PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

An Account of the Devonian Fish, Palaeospondylus gunni, Traquair

W. J. Sollas and Igerna B. J. Sollas

Phil. Trans. R. Soc. Lond. B 1904 **196**, 267-294
doi: 10.1098/rstb.1904.0009

IX. *An Account of the Devonian Fish,* Palæospondylus Gunni, Traquair.

By W. J. Sollas, *F.R.S., Professor of Geology and Palæontology in the University of Oxford, and* Igerna B. J. Sollas, *B.Sc., Lecturer on Zoology in Newnham College, Cambridge.*

Received May 19,—Read June 11, 1903.

[Plates 16 and 17.]

The small and obscure Devonian fossil, first described by Dr. Traquair in 1890 (1),* under the name of *Palæospondylus Gunni*, has excited a keen interest among Zoologists, owing to its asserted resemblance to the Lampreys; so that although but a short period has elapsed since its discovery, it already fills an important place in our literature. Its position in the animal kingdom has been made the subject of controversy, and is still open to discussion. Dr. Traquair, whose extensive knowledge of fossil fishes gives great weight to his opinion, concludes that "it not only appears to be, but actually is a Marsipobranch" (7); Professor Howes is no less positive and speaks of it as "an unmistakable Marsipobranch" (26); Dr. Smith Woodward, while expressing himself more cautiously, definitely includes it among Cyclostomes (4), as the sole representative of a new order, the Cycliæ, a term which had been previously proposed by Professor Gill (14), to designate a group of uncertain rank, of which Palæospondylus is the only known member.

In face of this agreement, an equally imposing array of authorities may be cited as holding different views. Professors Gegenbaur (21), Wiedersheim (17), and Zittel (12), regard the claims of Palæospondylus to a close alliance with Marsipobranchs as at least doubtful; Dr. Bashford-Dean, who has made a special study of recent Marsipobranchs, is even more sceptical (23), Huxley is said to have styled the fossil a "baby Coccosteus," the late Sir J. W. Dawson (8) suggested a comparison with larval Amphibians, and Professor Graham-Kerr claims it for a Dipnoan (24).

That competent observers should thus be divided in opinion will occasion but little surprise, when we recall how imperfectly the remains of the organism appear to be preserved and how incompletely they are exposed to view. On the other hand, the large amount of genuine information, which has been extracted from this obscure material, may well be a matter for astonishment; it affords a striking testimony to the powers of skilled investigators, provided with abundant specimens for comparison.

If on the present occasion, we are able to throw any fresh light on the subject, this

* These numbers in parentheses refer to the entries in the Bibliography at p. 291, 292.

is entirely owing to our employment of a new method of research, that of studying the fossils in a series of sections taken at minute and regular intervals apart. This —though applied to comparatively few specimens, none of them, as originally exposed to view, so perfect as some which have passed through the hands of Dr. TRAQUAIR, or as some examples displayed in the collections of the British Museum—has given definiteness and precision to much that was imperfectly known or only surmised before, and has exposed the general anatomy of the organism with unexpected completeness.

Dr. BASHFORD-DEAN (23) has remarked that "even in fairly good specimens, the structures are not only difficult to determine, but individuals will be found to vary in important details." This is perfectly true when the fossil is studied in the usual manner, but not when more searchingly investigated, indeed, that which has inspired us with the greatest confidence in our results has been their singular consistency. Having once obtained a correct representation of the complete skeleton, it becomes possible to identify without difficulty all the parts of even the most fragmentary remains.

Still, much remains obscure, as must necessarily be the case when sutures are absent, articulations vague, and a possibility exists that soft cartilaginous parts may have vanished in the natural course of petrifaction.

Mode of Occurrence.—The fossil occurs, apparently in not inconsiderable numbers, in beds of lower Old Red Sandstone age, which are worked in a shallow pit at Achanarras, Caithness; it is most abundant in bands 2 or 3 feet in thickness, met with at a depth of about 6 feet below the surface (6). The rock is a hard flaggy sandstone, composed of minute angular grains of quartz, and a few scales of muscovite mica, cemented by carbonates of lime and iron; fragments of coaly matter, and occasional granules of pyrites are also present: when fresh it is bluish-grey in colour, or when much carboniferous matter is present, almost black; it weathers usually to a yellowish-grey, sometimes to an ochreous tint. The fossil consists of a black lustrous substance, to be described later, which is very resistant to the weather, so that fairly good specimens, with their black tint unimpaired, are sometimes to be seen as conspicuous though minute objects on the rotten surface of flagstones, which must have lain for a long time exposed to the air, as is shown by their having weathered inwards for a depth of a quarter of an inch or more. The best specimens, however, are always comparatively fresh.

The fossil is often fairly complete, presenting sometimes the ventral, sometimes the dorsal surface to view; as hitherto some doubt has been felt on this point, it may be as well to add that serial sections place the matter beyond dispute, on grinding down examples in which the dorsal surface is exposed, the ventral is revealed and *vice versâ*, in those exhibiting the ventral surface the dorsal becomes revealed.

Not infrequently the fossil is incomplete, the dorsal or ventral moiety alone being present. This difference as regards completeness, is in many cases connected with the manner of splitting of the rock; under favourable circumstances, as when a thin shaley parting determines the splitting, a plane of separation may be produced, which will expose the fossil and yet leave it intact, but when such partings are absent or of comparatively insignificant thickness, then the plane of fracture must pass through the fossil itself, if this is to be exposed to view, and the nearer the fracture passes to the middle of the fossil, the better it will be displayed. In this way slabs of rock may be obtained, one bearing the ventral, and the other the dorsal moiety of the fossil. The splitting of the rock takes place naturally during the winter frosts, and the specimens thus set free are those which most readily catch the eye of the collector.

Most of the specimens which we received from the collector, Mr. Donald Calder of Thurso, were exposed on a more or less weathered surface, but at our request he sent us some obtained by splitting the rock with a hammer; on taking serial sections of one of these slabs and its counterpart, we found, as we had expected, that the dorsal moiety lay in one slab and the ventral in the other. Nothing, however, was gained beyond the knowledge of this fact; our best specimens were those naturally exposed.

Good specimens are said to be rare, a collector who in a gathering of 20 finds a single good one may be regarded as fortunate. The excellence of a specimen is usually judged, however, not only by its completeness, but also by the perfection of its exposure at the surface; a factor of no account when the fossil is studied by serial sections. Hence many a specimen which to superficial observation would appear far from good, will yield excellent results on grinding down.

As regards the outer part of the fossil which has lain exposed to the air, considerable imperfection might be expected, since although very resistant, the fossil is not absolutely weather-proof. Greater interest attaches to the deeper part, included in the unaltered substance of the rock, for this has remained hermetically sealed up, and thus protected from all destructive action, since the time when its petrifaction was first completed. Judging from these parts alone, we find that the organism was preserved in very various stages of decay, in some cases decomposition was far advanced and only fragmentary remains of the skeleton are left; in others it was arrested at an early stage and the general anatomy of the hard parts is almost as well displayed as it would be in a recent specimen. Still even in the best examples, parts are missing here and there; the auditory capsules, probably on account of the thinness of their walls, are never quite complete, and the same is true of the rostral processes. The outlines also are rarely even and flowing, but usually present an eroded and jagged edge. The specimen in which this defect is least marked is also the smallest we have encountered, it measures nearly 14 millims. in length and the length of the head is only 2·5 millims.; the contours of this, particularly in the region of the skull, are remarkably smooth and even.

The parts of the skeleton are, as a rule, singularly little displaced, not more than can be accounted for by gentle movement in the water, which surrounded them at the time of their death, or by the increasing pressure of accumulating sediment. The delicate fin-rays still retain their association with the vertebral column, and even movable parts, such as the so-called "post-occipital plates," suffer disarticulation only in the rarest cases; a neural arch may be detached from its centrum, but is never carried far away.

The effects of pressure are evident, but extremely slight; the hollow cylindrical vertebræ have been squeezed into a flattened band, and the skull has suffered more or less distortion, parts originally separate have been fused together, and a general compression has taken place from above downwards; but these changes, although greatly increasing the difficulties of interpretation, are the result of very trifling movements, so trifling as to suggest that the consolidation of the rock must have followed speedily upon deposition; a suggestion which is strengthened by the extraordinary state of preservation of such specimens as are represented by fig. 1, Plate 16, fig. 7, Plate 17, in which the thin cranial walls rise vertically upwards, with but little indication of having been deformed by pressure. As a consequence of the absence of disturbance during interment and petrifaction, the organisms retain the attitude in which they were left by death. The head always lies with its dorsal and ventral surface parallel to the lamination of the flagstone, a rule to which we have found no exception, notwithstanding the large number of specimens we have studied; this is obviously the result of its depressed tadpole-like or skate-like form.

The vertebral column as invariably lies on its side, except in the immediate neighbourhood of the head: this position having evidently been determined by the dorso-ventral extension of its median fins. The different disposition of the skull and vertebral column naturally involves a twist somewhere, and the effects of this are manifest in the case of the first few vertebræ, which lie next the skull; these are overturned so as to lie on their articular face, and are sometimes imbricated, or even in rare cases piled on one another; this latter derangement can scarcely be accounted for by spasmodic muscular contractions, but would seem rather to have resulted from the position of the cranial base, which was raised slightly above the sea-floor by the underlying visceral arches.

Judged by their various size, specimens of nearly all ages are associated in the flags of Achanarras; the smallest specimen we have examined measures 14·0 millims. in length, the smallest described by Dr. BASHFORD-DEAN only 6 millims., but since the head of this is said to measure as much as 3 millims. while that of ours measures only 2·5 millims. in length, the specimen is probably incomplete. The largest specimen is said by Dr. BASHFORD-DEAN to attain a length of 52 millims. and may have slightly exceeded this, since the head is imperfect. The average length is about 25 or 30 millims.

Numerous species of other Lower Devonian fishes are found with Palæospondylus, of which a list is given by Dr. TRAQUAIR (6), but fish and some ill-preserved plants are its only associates.

The substance of which the fossil consists closely resembles ordinary coal in appearance; it is black, lustrous, of considerable hardness, just below 4 of MOHR's scale, brittle, breaks with a conchoidal fracture, has a density of from 1·35 to 1·7, and burns with a smoky flame, leaving a considerable quantity of ash. It does not dissolve in xylol, benzol, chloroform, or carbon tetrachloride. Its mineral characters thus closely correspond with those of coal. It is structureless in thin slices, which thus afford no help in an attempt to determine its original histological character.

Associated fish remains, such as those of *Coccosteus decipiens*, are formed of a similar material, having all the properties just enumerated, but with a slightly lower average density. The mass of a *Coccosteus* is very considerable, so that it is possible to obtain enough of its substance for a complete chemical analysis. Accordingly the black coaly matter of a specimen of *Coccosteus decipiens* from Achanarras was chiselled out of its matrix, crushed in a steel mortar, passed through the meshes of a fine sieve, and then placed in a separating apparatus filled with chloroform to remove associated shale and other impurities. The lighter part, of density below 1·5, was removed, dried, and again placed in the separator, this time filled with a mixture of chloroform and xylol, having a density of 1·37; the heavier portion, which thus had a density of between 1·37 and 1·5, was removed, and dried in a water-oven. It amounted in weight to about 2 grammes. Mr. J. E. Marsh, M.A., very kindly undertook its analysis, with the following results:—

Composition per Cent.

	I.	II.	III.	Mean.
Hydrogen	4·7	4·5	4·6	4·5
Carbon	68·1	68·7	68·3	68·4
Oxygen, &c.	11·4	11·1	11.1	11·3
Ash	15·8	15·7	15·0	15·8
	100·0	100·0	100·0	100·0

An examination for nitrogen showed that this element was not present in any considerable amount, certainly not more than 0·5 per cent. Sulphur was not estimated. The "oxygen, &c.," in the tables given above is obtained by difference.

An analysis of the ash, made by one of us, showed the presence of 31·73 per cent. of phosphoric anhydride, equivalent to 68·77 per cent. of calcium phosphate.

The composition approaches very closely that of an impure cannel coal, as will be seen from the following table:—

	Coal from Coccosteus.	Cannel coal.
Carbon	68·4	66·44
Hydrogen	4·5	7·54
Oxygen, &c.	11·3	12·2
Ash	15·8	13·82
	100·0	100·00

If the ash be disregarded it even more closely resembles an ordinary non-caking coal, such as that of the South Staffordshire coal-fields; as is shown in the next table :—

	Coal from Coccosteus.	Non-caking coal.
Carbon	81·1	79·39
Hydrogen . . .	5·3	5·36
Oxygen, &c. . .	13·6	15·25
	100·0	100·00

Thus both in physical characters and chemical composition the substance of the *Coccosteus* fossil, and consequently of Palæospondylus, is a true coal. That coal might in some instances result from the decomposition of fish remains has often been conjectured, but never yet conclusively proved.

These results gain greatly in interest by the fact that *Coccosteus* occurs in another and very different state of fossilisation, as for instance in the calcareous nodules of the Moray Firth. Within these the skeleton has been protected from the effects of pressure, so that the bones are not squeezed together as in the Achanarras specimens, but retain a separate individuality; at the same time their organic basis has disappeared, leaving only the mineral matter, so that instead of being compacted into a black structureless coal, they are preserved as white clearly defined plates, in which histological characters are still plainly decipherable. Thin slices under the microscope are seen to be crowded with the characteristic cavities left by bone-corpuscles, and to be traversed by numerous minute canals. The corpuscular cavities are best displayed at the instant when the preparation of the thin slice is completed by the addition of balsam and a cover-glass; they are then filled with air and consequently obvious, but as this is driven out by the balsam they rapidly disappear, only a single one here and there remaining visible.

