EESTI LOODUSTEADUSE ARHIIV

VÄLJA ANTUD LOODUSUURIJATE SELTSI POOLT
TARTU ÜLIKOOLI JUURES

ARCHIV FÜR DIE NATURKUNDE ESTLANDS

(VORMALS LIV-, EHST- UND KURLANDS)

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REVISION OF THE ESTONIAN ARTHRODIRA

PART I

FAMILY *HOMOSTIIDAE* JAEKEL

BY

ANATOL HEINTZ

TARTU 1934

TARTU ÜLIKOOLI JUURES OLEVA LOODUSUURIJATE SELTSI KIRJASTUS
KOMISJONIS J. G. KRÜGER'I JUURES
TARTUS

VERLAG D. NATURFORSCHER-GESELLSCHAFT BEI D. UNIVERSITÄT TARTU
IN KOMMISSION BEI J. G. KRÜGER, TARTU
(EESTI)

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K. Mattieseni trükikoda o-ü., Tartu 1933.

Dedicated to the memory of my teacher and friend

PROFESSOR, DOCTOR JOHAN KIÆR.

I. Introduction.

During the summer of 1927 I visited the Geological Institute of Tartu University in Estonia and was at once very interested in the astonishing collection of fossil fishes from the Estonian Old-Red, preserved there. This material was mainly collected in the middle of the nineteenth century, but has never before been described in detail.

Soon after my visit I began to negotiate with the authorities of the Geological Institute in Tartu to obtain permission to work out and describe this remarkable collection. Thanks to the courtesy of Professor Tammekann, the Keeper of the Geological Department at the University of Tartu, and Doctor Luha (at the same institution) I was privileged to spend the summer 1929 in Tartu and to study the collection of fossil fishes there.

During my short visit to England in 1930, it proved possible to supplement my researches by studies of the material in the British Museum and especially of that in the Edinburgh Museum. This paper is a result of all these investigations.

I must here with a feeling of deep thankfulness and sorrow remember the late Professor Johan Kiær — my teacher and friend. He has always shown me and my work the greatest interest and has always helped me in all directions. Without his help this paper also would never have been written, and I therefore allow myself to dedicate it to the memory of Professor Kiær.

I must also express here my best thanks to all who helped me in my work, in the first place to Professor Tammekann of the University of Tartu for his kind permission to study the collection there.

I also wish to express my best thanks to Professor Öpik — and especially to Doctor Luha — both of the same University for all their courtesy and help during my visit to Tartu.

Finally, I wish to express my gratitude to Doctor I. E. White — British Museum, and to Doctor Grimshaw, Edinburgh Museum, for the privilege of being allowed to study the collections in these two Museums. Dr. Grimshaw has also kindly sent me

some plaster-casts and photographs of *Homostius milleri* Ag. (Pl. III, fig. 1, and Pl. XIX, fig. 4).

Two foundations, which I received from the University of Oslo made it possible for me to visit Tartu twice, and I am glad to have an opportunity of expressing my gratitude to the University authorities.

The majority of the photographs illustrating this work were taken by Mr. Kalamees, Tartu; two I received from Dr. Grimshaw, Edinburgh Museum, and some were taken by Miss Thorbjørnsen of the Paleontological Museum, Oslo. All the drawings are by the author himself.

II. Historical.

In 1835 Kutorga published a paper „Beitrag zur Geognosie und Palæontologie Dorpats und seiner nächsten Umgebung", in which for the first time were described and pictured the fragments of fossils found in the Old-Red sandstone in the neighbourhood of Tartu. Two years later he published a second report about the same discovery (1837), describing and picturing some new bones. Kutorga considered the fossil bones as belonging to reptiles and described a number of new reptilian specimens.

About the same time Asmuss began to collect fossil bones in the same locality — a work he continued for nearly 20 years. The first result of his investigations was a short letter to Professor Baer in 1840, in which he expressed the opinion, that the fossil fragments from Tartu belonged to fishes, but not to reptiles. Some years later Asmuss prepared some very fine plaster-casts from his best specimens and sent series of them to different museums in Europe. (To-day these casts are exhibited for instance in the British Museum.) One set of these casts belonged to L. Agassiz — the greatest expert on fossil fishes in the middle of the nineteenth century. On account of their tuberculated surface Agassiz determined them all as belonging to the family *Asterolepis*, a family described by Eichwald, from the Russian Devonian. In Agassiz' monography (1844) we find drawings of Asmuss's plaster-casts on pl. 32.

At the same time as Asmuss was collecting fossils in Tartu, H. Miller was doing the same in Scotland, but whereas the first only found fragments of single bones, the latter also collected more or less complete examples of the head of *Homostius* Unfortunately, misled by Agassiz' determination, Miller described (1849, 2) the *Homostius* head from Scotland as „*Asterolepis*". As the paper of H. Miller was widely distributed both in England and America the wrong name „*Asterolepis*" has for many years been fixed to an animal, which in reality had very little to do with the real *Asterolepis*.

The names *Homostius* and *Heterostius* were proposed some years later by Asmuss in his paper „Das vollkommenste Hautskelet der bisher bekannten Thierreihe", printed in Tartu in 1856. This short, but in many respects remarkable and interesting paper, is in reality the only more or less complete description of the collections in Tartu. It is in fact wonderful that Asmuss was able to give such a complete and perfect description of the single plates and such fine reconstructions of the whole carapace of these two gigantic *Arthrodira*. To him the papers and drawings of H. Miller were unknown and he based all his descriptions only on the fragments of isolated plates he himself had gathered. Although Asmuss correctly described the single plates, he was mistaken in the placing of the carapace. He supposed that its largest part, which we now know covered the head, protected the caudal region of the animal and the body carapace — covered the front of the body. According to him, the joint, which he was the first to describe, was placed between the caudal region and the front part of the body.

The following year Pander published his classical work about „*Placodermen*" (1857) in which he for the first time gave a somewhat complete and correct description of the *Arthrodira*. One chapter in this paper is dedicated to *Homostius* and one to *Heterostius*, the forms of which he knew from Kutorga's originals and Asmuss's descriptions and casts only. Nevertheless, Pander's description is quite correct and his drawings very clear and good. He pointed out the gread similarity between *Coccosteus* and these two gigantic forms, and stated that Asmuss had inaccurately described the head shield as a caudal part of the carapace. He also remarked that H. Miller had wrongly determined the fossil fishes from Stromnes, a form identical with Asmuss's *Homostius*, as „*Asterolepis*". Furthermore, he pointed out that Miller described many bones as belonging to „*Asterolepis*", while, in reality, they belonged to different other fossil fishes; he determined also some „*Asterolepis*“ bones incorrectly.

The next and last paper of importance dealing with *Homostius*, is Traquair's well-known work „*Homosteus* Asmuss compared with *Coccosteus* Agassiz“ (1889). This paper gives the most complete and correct description of *Homostius* available, showing that all the single plates of this form easily can be compared with the plates in *Coccosteus*.

Since then only short papers or notes about the structure of *Homostius* and *Heterostius* have been published, the most important being two papers by A. Sm. Woodward (1891, 3, and 1916). The first paper especially is very interesting, as it describes the ventral plates of the body carapace for the first time. In 1916 Bogoljuboff published a short paper about the structure of *Heterostius* basing his description on the material preserved in Tartu Museum. Also Abel in 1927 gave a detailed description of the joint structure in *Heterostius*. The most recent contributions to the literature on the subject are two short papers on the Tartu forms published by the present writer (1928 and 1930, 1).

Thus the number of papers actually dealing with the remains of *Homostius* and *Heterostius* is relatively modest, but, on the contrary, in many other papers we find different speculative discussions on these forms. The unusual position of the eyes in *Homostius* led to the result that this form was very often mentioned in discussions about the relationship of *Arthrodira*. Newberry, in his description of *Dinichthys* (1875) was the first to mention these forms. Jaekel (1903, 2), who personally studied the collection in Tartu, was of the opinion that *Homostius* is a form which combines *Arthrodira* with *Antiarchi*, and Hussakof held the same view (1906). On the other hand, Dean pointed out that *Homostius* may be regarded as an intermediate form between *Macropetalichthys* and *Arthrodira* (1900, 1901). Finally Stensjø (1925) wrote that „it approaches *Phlyctænaspis* on the one hand and *Macropetalichthys* on the other“.

As we have seen, it is remarkable how little attention has been paid to these two *Arthrodira* which are among the most interesting representatives of the whole group, especially when we remember that a large collection of *Homostius* and *Heterostius* fragments has been preserved in the Museum of Tartu University for nearly a hundred years.

III. Material. Methods.

As mentioned above, the nucleus of the collection in Tartu consists of the material gathered by Asmuss from the years 1836 to 1856. After Asmuss's death, Grewing continued the work and collected a great number of different bone fragments, many of his pieces being particularly good as, for instance, the almost complete head shield of an *Heterostius*. Later V. Paul also collected some fragments of these remarkable fishes.

Nearly all the specimens collected by Asmuss and Grewing are from the same locality — Aruküla — a small village near the river Emajõgi about two kms. from Tartu. In earlier times some underground caves were known to be there. The occurrence of such caves in the very soft Old-Red sandstone is quite common in different districts both in Estonia and Latvia. The caves in Aruküla are especially well-known owing to the unusually fine white sandstone which is found there. This sandstone is so soft that it is easily dug out with a spade and crushed to the finest and cleanest sand, which, in earlier days, was used by the neighbouring peasants for spreading on the earthen floors of their houses.

Even at that time it was known that this sand contained remains of remarkable bones and shields. As is known, Kutorga was the first to collect them (1830—40), and immediately after him, Asmuss also began a systematic excavation and collection of the fossil bones in Aruküla (1836—56) a work which Grewing continued (1856—70). Each piece Asmuss collected is marked with a small label on which the date is given (Pl. I, 4; Pl. IV, 3 and others) showing that he collected his fossils not only during the summer, but also during the winter months — a work which must have proved a very difficult and strenuous task.

At the present time the entrance to the caves in Aruküla is blocked by a landslide of sandstone, and complicated excavations will be necessary before the caves can be entered.

The bone fragments found in the sandstone in Aruküla are excellently preserved but immediately after excavation they are very soft, breakable and difficult to transport. When dried, however, they become more solid, but they always remain somewhat fragile. The majority of the excavated bones are accordingly broken up into many, often very small pieces. They are quite easily cleaned from the traces of sandstone — a work usually done with a stiff brush, but sometimes also with a needle. It is only with great difficulty, however, that all the fragments can be put together. Some of the larger plates of *Heterostius* and especially of *Homostius* are broken into thousands of small pieces (Pl. II, 1, Pl. IV, 1).

The colour of the bones varies greatly, according to a more or less strong infiltration of ferrous salts, from almost white to yellow, yellow-brown and dark brown. The microscopical structure shows, as a rule, unusually fine preservation. In some cases it is difficult to determine, even when seen through the microscope, whether we have to do with a recent or a fossil bone. In a later paper I shall discuss this question in greater detail. I will only mention here, that in some microscopical sections of the bones, I was able to observe that the bone canals were sometimes open as in recent bones, and not filled with sediment. This very remarkable circumstance prompted me to undertake a chemical analysis of these bones Thanks to the kindness of Doctor Luha, a series of analyses was undertaken at the Chemical laboratory of Tartu University and at the same time a parallel series of analyses on recent bones was carried out (of *Perca fluviatilis* and of *Bos taurus*).

The result of these analyses was quite unexpected as is seen from Tables I and II. These tables give the results of the analyses of both fossil and recent bones. Table I shows the remarkable fact that the bones of *Homostius* and *Heterostius* have still preserved 5% organic substance. Table II gives the result of the same analysis, calculated for the inorganic part only, indicating particularly clearly the minimum difference in the composition between recent and fossil bones. The absence of Cl, SO_3 and Na_2O in the bones of *Homostius* and *Heterostius* is intelligible, as these very active elements in recent bones are also only represented in parts of one per cent (except SO_3 in *Perca fluv.*). The percentage of F is high, more than seven times higher than in recent bones (2,57 and 0,35), this may have been caused by a secondary application of F. The percentage of P_2O_5 and CaO nearly corresponds to the contents in recent bones. The total absence of SiO_2 is remarkable as the fossils are inbedded in quartz sand and the presence of this substance could therefore be expected. The percentage of Fe_2O_3 is high and variable (from 2,72 to 1,99). It gives the fossil bones a more or less strong *yellow-brown colour*,

TABLE I.

	Heterostius sp. PtO	Heterostius sp. AL	Homostius sp. Fragm.	Perca fluv.	Bos taurus Femur.
hygroscopic water	2,24	2,46	2,06	—	—
indissoluble in HCl	2,16	0,43	1,74	—	—
loss on ignition	4,81	5,03	4,86	46,76	29,82
CO_2	2,17	2,03	2,21	1,62	2,52
P_2O_5	35,57	36,40	36,08	21,86	29,28
F	2,50	2,25	2,37	0,18	0,25
Cl	—	—	—	0,22	0,12
SO_3	—	—	—	0,80	0,11
CaO	49,67	50,20	49,86	27,50	37,02
MgO	0,20	0,28	0,38	0,54	0,72
Na_2O	—	—	—	0,30	0,10
Fe_2O_3	2,29	1,98	1,83	—	—
	101,61	101,06	101,39	99,68	99,94
	1,00	0,90	0,95	0,12	0,13
Totals	100,61%	100,16%	100,44%	99,56%	99,81%

which without doubt is secondarily supplied, as it is absent in recent bones.

We have thus seen that, on the whole, the changes in the composition of the bone substance are minimum where our fossils are concerned.

This remarkable degree of preservation of *Homostius* and *Heterostius* bones must be in accordance with the good preserva-

TABLE II.

The same analysis calculated for inorganical part only.

	Heterostius sp. PtO	Heterostius sp. AL	Homostius sp. Fragm.	Perca fluv.	Bos taurus Femur.
Cl	—	—	—	0,42	0,17
SO_3	—	—	—	1,33	0,16
CO_2	2,26	2,23	2,41	3,07	3,60
P_2O_5	38,89	39,41	39,32	41,40	41,83
F	2,70	2,42	2,58	0,34	0,36
CaO	54,32	54,48	54,33	52,08	52,89
MgO	0,21	0,30	0,41	1,02	1,03
Fe_2O_3	2,72	2,14	1,99	—	—
Na_2O	—	—	—	0,57	0,14
Totals	101,10	100,98	101,04	100,28	100,18
	1,10	0,98	1,04	0,28	0,18
	100,00	100,00	100,00	100,00	100,00

tion of the sediment itself in the Kambro-Devonian deposits in Estonia. As mentioned above, the “sandstone“ where the fossils are found is, in reality, not harder than some deluvial deposits. The layers of clay, which in some parts of the Estonian Old-Red interchanges with the sandstone, are also more or less plastic and are used by the peasants as ordinary clay.

As mentioned above the *Heterostius* and *Homostius* bones are usually broken into many pieces. To glue all these fragments correctly together is a very difficult task, which often takes a very long time.

Asmuss must have found this work particularly difficult, as he had no prior idea as to the size and shape of the plates he eventually reconstructed, but in spite of this both Asmuss and Grewing have rebuilt a great number of the single plates of both the gigantic forms from Aruküla. This excellent collection was, of course, preserved in the Tartu University. Unhappily, during the Great War it was, together with the whole University of Tartu, removed to Central Russia (Rjasan) and only returned to Tartu after the conclusion of peace between Estonia and Russia. It is obvious that such a removal — with badly-packed cases — greatly damaged the fossils, some of the reconstructed and glued plates being broken into so many minute pieces, that reconstruction was rendered impossible. The whole collection was therefore in quite a chaotic condition when I started my work in Tartu in the summer of 1929, although the first curator at the Geological Museum in Tartu, Prof. Becker, had very energetically tried to put the collection in order. It took about a month of hard work to determine all the fragments and to glue together what was still possible to reconstruct, although a great many undeterminable fragments had to be left.

When this initial work was finished I had assembled a relatively large number (about 800) of more or less complete bones of *Homostius* and *Heterostius.*

With very few exceptions each piece represented only one plate or a fragment of a plate. It was very rare to find plates in a natural connection with each other and only one specimen showed a more or less complete head-shield.

Usually the fragments of both the genera — *Homostius* and *Heterostius* — are not very difficult to separate from each other, first, owing to their different ornamentation and, secondly, because the plates in *Heterostius* are as a rule more massive than those in *Homostius*.

Undoubtedly the collection represents a number of different species of both genera. As is known Asmuss distinguished no less than 5 different species of *Homostius* only. In my opinion, however, it is difficult with certainty to determine such a great number of species, as in reality the difference between the single forms is small, thus making it difficult enough to give a satisfactory definition of only the three I propose.

IV. General Part.

Homostius is known from the middle Old-Red of Scotland, Estonia and Latvia. I have also recently ascertained its presence in the middle Devonian in Spitsbergen (Wijde Bay Series).

Like all other *Arthrodira*, the bony armour in *Homostius* covers the whole head and the front part of the body. The head and body carapaces are connected by means of a movable joint. The points especially characteristic in *Homostius* are: 1) Unusually flat head and body carapace. 2) The hind part of the head strongly developed. 3) The position of the orbits is close to each other and to the front margin of the head. 4) The shortness of the body carapace. 5) The shape and development of the Infero-Gnathal plate. 6) The shape and position of the Antero-Lateral and Intero-Lateral plates and, finally, 7) the reduction of the number of plates in the ventral carapace.

A. The Head Shield.

As is the case with many other *Arthrodira* the head shield in *Homostius* is naturally divided into two parts: the head roof and the side plates of the head. This division is especially sharp in our form. I was unable to find any traces of a contact between these two parts and, also in perfectly preserved specimens from Scotland, their natural relationship is more or less destroyed. The head roof is best known as, in some of the Scotch specimens, it shows complete preservation, whereas the number and shape of the plates composing the side parts of the head, has not yet been determined with certainty.

1) **The Head Roof.**

The head roof is composed of 13 single plates: 5 pairs of unsymmetrical side plates and 3 symmetrical median plates. Thus compared with some other forms, one pair of unsymmetrical plates has been reduced in *Homostius* (post-marginal). The material from Estonia comprises isolated plates exclusively, but the collection in Edinburgh also contains a complete head roofs. This very fortunate combination gave me the opportunity of studying the structure of the head roof in *Homostius* especially closely.

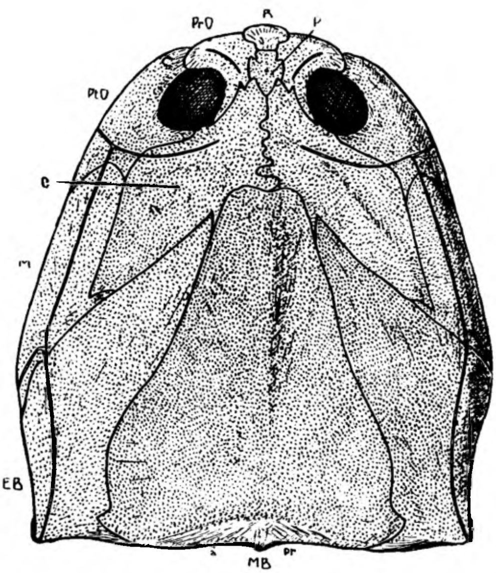

Fig. 1. The head roof of *Homostius sulcatus* Kut., outside view. Strongly reduced. *a* — part without tuberculation. *EB* — externo-basal, *C* — central, *MB* — median-basal, *M* — marginal, *P* — pineal, *Pr* — median projection on *MB*, *PrO* — pre-orbital, *PtO* — post-orbital, *R* — rostral.

The flat and oblong head roof (Fig. 1, 2) is nearly semicircular in front and straight at the basis. Its side margins are slightly curved; the broadest part of the head roof is thus placed about 1/3 from the hind margin (Fig. 1, 2, 3). When characterizing the relation between the breadth and length of the head, it is very useful to calculate the so-called breadth-length index, by which name is meant the relation between the breadth and length of the head multiplied by a hundred, thus when the breadth-length index is a hundred it indicates that the head is as broad as it is long. If the number is less than a hundred the head roof is longer than it is broad, the head being broader if the breadth-length index is over a hundred. The latter is the case in the majority of *Arthrodira*. In *Dinichthys* the b/l index = 130, in *Coccosteus* = 140, in *Stenognathus* = 175[1]). Only in *Acanthas-*

1) In the forms from Wildungen it is more difficult to define the b/l index, as here the head roof is not always sharply divided from the side plates of the head.

pida from the lower Devonian is the index smaller; in *Jaekelaspis* = 84, in *Arctaspis* = 98, in *Phlyctænaspis* = 100. The b/l index in *Homostius* is exceptionally low, being only 81. The lower numbers are probably only to be found in some unusually small forms from Wildungen as, for example, *Oxeosteus* and *Leptosteus*. The reduction in the indexes in the two latter can be referred, however, to the strongly developed rostral part of the head, not of the basal, as is the case in *Homostius*.

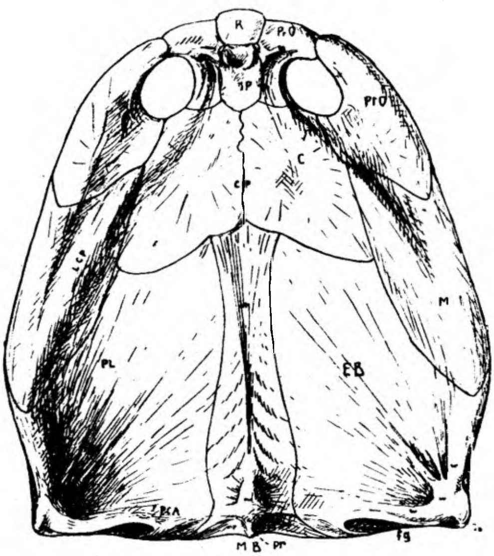

Fig. 2. The head roof of *Homostius sulcatus*. Kut., inside view. Strongly reduced. *CP* — central part, *ds* — double sockets, *fg* — fossa condylus, *im* — central impression on *EB*, *Jp* — hind side corner of the head (joint process). *LCP* — lateral consolidated part, *mp* — thin hind part of *MB*, *mr* — median thickened ridge, *PCA* — posterior consolidated arch, *PL* — postero-lateral impression, *ts* — socket behind orbital impression. Rest as on fig. 1.

The eye-openings are relatively small and placed quite near to each other, with the result that the orbits are surrounded by the pre-orbital, post-orbital and central plates only (Fig. 1, 2, 3). In the majority of other *Arthrodira* the eyes are limited by the pre-orbital, post-orbital and sub-orbital, in some forms also by the post-nasal. Finally, in some others (from Wildungen) the marginal also (Gross, 1932) helps in limiting the eyes. *Homostius* displays an unusual feature, as the central and not the sub-orbital plays a part in limiting the orbits, a characteristic which is absolutely unknown in other *Arthrodira*.

Besides this, the eye openings in *Homostius* are pushed very near to the front margin of the head roof. This remarkable position can be particularly clearly seen if we compare the condition in *Homostius* with that in other *Arthrodira*. The relation between the distance from the middle of the line connecting the orbits, to the top of the rostral plate on one side and to the hind margin of the median-basal plate on the other, multiplied by 100, gives the best expression for the position of the orbits. We will call it the orbit index, which in different forms is as follows:

1) *Homostius* . . . 17	4) *Dinichthys* . . 47	7) *Stenognathus* 71
2) *Jaekelaspis* . . 19	5) *Pachyosteus* . . 50	8) *Brachydirus* 90
3) *Coccosteus* . . 29	6) *Leptosteus* . . . 67	9) *Oxyosteus* . . 210 [1]

From the outside the head roof in *Homostius* is quite smooth, even, and covered by fine, distinct tubercles (fig. 1; Pl. XIV, 1; Pl. XVII; 1). As is known Asmuss has linked this characteristic to the name *Homostius*=homogenous, to emphasize the difference from the other Aruküla form *Heterostius*=heterogenous, with tubercles of very different size.

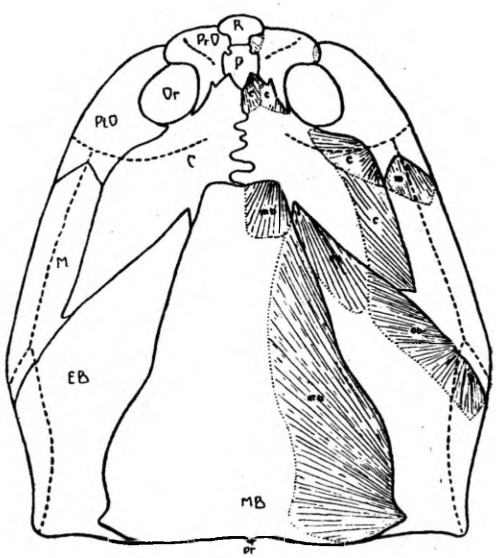

Fig. 3. Limits between the single plates of the head roof of *Homostius sp.*, outside one in continuous lines, inside one dotted. Overlapping margins are hatched. *c*, *eb*, *mb*, *m*, *pro* — parts of the corresponding plates (*C* *EB*. *MB*, *M* and *PrO*) which overlap neighbouring plates.
Or — orbital opening. Else as on fig. 1.

As pointed out, the head roof (fig. 1, 2, 3) is nearly level and only slightly bent along the front and side margins, but opposite to *Coccosteus* and *Dinichthys* (See Heintz 1932, 1, de 2) we have no reason to suppose, that secondarily it has been more or less strongly flattened. In the first place no trace of strong pressure in form of clefts, crushed portions or microstructural

1) The very high orbital index in *Oxyosteus* is due to the enormous size of the rostral plate in this form.

deformation can be seen on any of the bones from Estonia[1]), and in the second the position of the long and well-developed fossa condylus shows clearly that the head roof could not have been strongly bent. As is known, to allow the movement of the head roof, the axis of the right and left fossa condylus must be placed on one straight line, which I have called the "axis of the head" (Heintz, 1932, 2). When looking at the head roof of *Homostius*, from behind, we can see at once that the angle between the axis of the fossa condylus and the upper surface of the head is very small, measuring scarcely 12—15 degrees; for comparison it may be mentioned that the corresponding angle in *Dinichthys* measures about 50—60 degrees. Thus in a relatively large specimen of *Homostius*, measuring about 30 cm. between the hind side corners of the head, the distance between the middle point of the hind margin of the median-basal plate and the axis of the head is not more than 3,5 cm., the "breadth-height index" being 12. The same index in *Dinichthys* is about 25.

As we do not know any facts indicating that the head roof in *Homostius* was more or less strongly bent from back to front, we must regard this form as an unusually flat one.

All the sensory canals of the head, except the externo-basal (superatemporal cross commisure Stensiø 1925) are well-developed. They form relatively deep and distinctly marked grooves, much more obvious than in many other *Arthrodira*. The pre-orbital canal (supra-orbital Stensiø), which Traquair did not observe in the examples of *Homostius milleri* Traq., is in reality well-developed. I was able to find it, not only in all examples from Estonia, but also in those described by Traquair (s. Pl. XVII, 1); in the latter, however, it is not so clearly seen. This canal begins at the side front margin of the pre-orbital plate and runs obliquely downwards in the direction of the limit between this plate and the central, but does not cross the limit as is usual in other *Arthrodira*.

The strong development of the central affects the course of the post-sub-orbital (upper part of the infra-orbital Stensiø) canal. It runs, rising, slightly upwards on to the central, instead

1) The circumstance that the majority of bones preserved in Tartu are broken into many pieces does not contradict the above-mentioned statement. The bones found in the sandstone are more or less complete, but they have been broken during the excavation, transport and preservation.

of running obliquely downwards, as in other *Arthrodira.* It is interesting to point out how two different changes in the structure of the head have had the same influence on the course of the sensory canal. If we look at the development of this canal in *Stenognathus* (Heintz, 1931, 3) (or in some of the Wildungen forms), we will notice, that the post-sub-orbital canal here also runs obliquely upwards, exactly as in *Homostius*, but the reason

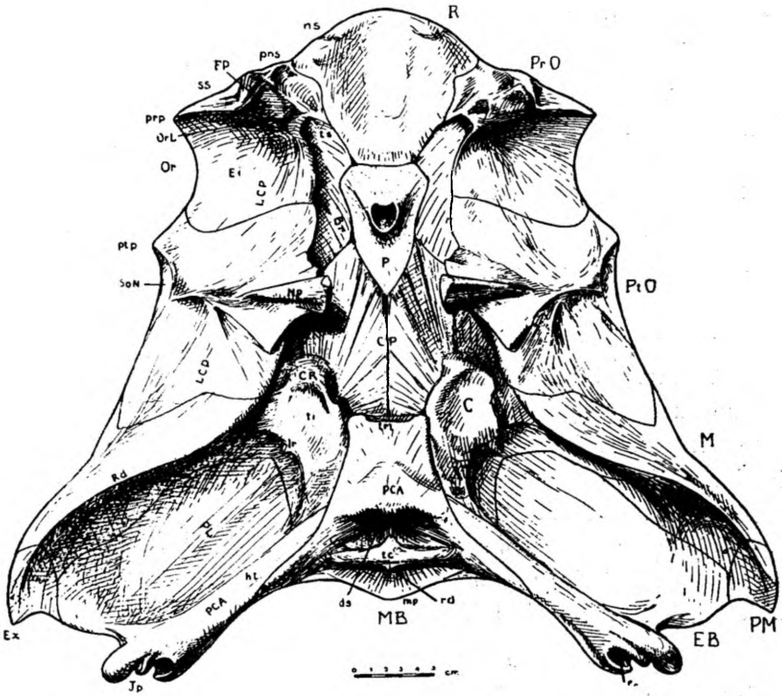

Fig. 4. The head roof of *Dinichthys intermedius* Nwb., inside view. Explanation as in fig. 1 and 2 (after Heintz, 1932, 2).

for the displacement in this case is not due to the strongly-developed C. and MB. plates, but to the enormously enlarged eye-openings.

The very distinct marginal canal (part of the infra-orbital and part of the lateral line grooves Stensiø) runs parallel with, and quite near to, the side margin of the head roof. The short post-marginal (pre-opercular Stensiø) canal branches from the marginal in the posterior portion of the marginal plate at exactly the broadest part of the head roof. Thus the point where this canal crosses the side margin of the head roof, corresponds to the external angle in *Dinichthys*, which is also the broadest part of the shield (fig. 4, Ex).

The fossa condylus is unusually long and strongly developed. Each one occupies nearly 1/4 of the whole hind margin of the head roof (fig. 2, fg). For purposes of comparison it may be mentioned, that in *Dinichthys*, for instance, each fossa condylus is not larger than 1/10 of the hind margin of the head roof (fig. 4, fg). I will later describe the fossa condylus in greater detail.

From the inside (fig. 2) the head roof is quite flat and even with thickened margins. The thickening is especially well developed along the hind margin of the head. This part corresponds to the "hind consolidated arch" in *Dinichthys* (Heintz 1932. 2. fig. 4, PCA). The hind side corner of the head, (fig. 2, Ip) with the fossa condylus is very massive, equal to *Dinichthys*, where the joint process is placed in the corresponding position (fig. 4, Ip).

Another consolidated ridge runs from the posterior corner of the marginal obliquely upward in the direction of the pineal plate (fig. 2, LCP) corresponding to the "lateral consolidated portion" in *Dinichthys* (fig. 4, LCP). It becomes narrower near the orbits and here forms the thickened side margin of the pre-orbital plate. The front of the head is also considerably thickened, the anterior part of the pre-orbital being particularly massive like the conditions in *Dinichthys* (fig. 4, FP).

In the middle, the median-basal plate is also thickened. Gradually decreasing, this thickening runs on to the central plate.

Two symmetrical, relatively thin parts of the head roof, marked on fig. 2 as "PL" can be compared with the "posterior lateral impressions" in *Dinichthys* (fig. 4, PL). The median, somewhat thin part CP (fig. 2) is equivalent to the „central impression" in the same form (fig. 4, CP). Corresponding to the condition in *Dinichthys* the central impression is also here divided in front, into two branches, by the relatively thick pineal plate. The two extreme points of the branches, which bend slightly outward and end in a clear impression, show a great likeness to *Dinichthys* (fig. 2 and 4, ts).

The Single Plates of the Head Roof.

It is a characteristic of all the head roof plates in *Homostius* that they are:

1.) Relatively thin and level, and 2.) Overlap each other unusually strongly. As a result, the course of the limits between the single plates, on the outside and the inside of the head shield is very different (fig. 1, 2 & 3). It is clearly seen in fig. 3 where the parts of the plates, which overlap each other, are scratched.

In spite of the solid connection, which in some cases was strengthened by the help of long spines, we find, that in the material from Estonia, the plates of the head roof are, as a rule, isolated. On the other hand, the material from Scotland shows very completely preserved head roofs with all the plates in their natural position.

The Median-Basal Plate (MB, fig. 1, 2, 3, 5, 48 & 49; Pl. I; Pl. II; Pl. III, 1). This plate is the largest in the head roof. From the outside it shows no overlapping margins, and forms the greatest part of the anterior region of the head (fig. 1). It is very long, its breadth-length index measuring ca 85. For comparison, it may be mentioned that in *Dinichthys* the same index measures 140, in *Coccosteus* 160, in *Pholidosteus* 270, and only in some *Acanthaspids* and in very narrow forms from Wildungen is the index less than 85. It thus follows that MB stretches exceptionally far forwards, covering nearly 2/3 of the whole length of the head. The corresponding condition in *Dinichthys* is somewhat more than 1/4, in *Coccosteus* about 1/3 and in *Oxyosteus* only 1/6. Finally MB's surface comprises nearly 1/3 of the whole area of the head roof, while in *Dinichthys* the surface of MB composes not more than 1/10 of the whole head roof surface.

The shape of MB, taken as a whole, is oblong trapezoid (fig. 1, 2, 3 & 5; Pl. II, 1; MB. Pl. XIV, 1; Pl. XVII, 1) but the course of the single limits vary strongly in different examples. Unfortunately, I have not had material enough always with certainty to define if this is only an individual variation or a specific character. In some specimens, for instance, the side margins have a sharp impression on the upper part, the front margin being more or less strongly bifurcated (Pl. II, 1).

The posterior margin of MB is somewhat concave, with a small sharp projection developed exactly at its median point (Pr. fig. 1, 2, 3 & 5 Pl. I, 3, 4).

The surface of MB is even and is covered with fine tubercles. As Asmuss (1856) said: "die Oberfläche erscheint ungefähr wie mit gleichmässiger feiner Manna dicht bestreut" (Pl. I, 3; Pl. II, 2). The tubercles differ according to their position — those in the hind median portion (around the region of the ossification

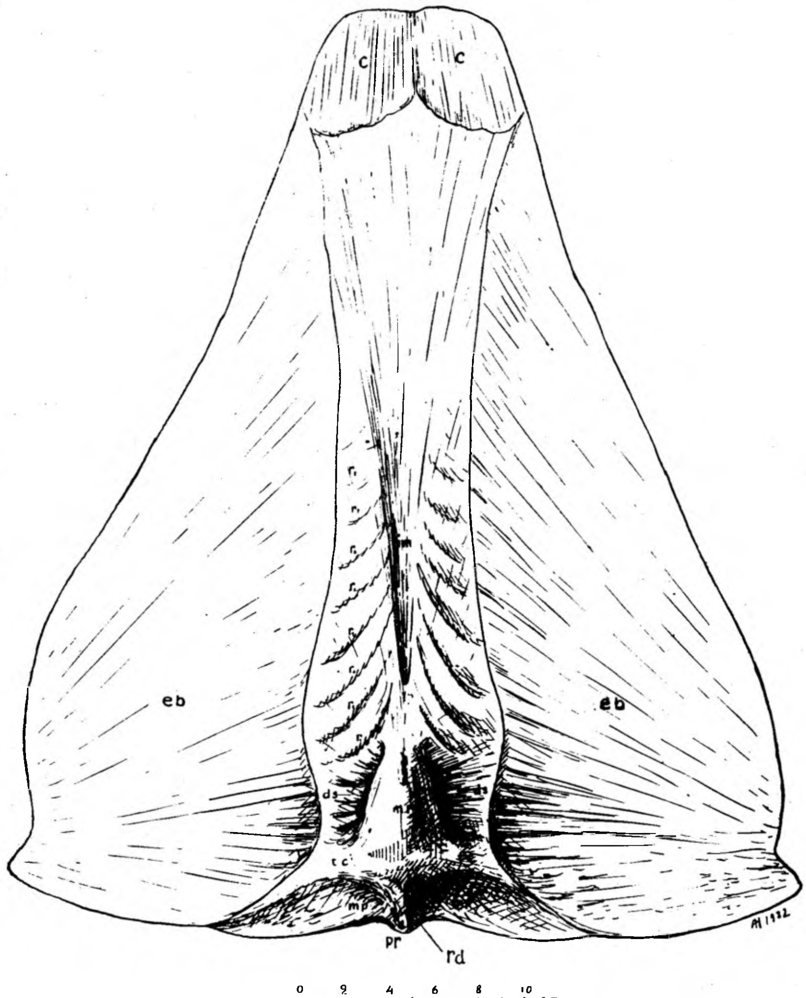

Fig. 5. The median-basal plate of *Homostius* sp. (after *H. sulcatus* Kut. and *H. milleri* Trq.) from the inside. *c* — overlapping margin covering *C* plate, *eb* — overlapping margin covering *EB* plate, *rd* — hind median ridge, $r_1, r_2, r_3 \ldots$ — ribs on side of median impression, *ts* — transversal wall. Else as in fig. 2.

centre or "focus" as Asmuss called it) are the smallest. They increase gradually towards the side and front margin of the plate. A small triangular-shaped part along the posterior margin of MB (a, fig. 1; Pl. I, 3; Pl. II, 2) is not covered with tubercles. The corresponding smooth area is to be found, as we shall see later, along the front margin of the median-dorsal plate; these places indicate the part of the plates where ligament was attached.

