II—THE ACANTHODIAN FISHES

By D. M. S. WATSON, F.R.S., *Jodrell Professor of Zoology and Comparative Anatomy, University College, London*

(*Received* 22 *December* 1936—*Read* 29 *April* 1937)

[Plates 5–14]

CONTENTS

Introduction

The Acanthodian fishes form one of the most sharply demarcated and recognizable groups of vertebrate fossils. Their characteristic squamation of square, exceedingly minute ganoid scales, and the fact that all the fins except the caudal fin are supported by large anterior spines, distinguish them sharply from all other fishes, and enable even fragmentary specimens to be recognized without doubt. They are worldwide in distribution, and their range in time is thus known with considerable certainty.

The first fragments, attributed on very good evidence to the group, are isolated fin spines, found in Upper Silurian rocks perhaps not earlier than the Downtonian, which seem to be identical with those found in complete fishes of Lower Devonian age.

The group was more varied in structure and played a larger part in the world in Lower Devonian times than at any other period. Even in the Middle Old Red Sandstone the range in structure had been reduced, and by Carboniferous times very few forms remained.

Finally the group disappears during the Lower Permian, occurring, essentially in the form of a single species, in the Rothliegende of Europe.

Thus the Acanthodians were the earliest group of vertebrates, apart from the Ostracodermi, to reach their maximum and decline, antedating all certain Elasmobranchs and all bony fishes, and even the Arthrodeirs and Antiarchi. They have therefore a special interest because now it is known from the work of Professors Stensio and Kaeir that the Ostracodermi are related to the lampreys, the Acanthodians become the most archaic and earliest of gnathostomes, and their morphology, when fully understood, may be expected to throw light on all the various problems connected with the formation of the jaws and the backward migration of the mouth which is associated with them.

Material representing Acanthodian fishes is locally abundant at all periods from the Lower Devonian to the Permian, but very little of it is sufficiently well preserved to display much of the structure of the head. The fishes from the Lower Old Red Sandstone of Turin Hill and Farnell in Forfarshire are often perfectly preserved so far as their external surface is concerned, but they give exceedingly little evidence as to the character of the endoskeleton, either of the head, trunk or fins.

The Middle Old Red Acanthodians from the nodule localities of the Moray Firth are sometimes beautifully preserved, but they also are crushed flat, and consequently the traces of neural cranium visible in them are unintelligible.

Specimens of *Acanthodes* from the Coal Measure Ironstones may be little crushed and well preserved, but they are remarkably rare and I have been able to do little with them.

There remains therefore only "*Acanthodes bronnii*", which is common and in many ways exceedingly well preserved in the Ironstone nodules from the Lebach shales near Saarbruck. This fish is indeed the only Acanthodian the structure of whose head can be determined at all completely, but as it is the last surviving member of the group it is not necessarily representative of the structure of the majority of the genera, although it must conform to the underlying morphology of the group.

The literature dealing with Acanthodians is exceedingly extensive. Beginning with the foundation of the genus *Acanthodes* by Agassiz in the "Poissons Fossiles", they have been dealt with by nearly every author who has concerned himself with fossil fishes, but few have added materially to our knowledge of the structure of any member of the group. Roemer (1857), Kner (1868), Powrie (1864, 1870), Traquair (1894), and Smith Woodward (1891) are the most important references for our general knowledge, otherwise than of the head.