Owing to the fortunate occurrence of species of *Coccosteus* in two different states of fossilisation, we are furnished with precise information as to the nature of the material which has been converted into coal; it was evidently bone. The organic basis of this may be presumed to have closely approached chondrin in composition, and this as regards the relative quantities of carbon and hydrogen, which enter into it, is so similar to cellulose that its transformation into coal need not occasion surprise. The composition of the two substances is given below :—

	Carbon.	Hydrogen.	Oxygen.	Nitrogen.	Rest.
Chondrin . .	47·74	6·76	31·04	13·87	0·59
Cellulose . . .	44·2	6·3	49·5	—	—

To convert chondrin into coal it must lose all its nitrogen, a little more than one half its hydrogen, and about three-quarters of its oxygen, the total loss of substance amounting to about 41 per cent. This is a minimum estimate and may have been much exceeded. To what extent the mineral constituents of the skeleton would be added to or diminished we have no means of judging. Evidently the chances are that a considerable contraction in bulk accompanied the process of carbonisation; but the matrix about Palæospondylus adheres to it closely, no interspace exists between the rock and the fossil, either empty or filled with a mineral deposit, the sand-grains of which the rock chiefly consists are in immediate contact with the fossil. Hence carbonisation may be inferred to have been practically completed before the rock was consolidated. Taking all the facts into consideration we are inclined to think that the transformation into coal was not effected very slowly.

An important question next arises as to what was the original character of the skeletal substance of Palæospondylus. As already pointed out it now consists of coal, which, so far as can be seen, differs from that of Coccosteus solely by a slightly greater density, due probably to the presence of a somewhat larger proportion of mineral salts. That it has been derived from a substance not greatly differing in composition from bone is highly probable, but there is no evidence to show that this substance actually possessed the histological structure of bone, nor, on the other hand, is there any direct evidence to prove that it did not. The assumption has been made, that it consisted, not of cartilage bone, but of calcified cartilage (5, 7); this may very well have been the case, but the suggestion arises solely from zoological analogies. That the skeleton consisted of fairly hard substance is suggested by the remarkable manner in which thin walls and delicate processes are sometimes preserved.

In concluding this account of the mode of occurrence of Palæospondylus, we may endeavour to reach some conclusion as to the physical conditions under which the sediments of its "gisement" were deposited. The rarity of any fossils in the Old Red Sandstone, except fishes and Crustacea, and of these except sporadically or at special horizons, where they suddenly become abundant, is a very remarkable fact, and becomes all the more so when the rich and diversified nature of the contemporaneous marine faunas is recalled to mind.

Had the Old Red fish inhabited a fresh-water lake, it would have been strange if fresh-water molluscs had not lived along with them, and this argument is strengthened rather than weakened by the isolated occurrence of the so-called *Anodonta Jukesii* of Kiltorcan, in Ireland; since, if this fossil has been correctly referred to the genus, it proves that fresh-water molluscs were in existence, and flourished in considerable numbers where conditions were favourable. That these conditions were not general over the Old Red area seems fairly certain. In Russia there is much evidence to suggest that some parts of the system were deposited in salt lakes, pseudomorphs of rock-salt occurring in some localities, and the generally unfossiliferous character of the Old Red Sandstone of the British Isles may be most readily explained by regarding it as the deposit of "dead" seas. Perhaps no precise analogy can be pointed out amongst existing basins; in some respects we are reminded of the Black Sea, in others of the Caspian or the Great Salt Lake of Utah.

The hypothesis of a lifeless sea leads naturally to the suggestion that the Old Red Sandstone fish were inhabitants of the freshwater rivers of the adjacent land, and were washed into the lakes by sudden freshets, just as happens at the present day to the fish which live in the rivers tributary to the Great Salt Lake of Utah. The fish carried into this lake are said to perish instantly; an equally sudden death, followed by a rapid burial, seems to have overtaken the assemblage of fishes now preserved in the flagstones of Achanarras.

Description of the Anatomy.

The Head: Dorsal Aspect (Plate 16, figs. 1, 3; Plate 17, figs. 7, 9).—Viewed from above the skull presents a median longitudinal trough, bordered on each side by paired lateral structures, and produced in front into numerous spine-like processes.

The trough, which extends throughout the length of the skull and occupies the middle third of its breadth, clearly represents the cranial cavity.

The most posterior of the lateral structures are a pair of cavernous bodies, which, as Dr. Traquair (5) rightly conjectured, represent the auditory capsules.

The most anterior are a pair of arcades, applied to the cranial walls, and partially divided by a transverse partition; these we regard as the nasal capsules.

An important element, having somewhat the form of an inverted "L," lies on each side, immediately behind the nasal capsules, and was probably related to the eye, which was situated above it. This element is indicated in Dr. Traquair's figures by the letter *a*, and is spoken of by him as "the additional lobe." As it will be frequently referred to, it requires a distinctive name, and in order to avoid as far as possible the introduction of hypothesis into description, we propose to call it the "gammation," from its fancied resemblance to the Greek letter "Γ."

Another element, lying immediately in front of the gammation and nearer the middle line, is almost entirely concealed by the nasal capsules, but is partly visible in the posterior compartment of the nasal capsule of the left side in Plate 16, fig. 3. This may be termed the pre-gammation.

A transverse division of the skull into a somewhat larger anterior and smaller posterior portion may be made, owing to the fact that the gammation is more closely connected with the nasal than with the auditory capsule, with which, indeed, it never appears to come actually in contact. In one specimen—the smallest—an obvious deep groove divides the coherent anterior region from the posterior (Plate 17, fig. 9).

The cranial cavity is open in front, behind and above. In the least distorted specimens of large size its walls are steep, for the most part vertical, and thin, about 0·1 millim. in thickness, but in the smallest specimen at least twice as great. Their height in proportion to the length of the skull is by no means inconsiderable;

in the case of one skull, which measures 5·3 millims. in length, their height is 1·0 millim.; in another, 3·75 millims. in length, the height is 0·4 millim. They pursue an almost parallel course for the greater part of their length, that is for the posterior four-fifths, and are then bent slightly outwards (Plate 16, fig. 1) at about the anterior termination of the nasal capsules, after which they resume a parallel course, but at a greater distance apart, and with diminished height. These low anterior walls are not visible in all specimens, they appear to be absent in the one shown by Plate 16, fig. 3, probably as a result of displacement.

At their posterior extremity the cranial walls are confused with the walls of the auditory capsules, but they retain their individuality in the anterior region of the capsules.

The upper edge of the posterior cranial walls is frequently more or less curved over towards the middle line; this is evidently in part a result of distortion by pressure, but also may also indicate the presence of an incomplete cranial roof of which only the margins are preserved (Plate 17, fig. 7).

The cranial walls are perforated by large vacuities, which are constant in position in all our specimens; most posterior is a wide gap on each side by which the cavity of the auditory capsule is put into communication with that of the skull; this, indeed, is a complete solution of continuity, for it is not roofed over. A communication between the cavity of the ear capsules and the brain case is characteristic of some Teleosteans, but it might easily be produced in Palæospondylus as the result of *post-mortem* changes.

The next opening lies in front of the auditory capsule, opposite the concavity of the gammation; as this is roofed over, it is not visible from above, a strip of paper has, therefore, been passed through to indicate it in the figures (Plate 16, figs. 1, 3). The aperture from its constancy in occurrence and position may be regarded as indicating some feature original to the skull, most probably a foramen, which has been enlarged by subsequent decomposition. We consider that it gave exit to the optic nerve, possibly to the fifth and seventh as well.

In front of the enlarged optic foramen no constant vacuity is met with in the side walls of the skull, we look in vain for such an aperture as might have afforded egress to the olfactory nerve. But precisely at that point, where the sudden flexure of the cranial walls occur, there is an easy way into the anterior compartment of the nasal capsule, through which the nerve may have passed.

The posterior opening of the cranial cavity, corresponding to the occipital foramen, is not completed by a roof, a fact rendered all the more remarkable by the presence, immediately behind it, of the neural arch of the first vertebra, still retaining its original position with regard to the skull or only slightly displaced to a lower level, although the body of the vertebra has been separated from it, and turned over so as to lie on its articular face. The arch is far from well preserved, however, and is usually in a very fragmentary condition. The absence of an occipital arch in the fossil does not necessarily prove that it was not present in the organism; the apparently capricious way in which parts are preserved in one specimen and not in another, offers a warning against putting too much faith in merely negative evidence; the number of specimens we have examined in which the dorsal surface was embedded in the rock, and, therefore, most likely to be well preserved, is not great, (some six or seven in all), and with regard to these it must be borne in mind that if the organism came finally to rest on its ventral surface, the upper part of the skull would be the last to be covered up with sediment, and would thus be the longest exposed to oxidising and destructive action.

The floor of the cranium, as rightly surmised by Dr. TRAQUAIR, is continuous, save for a slight interruption in front, and there are no signs of a basi-cranial fontanelle. It is fairly level in the posterior region, between the auditory capsules, such irregularities as do occur being obviously due to decomposition; but just on a line with the anterior border of the auditory capsules or between this and a line joining the optic foramina of opposite sides, it makes a sudden step-like descent to a lower level, recalling in a striking manner the "saddle-ledge" which occurs in a corresponding position in many Elasmobranchs, and which marks in them the position of the pituitary fossa.

Beyond this region the floor descends very gently, and becomes slightly narrower; the cranial walls ceasing to be quite vertical near their base, curve slightly inwards as they pass into the floor, so that the cranial cavity in this region, *i.e.*, between the nasal capsules, is narrower, as well as deeper than elsewhere.

The floor then gently rises and widens forwards, but again deepens near its termination between the low anterior walls; in this region it is crossed by a fissure which extends transversely across it and separates two distinct elements of the skull from each other. Beyond this it makes an upward rise and continues at this level to its termination.

The two elements just mentioned will be referred to again in treating of the ventral aspect of the skull, but the most anterior of them may conveniently be noticed here. So far as it contributes to the floor of the skull it may be described as a transverse bar or fillet, somewhat higher in front than behind, providing a support on each side for the terminal half of the low anterior cranial walls. The thickness of the bar, which for brevity may be called the "ampyx," is considerable, and it extends downwards to the ventral face of the skull, where it is seen as a very conspicuous ridge (Plate 16, fig. 5; Plate 17, fig. 10). Further description of this element is rendered difficult, owing to its extension into other regions not sharply marked off from it, it is confused laterally with the walls of the nasal capsules and may be produced beyond them as a thin broad lamella which fills the angle between the capsules and the lateral rostral process.

The rostral processes or rostralia are forward extensions of the ampyx, arising from it at different levels, and imperfectly distinguished into a dorsal and ventral series.

They are most completely preserved and displayed in a unique specimen described and figured by Dr. TRAQUAIR (7, Plate 9, fig. 1). In this they number altogether 11, of which 2 are lateral, and by far the longest and strongest, 5 are dorsal, and continuously united by a thin membranous-like expansion, and 4 are ventral; 1 of the dorsal series is median in position, the others are symmetrically disposed on each side of it, the ventral processes are symmetrically arranged 2 on each side of the middle line.

No signs of dorsal rostralia were discernible in any of our specimens as naturally exposed, but clear evidence of their existence was obtained in sections. The ventral and lateral, on the other hand, are generally visible in hand specimens.

The ventral rostralia are evidently extensions of the ampyx, as may be learnt from Dr. TRAQUAIR'S figures. They proceed from its front margin near the ventral surface; thus in the specimen shown in Plate 17, fig. 11, they make their first appearance in the third section upwards from the base, or 0·2 millim. from the ventral surface. This specimen, however, being one of the first experimented on, was cut at intervals of 0·1 millim.; had the intervals been smaller the processes might have appeared sooner, but not by more than 0·025 millim.

Lateral processes appear in the same specimen a little above the ventral, and are followed by dorsal ones, of which only the basal portions are present. The left lateral process is bent near its termination towards the right side.

A specimen in which the ventral surface is unusually well preserved (Plate 16, fig. 5) shows four processes in the first section by which the ventral face of the ampyx is revealed (counting from below upwards); these are both unusually large for ventral rostralia, and are not exceeded in length or breadth by the lateral processes, which appear in the succeeding sections, and are followed later by dorsal processes. These, like the ventral, appear to be extensions of the ampyx, but are given off at a higher level.

An interesting series of sections is afforded by the specimen shown in Plate 16, fig. 1, the ventral surface is not particularly well preserved, but traces of the ventral rostralia appear in the second section, and continue through to the eighth, when others, apparently both dorsal and ventral appear. The dorsal are the three anterior, two of which are conjoined by their expanded base, they are continued no farther than the next section, where the outer one on the left joins the adjacent outer process of the series behind. Beyond this ragged fragments of broadly extended thin processes are seen in the succeeding four sections; these are not connected with the ampyx, which is much reduced in breadth (antero-posterior extension) in the first of these sections, is interrupted in the middle in the second and third, and has wholly disappeared in the fourth.

The basal or proximal ends of the rostralia—whether ventral or dorsal is difficult to say—are well exposed on the upper surface of the ampyx in the fine specimen shown in Plate 16, fig. 3; judging from their number and position they would seem to be dorsal. They occur as sharply marked ridges symmetrically arranged on each side of the middle line. The innermost are the smallest, scarcely extending beyond the front margin of the ampyx; the second pair are larger and broader, extending for more than one-third of their length forwards beyond the ampyx, as well as slightly backwards, the ampyx accompanying them, so that its posterior margin is rendered sinuous, a median sinus corresponding to the space included by the innermost rostral pair, and a lobe on each side of this to the second pair. The third or outermost pair are by far the largest, extending 1 millim. in front of the ampyx.

A median dorsal rostralium is not clearly expressed, but a minute rounded projection in the middle line, just below the groove which separates the first pair, may possibly represent it.

