*, portion of the pars basalis of the sphenoid anterior to the fenestra optica; *fen. bas. post.*, probably a remaining part of the fenestra basicranialis posterior; *fen. opt.*, fenestra optica; *f. hyp.*, fossa hypophyseos; *fi.*, fissure probably pierced by the n. abducens; *my.*, fossa in which the external rectus muscle of the eye has originated. Corresponds to an antero-lateral part of the middle compartment of the myodome in *Amia* and Teleosts; *ophth. lat.*, exit of the n. ophthalmicus lateralis; *ophth. lat. 1.*, posterior opening of the canal for r. ophthalmicus lateralis on the pars lateralis of the sphenoid, and *ophth. lat. 2.*, anterior opening of the same canal; *pc.*, the basal parachordal plate of the sphenoid; *r.*, dorsal opening of small canal issuing from the ophthalmicus lateralis canal and which has contained vessels and nerve branches to the cranial roof; *v. 1.*, *v. 2.*, *v. 3.*, *v. 4.*, openings of small canals for nerves and vessels to the cranial roof; *v. 4* foramen which has probably transmitted the vena cerebialis anterior. *II.*, foramen opticum; *III.*, foramen oculomotorii; *IV.*, foramen trochlearis; *V.*, place of exit for the n. trigeminus with the exception of r. ophthalmicus profundus. The n. buccalis lateralis was also transmitted at this place; *Vte.*, external opening of the canal for the nervus ophthalmicus profundus or a somewhat equivalent nerve.

Plate 22.

- Fig. 1. *Birgeria mougeoti* (AGASSIZ), the neurocranium in ventral aspect. (P. 165).
 » 2. » » » part of the axial skeleton and the endoskeleton of the dorsal fin (P. 157). $\frac{4}{5}$.
 » 3. » » » the neurocranium (P. 165) in ventral aspect with parts of the parasphenoid and prootico-opisthotic removed.
 » 4. *Boreosomus reuterskiöldi* n. sp., scales (P. 116). $\frac{3}{1}$.
 » 5. Genus et Species indet. Tooth in coronal aspect. (P. 14). $\frac{3}{2}$.

Explanation of index letters.

Ausph., autosphenotic; *Bd.*, basidorsal; *Bo.*, basioccipital; *Lp.*, lepidotrichia; *Ms.*, baseost; *Pro. o.*, prootico-opisthotic; *Ps.*, axonost; *Psph.*, parasphenoid; *Sph.*, sphenoid; etc. as in Pl. 21; *c. sem. ext.*, canalis semicircularis externus; *c. sem. post.*, canalis semicircularis posterior; *pl.*, profound lamella of the parasphenoid; *pr. asc.*, processus ascendens of the parasphenoid; *vl.*, ventral lamella of the supratemporo-intertemporal; *vp.*, processus from this lamella; *VII.*, posterior opening of the facialis canal; cf. also Pls. 20, 21.

Plate 23.

- Fig. 1. *Birgeria mougeoti* (AGASSIZ), part of the visceral skeleton in ventral aspect (P. 171).
 » 2. » » » parts of the visceral skeleton with the parasphenoid in dorsal aspect (P. 171).
 » 3. » » » skeleton of the ventral fins. (P. 154).
 » 4. *Acorrhaddus asplundi* n. sp., pectoral fin (P. 173c).

Explanation of index letters.

Cbr₁—Cbr₄, ceratobranchials of the gill-arches I—IV; *Co₁—Co₂*, ossifications in the copular series; *Ebr₁—Ebr₃*, epibranchials of the gill-arches I—III; *Ecpt.*, ectopterygoid; *Enpt.*, entopterygoid; *Hbr₁—Hbr₃*, hypobranchials of the gill-arches I—III; *Iibr₂*, ossified infrapharyngobranchial of the

second gill-arch; *Mco*, mixicoronoid; *Mx*, maxillary; *Pc*, pectoral fin; *Pv*, pelvic bone; *do*, ossifications in the distal segments of certain endoskeletal radials of the ventral fins; *po*, ossifications in the proximal segments of the endoskeletal radials of the ventral fins; *pr. int.*, process perhaps developed in connection with the ligamentum interarcuale ventrale.

Plate 24.