MB overlaps the externo-basal plate especially strongly, covering nearly $^1/_2$ of the latter (eb, fig. 3, 5; Pl. I, 4; Pl. II, 1). The front part of MB somewhat overlaps the hind portion of the central plates (c, fig. 3, 5; Pl. II, 1). Thus the inside of MB shows large and distinct overlapping margins, with the result that in a complete head roof only a very small stripe of the plate is seen from the inside (fig. 2 & 5; Pl. III, 1). Nearly $^3/_4$ of the whole plate is covered from this side partly by EB, partly by C. Its central portion, visible from the inside, shows a very interesting structure which can be compared with the corresponding part in other *Arthrodira*. Unfortunately this part of MB is described in greater detail in a few forms only, namely in *Dinichthys* (Newberry, 1875, 1889, and Heintz, 1932, 2), in *Coccosteus trautscholdi* (Trautschold, 1889, and Obručev, 1931), in *Heterostius* (Asmuss, 1856, Pander, 1857, and Heintz, 1930, 1) and in *Stenognathus* (Heintz, 1931, 3). Besides these, I have seen an MB plate from Sjass, by Professor Jaekel, which Trautschold collected in 1891, with a very well-preserved interior. As far as I know this form has not as yet been described,[1] I therefore give a sketch of this plate (fig. 8) and designate it below as *Coccosteus* sp. from Sjass, a name written on the labels by Trautschold.

As the conditions in *Dinichthys* are very well known, we will first compare *Homostius* with that form (fig. 4). Like *Dinichthys* the hind part of the plate is relatively thin (mp, fig. 2, 4 & 5; Pl. I, 4; Pl. II, 1; Pl. IV, 3) and divided into two parts with the help of a small ridge running from the projecting point on the posterior margin upwards along the median line (rd. fig. 3, 4 & 5; Pl. I, 4; Pl. II, 1; Pl. IV, 3). The same condition can be observed in *Coccosteus trautscholdi* (mp, rd, fig. 6) (Obručev,

1) Obručev described this form in his latest paper (1933) as *Holonema radiatum* Obr.

1931), in *Coccosteus* sp. from Sjass (mp, rd. fig. 8), *Stenognathus* (mp, rd, fig. 9), *Heterostius* (mp, rd, fig. 7) and other forms. This thin division is limited from the front part of the head by a more or less clearly developed transversal wall (tc, fig. 4, 5, 6, 7, 8 & 9), which is especially distinct in *Dinichthys* (fig. 4) where it forms a really well-marked ridge. In other forms as *Coccosteus trautscholdi* and *Heterostius* (tc, fig. 6 & 7) this part is not so sharply limited and forms only a thickened broad wall, running in a transversal direction. In *Coccosteus* sp. from Sjass this part is developed as a narrow crispa (tc, fig. 8). In *Homostius* the transversal wall is clearly seen as a short flat ridge, running on the posterior part of the plate (tc, fig. 2 & 5; Pl. I, 4; Pl. II, 1; Pl. IV, 3).

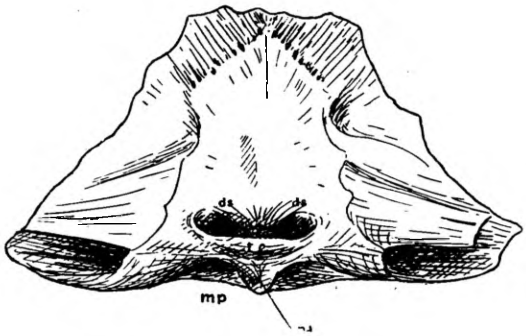

Fig. 6. The median-basal plate of *Coccosteus trautscholdi* Eastm. from the inside. Explanation as in fig. 5.

Immediately in front of this transversal wall we find in *Dinichthys* the so-called "double sockets" — a quite deep impression, divided by a longitudinal median ridge into two parts (ds, fig. 4). These double sockets are very characteristic of all *Arthrodira* and can always be found of more or less varied shapes. In *Coccosteus trautscholdi* (fig. 6) and *Heterostius* (fig. 7), for instance, the condition is reminiscent of that in *Dinichthys*: both sockets are placed relatively near each other in a common impression, with a small median ridge between them (ds, fig. 6 & 7). On the

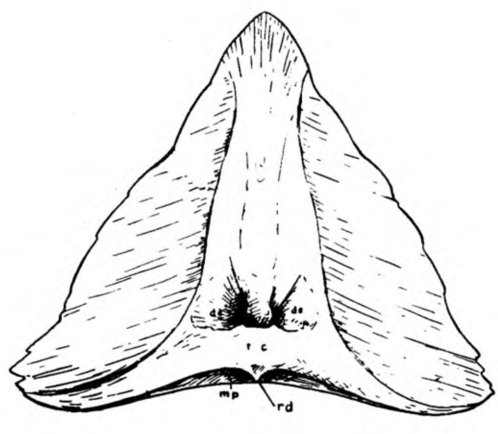

Fig. 7. The median-basal plate of *Heterostius* sp. from the inside. Explanation as in fig. 5.

contrary, in other forms as *Coccosteus* sp. from Sjass (fig. 8) and *Homostius* (fig. 5) the distance between the sockets is large and the median ridge between them strongly thickened. In *Homostius* this ridge is particularly well-developed (mr, fig. 2 & 5; Pl. I, 1, 2, 4; Pl. II, 1; Pl. IV, 3). Melted together with the transversal wall (tc) it continues immediately forward from the central part, forming the hind central thickened part of MB. This median ridge has a characteristic outline — broader behind, narrower in front (mr. fig. 2 & 5; Pl I, 1, 2, 4; Pl. II, 1) with the sockets developed as oblong, narrow clefts on its sides (ds, fig. 2 & 5; Pl. I, 1, 2, 4; Pl. II, 1; Pl. IV, 3).

The position of the openings of the sockets are directed differently in the various forms, in *Dinichthys* (fig. 4) more upward, in *Coccosteus trautscholdi* (fig. 6) and *Heterostius* (fig. 7) more forward and finally in *Homostius* more sideward.

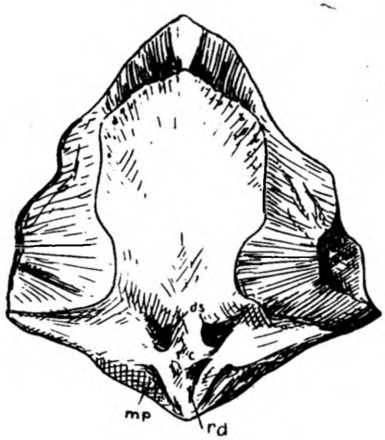

Fig. 8. The median-basal plate of *Coccosteus* sp. from Sjass (Trautschold) from the inside. Explanation as in fig. 5.

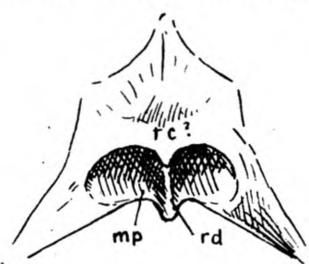

Fig. 9. The median-basal plate of *Stenognathus gouldi* Nwb. from the inside. Explanation as in fig. 5.

Obručev in his paper about *Coccosteus trautscholdi* (1931) pointed out, that possibly the "cranio-spinal process" (Stensiø, 1925) of the neurocranium fitted into the double sockets. The same explanation was given for their function in *Dinichthys* by Stetson (1931). In the latter the double sockets are divided from the front part of the head roof by a high, thick ridge — the posterior consolidated arch (fig. 4, PCA). This ridge is much higher and more strongly developed than the transversal wall (tc). The double sockets are therefore more naturally connected with the hind thin part of MB, than with its thickened front part (fig. 4), what led me to suppose (Heintz, 1932, 2) that musculus levator capitis was also attached to the double socket. New investigations have, however, shown me that in many other forms the hind consolidated arch has a course other than that in *Dinichthys*, becoming one with the transversal wall (tc), which therefore becomes greatly strengthened (see below). At the same time, the double sockets are moved forward and are divided from the hind thin part of MB by a solid, thick ridge (transversal wall, tc, fig. 2, 5, 6 & 7). Thus my explanation of the function of the double sockets proves to be unacceptable, as it is difficult to expect that the muscle was attached to the MB plate far forward, in front of the transversal wall. The explanations proposed by Obručev and Stetson, however, are also problematic, firstly because the presence of the cranio-spinal processes in *Arthrodira* cannot be regarded as certain, as this structure is, as yet, only known from *Macropetalichthys*, and secondly, if the cranio-spinal processes were developed in *Arthrodira* they would form the most posterior point of the neurocranium. But as I have tried to point out (1932, 2), the neurecranium in *Arthrodira* extends behind the head roof, so the cranio-spinal processes, if existing, would be situated in the opening between the head and body carapaces, but not as far forward as the double sockets. The significance of this impression is thus hitherto unknown.

In front of the double sockets in *Dinichthys* is a strong thickened portion — forming the central part of the hind consolidated arch (fig. 4, PCA). More in front MB becomes thinner, ending in a distinct transversal limit (trl, fig. 4). A quite different picture is shown us by those *Arthrodira* where the hind border of the head roof is not so strongly concave as in *Dinichthys*, or not concave at all. The thickened ridges, always running from the fossa condylus along the hind margin of the head to the median line, forming the wings of the posterior consolidated arch, meet here at an angle not so sharp as in *Dinichthys*. They form a somewhat bent (as in *Heterostius*, fig. 7) or a nearly straight (as in *Coccosteus trautscholdi*, fig. 6, and *Homostius*, fig. 5) line, with the result, that the thickened central part of the posterior consolidated arch is moved downward, from the position in front of the double sockets to the position behind them, becoming one with the transversal wall (as pointed out before) (fig. 2, 5, 6 & 7). Thus the anterior part of MB in front of the double sockets, in these forms is relatively thin and decreases in thickness gradually forwards. In *Homostius* this part is very long (fig. 2 & 5) so that the part of MB in front of the double sockets is about four times as long as the part behind them. In front of the median ridges we find (mr, fig. 2 & 5; Pl. I, 4; Pl. II, 1; Pl. IV, 3) a small, quite deep impression, which becomes broader and at the same time flatter, in an anterior direction (im, fig. 2 & 5; Pl. 1, 2; Pl. II, 1). On both sides of this impression, in some forms, remarkably symmetrically arranged ribs are developed, placed under a more or less sharp angle to the median line (r_1—r_8, fig. 2 & 5; Pl. I, 1, 2; Pl. III, 1). The pairs farthest back are most distinct and deep, and are placed at an especially sharp angle (r_1—r_3). Forward, the ribs become more and more flat and obtuse, their angles to the median line increasing gradually (r_4—r_8). In the best preserved specimens (from the Edinburgh Museum Pl. III, 1) I was able to count 10—11 ribs which, however continue to the EB plates also. On the largest single MB plate (from Tartu Museum) no traces of ridges are preserved at all (Pl. II, 1). The presence of this ridge was pointed out for the first time by Asmuss (1856). Woodward (1893, 3) when describing the MB plate in *Homostius milleri* Traquair also mentioned this unusual structure and explained it as follows: "These markings behind are very suggestive of an impression of the anterior part of the spinal cord with its divergent nerves, but in front they appear rather as if corresponding to the septa between the myocommas of the muscular system. The brain itself would certainly have occupied a more anterior situation." As we shall see later it is difficult to admit that the brain in *Homostius* did not stretch into the hind limit of the head shield. The explanation of these impressions given by Woodward seems, therefore, hard to acknowledge, and as I am not yet able to give another explanation, the significance of these ribs must still be regarded as unknown. As far as I know, a corresponding structure on the inside of MB has not been observed in any other *Arthrodira*.

The Externo-Basal Plate (EB, fig. 1, 2, 3, 10, 11, 46 A, B, C, 48 & 49; Pl. II, 2; Pl. III; Pl. IV; Pl. V, 1, 2, 3, 4; Pl. XIV, 1; Pl. XVII, 1; Pl. XXIII, 1). Corresponding to the elongated shape of the MB plate, the EB is also unusually long and narrow. It is nearly triangular, with a straight hindside (A—D), a convex outside (A—B) and a somewhat concave inside

(D—B) limit. Its upper corner is sharp (B). On the contrary both the lower (D & A) are nearly at a right-angle, the outside hind corner (A) in particular measures nearly 90°. More than half of the hind limit is occupied by a very long fossa condylus (fg, fig. 10, 11 & 46; Pl. III, 2; Pl. IV; Pl. V, 1, 2, 3, 4). The strongly developed processus glenoidalis (pg, fig. 10, 11 & 46; Pl. III, 2; Pl. IV; Pl. V) is placed on the basal part of the outside limit. Its surface like that in *Dinichthys*, is placed nearly perpendicular to the longitudinal axis of the fossa condylus. On the other hand, the angle between the upper surface of EB and the surface of processus glenoidalis is quite different from that in *Dinichthys*. In the latter form this angle measures ca. 150°, in *Homostius* not more than 110°. Corresponding to these conditions, the angle between the length axis of the fossa condylus and the upper surface of the head is also very different in both forms. In *Dinichthys* it measures ca. 70°, in *Homostius* only ca. 20°. It is obvious that the difference in these angles correlates with the fact, that *Homostius*' head roof is very slightly curved in relation to the head roof in *Dinichthys*.

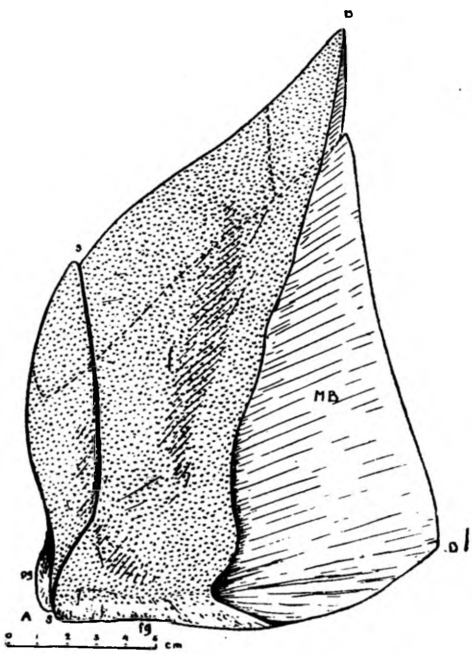

Fig. 10. The left externo-basal plate viewed from the outside. *A* — hind side corner (joint process), *B* — upper corner, *D* — inside lower corner, *fg* — fossa condylus, *MB* — overlapping margin covered by *MB* plate, *pg* — processus glenoidalis, *s* — *s* — sensory canal.

From the outside, the whole plate is evenly covered with fine tubercles (fig. 10; Pl. II, 2; Pl. III, 2; Pl. IV, 1; Pl. V, 1). A distinct and deep sensory canal runs near its outside limit (s-s, fig. 10; Pl. III, 2; Pl. IV, 1; Pl. V, 1; Pl. XXIII, 3). In the lower part it turns in a sideward direction, towards the hind side corner of the plate, where it crosses the limit of the plate and continues on to the plate of the body carapace (ADL).

From the inside EB is quite smooth (EB, fig. 2 & 11; Pl. III, 1; Pl. IV, 2, 3; Pl. V, 4). The thickened parts are only developed along its hind margin, where the fossa condylus is placed, and partly on the hind part of the outside margin, where processus glenoidalis is developed. Thus the thickened hind and outside margins of EB form a kind of wall (w-w-w, fig. 2 & 11; Pl. IV, 2, 3; Pl. V, 4) which surrounds the hind side corner of the plate. From this thickened corner radiate two or three more or less indistinct ridges (rd, fig. 3 & 11; Pl. IV, 2; Pl, V, 4) to the inner, thinner part of EB.

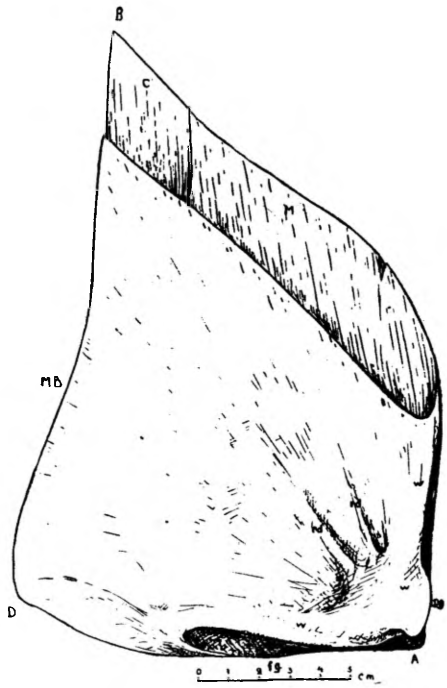

Fig. 11. The left externo-basal plate seen from the inside. *C* — overlapping margin covered by *C*, *M* — overlapping margin covered by *M*, *rp* — ridges radiating from the hind side corner, *w* — *w* — *w* — thickened wall which surrounds the hind side corner. Otherwise as in fig. 10.

In this corner is developed a remarkable incrustation, which Asmuss (1856, p. 18) has already noted and described as follows: "Ihre (Externo-Basal plate) inneren Wandungen sind . . . mit einer emailähnlichen, harten und spröden, auf ihrer Oberfläche sonderbar gerunzelten Masse ausgekleidet, die an noch so blassen Knochen immer rotbraun gefärbt und etwas durchscheinend ist" (* Pl. IV, 3; Pl. V, 4). This remarkable red coating is not known from other parts of the skeleton in *Homostius* and has never before been observed in any other *Arthrodira*. Unfortunately, I was not able to obtain a microscopical section of this part. Its function is hitherto unknown.

EB, like the condition in other *Arthrodira*, comes in contact with three other plates of the head roof: 1) the median-basal, which greatly overlaps the outside of EB (MB, fig. 1 & 10; Pl. II, 1, 2, 3; Pl. IV, 1; Pl. V, 1), 2) the marginal, which is considerably overlapped by EB (M, fig. 1, 2, 3 & 11; Pl. IV, 2; Pl. V, 4) and finally 3) the central, which is only somewhat overlapped by the front part of EB (C, fig. 1, 2, 3 & 11; Pl. IV, 2). All the overlapping margins, both from the out and inside are clearly seen and strongly developed.

The Marginal Plate (M, fig. 1, 2, 3, 12, 13, 48 & 49;

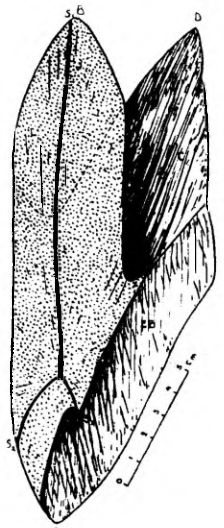

Fig. 12. The left marginal plate figured from the outside. *A* — posterior point, *B* — upper outside point, *C* — margin overlapped by *C*, *D* — upper inside point, *EB* — margin overlapped by *EB*, s_1-s_2-s_3 — sensory canals, x — protuberated part of the tuberculated surface.

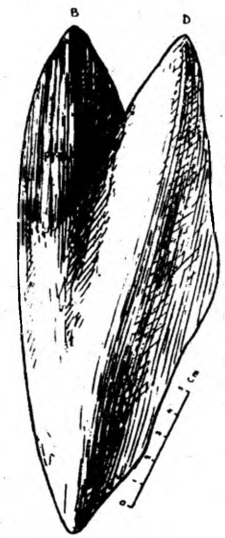

Fig. 13. The right marginal plate viewed from the inside. *PtO* — margin overlapping the *PtO* plate. Otherwise as in fig. 12.

Pl. III, 1; Pl. VI; Pl. XIV, 1; Pl. XVII, 1). This plate is relatively narrow and long and is situated along the outside margin of the head roof. Its outline (fig. 12 & 13; Pl. VI, 1, 2) is bifurcated: running from its rear point (A) it becomes divided into two parts at the top (B & D). Its outside margin is straight in the median part, but curves slightly inwards at both ends. From the outside is seen an almost spindle-shaped tuberculated portion and two quite distinctly divided overlapping margins, one upper

(C) and one lower (EB). In some specimens a more or less narrow, long protuberance from the tuberculated surface continues obliquely upward, exactly along the limit between both overlapping margins (x, fig. 1; Pl. VI, 1). In other specimens the protuberance is short (x, fig. 12; Pl. VI, 3), or not present at all (Pl. VI, 4).

A very distinct sensory canal runs from the upper point of the plate (s_1) downward, parallel to the outer and inner margin of the tuberculated part of the plate. Not far from its lower point the canal curves slightly and branches into two — the one going outward and crossing the outward margin (s_2), the other (s_3) crossing the limit to the EB plate on which it continues (fig. 1, 12, 48 & 49; Pl. VI, 1, 3, 4; Pl. XIV, 1; Pl. XVII, 1). Thus the course of the sensory canal on the marginal is similar to the condition known in other *Arthrodira*. The greatest divergence lies in the fact, that the ossification centre and the branching point of the sensory canals are removed farther to the rear.

The lower overlapping margin was covered with the externobasal plate (EB, fig. 12; Pl. VI, 1, 3, 4), the upper with the central plate (C, fig. 12; Pl. VI, 1, 3, 4).

From the inside (fig. 2 & 13; Pl. III, 1; Pl, VI, 2) the plate shows two distinctly developed thickenings, which run from the lower point (A) to the right and left upper points (B and D) respectively. The ridge A—D corresponds in the position and direction with the side thickening ridge in *Dinichthys* (fig. 4 Rd).

Only one overlapping margin is seen on the inside. It is developed on the outer upper point of the plate (B) and was covered by the post-orbital plate (PtO, fig. 13; Pl. VI, 2).

As is known, in many other *Arthrodira* (*Coccosteus*, *Phlyctænaspis*, *Stenognathus*, *Dinichthys*, *Heterostius*, *Pholidosteus* and others) a small plate is developed immediately behind the marginal. The plate is known by different names: angulare (Traquair, 1894), post-genale (Gross, 1932), post-marginal (Heintz, 1931, 3, 4, 1932, 2). In the majority of forms this plate also touches the EB plate. It seems to be completely reduced in *Homostius*, and I was not able to find it either in the complete specimens from Scotland or among the isolated plates from Estonia.

The Central plate (C, fig. 1, 2, 3, 14, 15, 48 & 49; Pl. III, 1; Pl. VII; Pl. XIV, 1; Pl. XVII, 1). It comprises a large, even, rhomboidal-shaped plate. Like all the plates described above C is unusually long and narrow. Especially characteristic for *Homostius* is the circumstance that C takes part in limiting the orbits (or, fig, 1, 2, 14 & 15; Pl. III, 1; Pl. VII; Pl. XIV, 1; Pl. XVII, 1).

As the central is relatively long and thin with many protuberated parts, it is only seldom found as a complete isolated

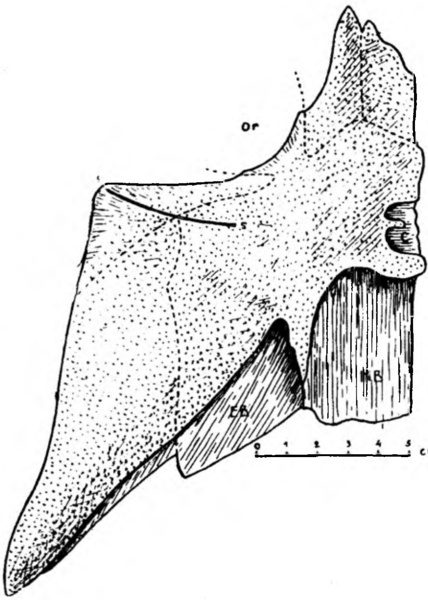

Fig. 14. The left central plate seen from the outside. *C* — overlapping margin covered by adjoining right *C* plate, *EB* — overlapping margin covered by the *EB* plate, *MB* — the same covered by the *MB* plate, *Or* — margin of the orbital opening, *s-s* — sensory canal.

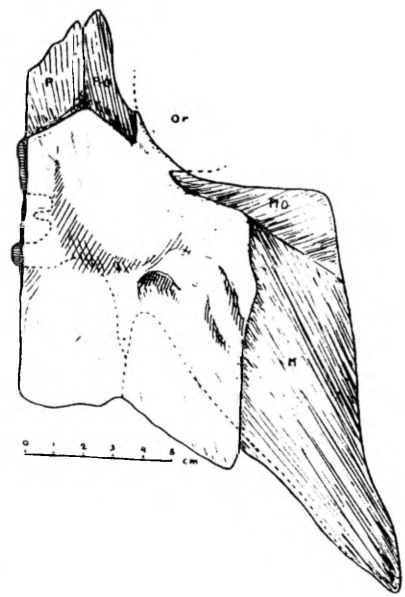

Fig. 15. The left central plate seen from the inside. *M* — overlapping margin covering the *M* plate, *Or* — margin of the orbital opening, *P* — overlapping margin covering the *P* plate, *PrO* — the same covering the *PrO* plate, *PtO* — the same covering the *PtO* plate.

plate. Among the collection in Tartu only one more or less complete specimen (Pl. VII, 1, 2) and some fragments are known.

From the outside (C, fig. 1, 14 & 48; Pl. VII, 1; Pl. XIV, 1; Pl. XVII, 1) the plate is evenly covered with tubercles. Only on the upper part along the margin of the orbital opening are the tubercles absent, and the radiant bone structure is clearly seen (or, fig. 14; Pl. VII, 1).

Only one sensory canal is developed running from the limit with the post-orbital plate in the direction of the ossification centre, which, however, it does not reach (ss, fig. 1, 3, 14, 48 & 49; Pl. VII, 1; Pl. XIV, 1; Pl. XVII, 1). As is known, in the majority of other *Arthrodira*, we usually find another canal — the pre-orbital — on C. In some forms is also developed a third — the externo-basal — which runs from the ossification centre of the EB plate upwards to C. No trace of these last two canals can be seen in *Homostius*.

From the inside (C, fig. 2 & 15; Pl. III, 1; Pl. VII, 2) C is smooth, with only weakly developed thickenings in the middle part. As usual, it comes in contact with all the plates of the head roof except the rostral, thus touching 7 different plates. Its lower part is greatly overlapped from the outside by MB and EB (MB, EB, fig. 3 & 14; Pl. VII, 1). With the upper and side margins it overlaps the M, PtO, PrO and P plates. (M, PtO, PrO and P, fig. 3 & 15; Pl. VII, 2). Finally, it is combined with the adjoining central plate with the help of a very complicated suture (C, fig. 1, 14 & 15; Pl. VII, 3).

The Pre and Post-Orbital Plates (PrO & PtO, fig. 1, 2, 3, 48 & 49; Pl. III, 1; Pl. XIV, 1; Pl. XVII, 1) are the two most characteristic plates in the head roof of *Homostius*. Firstly, they are unusually small compared with the other plates of the head. Thus, for instance, in *Dinichthys*, the post-orbital is nearly of the same size as the externo-basal, and the pre-orbital is even larger than the EB. In *Homostius* PtO measures not more than 1/3 and PrO 1/5 of EB.

Secondly, the pre-orbital and post-orbital processes are so strongly developed that they meet in front of the orbital openings. Thus the orbits are almost entirely surrounded by these two plates, an arrangement not known in any other *Arthrodira*. Thirdly, the orbital openings are removed so far inward toward the median line (bentonic forms), that the PtO and PrO plates do not touch each other with the basal parts, but are divided by C [1]. In all other *Arthrodira* the limit between the basal parts of PrO and PtO is particularly strongly developed.

The Post-Orbital Plate (PtO, fig. 1, 2, 3, 16, 17, 48 & 49; Pl. III, 1; Pl. V, 5; Pl. VIII; Pl. IX, 1, 2; Pl. XIV,

1) In one specimen from Spitsbergen the basal parts of the PrO and PtO plates also touch each other (See later).

1; Pl. XVII, 1) is the largest of these two plates. Its nearly triangular-shaped basal part, with the help of two strongly developed overlapping margins is connected with M and C (M & C, fig. 3 & 16; Pl. VIII, 1; Pl. IX, 1, 2). The post-orbital process is developed as a long thick curved offshoot, limiting nearly half of the orbital opening (ptp, fig. 16; Pl. VIII, 1, 2; Pl. IX, 1, 2). The outside of the plate is covered with tubercles in the centre, the post-orbital process and the outside margin only revealing ossi-

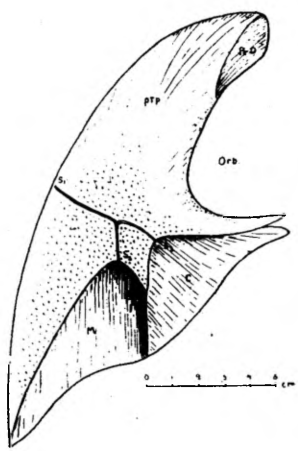

Fig. 16. The left post-orbital plate from the outside. *C* — overlapping margin covered by the *C* plate, *M* — the same covered by the *M* plate, *Orb* — margin of the orbital opening, *ptp* — post-orbital process, *PrO* — part covered by the pre-orbital process, s_1-s_2-s_3 — sensory canals.

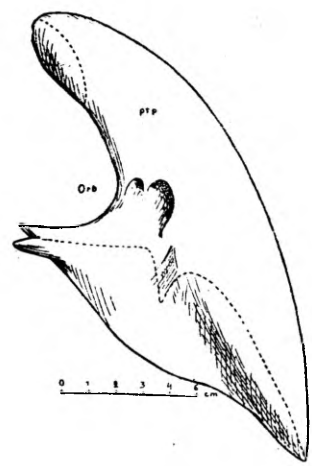

Fig. 17. Inside view of the left post-orbital plate. Explanation as in fig. 16.

fication rays (fig. 16; Pl. VIII, 1; Pl. IX, 2). As usual, a strongly developed sensory canal (s_1, s_2, s_3, fig. 1, 3, 16, 48 & 49; Pl. VIII, 1; Pl. IX, 1, 2) runs from the outside margin of the plate (s_1) obliquely downward to the limit of the C plate (s_2). This canal continues, as we see on the C plate. A short canal branches from the former and runs directly downward to the limit of the M plate (s_3), on which it continues further on to the EB plate. From the inside (fig. 2 & 17; Pl. III, 1; Pl. VIII, 2) the PtO is relatively smooth and shows no clear ridges or impressions. On the whole it is very solid and thick. Nevertheless, only a few fragments are known from Estonia. The best one represents a nearly complete plate (Pl. VIII, 1, 2). Unfortunately, the original of this is lost, and there is only left the plaster-cast which Asmuss prepared. Another is pictured on Pl. IX, 2. It represents a much worn fragment. The surface ornamentation is indistinct and all the corners are partly broken off and rounded, only the sensory canals being well preserved. A perfectly preserved small fragment (Pl. VIII, 3) shows the outside of a plate, with overlapping margin on to C and M and clearly developed sensory canals. Finally, the little piece depicted on Pl. V, 5 represents a fragment with the margin against C and the limits of the lower part of the orbit. The fine nearly complete plate figured on Pl. IX, 1 represents one of the few undoubted fragments of *Homostius* known from Spitzbergen. This plate shows an interesting new overlapping margin, immediately behind the orbit limit and in front of the overlapping margin to C (pro Pl. IX, 1). It seems that the last does not continue so far forward as to the orbital openings. This new overlapping margin could only be covered by the pre-orbital plate, which in all other specimens, just at this point, comes very near to the post-orbital plate (compare fig. 1, 2, & 3; Pl. XIV 1; Pl. XVII, 1). It is also very probable, that in the form from Spitsbergen the pre and post-orbital plates touch each other not only with the pre and post-orbital processes, but also with the basal part of the plates. This Spitzbergen form must in that case be regarded as a more primitive form, where the migration of the eye-opening in the direction of the median part of the head roof is not so far advanced as in other specimens of *Homostius.* The eye-opening in this form is only limited by the pre and post-orbital plates and neither the sub-orbital nor the central take part in encircling the orbit.

The Pre-Orbital Plate (PrO, fig. 1, 2, 3, 18, 19, 48 & 49; Pl. III, 1; Pl. IX, 3, 4, 5; Pl. XIV, 1; Pl. XVII, 1) is a small, narrow, bent plate. The pre-orbital process is especially strongly developed (prp., fig. 18 & 19; Pl. IX, 5). Only on the inside limit of the plate is the overlapping margin more or less strongly developed. The hind part was covered with the offshoot of C (C, fig. 3, 18 & 19; Pl. IX, 3). The side part comes in contact with the pineal (P, fig. 3, 18 & 19, Pl. IX, 3). Here in the upper part, is situated a long spine (sp. fig. 18 & 19; Pl. IX, 3), fitting into the corresponding cavity on the upper part of the pineal plate, thus strengthening the connection between these two plates. On the contrary, the contact with the rostral plate is quite weak, with only a narrow overlapping margin on the inside of the plate (R, fig. 3, 18 & 19, Pl. IX, 4). On the outside only the central and lower parts of the plate are tuberculated (fig. 18; Pl. IX, 3, 5). Along its front margin and on the pre-orbital process only the ossification rays are clear. A distinct sensory canal — the pre-orbital — runs from the upper limit of the plate obliquely downward in the direction of the pineal plate (s, fig. 1 & 18; Pl. IX, 3, 5). This canal was not observed by Traquair (1889), but is very clearly developed on all the fragments from Tartu (s, Pl. IX, 3, 5). Similarly, in all the specimens from Scotland, this canal is

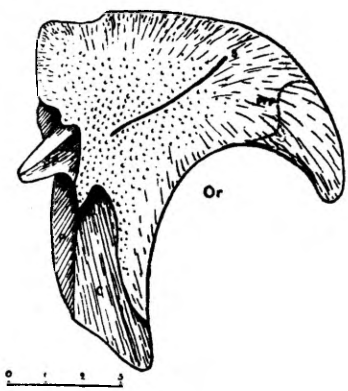

Fig. 18. The right pre-orbital plate seen from the outside. *C* margin overlapped by the *C* plate. *Or* — position of the orbital opening, *P* — margin overlapped by the *P* plate, *prp* — pre-orbital process, *s* — sensory canal, *Sp* — spine fitting into the cavity on the upper part of the *P* plate.

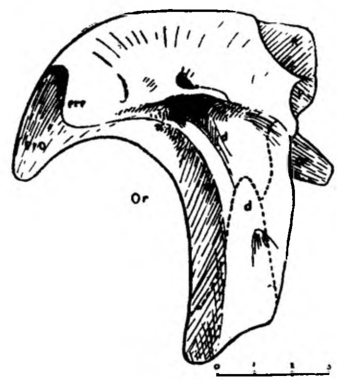

Fig. 19. The right pre-orbital plate seen from the inside. *a-a* — thickening around the orbital limit, *b* — groove on the end of the curved impression, *d-d* — curved impression, *PtO* — margin overlapping the post-orbital process, *R* — margin overlapping the *R* plate. Rest as in fig. 18.

also well developed, but is not so easily seen (s, Pl. XIV, 1; Pl. XVII, 1).

On the inside (fig. 2 & 19; Pl. IX, 4) the arrangement of the thickenings and impressions is very reminiscent of the condition in *Dinichthys* (PrO, fig. 4,). Also here we have a thickening around the orbit limit (a-a, fig. 19; Pl. IX, 4) and a curved imression (d, fig. 19; Pl. IX, 4), which ends in a comparatively deep groove (b, fig. 19; Pl. IX, 4) (the "side branches" in *Dinichthys* see fig. 4, Br and ts). The front part of the plate is thickened (fig. 19; Pl. IX, 4). As mentioned before, the point of the pre-orbital process "overlaps" the point of the post-orbital process. This "overlapping" is, however, of a somewhat divergent character from what we usually find between two plates in the head roof. The overlapping margin is indistinct, as the plates in reality only lie on top of each other, not being connected by sutures

The Pineal Plate (P, fig. 1, 2, 4, 20 & 48; Pl. III, 1; Pl. X, 1, 2, 3, 4, 5; Pl. XIV, 1; Pl. XVII, 1) is a small, thick nearly quadrangular plate. With the help of strongly developed sutures and spines it is connected with the PrO and R plates and is strongly overlapped by the upper part of C (PrO, R and C, fig. 3 & 20; Pl. X, 1, 2, 3, 4, 5). From the outside (fig. 1 & 20 A; Pl. X, 1, 2, 5; Pl. XIV, 1; Pl. XVII, 1) the tuberculated, not overlapped, part of the plate forms a somewhat cross-shaped figure. On its upper side, between the central and side branches of the cross, are two deep cavities, into which the above-mentioned spine on PrO fits in (PrO, fig. 20 A; Pl. X, 1, 3, 5). The upper part of the central branch (R, fig. 20; Pl. X, 1, 2, 3, 4) of the cross is not sculptured; it fits into a cavity on the hind margin of the rostral plate.

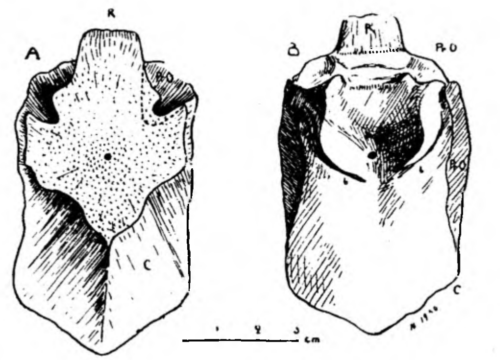

Fig. 20. The pineal plate seen from the outside (*A*) and from the inside (*B*), *a* — funnel-shaped impression, *b* — semi-circular row limiting the funnel-shaped impression. *C* — overlapping margin covered by the *C* plate. *PrO* — overlapping margin covering the *PrO* plate (*B*) and cavity where the spine from the *PrO* plate fits in (*A*). *R* — protuberated front part, fitting into the cavity on the *R* plate.

On the inside of the upper part of the plate (fig. 2 & 20 B; Pl. III, 1; Pl. X, 2, 4) a funnel-shaped impression (a) is developed, limited from above by a nearly semi-circular row (b). In the middle of this impression we find a small opening — the pineal opening. As mentioned by many authors, the pineal plate is only very thin in its central part, but it is not perforated with a real opening. It is therefore interesting to point out, that in the specimens of *Homostius* I have examined, the pineal opening is more or less clearly developed.