The lateral rostralia do not differ greatly in size from the outermost dorsal, they appear to arise just below the latter, and that on the right side is bent sharply in the middle, so that its distal half crosses underneath the adjacent outermost dorsal process, of which it deceptively appears to be a branch. The occurrence of this flexure in other specimens affecting the corresponding rostralia leads to the suggestion that the lateral rostralia pointed not only forwards and outwards but also downwards, bending would then naturally result from the action of pressure, such as might be produced by the mere weight of the organism. A general shifting of the rostral apparatus backwards seems to have taken place in this specimen, leading to a concealment of the anterior cranial walls and carrying the base of the outermost dorsal process into the anterior compartment of the left nasal capsule. In another specimen (Plate 16, fig. 5) two of the rostralia are seen to extend backwards into the cranial cavity for a distance of at least half a millimetre, while the base of another is found within the aperture of a nasal capsule. Dr. TRAQUAIR seems to have observed something similar in his specimens, since he speaks of the lateral processes as passing "within the rim of the opening." From the facility with which they undergo displacement one can only infer that their attachment must have been very loose.

The rostralia seem to have retained their original disposition most completely in our smallest specimen (Plate 17, figs. 8 and 9). In this the ventral are very diminutive, the lateral well developed, but several others are confused with them; two of the dorsal processes are seen on the upper surface of the ampyx, bordering a deep narrow groove. The general appearance in this case strongly suggests that the rostralia formed a terminal fringe around the anterior aperture of the cranial cavity. It is worthy of note that in this specimen the cranial cavity is slightly constricted just in front of the anterior walls of the nasal capsules, so as to be divided into a larger posterior portion, the true cerebral cavity, and a much smaller anterior one, with which the rostralia seem to be directly associated.

The Nasal Capsules.—The structures, which we think may have supported the olfactory organs, occupy the greater part of the anterior half of the sides of the head;

they have the form of a half boat, longitudinally divided and inverted, the parts corresponding to the cut surfaces being applied to the walls of the skull. A transverse vertical wall or bar crosses the cavity of each half-dome, almost in the middle, thus dividing it into nearly equal compartments, one anterior, the other posterior. One end of the transverse bar is closely applied to the inner wall of the dome, with which it seems to be confluent, the other meets the wall of the skull, and in some well-preserved and scarcely distorted specimens seems to be continuous with it; in others, which have yielded to pressure, it retains a separate existence, even when closely adpressed to the skull walls. Usually both compartments of the capsules are open above, but in some cases the anterior is roofed completely over. Both are freely open below.

Several small apertures in the cranial walls place its cavity in communication with that of the capsules, but these are not so constant in position as we should expect if they were original. It does not seem likely that foramina, large enough to give exit to the olfactory nerves, would become obliterated by a secondary deposit of coal during the process of fossilisation, nor can we suppose that they have been closed up by pressure, at least in the case of such specimens as still present thin vertical cranial walls, which have certainly not been exposed to any adequate downward compression. There is nothing, however, to interrupt the free communication of the cranial cavity with the anterior compartment at the point where the cranial walls are suddenly diminished in height (Plate 16, fig. 1), and the exit of the olfactory nerves at this comparatively high level would not be inconsistent with analogy.

The use of the term nasal capsules may be objected to as a *petitio principii;* if a purely descriptive name should be thought preferable, they might be spoken of as the "anterior hemidomes."

The Auditory Capsules.—As will be seen from the figures, these are of considerable size; in a young Skate, of which the cranial cavity measures 24 millims. in length, the auditory capsules have a length of 6 millims., giving a ratio of 1 : 4; in a specimen of Palæospondylus the length of the cranial cavity was found to be 4·2 millims., that of the auditory capsules 1·5 millims., giving a ratio of 1 : 2·8. The capsules extend very nearly the whole length of the postero-lateral mass, but not over its outermost lateral portion, this is covered by a thin plate, which overlies the gills. The walls of the capsules were evidently very thin, as is shown by the generally fragmentary character of their remains, yet in one instance they are well enough preserved to still show traces of the course of the anterior and posterior semicircular canals.

The free communication which exists between the cavity of the capsules and that of the cranium has already been mentioned.

The Ventral Aspect of the Head. (Plate 16, figs. 2, 5; Plate 17, figs. 8, 10.)—The ampyx with its rostralia forms the most anterior portion of the skull, and is succeeded immediately behind on the ventral surface by a somewhat "T"-shaped element, which may be termed the "tauidion." The front margin of the "T" fits against the posterior margin of the ampyx, from which it is clearly defined, and from which it was readily separable, as may be seen in specimens where the parts have been slightly displaced by pressure (Plate 16, fig. 5). The slender shaft of the "T" is directed backwards in the middle line. The tauidion forms the anterior part of the floor of the skull, and there is nothing to show that it does not pass insensibly into the cranial walls. In specimens showing the ventral surface naturally exposed, a separation appears to exist, but in sections of these specimens it can no longer be traced. The tauidion may consequently prove to be a region rather than a separate element of the skull.

Two small foramina perforate it on each side in the angle formed by the junction of the arms with the shaft, they are about 0·1 millim. in diameter, and occur 0·15 millim. above its most ventral surface. They are indicated in Plate 16, fig. 5, by inserted slips of paper.

The Visceral Arches.—Branchial arches are present, more or less completely preserved in all the specimens we have examined; they are best displayed by the specimen shown in Plate 16, fig. 5. Their position is invariably below the posterior region of the skull, concealed almost completely by the auditory capsules and the epibranchial plates. They are four in number, and appear as a paired series of stout well-developed rods, diverging from the middle line outwards and backwards, those of each side remaining in general parallelism with each other. The second and third are the longest and strongest, the fourth the shortest of the series; thus, in the specimen just mentioned, the second measures 2·8 millims. in length, 0·5 millim. in height, and 0·3 millim. in breadth; the fourth nearly 1·3 millims. in length; in its other dimensions it resembles the second, but is slightly stouter.

Notwithstanding their difference in length, all four of the branchial bars terminate not far from the same straight line, and their anterior extremities in consequence make very different degrees of approach towards the base of the skull. The second pair meet each other over the base just behind the tauidion, the third likewise, a little behind the second, but the distal ends of the first and fourth do not meet, and lie somewhat remote from the middle line.

The several bars are united dorsally near their posterior extremities, in the case of the second and third bars an apparent coalescence takes place, the two, in the specimen under description, becoming one for the last 0·1 millim. of their length; the precise nature of the union is not always easy to make out, in some cases an evident bridge crosses from one to the other; in others, the extremities pass into each other, the two bars forming a loop. The third and fourth bars are united by a bridge near their extremity, and in addition by a broad plate, which lies transversely over their dorsal surface and looks like a separate structure. The bars of the first pair are free at their anterior extremity, but attached posteriorly to the second, and are thus liable to a displacement, the anterior ends moving outwards, and the whole bar coming nearly into parallelism with the long axis of the skull. The parts just described are probably cerato-branchial, but traces of epi-branchials are sometimes met with; it is difficult to interpret otherwise the processes seen in connection with the back of the skull in Plate 17, fig. 10. It has sometimes appeared as though basi-branchials might be present, but, if so, they are for the most part confused with the base of the skull.

The cerato-branchial bars are interrupted by perforations, revealed by sections, but whether these are original or not there is nothing to show.

In front of the branchial arches lies a pair of large and important structures, one on each side of the middle line, separated from each other by the base of the skull or the backward extension of the tauidion. Looked at *en face* each has somewhat the form of a trapezium, and bears two bars, one over its anterior, and the other over its posterior edge. The anterior is much the smaller of the two; it is separated by an interval from the overlying mass, and in one instance is brought into connection with this by its outer end alone. A strip of paper has been inserted between the two parts in Plate 16, fig. 5. The posterior, which is situated so as to continue the direction of the first branchial bar towards the middle line, is not separable in its present state from the skeletal mass immediately above it, but it has the appearance of having been originally a separate element.

In the identification of these structures lies in all probability the key to the interpretation of the affinities of Palæospondylus; for facility of reference we propose to term them provisionally the anterior and posterior trapezial bars.

From a careful comparison of sections it would seem to result that the trapezium-like mass consists of the pre-gammation and the gammation; the posterior trapezial bar is supported above by the gammation, while the anterior trapezial bar is borne by the pre-gammation. Conflicting explanations will probably be found by different thinkers for these relationships; that which we are inclined to regard as the most probable would identify the anterior trapezial with the mandible, the posterior with the hyoid, the gammation with the hyo-mandibular, and the pre-gammation with the palato-quadrate. In this case the opening of the mouth must have been transverse.

The right and left trapezial bars are always separated by the base of the skull, perhaps as a consequence of the pressure of this upon them.

The Post-branchial Plates.—These are the problematical "post-occipital" plates of Dr. TRAQUAIR, marked x in his figures. They are comparatively large and important structures, found in the least distorted specimens lying immediately behind the skull, parallel with the vertebral column, one on each side of it. Anteriorly, they extend for a short distance beneath the posterior region of the skull, so that their relation to other underlying structures can only be studied in specimens showing the ventral surface, or in sections. These show, in the clearest manner, that the problematical plates have no connection with the cranium, but are directly related to the last pair of branchial bars, the rounded end or head of the plate resting in contact with the thick rounded anterior extremity of the bar, as though making articulation with it.

That the post-branchial plates were freely movable in a horizontal plane is shown by the positions in which they lie; sometimes one, sometimes the other crosses obliquely over the middle line, and in one beautifully preserved example both alike take a parallel oblique course, while their capitular ends remain in contact with the posterior branchial bars. In this case the vertebral column is seen to overlie the plate that crosses its course. Whether they were also capable of movement in a vertical plane we are unable to say, there is no evidence to show that they were, and equally none to suggest that they were not.

It is difficult to be sure of the precise form of the plates, in some cases (Plate 16, fig. 6) they have the appearance of somewhat flattened cylinders, with a cavernous interior. In the specimen referred to they measure 2·8 millims. in length, 0·5 millim. in breadth, and 0·3 millim. in thickness, but may have been somewhat thicker, since their dorsal surface is somewhat corroded; in other cases (Plate 16, fig. 1) they resemble a plate curved from side to side into the form of a hollow half-cylinder, as if in conformity to the vertebral column which lies between them.

It seems not unlikely that the post-branchial plates may represent a modified branchial arch: in modern Elasmobranchs, as GEGENBAUR has pointed out, the last branchial arch, whatever its number, is usually both stronger than those which precede it, and turned backwards to a greater extent, so as in some cases to assume a nearly parallel position to the vertebral column. It is true that at the same time it becomes less movable, acting as a strut, or as a protection to the pericardium, but probably modern Selachians do not exhaust all the possibilities of modification which the last arch may undergo.

If the plates were capable of movement in a vertical plane, then they may have served as limbs, and the fourth branchial bar might be regarded as a potential coracoid, while the transverse plate overlying it and the third bar might represent a potential scapula. In this case the homology with a fifth branchial arch would fail. On the other hand, if their movement were limited to a horizontal plane, it might be maintained, and the function of the plates would then appear to have been to assist in securing the head to the vertebral column. Specimens show that the neck was very liable to dislocation.

The Vertebral Column.—The vertebræ, as displayed in reconstructions, confirm in all essential respects the description of Dr. TRAQUAIR. The large centra have the form of hollow cylinders, with rounded ends, which are complete throughout the vertebral column, except in the region of the caudal fin, where only the ventral half appears to be well developed. The neural arch roofs over a large canal, and seems not to have been very firmly attached to its centrum, since it is frequently found detached. The backwardly directed processes which are given off from the ventral aspect of the caudal vertebræ are single and median. They appear to be directly continuous with the centra. We have not found any evidence to suggest that the notochord was more constricted in the middle region of the vertebral column than elsewhere; as Dr. BASHFORD-DEAN has asserted, the centra are somewhat longer and not so high as in the neighbourhood of the head, but are not distinguished by other differences. In the cervical region, a vertebra favourably situated for measurement was found to have a length of 0·35 millim. and a breadth of 0·7 millim., giving a ratio of 1 : 2. In an overturned vertebra, showing the ring-like form, the height and breadth were nearly equal, and measured 0·7 millim. The length in this case was 0·3 millim.; further back, five or six vertebræ behind the post-branchial plates, the length and height of the centra had become equal, and measured 0·55 millim.

Judged by the lumen of the ring-like centra, the notochord must have been of great relative thickness, thus in one case the outer diameter of a ring was found to measure 0·9 millim. the inner 0·7 millim., the walls being only 0·2 millim. in thickness; so that, making no allowance for the enlargement which the central cavity may have undergone as a result of *post-mortem* changes, the notochord would have formed more than three-quarters of the diameter of the centrum. There is nothing very remarkable in this, however, and ring-like remains of cyclo-spondylous vertebræ are not uncommon among fossil Elasmobranchs.

The first vertebra is distinguished from the rest by its very large and strong neural arch, which is intimately associated with the posterior region of the skull, so that in several cases it retains its original position more or less perfectly, although the centrum corresponding to it has been displaced and overturned. The fact is interesting in connexion with the apparent absence of an occipital arch, and the suggestion naturally arises that this element may be represented by the neural arch of the first vertebra, which though not actually incorporated with the skull seems to be on the point of becoming so. In the specimen shown on Plate 16, fig. 3, the arch of the first vertebra has been displaced as well as the centrum, and lies on its face; it has a span of 1·3 millims. and a height of 0·6 millim., while the centrum measures 0·9 millim. in height and breadth. The total height of this vertebra is now 1·5 millims., while the length of the head, measured from the front margin of the ampyx to a line joining the posterior margin of the posterior lateral masses, is 5·5 millims.