Fig. 1. *Birgeria mougeoti* n. sp., caudal fin. (*P. 151*) Somewhat less than nat. size.

- » 2. » » » » the head from above (*P. 165*). The same as that reproduced in Pl. 20, fig. 6, Pl. 22, figs. 1, 3.
 » 3. *Birgeria* sp., tooth from the bone-bed 263 m above the fish horizon, Mt Bertil (*P. 715*). $\frac{5}{2}$.
 » 4. *Boreosomus?* *scaber*, scales (*P. 877*). $\frac{3}{1}$.

Explanation of index letters.

Dsph, dermosphenotic; *Fr*, frontal; *Pa*, parietal; *Pro. o*, prootico-opisthotic; *Stemp. it*, supra-temporo-intertemporal; *So?* supraorbital? *cv*, cranial cavity; *hsp*, haemal spines;

Plate 25.

Fig. 1. *Glaucolepis gyrolepidoides* n. sp., parts of the body preserved as impression in the stone (*P. 671*) $\frac{2}{1}$.

- » 2. » » » » detached scale from the bone-bed 33 m above the fish horizon, Mt Viking (*P. 7*). $\frac{2}{1}$.
 » 3. *Pygopterus de geeri* n. sp., small specimen lacking the dorsal parts of head and body (*P. 110*). $\frac{3}{2}$.

Explanation of index letters.

A, anal fin; *D*, dorsal fin; *Icr*, endoskeletal radials of the epichardal lobe of the caudal fin; *Ma*, mandible; *Mx*, maxillary; *Pc*, pectoral fin; *V*, ventral fin; *hsp*, haemal spine.

Plate 26.

Fig. 1. *Pygopterus de geeri* n. sp., parts of the head and abdominal region of a rather large specimen (*P. 112*).

- » 2. » » » » much crushed and weathered specimen (*P. 671*) lacking the tail and the posterior part of the caudal region. $\frac{3}{2}$.
 » 3. *Boreosomus?* *scaber* n. sp., scales (*P. 18*). $\frac{4}{1}$.

Explanation of index letters.

Bd, Basidorsal; *Cl*, cleithrum; *Hb*, parts of haemal arches; *Icl*, clavicle; *Ma*, mandible; *Mx*, maxillary; *Nsp*, unpaired neural spine; *Op*, operculum; *Pc*, pectoral fin; *Po*, preoperculum; *R*, endoskeletal radials of the pectoral fin; *Ra*, endoskeletal radials of the anal fin; *Rbr*, branchiostegal ray; *Rd*, endoskeletal radials of the dorsal fin; *Scl*, supracleithral; *Sop*, suboperculum; *V*, Ventral fin; *ifc*, supraorbital sensory canal; *soc*, infraorbital sensory canal.

Plate 27.

Fig. 1. *Pygopterus de geeri* n. sp., parts of the visceral skeleton (*P. 109*).

- » 2. *Boreosomus arcticus* (A. S. WOODWARD) scales (*P. 695*). $\frac{3}{1}$.
 » 3. » *reuterskiöldi* n. sp., parts of the body and the head. (*P. 117*), mainly preserved as impressions in the stone.
 » 4. *Platysomus nathorsti* n. sp., scale (*P. 879*).

Explanation of index letters.

D, dorsal fin; *Ext*, extrascapular; *Fr*, frontal; *Op*, operculum; *Pa*, parietal; *Po*, preoperculum; *Rbr*, branchiostegal ray; *Scl*, supracleithral; *Sop*, suboperculum; *Stemp.it*, supratemporo-intertemporal; *ifc*, infraorbital sensory canal; *l*, lateral canal; *md*, middle pit-line of head organs; *poc*, preopercular sensory canal; *s.com*, supratemporal transversal commissure between the cranial sections of the two lateral canals; *soc*, supraorbital sensory canal.

Plate 28.

Fig. 1. *Boreosomus reuterskiöldi* n. sp., impression of the ventral side (*P. 119*). Somewhat magnified.
 » 2. *Platysomus nathorsti* n. sp., some scales (*P. 142b*), preserved as impression of the medial surface.
 » 5. *Perleidus woodwardi* nom. nov., posterior portion of fish with dorsal and anal fins (*P. 185*).

Explanation of index letters.