The Rostral Plate (R, fig. 1, 2, 3, 21 & 48; Pl. III, 1; Pl. X, 6; Pl. XIV, 1; Pl. XVII, 1) is unusually small, quite flat on both sides, with three distinct overlapping margins on the outside: one in the middle with a deep cavity for the upper point of the pineal plate (P, fig. 21; Pl. X, 6) and two on each sides for both the PrO plates (PrO, fig. 21; Pl. X, 6). No tubercles are developed on its outside. The front part of the plate is quite thin.

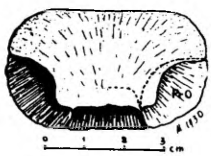

Fig. 21. The rostral plate from the outside. *PrO* — overlapping margin covered by the *PrO* plate. *R* — cavity, where the protuberated front part of the *P* plate fits in.

The rostral plate is the smallest in the whole head roof of *Homostius* (fig. 1, 2 & 3). In relation to other *Arthrodira* it is exceptionally reduced, as can be seen from the following table, showing the so-called "rostral index" that is: The relation between the length of the rostral and the length of the whole head roof multiplied by 100.

Homostius	*5*	*Dinichthys intermedius*	*24*
Coccosteus decipiens	*11*	*Oxyosteus rostratus*	*27*
Svalbardaspis stensiøi	*12*		

No trace of impressions for the nasal openings can be seen on the rostral plate.

2) The Side Plates of The Head.

In *Homostius* the side plates of the head are imperfectly known, therefore we are not able to get a clear picture of their arrangement and relative position. Of the 8 paired and one unpaired plates as known in *Coccosteus* (Heintz, 1931, 4) for instance we find in our form only 4 paired plates, and of these two only can undoubtedly be homologized with the similar plates in other *Arthrodira,* while the position and relation of the other two are more or less problematic.

H. Miller (1849, 2) was the first to picture and describe three of them, but determined them as the "internal bone", "clavicle" and "latero-cerebral plate" in his *Asterolepis (= Homostius).* Traquair in 1889 also pictured three, and correctly determined the two as sub-orbital (his plate A) and mandibular (his plate B). Finally Woodward (1916) described one pair as the right and left "upper jaw (?)."

The largest of these plates is the Sub-Orbital (Lateral-cerebral by H. Miller, 1849, 2, plate A by Traquair, 1889) (SO, fig. 22, 23, 24, 48 & 49; Pl. XI; Pl. XII, 5, 6; Pl. XIV, 11; Pl. XVII, 1).

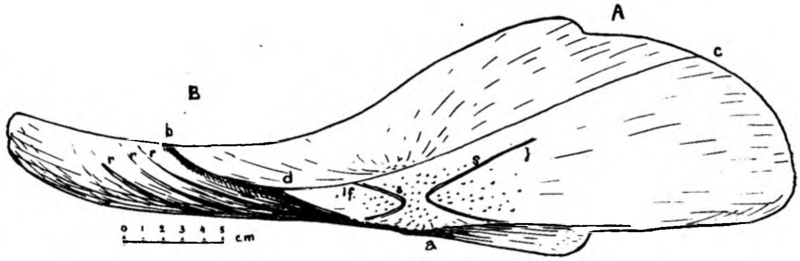

Fig. 22. The left sub-orbital plate seen from the outside. *A* — the blade *B* — the handle, *a-b* — limit dividing the front part of the handle from the blade. *c-d* — limit dividing blade into two portions. *if* — lower portion of the sub-post-orbital canal. *j* — gnathal canal. *r-r-r* — cuts on the front part of the handle. *s-s* — sensory canals.

Unlike all other *Arthrodira*, SO in *Homostius* did not limit the orbital opening from beneath. As mentioned above, the orbital openings are moved nearer to each other (and to the median line) and are thus limited by the pre and post-orbital and central only.

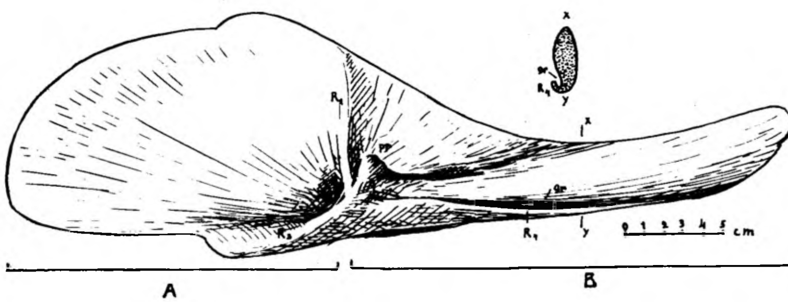

Fig. 23. The left sub-orbital plate viewed from the inside. *gr* — impression running along the handle. *pr* — projection in front of the ridge R_1; R_1 — ridge running from the upper margin of *SO* downward. R_3 — ridge running along the lower margin of the blade. R_4 — ridge running along the lower margin of the handle. *x-y* — cross-section of the handle. Rest as in fig. 22.

Nevertheless the SO has preserved nearly the same form as in other *Arthrodira*. We can clearly distinguish — a more or less broad part — the "blade" (A, fig. 22 & 23) and a narrow and relatively thick "handle" (B, fig. 22 & 23; Pl. XI, 1, 2) in front. But the distinctly marked incut for the orbit, which always clearly divides these two parts, is not sharply developed in *Homostius*.

The handle and the hind margin of the blade are thickened and solid, the upper part of the blade, on the contrary, is relatively thin.

From the outside a distinct limit formed like a step divides the front part of the handle from the blade (a-b, fig. 22; Pl. XI, 2, 4; Pl. XII, 5). It runs from the hind margin of the blade obliquely upward to the upper margin of the handle. Possibly the part of the handle in front of this limit, may be an homologue of the "tongue-shaped part" of the handle in *Dinichthys* (see Heintz, 1932, 2, fig. 21, 22 & 23), a portion which was situated lower down, and partly served as an attachment for the supragnathal elements. The front part of the handle shows clear cuts or impressions, running more or less parallel to the limit a-b disappearing more forward (r, r, fig. 22; Pl. XI, 2, 4; Pl. XII, 5).

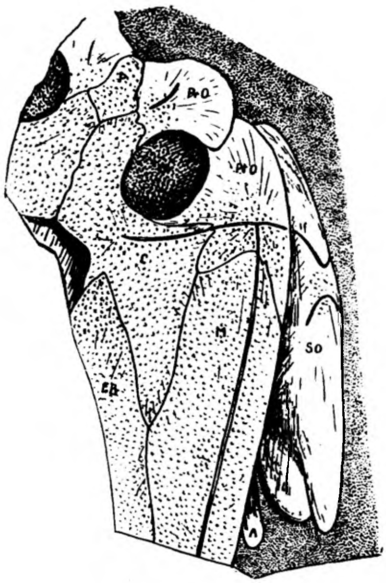

Fig. 24. The right front part of the head of *Homostius milleri* Traquair. A sketch made from specimen № 1162 from Edinburgh Museum. *A* — the plate „*x*", *IG* — infero-gnathal, *if* — post-sub-orbital sensory canal, *SO* — sub-orbital plate. Rest as in fig. 1.

Nearly in the middle of the limit a-b, another limit less distinct begins (c-d, fig. 22; Pl. XI, 4; Pl. XII, 5), which almost runs parallel to the upper front limit of the blade crossing its hind margin (c). It divides the blade into two portions — an upper, thinner and somewhat incurved, and a lower, thicker, and smoother. The upper part was, as we shall see later, covered by the sides of the head roof (fig. 24, 48 & 49), thus in reality representing a kind of overlapping margin. On the hind thickened part of the blade two independent sensory canals are developed. They form two V-shaped figures pointing towards each other (s-s, fig. 22, 24, 48 & 49; Pl. XI, 3, 4; Pl. XII, 5). As is known, in other *Arthrodira*, the sensory canals on SO always form a three-branched figure. Another exception, besides our form, is *Titanichthys*, which, according to Dean (1909), also has two independent canals. The front canal is an immediate prolongation of the sub-post-orbital canal (= infraorbital) (fig. 24), the hind one corresponding to the gnathal (= jugal) canal.

On a relatively small space between and round the sensory canals the surface of SO is covered by tubercles (fig. 22, 24, 48 & 49; Pl. XI, 3), which, however, I did not find in all specimens. In larger forms the tuberculation is mostly absent. (Pl. XI, 4; Pl. XII, 5; Pl. XIV, 1, SO).

From the inside SO is more like the corresponding plate in other *Arthrodira*. The handle continues far backwards as a thickened ridge along the lower margin of the plate (fig. 23; Pl. XII, 6). A more or less strongly developed ridge runs from the upper margin of SO downward, nearly perpendicular to the lower margin (R_1, fig. 23; Pl. XII, 6). This ridge certainly marks the original position of the hind limit of the orbital incut, and corresponds to the ridge R_1 in *Dinichthys* (Heintz, 1932, 2, pg. 139, fig. 22). Thus in reality the handle in *Homostius* represents not only the relatively narrow front portion of the plate, but also the part of the broader deal in front of the ridge R_1.

Immediately in front of the point where the ridge R_1 touches the thickening on the lower margin of the plate, a sharp projection is developed, directed upward (pr. fig. 23; Pl. XII, 6). This projection corresponds probably to the high crest on the ridge R_3 in *Dinichthys* (Heintz, 1932, 2). This last ridge in *Homostius* is shaped as a thickening running along the lower margin of the blade (R_3, fig. 23; Pl. XII, 6).

The handle is more uniform, not showing any certain homology with the structure of that in *Dinichthys*. An obvious, deep impression begins almost in front of the above-mentioned projection (gr. fig. 23; Pl. XI, 1; Pl. XII, 6). It becomes gradually deeper while running obliquely downward and forward, crossing the lower margin of the handle not far from its front point. Possibly this impression may be regarded as corresponding to the "groove" on the tongue shaped portion in *Dinichthys* (Heintz, 1932, 2). If this supposition is right, the distinct border, which limits this impression from above (R_4, fig. 23; Pl. XI, 1; Pl. XII, 6), corresponds to the ridge R_4 in *Dinichthys*. Nothing directly homologous with the ridge R_2 in *Dinichthys* can be found in *Homostius*.

It must be pointed out here, however, that in specimens from

Scotland the structure of SO is not so clearly seen, thus all these elements are difficult to perceive (SO, Pl. XVII, 1).

As mentioned, SO in *Homostius* was strongly overlapped by the head roof (Fig. 24, 48 & 49; Pl. XIV, 1). The side margin of the head roof covers the whole upper thin part of the blade but only touches the handle along its upper margin. Thus the post-sub-orbital (= Infra-orbital) sensory canal continues immediately on the SO plate (If, fig. 22 & 24; Pl. XI, 2, 3, 4; Pl. XII, 5). The front point of SO projects nearly to the limit between the PrO and PtO, while the hind part stretches as far as the middle of M (fig. 24).

In some Scotch forms, between the hind upper margin of SO and the head roof can be seen a clear cleft, which, however, was not originally so large as it looks, as SO in these specimens was partly displaced by pressure (fig. 24, Pl. XIV, 1). In this cleft we can often see the hind part of two other plates — one large and relatively broad, the other small and narrow (fig. 24; Pl. XIV, 1; Pl. XVII, 1). The first is the infero-gnathal, which we shall describe later, the second is more doubtful, and may from its position represent one of the following three plates in other *Arthrodira:* 1) the post-marginal, 2) the internal, or 3) the post-sub-orbital.

All these three plates in other *Arthrodira* are placed somewhere in this region of the head roof and in the same relation to the marginal and sub-orbital.

That our plate is the post-marginal, however, is quite improbable, as in all hitherto known forms this plate is more or less strongly connected with the head roof and composes a part of it. The plate in question is not connected with the head roof, which as we know, shows no overlapping margin in this region.

It is also improbable that we here have a post-sub-orbital plate, as in all known forms this broad and flat plate is connected with the sub-orbital. Thus it seems more plausible to suppose that our plate is the "Internal", a plate for the first time described in *Coccosteus* (H e i n t z, 1931, 4), and which probably corresponds to the "post-cuspidale" described by G r o s s (1932) in some Wildungen forms. In *Coccosteus* it is a small narrow plate, placed between M and SO, and both its form and position remind one strongly of our plate.

Unfortunately, I did not find any remains of this plate among the material in Tartu, but, as mentioned above, in four specimens from Scotland (preserved in Edinburgh Museum) it is found in situ (E. M.

1162 (fig. 24), E. M 1878/5/426, E. M. 1878/5/410 (Pl. XVII, 1) and E. M.? (Pl. XIV, 1)); one isolated plate is also preserved in the Edinburgh Museum (Original of Miller's (edit. 1861), fig. 45 "Clavicle", E. M. 1893, P. 3).

In fig. 25 is given a reconstruction of the outside of this plate, based on the material in the Edinburgh Museum. The long narrow plate ends on one side in a point (fig. 25, a) and is rounded on the other (b). This part is also bent upwards and a narrow small portion on the rounded point is tuberculated (c). Probably, only this part was visible from the outside of the head, the other was covered partly by the marginal, partly by the suborbital. On its upper margin in front of the tuberculated part is a short projection (fig. 25, d). From this a ridge runs obliquely downward and forward (e), and disappears towards the front point of the plate. The plate is thin along the upper margin (a-b-d) and more or less thickened along the lower (a-c-b). Apparently another ridge is developed on its inside, but I have not been able to study it more closely, as the inside of the plate has not been well preserved. I provisionally propose to call this plate: "plate X".

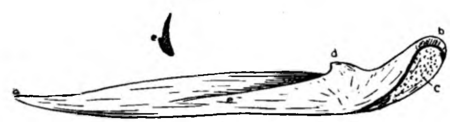

Fig. 25. The reconstruction of plate "X" of a *Homostius* sp. from the outside (chiefly after *H. milleri* Trq.), *a* — the sharp front point. *b* — the rounded hind point. *c* — tuberculated part, *d* — projection on the upper margin, *e* — the ridge.

The most remarkable plate in *Homostius* is, however, the Infero-Gnathal, well-known both from isolated plates in Tartu Museum (fig. 27, 28 & 29, Pl. XIII) and from complete specimens from Scotland (Pl. XIV, 1; Pl. XVII, 1). This plate was formerly pictured by Traquair (1889) in a drawing of *Homostius*, and its hind part was also depicted by Woodward in 1916. In his description Traquair mentioned that "we may assume that bone B . . . is the mandible, but no traces of teeth can be found on it." Woodward in the "Catalogue" (1891) remarked that "mandibular rami are suturally united at the symphysis, apparently toothless". This is the only description of the "mandible" in *Homostius*, hitherto known. The outline of this plate is in reality very remarkable and can hardly be compared with the infero-gnathal in other *Arthrodira*. However Newberry (1889) pointed out its likeness to the jaw in *Titanichthys*. The likeness is not so great, as the very characteristic twisting and sickle-shaped bending for *Homostius* is unknown in *Titanichthys*, where the IG is level and only slightly bent at the point. I have studied it closely without any positive result, until the description and picture of the "spleinale" in *Angarichthys* (fig. 26) by Obručev (1927) caught my attention. Obručev pointed out (pp. 682, 683, 684, 685, 690, 691) that *Angarichthys*, in some respects, reminds one of *Homostius*. If we try to compare IG (= speinale) in the first form with IG in other *Arthrodira* on one hand, and in *Homostius* on the other, we will

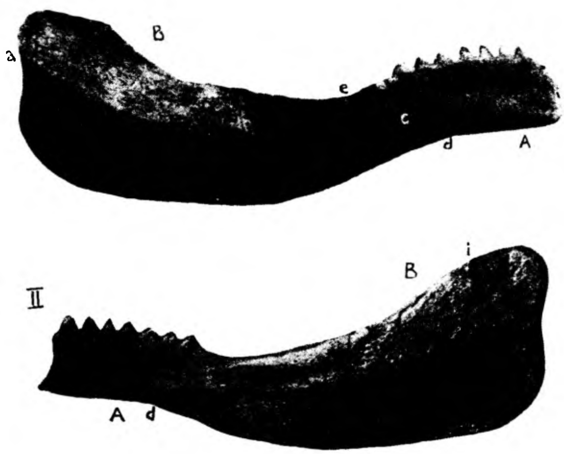

Fig. 26. *Angarichthys hyperboreus* Obručev. The infero-gnathal plate from "outside" (I) and from "inside" (II). *A* — functional portion, *B* — blade. Explanation as in fig. 27. After Obručev 1927. ca. 1/2 nat. s.

notice that IG in *Angarichthys* can be regarded as an intermediate form, which, quite unexpectedly, shows a resemblance both to IG in *Homostius* and in other *Arthrodira*.

Thanks to the kind generosity of Dr. Obručev, I received from him a great number of drawings and photographs of IG in *Angarichthys*, together with a very minute description of this remarkable bone. I therefore here wish to express my best thanks to him for all his kindness, and especially for the permission to reproduce his drawings, which are to be published in one of his papers.

In his paper published in 1927, he described the IG in *Angarichthys* (fig. 26) as follows: (pag. 689) „Es ist ein Knochen mit abgebrochenem Vorderende, 15 cm. lang und 5-3-2 cm. breit, stark sigmoidal gebogen. Seine Aussenseite (fig. 26, I, 2) ist mit einer Längsleiste versehen, die am hinteren Rande stark hervorragt und allmählich auf dem Mittelteile verschwindet. Der zahntragende Teil (A) ist sehr verdickt. Auf der Innenseite (fig. 26, II) erstreckt sich diese Verdicktung längs dem Oberrande weit nach hinten und ragt mit einer steilen Abstufung über dem übrigen Knochen. Letzterer bildet eine dünne Platte. Die sieben erhaltenen Zähne sind von dem Knochen nicht abtrennbar, elliptisch-kegelförmig und nach innen gebogen." In the figures 26, 27, III & IV and 28, I & III are reproductions of Obručev's photographs and drawings, giving a very good picture of IG in *Angarichthys.* If we compare these figures with the corresponding ones of IG in *Homostius* fig. 28, II & IV; fig. 29; Pl. XIII) the likeness between them perhaps does not appear to be too great. The fact is, however, that the IG in *Homostius* is not only strongly sickle-shaped, but is also twisted, and consequently the "blade" (B) and the "functional portion" (A) are not placed on the same plane, but with their surfaces nearly perpendicular to each other (fig. 29, especially obvious on I and V). If we "retwist" IG in *Homostius,* so that the blade and the functional portion are on the same plane, the likeness between IG in *Angarichthys* and in *Homostius* becomes more striking. Such a "retwisted" IG in *Homostius* is depicted on Fig. 27, I & III, besides an IG in *Angarichthys* (II & IV).

As seen on Pl. XIII and fig. 27, 28 & 29 the IG in *Homostius* as in other *Arthrodira* is composed of two parts — the blade (B) and the functional portion (A). Thanks to the strongly sickle-shaped form of IG these two parts are bent in opposite directions: thus on the side where the blade is convex the functional portion is concave (fig. 28, II; fig. 29, I) and, on the contrary, on the side where the blade is concave the functional portion is convex (fig. 28, IV; fig. 29, IV). As we know, exactly the same is the case in *Angarichthys* (fig. 28, I & III).

The blade (B, fig. 27, 28 & 29; Pl. XIII) is broadest in the hind, moderately thickened part and narrower in front, where it comes in contact with the functional portion. On the concave side (B, fig, 27, I; fig. 28, II; fig. 29, III & IV; Pl. XIII, 1) from the middle of the hind margin, a distinct ridge (a) runs directed inward and slightly upward, disappearing somewhere in the middle of the blade. The same ridge is also known in *Angarichthys* (a, fig. 26; a - a, fig. 27, II). The lower limit of the blade (b-d-c) runs arch-

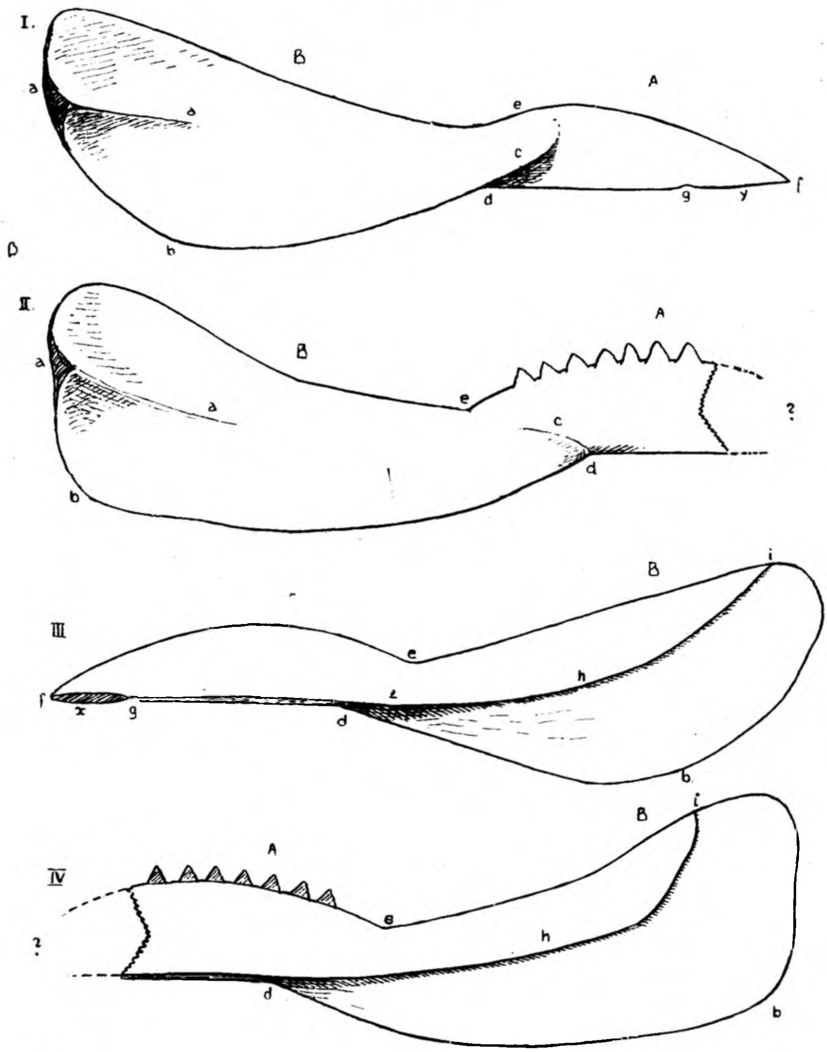

Fig. 27. The infero-gnathal of *Angarichthys* (II and IV, after Obručev) compared with the "retwisted" infero-gnathal of *Homostius* (I and III), *A* — functional portion, *a* — ridge on the hind part of the blade. *B* — blade, *b* — lower margin of the blade. *c* — step between the blade and the functional portion. *d* — point where the lower margin of the blade runs "under" the functional portion, *e* — upper, thickened, part of the functional portion, *f* — front point of the functional portion, *g* — incut in the lower margin of the functional portion, *h* — thickened prolongation of the functional portion, *i* — the hind point of the functional portion, *x* — large worn area on ovoid part, *y* — small worn area on ovoid part, *z* — the hind point of the worn area.

shaped forward and upward to the functional portion, which it strongly "overlaps" (d-c), thus forming a clear step between these two parts (c, fig. 27, 28 & 29, I; Pl. XIII, 2). This step, however, gradually vanishes on the upper, thickened part of the func-

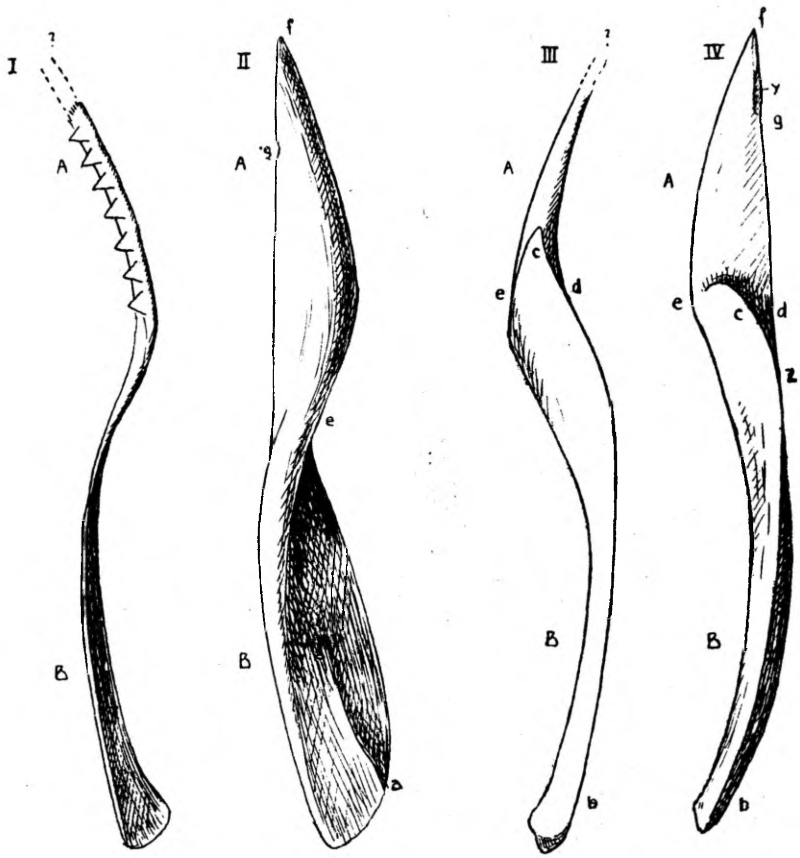

Fig. 28. The infero-gnathal plate of *Angarichthys* (I and III, after O b r u č e v) compared with that of *Homostius* sp. (II and IV) seen from above (I and II) and from below (III and IV). Explanation as in fig. 27.

tional portion (e). In *Angarichthys* we also find nearly the same development, only with the difference, that the "overlapping" on the functional portion by the blade is not so distinct, but the limit between these parts is still clearly seen (d-c-e, fig. 26, I; fig. 27, II).

On the convex side (B, fig. 27, III; fig. 28, IV; fig. 29, I, II, V; Pl. XIII, 1, 2, 4) along the upper margin runs a thickening forming the prolongation of the functional portion (h). It will be described later. In front, the lower margin of the blade runs under the functional portion (d), and forms a step (c-d) as mentioned above. The development of this side of the blade in *Angarichthys* is almost identical with that in *Homostius* (fig. 26, II; 27, IV).

As we now have seen, the blade in *Homostius* is developed quite like the corresponding part in other *Arthrodira*.

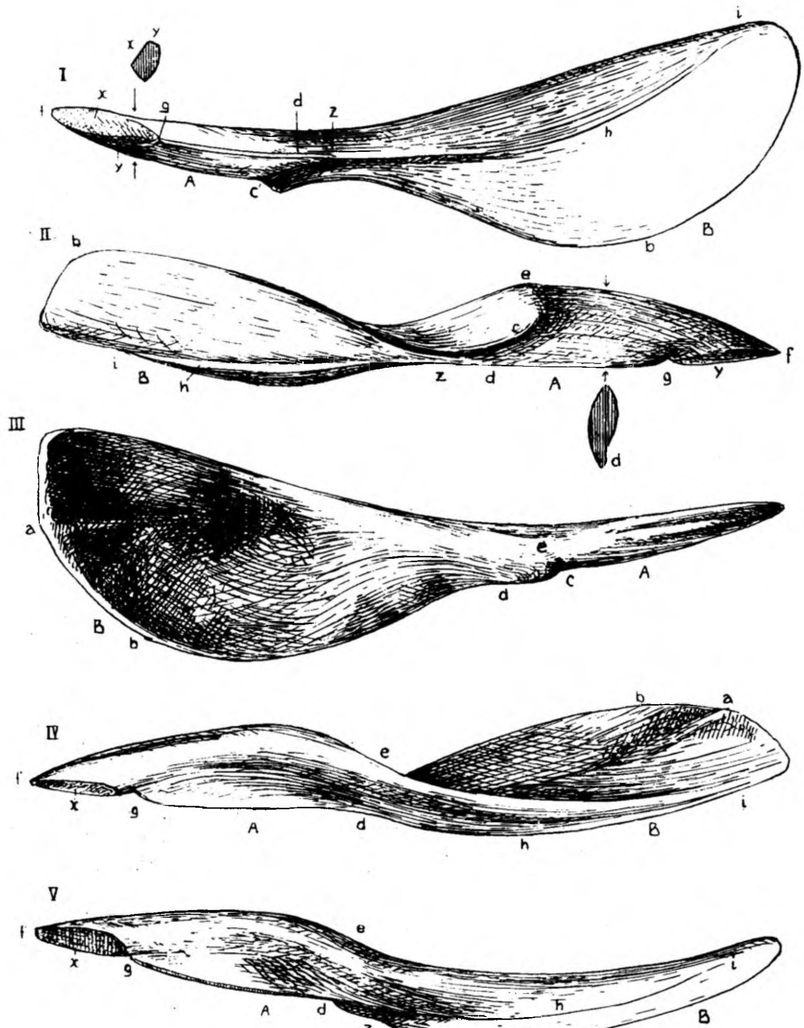

Fig. 29. The infero-gnathal plate of *Homostius* sp. from different sides. I — from the "outside", II — from side, III — from the "inside", IV — from above, V — from side. Explanation as in fig. 27.

The structure of the functional portion (A, fig. 27, 28, 29; Pl. XIII) on the other hand, is more exceptional. Its arched upper margin (e-f) is strongly thickened. In some forms the cross-section is roundish, with a marked impression on the top, in others, it is more or less angular. The almost straight lower margin (d-g-f) on the contrary, is relatively thin, except in front, (f) where it meets the thickened upper margin.

The functional portion in *Angarichthys* (A, fig. 26, 27, II, IV; fig. 28, I, III) is more uniformly thick, with the lower margin not especially thinner than the upper. Unfortunately, the front point of the functional portion in *Angarichthys* is broken off, so the configuration of this part is unknown but as its upper margin is arched, like that in *Homostius*, and its lower is straight, also like our form, it seems not improbable that the point was also developed correspondingly.

On the concave side (fig. 27, I; fig. 28, IV; fig. 29, I, II; Pl. XIII, 1, 5) the functional portion in *Homostius* is absolutely smooth without any traces of worn area or teeth. As is known, its hind portion is strongly "overlapped" by the front part of the blade (c-d).

From the convex side the functional portion (fig. 27, III; fig. 28, II; fig. 29, I, IV, V; Pl. XIII, 3, 4) is strongly developed (f-g-d-h-i). It continues backwards nearly to the hind limit of the blade (i), and composes, as before mentioned, the thickened upper part of IG, sharply divided from the blade by a distinct step (d-h-i), which increases forwards (i-d). We find a congruent condition in *Angarichthys* also (fig. 26, II; fig. 27, IV).

It is surprising to find on the lower straight margin of the blade, on this side a well-developed w o r n a r e a (d-g-f, fig. 27, III; fig. 29, I, V; Pl. XIII), which composes only a narrow stripe on the hind thin part of IG (d g), but which has an ovoid form on the thickened front portion (g-f). The presence of this area in such an unexpected part of IG has made the identification of the relation of this plate extremely difficult. I tried, naturally, first to place the worn area upwards, not downward, until a comparison with *Angarichthys* showed me that the worn area in *Homostius* is moved from the upper to the lower margin of the plate.

As mentioned, the worn area, the only real "chewing marks" we know in *Homostius*, is divided into two parts: the front ovoid-shaped, and the hind, narrow, straight part. These parts are separated by an incut (g). The ovoid area (g-f) consists of two worn planes — one large (x, fig. 27, 28, 29; Pl. XIII) and one small narrow (y, fig. 27, 28, 29; Pl. XIII), placed at an obtuse angle to each other. This circumstance may indicate that IG, during chewing not only moved up and down, but could also perform more complicated movements. As the straight narrow worn area on the thin hind part of the lower margin lies on the same plane as the large one (x) on the front ovoid part, it seems likely that they were both produced by contact with one and the same plate in the upper jaw. It is also interesting to note here that the worn area continues backward (z, fig. 27, 28, 29; Pl. XIII) — behind the point, where the front part of the blade touches the functional portion (d).

At the same time I would mention that in one specimen from Tartu (T. M. 73) I saw another worn mark on the upper thicker part of the functional portion on the concave side. This mark is relatively small. It is clearly seen on Pl. XIII, 3 (w). How this mark was caused and whether it was done while the animal was still alive, or only accidentally on the already isolated bone, it is difficult to say.

From this description the great resemblance between IG in *Angarichthys* and the "retwisted" IG in *Homostius* is obvious. The blade and the functional portion are of nearly the same form and are sickle-shaped. On the convex side of the blade a ridge (a) is developed and on the concave the prolongated hind part of the functional portion "overlaps" the blade. The greatest differences are: 1) that in *Homostius* the limit between the blade and the functional portion is more clearly developed, 2) that *Angarichthys* has well-developed teeth and 3) that in *Homostius* we find a worn area on the hind margin of the functional portion. But all these characteristics are not of a greatly decisive value and they all point in the same direction — that *Homostius* is more highly specialized than *Angarichthys*.

Hitherto, we have in our comparison only spoken about the "retwisted" IG in *Homostius*. The likeness, however, will not be reduced if we directly compare IG in both forms (fig. 28). Besides, we can, just in the twisting, find new similarities between these two forms. Obručev mentioned in a letter to me that the blade and the front part of IG in *Angarichthys* are not placed on the same plane, but slightly twisted in relation to each other. The position of the teeth on IG in *Angarichthys* also points in the same direction, not being placed on the same plane with the surface of the functional portion, but inclined in a direction from the concave to the convex side (fig. 26, 27, II, IV; 28, I, III). This circumstance also shows the beginning of the "twisting" of the functional part. Thus the "twisting" of IG, which is clearly developed in *Homostius*, has already begun in *Angarichthys*, in exactly the same direction (fig. 28). This characteristic makes a more or less near relation between these two forms still more certain.

We have now described IG in *Homostius* and ascertained its likeness to that in *Angarichthys*, but the problem of the "lower jaw" in *Homostius* is not thereby solved.

It is obvious from the description of Obručev quoted above, that he regards the side of IG, where the blade is convex and the functional portion concave (convex-concave side) as being the outside, and the opposite one (concave-convex side) as the inside.

If we compare IG in *Angarichthys* (or *Homostius*) with that in other *Arthrodira*, however, we get the opposite result. In fact, in the majority of known *Arthrodira*, the functional portion "overlaps" the blade on the outside, and is divided from it by a distinct step (cf. for instance *Coccosteus*, *Dinichthys*, *Diplognathus*, *Stenognathus*, *Oxyosteus* and others). As a rule, this limit runs from the lower margin of IG obliquely backward and upward to the upper margin. We find exactly the same condition in *Angarichthys* (and *Homostius*) on the concave-convex side, which Obručev determined as the "inside" (fig. 26, II; 27, III, IV; 29, I, V; Pl. XIII, 2, 5), only with the difference, that the hind part of the functional portion stretches farther backward, nearly reaching the hind margin of the blade, while the convex-concave side, which Obručev calls the "outside", shows no trace of this overlapping (fig. 26, I; 27, I, II; 29, III). On the contrary, it is from this side the blade more or less distinctly "overlaps" the functional portion, a trait well-developed in some other forms as well (*Dinichthys*, *Coccosteus*, *Stenognathus* and others). In *Homostius* this "overlapping", as stated before, is exceptionally strong.

The above-mentioned ridge, running from the median part of the lower margin of the blade obliquely forward and upward (a-a) on Obručev's "outside", is entirely unknown on the outside in other *Arthrodira*, but in some specimens of *Dinichthys* I was able to find an indistinct ridge on the corresponding place on the inside of the blade. This ridge, however, is too weakly developed to be of any great significance.

Also another character points in the same direction. As mentioned before we find the "worn area" in *Homostius* placed on the lower margin on the concave side of the functional portion (fig. 29, I, V; Pl. XIII, 3, 4). Such a remarkable position is easiest explained by the pronounced twisting of the lower jaw. Originally — as in all other *Arthrodira* — in the ancestors of *Homostius*, the functional portion was placed more or less horizontally, thus when the mouth was closed its upper margin was overlapped by the plates of the upper jaw (ASG and PSG). The worn area was situated on the outside of IG. In later forms the twisting of the functional portion has begun. The upper margin became more and more inwardly bent and the worn area was gradually moved to the lower margin (fig. 30, A), but still on the outside of IG. The configuration of IG in *Angarichthys* may be regarded as an intermediate stage, where the twisting only lasted long enough to influence the position of the teeth. This circumstance also points in the direction that the concave-convex side of IG in *Homostius* (and *Angarichthys*) must be regarded as the outside.

Obručev in his paper (1927) did not mention the reason why he regarded this side as an inside, but in a letter to me, he pointed out that it is difficult to expect that the front part of IG can have been concave because the outline of the mouth opening in that case would be too extraordinary (fig. 30, B, I). He also writes, that the position of the teeth in *Angarichthys* is more easily explained if the lower margin of IG is bent inwardly. To maintain the contact with the upper jaw the teeth in this case become bent inwardly (fig. 30 A, II). Obručev supposed that the presence of the worn area on the lower margin of the inside of IG is possibly due to its strong twisting, the upper jaw elements coming secondarily in contact with IG from the inside. He remarked, however, that this explanation is hardly acceptable.