The Absence of Ribs.—The presence of ribs has been both asserted (15 and 19) and denied (16), we have, therefore, made a very careful search for them, but without success. Twice structures were found in connexion with the fossil which might have easily been taken for ribs, but when their true nature was ascertained by sections, they proved to be the remains of other parts slightly shifted out of their proper position; in one case they were displaced post-branchial plates (Plate 17, fig. 10), in the other detached neural arches (Plate 16, fig. 1). It is evidently almost as dangerous to assert the presence as the absence of parts from an examination of the specimens which are only superficially exposed.

The Absence of Limbs.—Structures which might possibly represent the fragmentary and confused remains of a pectoral and pelvic girdle with their associated fins have been met with in one specimen. The specimen was studied in sections, and reconstructed, but without adding anything definite to our knowledge; the vertebral column passes continuously through the confused problematical structures, but these cannot be resolved into definite parts.

The Affinities of Palæospondylus.—Suggestions have been made that Palæospondylus was a larval form, possibly of an Arthrodiran Fish, possibly of an Amphibian. Dr. BASHFORD-DEAN is much inclined to take this view, and has supported it by the assertion that the relative dimensions of the parts of the organism undergo great changes with growth, and, indeed, as represented by Dr. DEAN in the following table, these changes are by no means inconsiderable.

TABLE illustrating the Changes in the Approximate Proportions of Palæospondylus at various Stages of Growth. (Dr. BASHFORD-DEAN (23).)

Length of specimen in millimetres.	Length of cranium.	Percentage of total length.			
		Breadth of head.	Length of post-occipital plates.	Length of column.	Thickness of column.
6	50	30	—	50	4
13	30	23	15	70	2·2
17·5	21	12	7	79	2·0
22	17·7	11	6·8	83	1·8
24	16·5	11	6·6	83·5	1·7
52	15·4	10	—	84·6	2·2

These results are of great interest, and if trustworthy of great importance. Dr. BASHFORD-DEAN furnishes us, however, with very little material for a critical examination of the process by which they were obtained; no information is given as to how the length of the cranium was determined, nor as to the characters by which the completeness of the specimens was judged. An examination of the figures illustrating Dr. BASHFORD-DEAN'S paper does not inspire us with confidence as regards the latter point. The actual results of measurement are not stated, but they may be elicited from the table, and are given from our calculations in the table below:—

Length of specimen.	Length of cranium.	Breadth of head.	Length of post-occipital plates.	Length of column.	Thickness of column.
6	3	1·8	—	3	2·4
13	3·9	2·99	1·95	9·1	2·86
17·5	3·675	2·1	1·23	13·825	3·5
22	3·74	2·42	1·496	18·26	3·96
24	3·96	2·64	1·584	19·04	4·08
52	7·908	5·2	—	43·992	13·00

The measurements are given in millimetres.

A glance at these data is sufficient to show the laws of growth as represented by Dr. Bashford-Dean's table of percentages are the result of an illegitimate method of comparison. The fact that one specimen with a cranium measuring 3·9 millims. in length is provided with a vertebral column only 9·1 millims. long, while another with a head 3·96 millims. in length possesses a vertebral column 19·04 millims. long, does not illustrate a law of growth, but rather the danger of trusting to measurements made on specimens only superficially exposed to view. The smallest specimen in the table is represented by a figure (23, Plate 1, fig. 9) in Dr. Bashford-Dean's Memoir, which shows nothing but the vertebral column or a part of it, without any indication of a head; to draw important conclusions from so obscure and insignificant a fragment appears to us hazardous in the extreme; still more to make it the subject of measurements for comparison. Our own smallest specimen has a total length of 14·0 millims. measured from the front margin of the ampyx to the extremity of the vertebral column, which may not be complete; the length of the head between the front margin of the ampyx and a line joining the posterior margin of the postero-lateral masses is 2·5 millims. It does not differ in any structural character, so far as can be discovered, from our largest specimen, in which the length of the head is 5·5 millims., except in the close apposition of the posterior border of the gammation to the cranial wall.

To arrange the specimens in the order of their total length, as Dr. Bashford-Dean has done, is not a proceeding which commends itself to our judgment; any want of completeness in the length of the vertebral column cannot fail by this method to vitiate the whole of the results; a safer method would be to select some one organ, of which the completeness can be more successfully estimated, as a basis of reference, and this would appear to be the head.

In the following series the specimens are arranged in the order of magnitude of the length of the head (cranium), Dr. Bashford-Dean's smallest specimen being omitted and measurements made from ours substituted; measurements have also been added taken from Dr. Traquair's most perfect specimen, they appear in the second line of the table:—

Length of cranium.	Length of column.	Ratio of length of vertebral column to length of cranium*.
2·5	11·5	4·6
3·5	20	5·7
3·675	13·825	3·76
3·74	18·26	4·86
3·9	9·1	2·33
3·96	19·04	4·30
4·67	27·1	5·8
7·908	43·992	5·56

* Taken as unity.

The absence of regularity in the series of ratios shown in the last column is inconsistent with Dr. BASHFORD-DEAN'S conclusions, and we can only suppose that some concealed imperfections in his specimens have led him to over-estimate their completeness. On the other hand, the results suggest that the average ratio between the length of the head and "tail" is as one to five or six.

We are far from denying, however, that some change in the proportional size of the organs of Palæospondylus has taken place with growth; indeed, there seems to be some evidence to show that it has. Thus in our smallest specimen the length of the head anterior to a line joining the posterior border of the gammation (which corresponds to a line joining the anterior margins of the postero-lateral masses) measures 1·35 millims., the part behind this line, 1·1 millims., giving a ratio of 1·18 : 1; in another specimen, chosen for its apparent freedom from distortion, the length of the anterior part is 2·465 millims., of the posterior 1·785 millims., giving a ratio of 1·38 : 1, thus indicating a more rapid growth on the part of the anterior region, a result precisely corresponding to that found by SEWERTZOFF in his study of the early development of the Skate (27), but further, the same observer has shown that this more rapid growth is confined to the rostral region, and does not affect the rest of the skull behind this region; precisely the same fact is indicated by our two specimens: thus the low anterior walls of the skull measure 0·25 millim. in the small specimen and 0·765 millim. in the large one; deducting these quantities from the length of the anterior division first mentioned, we have in the small specimen $1·35 - 0·25 = 1·1$, and the ratio of this to 1·15, the length of the posterior region, is 1 : 1·05; in the case of the large specimen $2·465 - 0·765 = 1·7$; the ratio of this to 1·785 is 1 : 1·05, or identical with that found for the smaller specimen. This suggests that the low anterior skull walls are closely associated with the rostral apparatus. The ratio of 1 : 1·05 is so nearly unity as to show that the rate of growth of the parts to which it relates has been practically uniform.

It by no means follows, however, that Palæospondylus is a larval form; it would have been surprising if no change in the relative dimensions of parts had taken place during growth, from a length of 14 millims. up to a length of 52 millims., that of Dr. DEAN'S largest specimen.

On the other hand, the absence of any important structural changes, which might have been expected to distinguish our smallest from our largest specimens, is a remarkable fact, and suggests that the characters of the adult were attained at a very early age.

Regarding Palæospondylus as an adult form, we next pass to a discussion of its relations to other Vertebrates.

Its claims to alliance with the Marsipobranchs have been ably urged by Dr. TRAQUAIR, who regards the presence of rostralia about a single anterior aperture as indicating a narial character for that opening; if so, of course, the fossil must be regarded as a Monorhine; the presumed absence of jaws has naturally led to the conclusion that it is a Cyclostome. But the position of the rostralia at the anterior extremity of the cranial cavity is also that which they occupy in other fishes such as the Elasmobranchs, where they primarily serve as supports for the mucous glands. These fill the anterior end of the cranial cavity, and are only partitioned off from the brain by a membranous septum, as may be readily demonstrated in a young Skate or Dog-fish.*

The position of the rostralia is thus as much consistent with Elasmobranch as with Marsipobranch affinities.

As regards the presumed absence of jaws, we have already pointed out structures that are probably of this nature, and with this the last of the two most convincing arguments in favour of Marsipobranch relationship disappears.

There remain then features of indicative but not of fundamental importance, such as the asserted nature of the caudal fin-rays, which in their dichotomy do certainly recall a Marsipobranch character in a most striking manner. We can offer no observations of our own on the nature of these structures; our specimens were not well enough preserved, but Dr. BASHFORD-DEAN sees no reason why they should not be dermal, and he considers the fact that they twice dichotomise supports him in this view. The absence of ribs and limbs cannot by itself be regarded as furnishing an argument for a Marsipobranch alliance.

The arguments against such an alliance, however, have become much strengthened in the light of additional knowledge; the characters of the cranium are foreign to the Marsipobranch, the highly developed vertebral column equally so, while the visceral skeleton is absolutely unlike anything known among existing Marsipobranchs.

Professor GRAHAM KERR finds a remarkable agreement between the general features of Palæospondylus and the Dipnoi as illustrated by Ceratodus, he compares the post-branchial plates with the cranial ribs of a young Dipnoan, and remarks on the presence on the ventral surface of the fossil of a pair of plates, which recall the two moieties of the hyoid arch of Lepidosiren. These last are evidently what we should regard as a pair of branchialia, belonging to the second or third arch.

The post-branchial plates cannot be interpreted as cranial ribs, since they are not attached to the skull, but to the last branchial arch; a glance at Plate 17, figs. 8 and 9, will be sufficient to suggest their true nature.

That a certain similarity may be recognised between the head of Palæospondylus and that of a young Dipnoan, such as Ceratodus, can scarcely be doubted. If we turn to the figure by SEWERTZOFF (28) of a lateral view of the skull of an advanced embryo of Ceratodus, we shall find similar large auditory capsules, a cranial cavity not completed by a roof, with its walls higher behind than in front, and a large

* In a young skate, 8 inches in length, the brain entirely fills the cranial cavity, with the exception of that part occupied by the mucous glands, and the wide space in front of the brain met with in the adult is non-existent.

foramen immediately in front of the ear, giving passage in this case to branches of the fifth and seventh nerves. There is as yet nothing to correspond to the anterior hemidomes, but they might readily arise as developments about the eye and nasal capsules; in such a case the eye would be situate in the posterior, and the nasal capsule in the anterior compartment of the hemidomes.

The branchialia, though very much smaller, correspond in number and position with those of Palæospondylus, but the hyoid and lower jaw are immensely larger than the parts we have identified with these elements in the fossil; their suspension also is altogether different.

If Palæospondylus is to be interpreted as a Dipnoan, we must either suppose that the lower jaw has been lost, or we must find it articulating with the gammation, and biting against the quasi-maxillary cartilage. The first is not an impossible assumption, —it might be as logical to conclude that the Mammalian lower jaws of the Stonesfield slates had no heads, as that Palæospondylus had no lower jaw—but it would be made use of as a valuable admission by those who might still prefer to regard Palæospondylus as a Marsipobranch. As regards the other horn of the dilemma, it may be urged that we are mistaken in the identification of the lower jaw, and that it may occur in the requisite position. We have done our best to find it there, and, in one instance, thought we had succeeded. In a particularly fine specimen, of which the ventral surface is shown by Plate 17, fig. 13, a more or less distinct ridge may be traced running forwards from the gammation, conformable with the quasi-maxilla on the left side, close to it, and, as longitudinal sections show, below it. The ridge terminates near the extremity of the transverse arm of the tauidion. If this could be shown to be the lower jaw the resemblance to a young Ceratodus would be indeed remarkable. Unfortunately none of our other specimens have afforded evidence that would confirm this identification, and we are compelled somewhat reluctantly to abandon it in favour of that we have already proposed.

Again, as a matter of fact, structures corresponding to the hemidomes are not present in Ceratodus, nor if they were, is it easy to see how the eye could have been placed in the posterior compartment, which is unprovided with a foramen, through which the optic nerve could find issue to it.

Tempting as the Dipnoan interpretation certainly is, we are unable to adopt it, chiefly on account of the great apparent difference in the nature of the suspensorium and manducatory apparatus.

Sir J. W. Dawson, on what appear to us insufficient grounds, has suggested that Palæospondylus may prove to be a forerunner of the Batrachia or a primitive tadpole. There may be other arguments than those he urged in favour of such a view, but the remarks just offered with regard to the Dipnoi will, for the most part, apply equally to the Amphibia.

No one seems yet to have proposed to associate the fossil with the Elasmobranchs, and yet they have much in common.

Except for the presence of a roof in that of the latter, the crania of the two are not very dissimilar, and even as regards the roof, this is not complete in the Selachians.

If we take the similar aural capsules as a starting point in the comparison, we find the eye of the Elasmobranch situated immediately in front of them, and the optic nerve passes out, frequently through a large foramen, opposite to it. In Palæospondylus a large aperture exists in a similar position, and if it represents an optic foramen, then the eye must also have occupied a corresponding position. The saddle-ledge, which marks the place of the pituitary body in the floor of the Selachian skull, is met with similarly placed in Palæospondylus.

If the hemidomes of Palæospondylus are really nasal, then the nasal capsules have a similar position to that which they occupy in the Elasmobranchs. In the latter, however, there is no such marked transverse bar or median septum as occurs in the hemidomes. Professor BRIDGE suggests that this may be represented by the partition between the nares, as seems very possible; it would also seem possible that the posterior compartment might represent the ethmoidal incisure of some Elasmobranchs, such as Prionodon or Pristiurus: its posterior wall would then correspond with a pre-orbital process, and its lateral wall to the lateral ethmoidal process.

The pre-frontal gap of the Elasmobranch skull occurs in a region corresponding to that which lies between the low anterior walls of the fossil skull. The position of the rostralia is similar in both.

There is nothing in the Elasmobranch skull to correspond with the transverse line of separation between the ampyx and the tauidion of Palæospondylus.