The head skeleton of *Acanthodes bronnii* was described by O. M. Reis in a series of papers, of which the latest and most important are two published in 1895 and 1896. One of them (1895) consists of a series of plates containing admirable and, in the only case in which I have made direct comparison with the original, scrupulously accurate drawings of the head. The other (1896) contains a detailed description and discussion of the morphology of the whole skeleton. This paper has never received the attention that it deserves because it is exceedingly difficult to follow without actual material at hand, and it contains one or two suggestions which cannot be supported; but it is in general, so far as I can claim to understand it, accurate as to its facts, as distinguished from the interpretation sometimes placed on them. The only two authors who seem seriously to have considered REIS's papers are JAEKEL and BASHFORD DEAN. The former made a series of magnificent preparations of the material of *Acanthodes bronnii* in Berlin and elsewhere, but never gave a connected account of the structure which they showed, contenting himself with partial drawings and descriptions scattered throughout papers dealing with very different subjects over a period of a quarter of a century, and indulging in occasional polemics with REIS. Professor BASHFORD DEAN (1907) examined some of Professor JAEKEL's material and gave, in a short paper in the *American Journal of Anatomy*, a discussion of certain parts of the anatomy of "Acanthodian sharks" which contained many important observations and criticisms of the views of REIS, JAEKEL and SMITH WOODWARD, together with some admirable drawings illustrating anatomical details.

Thus, despite the extent of the literature, our real knowledge of the Acanthodians is limited in extent, and scarcely justifies the certainty with which these fishes have been referred to the Elasmobranchii, or to some other position in the class Pisces. Acanthodian material is abundant; in connexion with this paper I must have examined about 1000 specimens, but of these very few are of value for the study of the morphology of the head. The general absence of dermal bones which are individually recognizable, the exceedingly small size of all the scales and head plates, and the fact that when crushed flat, as with very few exceptions all Acanthodians are, the two surfaces of the head become so closely pressed on to one another that it is difficult to distinguish their structures no matter how well the individual bones may be preserved, probably account for the fact that the Acanthodians are now the only group of primitive fishes of whose morphology we have no detailed knowledge.

The method of investigation I used is as follows.

The head of the specimen was photographed with carefully considered lighting and often through a coloured screen, and an enlargement at a magnification of from 3 to 10 diameters was made from the negative.

Miss JOYCE TOWNEND then inked in on the enlargement the borders of all the individual bones visible in the specimen when examined under a fairly high-power (30 diam.) binocular microscope. I then discussed any doubtful points with Miss TOWNEND until we reached agreement.

Then from the photograph of the best available specimen outlined in this way, we made a reconstruction of the head, controlling the results by making hypothetical transverse sections, and projections on other planes.

We then checked the restoration by comparison with the inked-in photographs of all other specimens, determining the proportionate sizes by direct comparison of some well-marked structure like Meckel's cartilage or a pectoral fin spine. By such comparisons additional details can often be added to the restoration. The whole process is exceedingly laborious, but it does give considerable certainty and leads to the discovery of many otherwise unobserved facts.

As no existing account of any Acanthodian is reasonably complete, accurate and intelligible, I have thought it well, in view of the great morphological importance of their structure, to give straightforward accounts of the structure (so far as it is known to me) of *Climatius reticulatus*, *Euthacanthus macnicoli*, *Brachyacanthus scutiger*, *Parexus incurvus*, *Mesacanthus mitchelli* and *Ischnacanthus gracilis* from the Lower Old Red Sandstone of Forfarshire, of *Diplacanthus striatus* and *Cheiracanthus* from the Middle Old Red Sandstone of the Moray Firth and of *Acanthodes* from the Upper Carboniferous Ironstones of Lebach in the Saar.

Climatius reticulatus

Climatius reticulatus is the third most abundant fish in the Lower Old Red Sandstone of Turin Hill, but is none the less an uncommon fish, contrasted with the numbers of *Mesacanthus* and *Ischnacanthus* to be found there.

The more important specimens are: B.M.N.H. No. 38596, and its counterpart Powrie Collection 1891, 92, 198 in the Royal Scottish Museum. This fish has been so preserved that the dorsal surface and right lateral surface of the head are seen on one slab, and the left lateral and ventral surfaces on the other. The dermal bones are displayed from their visceral surface and are in perfect condition.

L. 12096, A and B, Manchester Museum, is the most complete existing specimen and is valuable for the structure of the head, dentition, fins and body shape.

Powrie 1891, 92, 206, R.S.M., and its counterpart P. 6961, B.M.N.H., show the ventral surface of the head and shoulder girdle very well.