We will now consider whether the configuration of the mouth is in reality so improbable, if we admit that the concave-convex side of IG is the outside. When we recollect, that *Homostius* (and probably also *Angarichthys*) were very broad and flat forms, with relatively short "jaws", the hind part of the right and left rami could not have been placed nearly parallel to each other, as for example in *Dinichthys*, but, on the contrary, met at an almost straight angle (fig. 30, C). Besides, in all cases in *Homostius*, the worn area is itself straight, in spite of the concave functional portion (cf. fig. 28, II, IV; 29, II, IV; Pl. XIII, 2, 5) making the configuration of the mouth more natural. As seen on fig. 30,

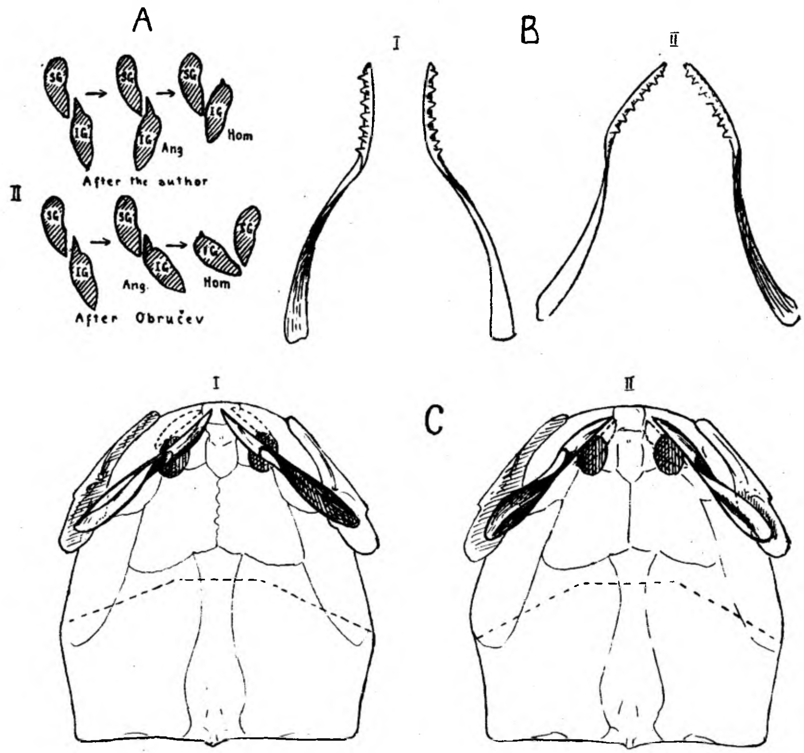

Fig. 30. The position of the infero-gnathal in *Homostius* sp. and *Angarichthys*. *A* -- possible development of the relation between the upper *(SG)* and the lower *(IG)* jaw in: 1) ordinary *Arthrodir (a)*, 2) *Angarichtyhs (Ang.)* and 3) *Homostius (Hom.)* after the author *(I)* and after Obručev *(II)* Cross-sections. *B* -- relation of both rami of lower jaw in *Angarichthys* after the author *(I)* and after Obručev *(II)*. *C* — the same in *Homostius* afer the author *(I)* and after Obručev *(II)*.

C, I and II both possible positions of IG do not differ much from each other. With regard to the condition in *Angarichthys* it is, as yet, difficult to say anything definite and the connection of IG with a possible cartilaginous part of the lower jaw, is also difficult to discuss at present. There are different circumstances, however, which point favourably to Obručev's interpretations:

Firstly, in the majority of *Arthrodira* the side surface of IG is not placed strictly horizontally, but inclined (comp. f. inst. *Dinichthys*), with the lower margin more inwardly. It is accordingly easier to suppose that in *Angarichthys* and *Homostius* this trait has been strongly developed and finally resulted in the twisting of IG with the lower margin directed inwardly. At the same time, the declined position of the teeth, as mentioned before, can clearly be explained in connection with the twisting.

Secondly, in one specimen of *Homostius* in Edinburgh (E. M. 1878/5/410; the original of Traquair's drawing), I found IG with the convex-concave side outwards (Pl. XVII. 1). In favour of an opposite opinion, however, it may be mentioned, that in another specimen in Edinburgh (EM. 23) it seems as if IG is placed with the concave-convex side outwards. The most important argument, however, is the position of the worn area, as, if Obručev is right, the worn area in *Homostius* must be placed on the inside of IG. In other words, the supro-gnathal elements are situated inside on IG such position being unknown in any *Arthrodira*.

As we see, the "jaw problem" in *Homostius* is very difficult, and at the present time we cannot with certainty say that we know how the jaws were placed, either in this form, or in *Angarichthys*. Undoubtedly, however, the detection of the upper jaw elements in *Angarichthys* or *Homostius*, which is of the greatest interest, will in all probability solve this problem.

The next and last plate, known as a side plate of the head in *Homostius*, is a small narrow plate, which has already been pictured by H. Miller (his fig. 46, c) and determined as one of the "internal bones of *Asterolepis*". In 1916 Woodward shortly described and depicted a pair of these plates. He determined them as the right and left "upper jaw?". As mentioned by Woodward this plate (fig. 31, Pl. XIII, 1, 2, 3 & 4) is composed of two parts: one flatter and broader (fig. 31, b, Pl. XII, 3 & 4) and one narrower and longer (fig. 31, b, Pl. XII, 1 & 2). On one side the surface of the front part is uneven and rough with very distinct bone structure; it therefore probably served as an attachment for cartilage (fig. 31, B, b, Pl. XII, 4). On this side the front part is sharply separated from the hind part, which is perfectly smooth and somewhat concave (fig. 31, B, a, Pl. XII, 2). On the other side both parts are more or less level, and not divided by any clear limit (fig. 31, A, Pl. XII, 1, 3). The hind part is slightly convex and moderately thickened, the broader front part showing some indistinct impressions and ridges (fig. 31, A, b, Pl. XII, 3). Woodward pointed out, that the hind (narrow) part on this side is "slightly tuberculated". I was unable to find any traces of tuberculation on the specimens from Tartu (only 2) and on the original of H. Miller's figure in Edinburgh Museum.

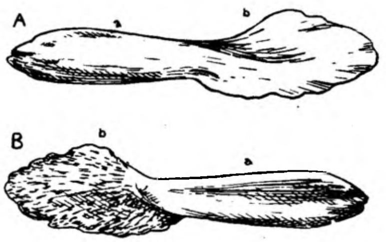

Fig. 31. The reconstruction of a left (?) plate "Y" of *Homostius* sp. *A* — from the outside, *B* — from the inside. *a* — the front part, *b* — the hind part.

It is very difficult to determine this bone with certainty, as it is not like any known plates in other *Arthrodira*. Besides, we do not know its position on the head shield or its relation to other plates as it has always been found isolated and we have no evidence that it is a representative of the upper jaw elements as it shows no trace of teeth or worn area. It might be the post-nasal plate, which limited the nostrils from above but this supposition is also not very probable and we cannot therefore say anything definite about the real nature of this plate. I propose to call this plate provisionally "plate y".

We have now finished the description of the head plates in *Homostius* and shall pass on to the body carapace. The reconstruction of the head and the position of the single plates of the cheek in this form will be discussed later, together with the reconstruction of the body carapace.

B. The Body Carapace.

The body carapace in *Homostius* shows a relatively high degree of specialization and differs in many respects from the "typical" carapace found for instance in such forms as *Coccosteus* or *Pholidosteus*.

Firstly, 7 of the 19 plates in an "ideal *Arthrodira*" are absent, probably reduced, these being postero-lateral, spinal, postero-ventro-lateral and median-ventral. Secondly, the majority of the other plates are in many ways unusual and highly specialized.

The whole carapace is very short and broad, especially compared with the head roof (fig. 43, 48; Pl. XIV, 1; Pl. XVII, 1). The relation of the length of the head roof to the length of the median-dorsal plate in different *Arthrodira* is as follows: *Jaekelaspis decipiens* — 0,8. *Coccosteus decipiens* — 1,1. *Dinichthys* — 1,6

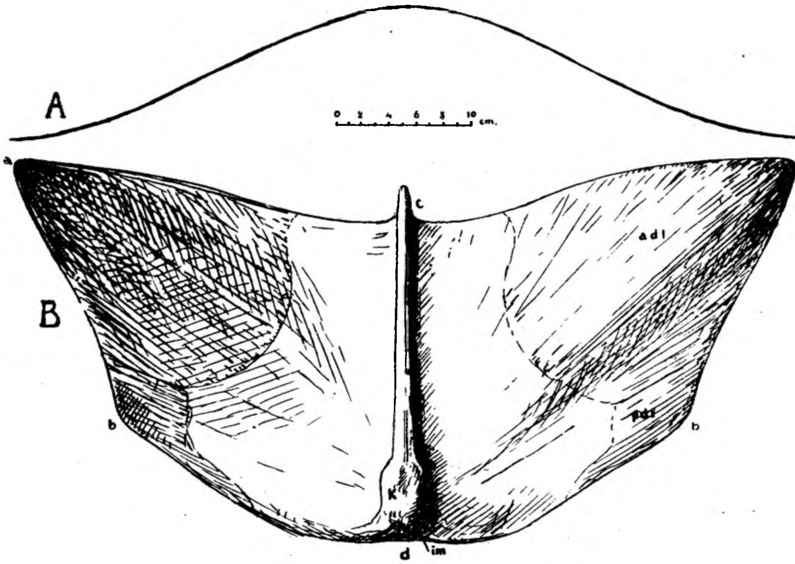

Fig. 32. The median-dorsal plate seen from the inside *(B)* and profile *(A)* *a* — acute front angle, *adl* — overlapping margin covering the *ADL* plate. *b* — obtuse hind angle, *c-d* — median keel, *im* — symmetrical impressions on the hind margin of the knot, *k* — knot on the median keel, *pdl* — overlapping margin covering the *PDL* plate.

Brachyosteus — 1,9. *Homostius* — 2,7 and *Oxyosteus* — 4,1. In the last form the high index is due to the enormous rostral part of the head.

1) The Single Plates of the Body Carapace.

Corresponding to the head roof, the body carapace is also very flat, only somewhat more curved (fig. 44 and 45). As usual, the largest plate of the dorsal shield is the Median Dorsal Plate (fig. 32; Pl. XIV; Pl. XV, 1; Pl. XVII, 1; Pl. XXIII, 1). It is nearly trapezoidal, broadest in front, narrower towards the rear. Contrary to the majority of other *Arthrodira*, it is nearly twice as broad as long. Usually, MD is rather longer than broader, (*Coccosteus*, *Acanthaspis* and many Wildungen forms), or its length and breadth is the same (*Dinichthys*).

The front margin (fig. 32, a-c-a. Pl. XV, 1) is concave and the side margins (fig. 32, a-b, Pl. XV, 1) curved inwardly. The hind margin, on the contrary, is strongly convex (fig. 32, b-d-b, Pl. XV, 1). The front angles (a) are thus acute, the hind (b) obtuse. As usual, the whole plate is arched, but not like the majority of other forms, where the sides of the plate are more strongly bent than in the median portion, but on the contrary, the median part in *Homostius* is most strongly arched, at the same time as the side parts are flat, even concave (fig. 32, A).

On the outside the whole plate is covered with tubercles (Pl. XIV, 1; Pl. XVII, 1). Some well-preserved specimens have a small smooth triangular-shaped area developed along the front margin, like a corresponding area on the hind margin of the median-basal plate of the head roof (Pl. XIV, 1, c). Two weak impressions are seen on the outside running from the hind median part of the plate obliquely upward to the front angles (Pl. XIV, 1).

On the inside (fig. 32; Pl. XIV, 2; Pl. XV, 1; Pl. XXIII, 1) along the median line, is the usual median keel (c-d). In *Homostius* this keel is relatively very low, and reminds one of that in *Acanthaspida*. It retains nearly the same height throughout its whole length, becomes only slightly broader in the rear, while the most posterior portion suddenly becomes broader, forming a knot (k, fig. 32, Pl. XIV, 2; Pl. XV, 1, Pl. XXIII, 1). As is known, H. Miller (1849, 2) has described this ridge with its thickened point as "Nail-like bone" — a very adequate name. In the only completely preserved MD plate from Tartu (Pl. XV, 1) and in two specimens in the Edinburgh Museum the median keel continues forward along the front margin of the plate, forming a remarkable point at the front of the plate (c, fig. 32; Pl. XIV, 1; Pl. XV, 1). It is difficult to determine whether this remarkable condition was always developed in *Homostius* to a more or less great extent, or if it is due to disintegration of the plate after the death of the animal. The last proposition is, however, not very probable, as on the plate with sharply protruding keel, the side angles of the plate, which should be the first to be worn off, are still very sharp. On the hind margin of the above-mentioned thickened knot are two symmetrical small impressions (im. fig. 32, Pl. XV, 1, Pl. XXIII, 1), which obviously correspond to the impressions on the hind part of the keel, commonly found in other *Arthrodira* (*Dinichthys*, *Heterostius*). The hind margin of MD is relatively thick, with two thickenings running obliquely upward to the upper angles (a), corresponding to the above-mentioned impressions on the outside. On the side of the plate are clearly seen two overlapping margins. The front one, which is the larger, covered the ADL plate (ADL, fig. 32, Pl. XV, 1) and occupied the whole front angle running deeply inward, the other, much smaller one, placed round the hind angle (PDL, fig. 32, Pl. XV, 1), covered the PDL plate.

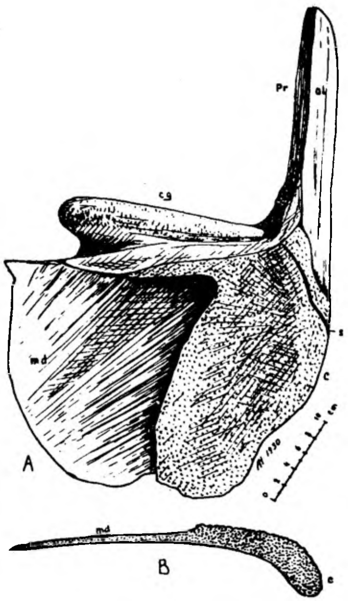

Fig. 33. The antero-dorso-lateral plate figured from the outside *(A)* and in section *(B)*, *al* — overlapping margin covered by the *AL* plate, *c* — thickened outside margin, *cg* — condylus, *md* — overlapping margin covered by the *MD* plate, *Pr* — forward directed process, *s* — sensory canal.

The Antero-Dorso-Lateral Plate (fig. 33, 35; Pl. XV, 2, 3; Pl. XVI; Pl. XVIII, 3, 4) is remarkably developed and at first glance quite unlike the corresponding plate in other *Arthrodira*. The easiest way to understand its construction is by comparing it with an ADL in another, more typical *Arthrodira*, for instance, *Dinichthys* (fig. 34).

We find in both plates (fig. 33 and 34) on the left side (the right plate) a distinct overlapping margin (md), which was covered by the MD plate. In *Dinichthys* the size of this overlapping margin is relatively moderate, but in *Homostius*, on the contrary, it constitutes nearly half of the whole plate. The tuberculated part of the plate in *Homostius* corresponds to the thickened central part in *Dinichthys* (as is known *Dinichthys* does not show any tuberculated sculpture on the surface of the plate) where this part is divided into two nearly equal portions by a sensory canal, running from the condylus in an almost perpendicular direction to the front limit (fig. 34, s). We find the same canal developed in *Homostius* as well (fig. 33, s), but here it is removed farther to the side, and runs very near and parallel to the outside margin of the tuberculated part.

On the other side of the central part in *Dinichthys* is developed another overlapping margin (fig. 34, al), which was covered by the AL plate, and at first glance there seems to be nothing equivalent to it in *Homostius*. Here we have only a narrow, but very solid process running forward, nearly perpendicular to the front limit of the plate (fig. 33, Pr). Nevertheless it is not so difficult to find analogies. On the outside of the process is developed a distinct overlapping margin (fig. 33, al) limited from behind by the sculptured part of the plate. Thus this part corresponds to the second overlapping margin in *Dinichthys*, and if we suppose, that this part of ADL in *Dinichthys* is strongly bent forward (fig. 34) we obtain an outline almost like that of ADL in *Homostius*.

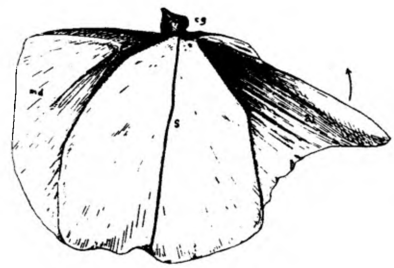

Fig. 34. The antero-dorso-lateral plate of *Dinichthys* sp. seen from the outside. Explanation as in fig. 33 (After Heintz, 1932, 2).

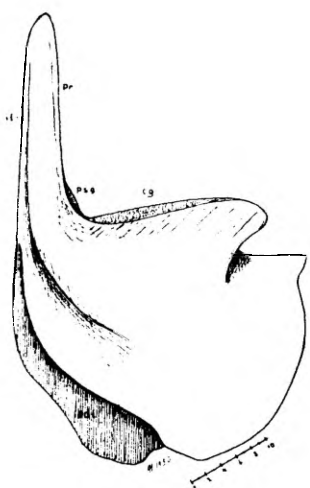

Fig. 35. The antero-dorso-lateral plate of *Homostius* sp. viewed from the inside. *pdl* — overlapping margin, which covered the *PDL* plate, *psg* — processus-subglenoidalis. Rest as in fig. 33.

The position and shape of the condylus (cg) is also unusual in our form. Firstly, it is very long, occupying nearly the whole front margin of the plate (cg, fig. 33, 35, 47). Secondly its longitudinal axis runs almost parallel to the upper surface of the plate, while in *Dinichthys* (fig. 34) the condylus is shorter and its longitudinal axis placed nearly perpendicular to the surface of the plate. Especially the last trait is of great interest, as it indicates the position of ADL. In reality, the angle between the longitudinal axis of the condylus and the upper surface of the plate in

Dinichthys, measures nearly 70°. But as the longitudinal axis of the condylus must always be placed horizontally (see Heintz, 1932, pp 153, 154) it shows that the surface of the ADL was situated at an angle of nearly 20° to the vertical line. As mentioned in *Homostius*, the angle between the longitudinal axis of the condylus and the surface of the plate is very small, about 10—15°, showing clearly that in this form the surface of ADL, instead of being nearly vertical as in *Dinichthys*, is nearly horizontal (at an angle of about 75—80° to the vertical line). This circumstance confirms my statement, that *Homostius* was an unusually flat form.

The greatest part of ADL is slightly bent — or nearly straight. Only the quite strongly thickened outside margin (fig. 33, A, c) is sharply bent downwards (fig. 33, B, c). This part as we know continues into the forwardly-directed process, with the overlapping margin covered by the AL plate (Pl. XV, 3; Pl. XVIII, 4).

On the inside (fig. 35; Pl. XV, 2; Pl. XVI, 3; Pl. XVIII, 3) the ADL is much smoother and strongly thickened in front, where the condylus (cg) is situated. The condylus ridge, so strongly developed in *Dinichthys*, is not so strong here, as the axis of the condylus and the surface of the plate lie nearly on the same plane. As mentioned, the outside of the plate is strongly thickened, and from this side is clearly seen how this thickening bends upwards and continues into the forwardly directed process. In some forms a very distinct impression divides this thickening from the outside margin of the plate (Pl. XV, 2), which is not the case in other forms.

On the posterior side margin is developed a distinct overlapping margin, which overlaps the PDL (PDL, fig. 35, Pl. XVI, 3). On the inside of the process we find the "processus-sub-glenoidalis", (PSG, fig. 35, 47; Pl. XV, 2; Pl. XVI, 3; Pl. XVIII, 3), which, as usual, is placed nearly perpendicular to the axis of the condylus. However, a more detailed description of the joint will be given below.

The Postero-Dorso-Lateral is a very small plate (fig. 36; Pl. XVII, 1, 2, 3, 4). Its hind margin is rounded, the front is more or less angular, with two well-marked overlapping margins. The relatively small one in front was covered by ADL (adl, fig. 36; Pl. XVII, 2, 3, 4) the other — larger by MD (md, fig. 36; Pl. XVII, 2, 3, 4). The tuberculated part forms a small brim along the outside margin, and continues as a triangular offshoot forward between both the overlapping margins. A short sensory canal is developed on the front part of the plate. It runs from the front point very near and parallel to the outside margin, disappearing about the middle of the plate (s, fig. 23; Pl. XVII, 2). This canal is a prolongation of the canal on ADL. I was unable to find, however, any traces of it on the PDL plate in the specimens from Scotland (Pl. XVII, 1). The whole plate is slightly bent from side to side and from front to rear. It composes the

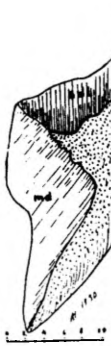

Fig. 36. The postero-dorso-lateral plate seen from the outside. *adl* — overlapping margin covered by the *ADL* plate, *md* — overlapping margin covered by the *MD* plate.

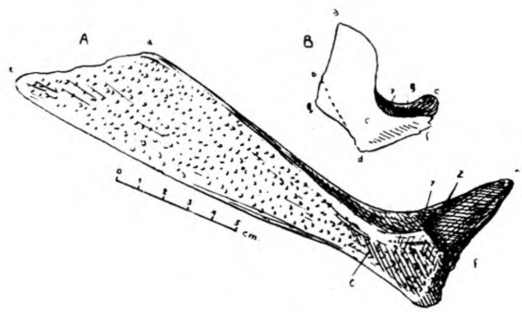

Fig. 37. The antero-lateral plate of *Homostius* sp. seen from the outside *(A)* compared with the corresponding plate of *Dinichthys* (*B* — strongly reduced). *a* — upper front angle, *a-b* — upper margin, *a-y* — front margin, *b* — upper hind angle, *b-d* — hind margin, *d-f* — lower margin, *e* — hind wing, *f* — lower front part, *g* — upper margin of the hind wing, *y* — front thickening, *z* — impression in front of sculptured part.

hind side corners of the body carapace, and, contrary to all other forms, is placed chiefly on the dorsal side of the carapace, not on the lateral (fig. 43). On the inside the plate is smooth and shows nothing of interest.

The Postero-Lateral Plate is absent. It is probably reduced, as no traces of it have been found, either in complete specimens or among isolated plates.

On the other hand, the Antero-Lateral Plate is well and remarkably developed. As, in 1928, I already described and depicted this plate in a short paper, I shall here only point out some remarkable characteristics and try to compare it with the corresponding plate in *Dinichthys*. In the above-mentioned paper I pointed out that AL in *Homostius* "was Form und Grösse anbetrifft, hat sich bis zur Unkenntlichkeit verändert . . ." My latest investigations, however, lead to another result, showing that in AL we recognize all the elements, which are characteristic of this plate in other forms (fig. 37, 38, 39; AL, fig. 43, 44 & 45; Pl. XVIII; Pl. XX; Pl. XXIII, 2 and Heintz 1928, Pl. I).

On the outside (fig. 37; Pl. XVIII, 4, 6; Pl. XX, 1, 3) we can easily identify the outline of AL in *Dinichthys*, with the difference, that the whole plate is narrower and longer. The front limit (a-y) is not convex as in *Dinichthys*, but straight. The upper limit (a-b) does not run obliquely downward, but upward. The small triangular shaped part b-q-d, which comes in contact with PL is not developed at all, this being one of the reasons why the AL in *Homostius* is so narrow. The hind margin (b-d) is also straight, longer than the front margin (in *Dinichthys* it is shorter). The lower margin (d-f) is very short. The strongly developed impression on the lower part of the front margin (c) is also present in *Homostius*, but, as mentioned, the lower part of the plate, which is slightly bent inward, is much shorter than the corresponding part in *Dinichthys* and this impression therefore is not so clearly seen. For the same reason, the deep cleft (z), which in *Dinichthys* lies between the hind wing (e) and the lower front part of the plate (f) is not developed in *Homostius*, and is only represented by a small impression immediately in front of the lower limit of the sculptured part (z, fig. 37 & 39). On the other hand the thickening (y) developed in *Dinichthys* in the upper part of

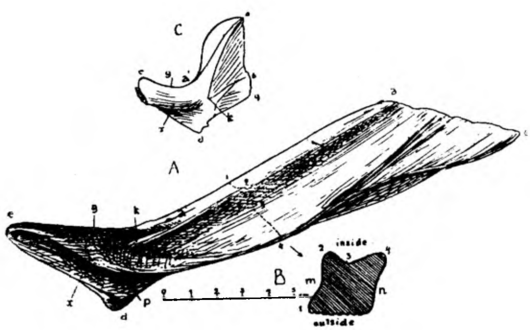

Fig. 38. The antero-lateral plate of *Homostius* sp. viewed from the inside *(A)* and in cross-section. *(B)* compared with the corresponding plate of *Dinichthys* sp. (*C*, strongly reduced) *a-a*[1] — ridge in front of the overlapping margin, *a-k-b* — overlapping margin covering the *ADL* plate. *e-p* — impression on the underside of the hind wing. *m* — front margin of the ridge, *n* — hind margin of the ridge. Rest as in fig. 37.

this cleft is also obvious in *Homostius* only moved somewhat downward (y, fig. 37 & 39; Pl. XVIII, 6; Pl. XX, 2, 3).

On the inside (fig. 38; Pl. XVIII, 1, 2, 3; Pl. XXIII, 2) AL also corresponds with *Dinichthys*. We find a well-developed overlapping margin, which covered the ADL (a-k-b). In *Homostius* it is somewhat narrower, but, in general, of the same triangular form, with the difference that its surface carries much stronger developed ridges and impressions serving as a connection with the ADL. Like in *Dinichthys* this overlapping margin forms the upper part of a distinct ridge (a-a[1]), which, increasing in height, runs from the upper part of the plate downward, and in the lower part continues into the hind wing (g). In *Dinichthys* this ridge, however, is not so sharply limited from the side as in *Homostius*, where both the front and hind margins are very distinct (m and n, fig. 38, 39; Pl. XVIII, 1, 2). As these two margins are placed nearly parallel to each other and almost perpendicular to the upper surface of the ridge (and to the tuberculated outside of the plate) the cross-section of AL in *Homostius* is nearly quadrangular (fig. 38, B). Another specific characteristic for *Homostius* is the development of the hind wing. In *Dinichthys* it is only a relatively thin lamella, while in the former it is very strong and thick, bent along the longitudinal axis, and, therefore, when viewed from underneath, it shows a distinct groove (e-p) unknown in *Dinichthys* (fig. 38, Pl. XVIII, 1, 2).

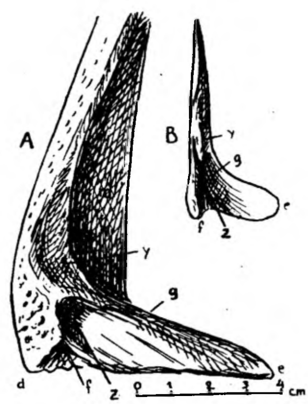

Fig. 39. The lower part of the antero-lateral plate of *Homostius* sp. seen from the front (*A*) compared with the corresponding plate of *Dinichthys* (*B*, strongly reduced). Explanation as in fig. 37 and fig. 38.

As mentioned, the overlapping margin of AL covers the front offshoot of ADL, thus forming an immediate prolongation of the latter. Asmuss was the first to point out this position of his "Sandalenstück" (AL). He mentioned that: AL was connected "unbeweglich mit dem äusseren Fortsatz des Adminiculum laterale" (= ADL) (Asmuss 1856 pag. 25). In spite of this clear description, none of the later investigators was able to determine this bone and homologize it with AL in other *Arthrodira*. Pander pictured it in "*Placodermen*" (Pl. VII, fig. 33 a & b), but, in the description, pointed out that it is a bone "dem wir bis jetzt noch nicht seine Stelle anweisen können". Traquair (1889) wrote that he "cannot speculate upon its position" (pag. 56). Woodward in Catalogue (p. 306), says that it is an "undetermined bone" (cat. nb. 15142 z). In 1928 I pointed out its position and mentioned that among the plates in Tartu Museum was one, where these two plates are preserved in their natural connection. This piece is pictured on Pl. XVIII, 3 & 4. Moreover, in complete specimens from Edinburgh AL is also found in its normal connection with ADL, only here it was more difficult to recognize their outlines, as they were partly broken, and partly strongly pressed (Pl. XIV, 1; Pl. XVII, 1). In addition, on a drawing in Woodward's paper (1916) the limit between AL and ADL is quite clearly seen. As the shape of AL varies in different species, it can serve as a very good specific characteristic. On Pl. XVIII, 1, 2, 5 & 6 two divergent types of AL are seen. In a later description of the species this difference will be discussed in greater detail.

The Intero-Lateral Plate corresponding with the AL was also well known in older times, but its relation to other plates and its real characteristics were never before correctly defined.

The first to depict and describe it was Kutorga (1837). On Pl. II, fig. 1, 2, 3 & 4, he gives some beautiful pictures of this interesting plate. He described them, however, as ribs of a turtle — *Trinyx sulcatus*.

In H. Miller's "Footprints" (1849, 2) the same plate is depicted on fig. 43 and determined as "Shoulder (i. e. Coracoid?) plate of *Asterolepis*".

Traquair (1889) wrote about this plate as one of the undoubted remains of *Homostius*, whose position in the body he cannot speculate upon. Woodward (1916) mentioned this bone as an "undetermined plate" (x), notwithstanding that in his specimen it was placed in a nearly natural relation to the other plates of the body carapace. Obručev (1927) depicted the corresponding bone in *Angarichthys* and pointed out its great likeness to the bone described by Kutorga and Miller. He calls this bone the "spinale". Finally Gross probably meant this bone, when he (1930, pg. 19) wrote that "Gewisse Knochen . . . mit typischem heterosteusartigem histologischem Aufbau scheinen mir zur Mundregion zu gehören. Sie zeichnen sich durch regelmässig angeordnete schräge Querleisten aus, die aus Knochengewebe bestehen" (see also Gross 1933). My investigation in Edinburgh Museum has shown me that this bone is an intero-lateral in *Homostius*.

It is a long and narrow plate (fig. 40, 41; Pl. XIX; Pl. XX, 1, 2), broader in one (lateral) part (a—b), and gradually narrowing towards the other, where it runs into a point (c). It is thinner along the upper margin (a—c) and thicker along the lower (b—c). On the outside (fig. 40, Pl. XIX, 1, 2; Pl. XX, 1, 2) it is moderately convex (fig. 41, B, C) from the upper to the lower margin, and slightly concave along its longitudinal axis. This part is remarkably sculptured, and shows two distinctly different patterns: on a more or less small triangular portion in the broadest part of the plate (abe) we find the sculpture corresponding to all other plates in *Homostius* (small stellar tubercles evenly covering the surface). In some specimens this tuberculated part runs somewhat forward along the lower limit of the plate. The remaining, greater part of the plate (aec) is covered with sharp and distinctly developed ridges, running from the upper margin of the plate obliquely downward and forward. The single ridges are high and divided by deep clefts. They are situated more vertically on the hind part of the plate, becoming gradually horizontal, towards its points. At the same time, each single ridge is not straight, but bent slightly backward in the upper part (at the margin of the plate) and forward in the lower. Thus each ridge is more or less clearly S-shaped. Some ridges anastomose with each other, while some are divided into two (Pl. XIX, 1; Pl. XX, 2). In different species the pattern of the ridges varies strongly. They are either placed more horizontally, or more vertically, and, in some, I have observed two or three ridges, running parallel to the upper margin of the plate throughout its whole length. The tuberculated part and the other part covered with ridges, are always sharply divided from each other. The hind limit of the plate (ab) is uneven, with small depressions and ridges.

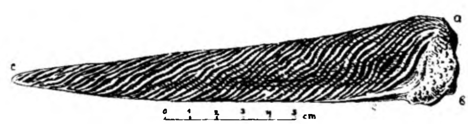

Fig. 40. The intero-lateral plate from the outside. *a-b* — hind margin, *c* — front point.

On the inside (fig. 41; Pl. XIX, 3, 4) the plate is slightly concave. The upper hind part (ad) is relatively thin, while more forward the plate is thicker (dc). Along the lower margin (bc) runs a strongly-developed ridge (x—x) beginning as a relatively broad thickening on the lower hind margin of the plate (z), which soon afterwards is divided into two ridges: one, the smaller running obliquely forward and upward and finally disappearing (y), the other, the head ridge, (x), running into the point of the plate. Ridge x—x is relatively high and narrow (fig. 41, C, x) placed nearly perpendicular to the inside of the plate, and is divided from the lower margin with a small but distinct step (s).

As seen in the figures, the second, smaller ridge (y) divides the upper, thinner part of the plate from the lower, thicker part. On the hind margin (ab) also on this side are some small ridges and impresions.

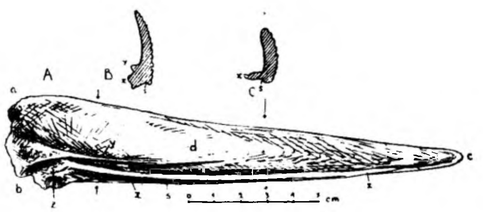

Fig. 41. The intero-lateral plate from the inside (*A*) and two cross sections of it (*B* & *C*), *a-d-b* – thin part overlapping the hind wing of the *AL* plate. *s* — step under the ridge *x-x*. *x-x* — lower ridge, *z* — thickened hind part, *z-y* — upper ridge.

Unfortunately the outline and structure of the IL in other *Arthrodira* are not very well known. They are only described in detail in *Dinichthys* (Heintz, 1932, 2) and the outline is also partly known in *Coccosteus* (Heintz, 1931, 4, Gross 1933.) and *Jaekelaspis* (Heintz, 1929, 1 and 2). Thus we must again compare our IL with that in *Dinichthys*. It is not difficult to ascertain a likeness between these two plates (cf. Heintz, 1932, 2, fig. 62). Also in *Dinichthys* the plate on the outside is divided into two parts with different sculptures. The hind outside corner is without sculpture, as are all the other plates in *Dinichthys*, while the front part on the other hand is covered with flat relatively broad ridges, running nearly in the same direction as the ridges in *Homostius*. Also, as in the latter form, the hind margin of the plate is thickened, and on the inside we find a thinner hind part (ov) a thicker front part and an especially solid hind margin.

If we try to combine this plate with the AL, we find that they fit perfectly together, thus confirming, in the clearest way, that the definition of this plate as an IL is correct. Its hind margin (ab) (Pl. XX, 1, 2,) fits exactly into the front limit of the sculptured part of AL (fd, fig. 34, 36, 43, 44, 45; Pl. XVIII, 4, 5, 6; Pl. XX, 1, 2) so that each ridge and impression on the one corresponds to an impression and a ridge on the other, the tuberculated part of IL forming an immediate prolongation of the tuberculated part of AL. The wing of AL (gef, fig. 37, 38, 39) fits perfectly into the thinner, upper part of the inside of IL (ad, fig. 40) and the above-mentioned thin ridge (z-y, fig. 41) runs along the lower margin of the wing.

On the hind lower corner of IL (b) and on the front lower corner of the sculptured part of AL (d) is developed an impression with a rough surface, pointing out, that it apparently served as an attachment for another plate, in which case it must have been the spinal. I was unable to find any traces of this plate either in the complete specimens from Scotland or among the fragments in Tartu, but on the drawing given by Woodward (1916) of *Homostius* from Cathness Flagstone, a small plate is depicted in this region, apparently attached to AL, and at the same time touching IL. It is not impossible that this plate, in reality, represents the spinal in *Homostius*.

Finally, it may be of interest to point out that, in the specimen described and depicted by Traquair (1889) (Pl. XVII, 1), the IL is quite clearly seen in situ. The specimen is so greatly flattened, that the IL is seen as a ridge-like thickening on the surface of the head (Pl. XVII, 1 **)· Besides, on the counterpart of the original specimen, some traces of the remarkable sculpture of this plate are preserved.

The Ventral Shield was very imperfectly known formerly. Asmuss, Miller and Pander mentioned nothing about the ventral shield, notwithstanding that the two latter described some of its plates as belonging to different other parts of the fish. Traquair (1889) only mentioned that: "It is curious that no undoubted remains of a ventral body carapace . . . . have occurred in connection wiht *Homostius*", and Woodward in his Catalogue pointed out that "Ventral armour is unknown". But already the same year (1891, 3) he described three plates of *Homostius*, which, in his opinion, belonged to the ventral armour. In a short description of *Homostius* (1928) the present writer also expressed the opinion that: "bis jetzt keinerlei Reste vom Bauchpanzer gefunden sind". Gross was of the same opinion, when he (1930) pointed out that: „Der Verlust des Ventralpanzers . . . muss ganz sicher bestätigt werden".

But my investigation in Edinburgh has shown me that the ventral shield was well-developed in *Homostius*, despite the fact that three of its plates are reduced, which confirms the opinion expressed by Woodward as early as in 1891. The first time I mentioned and depicted the ventral shield in *Homostius* was in my paper: "Untersuchungen über den Bau der *Arthrodira*" (1932, 3).

As mentioned, of the normally developed 6 ventral plates only three frontals are left in *Homostius* (the right and left antero-ventro-lateral and the antero-median-ventral). The other three plates have never been found, and as we shall see below, we have every reason to suppose, that they have been reduced.

The Antero-Ventro-Lateral Plate (fig. 42, 43; Pl. XIV, 1; AVL, Pl. XX, 3; Pl XXI, Pl. XXII) was for the first time depicted and described by Kutorga (1837, Pl. I & IX) and determined as "Schuppenförmig ausgebreitete hintere Ribbe des *Trionyx spinosus*". Miller and Pander also gave a picture of this plate, but determined it as "operculum" in *Homostius* (H. Miller, 1849, 2, fig. 39; Pander, 1857, Tab. B., fig. 16a and 16b). Finally Woodward in 1891 (3) determined it correctly as AVL in *Homostius*.

It is a large, nearly quadrangular plate. Its shape varies, however, in different forms, the single angles can be more or less rounded or, on the contrary, very sharply pointed. On the outside (Pl. XXI, 1; Pl. XXII, 2) the plate is nearly level being only slightly bent along the margins, and evenly sculptured. Remarkably enough, the sculpture varies greatly in different forms: in some it corresponds exactly to the sculpture on other plates in *Homostius* and is composed of small, even stellar tubercles (Pl. XXI, 1) but in others the sculpture is composed of more or less distinctly developed ridges, which form a complicated network. In some parts, however, the network is broken up into rows of single tubercles (Pl. XXII, 2). As this sculpture is otherwise unknown on the plates belonging to *Homostius*, we must suppose, that this remarkable trait only appears on the ventral plates in those forms which have ordinary sculpture on the dorsal plates.