On reviewing the resemblances and differences between the two skulls, it would appear that the former outweigh the latter; on the whole, the general topography of the two is strikingly concordant.

In strong contrast with this conclusion is the evidence of the visceral skeleton. The branchial arches in their number, limited to four, and in their position beneath the skull afford a character, which finds no parallel among the Elasmobranchs, and it is not till we reach the higher groups of Dipnoi and Amphibia, and then only in larval forms, that we again encounter it, but in these it is precisely repeated.

With an agreement so close in this respect, we might reasonably expect to find an equally marked correspondence between the jaws and suspensory apparatus, but, as we have already seen, this expectation is disappointed. These structures in Palæospondylus remain, we believe, without any precise analogy. Reasoning upon the observed facts alone the position of the gammation and pre-gammation is as anomalous on a Selachian as upon a Dipnoan interpretation; they suggest the idea of a divided sub-orbital bar, but this, though ending close to the middle line of the skull on the one hand, and to the auditory capsules on the other, is united to neither. The primitive connection of the quadrate bar with the trabecula in the Dipnoi and

Amphibia is behind the eye, and this is the connection of the gammation with the cranial walls in our youngest specimen, but in larger specimens, though apparently freed from this connection, the gammation has not entered into union with the auditory capsules; it may have done so, but there is no absolute proof that it did. Still, our friend, Professor BRIDGE, who has carefully studied our reconstructions, remarks that "it looks as though such a connection must have existed"; in this we fully concur, and if we may assume that the appearance represents the fact, we may identify, as we have done, the gammation with the hyomandibular, the pre-gammation with the palato-quadrate, the posterior trapezial with the hyoid, and the anterior trapezial bars with the mandible. The lower jaw would, in this case, have been singularly diminutive; it could have bitten against the palato-quadrate, and its position would have been transverse. Its two halves are now separated in the middle line, and it is unprovided with teeth. Teeth might, however, have been originally present; they would have been very minute, and highly calcified. Under the conditions which were favourable to the conversion of cartilage into coal, much carbonic acid would be evolved, in presence of which calcareous structures, such as teeth, might easily pass into solution. The interpretation of the anterior arches which seems most probable is thus frankly Selachian, but no known Elasmobranch is provided with jaws so insignificant in size, or with a hyoid which, as in this case, greatly exceeds them in magnitude. Dr. GOODRICH, commenting on the relative dimensions of the trapezial bars, would regard the anterior as labial, and the posterior as mandibular. On this view, of the four branchial arches the anterior would be the hyoid.

There is evidently room for a difference of opinion as regards the precise interpretation of the anterior arches, but that their facies is Selachian seems to us evident.

The position of the branchial arches is apparently a primitive character, and when persistent, correlated with comparatively small jaws. In Dipnoi, although the jaws are large, they are placed far forward; in Amphibia they are small, so long as the branchial arches are present beneath the skull; their backward position in Selachians seems to be a direct consequence of the enormous development of the jaw apparatus, with its large posteriorly placed suspensorium. The number of the branchial arches may or may not be primitive; in the advanced embryo of Ceratodus, as described by SEWERTZOFF, there are only four, but in the adult Dipnoi there are five, an increase which suggests the possibility that the larger number of the Selachians may not have been an original character.

If the branchial arches present us with merely primitive, indifferent characters, generally possessed by ancestral fishes, then the remaining characters of Palæospondylus which can be looked upon as distinctive are those connected with the jaws, and these seem to point rather in a Selachian direction than any other. If Palæospondylus took its origin near the base of the Elasmobranch stem, it proceeded in its subsequent development along an independent course, losing its limbs, if it ever possessed them, and acquiring a highly organised vertebral column, homoplastic in character with that of cyclo-spondylous Selachians.

It thus does not seem possible to place Palæospondylus in any of the accepted sub-classes of fishes; it probably belongs to that legion of primitive forms which must have peopled the Devonian waters, but of which the vast majority have disappeared without leaving any trace of their existence.

We desire in conclusion to express our warm thanks to our numerous friends who have interested themselves in the progress of this investigation, to Dr. SMITH WOODWARD and Dr. TRAQUAIR, who made special journeys to Oxford to examine our specimens, to Professor WELDON, to Dr. GOODRICH, and particularly to Professor T. W. BRIDGE for much useful information and suggestive criticism.

BIBLIOGRAPHY.

1. TRAQUAIR, R. H. "On the Fishes found at Achanarras Quarry, Caithness," 'Ann. and Mag. Nat. Hist.' (6), vol. 6, pp. 485, fig. 4. 1890.
2. WOODWARD, A. SMITH. 'Catalogue of the Fossil Fishes in the British Museum,' part 2, p. 553. 1891.
3. HOWES, G. B. "On the Affinities, Inter-Relationships, and Systematic Position of the Marsipobranchii." 'Trans. Biol. Soc. Liverpool,' vol. 6. 1891.
4. WOODWARD, A. SMITH. "The Forerunners of the Backboned Animals," 'Nat. Science,' pp. 597–599. 1892.
5. TRAQUAIR, R. H. "A Further Description of *Palæospondylus Gunni* (TRAQUAIR)," 'Proc. Roy. Phys. Soc. Edin.,' vol. 12, pp. 87–94. Plate 1. 1893.
6. ——————— "Achanarras Revisited." *Ibid.*, p. 279. 1893.
7. ——————— "A Still Further Contribution to Our Knowledge of *Palæospondylus Gunni*." *Ibid.*, pp. 312–321, Plate 9. 1893.
8. DAWSON, J. W. 'Salient Points in the Science of the Earth.' London, pp. 285–286. 1893.
9. TRAQUAIR, R. H. "*Palæospondylus Gunni* (TRAQUAIR) from the Caithness Flagstones," 'Ann. Scot. Nat. Hist.,' pp. 94–99, Plate 3. 1894.
10. NEUMAYR, M. 'Erdgeschichte,' vol. 2, pp. 12, 112. 1895.
11. DEAN, BASHFORD. 'Fishes Living and Fossil.' New York, pp. 65, 70–71. 1895.
12. ZITTEL, K. A. VON. 'Grundzüge d. Palæontologie.' Munich and Leipzig, p. 527. 1895.
13. GILL, THEODORE. "Note on the Systematic Position of Palæospondylus," in a Review of DEAN'S 'Fishes,' 'Science,' N.S., vol 3, pp. 914, 915. 1896.

14. GILL, THEODORE. "Note on the Devonian Palæospondylus." *Ibid.*, vol. 4, pp. 10, 11. 1896.

15. DEAN, BASHFORD-. "Is Palæospondylus a Cyclostome?" 'Trans. N.Y. Acad. Sciences,' vol. 16, pp. 101–104, Plate 5. 1896.

16. TRAQUAIR, R. H. "Note on the Affinities of *Palæospondylus Gunni* (TRAQUAIR), In Reply to Dr. BASHFORD-DEAN of New York," 'Proc. Zool. Soc. Lond.,' pp. 314–317. 1897.

17. WIEDERSHEIM. 'Elements of Comparative Anatomy,' p. 74. 1897.

18. PARKER and HASWELL. 'A Text-book of Zoology,' London, vol. 2, pp. 133–134. 1898.

19. DEAN, BASHFORD-. "Remarks on the Affinities of *Palæospondylus Gunni*. In Reply to (Dr. TRAQUAIR)," 'Proc. Zool. Soc. Lond.,' pp. 343–347. 1898.

20. WOODWARD, A. SMITH. 'Outlines of Vertebrate Palæontology,' Cambridge, pp. 1–3. 1898.

21. GEGENBAUR, C. 'Vergl. Anat. d. Wirbelthiere,' Leipzig, vol. 1, pp. 65, 363–365. 1898.

22. DEAN, BASHFORD-. 'On the Embryology of Bdellostoma Stouti' (Festschrift CARL VON KUPFER), Jena, p. 221. 1899.

23. ——————— "The Devonian 'Lamprey,' *Palæospondylus Gunni* (TRAQUAIR)," 'New York Acad. Sciences Memoirs,' vol. 2, pp. 1–32, Plate 1. 1900.

24. KERR, GRAHAM. "The Zoological Position of Palæospondylus (TRAQUAIR)," 'Cam. Phil. Soc. Proc.,' vol. 10, p. 298. 1900.

25. SOLLAS, W. J. "The Investigation of Fossil Remains by Serial Sections," 'Rep. Brit. Assoc.' 1901, p. 643.

26. HOWES, G. B. "Presidential Address to Sec. D. Brit. Assoc." 'Rep. Brit. Assoc.' 1902, p. 626.

27. SEWERTZOFF, A. N. 'Die Entwickelung des Selachier-Schädels' (Festschrift CARL VON KUPFER), Jena. 1899.

28. ——————— "Zur Entwickelungsgeschichte des Ceratodus Forsteri," 'Anat. Anzeiger,' vol. 21, pp. 593–608. 1902.

EXPLANATION OF PLATES.

Plate 16.

Fig. 1. Dorsal aspect of a reconstruction. In the specimen from which the reconstruction was obtained the ventral surface was exposed to view, the dorsal was embedded in the rock.

Fig. 2. Ventral surface of the same reconstruction.

Fig. 3. Dorsal aspect of a reconstruction. The specimen was embedded in the same way as that of Fig. 1. The ventral surface was consequently imperfect. A slight distortion has led to a shortening of the anterior region of the head, and to the concealment of the anterior cranial walls.

Fig. 4. The same reconstruction with the dorsal moiety removed. The left hemidome, with the gammation, pregammation, and a part of the cranial wall, is shown in the upper left-hand corner.

Fig. 5. Ventral aspect of a reconstruction. The specimen from which the reconstruction was obtained was embedded by the ventral surface, the dorsal side is therefore the less perfect.

Fig. 6. Dorsal aspect of the same reconstruction.

(The magnification of the figures on this plate is 10 diameters.)

Plate 17.

Fig. 7. Dorsal aspect of a reconstruction. The specimen was embedded on the dorsal side, but it had suffered much disturbance and decay before petrifaction. The reconstruction shows the cranial wall of the right side curving roof-like over the cranial cavity at the point marked *c.w.*

Fig. 8. Ventral aspect of a reconstruction. The specimen, which was the smallest in our collection, was embedded by the ventral surface.

Fig. 9. Dorsal aspect of the head of Fig. 8.

Fig. 10. Dorsal aspect of another reconstruction. The specimen was embedded on the dorsal side, and had been much compressed from above downwards.

(Figures 7 to 10 are magnified 15 diameters.)

Note.—The specimens from which the reconstructions shown in figs. 1 to 10 were obtained were cut at intervals of 0·025 millim.

Fig. 11. Ventral aspect of a reconstruction. The specimen was embedded on the ventral side. (Cut at intervals of 0·1 millim. $\times 7\frac{1}{2}$.)

Fig. 12. Both aspects of another reconstruction. (Cut at intervals of 0·1 millim. $\times$ 15.)

Fig. 13. Ventral surface of an actual specimen ($\times 7\frac{1}{2}$).

Explanation of Abbreviations used in Figures.

am. Ampyx.
br.c.$_{1-4}$. First to fourth cerato-branchials.
br.$_{1-2}$*e.* Epibranchials.
br.b. Basi-branchial.
br.p. Post-branchial plates.
c.w. Cranial wall.
c.w.a. Anterior cranial wall.
e.br.p Epibranchial plate.
for. Foramen in front of auditory capsule.
g. Gammation.
g.p. Pre-gammation.
h. Hemidome.
h.a. Anterior wall of hemidone.
h.p. Posterior wall of hemidome.
h.a.c. Anterior compartment of hemidome.
h.m.s. Median septum of hemidome.
h.p.c. Posterior compartment of hemidome.
h.p.w. Posterior wall of hemidone.
mx. Quasi-maxillary cartilage.
r. Rostralia.
r.l. Lateral rostralia.
r.d. Dorsal rostralia.
s.c.a. Anterior semi-circular canal.
s.c.p. Posterior semi-circular canal.
t. Tauidion.
t.f. Foramen in tauidion.
tp.b.a. Anterior trapezial bar.
tp.b.p. Posterior trapezial bar.
v. Vertebra.
v.b. Centrum of vertebra.
v.n.a. Neural arch.

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

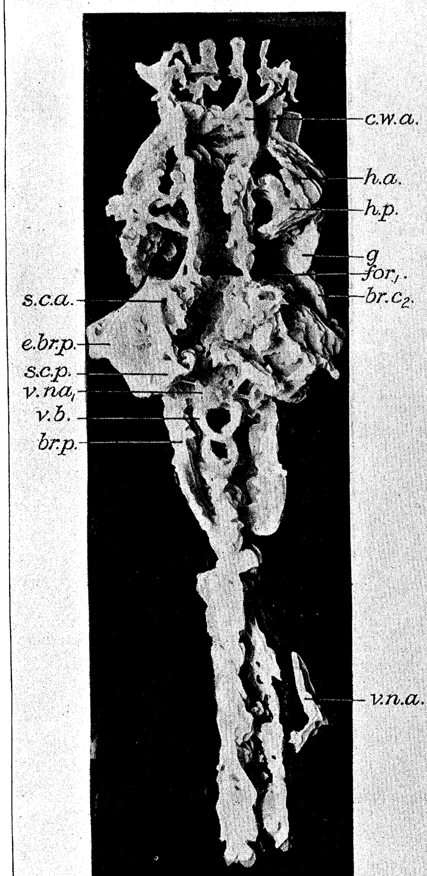

Fig. 1.

