8. Notes on a Crossopterygian fish from the upper Devonian of Spitzbergen.

By

Erik A:son Stensiö.

(With Plates IV—VI.)

Introduction.

In my paper entitled »Zur Kenntnis des Devons und des Kulms an der Klaas Billenbay, Spitzbergen» *(10)* I showed that fish remains are very common in the Devonian of Spitzbergen, especially in certain strata of its upper part in Mimer Valley. In this respect the black schists with ironstone-nodules, found already in 1882 by NATHORST *(7)* at a locality called by him »the fish cleft» (*7*, p. 315) are noticeable. All the upper-devonian fish remains described by LANKESTER *(5)* and WOODWARD *(18)* are probably obtained from this locality. During the summers of 1916 and 1917 I have myself for short periods had opportunities of working in Mimer Valley, and thus a large amount of material has been collected, partly from other localities as well. The fish cleft, however, has always been the most fruitful.

The following is a list of the fossil fishes hitherto found in the fish cleft: *Acondylacanthus?* sp., *Psammosteus arenatus* AGASSIZ, *Asterolepis scabra* (A. S. WOODWARD), *Asterolepis* sp., remains of *Coccesteidean* jaws not nearer determinable, teeth of *Dendrodus*-type and scales of *Rhizodontids*. Especially interesting, however, is a large cranium of a Crossopterygian, *Dictyonosteus,* the osteology of which shows several points of resemblance with the Coelacanthids, as already mentioned in my paper quoted above. This cranium is the subject of the following description.

Description.

Dictyonosteus arcticus n. g. n. sp.

(Plates IV, V, VI.)

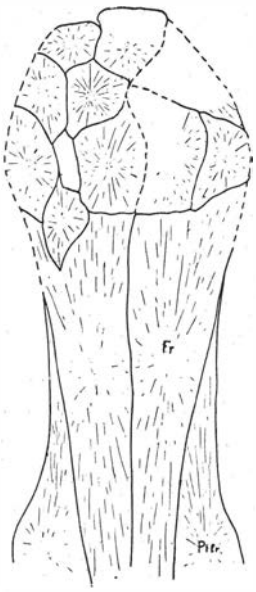
Remains of large Crossopterygian fishes, belonging to the *Rhipidistia* and among them most closely related to the Rhizodonts are commonly found in the upper Devonian of Mimer Valley. Most of them may perhaps belong to *Dictyonosteus arcticus* or some closely related species. Their state of preservation is, however, not sufficiently good, or most of the remains are too fragmentary to establish with certainty anything of this sort. I shall accordingly confine myself to the cranium mentioned.

In this connection, however, it is worth while pointing out that hitherto only teeth of the *Dendrodus*-type have been found in conjunction with the numerous remains of Rhizodontids. In a large nodule containing two large poorly preserved Rhizodontid fishes, coming from a level somewhat below that of the fish cleft in question, there are also found large *Dendrodus* teeth, occurring together with the fish remains mentioned in such a way that one feels inclined to refer all the remains to one and the same species. The scales of these two specimens strongly resemble a type often found in the schist of the fish cleft and they exhibit a sculpture indicating to a certain degree *Dictyonosteus,* as will be described below. Thus we may put forward the possibility, although as yet there is no decisive evidence forthcoming, that all the fish remains under discussion may belong to *Dictyonosteus,* and that this consequently may perhaps be identical with *Dendrodus*.

The above mentioned cranium, the only representative of the typical specimen of *Dictyonosteus arcticus,* has unfortunately the whole regio occipitalis and auditiva missing. Only the orbitotemporal and ethmoidal regions have been preserved. The visceral skeleton and dermal cheek plates are likewise entirely absent. But merely from these remains it is clear that *Dictyonosteus arcticus* attained a pretty considerable size. The broken part present measures about 18 cm. in length. It lies embedded in hard ironstone and the state of preservation is comparatively good, only it is somewhat compressed from the sides, so that it appears somewhat narrower than it was in its natural state. The bone substance being black and the nodule of a rusty red colour caused considerable difficulties in photographing as orthochromatic plates could not be obtained under present conditions. The pictures given below therefore show, as a matter of fact, few of the finer details of the original.