On the inside (fig. 42, 43; Pl. XIV, 1 — AVL; Pl. XX, 3 — AVL; Pl. XXI, 2, 3, 4; Pl. XXII, 1) the plate reminds one of that in *Dinichthys* (see Heintz, 1932, 2, p. 171, fig. 56). As in the latter form, ridges are also developed along the front (b-c) and the outside margins (a-b), while the hind (a-d) and the inside (c-d) margins are relatively smooth and thin. The protuberated angle "b" in *Homostius* corresponds in form and position with the angle "Sp" in *Dinichthys*. It is strongly thickened and shows many small clefts and ridges. The very strongly-developed ridge on the outside of the plate (a — e — a [1], fig. 42, Pl. XXI, 2, 3, 4; Pl. XXII, 1), corresponds to the ridge "sk" in *Dinichthys*. In *Homostius* this ridge begins at the angle "a" and rises quite high in the middle of the plate (fig. 42, B; Pl. XXI, 2, e), and slackens gradually downward before it reaches the angle "b". In an inward direction the ridge gradually passes into the surface of the plate, while outward it runs directly downward and partly inward thus forming a groove-like impression along the outside margin (fig. 42, B, m; Pl. XXI, 2, 4, m.). On the front margin the ridge is not so clearly developed, but we find a thickening similar to *Dinichthys*, forming a semi-circle from the outside margin, forwards and inwards, until it crosses the front margin of the plate. (w — w — w — wr, fig. 42, Pl. XXI, 3, 4; Pl. XXII, 1) The last part, before it reaches the front margin, looks more like

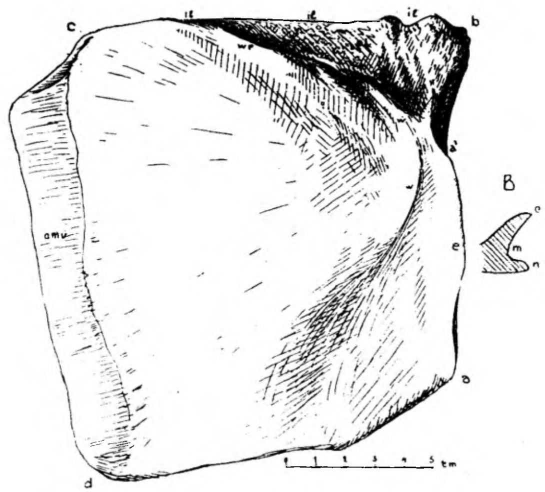

Fig. 42. The inner view of the antero-ventro-latera plate *(A)* and cross-section of the outside margin *(B)*. *a-b* — outside margin, *a-e-a*[1] — ridge on the outside margin, *al* — overlapping margin covered by the hind wing of the *AL* plate, *amv* — overlapping margin covering the *AMV* plate, *b* — thickened, protuberated outside front angle, *b-c* — front margin, *c-d* — inside margin, *d-a* — hind margin, *il-il* — part of the front margin, where the inside of the *IL* plate comes in contact with the *AVL* plate. *m* — groove along the outside margin, *n* — the lower outside margin, *w-w-wr* — the ridge on the front margin of the plate, *wr* — the thickenings on the front margin.

a sharp-edged ridge (wr). Thus this thickening and ridge clearly divide off a triangular part on the inside of the front margin (al, fig. 42, Pl. XXI, 3, 4; Pl. XXII, 1) from the rest of the plate. Into this triangular-shaped impression with its rough surface the triangular shaped "wing" of the AL plate fits perfectly

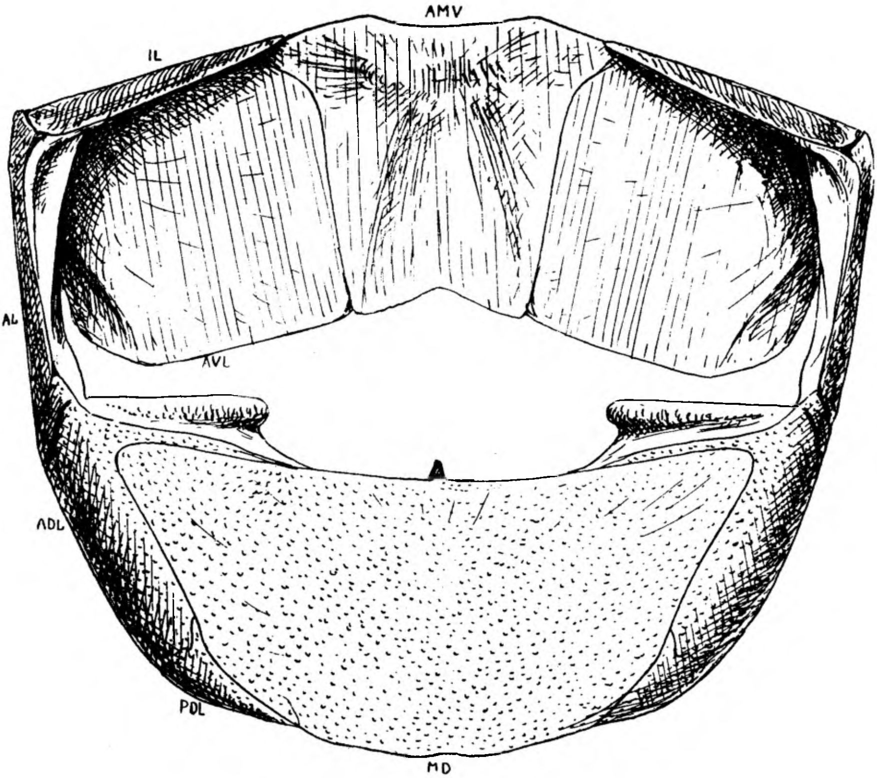

Fig. 43. The reconstruction of the body carapace of *Homostius sulkatus* Kut. seen from above. *ADL* — antero-dorso-lateral plate, *AL* — antero-lateral plate, *AMV* — antero-median-ventral plate, *AVL* — antero-ventro-lateral plate, *IL* — intero-lateral plate, *MD* — median-dorsal plate, *PDL* — postero-dorso-lateral plate.

(Pl. XX, 3). Along the thickened front margin with a rougher surface (fig. 42, Pl. XXI, 3, 4, il) the inside of the IL came in contact with the AVL.

On the inside margin (c—d) is a very distinct and broad overlapping margin (amv, fig. 42; Pl. XXI, 3; Pl. XXII, 1), which was covered by the antero-median-ventral plate, but no trace of an overlapping margin can be seen on the hind margin of the plate (a—d), which is very smooth and thin. It is therefore natural to expect that the PVL plate was not developed at all.

The Antero-Median-Ventral Plate (fig. 43, AMV; Pl. XIX, 4, AMV) was depicted for the first time by H. Miller as "Palatal plate of *Asterolepis*" (H. Miller, 1849, fig. 37). Traquair (1889) mentioned that it "looks to me as if it might be the anterior median ventral, so far as its shape is concerned". Finally, Woodward (1891, 3) was the first to determine it for certain as the AMV plate. In the collection in Tartu this plate is not preserved, while it is present both in the Edinburgh Museum (two specimens Ed. M. 1896/6/1 and Ed. HMC, 3) and in the British Museum.

Antero-median-ventral (fig. 43, Pl. XIX, 4) is an unusually large plate, of nearly the same size as AVL. In other *Arthrodira* it forms only a small part of the latter. Its outline is mushroom-like, with a relatively broad front (a—b—a; Pl. XIX, 4) and a narrow hind part (a—c—a). From the sharply protuberated side angles (a—a, Pl. XIX, 4) on the rounded or trapezoid front part, the plate rapidly narrows, stretching backward with almost parallel side margins. The hind margin shows a more or less deep angular impression (fig. 43, AMV, compare the picture of Miller and Woodward). On the outside the plate is covered with typical stellar tubercles (but only one plate in the Ed. Mus. shows the outside). Distinct overlapping margins begin from the protuberated side corners proceeding downward along the side margins, which are overlapped by AVL. Also along the front margin a small border without tubercles is developed, a part of this coming in contact with the IL plate. On the hind part no overlapping margin is found, which indicates that the MV plate was also not developed in *Homostius*. On the inside the plate is quite smooth without any trace of overlapping margins.

2) The reconstruction of the body carapace.

As we have now seen, the ventral shield in *Homostius* was composed of three almost equally large plates only, forming a comparatively short, but broad carapace, connected to the dorsal with the help of the AL and the IL plates. The AL, as mentioned, fits into the triangular depression on the front of AVL, and IL was attached with its side margin to AL, while its lower margin was connected to the front margin of AVL and partly AVM. Thus, as usual, the body carapace in *Homostius* represents a solid ring (fig. 43, 45), broad in the dorsal and ventral parts, but with very narrow sides (fig. 44) as in *Dinichthys*, (Heintz, 1932, 2). In comparison with all hitherto known *Arthrodira*, the body carapace in *Homostius*, corresponding to the head shield, was unusually flat, with the result that the distance between the dorsal and ventral shields was very moderate (fig. 44 & 45). The MD plate is only slightly bent, similar to the upper part of the ADL plate (fig. 45). Only the lower part of this plate with its long forwardly directed offshoot, is sharply bent downward, its tuberculated surface being placed nearly vertically (fig. 44). The AL, attached to the offshoot of ADL and forming its immediate prolongation, continues mainly forward and little downward (fig. 43 & 44). The ventral shield is completely flat.

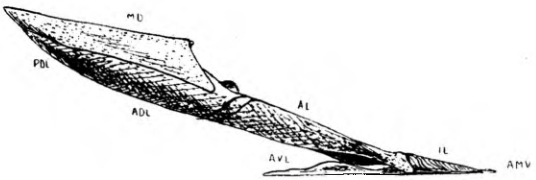

Fig. 44. The same reconstruction as in fig. 43 seen from the right side.

Another characteristic trait in *Homostius* is the position of the ventral shield which is pushed forward with the result that the dorsal shield is placed behind the ventral, its front margin not even reaching the margin of the latter (fig. 43 & 44). In *Coccosteus* (Heintz, 1931, 4) or *Dinichthys* (Heintz, 1932, 2), for instance, the hind margin of the ventral shield is situated somewhat below the hind margin of the dorsal. The unusual shape of the body carapace in *Homostius* is very clearly seen on the reconstruction in fig. 43, 44 and 45.

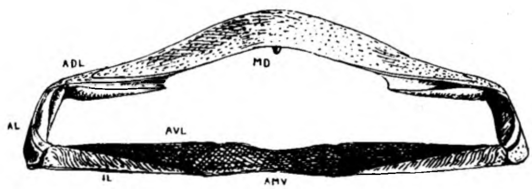

Fig. 45. The same reconstruction as in fig. 43, in front view.

C. The connection between the head and body carapace.

As mentioned above, the joint between head and body is strongly developed in *Homostius*, but, owing to the very flat shape of the head and body, the joint has somewhat changed its form and proportions (fig. 46 and 47).

We will begin with the fossa condylus (fig. 46, A, B, C) which as is known, is situated on the EB plate of the head, and shall compare it with the corresponding part in *Dinichthys* (fig. 46, D & E). It has already been pointed out that the fossa condylus in *Homostius* is unusually long (fg. fig. 46, A & C; Pl. II, 2; Pl. IV; Pl. V, 1, 2, 3 & 4) but, on the other hand, it

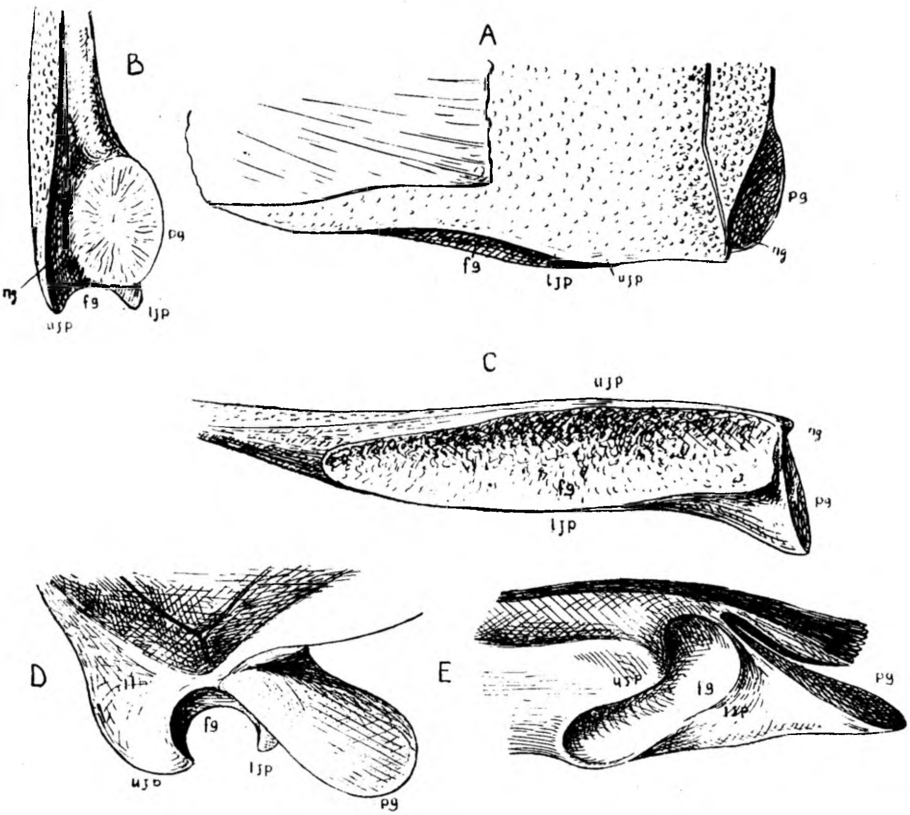

Fig. 46. Fossa condylus in *Homostius (A, B, C)* compared with that in *Dinichthys* (D & E, after Heintz, 1932, 2) *A* and *D* from outside, *B* — from side, *C* and *E* — from underside, *fg* — fossa condylus (fossa glenoidalis) *fjp* — lower joint process, *ng* — small protuberated ridge, *pg* — processus glenoidalis, *ujp* — upper joint process.

is not so deep as in *Dinichthys* (fig. 46, B; Pl. V, 3) where it forms nearly 3/4 of a circle (fig. 46, D). The processus glenoidalis is well-developed (pg, fig. 46, A, B, & C: Pl. III, 2; Pl. V, 1, 2, 3 & 4) but does not protuberate as sharply as in *Dinichthys* (pg, fig. 46, D & E). It is placed on the outside limit of the

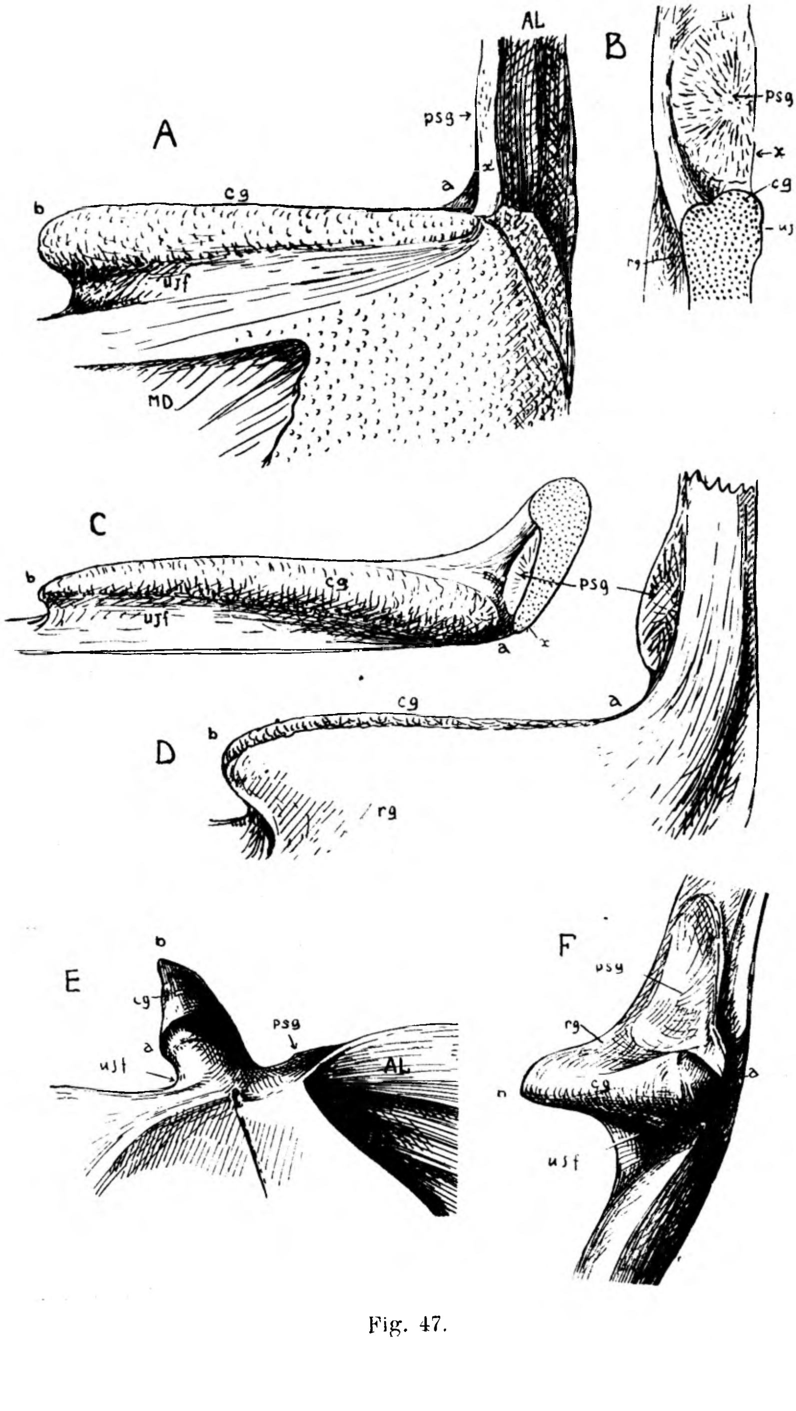

Fig. 47.

head roof, nearly perpendicular to the longitudinal axis of the fossa condylus (fig. 46, C; Pl. V, 2) and at the same time almost perpendicular to the tuberculated surface of the plate (fig. 46, A, B and C; Pl. III, 2; Pl. V, 1, 2, 3 & 4). The upper joint process in *Dinichthys* so sharply developed, (ujp, fig. 46, D & E) is indistinct in *Homostius*, because the front limit of the fossa condylus coincides with the hind limit of the EB itself (ujp, fig. 46, A, B & C; Pl. V 1, 2, 3 & 4), while, on the contrary, the lower joint process is as distinctly developed as in *Dinichthys* (ljp, fig. 46; Pl. V, 2, 3 & 4).

The condylus is also very long and, corresponding to the fossa, not so strongly rounded as in *Dinichthys* (cg, fig. 47; Pl. XV, 2, 3; Pl. XVI; Pl. XVIII, 3, 4), but, as with the condylus in *Dinichthys*, it is broader outwards (a, fig 47, A, C, D, E, F) and narrower inwards (b, fig. 47, A. C, D, E, F). The condylus ridge, strongly developed in *Dinichthys* (fig. 47, F, rg), is not particularly distinct, as the axis of the condylus (a—b) and the upper surface of the plate (ADL) nearly coincide with each other (fig. 47). This ridge forms only a thickening on the inside of the plate (rg, fig. 47, B, D; Pl. XV, 2; Pl. XVI, 3; Pl. XVIII, 3).

The processus sub-glenoidalis (psg — fig. 47; Pl. XV, 2; Pl. XVI, 3; Pl. XVIII, 3), which, as is known, comes in contact with the processus glenoidalis on EB, is well-developed. It is placed on the inside of the offshoot of the ADL, and like *Dinichthys* (fig. 47, F) is nearly perpendicular to the longitudinal axis of the condylus. An impression, corresponding to the upper joint fossa in *Dinichthys* (ujf, fig. 47, E, F) is not clearly developed in *Homostius*, but it can easily be recognized as the impression lying between the condylus and the front limit of the ADL plate (ujf, fig. 47, A, B, C; Pl. XV, 3; Pl. XVI, 1, 2; Pl. XVIII, 4).

The joint itself is a typical "Sperr-Gelenk". The movement possibilities of the head in relation to the body are strongly reduced because of the processus glenoidalis and the processus sub-gle-

Fig. 47. Condylus in *Homostius (A, B, C* and *D)* compared with that in *Dinichthys* (*E* and *F*, after Heintz, 1932, 2), *A* and *E* from outside, *b* — from inside (condylus in cross-section), *C* and *F* — from above (the upwards directed process of *ADL* is depicted in cross-section), *D* — from inside. *a-b* — the longitudinal axis of condylus. *AL* — overlapping margin covered by the *AL* plate, *cg* — condylus glenoidalis, *MD* — overlapping margin covered by the *MD* plate, *psg* — processus sub-glenoidalis, *rg* — condylus ridge, *ujf* — upper joint fossa, *x* — inside limit of the process on *ADL* plate.

noidalis. In fact, the processus glenoidalis is not quite perpendicular to the longitudinal axis of the fossa condylus, and the processus sub-glenoidalis not quite perpendicular to the longitudinal axis of the condylus both forming an angle somewhat greater than 90^0. Thus when moving the head upwards the surface of the processus glenoidalis becomes more and more strongly pressed against the surface of the processus sub-glenoidalis, finally preventing any upward movement. Another simultaneous mechanism also limited the movement: as is known, the upper limit of the fossa condylus forms the upper joint process (ujp, fig. 46). When lifting the head this process finally slid into the upper joint fossa (ujf, fig. 47) on the ADL, thus also stopping the movement. It seems, however, quite improbable that the head was ever lifted so high, that this mechanism began to function.

At the same time, other accommodations confined the movement of the head downward. Firstly, when the head was strongly moved downward, the lower joint process (ljp, fig. 46) came in contact with the ridge of the condylus (rg, fig. 47, B & D) thus preventing any further movement. Secondly, a small protuberated ridge on the side margin of the EB, beginning immediately at its outside angle (ng, fig. 46) came in contact with the upper limit of the offshoot on the ADL (x, fig. 47; Pl. XV, 3; Pl. XVIII, 3) thus stopping the movement. In this manner the movement possibility of the head was greatly limited and at the most was about 15—20^0. But if we consider the very long outline of the head, we must acknowledge that, in spite of everything, the movement of the front part of the head was quite strong. In fact, when raising the head of a medium-sized *Homostius* (the head shield about 30 cm) only about 10^0 upwards, it means that the point of the head was lifted about 6 cm.

Even a relatively moderate movement needs a very strong musculus levator capitis, as, according to the laws of mechanism, in flat forms like *Homostius* where the musculus levator capitis was placed immediately above the movement axis of the head (fig. 49), great power was required to lift the head.

The musculus depressor capitis, on the contrary, was probably not particularly strong. Its upper part is attached to the side margin of the EB (from the inside) just in front of the processus glenoidalis, and its lower part to the inner ridge on the AL in ront of the processus sub-glenoidalis.

We cannot say anything with certainty about the muscles of the real jaw elements, before the relation and position of the infero-gnathal is clearly defined. For the same reason it is difficult to discuss the jaw mechanism in *Homostius*. In my opinion, however, the lifting of the head with the help of the musculus levator capitis is closely related to the opening of the mouth.

D. Some remarks about the total reconstruction of the carapace in *Homostius*.

On fig. 48 and 49 is given a total reconstruction of the head and body carapaces in *Homostius*. From this picture we get the impression that *Homostius* was a very flat form, perfectly adapted to a bentonic life.

New points shown in this reconstruction are as follows: The position of the SO plate, which in *Homostius*, as in all other *Arthrodira*, is the largest side plate of the head. At the back of its hind margin is still a large uncovered portion, probably filled with the plate marked "X" (see pag. 216) but nevertheless leaving open a relatively great space. At the present time it is difficult to determine whether this part was covered by some hitherto unknown plate, or only by skin. In front of the SO we find developed in other *Arthrodira* a small post-nasal plate. No traces of this plate are known in *Homostius*, and we must therefore expect that this plate was reduced, and that the nostrils were placed in soft tissue.

The other new points are the position of the AL, the IL and the development of the ventral carapace. It can be mentioned here, that because of the great flatness of the head and body shields the complete specimens found in Scotland are little changed in spite of their being strongly pressed. In fact, they represent a very fine "reconstruction" of *Homostius* (Pl. XVII, 1) with all the plates in their natural position, not only the dorsal, but also the ventral shield, being quite clearly seen as an impression on the dorsal (Pl. XVII, 1 **).

We now turn to the inner part of the head, which apparently was built of cartilage. The gill openings similar to those in *Dinichthys*, were placed on the underside of the head roof immediately in front of the IL, and probably continued partly backwards and upwards, between the AL and the M plate. It is difficult to say anything definite about the position and construction of the gill arches.

The shape and position of the primordial neurocranium are also difficult to determine more precisely. It was certainly very

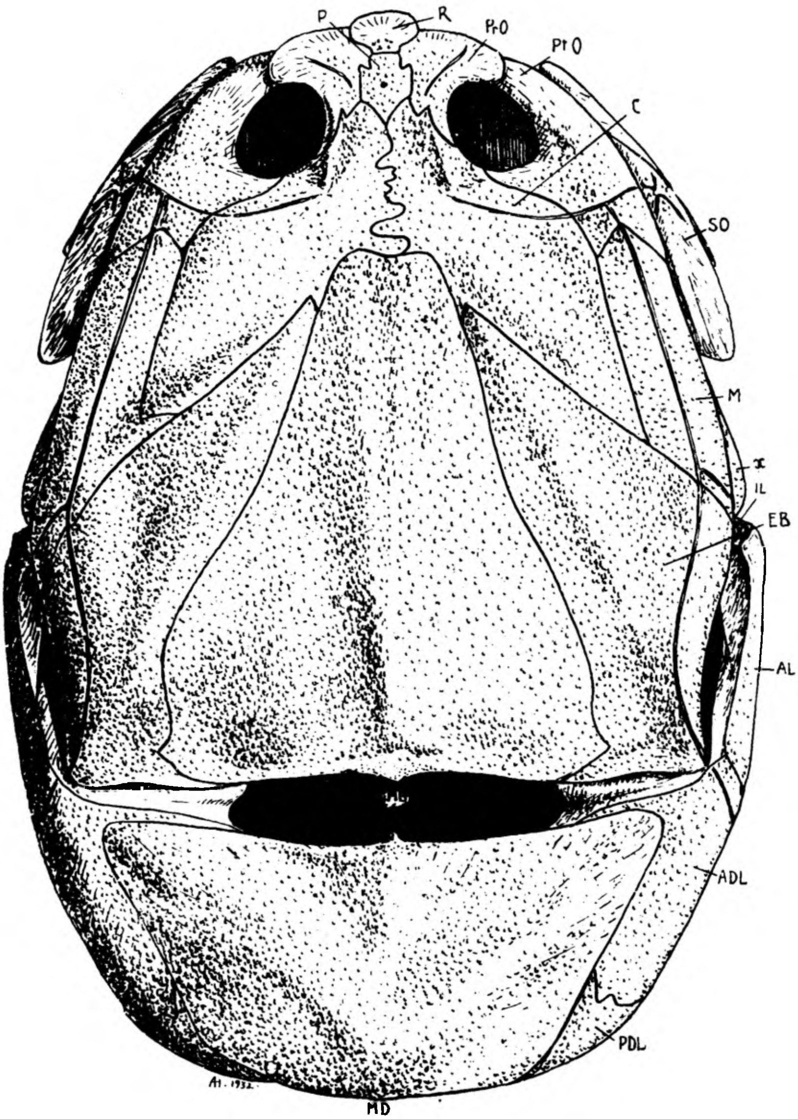

Fig. 48. The reconstruction of the head and body carapace of *Homostius sulkatus* Kut. from above. Explanation as in fig. 1 and fig. 43.

flat and broad with strongly developed occipital and otica (?) regions, and relatively short orbital and olfactory parts. (In this respect, probably not unlike the primordial neurocranium in *Phlyctænaspis.*) In his description of some plates in *Homostius* Woodward (1891, 3) mentioned, that the "head shield" most likely covered not only the head, but also the front part of the body. Looking at the head shield, with its very weak front and enormously long hind part, this idea seems very possible. But in other forms (e. g. *Dinichthys*, Heintz, 1932, 2) and forms from Wildungen (Gross, 1931, 1)) we know that the hind limit of the occipital region of the primordial neurocranium in *Arthrodira* was situated even behind the hind limit of the MB plate. As the

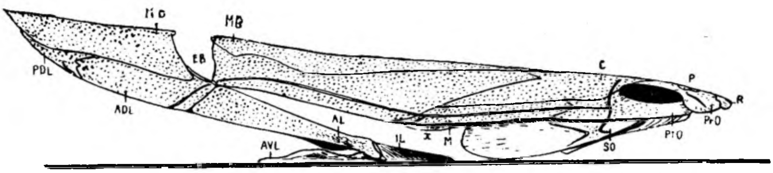

Fig. 49. The same reconstruction seen from the right side. Explanation as in fig. 1 and fig. 43.

arrangement of all the plates and sensory canals of the head shield in *Homostius* are similar to those in other *Arthrodira*, we must expect that the primordial neurocranium in our form also extended somewhat behind the hind limit of the MB until the movement axis of the head.

No traces of the vertebral column, paired or unpaired fins or scale cover were ever found in connection with *Homostius.* We should remember in this connection that the "inner skeleton bone", "teeth" and "scales" of *Asterolepis (=Homostius)* described and pictured by H. Miller (1849) have nothing to do with our form, but belong to different other fish remains from Devonian, as already pointed out by Pander (1857) and Traquair (1889).

V. Special part.

As already mentioned on several occasions, the first descriptions and pictures of the fragments of *Homostius*' bones were given by Kutorga in 1835 and 1837. He, however, described them as belonging to reptiles (different species of *Trinyx* and lizards and crocodiles), thus clearly indicating that it is impossible to use his genus name at the present time. Also the genus name "*Asterolepis*" used by Agassiz (1844) and H. Miller (1848, 1849, 1) and later by other English and American ichthyologists (e. g., Ph. Egerton, Newberry in his earlier publications, and others) cannot be accepted, as Eichwald (1840) originally under this name has described fish fragments belonging to *Antiarchi*.

Thus the genus name used by Asmuss (1856) "*Homostius*" must be regarded as the correct one. He also further proposed to combine the genus *Homostius* and the genus *Heterostius* in one family *Chelonochithydes*, but with our recent knowledge of the structure of these two forms it is difficult to acknowledge such a family. Although *Homostius* and *Heterostius* show some likeness in their specialization, they are in other ways too divergent to be united into one family. As *Homostius*, however, in many respects is so sharply divided from all other known *Arthrodira*, we are fully privileged to establish an independent new family and gather into it all *Homostius*-like forms. In accordance with the international rules for nomenclature we cannot accept the family name *Chelonochithydea* proposed by Asmuss, and later (1901) again introduced by Dean, and it therefore seems most natural, together with Jaekel (1903), later Gross (1931), and Woodward (1933), to adopt the name Fam. *Homostiidae* Jaekel.

This family, in my opinion, must contain two genera: first, the head genus *Homostius* Asm. with a number of different species and second, *Angarichthys* Obr. with one species. The latter genus, however, is still too imperfectly known, and later investigations may reveal that it differs too much from *Homostius* to be united into one family. But in all cases *Angarichthys* is that of *Arthrodira* which may be regarded as more or less closely related to *Homostius*.

Obručev on the other hand, in his paper in 1927, is not of the same opinion, and several times points out that *Angarichthys* cannot be regarded as being nearer related to *Homostius*. I shall, therefore, briefly recapitulate below what is known about *Angarichthys* and discuss its relation to *Homostius*.

The systematic position of *Angarichthys* Obr.

Hitherto, only 6 plates of this form have been described: three determined and three more or less uncertain. The best known plate is the bone described by Obručev as "Spleinale" (= intero-gnathal). In the description of this bone in *Homostius* we have already discussed and re-described the same bone in *An-*

garichthys and have seen that, in many respects, it is more like that in *Homostius* than IG in other *Arthrodira*. (See page 217 ,)

The next bone is O b r u č e v's "Spinale", which we also have mentioned before, and seen (see page 238) that it is identical with the intero-lateral in *Homostius* (as O b r u č e v himself pointed out). The likeness between these two bones is so great, that, if found isolated, the "Spinale" in *Angarichthys* would, without doubt, be taken for an IL in *Homostius*. Their greatest difference is that IL in *Angarichthys* is somewhat broader than the corresponding bone in *Homostius*, indicating that *Angarichthys* was not so flat as the latter.

Finally, the third determined bone is marginal, and O b r u č e v himself points out its great similarity to the corresponding bone in *Homostius*. A comparison of O b r u č e v's picture with those in fig. 12 and 13 and Pl. VI in this paper shows clearly that the bone concerned is really a marginal of a form closely related to *Homostius*.

O b r u č e v calls one of the more doubtful bones "Pterygiale", a name J a e k e l proposed for the postero-supro-gnathal, but as he only determined it after a comparison with a figure in J a e k e l's papers, this determination cannot be regarded as certain. I find that this bone is much more reminiscent of the narrow, long, bent bone in *Homostius*, described on page 216 as "plate X". The two other fragments are completely indefinable.

As seen, all the three determinable bones in *Angarichthys* show a more or less great likeness to those in *Homostius*, and also one of the indefinable bones reminds one of a bone in the latter. Moreover, the tuberculation of the bones is absolutely *Homostius*-like. These conditions, in my opinion, help to prove that *Angarichthys* is related to *Homostius*, whereas O b r u č e v as a disproof mentions the following arguments: 1) The likeness in the position and outline of the tubercles on the surface structure of the plate, cannot prove the relation between these two forms. Without doubt this argument is perfectly true, but when other characteristics show great similarity, the pattern of the ornamentation can also be of interest and serve as a support. 2) The resemblance between the two marginals is less than might be thought at first glance. O b r u č e v particularly points out the development of the ridge on the overlapped part of the plate in *Angarichthys*, a ridge unknown in any specimens of *Homostius*. In my opinion, one cannot lay too great weight on the presence or absence of a ridge if the form and relation between the different parts of the plate are alike. The development of the connecting ridges is known from other plates both in *Homostius* (e. g. , PrO) and other *Arthrodira.* In *Angarichthys* a ridge was developed on the M plate, and its presence may be considered as a specific character for Gen. *Angarichthys,* being unknown not only in gen. *Homostius,* but in all other *Athrodira.* 3) *Homostius* is a "tooth-less" form whereas *Angarichthys* has well developed "teeth". As we have already seen, this characteristic is less important, as these two forms show the greatest conformity in the very structure of the jaw. The reduction of the "teeth" in *Homostius* can be explained by the fact that the "biting part" was moved from the upper to the lower margin of the jaw. 4) According to Dean, *Homostius* is separated from all other *Arthrodira* in a special sub-order *Termnothoraci,* while *Angarichthys* must be ascribed to Dean's sub-order *Arthrothoraci.* The investigations of recent years, however, have clearly shown that we cannot accept Dean's classification, which incorrectly separates *Homostius* from all the other *Arthrodira.* We will discuss this question in a later chapter.

Thus we see that the arguments Obručev adduces to prove that *Angarichthys* is not related to *Homostius* are not indisputable. On the contrary, not a single one states with certainty that they are not related forms. Considering all the similarities mentioned above, it seems natural to regard these two forms as closely related and to collect them into one family *Homostiidae.*

Definitions of the Family and Genera.

Taking all the above-mentioned characteristics into consideration we can give the following definition of the Fam. *Homostiidea* Jaekel:

Comparatively large *Arthrodira* with a flat head and body carapace, composed of flat and relatively thin plates, strongly overlapping each other, with the outside covered with stellar, even, tubercles; the sensory canals developed as deep grooves; the head roof with a stronger hind part (MB and EB plates) and somewhat short front part (PtO, PrO, P and R plates); the orbits situated quite near to each other, and in the majority of forms, limited from the outside by the post and pre-orbital processes,

but not by the SO; the side plates of the head imperfectly known; the IG plate much bent and more or less clearly twisted; the hind part of the blade carries a distinct ridge running inwardly and disappearing somewhere in the middle of the blade; the thickened functional portion continues far backward nearly to the hind limit of the blade; cutting edge or "teeth" developed on the functional portion; other gnathal elements hitherto unknown.

The body carapace is short and broad. AL is long and narrow, as is also the strongly developed IL, with its typical sculpture composed of oblique ridges. The more or less strongly reduced ventral shield is moved far forward under the head shield.

No traces of the inner skeleton, fins or scales are known.

Lower (?) and middle Devonian (old red) Siberia, Spitsbergen, NW Russia, Estonia, Latvia and Scotland.

To this family belong two genera: *Angarichthys* Obr. and *Homostius* Asm. They can be defined as follows:

1. Gen. *Angarichthys* Obručev (1927).

Quite large forms (head shield about 40 cm). The marginal with a well-developed ridge running on the part overlapped by C, parallel to the inner limit of the sculptured part. The inferognathal is only slightly twisted. Seven or more strong „teeth" placed on the upper limit of the functional portion. IL relatively broad and solid. Other plates of the carapace are hitherto unknown. Siberia.

We know only one species *Angarichthys hyperboreus* Obručev (1927) from lower (?) Devonian, river Bachta, Jenissei Govern., Siberia. The author has hitherto not chosen any GENO or HOLOTYPE, but, as the most characteristic and best described and depicted bone is the infero-gnathal, it seems probable that later he will choose this bone as a LECTOTYPE. Preserved in the Museum of the Geological Committee, Leningrad, (No. 1661 (1—7).)

2. Gen. *Homostius* Asmuss (1856).

Comparatively large and very large forms (head shield up to 1 m) with a flat head and body carapace. All the sensory canals clearly developed except the EB canal, which is always absent. The canal on the SO plate is represented by two independent V-shaped canals. Only one canal on the ADL and PDL, and no canal on the MD or on the ventral shield.

The head shield is nearly of the same length and breadth with indistinct hind-side angles. The fossa condylus is not deep, but long, occupying nearly $^1/_3$ of the whole posterior margin of the head.