Royal Scottish Museum 1887, 35, 5, and counterpart P. 6961*a*, B.M.N.H., are important for the shoulder girdle, the orbits and anterior end of the head.

No. 49785, Museum of Practical Geology, has a good palato-quadrate and Meckel's cartilage.

Powrie 1891, 92, 204, R.S.M., is the only well-preserved laterally compressed fish.

The majority of the specimens of this species are crushed dorso-ventrally as far back as the pectoral region, but the posterior part of the body is seen in direct lateral view. As a result of this condition the intermediate spines of the two sides, which lie between the pectoral and pelvic fins, fall on one another and become singularly difficult to count.

Head—No traces of the neural cranium are ever to be seen, and it is certain that it lacked completely all calcifications. The palato-quadrate and Meckel's cartilage are, however, usually calcified; they are never well preserved, and it is probable that the hardened layer was entirely superficial. It appears very finely granular, differing from the bone of the scapula and from all the dermal elements in its texture. The material has not been investigated microscopically but is quite obviously not comparable with Elasmobranch cartilage calcification.

The jaws are best shown in No. 49725, Geological Survey, and in the Edinburgh specimen Powrie 206. The palato-quadrate is in principle like that of a dogfish; it has a deep posterior portion whose upper border is turned outward as a ridge but forms a smoothly curved margin which gradually sinks to the shallow anterior end, where it is cut out into two shallow bays. It is certain that there is no otic process homologous with that of *Acanthodes*, *Heptanchus*, etc.

Meckel's cartilage appears to extend forward to meet its fellow at a place a little in front of the anterior extremity of the palato-quadrate. It has a typical Elasmobranch appearance with a deep rounded posterior part, becoming shallower anteriorly but remaining rather massive to its end.

There are no teeth visible in the upper jaw but many specimens show the lower dentition, always very imperfectly because of its remarkable nature. The lower dentition seems to extend uninterruptedly and without any recognizable change of character from a point half-way along the length of the jaw, round a semicircular symphysis to the corresponding point on the other jaw. It is throughout composed of fused whorls of teeth whose bases coalesce to form a smooth cylindroid surface which was attached to the oral margin of Meckel's cartilage. The whorl seems to consist of at least three teeth. The individual teeth are most curious; each is thin in proportion to its width, and unexpectedly high. Its free extremity is broken up into three or five needle-pointed cusps by grooves on each surface of the tooth. These teeth are in detail quite unlike any others with which I am acquainted; in particular they do not in the least recall those of Elasmobranchs, although of course the whorl is in principle similar to the dentition of these far more recent fish.

The only other cartilages visible in the head are a crushed series of cerato-hyals, and probably two pairs of cerato-branchials seen from below in Powrie 206. They appear to be unsegmented and are so badly preserved that they cannot be further described.

The Dermal Bones of the Head—The whole external surface of the head is covered with an irregular mosaic of small polygonal ossicles, each one of which has a flat inner surface, whilst its outer surface is raised into a series of one or more denticles, each having its surface sculptured into a radiating series of angular ridges and grooves.

The dorsal surface of the head is perfectly shown from its inner side in No. 38596, B.M.N.H. In this specimen the normal regular squamation of the dorsal surface of the trunk suddenly passes over to a much more irregular arrangement of minute bones which in the mid-region of the head are no larger than ordinary scales. Farther to the side these bones gradually become larger until, above the gill chamber, the surface suddenly terminates in a row of relatively large elements, each about 2 mm. long. The whole width of the top of the head between the margins of the gill chambers is covered by about 15–17 bones. The marginal row of larger bones has attached to its lateral border a row of very narrow elements which perhaps turned downward to the inner surface of the gill chamber. At two neighbouring points the marginal row is produced downward on to the summits of the hyoid and first branchial arch.