Of the superficial bones on the cranial roof, there are preserved posteriorly two extended, comparatively narrow bones, which, to judge from their situation, can scarcely be anything else but frontals (Text fig. 1, *Fr*, Pl. IV, Fig. 1). The are separated medially by a straight

longitudinal suture. The centre of ossification is nearest to the front end and from the centre radiate the fairly distinct ossification stripes. As shown by a section (Fig. 3, Pl. V *Sc*) the sensory canal passes the lateral edges of the frontals as a groove, a phenomenon, which according to WOODWARD (*17* p. 321) is only found in the family *Holopthychidae* among *Rhipidistia,* while in *Rhizodontidæ* and *Osteolepidæ* the sensory canal forms a closed canal in the interior of the bones, communicating with the outside only by small pores. The great length of the frontals, however, has, on the other hand, no correspondence in the *Holopthychidæ* as far as is known (WATSON and DAY *15*). On the contrary *Gyropthychius* among the Rhizodontids and the *Osteolepidæ* more resemble *Dictyonosteus* and this seems also to be the case with the Coelacanthid fishes *(16)*. The centre of ossification is, at least in the latter, very near the posterior end of the bones. Caudally along the lateral side of the left frontal there is in the *Dictyonosteus* specimen under question an ossification, growing narrow towards the front, which seems to correspond most closely to a postfrontal (Text fig. 1 *Pfr,* Pl. IV, Fig. 1). The ethmoidal region is covered by a large number of rather small irregular bony plates (Text fig. 1; Pl. IV, Fig. 1), which on the left side are well preserved and easy to distinguish one from another. The right side is more crushed and compressed, and the limits of the medial ossifications thus cannot be fully ascertained. Taking all the evidence into consideration, however, it cannot be denied that there is a certain indication of bilateral symmetrical arrangement, though the bones on the right and those on the left side do not quite correspond to each other.



Text fig. 1. *Dictyonosteus arcticus.* Front part of the cranial roof. *Fr,* Frontals, *Ptfr,* Postfrontals.

In most other fossil forms of Crossopterygians little is known about the superficial dermal plates of the snout. According to the opinions of several earlier authors, fusion of elements may have taken place there to a very considerable extent. *Osteolepis,* however, shows clearly that at least in some of them the dermal plates were separate and bilaterally symmetrical (WATSON and DAY *15*, p. 20). I have found a fairly similar arrangement in Coelacanthids. *Gyropthychius* also has its snout covered with such polygonal plates (WOODWARD *17*, p. 358—359), but their arrangement cannot be clearly made out.

The sculpture on the dermal cranial roof bones consists in *Dictyonosteus arcticus* of a thin layer of ganoin-like, shining substance, arranged so as to form extremely fine tubercles and ridges, which, separated

by small hollows and pores, anastomose with each other to form a fine network, somewhat resembling *Sauripterus* (AGASSIZ *1*). A fact more worthy of attention is, however, that even in the interior of the bone substance of certain bones there often occurs a net-shaped arrangement of canals, showing a clear connection with the groove of the sensory canal, inasmuch as they radiate from the latter. As these conditions were difficult to reproduce in the *Dictyonosteus* cranium I have instead in Fig. 2, Pl. IV given the photograph of a loose bone showing essentially the same things in a particularly successful way. — The ramifications often anastomose with each other, and it is the peculiar net-shaped figure thus formed when the bones are weathered or split that has given rise to the generic name *Dictyonosteus*. — In connection with this it may be pointed out that the *Strepsodus*-like scales described from Mimer Valley show, when developed with grooves, that these are of the same nature as the ones just described, and it seems certain that such scales belong to the lateral line.

The brain case in *Dictyonosteus* appears, as far as it is preserved, strong and well ossified. By earlier authors it has already been shown that several ossifications are developed in fossil Crossopterygians. Thus YOUNG (*20,* p. 605) describes the brain case of *Megalichthys* in the following way: »The well-ossified basilar region includes a massive basioccipital which projects behind the vertical wall of the cranium, and sometimes has its length increased by the coalescence with it of at least the first vertebrate ring, whose neural processes remained distinct. The anterior part of the cranial is sometimes deficient, the sphenoidal (and prootic?) portion becoming detached. In a lateral view the ascending alisphenoidal plates and incomplete interorbital osseous septum are well seen.» In the same Genus COPE has also observed ossifications in the brain case and he gives the following brief account of his observations (*2,* p. 628): »The base of the skull consists of ossified parachordals, which embrace the chorda dorsalis posteriorly and are continued for a short distance posteriorly as a tube. Anteriorly the chordal groove is open. Trabeculæ not ossified. The cranial structure is an excellent illustration of a permanent embryonic type. Above and in front of the opening for the chorda the neural canal enters the groove. The parachordals are subtriangular, presenting one angle forward, and having the internal side that bounds the groove straight and longitudinally grooved. The anteroexternal side is oblique and nearly straight and is overhung by the osseous roof of the skull . . .» COPE has unfortunately confined himself to this brief description. No figure is given and consequently it is impossible to get a really clear idea of the character of the skeletal parts in question.

WATSON (*14,* p. 9) has briefly mentioned the occurrence of a basisphenoid in *Megalichthys*.