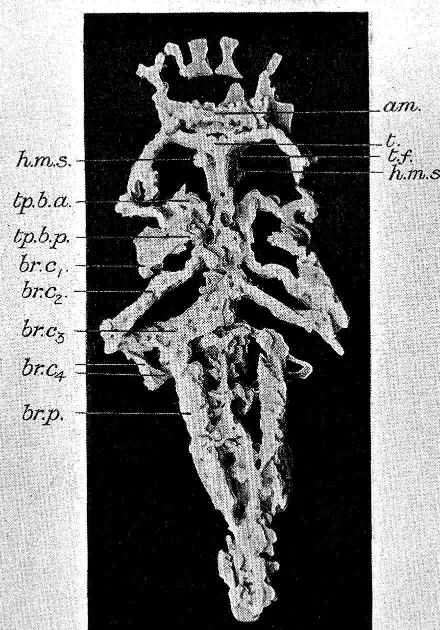

Fig. 2.

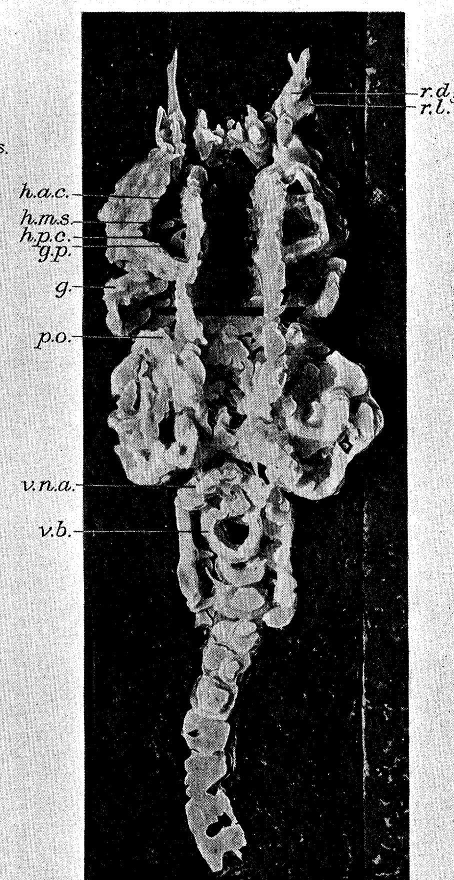

Fig. 3.

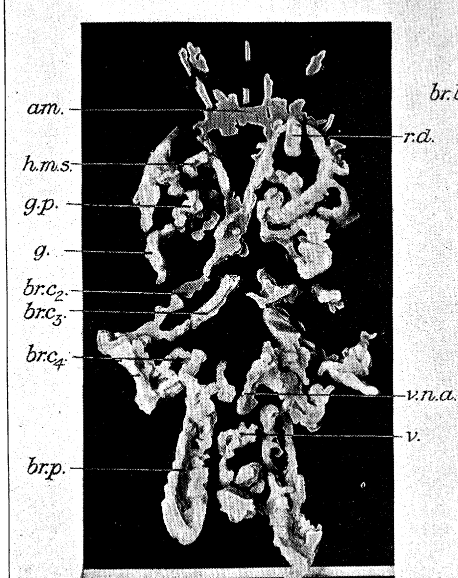

Fig. 6.

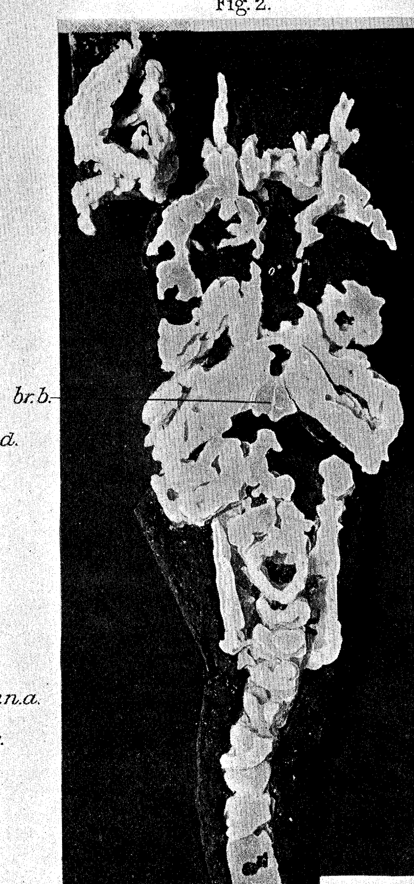

Fig. 4.

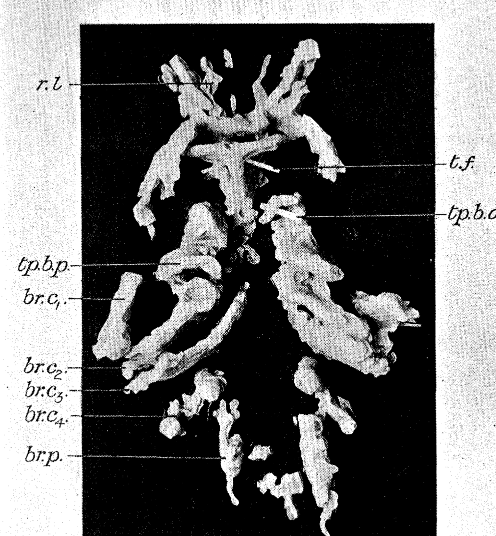

Fig. 5.

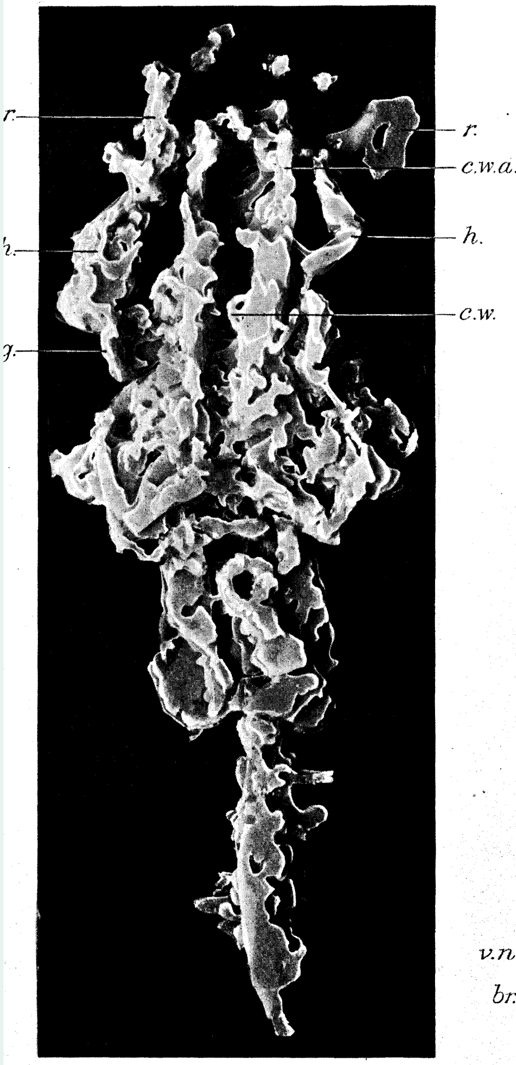

Fig. 7.

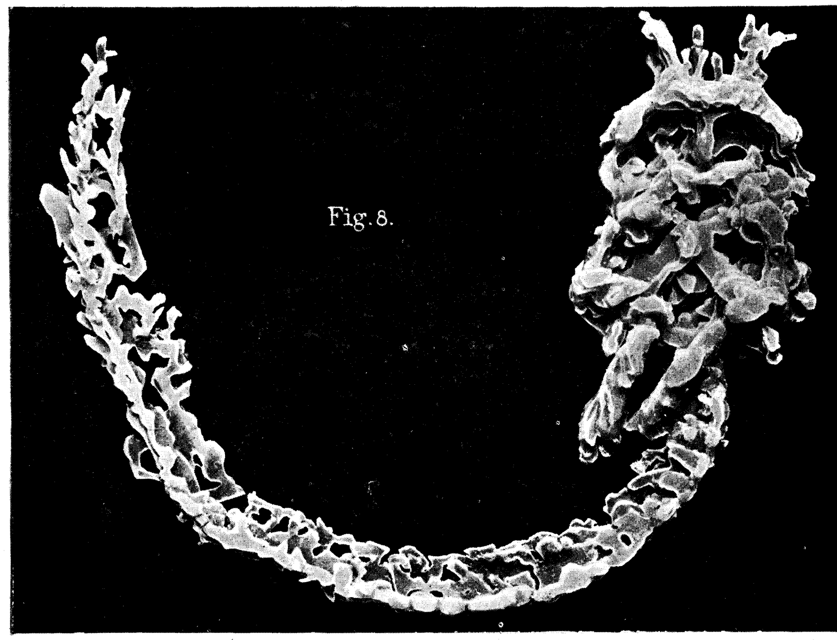

Fig. 8.

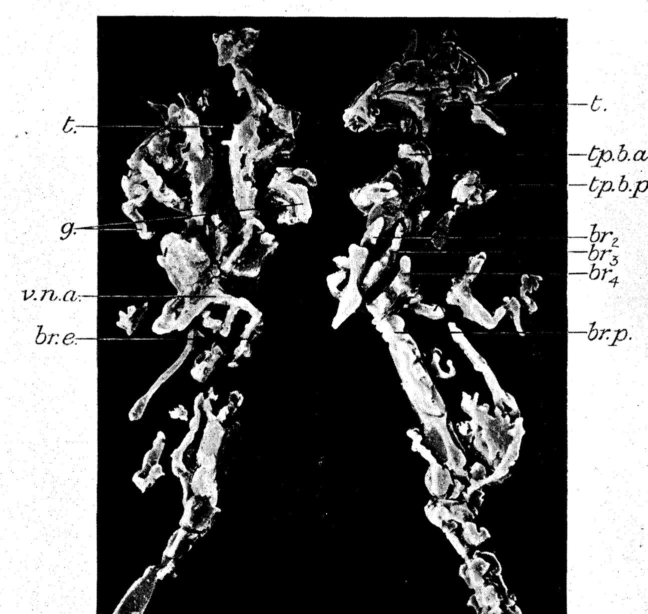

Fig. 12.

Fig. 9.

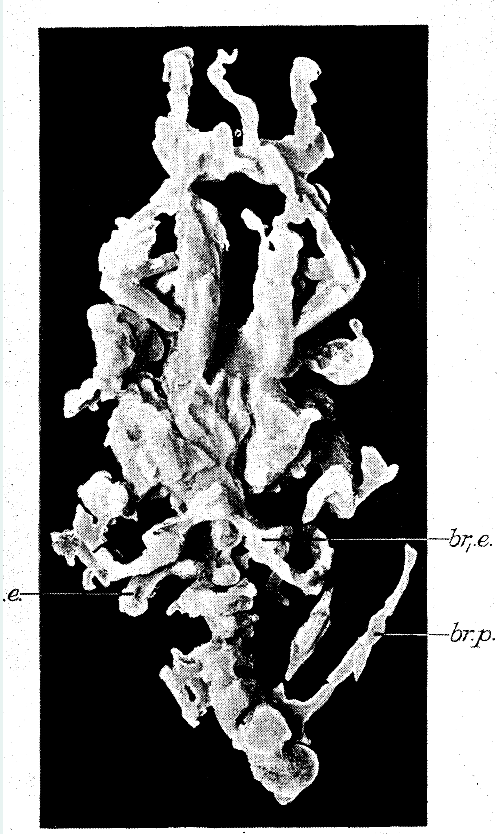

Fig. 10.

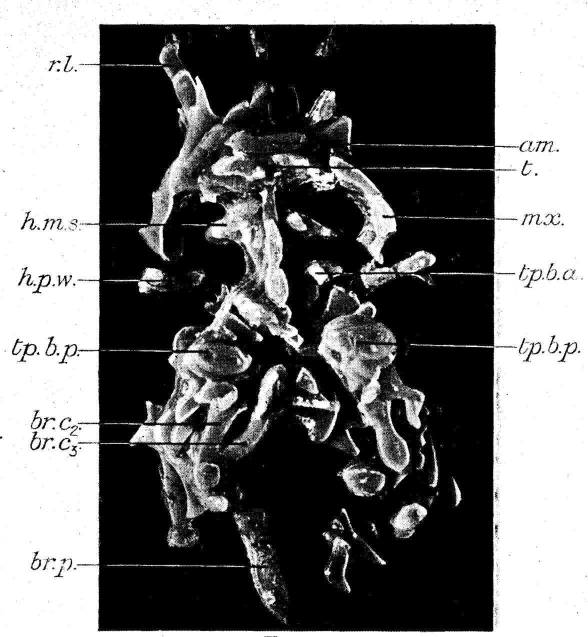

Fig. 11.

Fig. 13.

T.P. Collings.