The small orbital openings moved far forward are completely surrounded by the PrO and PtO, and in the majority of forms by the C plate as well. The SO is quite small and shows no visible impression for the orbits. The IG is so greatly twisted, that the surface of the functional portion and the blade are placed almost perpendicular to each other. No "teeth" are developed, but a distinct worn area is seen on the lower margin of the functional portion.

The MD plate is nearly twice as broad as long. The median keel on the underside of MD is low, with a thickening on its hind part. ADL is flat, its outside margin greatly bent downward, and its posterior part developed as a narrow, but solid offshoot, running forward nearly perpendicular to the axis of the very long condylus, which occupies almost the whole front part of the plate. The PDL plate is small, nearly triangular. The AL is narrow, long, and solidly connected to the offshoot of the ADL, forming its immediate prolongation. On the inside of AL is developed a distinct ridge, its front part continuing into the "hind wing", which runs from the front point of the plate obliquely in an inward and forward direction. To the front part of the hind wing the long, narrow IL is connected. The PL is reduced, the spinal is unknown. The ventral shield is composed of 3 almost equal very flat plates — 2 AVL and 1 AMV. The ventral shield is connected with the dorsal with the help of the AL and IL plates.

It is obvious that the Gen. *Homostius* must be regarded as the type genus of the Fam. *Homostiidea*, while, on the other hand, the question of the Genotype to the Gen. *Homostius* is more complicated.

As is known the first description and picture of *Homostius* fragments were given by Kutorga. In 1835 he depicted on Pl. III five different fragments of "*Trionyx spinosus*", of these two (1 and 2) belong to *Heterostius*, one is indefinable (4) and the two last, in all probability, represent fragments of *Homostius* (3 and 5); this, however, can hardly be determined. In 1837, Kutorga described and depicted a number of *Homostius* fragments: on Pl. I, AVL determined as "Schuppenförmig ausgebreitete hintere Ribbe des *Trionyx spinosus*", on Pl. II, fig. 1, 2, 3 & 4 two IL plates of different *Homostius* sp., determined as ribs of *Trionyx sulcatus*. On Pl. II, fig. 5 & 6, a plate of *Homostius*, described in this paper as plate Y, determined as "Schlüsselbein einer Eidexe" On Pl. VII, fig. 5, apparently the plate of *Homostius* described in this paper as plate X — determined as "Ribbe des Crocodilus", further, some other fragments determined as ribs of *Trionyx sulcatus* and *millaris* (Pl. VII, fig. 3 & 4) may represent fragments of *Homostius*.

Thus Kutorga has described 3 plates, which doubtless belong to *Homostius* and has proposed names for two different species — "*sulcatus*" and "*spinosus*", but as the name "*spinosus*" in 1835 was used for some certain *Heterostius*-fragments, this name cannot be accepted for *Homostius*, in spite of the fact that the plate described and depicted under this name in 1837 is very well preserved.

Thus the name "*sulcatus*" must be selected as the name of the Genotype. Under this name, however, also two different IL plates are described. I propose to regard the plates depicted on Pl. II, fig. 1 and 2 as belonging to this species, and count the plates on fig. 3 and 4 for another species (*Homostius latus* Asm.). It would also be the most natural thing to regard the bone depicted by Kutorga 1837 on Pl. II, fig. 1 and 2 as the GENOTYPE for the whole genus *Homostius* and as a LECTOTYPE for *Homostius sulcatus* **Kutorga**, but, unfortunately, according to the information of Dr. Obručev, the original material of Kutorga's papers is probably lost, and it is therefore necessary to find both a new GENOTYPE and LECTOTYPE. This must be chosen from among the pieces, which are collected in the same locality as Kutorga's material — in other words — from Asmuss' collection (but not H. Miller's from Scotland). As Kutorga's *Homostius sulcatus* seems to be identical with Asmuss' *Homostius cataphractus*, the LECTOTYPE for the latter must be regarded as a GENOTYPE for the Gen. *Homostius*. It is a fragment of the median basal plate, Tartu Museum, No. 39 (Pl. I, fig 1). Asmuss' plaster-cast No. 7.

The genus *Homostius* unites not less than 6 different species. As is known, Asmuss, as early as in 1856, described 5 species, but according to my investigation it is difficult to give a satisfactory definition of more than 3 of the species from Estonia and to these 3 are now added one from Latvia, one from Scotland and one from Spitsbergen. Remarkably enough, it seems that these 3 groups of species, the one from Spitsbergen, one from the Baltic and, finally, that from Scotland differ in some characteristics, thereby forming three "types". The difference, however, is not so great that it is necessary to establish a new genus or sub-genus for these groups. In my opinion, they show an increasing degree

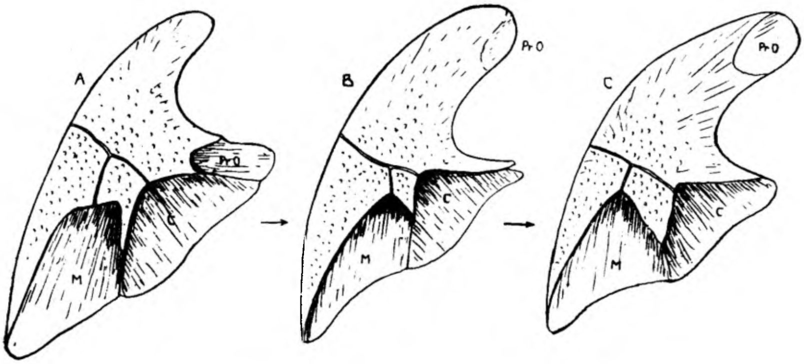

Fig. 50. The sub-orbital plates in three different groups of *Homostius*. *A* — Spitsbergen group *(H. arcticus)*, *B* — Baltic group *(H. latus)* and *C* — Scotch group *(H. milleri)*.

of specialization, the form from Spitsbergen being the most "primitive", and that from Scotland the most highly "specialized". Before beginning a description of the single species, I shall try to give a short characterisation of these three groups.

As we practically know only one plate of the Spitsbergen form, we must limit our characterisation to the arrangement of the plates round the orbital openings only.

In the first group the orbits are not placed especially near each other but lie very near the side margin of the head (fig. 50, A, fig. 51, B). The post-orbital process on the PtO plate is not so strongly developed in spite of its typical *Homostius*-like outline, and apparently the pre-orbital process on the PrO plate was indistinct and only just touched the post-orbital process. On the other hand, similar to all other *Arthrodira*, the basal parts of the

PrO and PtO plates came in contact with each other. Thus, in the form from Spitsbergen, the orbital opening is limited only by two plates, the PrO and PtO. It has already lost its connection with the SO, but as yet, does not reach the C. This group, as mentioned above, is imperfectly known and is only represented by one certain determined plate. We suggest calling it the Spitsbergen group. At the same time, it can be pointed out that it does not seem impossible that this group is closely related to *Angarichthys* — perhaps identical with the latter. New finds from Spitsbergen or Siberia, may show a relation between these two forms.

The second group, which we may call the Baltic group is much better known. Here the orbits are moved farther into the head shield and have reached the C plate (fig. 50, B, fig. 51, C). Both the pre and post-orbital processes are strongly developed, but overlap each other only moderately. The contact between the basal

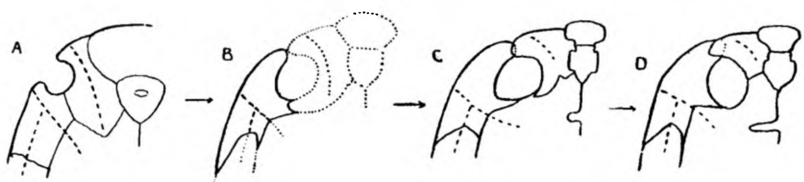

Fig. 51. Possible change of the front part of the head roof in the development line *Acanthaspis* — *Homostius*. *A* — *Jaekelaspis solnördali* Htz, from Spitsbergen. *B* — *Homostius arcticus* Htz. *C* — *Homostius latus* Asm. *D* — *Homostius milleri* Trq.

part of the PrO and PtO plates is already broken and the lower part of the orbit is now partly limited by the C plate, which thus separates the orbital plates, but the distance between their basal parts is very short. This group, so far as may be judged at present, is represented by all the species from Estonia, Latvia and NW Russia.

Finally, in the third group the orbits are moved still farther inward. The contact between the massive pre and post-orbital processes becomes stronger (fig. 51, D) and the basal parts of the orbital plates are moved so far from each other, that C composes nearly $^1/_3$ of the whole limit of the orbital opening. The PtO plate is still of the same size as in both the above-mentioned groups, but the PrO plate is clearly reduced. This group is represented by the form from Scotland and we may call it the Scotch group.

Thus these three groups represent a gradual change in the structure of the head of *Homostius*, a change which certainly must be regarded as the result of a progressive adaption to a bentonic life. On fig. 51 is given a drawing of the gradual movement of the orbits in a direction deeper and deeper into the head roof and steadily nearer to each other. A represents a *Jaekelaspis* from Spitsbergen, showing the more or less normal position of the orbits in a typical *Arthrodir*, B, C and D are *Homostius* forms from Spitsbergen, Estonia and Scotland respectively.

Description of different *Homostius* species.

I. Spitsbergen Group.

Definition. **Forms with the orbital openings limited completely by the PrO and PtO plates.**

This group, as mentioned, is represented only by one imperfectly known form from Spitsbergen, which I propose to call

Homostius arcticus nov. sp. (fig. 50, A, fig. 51, B, Pl. IX, 1).

The material of this form consists of one nearly complete left PtO plate and a number of different fragments of single plates and parts of the head shield (?), which, however, can hardly be determined because of their bad preservation.

As HOLOTYPE is chosen the only complete plate, the left PtO (Pl. IX, 1. Pal. Mus. Oslo, B 114).

The definition can therefore only be very imperfect: ***Homostius* with the orbital openings near the outside margin, entirely surrounded by the PtO and PrO plates. The basal part of the plates is in contact with each other, while at the same time the post and pre-orbital processes just touch.**

Description. The PtO plate (Pl. IX, 1) is of medium size. The point of the post-orbital process is broken off, but its outline is clearly seen from the impression on the stone. The complete plate measures about 15 cm in length and about 8 cm in breadth, being somewhat larger than the similar plate in the Scotch forms, but smaller than the largest plate known from Estonia. The sensory canals are developed as deep and distinct grooves. The most characteristic trait in the plate is its relatively weak post-orbital process and strong basal part. On the right side of the plate can clearly be seen three overlapping fields: The upper, comparatively small and not very deep was covered by the PrO plate (Pl. IX, 1, PrO). The middle one — the largest (Pl. IX, 1, C) was covered by C and the lower one (Pl. IX, 1, M) was overlapped by M. The last overlapping margin is more quadrangular-shaped than in any other *Homostius* forms, where it has a more triangular outline (fig. 16; Pl. VIII, 1, 2, M). The inside of the plate is unknown, as it was impossible to clean away the stone from its underside.

This plate was found north of the ridge Graakammen on the west side of Wijde Bay in North Spitsbergen, by Th. Vogt's expedition in 1928. Together with this plate on the same spot and on the ridge Graakammen, 775 m. above sea-level, other fragments were collected certainly belonging to the same form, but they cannot be determined in greater detail.

II. Baltic Group.

Definition. **Forms with the orbits limited principally by the PtO and PrO plates, and only slightly by the C plate.**

Material. To this group belong probably all the species known from Estonia and the adjacent districts, NW Russia and Latvia. Kutorga (1835—37) distinguished between 4—5 different forms from Tartu, Asmuss (1856) — 5 from the same locality (*Homostius formosissimus*, *H. latus*, *H. cataphractus*, *H. ponderosus* and *H. anceps*). Eichwald also described a fragment from Russia as *Homostius latus* (1860) and, finally, Woodward in II part of "Catalogue" connected all species from Estonia under one name *Homosteus formosissimus.*

As it is very difficult to reconstruct and determine the single species from the number of isolated plates known from Tartu, it is very tempting to establish a great number of new species. I have, however, made an attempt to reduce the number of the new species as much as possible, and propose to keep only three species among those described by Kutorga and Asmuss. These species can be more or less satisfactorily determined, but, of course, the single plates and fragments cannot always be determined with complete certainty as we must chiefly use such variable characteristics as size, kind of tuberculation, general outline etc., for determination, and only in a few cases have a distinct characteristic.

A relatively great number of fragments from Estonia can therefore only be preliminarily determined and many plates not at all. It seems quite obvious that the number of species from Tartu in reality was more than three, but it is doubtful whether we ever shall get a better insight into the composite of this remarkable fauna.

Homostius sulcatus Kutorga (1837).

Trionyx spinosus, Kutorga 1835, Pl. III, fig. 5 (?)
Trionyx sulcatus, Kutorga 1837, Pl. II, fig. 1 and 2.
(?) "Eidexe" Kutorga 1837, Pl. II, fig. 5 and 6.
(?) "Crocodilus" Kutorga 1837, Pl. VII, fig. 5.
Asterolepis sp., Agassiz 1844—45, Pl. 32, fig. (?) 3, 4 and 9, 10.
Homostius cataphractus, Asmuss 1856, Plaster-cast No. 7 (GENOTYPE and LECTOTYPE) and Plaster-cast No. 32.
Homostius latus, Asmuss 1856, Plaster-cast No. 34.
Homostius formosissimus, Asmuss 1856, Plaster-casts No. 12, 13, 31 and 35.
Homostius anceps, Asmuss 1856, Plaster-cast No. 28.
Homostius ponderosus, Asmuss 1856, Plaster-cast No. 33.
Homostius Asm., Pander 1857, Pl. 7, fig. 5, Pl. 8, fig. 2 (9, 10, 11) fig. 6 and 7.
Homosteus formosissimus Asm., Woodward 1892, BM, 15142 b, f, g, h, i, z.
Homosteus sp. Asm., Heintz, 1928. Pl. I.

Diagnosis. *Homostius* of medium size. The single plates relatively thick with well-developed ridges and thickenings, covered with grooves and somewhat uneven tubercles. On the inside of the MB plate the central hind thickening is moderately developed, while, on the contrary, the segmentally, obliquely arranged impressions in front are very clearly seen. The EB plate is rather short and broad. On the IG the cleft between the functional portion and the blade is strongly developed with the result that the blade is limited by a comparatively broad, roundish upper margin with a moderately developed impression (?). The MD plate is slightly curved with a well-developed median ridge. The ADL shows no tuberculation between the front limit of the overlapping margin covered by the MD, and the basal part of the condylus. On the inside the thickened ridge, running from the forwardly-directed lower part of the plate, gradually disappears in the hind part of the plate. The AL is somewhat coarse with a solid ridge on the inside. The overlapping margin covered by the ADL is nearly vertical — as is also the sculptured part of the plate — which makes the cross-section nearly rectangular. The "hind wing", broad in its basal part and becoming rapidly narrower towards the point, is not particulary long. It is placed at an angle of about 100^0 to the sculptured surface of the plate. The IL, with nearly straight upper and lower margins, is slightly curved and quite solid. The impression on the inside covered by the "hind wing" of the AL is comparatively short and broad. The AVL is more or less rectangular, both the hind and front margins and the side margins are almost parallel. The thickened ridge along the outside margin is very strongly developed.

Known from the middle Devonian (Old-Red) sandstone in Estonia and probably NW Russia.

As the IL described and depicted by Kutorga in 1837 (Pl. II, fig. 1) is lost, it is necessary to choose a new LECTOTYPE for *Homostius sulcatus* Kt. As mentioned, it is best to take the MB plate mentioned by Asmuss (1856) as plaster-cast No. 7 (Pl. I, 1). The same bone thus becomes a GENOTYPE for Gen. *Homostius.*

To this form, the most common in the collection in Tartu, belong a great number of isolated plates. The description of the single bones given in the general part of this paper is principally based on the bones of this form. Among Asmuss plaster-casts the following pieces belong to this form:

No. 7. — MB (*H. cataphractus* Asm.) GENOTYPE and LECTOTYPE; No. 12 and 13 — P (*H. formosissimus* Asm.) No. 14 — R (undetermined by Asmuss) No. 28 — AL (*H. anceps* Asm.) No. 31 — EB (*H. formosissimus* Asm.). No. 33 — EB (*H. ponderosus* Asm.) No. 34 — EB (*H. latus* Asm.) No. 35 — ADL (*H. formosissimus* Asm.) No. 44 — IG (undetermined by Asmuss) No. 54 and 55 — IL (undetermined by Asmuss).

In the Tartu Museum collections the following numbers belong to this form (of course the determination is not always absolutely certain).

Median-Basal plate, Tartu Museum No. 39 GENOTYPE and LECTOTYPE (Pl. I, 1) No. 38 (Pl. I, 2) No. 14 (Pl. II, 2; Pl. IV, 3) Nos. 243—254 No. 331 and No. 361.

Externo-Basal plate, Tartu Museum No. 11, No. 12

(Pl. V, 1, 4) No. 14 (Pl. II, 2) No. 41, No. 42 (Pl. III, 2) Nos. 255—261, Nos. 263—277, Nos. 363 and 432.

Marginal plate, Tartu Museum No. 16 (Pl. VI, 1, 2) No. 18, Nos. 278—292.

Central plate, Tartu Museum No. 25 (Pl. VII, 1, 2) No. 27 (Pl. VII, 3) No. 28 (?), nos. 294—306, No. 373. Paleontological Museum, Oslo, No. F 64.

Post-Orbital plate, Tartu Museum No. 31, (Pl. V, 5) No. 32, No. 33 (Pl. VIII, 3) Nos. 34 and 307.

Pre-Orbital plate, Tartu Museum No. 43 (Pl. IX, 3, 4) No. 44 (Pl. IX, 5) and No. 308.

Pineal plate, Tartu Museum No. 21 (Pl. X, 1, 2) No. 22 (Pl. X, 3, 4) No. 23 (Pl. X, 5) and No. 24.

Rostral plate, Tartu Museum No. 45 (Pl. X, 6).

Sub-Orbital plate is only represented by a few fragments, which are difficult to determine with certainty. Tartu Museum No. 68 (Pl. XI, 1, 2) Nos. 377, 378, 379, 399 and probably also Nos. 380 and 381.

Plate X, Tartu Museum No. 77 (Pl. XII, 1, 2) No. 78 (Pl. XII, 3, 4) Nos. 402, 403 and 404.

Infero-Gnathal plate, Tartu Museum No. 71 (Pl. XIII, 1, 2) and probably Nos. 382—394.

Median-Dorsal plate, Tartu Museum No. 36 (Pl. XIV, 2) Nos. 169—185, 348, 362 and 365.

Antero-Dorso-Lateral plate, Tartu Museum No. 1 (Pl. XVI, 1) No. 3 (Pl. XVIII, 3, 4), Nos. 190—211, 213—223, 314, 352 and 367. Paleontological Museum, Oslo No. F 150.

Postero-Dorso-Lateral plate, Tartu Museum No. 8 (Pl. XVII, 2) and No. 10 (Pl. XVII, 4) Nos. 186—189.

Antero-Lateral plate, Tartu Museum No. 3 (Pl. XVIII, 3, 4) No. 7 (Pl. XVIII, 1, 6. Pl. XX, 3) Nos. 224, 226—242, 358, 359, 366, 368, 371, 372, 797 and 798. Paleontological Museum Oslo No. F 65 (Pl. XX, 1, 2).

Intero-Lateral plate, Tartu Museum No. 82 (Pl. XIX, 1, 2, 3, Pl. XX 1, 2) Nos. 83, 116 and 6 unnumbered fragments.

Antero-Median-Ventral plate unknown.

Antero-Ventro-Lateral plate, Tartu Museum No. 119 (Pl. XXI) Nos. 120, 122, 123, 124, 127, 128 and 130.

Homostius formosissimus Asmuss (1856).

(?) *Trionyx spinosus*, Kutorga 1835, Pl. III, fig. 5.
Homostius formosissimus, As. 1856 in part.
Homostius Asm., Pander 1857, Pl. 7, fig. 33 Pl. 8, fig. 2, 12.
Homosteus formosissimus Asm., Woodward 1892 in part BM 15142 a.

Diagnosis. *Homostius* forms of small to middle size. The single plates are relatively thin, with moderately developed ridges and thickenings, flat and covered with fine, even tubercles. The MB plate is imperfectly known. The central thickenings seem to be moderately developed. The EB is unusually flat, relatively short and broad. The M is flat and thin. The IG is slender, the upper margin of the functional portion is sharp. The MD is unusually flat with a very moderate, thin median keel. The ADL is flat with a somewhat broad tuberculated portion between the front limit of the overlapping margin which is covered by the MD, and the basal part of the condylus, which is narrow and long. The ridges from the inside of the ADL are slightly developed. The PDL is comparatively strongly curved and thin. The AL is very characteristic, slender, with a distinct but thin obliquely-placed ridge on the inside. The overlapping margin covered by the ADL is not vertical, as in *Homostius sulcatus,* but forms nearly an immediate prolongation of the upper side of the ridge. The "hind wing", long, narrow, not especially broad in the basal part, is placed at an angle of about 110^0 to the sculptured surface of the plate. IL is imperfectly known, probably thin and slender. The AVL is also represented by a few fragments only; it is probably quite thick, not rectangular, but more roundish from the inside and hind side margin, while the outside margin is comparatively very short. All the ridges on the inner surface are slightly developed. It is as yet only known from the middle Devonian (Old-Red) sandstone near Tartu.

As LECTOTYPE is chosen a fragment of the MD (Pl. XXIII, 1), which Asmuss mentioned as the first fragment of *Homostius* belonging to the species *formosissimus* (Asmuss 1854 pp. 35 plaster-cast No. 5). The same fragment is mentioned by Woodward in "Catalogue" as "Type" for *Homostius formosissimus.* The LECTOTYPE is preserved in Tartu Museum and numbered No. 35.

This form is represented only by a few fragments and as the single bones are small and very thin, they have had small chances of being preserved as fossils. The most characteristic trait in this form is the thin and slender structure of all the plates. It is, however, always difficult to determine the single bones with certainty — the bones of younger specimens of two other forms were apparently similar to those in *Homostius formosissimus*. Among Asmuss plaster-casts only a few belong to this form. They are: No. 5 — MD (LECTOTYPE *H. formosissimus*) No. 27 — AL (*H. formosissimus*) and No. 45 — IG (undetermined by Asmuss). In the Tartu Museum collections the following numbers belong to this form.

Median-Basal plate, Tartu Museum, No. 162.

Externo-Basal plate, Tartu Museum, Nos. 13, 163 and 164.

Marginal plate, Tartu Museum, No. 20 (Pl. VI, 4), Nos. 165—167 and 293.

Central, Post-Orbital, Pre-Orbital, Rostral and Pineal plates unknown.

Sub-Orbital plate, Tartu Museum, No. 69 (Pl. XI, 3).

Infero-Gnathal plate, Tartu Museum. Only the plaster-cast is known (No. 45) as the original is probably lost.

Median-Dorsal plate, Tartu Museum, No. 35 (Pl. XXIII, 1, LECTOTYPE), Nos. 151, 152 and 168.

Antero-Dorso-Lateral plate, Tartu Museum, No. 4 (Pl. XVI, 2), Nos. 150, 153—159.

Postero-Dorso-Lateral plate, Tartu Museum, No. 9. (Pl. XVII, 3).

Antero-Lateral plate, Tartu Museum, No. (?) 5, No. 6 (Pl. XVIII, 2, 5), Nos. 160 and 161.

Intero-Lateral plate, Tartu Museum, No. (?) 115 and two unnumbered fragments.

Antero-Ventro-Lateral plate, Tartu Museum, No. 121, No. (?) 131 and some unnumbered fragments.

Homostius latus Asmuss (1856).

Trionyx spinosus, Kutorga 1837, Pl. 1.
Trionyx sulcatus, Kutorga 1837, Pl. II, fig. 3 and 4.
Asterolepis Eichw., Agassiz 1844—45, Pl. 32, fig. 2.
Homostius latus, Asmuss 1856, in part.
Homostius cataphractus, Asmuss 1856, in part.

Homostius ponderosus, Asmuss 1856, in part.
Homostius Asm., Pander 1857, Pl. B, fig. 16, Pl, 8, fig. 2 (5) and fig. 6.
Homostius latus Asm., Eichwald 1860.
Homosteus formosissimus Asm., Woodward 1892, in part.
BM, 15142 c, d and e.

Diagnosis. *Homostius* forms of medium to large size. The single plates more or less long and narrow, relatively thick, with distinct ridges and thickenings. The tuberculation is quite uneven. The MB is long, quickly narrowing into the bifurcated anterior margin. The hind median thickening is strongly developed, while on the other hand, the paired oblique impressions in front of it are absent. The EB is somewhat flat, long and narrow. The M is very massive and narrow, with a broad overlapping margin covered by C. The SO has a strongly developed, thick front part. The IG is more slender, the cleft between the blade and the functional portion is not especially broad, the upper margin of the latter is quite sharp. The MD plate has a comparatively massive high median keel. The ADL has no tuberculated portion between the front limit of the overlapping margin covered by the MD, and the basal part of the condylus, which is broad and thick. From the inside, the thickened ridge running backward from the forwardly-directed side part of the plate, is divided by a distinct, sharp cleft from the outside margin of the plate. The AL is long and slender, and is reminiscent of the AL in *Homostius formosissimus*. Here also the hind ridge is large, quite thin and oblique, covered on its overside by the overlapping margin of the ADL. The hind wing is narrow and long, and is placed at an angle of about 110^0 to the sculptured part of the plate. The main difference between the AL in *H. latus* and *H. formosissimus* is their size. The IL is narrow and strongly bent, its upper limit somewhat S-shaped, not straight as in *H. sulcatus*, with the result that the hind part of the plate is obviously broader than the front. The AVL plate is not rectangular, its outside margin is short, while the inside is large and roundish giving the whole plate a rather oblong outline. In one piece, probably belonging to *H. latus*, the tuberculation on the outside is developed as anastomising, small ridges.

Known from the middle Devonian in Estonia and possibly from NW Russia.

As LECTOTYPE has been chosen a fragment of the MB plate (Pl. I, 3, 4), which Asmuss mentioned as the first fragment of *Homostius* belonging to species *latus* (Asmuss, 1856, p. 36, plaster-cast No. 6).

This form is quite common and a great number of the fragments from Tartu probably belong to it. It is the largest *Homostius* form hitherto known. One complete MB plate preserved in Tartu (Pl. II, 1) measures about 60 cm, equivalent to a head shield of about 1 m and a whole carapace of about 1,50 m. The characteristics of this specimen are not always distinct and in some cases, possibly the very large plates of *H. sulcatus*, may be regarded as belonging to *H. latus*, as these two forms seem similar in many characteristics, e. g., the determination that the post-orbital plate belongs to *H. latus* cannot be considered wholly certain, as the decision is chiefly based on its very large size.

On the other hand, however, in the development of MB and especially the AL plate, *H. latus* shows a great resemblance to *H. formosissimus*, making it hard to decide, especially with regard to the AL, whether we have an exceptionally large plate of *H. formosissimus*, or a very small *H. latus* before us.

Among Asmuss plaster-casts the following belong to *H. latus*: No. 6 — MB (*H. latus* Asm. LECTOTYPE), No. 29 — AL (*H. latus* Asm.) No 37 — PtO (*H. ponderosus* Asm.) No. 43 — SO (undetermined by Asmuss) Nos. 46, 47 and 48 — IG (Undetermined by Asmuss) and No 56 — IL (Undetermined by Asmuss).

Of the specimens in Tartu Museum I regard the following as belonging to this specimen:

Median-Basal plate, Tartu Museum No. 15 (Pl. I, 3, 4, LECTOTYPE) No. 40 (Pl. II, 1) Nos. 330, 332, 333, 334 and 360.

Externo-Basal plate, Tartu Museum, No. 48 (Pl. IV, 1, 2) Nos. 262, 335—340, 364, 370 and 433.

Marginal plate, Tartu Museum No. 17 (Pl. VI, 3) Nos. 49, 341—343, 795 and 796.

Central plate, Tartu Museum Nos. 26, 344—347 and 794.

Post-Orbital plate, Tartu Museum No. 29 (Pl. IX, 2) No. 30 (Pl. VII, 1, 2 — only plaster-cast known).

Pre-Orbital, Rostral and Pineal plates unknown.

Sub-Orbital plate, Tartu Museum, No. 65 (Pl. XI, 4) Nos. 67, 374, 375 and 376.

Infero-Gnathal plate, Tartu Museum No. 72 (Pl. XIII, 4, 5) No. 73 (Pl. XIII, 3) Nos. 74, 395—397 and 398.

Median-Dorsal plate, Tartu Museum, No. 37 (Pl. XV, 1) Nos. 313 and 744.

Antero-Dorso-Lateral plate, Tartu Museum No. 2 (Pl. XV, 2, 3) No. 46 (Pl. XVI, 3) Nos. 315—319, 350, 351 and 357.

Postero-Dorso-Lateral plate, — no fragments known.

Antero-Lateral plate, Tartu Museum No. 4 (Pl. XXIII, 2) Nos. 47, 225, 320—328, and 329.

Intero-Lateral plate, Tartu Museum, the plate depicted by Kutorga in 1837 Pl. II, 3 and 4 must be regarded as the most typical of this species. In Tartu Museum only fragments are preserved. Nos. 112, 113, 114, 117, 118 and one unnumbered fragment.

Antero-Ventro-Lateral, the best example of this plate is depicted by Kutorga 1837 Pl. I (The same bone is depicted by Pander 1857 Pl. B, fig. 16). In Tartu Museum are only preserved fragments No. 125 — (Pl. XXII) and No. 126.

Homostius sp.

Thanks to the kindness of Dr. N. Deli, Riga, I have received from him for examination a large *Homostius* plate, which he collected in Old-Red on the East shore of Lake Burtniek in Latvia. This plate represents a big fragment of the EB of a very large form. Its length as it is now measures about 55 cm., thus, in reality, it was about 65—70 cm. long, a size similar to the largest known EB in *H. latus* (Pl. II, 1, 2). The hind margin with the fossa condylus and the inside margin, is not preserved. The sculpture and general outline of this plate, as also the distinct thickened ridge, running along the outside margin on the inside, are also reminiscent of *H. latus*, but show some unusual curvings, wholly unknown in the latter. The whole plate is bent along two convergent lines: One running nearly alongside the sensory canal which runs not far from the outside margin, the other, the main "ridge", from the middle of the hind margin to the upper point of the plate. Thus the whole plate is divided into three parts: The one between the outside margin and the sensory canal is slightly concave, the other — between the sensory canal and the main "ridge" is almost level, and, finally, the third between the main "ridge" and the inside margin, is also more or less concave. The main ridge is sharply developed — the angle between the surfaces of the second and third part of the plate is nearly 140°. It would be most natural to suppose, that the inner concave part represents an overlapping margin covered by the MB but as this part has a distinctly developed tuberculated structure, this supposition is impossible. If we suppose, which seems quite reasonable, that this inner part, in reality were placed more or less horizontally (as in other forms of *Homostius*), the whole plate would become very strongly bent, and the outside margin situated almost vertically. In no other *Homostius* is such a distinct curving of the head shield known. If, therefore, this plate is not pathologically deformed, we must suppose that we here have a new species of *Homostius*. In my opinion, however, it is better to await new finds, which may give us a better picture of this Latvian form, before we establish a new name.

III. Scotch group.

Definition. **Forms with the orbital openings limited nearly equally by the PtO, PrO, and C plates.**

Material. To this form belong all the *Homostius* fragments collected in Scotland, and preserved in different British Museums (mainly in the Edinburgh Museum). I have had the opportunity of studying the material of *Homostius* in the Edinburgh and British Museums, and have thus been able to investigate the originals of H. Miller's, Traquair's and partly Woodward's papers.

As pointed out by Traquair and Woodward, all these fragments belong to one specimen, which Traquair has called:

Homostius, (Homosteus) milleri Traquair.

Asterolepis from Stromness H. Miller 1849 (fig. 25, 28, 29 (LECTOTYPE) 30, 31, 37, 39, 40, 41, 42, 43, 44, 45 and 46 of the 1861 edition.)
Asterolepis asmussi, J. Morts 1854.
Homostius, C. H. Pander 1867. Pl. VIII, fig. 3 a—c.
Asterolepis, J. Miller 1869.
Homosteus milleri, Traquair 1888.
Homosteus milleri, Traquair 1889.
Homosteus milleri, Woodward 1891. 1.
Homosteus milleri, Woodward 1891. 2.
Homosteus milleri, Woodward 1916.

D e f i n i t i o n. *Homostius* of medium size. The single plates relatively thick, with distinct ridges and thickenings, with quite fine and even tuberculation. On the inside of the MB the central hind thickening is slightly developed, while on the contrary, the segmentally arranged oblique impressions in front of it, are very clearly seen. The PtO plate is quite broad, with a well marked overlapping margin on the post-orbital process, which was covered by the pre-orbital process in the PrO plate. The PrO plate is rather small, with a moderately developed basal part. The SO with indistinct ridges and thickenings is slenderer than in other *Homostius* forms. On the IG, the upper margin of the functional portion, is somewhat broad and rounded. The MD plate is comparatively broad in the hind part, broader than in any other *Homostius* forms, and has thus a more rectangular outline. The ADL shows no tuberculation between the front limit of the overlapping margin covered by the MD, and the basal part of the condylus. The latter is quite solid and thick, but seems to be a little shorter than in forms from Estonia. The configuration of the plate from the inside is not as yet clear. The AL is imperfectly known, but it seems as if the hind ridge is strongly developed and oblique. The IL plate has nearly straight upper and lower margins, and the basal part is quite broad. The AVL plate is angular, more or less trapezoidal, with a rather short outside and a long inside margin. The AMV plate is large, broader in front, with bifurcated lower margin.

The LECTOTYPE is the nearly complete head roof described and depicted by H. M i l l e r on fig. 29 (the 1861 edition). This piece is preserved in the Edinburgh Museum.

R e m a r k s. As seen from the definition above, *H. milleri* T r a q. and *H. sulcatus* K u t o r g a, showgreat resemblance, but they can, however, clearly be distinguished from each other. The similarity in the development of the impressions on the inside of the MB (Pl. III, 1) and the shape and development of the IG and IL plates is interesting to note. On the other hand the AL and AVL plates are more reminiscent of *H. latus* A s m u s s. (Pl. III, 1; Pl. XIV, 1; Pl. XVII, 1; Pl. XIX, 4.)

It is not improbable that later finds and investigations will reveal that the material from Scotland represents more than one species, and the circumstance that the different plates preserved in Edinburgh Museum vary relatively much both in shape and size, points in that direction. Of course, it is evident, that none of the Estonian forms are represented in the material from Scotland.

VI. Some remarks about the relation of the Family HOMOSTIIDAE Jaekel.

As we have seen the Fam. *Homostiidae* Jaekel is sharply divided from all the other *Arthrodiran* families. This isolated position must be regarded as a result of the very high specialization and adaptation to a bentonic life, which characterizes *Homostius*. The remarkable structure of *Homostius* has been pointed out by many authors, (Dean, (1900, 1901), Hussakof (1906), Jaekel (1902, 1903, 2), Stensiö (1925) and others) and, by some, is used to show that *Homostius* occupied an intermediate position between one or another group of *Arthrodira* or between *Arthrodira* and *Antiarchi*.

In this respect, the attempt of Dean (1901) to place *Homostius* between the real *Arthrodira* and *Macropetalichthys*, and an attempt of Jaekel (1903, 2) to regard *Homostius* as a "missing link" between *Arthrodira* and *Antiarchi* is especially interesting.

Dean proposed, as is known, a quite complicated systematic division of his Class *Arthrognathi*.

I Sub-Class *Anarthrodira*, Ord. I. *Stegothalami* Fam. *Macropetalichthys*.

II Sub-Class *Arthrodira*, Ord. I. *Temnothoraci*, Fam. *Chelonichthyida*. Gen. *Homostius*. Ord. 2. *Arthrothoraci*, containing 6 different Fam. (*Coccosteidæ*, *Dinichthydæ* and others) with a number of genera.

In the text Dean pointed out that *Temnothoraci* differs considerably from all other forms belonging to *Arthrodira* and, to some degree, connects this Sub-Class with the Sub-Class *Anarthrodira* — in other words — it represents a "bridge" between *Macropetalichthys* and real *Arthrodira*. On the accompanying drawing is a picture of *Macropetalichthys* with the hind part of the head shield divided from the front, and the new "plates" thus produced are homologous with the plates in a "*Temnothoraci*" — a hypothetical form, based "in general after *Homostius*". It is obvious that the head shield in a *Macropetalichthys* can hardly be regarded as homologous with the head + body carapace in *Arthrodira*. (Stensiö's investigations have shown that the primordial neurocranium in *Macropetalichthys* extends into the hind limit of the head shield). Also Dean's definition and description of the Order *Temnothoraci* do not correspond with our recent knowledge of *Homostius.* According to him, the following definition can be given of this Order: "*Arthrodires* whose cranial and dorsal shields are closely apposed, separated only by a transverse fissure-like interval: interarticulation of cranial and dorsal shields little developed . . . The anterior rim of the shoulder shield flattened at its sides, suggesting a rudiment of the ventral portion of the *Anarthrodirian.* Suborbital plate is present, but takes no part apparently in the ventral boundary of the orbits, thus being formed, as in *Anarthrodira* by the pre and post-orbital elements. Jaws, ventral armouring and endoskeleton not definitely known".

With regard to this definition we may note: 1) The cranial and dorsal shields in *Homostius* are wholly separated by a relatively broad interval, which cannot be regarded as "Fissure-like". 2) The interarticulation between these two parts is in no case less distinctly developed than in any other *Arthrodira.* 3) The development of the "anterior rim of the shoulder shield" also shows nothing unusual and cannot be considered a "rudiment" of the vertical portion of the *Anarthrodira.* 4) The only point really showing similarity is the position of the eyes, which in both forms are moved nearer to the median line of the head. But the homology between the single plates in *Arthrodira* and *Anarthrodira* is not so obvious, and it is therefore impossible, to say with certainty that in both forms the orbits were "formed by the pre and post-orbital elements" only. The circumstance that SO "takes no part in the ventral boundary of the orbits" must be regarded as an advanced specialization, but not as a primitive character.