With ROHON's description of a snout belonging to *Cricodus* this is all we know so far concerning the brain case of the fossil Crossopterygian

fishes. But as ROHON *(9)* interpreted this fragment as an entire cranium his description was consequently incorrect, a fact which TRAQUAIR *(11)* has also incisively pointed out.

A braincase ossified to a certain extent seems also to have existed in primitive *Dipnoi* (WATSON and DAY *15,* p. 33) and TRAQUAIR *(13)* also mentions replacing bones in the primordial cranium of the Palaeoniscids, a phenomenon that I have had myself an opportunity of observing in certain forms of Catopterids and other lower *Chondrostei* from the triassic of Spitzbergen. Curiously enough, the brain case of a great number of primitive forms among Teleostomous fishes seems thus to be ossified to an unexpectedly great extent.

To return now to *Dictyonosteus* we find most posteriorly on the preserved part of the side wall of the brain case a powerful ossification stretching from the basis cranii almost to the ventral side of the frontals (Pl. IV, Fig. 3; Pl. V, Fig. 1; Pl. VI). At its basal part this portion of bone has laterally on each side a powerful process forming a clear posterior boundary to the orbital region (*Bp,* Fig. 3, Pl. IV; Fig. 1, Pl. V and Pl. VI). The ossifications in question of the two sides are connected with each other in the base of the skull by means of a thick portion of bone without any traces of sutures. Seen from the back the whole thing appears as in Fig. 1, Pl. IV. The basal parts of the bone seen here surround an oval foramen, which is apparently completed at the top by a narrow bridge of bone (*b,* Fig. 3; Pl. IV; Pl. VI). Even in this no indications of sutures are visible. From this the ossifications in question extend (Pl. VI) further dorsally and somewhat forward up to the frontals as already mentioned. There is no doubt that we have here an unpaired ossification, which may probably be characterized as a basisphenoid.

It is quite clear that this ossification, characterized as basisphenoid, passes in front without suture into a paired orbitosphenoid as in *Polypterus* (*12, 6,* Pl. VI; Pl. V, Fig. 2, 3). The two orbitosphenoids, bounded by the frontals above, by the parasphenoid below, extend forward to the evidently ossified prefrontals in the ethmoidal region (*Pfr,* Pl. VI; Fig. 1, Pl. V). A cross section through the posterior part of the orbital region (along the posterior of the two cross cracks seen in Pl. VI) is shown in Fig. 3, Pl. V. As this crack has, however, arisen obliquely from in front, sloping downwards and backwards, a part of the basisphenoid is seen in the figure forming the basal parts. Another cross section taken further forward (along the anterior of the two cross cracks Pl. VI) appears somewhat different (Pl. V, Fig. 2). Ventrally above the parasphenoid *(psph)* the two orbitosphenoidal lamellae have approached very near to each other, and in certain places they have even coalesced. Dorsally, on the other hand, the lamellae turn sharply aside at *a* and then continue wide apart dorsally towards the frontals. This peculiarity is due to the exit of the optic nerve. The crack, as Pl. VI shows, has traversed the foramen opticum *(fopt).* This accordingly lies far forward. Consequently,

in *Dictyonosteus,* as in other fossil Crossopterygians, the eye is situated far forward towards the snout. Four other foramina are to be recognised on the orbitosphenoidal ossifications. One is situated dorsally to the foramen opticum *(ftr)* and has probably transmitted the nervus trochlearis; another *(fo_1)* lies a little caudally, similarly in relation to the opticus foramen. Of the two remaining ones, the posterior has a rather high position just on the limit between the orbitosphenoid lamella and the more robust upper part of the basisphenoid *(fo);* probably it may have given exit to the nervus ophthalmicus. The anterior one is situated in front between the prefrontal and the anterior end of the orbitosphenoid and seems to have afforded a passage for vessels and nerves to the olfactory region *(fa).*

The prefrontals in their turn seems to be slightly ossified *(pfr).* Their interior consists of a thin spongy mass (Pl. VI). A canal passing *(olf)* away downward and somewhat laterally seems to indicate nostrils placed ventrally or near the edge of the mouth. Or else we possibly have, as WATSON's and DAY's *(15)* description of *Glyptopomus* indicates, an outer and an inner nostril, in which case the opening on the lower side of the snout indicated here by X in Pl. V, Fig. 1 would correspond to the inner one in *Glyptopomus.* What X_1 in the same figure refers to I cannot say for certain.