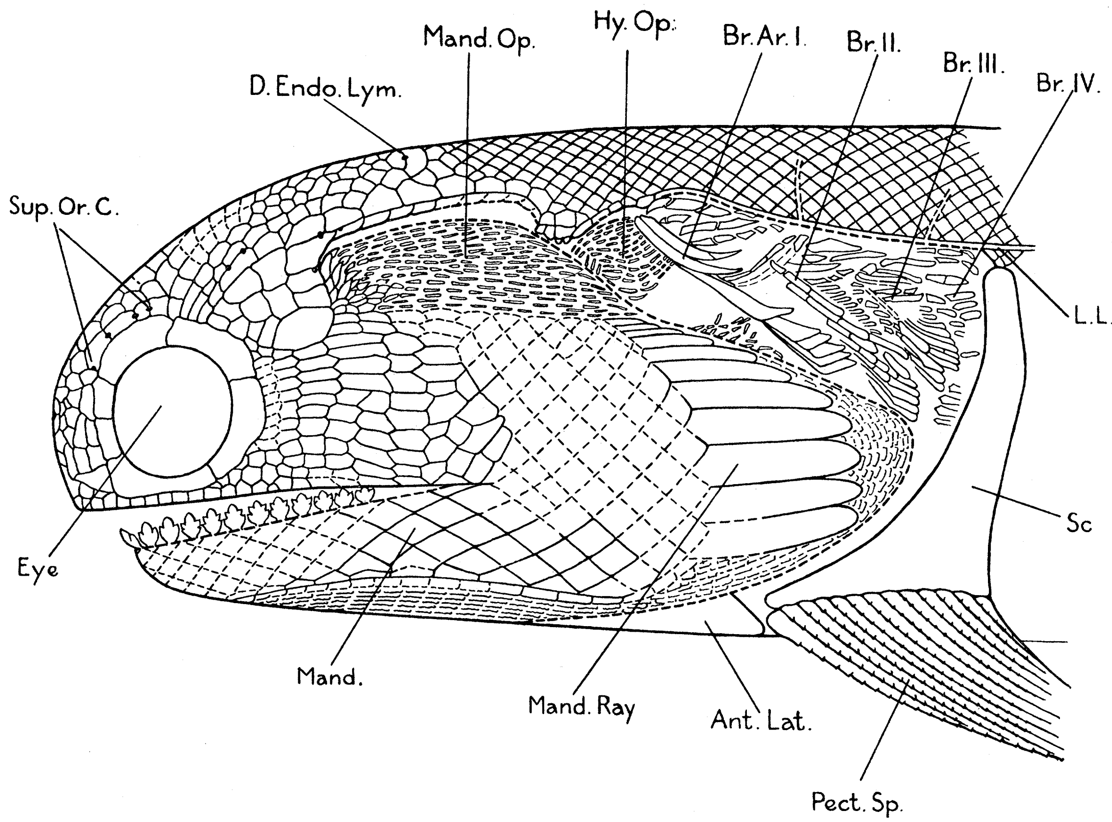


FIG. 1—*Climatius reticulatus* AG. × about 2·0. Reconstruction of the head founded almost entirely on the single specimen B.M.N.H. 38596 and Powrie 1891, 92, 198, from the L.O.R.S. of Turin Hill. All structures surrounded by continuous lines are accurate drawings from this specimen. *Ant.Lat.* antero-lateral dermal bone of the shoulder girdle; *Br.Ar.* I, *Br.* II, etc., the dermal elements of the branchial arches and their opercula; *D.Endo.Lym.* foramen for the ductus endolymphaticus; *Eye*, the orbit; *Hy.Op.* hyoid operculum; *L.L.* lateral-line; *Mand.* mandible; *Mand.Op.* mandibular operculum dorsal end; *Mand.Ray*, a "ray" in the mandibular operculum whose posterior margin is a thick broken line; *Pect.Sp.* pectoral spine; *Sc.* scapula; *Sup.Or.C.* supra-orbital canal.

There is only one recognizable irregularity in the roof of the skull in this region, the presence a little to each side of the mid-line of a pair of rather larger bones which meet one another in a straight transverse suture. On the left side in this suture there is a very minute foramen whose border lies mainly in the posterior bone; the opening is less clearly seen on the right. This foramen is no doubt for the ductus endolymphaticus.