A, anal fin; *D*, dorsal fin; *Md*, mandible; *Mg*, median jugular plate; *Mx*, maxillary; *Op*, operculum; *Pc*, pectoral fin; *Po*, preoperculum; *Rbr*, branchiostegal rays; *Rd*, endoskeletal radials in the dorsal fin; *Sop*, suboperculum; *V*, ventral fin.

Plate 29.

Fig. 1. *Boreosomus* sp., body and incompletely preserved specimen (*P. 120*) showing the position of the dorsal fin. $\frac{7}{10}$.
 » 2. » » scales from the lateral surface of the abdominal region (*P. 131b*). $\frac{3}{2}$.
 » 3. » » scales from the ventral parts of the abdominal region preserved as impressions on the stone (*P. 131a*). $\frac{3}{2}$.
 » 4. *Acrohabdus latistriatus* n. sp., abdominal region and parts of the head (*P. 170*).

Explanation of index letters.

D, dorsal fin; *Md*, mandible; *Mg*, median jugular plate; *Mx*, maxillary; *Op*, operculum; *Pc*, pectoral fin; *Po*, preoperculum; *Rbr*, branchiostegal rays; *Scl*, supracleithral; *Sop*, suboperculum.

Plate 30.

Fig. 1. *Acrohabdus asplundi* n. sp., parts of head and abdominal region (*P. 173*).
 » 2. » » » » scales (*P. 173*). $\frac{3}{2}$.
 » 3. » » *latistriatus* n. sp., scales from the lateral surface of the abdominal region (*P. 170*). $\frac{2}{1}$.
 » 4. » » » » scales from the ventral part of the abdominal region (*P. 170*). $\frac{2}{1}$.
 » 5. » » » » scales from the dorsal part of the abdominal region rather close behind the head (*P. 170*). $\frac{2}{1}$.

Explanation of index letters.

Ang, angular; *Cl*, cleithrum; *De*, dentalo-splenic; *Mx*, maxillary; *Op*, operculum; *Pc*, pectoral fin; *Po*, preoperculum; *Rbr*, branchiostegal rays; *Scl*, supracleithral; *Sop*, suboperculum.

Plate 31.

Fig. 1. *Acrohabdus bertili* n. sp., head seen from the right side (*P. 174*). The cheek plates are totally and the opercular plates are almost totally weathered away and by far the greater part of the neurocranium also very incompletely preserved.

Fig. 2. *Acrorhabdus bertili* n. sp., the same head as in fig. 1 (*P. 174*) with some parts removed to show the branchial skeleton.

- » 3. » » » » the same head as in the two figures above (*P. 174*), seen from the left side. On this side too the cheek plates and the opercular plates are weathered away.
- » 4. » » » » supporting gill-rays from the specimen (*P. 174*) reproduced in the three preceding figures. $\frac{2}{1}$.
- » 5. » » » » scales from the abdominal region of the specimen reproduced in figures 1—4 (*P. 174*). $\frac{2}{1}$.

Explanation of index letters.

Art, articular; *Bbr*, ossifications in the copular row; *Cbr*, ceratobranchial; *Chy*, ceratohyal ossification; *Cl*, cleithrum; *Ecpt*, ectopterygoid; *Enpt*, entopterygoid; *Hbr*, hypobranchial; *Hm*, hyomandibular; *Icl*, clavicle; *Mco*, mixicoronoid; *Mptg*, metapterygoid; *Op*, operculum; *Pro.o*, prootico-opisthotic; *Psph*, parasphenoid; *Qu*, quadrate; *Rbr*, branchiostegal ray; *Sec*, ossified primary shoulder girdle (scapulo-coracoid); *Scl*, supracleithral; *Sop*, suboperculum; *Sph*, sphenoid; *Sscap*, suprascapular; *Stly?* stylohyal? *Sympl*, symplecticum; *Uhy*, urohyal; *d*, process on the scapulo-coracoid; *ohy*, ossification in the posterior end of the ceratohyal cartilage. This ossification corresponds to the so-called epihyal of Teleosts; *pr. op*, processus opercularis; *V*, exit of the trigeminus.

Plate 32.

Fig. 1. *Platysomus nathorsti* n. sp., ornament of scale preserved as impression in the stone (*P. 142a*). $\frac{2}{1}$.