From the description above it is clear that *Dictyonosteus* represents a type of fish, which as regards certain replacing bones of the brain case greatly resembles *Polypterus* on the one hand and higher vertebrates on the other. The basisphenoid of *Dictyonosteus,* at least in its basal part, seems to correspond to the basisphenoid of the terrestrial vertebrates. Taking everything into consideration, I am of the opinion that the pituitary fossa must probably be located just at the cavity which is surrounded by the preserved part of the basisphenoid, ventrally of the above described apparent bridge *b.* This *(b)* is also situated, as shown by Fig. 1, Pl. V and Pl. VI, in a plane considerably behind the preserved base of the basisphenoid. In the Coelacanthid fishes, which I had an opportunity of carefully investigating in an extraordinary fine material from the triassic of Spitzbergen, I also found in the corresponding region of the skull an unpaired ossification, interpreted by HUXLEY *(4)* and REIS *(8)* as the prooticum. The conditions in Coelacanthids agree in general respects with *Dictyonosteus,* although in them there is no ossified orbitosphenoid. The unparied ossification must there too be characterized as a basisphenoid and this has on its front side a form difficult to understand, except in relation to the pituitory body. It is therefore probable that in *Dictyonosteus* as in Coelacanthids the real body of the basisphenoid was situated behind the pituitory fossa and then the bridge of bone *b* ought only to be remains of the upper part of the basisphenoidal body. In the Coelacantids the posterior part of the brain must have been situated dorsally to this body. It is thus probable that its corresponding part in *Dictyonosteus* has also been situated dorsally to *b.*

The ventral side of the preserved part of the brain case is covered, as shown in Fig. 1, Pl. V, by a powerful broad parasphenoid *(psph)*. Its most posterior part is not preserved, and it is therefore impossible to ascertain how far it has extended caudally. Anteriorly it is also incomplete, but seems to have reached far forward beneath the ethmoidal region. Its narrowest part lies almost exactly under the exits for the optic nerves and here too is situated its centre of ossification. In shape it resembles strikingly that of certain Coelacanthids, for instance the one reproduced in Text fig. 2 from a new Spitzbergen genus *Leioderma*. The agreement was so great that, when I first came across the *Dictyonosteus* skull under discussion and only the parasphenoid was to be observed, I was convinced that it must have belonged to a Coelacanthid fish, especially as representatives of this group have been found in the Devonian of both Europe and America *(3, 19)*.

Text fig. 2. *Leioderma sinuata* n. sp. from the Triassic of Spitzbergen. Parasphenoid from the ventral side.

Especially in mesozoic forms of Coelacanthids, as for instance *Undina* and *Macropoma*, the parasphenoid is considerably narrowed between the orbits. The edges directed dorsally and often of considerable size in Coelacanthids, which by several of the earlier investigators have often been interpreted as praefrontals or orbitosphenoids, do not appear in *Dictyonosteus*.[1]

Summary.

As seen from the short description above, *Dictyonosteus* shows in regard to the osteology of the skull several new points of interest. The brain case was, at least in its anterior part, well ossified. A powerful unpaired ossification is to be distinguished in the temporal region, extending from the base of the skull upwards to the frontals. This ossification may probably be homologized with a basisphenoid. From the basisphenoid posteriorly, and completely coalesced with it, a paired orbitosphenoid extends anteriorly right to the ethmoidal region, in the cartilage of which ossifications homologous with prefrontals could be recognised. A large broad parasphenoid covers the ventral side of the preserved part, and on the dorsal side are seen two extended frontals, while the ethmoidal region is covered by a rather large number of small polygonal ossifications, probably not quite symetrically developed on both sides.

[1] The broad parasphenoid of *Sauripteus* seems also to bear great resemblance to that of *Dictyonosteus*, and thus a similar form appears to be peculiar to several fossil Crossopterygians (EASTMAN, C. R., Fossil Fishes in the Collection of the U. S. Nat. Mus. Proc. U. S. Nat. Mus. Vol. 52, 1917, p. 254, Pl. 7, Fig. 5).

In many respects *Dictyonosteus* offers resemblances to the Coelacanthids. An essential difference, however, is that there are no orbitosphenoidal ossifications in the latter. In other respects the details also clearly show that *Dictyonosteus* cannot be refered to them. It must belong to the *Rhipidistia,* and among them it may probably be most closely related to the family *Rhizodontidæ.*

Specially interesting is also the correspondence with *Polypterus* in regard to the ossifications in the orbitosphenoid region, but *Polypterus* differs in the skeleton of the unpaired fins so essentialy from the known type of the fossil Crossopterygians, that it is difficult, in spite of the analogies now pointed out, to place it in any closer relation to the extinct forms.

In my description of the triassic Coelacanthids from Spitzbergen I shall return to the question of the basisphenoid bone of the early Crossopterygian fishes and to its agreement and possible homology with the ossifications in the corresponding region of the terrestrial vertrebrates.

Bibliography.