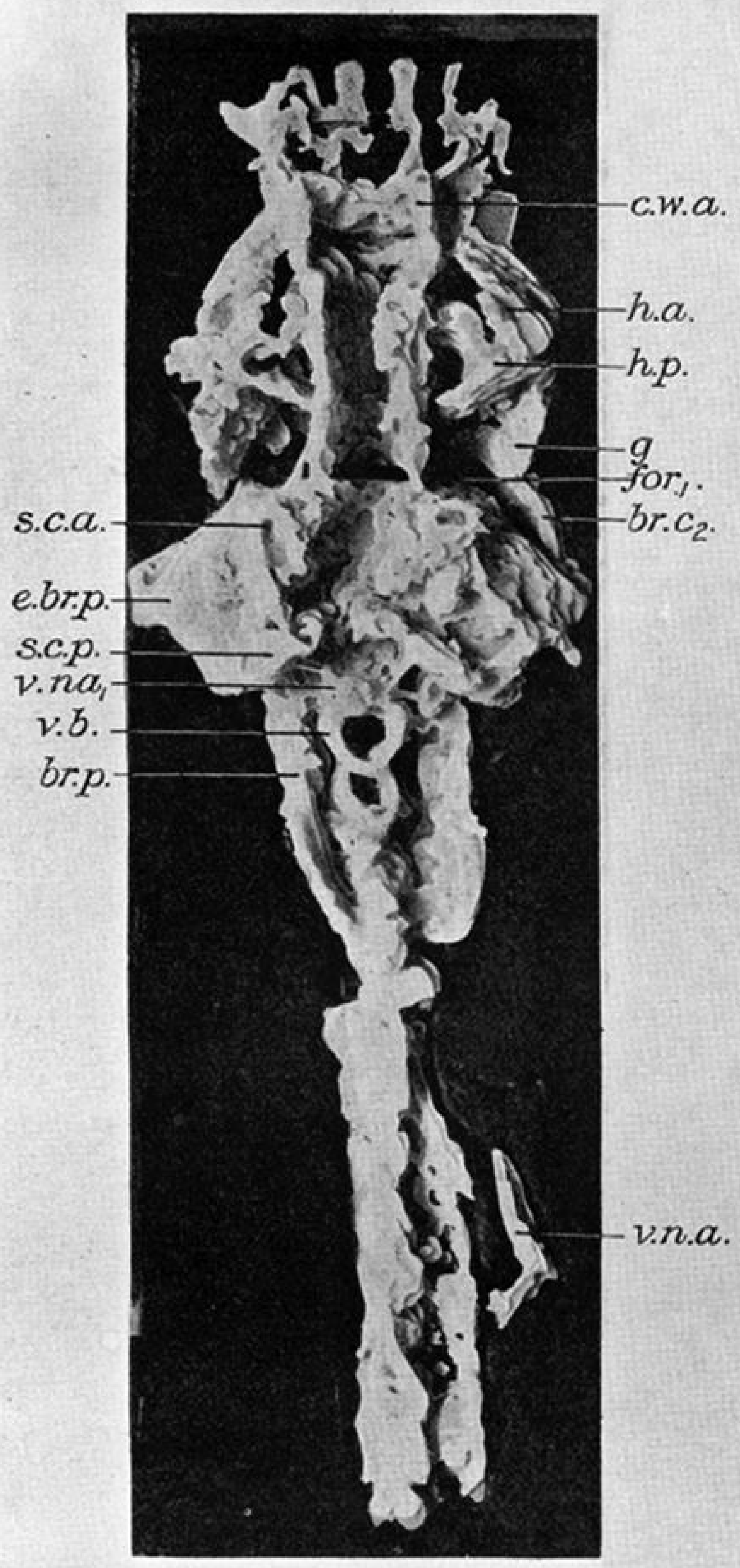

Fig. 1.

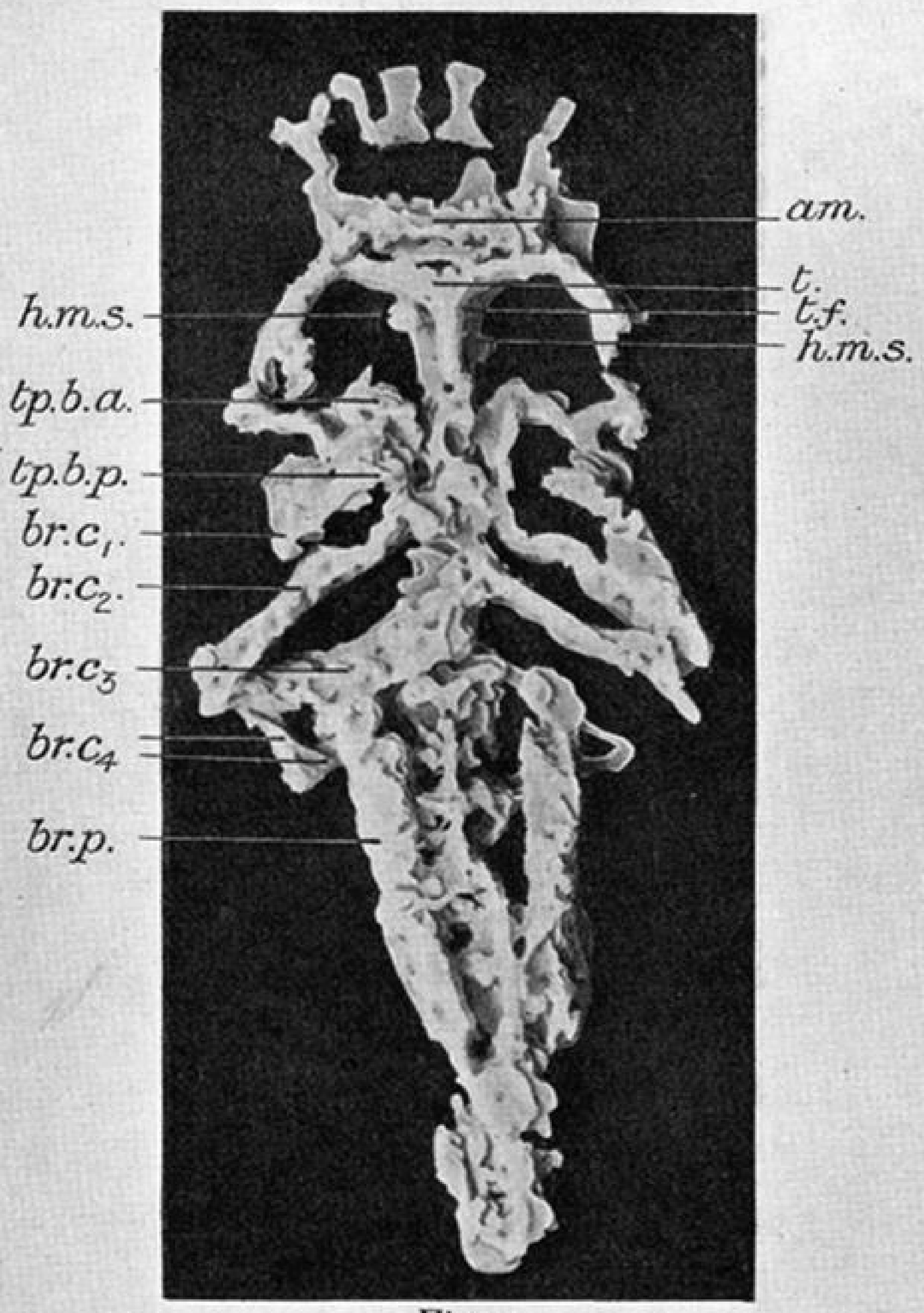

Fig. 2.

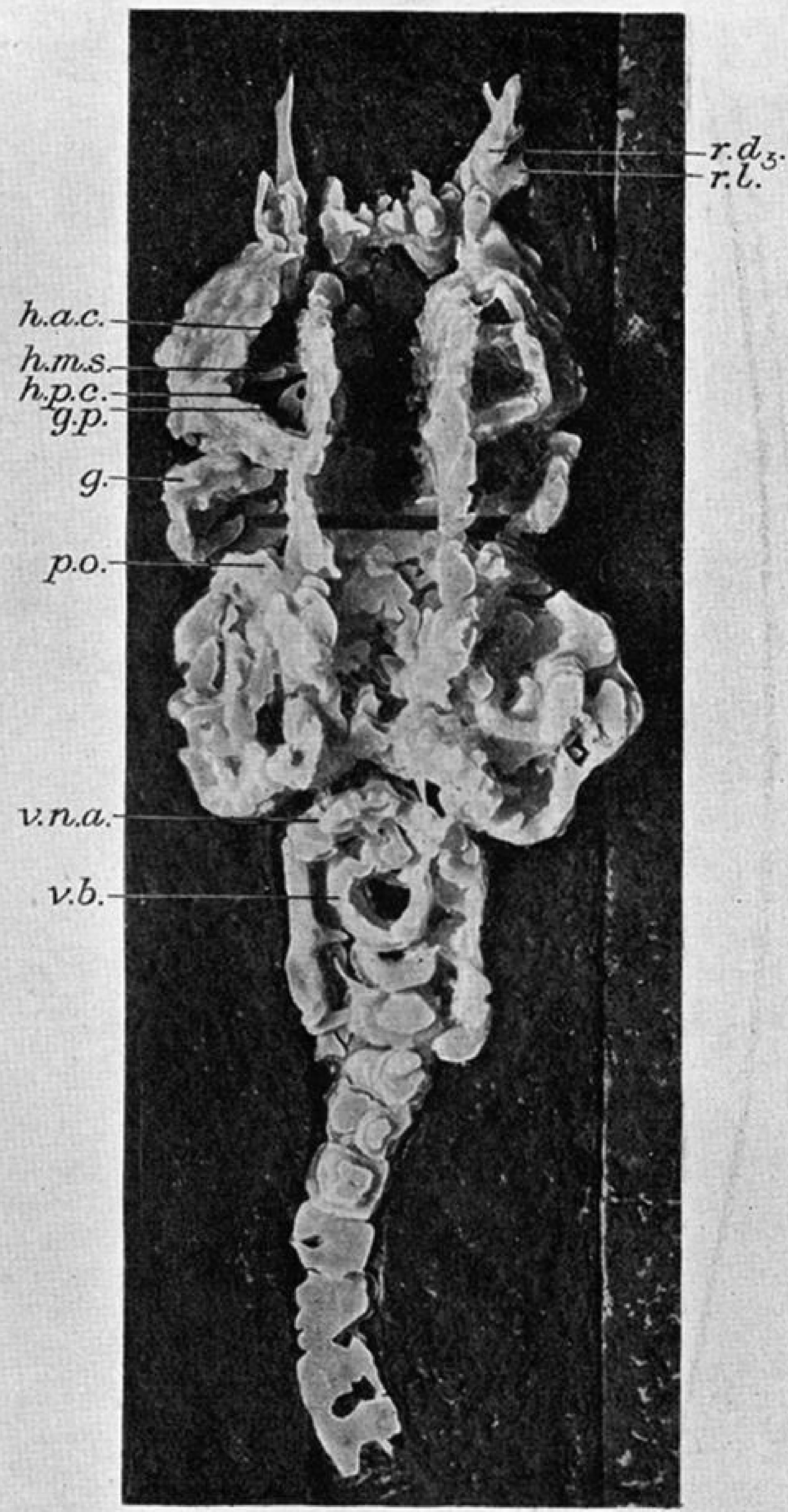

Fig. 3.

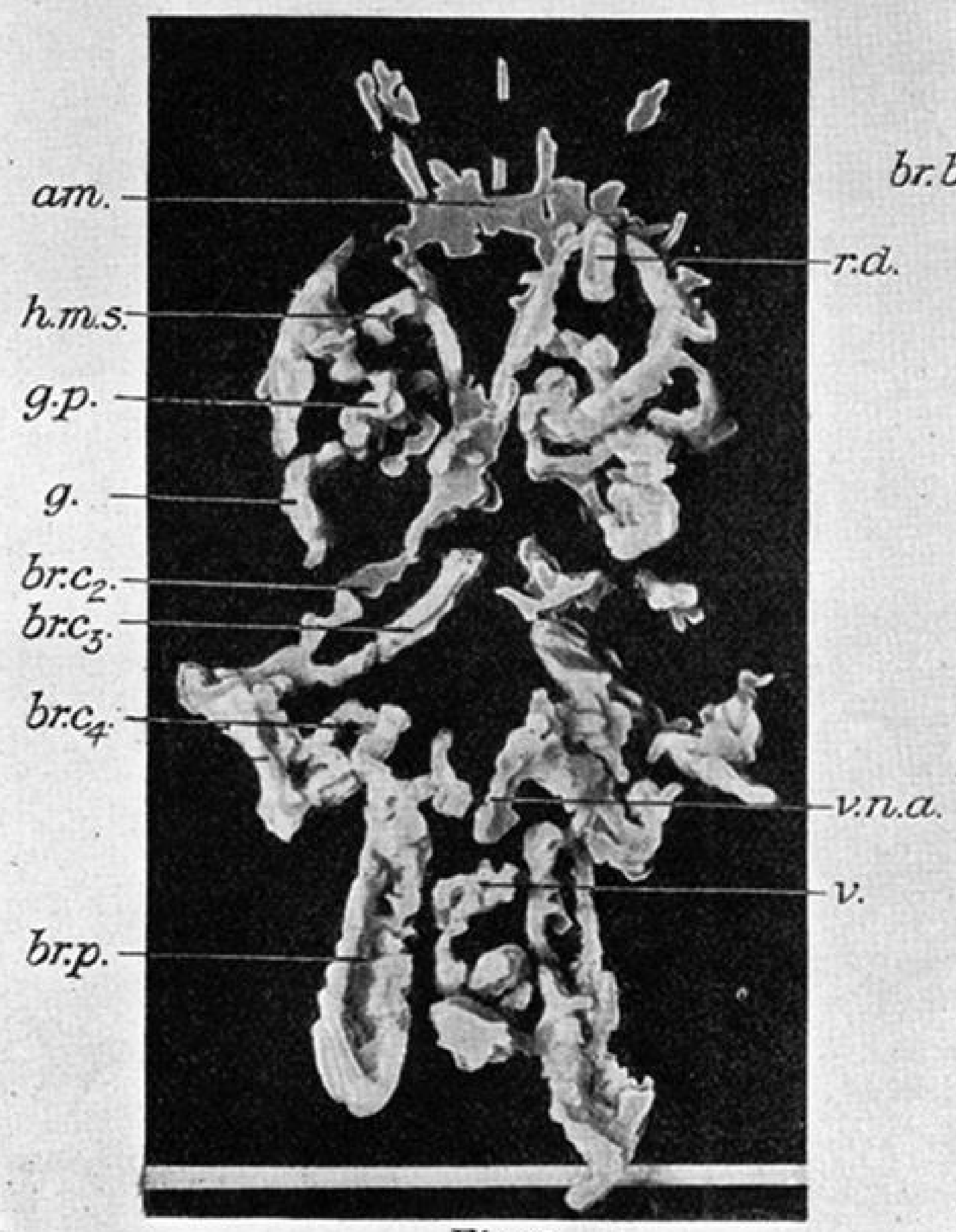

Fig. 6.