The marginal row of bones of the temporal region is continued forward until it terminates in a large ossicle, separated by a single small element from the circum-orbital ring. The inter-orbital width is great, about as wide as the temporal region, and is covered with the ordinary polygonal ossicles, those which lie laterally being rather larger than the medial series.

The orbit is surrounded by a series of six large, massive bones, each of which has a smooth concave inner surface terminated by a low, rounded ridge which forms the actual orbital margin. The outer surface of each bone is very heavily ornamented with ridges which radiate from the centre of the orbit and bear series of low points. The free margins of this ring of circum-orbitals are attached by sutures of normal character to the surrounding dermal bones, so it is certain that the whole is not composed of sclerotic plates.

The anterior end of the head scarcely projects in front of the orbits and forms a smooth snout covered by irregular transverse rows each of about nine small bones. Only one specimen (Powrie 206) gives any evidence of nostrils; here on the left side there is a very small hole surrounded, at least so far as its dorsal border is concerned, by four radiately arranged elements. If this structure be correctly determined the two nostrils must have lain very close to one another and have been directed forward at a distance of about half the diameter of the orbit above the margin of the mouth. Other specimens, Edinburgh 1887, 35, 5 and Powrie 198, show this region well and make it certain that no nostril exists below this point, they also show no signs of a ventrally directed nostril opening below the ventral border of the dermal bones of the snout.

The mouth has no distinct borders. Its upper margin is quite indefinite, being marked only by the disappearance of the small dermal bones attached to the circum-orbital bones, the most ventral of which seems actually to be separated from the border by a single row of small bones. In the mid-line there is a larger though still very small bone which is symmetrical and bears a median knob.

Behind the eyes, and immediately below the large bone which marks the anterior end of the marginal series of the temporal region, lie a series of very narrow elongated bones which form horizontal rows. Posteriorly these pass gradually into a quite irregular mosaic of larger polygonal ossicles which extend downward without any break to the lower margin of the lower jaw behind the angle of the rather short mouth. In B.M.N.H. No. 38596 this area of the cheek has a very definite upper and posterior limit, which coincides with that of the palato-quadrate cartilage, and is probably co-extensive with Meckel's cartilage. This border lies parallel to, but is far removed from, the lateral border of the temporal region and its continuation on the anterior part of the body squamation above and behind the gill chamber.

The characters of the pharyngeal region are only shown quite satisfactorily in B.M.N.H. No. 38596 and its counterpart Powrie 198, but other specimens provide confirmatory evidence for most of the more important features.

The well-defined, clear-cut edge of the gill chamber is very obvious and implies the presence of an opercular apparatus and the depression of the gill-bearing region. The anterior part of the operculum (*Mand.Op.*) is well shown as a sheet of skin containing very small elongated ossicles lying in irregular horizontal rows, a little separated from one another. The whole structure is attached to the cheek along a line on the level of the free upper border of the hinder part of the palato-quadrate. This operculum is bounded anteriorly by a series of larger but still very small bones arranged in a sickle shape; the upper border is bounded by a single row of similar bones, pulled away from the margin of the temporal region. This operculum is shown definitely to pass laterally to the downward projection of the temporal region on to the upper end of the hyoid arch. Below this point the operculum is destroyed, its place being in part occupied by five small opercular (?) rays, all misplaced, and in some cases lying on the inner surface of the operculum; it is uncertain whether these elements belong to the series described below or are misplaced hyoidean bones. The next visible element of the operculum consists of a series of very large thick bony rays (*Mand.Ray*), whose long dorsal and ventral borders are in contact with one another. The anterior ends of these rays are joined to the posterior ossicles of the cheek by ordinary attachments without any sign of a definite movable articulation. It is quite evident from the whole material (especially Powrie 204) that these opercular rays are attached by their anterior ends to the outer surfaces of the articular ends of the palato-quadrate and Meckel's cartilage. The most ventral of these rays lies in a single continuous opercular fold which is shown in Powrie 198 and 206 to stretch across between the two rami of the lower jaw and cover the whole ventral region of the pharynx until its hinder border overlaps the anterior ends of the large bones which form the ventral part of the shoulder girdle. This part of the operculum contains irregular rows of very elongated, narrow but thick ornamental bones which lie in festoons parallel to the lower jaw, with the ventral row of whose dermal covering they seem to be continuous.