1. AGASSIZ, L., Poissons fossiles du vieux grès rouge ou système dévonien. Neuchâtel 1844—45. Pl. 28, fig. 13.
2. COPE, E. D., Fourth contrib. to the history of the Permian formation of Texas. *Ectosteorachis ciceronicus* COPE, Amer. Phil. Soc. Philadelphia 1883.
3. EASTMAN, C. R., Devonian fishes of Iowa. Iowa Geol. Surv. Ann. Rep. 1907. Des Moines 1908, p. 246.
4. HUXLEY, TH. H., Illustrations of the structure of the *Coelacanthini.* Mem. Geol. Surv. of Unit. Kingdome. Figs and Descript. of Brit. org. Rem. Decade XII, London 1866.
5. LANKESTER, E. R., Report on the fragments of fossil fishes from the Palaeozoic strata of Spitzbergen. Vet. Akad. Handl. Stockholm, Bd. 20. N:o 9. 1884.
6. LEHN, CHARLOTTE, Beitrag zur Kenntnis des Primordialschädels von *Polypterus.* Zeitschrift f. angewandte Anatomie u. Konstitutionslehre. Bd. 2. Heft 4—6. Berlin 1918.
7. NATHORST, A. G., Beiträge zur Geologie der Bären Insel, Spitzbergens etc. Bull. Geol. Inst. Upsala. Vol. X. 1910—1911.
8. REIS, O. M., Die Coelacanthinen etc. Palaeontographica Bd. 35. 1888.
9. ROHON, J. O., Die Dendrodonten des devonischen Systems in Russland. Mem. Acad. Imp. de Sci. St. Petersbourg. T. 36. N:o 14. 1889.
10. STENSIÖ, ERIK A:SON, Zur Kenntnis des Devons etc. an der Klaas Billenbay, Spitzbergen. Bull. Geol. Inst. Upsala. Vol. XVI.
11. TRAQUAIR, R. H., On the systematic position of the »Dendrodont» fishes. Geol. Mag. Dec. III. Vol. VI. 1889.
12. ——, On the cranial Osteology of *Polypterus.* Journal of Anat. and Phys. Vol. 5. 1871.

13. TRAQUAIR, R. H., The ganoid Fishes of the Brit. Carboniferous Form. Palæoniscidæ. Palæontogr. Soc., vol. 31, 1877, p. 15.
14. WATSON, D. N. S., The larger Coal Measure Amphibia. Manchester Lit. and Phil. Soc. Mem. and Proc. Vol. 57. Part I, 1913, p. 9.
15. WATSON, D. N. S., and DAY, N., Notes on some palæozoic fishes. Manchester Lit. and Phil. Soc. Mem. and Proc. Vol. 60. Part I, 1916.
16. WELLBURN, E. D., On the Genus *Coelacanthus* as found in the Yorkshire Coal Measures. Yorkshire Geol. Polyt. Soc. Proc. Leeds 1900—1902, p. 474. Fig. p. 482.
17. WOODWARD, A. S., Catalogue of fossil fishes in the Brit. Mus. Part II.
18. ——, The Devonian fish-fauna of Spitzbergen, Annals and Magazine of Nat. Hist. Ser. 6, vol. 8. 1891.
19. ——, Note on a Devonian Coelacanthid fish. Geol. Mag. Dec. 4, vol. 5, p. 529, 1898.
20. YOUNG, J., New genera of carboniferous Glyptodipterines. Quart. Journ. Geol. Soc., vol. 22, 1866, p. 605.

Explanation of Plates.

The originals belong to the Geological Institution at Upsala. The photographs are taken by E. FINN, photographer, Upsala. The drawings were done by Miss AINA LAURELL, Upsala.

All the figures are reproduced in natural size.

Plate IV.

Fig. 1. *Dictyonosteus arcticus.* The cranial roof seen from the dorsal side. The limits of the bones shown in white. *Fr,* frontal; *Ptfr,* postfrontal.

Fig. 2. Ossification of a Crossopterygian, possibly *Dictyonosteus,* showing the sensory canal and radiating from it the net-shaped anastomosing canals in the bone substance, as seen from the medial side. Along the right edge a part of the bone substance has disappeared, and this shows clearly that the sensory canal with its ramifications was situated here within the bone substance.

Fig. 3. *Dictyonosteus arcticus.* Part of the basisphenoid seen from the back. The basisphenoid has had a greater extension backwards but nothing of it has been preserved on the cranium reproduced here. *Bp.* lateral side process at the base of the basisphenoidal bone; *b.* bridge of bone between the two lateral side-parts marking the upper and back boundary of the fossa hypophyseos.

Plate V.