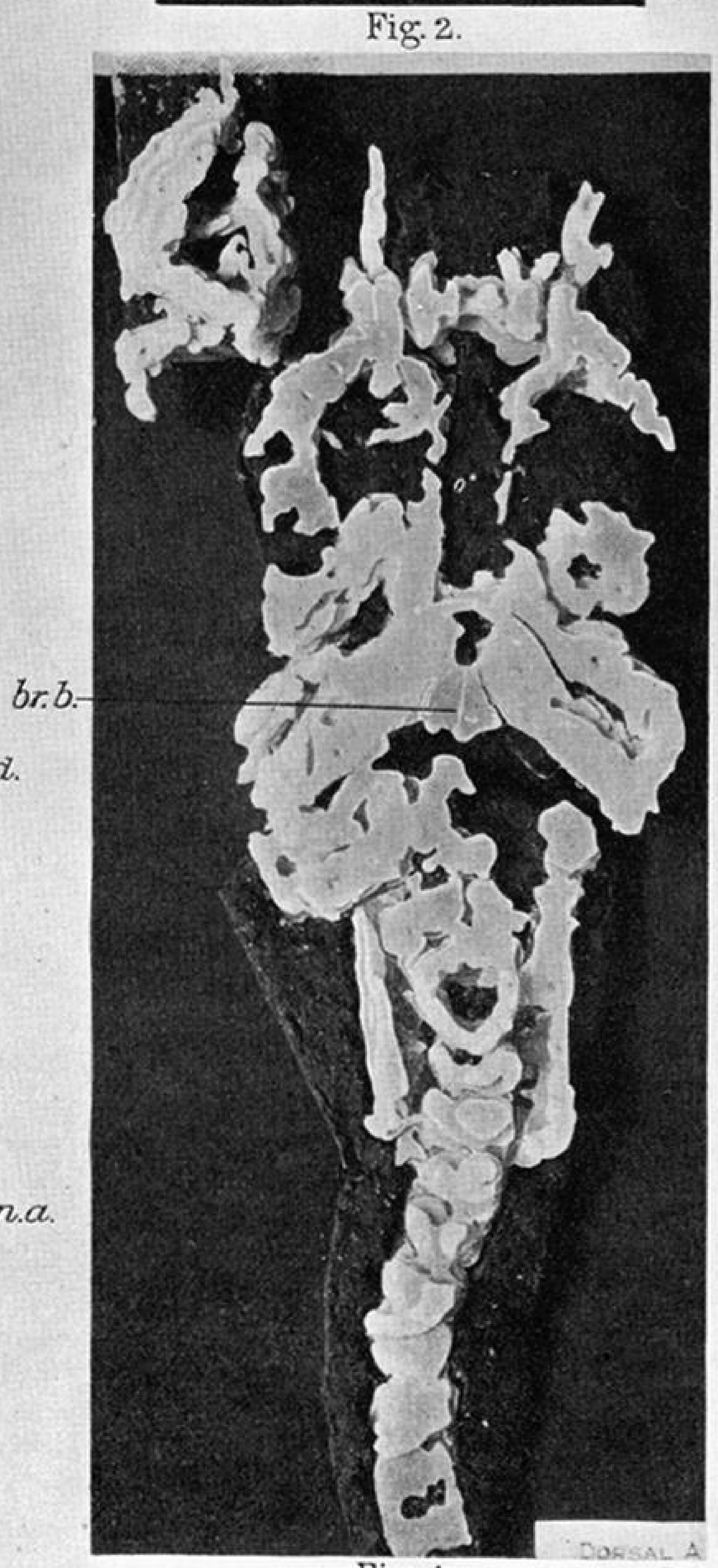

Fig. 4.

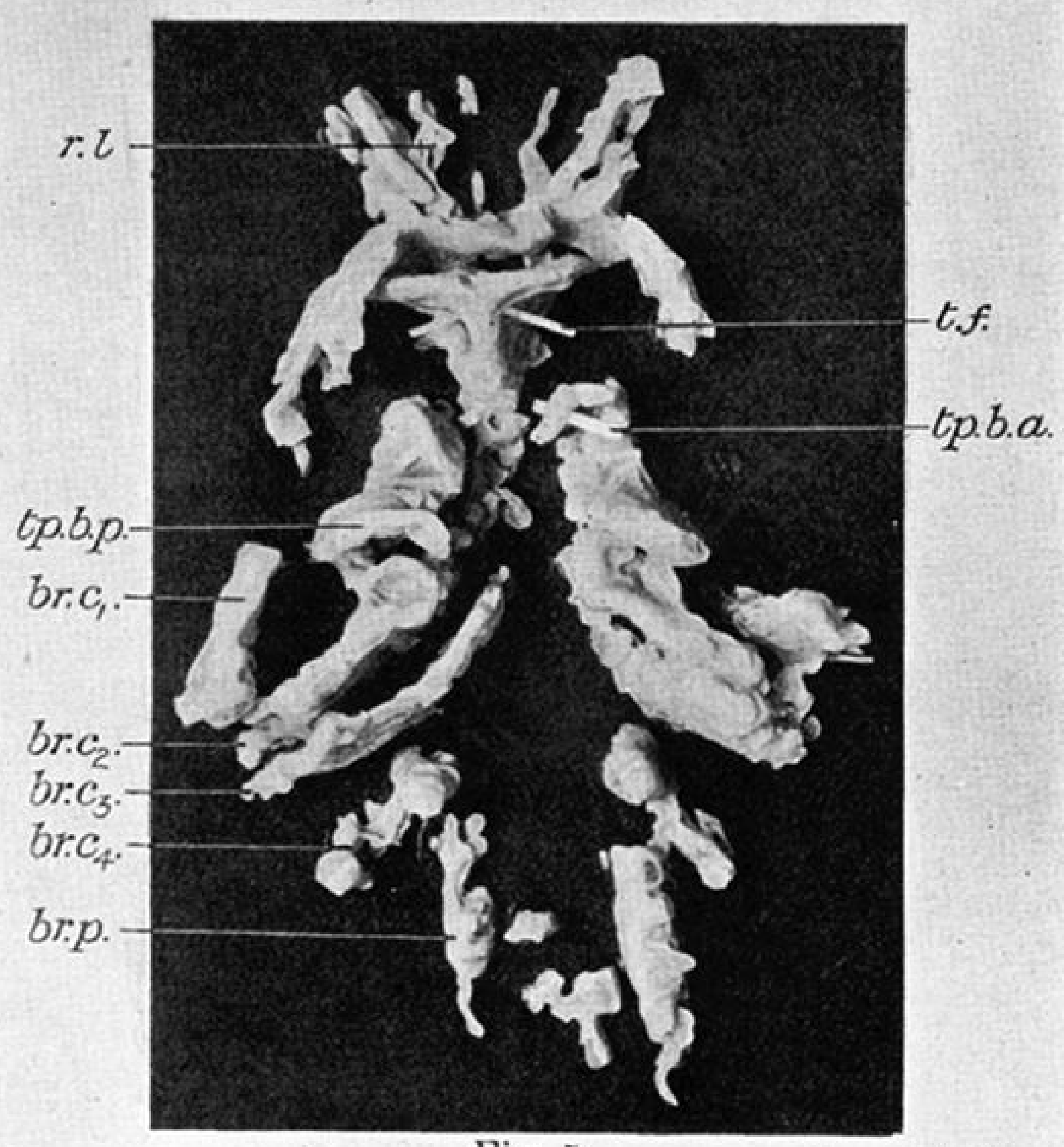

Fig. 5.

PLATE 16.

Fig. 1. Dorsal aspect of a reconstruction. In the specimen from which the reconstruction was obtained the ventral surface was exposed to view, the dorsal was embedded in the rock.

Fig. 2. Ventral surface of the same reconstruction.

Fig. 3. Dorsal aspect of a reconstruction. The specimen was embedded in the same way as that of Fig. 1. The ventral surface was consequently imperfect. A slight distortion has led to a shortening of the anterior region of the head, and to the concealment of the anterior cranial walls.

Fig. 4. The same reconstruction with the dorsal moiety removed. The left hemidome, with the gammation, pregammation, and a part of the cranial wall, is shown in the upper left-hand corner.

Fig. 5. Ventral aspect of a reconstruction. The specimen from which the reconstruction was obtained was embedded by the ventral surface, the dorsal side is therefore the less perfect.

Fig. 6. Dorsal aspect of the same reconstruction.

(The magnification of the figures on this plate is 10 diameters.)

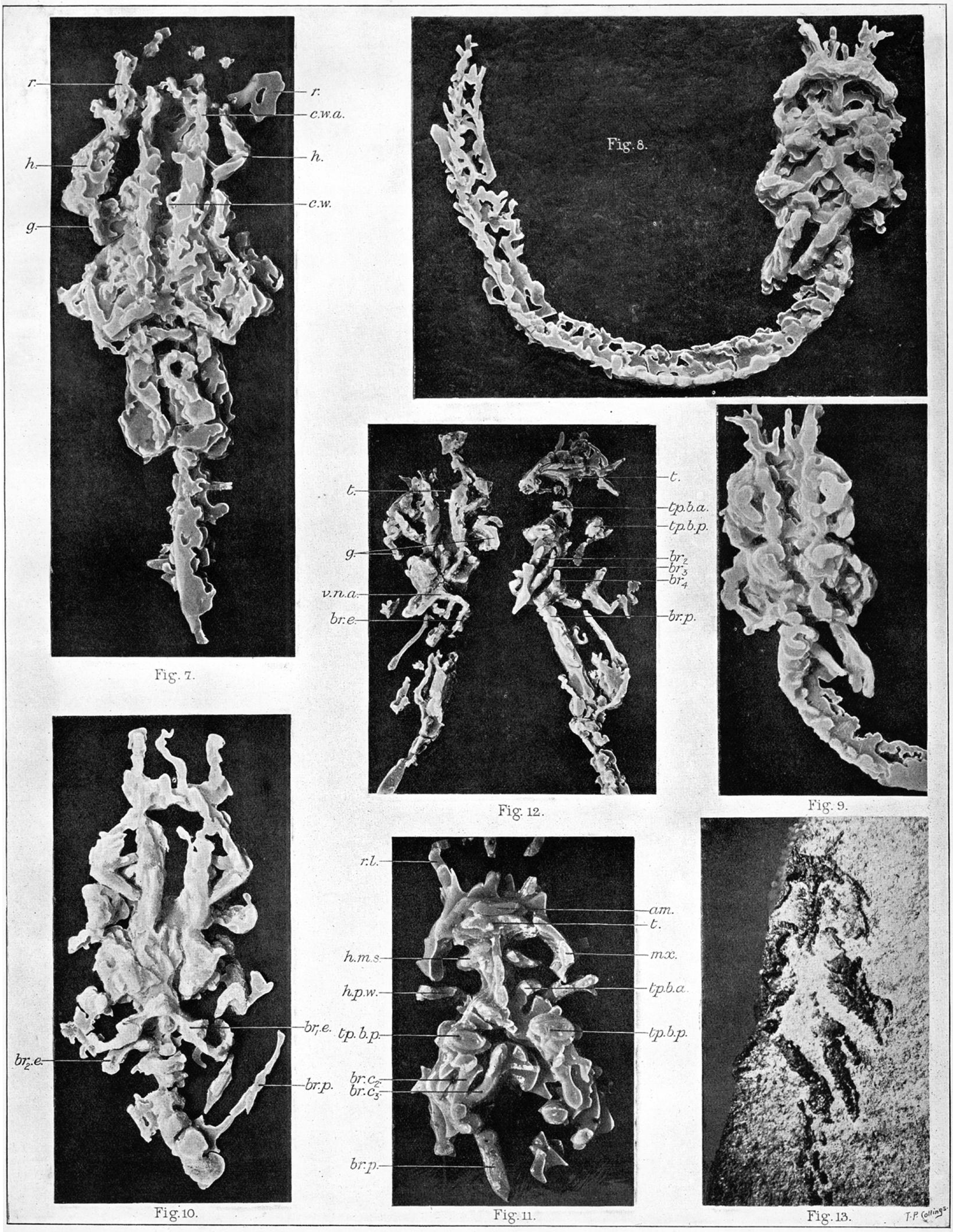

PLATE 17.

Fig. 7. Dorsal aspect of a reconstruction. The specimen was embedded on the dorsal side, but it had suffered much disturbance and decay before petrifaction. The reconstruction shows the cranial wall of the right side curving roof-like over the cranial cavity at the point marked *c.w.*

Fig. 8. Ventral aspect of a reconstruction. The specimen, which was the smallest in our collection, was embedded by the ventral surface.

Fig. 9. Dorsal aspect of the head of Fig. 8.

Fig. 10. Dorsal aspect of another reconstruction. The specimen was embedded on the dorsal side, and had been much compressed from above downwards.

(Figures 7 to 10 are magnified 15 diameters.)

NOTE.—The specimens from which the reconstructions shown in figs. 1 to 10 were obtained were cut at intervals of 0·025 millim.

Fig. 11. Ventral aspect of a reconstruction. The specimen was embedded on the ventral side. (Cut at intervals of 0·1 millim. $\times 7\frac{1}{2}$.)

Fig. 12. Both aspects of another reconstruction. (Cut at intervals of 0·1 millim. $\times$ 15.)

Fig. 13. Ventral surface of an actual specimen ($\times 7\frac{1}{2}$).