- » 2. *Acrorhabdus bertili* n. sp., scale from the first or second vertical row behind the shoulder girdly (*P. 174*). $\frac{2}{1}$.
- » 3. » » » » head seen from the right side. The same head as in Pl. 31, figs. 1—3 (*P. 174*). Parts of the clavicle have been removed to show the ossified primary shoulder girdle.
- » 4. » » » » opercular apparatus shoulder girdle and a proximal part of the pectoral fin. Belongs to the same specimen as the head in the preceding figure (*P. 174*) and in figures 1—3 Pl. 31. The bones partly preserved as an impression of the lateral surface in the stone.
- » 5. » » » » head seen from the left side with some parts removed to show the gill-arches. The same head as in figures 3—4 and Pl. 31, figs. 1—3 (*P. 174*).

Explanation of index letters.

Ebr, epibranchial; *Pc*, pectoral fin; *g*, process on the primary shoulder girdle plate, probably the place of articulation of the pectoral fin; *n*, nerve canal through the primary shoulder girdle plate; *v*, postero-ventral corner of the primary shoulder girdle plate; other index letters as in the preceding plate.

Plate 33.

Perleidus woodwardi nom. nov., nearly complete specimen (*P. 185*).

Explanation of index letters.

A, anal fin; *D*, dorsal fin; *Fr*, frontal; *Ifo*, infraorbital bone; *Md*, mandible; *Mx*, maxillary; *Op*, operculum; *Pc*, pectoral fin; *Pcl*, postcleithral plates; *Po*, preoperculum; *Rbr*, branchiostegal ray; *So*, supraorbitals; *Sop*, suboperculum; *Sscap*, suprascapular; *V*, ventral fin; *orb*, orbit.

Plate 34.

Fig. 1. *Perleidus woodwardi* nom. nov., head of the specimen (*P. 177*) in figure 2; magnification $1\frac{1}{3}$. The preserved parts of the sensory canals of the head stained white.

» 2. » » » » specimen lacking the caudal region (*P. 177*). Most parts preserved only as impressions in the stone (impression of the external surface).

Explanation of index letters.

Ant, antorbital; *Cl*, cleithral; *D*, dorsal fin; *Ext*, extrascapular; *Fr*, frontal; *Icl*, clavicle; *Ifo*, infraorbital series of bone plates; *Mx*, maxillary; *Na. ptr*, nasalo-postrostral (+ medial postral element); *Op*, operculum; *Pa*, parietal; *Pc*, pectoral fin; *Pcl*, enlarged postcleithral scales; *Po*, preoperculum; *R*, lateral rostral; *Rbr*, branchiostegal ray; *Sop*, suboperculum; *Stemp. it*, supra-temporo-intertemporal; *V*, ventral fin; *ap*, anterior head-line of pit organs; *dl*, pores of the dorsal lateral line on the body; *ethm. com*, ethmoidal transverse commissure between the two infraorbital canals; *ifc*, infraorbital sensory canal (in the infraorbital plates and in the antorbital); *l*, main lateral line of the body (pores and a shallow longitudinal furrow); *lc*, cranial section of the main lateral canal of the body; *mp*, middle head-line of pit organs; *na₁* and *na₂*, nasal apertures; *orb*, orbital opening; *poc*, preopercular sensory canal; *pp*, posterior head line of pit organs; *s. com*, supra-temporal cross commissure; *soc*, supraorbital sensory canal.

Plate 35.

Fig. 1. *Perleidus woodwardi* nom. nov., nearly complete specimen preserved as impression of the right side in the stone (*P. 176*).

» 2. » » » » some teeth in profile (*P. 183*). $\frac{1}{2}$.

» 3. » » » » part of fish showing the unpaired fins (*P. 181*).

» 4. *Boreosomus?* *scaber* n. sp., scale (*P. 18*). $\frac{4}{1}$.

Explanation of index letters.

A, anal fin; *D*, dorsal fin; *Ifo*, infraorbital bones; *Mx*, maxillary; *Op*, operculum; *Pc*, pectoral fin; *Po*, preoperculum; *Scl*, supracleithral; *Sop*, suboperculum; *Sscap*, suprascapular; *V*, ventral fin; *orb*, orbital opening.

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