Fig. 1. *Dictyonosteus arcticus.* Typical example seen from the ventral side. The parasphenoid *(Psph)* preserved for the greater part only as an impression. At the back is seen the powerful basisphenoid, especially its basal part. *Bp.* basal process on the basisphenoid; *b.* bridge of bone above and behind the fossa hypophyseos. *Pfr.* prefrontals; x and x_1 foramina, the first of which may possibly be an interior nostril.

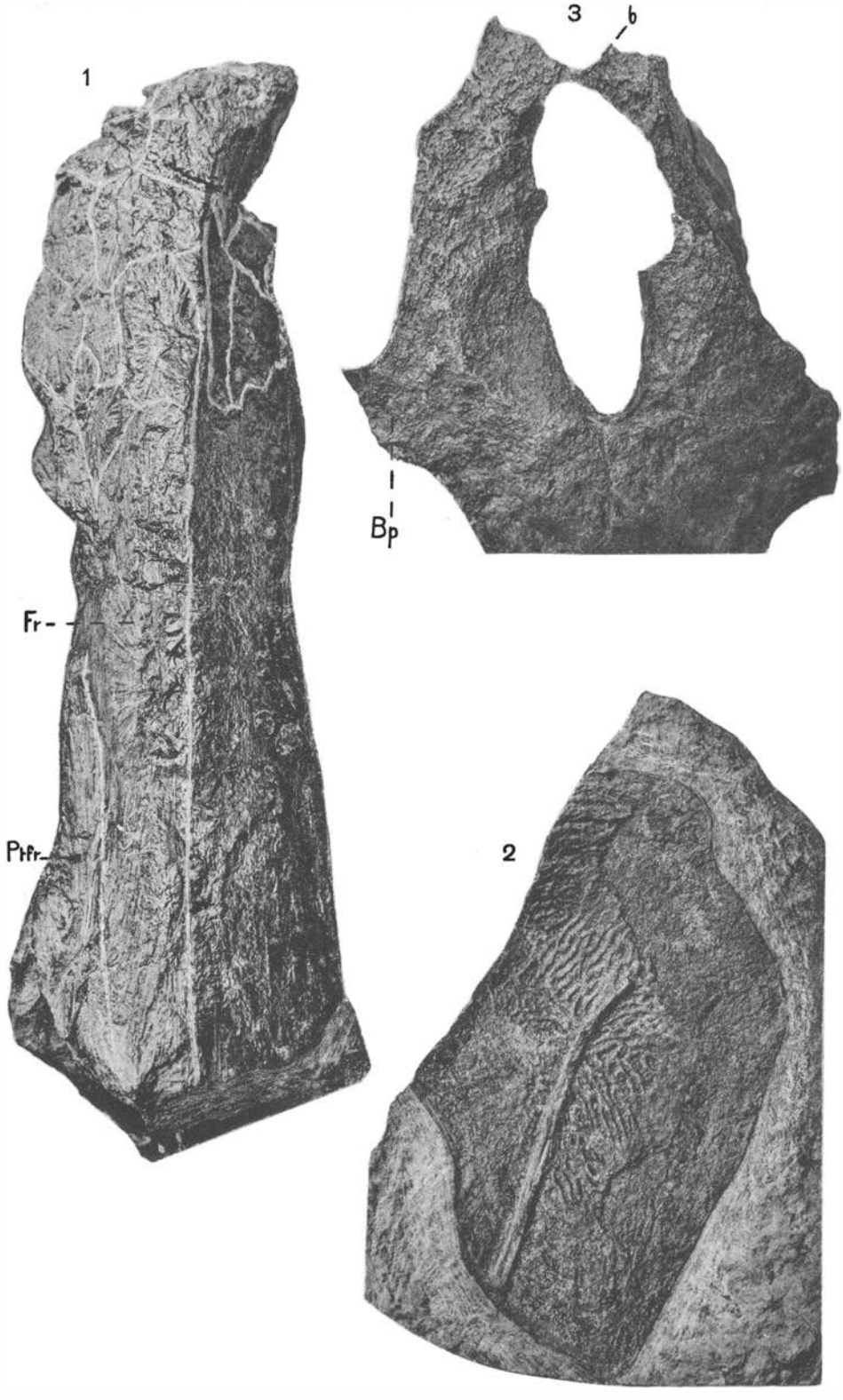
Fig. 2. *Dictyonosteus arcticus,* cross-section through the cranium along the anterior of the two cross cracks Pl. VI. The whole cranium towards the snout much compressed from the sides. Through this the right side especially is crushed and owing to this the orbitosphenoidal ossification is not preserved in its upper part on this side. Ventrally above the parasphenoidal bone the two lamellae of the orbitosphenoidal bones approach closely to each other, the section having passed immediately in front of the exit of n. opticus. *a,* edge belonging to the upper limit of the left for. opticum; *Fr,* frontal; *Orbsph,* orbitosphenoidal lamella; *Psph,* Parasphenoid; *Sc,* sensory canal.