Thus, in my opinion, all the reasons brought forward to divide *Homostius* from other *Arthrodira* and regard it as a more or less "intermediate" form between the later and *Macropetalichthys*, were in Dean's time only based on an unsatisfactory knowledge of our form, and cannot be acknowledged to-day; nor can we admit the systematic division of *Arthrodira* proposed by him.

In his review of Dean's above-mentioned paper, Jaekel (1903, 1) writes that "die *Pterichthyidee* sind durch *Homostius* (Asm.) und die *Coccosteiden* so eng angeschlagen, dass Platte für Platte ihres Schädeldaches homolog ist". The same year in a paper about "*Asterolepis*" (1903, 2) Jaekel, in fact, gives such a comparison of the single armour plates in *Arthrodira* and *Anti-*

archi. The proposed homology of the single plates in the head roofs of these two groups (later acknowledged by Hussakof (1906) is, however, only more or less probable, and of course cannot be taken for granted, especially as Stensiö (1931) and Gross (1931), for instance, have reached quite divergent results, in respect to this question.

We shall not here go through the different opinions concerning the homology of these forms, as they are of little interest to us in connection with *Homostius.* We can only point out, however, that *Homostius* cannot in every case be regarded as an intermediate form between these two groups. Jaekel in the above mentioned paper (1903, 2) depicted three head shields: one of *Pachyosteus*, one of *Homostius* (wrongly named *Heterostius*) and one of *Asterolepis*, probably to show, that *Homostius* occupied a position between the real *Arthrodira* and *Antiarchi.* In the text, however, he does not mention any special reasons why he regards *Homostius* as an intermediate form but they are easily conjectured; being, apparently, the position of the eyes and the position of the SO plate. Moreover, there are in fact some points in the structure and configuration of the head shield of *Homostius* and *Asterolepis*, which are somewhat similar. 1) The eyes in both forms are placed near each other, on the sides of the pineal plate. 2) The SO in *Homostius*, a long, narrow plate, is situated along the anterio-lateral part of the head roof and is thus reminiscent of the shape and position of the small movable plate on the side of the head in *Antiarchi.* It is by Traquair (1888) and Gross (1931) called the "Externolateral" by Patten (1912) "Sub-Orbital", by Jaekel (1903, 2) "Jugal" and by Stensiö (1931) "Opercular". 3) Finally, the configuration of the infero-gnathal in *Homostius* is not unlike that in *Antiarchi* (compare the picture in Patten (1912) and Stensiö (1931) with fig. 29 and Pl. XIII in this paper).

These similiarities — in my opinion — can only be looked upon, however, as convergences when compared with all the great differences which exist between these two groups, and are therefore not of much value. Some characteristics may be pointed out here: e. g., 1) The prominently developed posterior part of the head roof in *Homostius* compared with the strongly developed front part of that in *Antiarchi.* 2) The great reduction of the body carapace in *Homostius* opposite to the strong body armour in *Antiarchi.* It seems, therefore, that *Homostius* cannot be considered as a connecting form between *Arthrodira* and *Antiarchi*, but, on the contrary, as a highly-specialized form placed far above the common ancestors of these two groups.

The position of this family in relation to other families of *Arthrodira* is, however, not so easily found — as many characteristics are sharply divergent from all other known forms. Therefore, in all the systematic divisions of *Arthrodira* proposed of recent years (Gross 1931, Woodward 1932, Heintz 1932, 2) we find the family *Homostiidae* as an independent family not closely related to any other *Arthrodiran* family.

As a whole, investigations of the past few years show that the systematic division of *Arthrodira* is a difficult problem, especially when we try to draw up a more or less complete picture of their phylogeny.

It seems, however, that all scientists agree to count as the first group which shows many "primitive" characteristics, the principal lower Devonian *Acanthaspida* (= *Phlyctænaspida*) (called "Family" by Woodward, 1932, "Sub-Order" by Gross 1931, 1 and "Order" by Heintz 1932, 2).

As is known, they are especially characteristic because of the presence of a more or less distinctly developed spine on the body carapace, but, in actual fact, this group is not by far so homogeneous as it seems. If we examine its single representatives we find remarkable variations: Some forms have the orbits placed far forward, near each other (*Phlyctænaspis acadica* Traquair 1890, 3); others — quite far backward, far from each other (*Euryaspis brachycephalus* Bryant 1932). In some, the orbits make only a very slightly marked depression on the side margin of the head roof (*Ph. acadica*, *Arctaspis maximus* Heintz 1929, 2) in others, on the other hand, they make very deep incuts in the head roof (*Jaekelaspis solnördali* Heintz 1929, 2). In some, the rostropineal plate comes in contact with the central plate (*Jaekelaspis*, *Lunaspis*, Broili 1929), while in others the right and left PrO touch each other and divide the rostro-pineal from the central (*Svalbardaspis*, *Arctaspis*, Heintz, 1929, 1, *Phlyctænaspis*, *Euryaspis*). In some, the MB is relatively short and broad (*Euryaspis*, *Jaekelaspis*, *Phlyctænaspis acadica*) and in others long and narrow (*Phlyctænaspis anglica*, Traquar 1890, 3, *Svalbardaspis*). It is not difficult to multiply the variations in the structure of the single species in this group, and we could for example compare the structure of the body carapace, the relation between the size of the head and body, the course of the sensory canals and other factors. It all indicates that "*Acanthaspida*", in reality, is not a homogeneous group, but represents a kind of "central group" from which all the other *Arthrodira* radiate; but also among the "*Acanthaspida*" we find different lines of specialization which have probably given rise to various groups of later *Arthrodira*. In spite of all their divergences, the "*Acanthaspida*" constitute a unit, as in many respects they show more "primitive", or better still "original" characteristics, contrary to many characteristics in other *Arthrodira*, which must be regarded as more highly "specialized".

In the following table I have tried to give a general view of the different characteristics in the change from the more "original" to more "specialized".

"Original Characteristics".	**"Specialized Characteristics".**
1a) Small to average size.	1b) Large size.
2a) Thick carapace with solidly connected single plates.	2b) Thin carapace with comparatively loosely connected plates.
3a) Plates with sculptured surface.	3b) Plates without sculpture.
4a) Distinct and deep sensory canals.	4b) More or less indistinct and not deep sensory canals.
5a) Head shield almost of the same size or smaller than the body carapace.	5b) Head shield larger than the body carapace.
6a) All the head and body plates well developed.	6b) Some of the head or body plates reduced.
7a) Carapace nearly of same height as breadth.	7b) Carapace higher than it is broad.
8a) Rostral and pineal plates form a joined rostro-pineal plate.	8b) Pineal and rostral plates isolated.
9a) Small orbits.	9b) Large orbits.
10a) Orbits limited by the PtO, PrO and SO plates.	10b) Orbits also limited partly by other plates (as C, PN or M).
11a) Strongly developed hind part of the head roof (MB and EB).	11b) Hind part of the head roof not strongly developed.

12a) The side plates of the head not in close connection with the well limited head roof.	12b) Side plates of the head more or less closely connected with the head roof.
13a) The condylus (and fossa cond.) indistinctly developed, placed near each other.	13b) The condylus (and fossa cond.) clearly developed, situated quite far from each other.
14a) The opening between the head and body carapace narrow and small.	14b) The opening between the head and body carapace, broad and large.
15a) The MD plate narrow and long.	15b) The MD plate short and broad.
16a) The keel on the inside of MD poorly developed.	16b) The keel on the inside of the MD plate distinctly developed.
17a) The Sp plate strongly developed.	17b) The Sp plate more or less completely reduced.
18a) The contact line between the ventral and dorsal parts of the body carapace long.	18b) The contact line between the ventral and dorsal parts of the body carapace short.
19a) The ventral shield large, with all plates developed.	19b) The ventral shield more or less reduced.
20a) The axial skeleton and fins not calcified (or ossified).	20b) The axial skeleton more or less calcified or ossified.

This list of characteristics can easily be extended.

As is seen, the characteristics given as "originals" are almost clearly developed in "*Acanthaspida*", but not in all forms, as the different groups each show more "specialized" features at various points.

If we try to "analyse" the different species of *Arthrodira* and in that way define the relation between the various groups, we shall at once find it a very difficult task, as "crossings of specialization" is a very common phenomenon. This can be illustrated by some examples: *Pholidosteus* (Jaekel 1907, Gross 1932), a form from the upper Devonian from Wildungen, shows a remarkable combination of "original" and "specialized" characteristics. It is of smaller size, with solid armour, tightly connected, tuberculated single plates, with distinct sensory canals. The head shield of nearly the same size as the body carapace. All plates well developed, spinal strong and long, a large ventral shield, well combined with the dorsal, all these are more "primitive traits" known in *Acanthaspida*. *Pholidosteus*, however, shows many other more "specialized" characteristics: The pineal and rostral plates are completely divided, the orbits are large, the posterior part of the head moderately developed, and the side plates of the head well connected with the head roof. The condylus and fossa condylus clearly developed. The opening between the head and dorsal shields relatively large. The MD plate well developed, but somewhat short. The axial skeleton calcified.

Thus we here find the most complicated combination of different traits, some reminiscent of the lower Devonian *Acanthaspida*, others of the most specialized upper Devonian forms.

If we now turn to *Homostius* we will see that this form also displays many mixed characteristics: It has a thick carapace, covered with tubercles, with deep sensory canals, but the single plates are absolutely isolated, and P and R are independent plates. The orbits are small, but deeply incised into the head roof and not limited by the PrO, PtO, and SO, but by the two first and C. The posterior part of the head is very large and the side plates of the head are not connected to the head roof, while the body carapace is small with a short and broad MD plate. The condylus are strongly developed lying quite far from each other, but the opening between the head roof and dorsal shield is narrow. Sp has probably wholly disappeared and the contact line between the dorsal and ventral shields is strongly reduced and very short, while no traces of a calcified central skeleton is known.

I am fully aware that we cannot emphasise too much the proposed "differentiation of the characteristics". In some specialized forms from Wildungen (*Brachydirus*, *Oxyosteus* and finally *Synochenia* for example), the opening between the head and body secondarily becomes more and more reduced, finally completely disappearing together with the reduction of the condylus. But still these characteristics can, undoubtedly, help us to determine the possible relation between the single Genera and Families of the *Arthrodira*. As mentioned, the somewhat "primitive" group *Acanthaspida* apparently contains ancestors of all later forms. But only very seldom may we hope to be able really to recognize the development of the single lines, and, among *Acanthaspida*, find some form or other which may be regarded as the ancestor of a higher form, thus reconstructing a line of development. In the best cases we may find some forms which indicate a possible line of the development. Thus, for instance, *Phlyctænaspis angelica*, *Coccosteus minor*, *Coccosteus decipiens* and perhaps *Dinichthys* can be regarded as more or less natural groups of forms. Another more or less probable line of development runs from some *Acanthaspis* or other, with the deeply-incised orbits to *Angarichthys* and so to the three steps of development of *Homostius* (The Spitzbergen, Baltic and Scotch). We know only very few of the existing forms and our insufficient knowledge of *Arthrodira* will always make a reconstruction of a real ancestor line very problematic and uncertain.

On the other hand, there are more chances of ascertaining the gradual change and development of a single characteristic (shape of the plate, reduction of some organs and others). This kind of "evolution" has been pointed out earlier. I have in my recent paper (Heintz 1931) described the change of configuration of the AL plate in different forms and the gradual reduction of the ventral shield, and it can hardly be difficult to construct some other of these "lines of evolution", e. g., the development of the orbits, reduction of the spinal, configuration of the jaws and others.

If we now look at the systematic division of the *Arthrodira*, we must point out that our recent knowledge of this group is not sufficient to undertake a more or less satisfactory classification, corresponding to the phylogenetic development of the group. I therefore consider it better provisionally to establish a number of independent families, (as Gross proposed), which can later be connected into greater units. We can already with a great degree of probability regard the Sub-Order (or Order) *Acanthaspida* as a natural "Central Order", and also the Sub-Order *Coccosteida* (Heintz 1932, 2) as a more or less natural group. The Family *Homostiidae* is quite isolated, but shows some traits which indicate that at an early stage it became separated from the common "*Acanthaspida*" stock and soon afterwards (middle Devonian) obtained a very high degree of one-sided specialization.

With regard to the relation between *Arthrodira* and *Antiarchi* I would only point out that just the "*Acanthaspida*" — (in spite of the fact that they on no account can be regarded as connecting forms between these two groups) still show the greatest resemblance to *Antiarchi* e. g., in the shape of the body carapace, the presence of the spine, and the relation between the size of the head and body carapaces. All these points seem to indicate that these two groups originally had a common ancestor.

With regard to the relation of the group *Placoderma* to other vertebrates, I would point out that, after the last (unpublished) investigation of Stensiö, it seems that the jaw in *Arthrodira* must be regarded as a modified normal Gnathostom jaw. Thus my suggestion (Heintz 1932, 2) that *Arthrodira* was an independent class of Vertebrates, proves to be erroneous — it must be considered as related to one or another group of fishes, probably to *Elasmobranchii.*

Paleontological Museum Oslo.
May 1933.

VII. Bibliography.

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Explanation of plates.

Plate I.

1. *Homostius sulcatus* Kutorga. A fragment of the median-basal plate seen from the inside. GENOTYPE and LECTOTYPE. Tartu Mus. No. 39.
2. *Homostius sulcatus* Kutorga. A fragment of the median-basal plate from the inside. Tartu Mus. No. 38.

3 and 4. *Homostius latus* Asmuss. A fragment of the median-basal plate from the outside (3) and from the inside (4). LECTOTYPE. Tartu Mus. No. 15.

a — hind part of the plate not covered with tubercles, ds — double sockets, eb — overlapping margin covering the EB plate, im — median impression, mp — hind, thin part of the plate, mr — median ridge between the double sockets, pr — projection on the median point of the posterior margin, rd — hind median ridge, r_1-r_2-r_3 . . . — ribs on the side of the median impression, ts — transversal wall.

Plate II.

1. *Homostius latus* Asmuss. Nearly complete median-basal plate from the inside. Tartu Mus. No. 40.
2. *Homostius sulcatus* Kutorga. Fragment of the median-basal (MB) and externo-basal (EB) plates in natural connection. Tartu Mus. No. 14.

Explanation as in Plate I.

Plate III.

1. *Homostius milleri* Traquair. Nearly complete head roof from the inside. Edinburgh Mus. No. 1900—39.
2. *Homostius sulcatus* Kutorga. Fragment of the externo-basal plate seen from the outside. Tartu Mus. No. 42.

C — central plate, EB — externo-basal plate, fg — fossa condylus MB — median-basal plate, M — marginal plate, Or — orbital opening. P — pineal plate, pg — processus glenoidalis, PrO — pre-orbital plate, PtO — post-orbital plate, R — rostral plate, rd — ridges radiating from the hind corner of EB, r_1-r_2-r_3 . . . ribs on the side of the median impression, s-s — sensory canals, w-w — thickenings along the outside and hind margins of EB.

Plate IV.

1, 2. *Homostius latus* Asmuss. Complete left externo-basal plate from the outside (1) and from the inside (2). Tartu Mus. No. 48.

2. *Homostius sulcatus* Kutorga. The same piece as on Pl. II, fig. 2, from the inside.

A — hind side corner, B — upper corner, C — overlapping margin covering the C plate, D — inside hind corner, M — overlapping margin covering the M plate. * — the red incrustation. Rest as in Plate I and III.

Plate V.

1, 4. *Homostius sulcatus* Kutorga. Lower part of a left externo-basal plate seen from the outside (1) and from the inside (4). Tartu Mus. No. 12.

2, 3. *Homostius sulcatus* Kutorga. Fragment of the hind part of a left externo-basal plate, from behind (2) and from outside (3). Photographs after plaster-cast.

5. *Homostius sulcatus* Kutorga. Fragment of the right post-orbital plate seen from the outside. Tartu Mus. No. 31.

C — overlapping margin covered by the C plate, fg — fossa condylus, ljp — lower joint process, MB — overlapping margin covered by the MB plate, M — overlapping margin covered by the M plate, Or — orbital opening, pg — processus glenoidalis, rd — ridges radiating from the hind corner of EB, s-s — sensory canals, ujp — upper joint process, w-w — thickenings along the outside and hind margins of EB. * — the red incrustation.

Plate VI.

1, 2. *Homostius sulcatus* Kutorga. Nearly complete right marginal plate from the outside (1) and the inside (2). Tartu Mus. No. 16.

3. *Homostius latus* Asmuss. Fragment of a left marginal plate from the outside. Tartu Mus. No. 17.

4. *Homostius formosissimus* Asmuss. Fragment of a right marginal plate seen from the outside. Tartu Mus. No. 20.

A — posterior angle, B — upper outside angle, C — margin overlapped by the C plate, D — upper inside angle, EB — margin overlapped by the EB plate, s_1-s_2-s_3 — sensory canals, x — protuberated part of the sculptured surface.

Plate VII.

1, 2. *Homostius sulcatus* Kutorga. Nearly complete left central plate from the outside (1) and from the inside (2). Tartu Mus. No. 25.

3. *Homostius sulcatus* Kutorga. Fragment showing the contact between the right and left central plates, from the outside. Tartu Mus. No. 27.

C — overlapping margin covered by the adjoining C plate. EB — overlapping margin covered by the EB plate. MB — the same covered by the MB plate. Or — position of orbits. P — overlapping margin covering the P plate. PtO — the same covering the PtO plate. PrO — the same covering the PrO plate. s-s — sensory canals. M — overlapping margin covering the M plate.

Plate VIII.

1, 2. *Homostius latus* Asmuss. The left post-orbital plate seen from the outside (1) and the inside (2). Plaster cast, original lost. Tartu Mus. No. 30.

3. *Homostius sulcatus* Kutorga. Fragment of the right post-orbital plate seen from the outside. Tartu Mus. No. 33.
   C — overlapping margin covered by the C plate, M — the same covered by the M plate, Orb — position of the orbit, PrO — position of the pre-orbital plate, ptp — postorbital process. s_1-s_2-s_3 — sensory canals.

Plate IX.

1. *Homostius arcticus* nov. sp. The left post-orbital plate seen from the outside. Wijde Bay, Spitsbergen. Paleont. Mus. Oslo. B 114, HOLOTYPE
2. *Homostius latus* Asmuss. The left post-orbital plate from the outside. Tartu Mus. No. 29. Explanation as in Pl. VIII.

3, 4. *Homostius sulcatus* Kutorga. The right pre-orbital plate, nearly complete, from the outside (3) and from the inside (4). Tartu Mus. No. 29.

5. *Homostius sulcatus* Kutorga. Fragment of a right pre-orbital plate seen from the outside. Tartu Mus. No. 44.
   aa — thickening around the inner limit of the orbital opening. b — groove on the end of the curved impression. d — curved impression. Or — position of the orbits. P — position of the P plate. PtO — position of the PtO plate. prp — preorbital process. Sp — spine-like process serving to connect the PrO with the P plate. S — sensory canal.

Plate X.

Homostius sulcatus Kutorga.

1, 2. Complete pineal plate seen from the outside (1) and from the inside (2). Tartu Mus. No. 21.

3, 4. Fragment of the pineal plate seen from the outside (3) and from the inside (4). Tartu Mus. No. 22.

5. Upper part of a pineal plate seen from the outside. Tartu Mus. No. 23.
6. Rostral plate seen from the outside. Tartu Mus. No. 45.
   a — funnel-shaped impression, b — semi-circular row limiting impression a, C — overlapping margin covered by the C plate, P — cavity, where the protuberated front part of the P plate fits in, PrO — overlapping margin covered by the PrO plate, R — protuberated front part of the P plate.

Plate XI.

1, 2. *Homostius sulcatus* Kutorga. The "handle" of the right sub-orbital plate seen from the inside (1) and from the outside (2). Tartu Mus. No. 68.

3. *Homostius formosissimus* Asmuss. Fragment of the right "blade" seen from the outside. Tartu Mus. No. 69.
4. *Homostius latus* Asmuss. Fragment of the right sub-orbital plate seen from the outside. Tartu Mus. No. 65.
   a-b — limit dividing the front part of the handle, c-d — limit dividing the blade into two parts, if — lower portion of the sub-post-orbital canal, j — gnathal canal, gr — groove running along the lower limit of the handle, R_4 — ridge running along the lower margin of the handle, r, r — ridges on the front part of the handles, s-s — sensory canals.

Plate XII.

1, 2. *Homostius sulcatus* Kutorga. The front part of the left (?) plate "Y" from the outside (1) and from the inside (2). Tartu Mus. No. 77.

3, 4. The hind part of the right-(?) plate "Y" seen from the outside (3) and from the inside (4). Tartu Mus. No. 78.

5, 6. *Homostius latus* Asmuss. The central part of the left sub-orbital plate seen from the outside (5) and from the inside (6). Tartu Mus. No. 66.

Pr — projection in front of the ridge R_1; R_1 — ridge running from the upper margin of the plate; R_3 — ridge running along the lower margin. Rest as in Plate XI.

Plate XIII.

1, 2. *Homostius sulcatus* Kutorga. Infero-gnathal plate seen from the side (1) and from above (2). Tartu Mus. No. 71.

3. *Homostius latus* Asmuss. Fragment of the infero-gnathal plate. Tartu Mus. No. 73.

4, 5. *Homostius latus* Asmuss. Front part of the infero-gnathal plate seen from the outside (4) and from the inside (5). Tartu Museum. No. 72.

A — functional portion, B — blade, b — lower margin of the blade, c — step between the blade and the functional portion. d — point where the lower margin of the blade runs "under" the functional portion, e — upper, thickened part of the functional portion, f — front point of the functional portion, g — incut in the lower margin of the functional portion, h — thickened prolongation of the functional portion, i — the hind point of the functional portion, x — large worn area on the ovoid part, y — small worn area on the ovoid part, z — the hind point of the worn area, w — worn trace on the side of the blade.

Plate XIV.

1. *Homostius milleri* Traquair. A nearly complete head. The body carapace partly destroyed. Plaster casts. Original in Edinburgh Museum.

2. *Homostius sulcatus* Kutorga. A fragment of the hind part of the median-dorsal plate seen from inside. Tartu Mus. No. 36.

a — acute front angle of MD, AL — antero-lateral plate, ADL — antero-dorso-lateral plate, AVL — antero-ventro-lateral plate, b — obtuse hind angle of MD, c — front median point, d — hind median point, IG — infero-gnathal plate, im — symmetrical impression on the hind margin of the knot, K — knot on the median keel, SO — sub-orbital plate, x — the plate "X", Rest as in Pl. III.

Plate XV.

1. *Homostius latus* Asmuss. Complete median dorsal plate seen from the inside. Tartu Mus. No. 37.

2, 3. *Homostius latus* Asmuss. Nearly complete antero-dorso-lateral plate seen from the inside (2) and from the outside (3). Tartu Mus. No. 2.

a — acute front angle, adl — margin overlapping the ADL plate, al — margin overlapped by the AL plate, b — obtuse hind angle, cg — condylus, c-d — median keel. im — symmetrical impressions on the hind margin of the knot, k — knot on the median keel, md — overlapping margin covered by the MD plate, pdl — overlapping margin covering the PDL plate, pag — processus glenoidalis, rg — condylus ridge, s — sensory canal, ujf — upper joint fossa, x — inside limit of the process on ADL.

Plate XVI.

1. *Homostius sulcatus* Kutorga. The large fragment of a right antero-dorso-lateral plate, with broken process, seen from the outside. Tartu Mus. No. 1.
2. *Homostius formosissimus* Asmuss. The fragment of a left antero-dorso-lateral plate, with broken process, Tartu Mus. No. 4. Seen from the outside.
3. *Homostius latus* Asmuss. Large fragment of a left antero-dorso-lateral plate seen from the inside. Tartu Mus. No. 46. Explanation as in Pl. XV.

Plate XVII.

1. *Homostius milleri* Traquair. Complete head and body carapace. Photograph of a plaster-cast from specimen No. 1878/5/410 in Edinburgh Museum. Original of Traquair's plate (1889).
2. *Homostius sulcatus* Kutorga. The left postero-dorso-lateral plate seen from the outside. Tartu Mus. No. 8.
3. *Homostius formosissimus* Asmuss. Fragment of the right postero-dorso-lateral plate from the outside. Tartu Mus. No. 9.
4. *Homostius sulcatus* Kutorga. Fragment of the right postero-dorso-lateral plate, seen from the outside. Tartu Museum, No. 10.

adl — overlapping margin covered by the ADL plate, md — overlapping margin covered by the MD plate. * * — Impression after ventral shield (IL). Rest as in Pl. XIV.

Plate XVIII.

1, 6. *Homostius sulcatus* Kutorga. Nearly complete antero-lateral plate seen from the underside (1) and the upperside (6). Tartu Mus. No. 7.

2, 5. *Homostius formosissimus* Asmuss. Complete antero-lateral plate seen from the underside (2) and the upperside (5). Tartu Mus. No. 6.

3, 4. *Homostius sulcatus* Kutorga. The antero-lateral plate (with broken hind wing) in natural contact with the antero-dorso-lateral plate. Tartu Mus. No. 3.

a — upper front angle, a-a — ridge in front of the overlapping margin, a-b — upper margin, a-v — front margin, b — upper hind angle, b-d — hind margin, d-f — lower margin, e — hind wing. f — lower front part, g — upper margin of the hind wing. e-p — impression on the underside of the hind wing, m — front margin of the ridge, n — hind margin of the ridge, y — front thickenings, z — impression in front of the sculptured part. Otherwise as in Pl. XV.

Plate XIX.

1, 2, 3. *Homostius sulcatus* Kutorga. The hind part of an intero-lateral plate seen from the outside (1), from the underside (2) and from the inside (3). Tartu Mus. No. 82.

a-b hind margin, a-d-b — thin part overlapping the hind wing of AL, a-c — upper margin, b-c — lower margin, s-s — step under the ridge x-x; x-x — lower ridge, z — thickened hind part, z-y — upper ridge.

4. *Homostius milleri* Traquair. The antero-ventro-median (AMV) and the intero-lateral (IL) plates seen from the inside. Edinburgh Mus. No. 1896/6/1.
   a-side corners of the AVM plate, b — front margin, c — hind margin.

Plate XX.

1, 2. *Homostius sulcatus* Kutorga. Connection between the antero-lateral (Paleont. Mus. Oslo, F 65) and intero-lateral (Tartu Mus. No. 82) plates.

3. *Homostius sulcatus* Kutorga. Connection between the antero-lateral (Tartu Mus. No. 7) and antero-ventro-lateral (Tartu Mus. No. 119) plates.
   Explanation as in Pl. XVIII and XIX.

Plate XXI.

Homostius sulcatus Kutorga. The right antero-ventro-lateral plate. Tartu Mus. No. 119.

1. A part of the plate from the outside.
2. Plate seen from the side a-b (outside margin).
3. Plate seen from the inside.
4. Plate seen from the front.

   a-b — outside margin, a-e-a' — ridge on the outside margin, al — overlapping margin covered with the hind wing of the AL plate, amv — overlapping margin covering the AVM plate, b — thickened, protuberated outside front-angle, b-c — front margin, c-d — inside margin, d-a — hind margin, il-il — part of the front margin where the inside of the IL plate comes in contact with AVL. m — groove along the outside margin, n — the lower outside margin, w-w-wr — the ridge on the front margin, wr — the thickenings on the front margin.

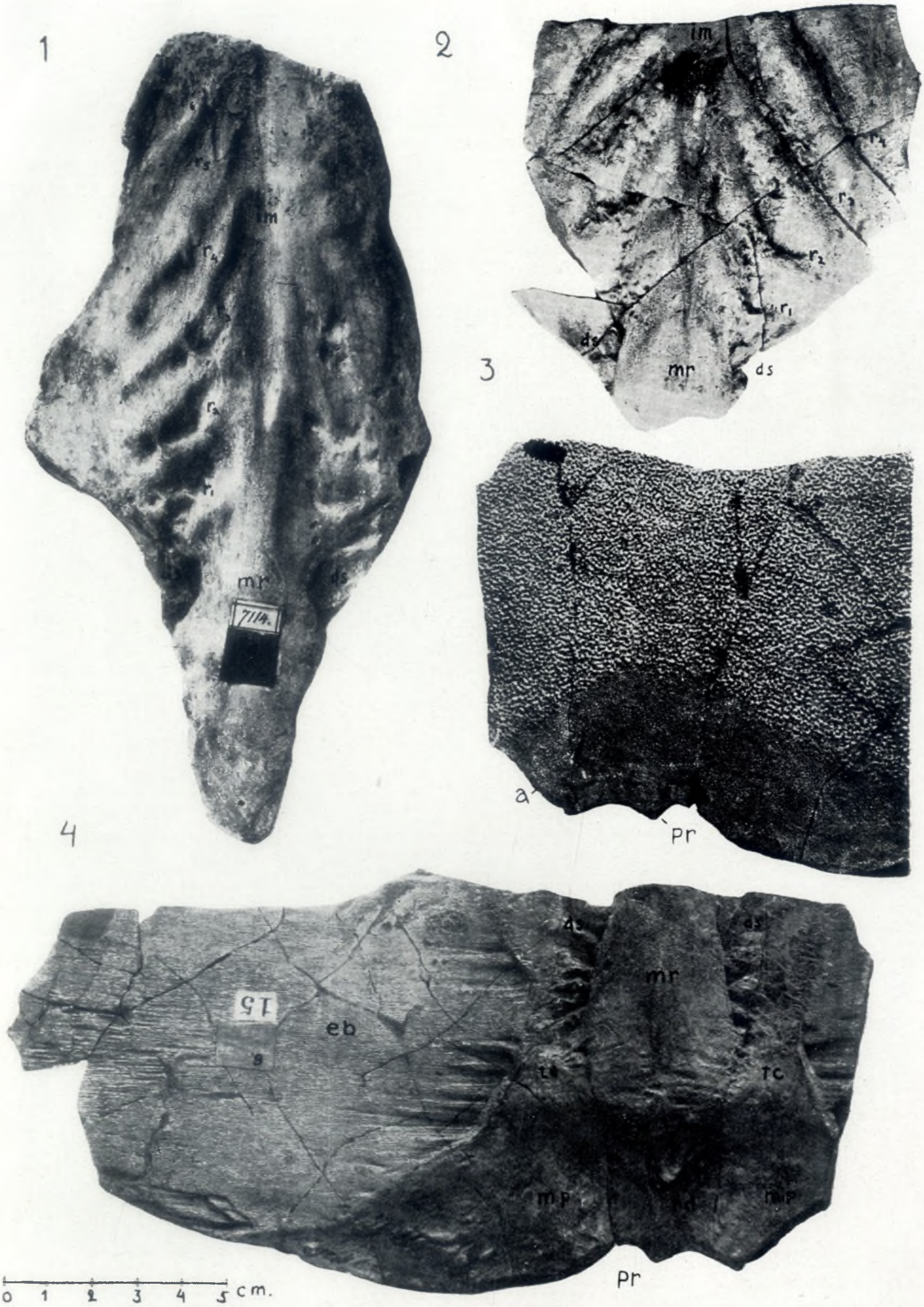
Plate XXII.

Homostius latus Asmuss. The right antero-ventro-lateral plate seen from the outside (2) and from the inside (1). Tartu Mus. No. 125.
   Explanation as in Pl. XXI.

Plate XXIII.

1. *Homostius formosissimus* Asmuss. The fragment of the median-dorsal plate seen from the inside. LECTOTYPE. Tartu Mus. No. 35.
   Explanation as in Pl. XV.
2. *Homostius latus* Asmuss. The hind part of the left antero-lateral plate seen from the inside. Tartu Mus. No. 5.
   Explanation as in Pl. XVIII.
3. *Homostius sp.* from Latvia. Fragment of the right externo-basal plate seen from the outside. Museum Riga.

Contents.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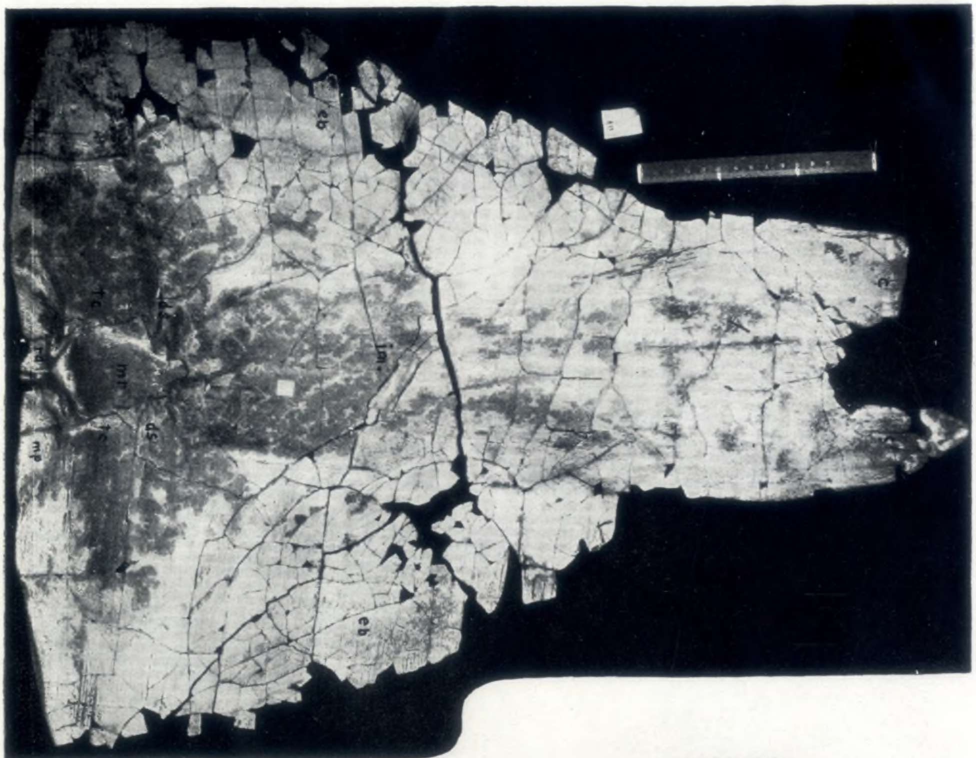

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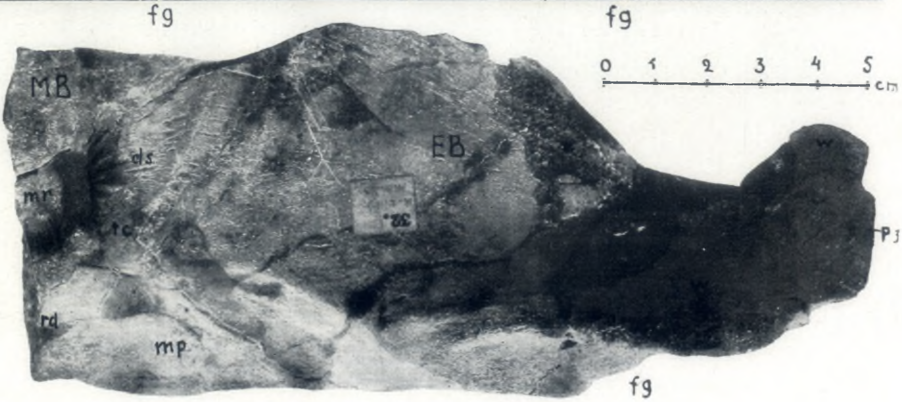


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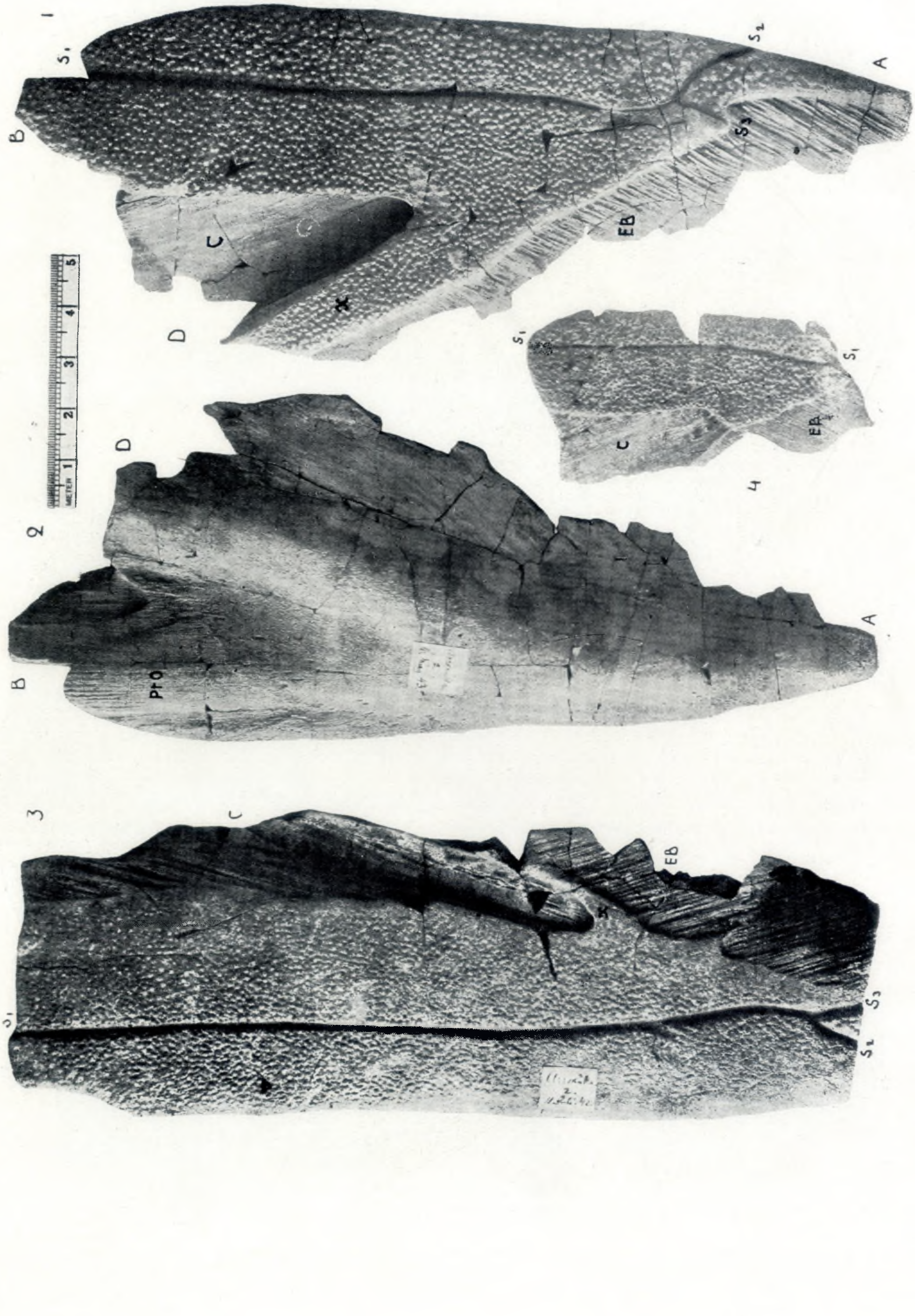

Plate VII.