Fig. 3. *Dictyonosteus arcticus.* Cross-section through the cranium along the posterior of the two crack lines Pl. VI. The section has passed obliquely downwards and backwards so that the basal parts shown in the figure are the anterior and lower parts of the basisphenoid. *Fr,* frontals; *Sc,* sensory canal.

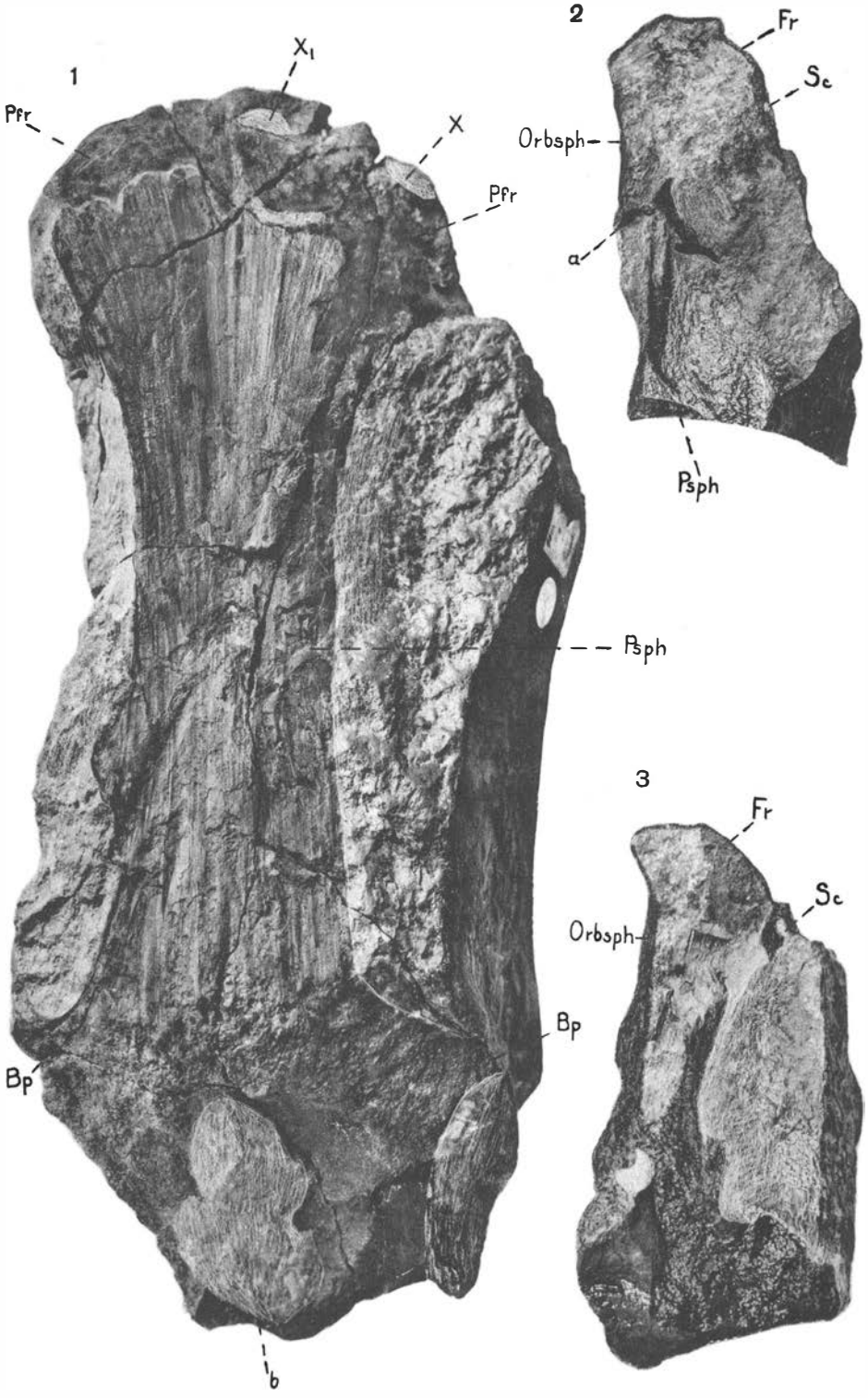
Plate VI.

Dictyonosteus arcticus. The cranium seen from the left side. The obitosphenoidal ossification completely preserved *(Orbsph),* passing at the back into the basisphenoid without any suture. In the snout ossifications are clearly distinguished in the ethmoidal region *(Pfr).* Observe the situation of the bridge of bone *b,* in relation to the frontals and the base of the cranium; *Bp,* the basal process on the lateral sides of the basisphenoid; *b,* bridge of bone behind the pituitary fossa; *fa,* foramen between orbital and olfactory region; *fo,* foramen probably for the ophthalmic nerve; fo_1, foramen probably for certain nerves for the eye-muscles; *Fr,* frontal; *fopt,* foramen opticum; *ftr,* foramen probably for n. trochlearis; *olf,* canal f. nervus olf.; *Orbsph,* orbitosphenoid; *Pfr,* prefrontal; *Psph,* parasphenoid.

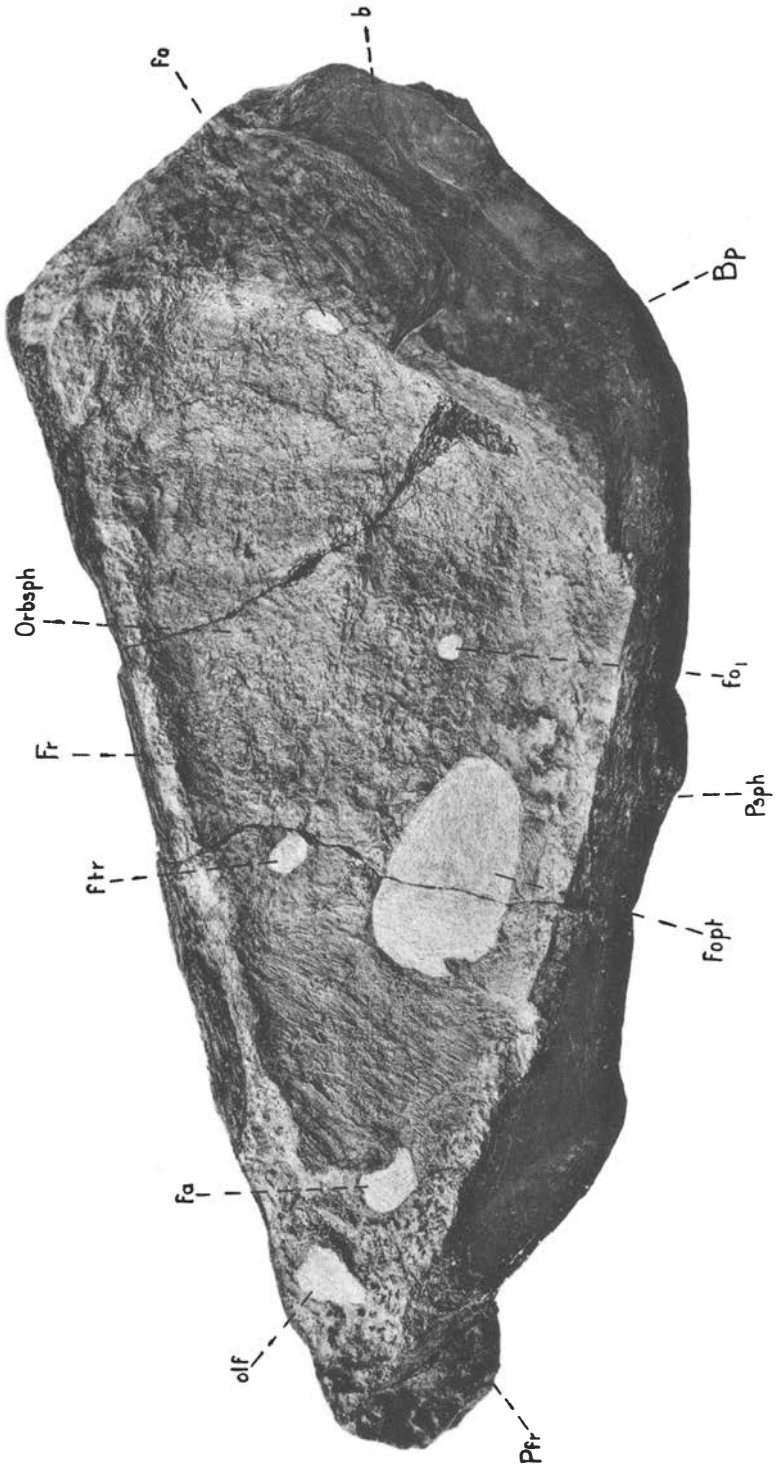
Gedruckt $^{19}/_{6}$ *1918.*



Ljustr. A. B. Lagrelius & Westphal. Stockholm



Ljustr. A. B. Lagrelius & Westphal. Stockholm



Ljustr. A. B. Lagrelius & Westphal. Stockholm