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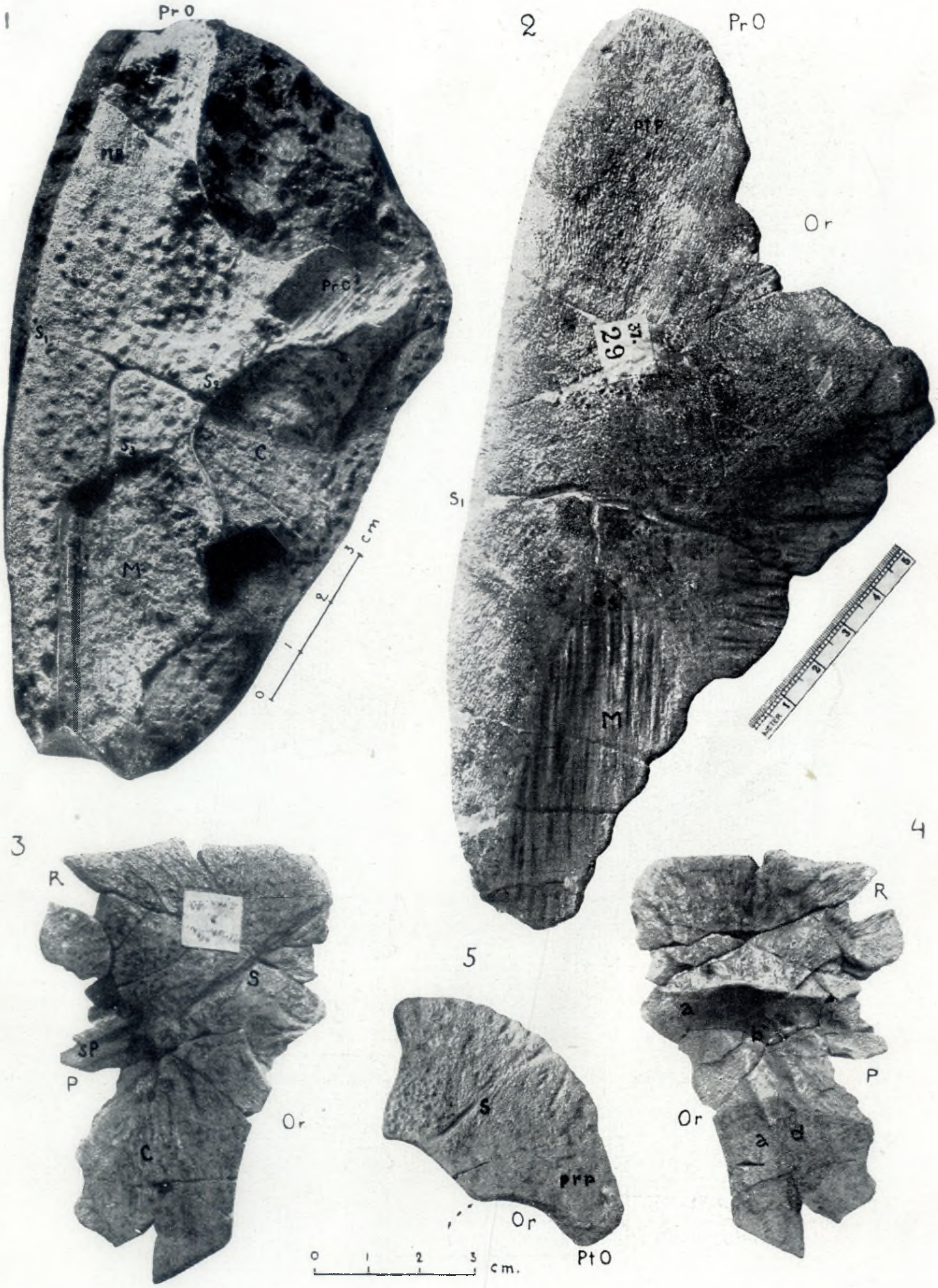
Plate IX.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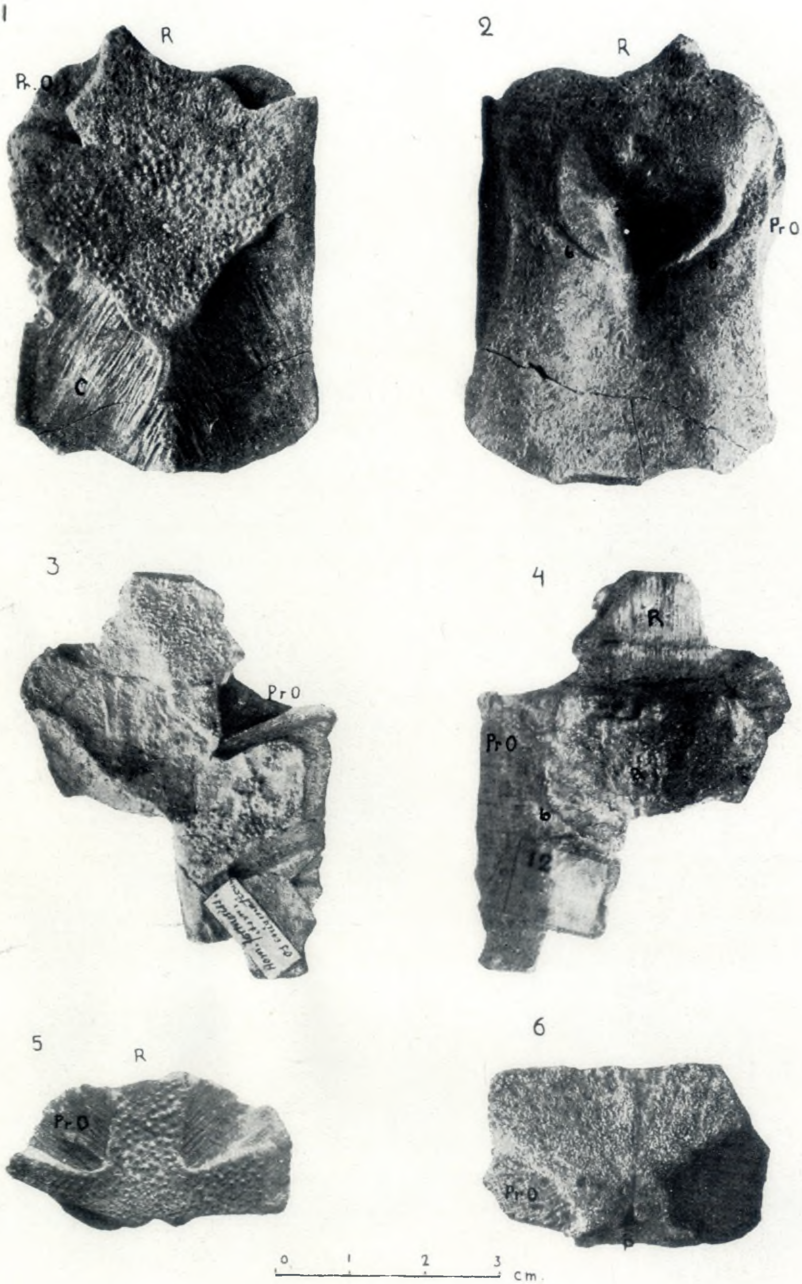
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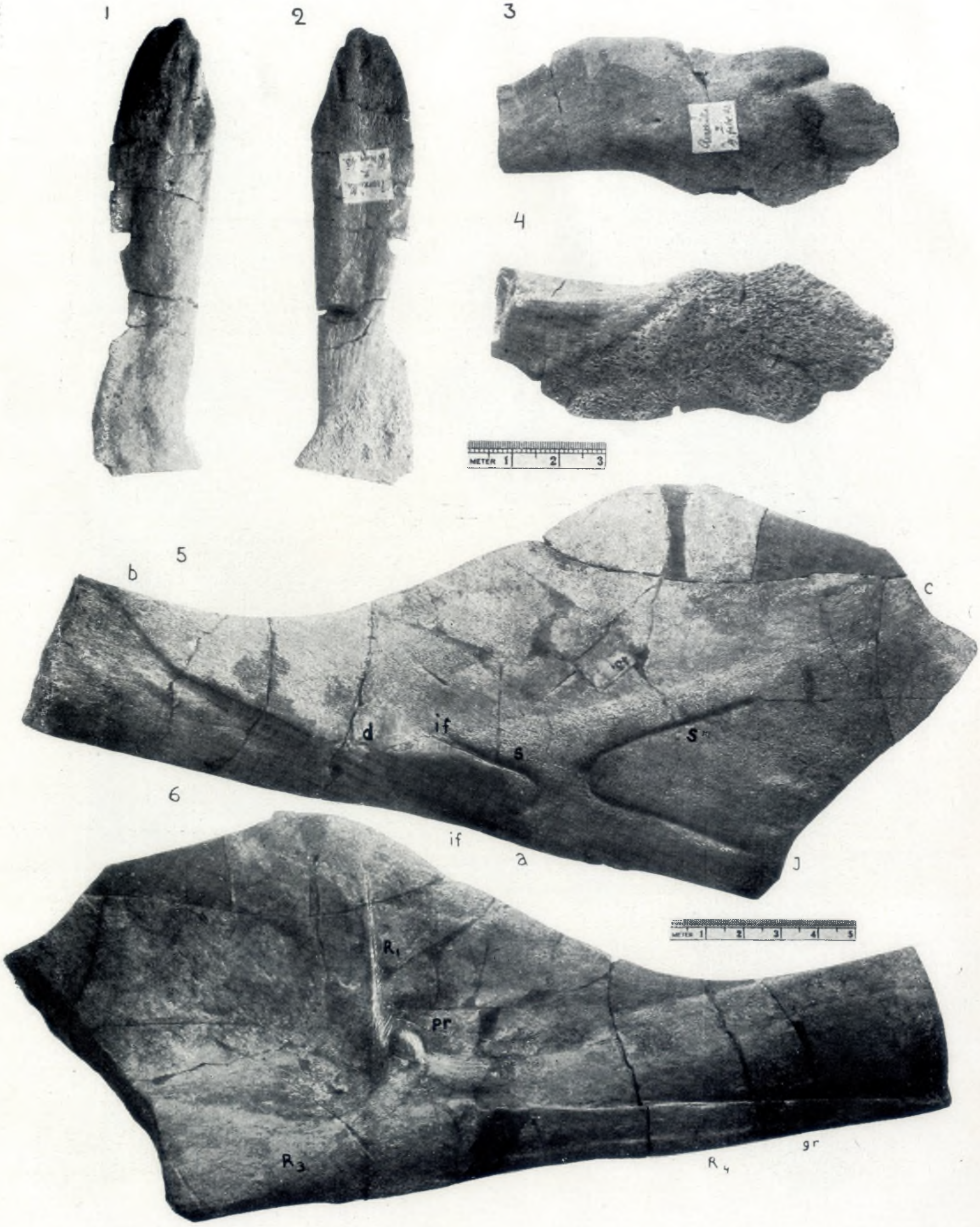
Plate XI.

Plate XII.



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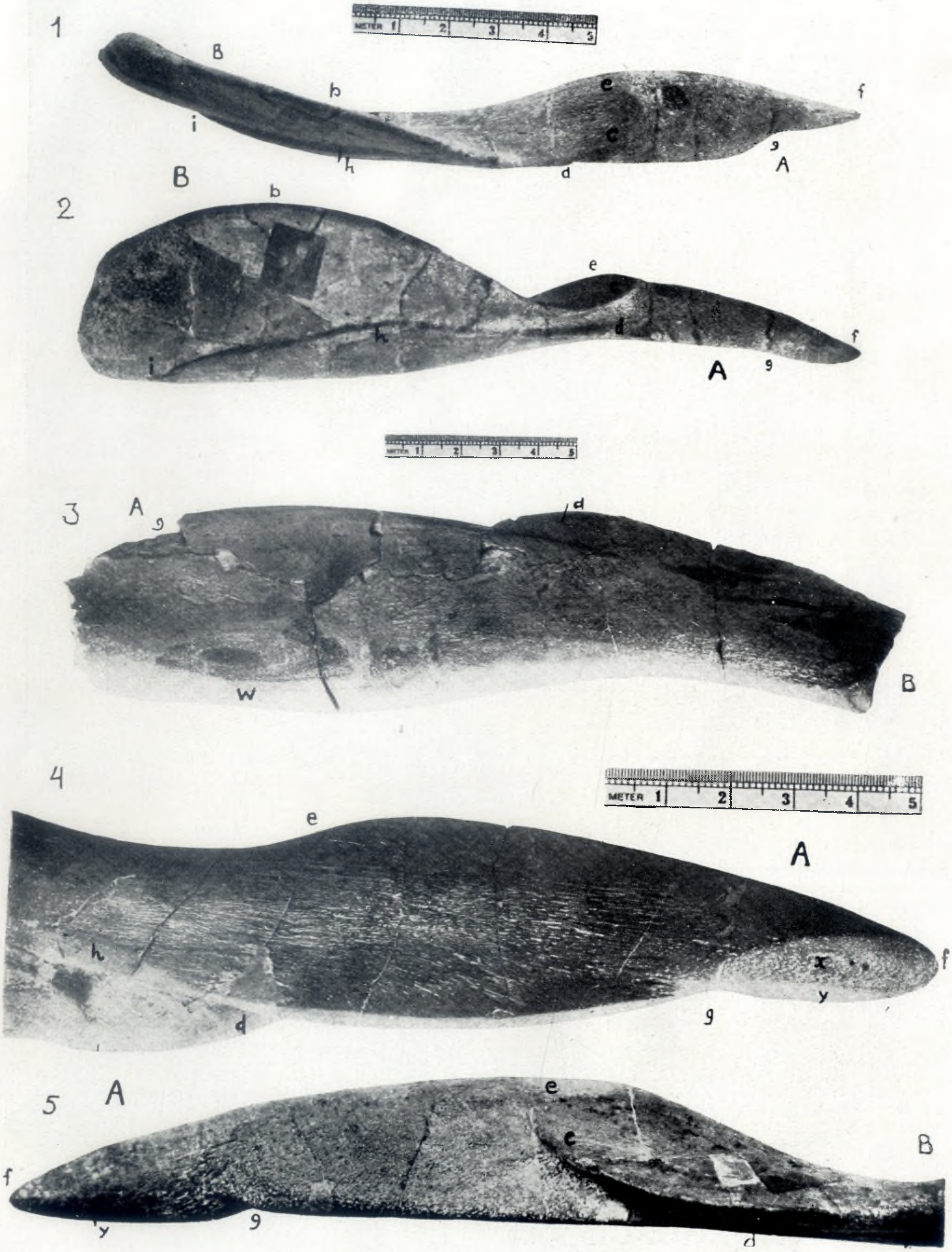
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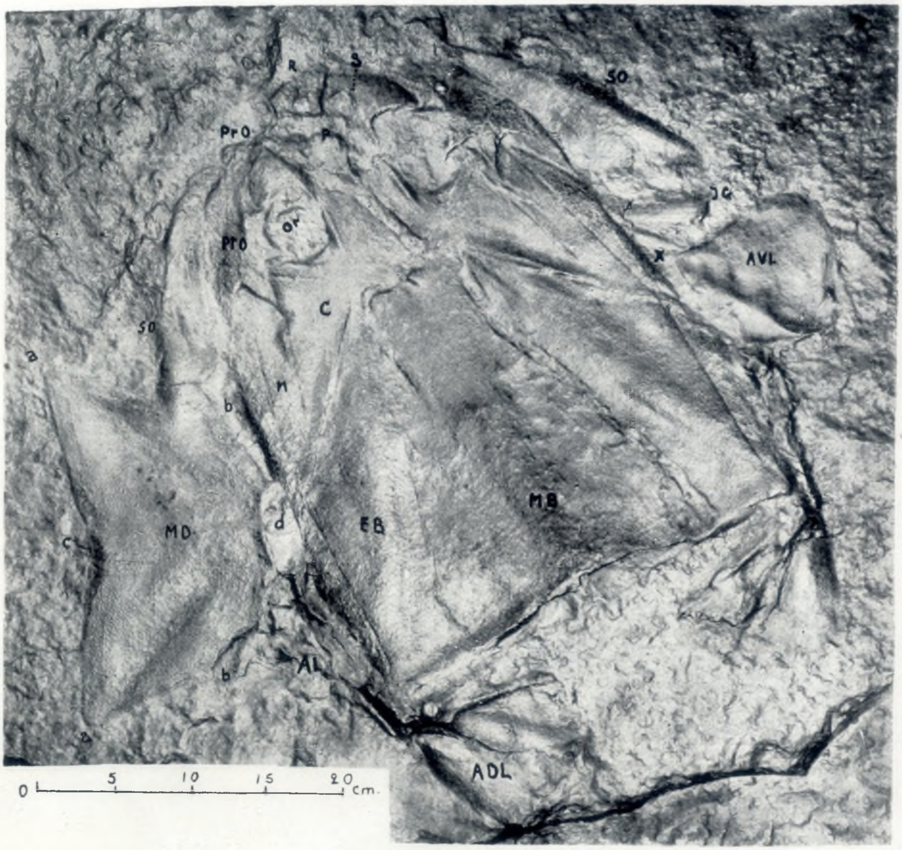
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Plate XV.

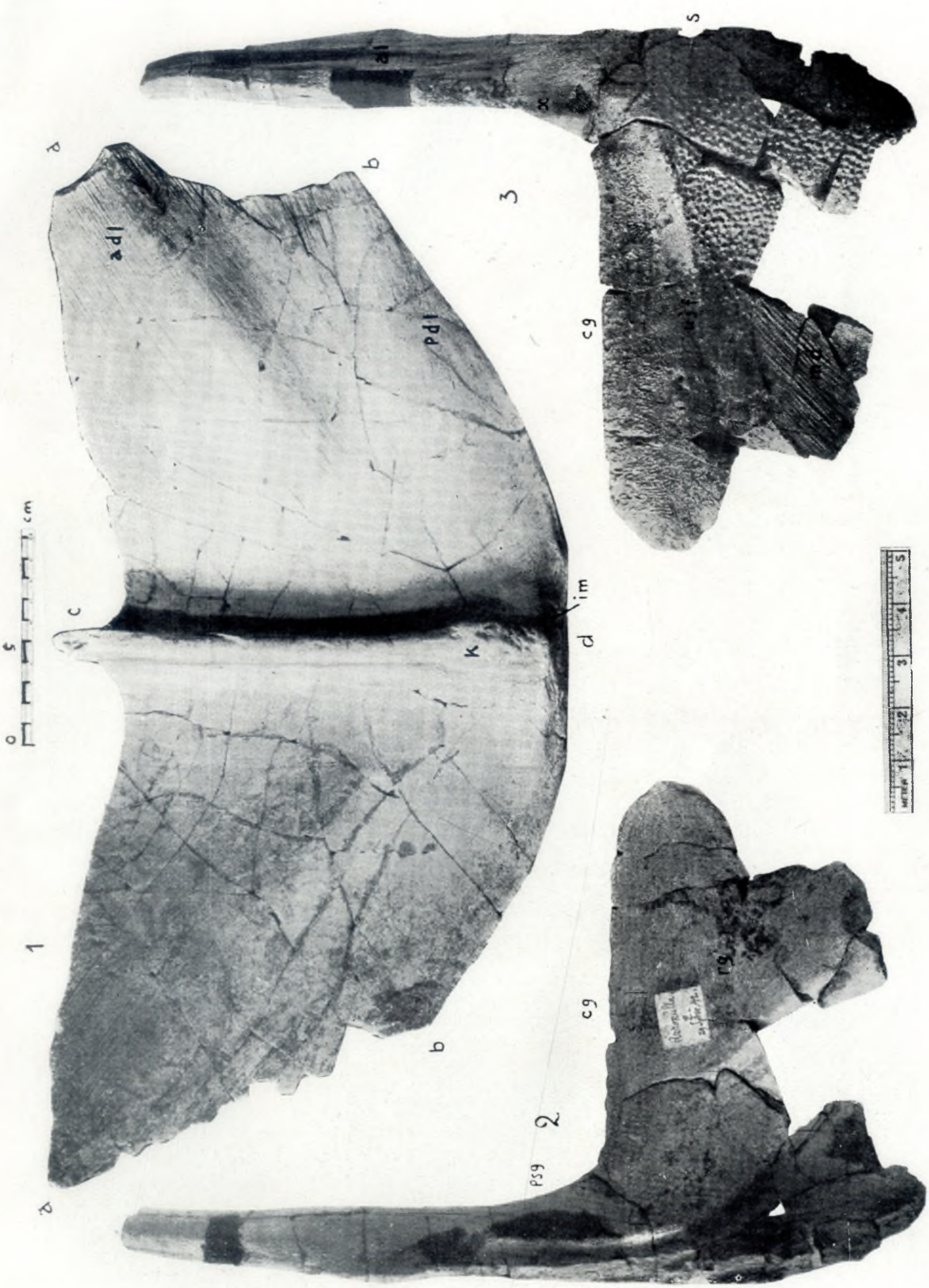
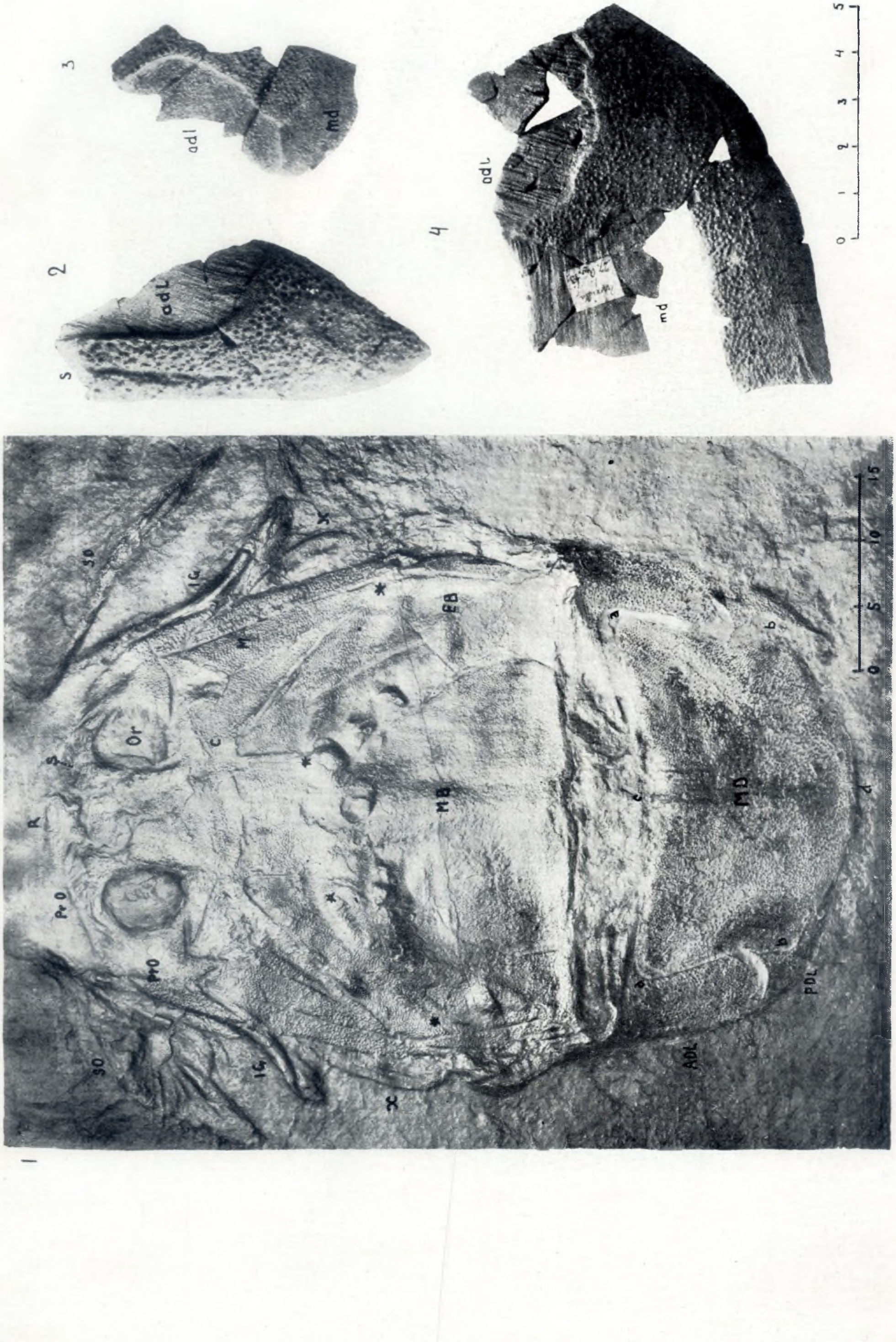


Plate XVII.

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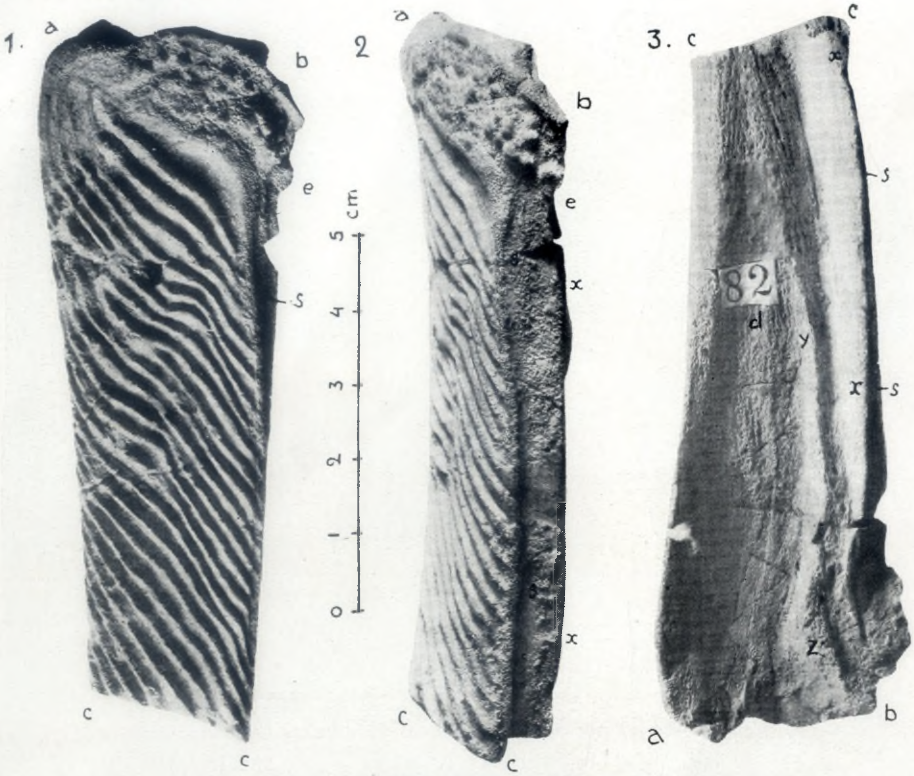
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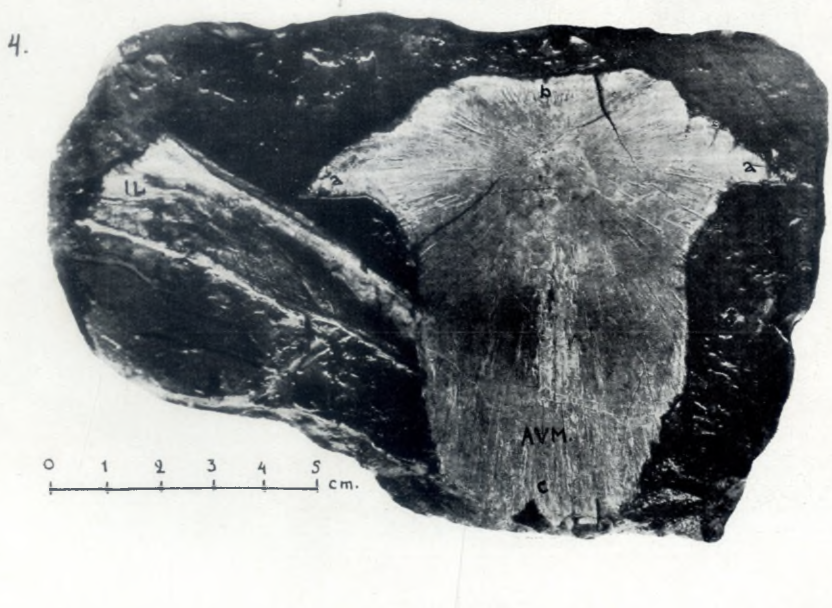
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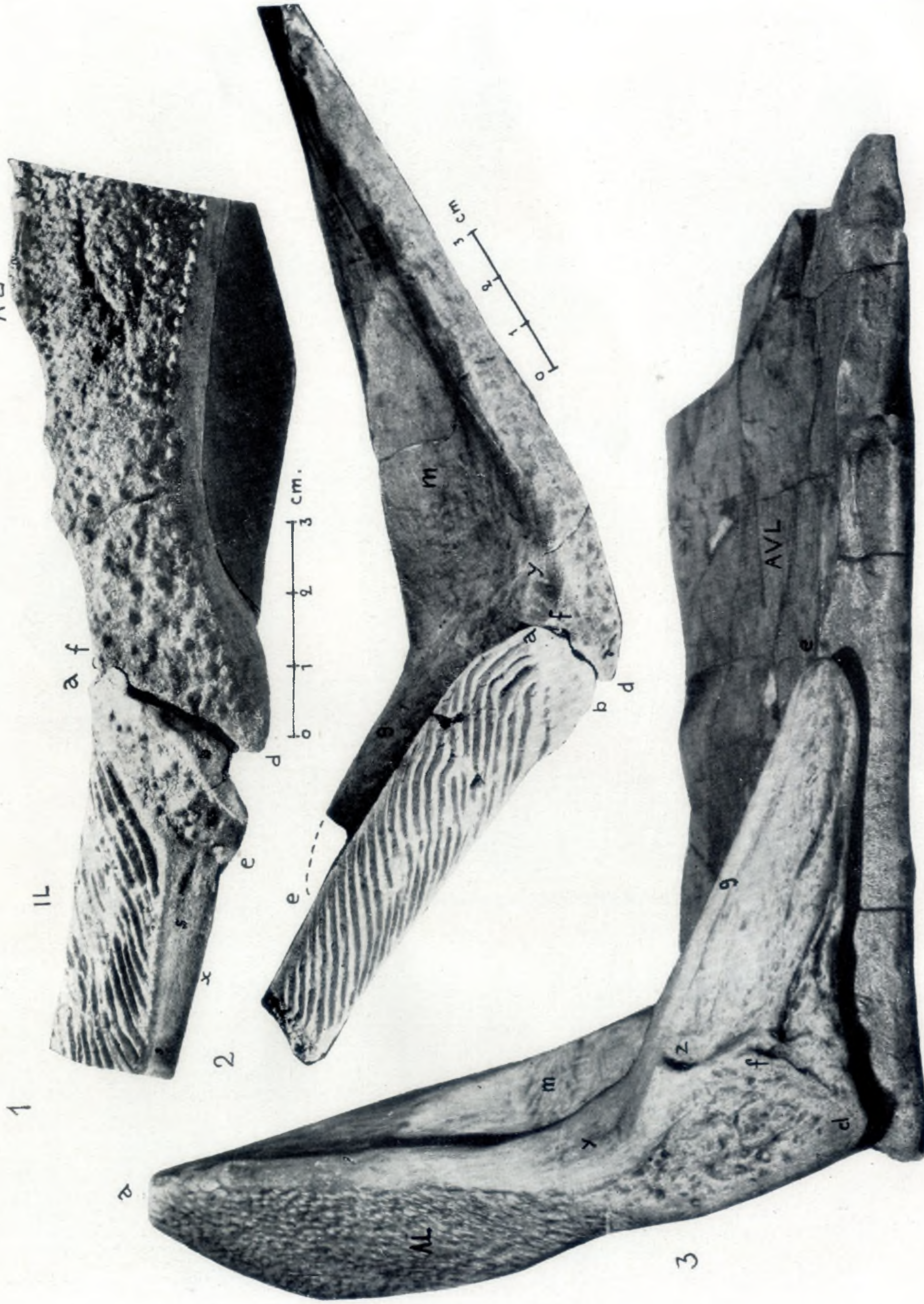
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Plate XXI.

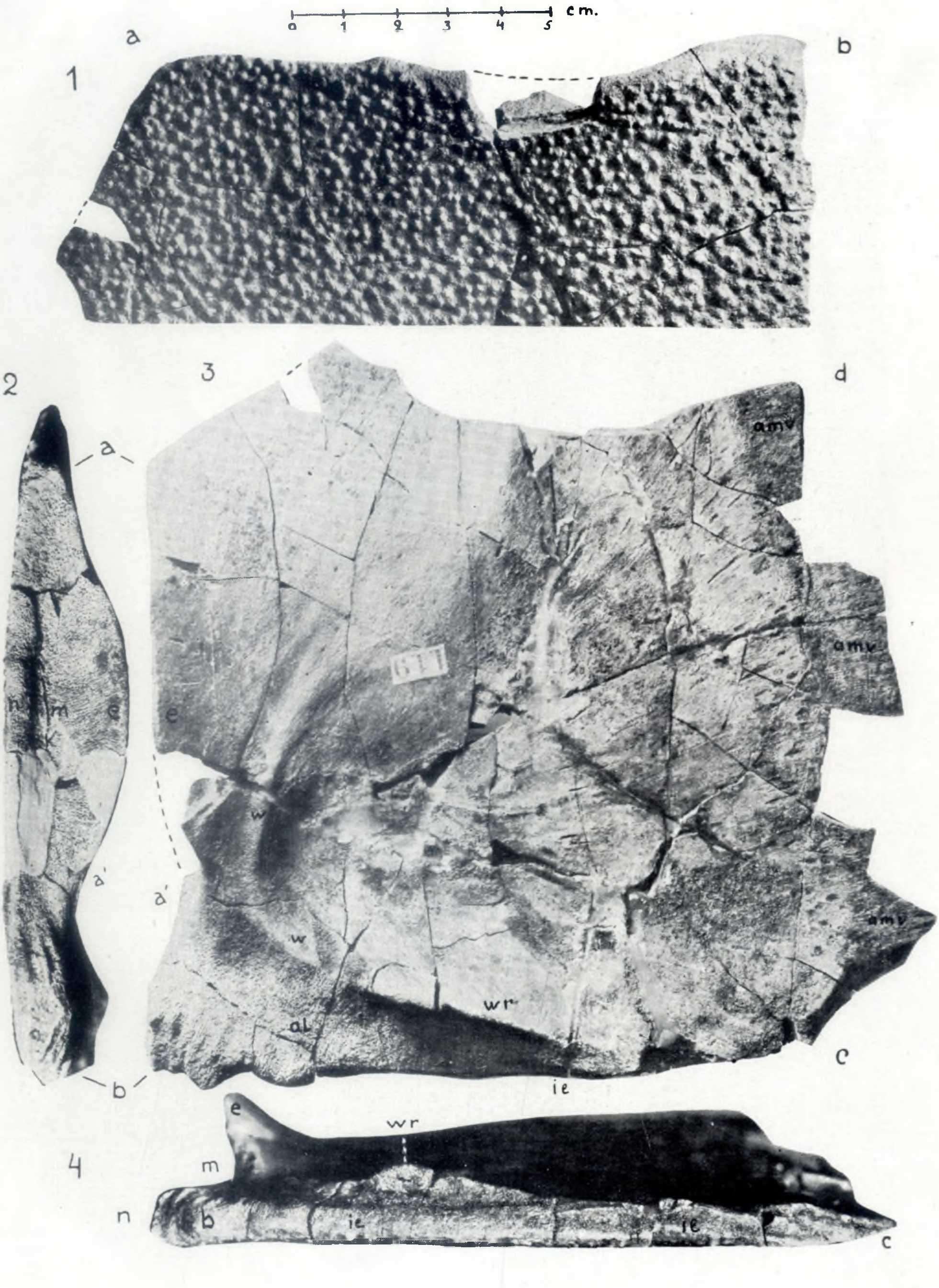
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Plate XXIII.

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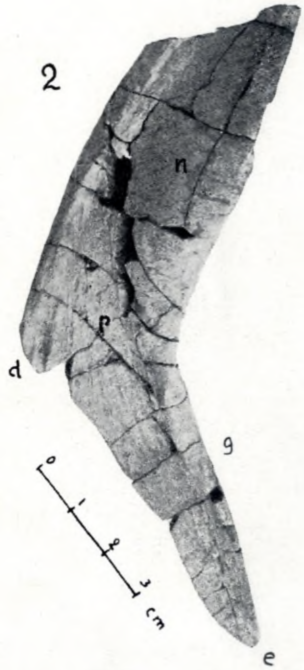

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