L. 1209*a*, Manchester, shows the opercular apparatus well. In this specimen it seems that the small displaced rays of B.M.N.H. 38596 are represented by similar structures in their natural position, and that they lie in series dorsally to the large opercular rays which are so well shown in that specimen. Part of the shoulder girdle hides the hyoid arch, but the first and second branchial arches are well shown and agree exactly with those in B.M.N.H. 38596.

It is thus obvious that the most anterior and dorsal part of this operculum is attached to the mandibular arch, and I think it probable that the whole structure I have just described belongs to that cranial segment. But the unfortunate break in the structure in B.M.N.H. 38596 makes it possible to regard the series of large rays, and of course everything lying below them, as of hyoidean position.

The hyoidean arch certainly supports an opercular fold. The upper extremity of the outer face of the hyoidean gill septum is covered by a small patch of polygonal bones, similar to, though smaller than those which pass downward behind the eye to the dermal covering of the cheek. From this area arises an operculum containing the customary very small bones capped by large and sickle-shaped elements exactly similar to those which mark the anterior and upper end of the mandibular operculum. This small patch of operculum can be traced ventrally to the area covered by the polygonal scales. The exactly similar elements which occur in the same position on the first branchial arch are attached anteriorly to a long, dorso-ventrally directed bony splint which lies in the skin of that gill septum. This condition makes it possible that the small rays in B.M.N.H. 38596, plausibly interpreted as parts of the mandibular operculum, really held a similar position on the hyoid arch. If this were the case then they must have passed downward to a point ventral to the upper border of the palato-quadrate and the mosaic of dermal bones lying over it, and we should have direct evidence that the gill slit between the mandibular and hyoid arches was of full size. I feel it difficult, however, to believe that these long splints could have been stripped away leaving undisturbed a small patch of operculum of much more delicate structure, to which they once gave support. It is thus probable that, in contrast to the first branchial arch, the hyoidean arch remained with a very delicate dermal coating, presumably because it lay for the greater part of its length mesial to the palato-quadrate.

The first branchial arch has its dorsal end covered by a patch of polygonal bones similar to, though smaller than that which occupies the corresponding region of the hyoid arch. Below this the outer surface is covered by a series of narrow, elongated bones in each of which the lower part of the long anterior border rests on the upper part of the posterior border of the one lying below it. The series forms a very narrow belt extending from above downward and a little backward. The whole carries an opercular fold whose dorsal part is supported by slender sickle-shaped bones below which is a region with small ossicles like those in the corresponding regions of the mandibular and hyoid opercula. At the level of the most dorsal of the large mandibular opercular rays one of these splints has a backwardly turned extremity, and from this point downward there is an alternation of free rays and backwardly directed lower ends of splints forming a structure which, though on a much smaller scale, reproduces that attached to the mandible. The whole series then ends abruptly.

The second branchial arch has no dorsal coating of polygonal bones attached to the margin of the gill chamber. It bears a long series of splints which extend downward to a point ventral to the termination of those of the first arch. The lower end of this series turns a little forward. The upper edge of the operculum of this arch has the usual sickle-shaped ossicles, but the series of definite rays begins higher and extends farther down than in the case of the first branchial arch.

The third arch stands more vertically than the second; it has the same structure and its forwardly turned lower end lies even more ventrally.

Finally there is evidence of a short but similar fourth arch.

The general structure of the whole arrangement is obvious. The fish possessed a series of one pre-hyoidean and five branchial gill slits, each of very great dorso-ventral extent. An independent operculum was attached to the hinder border of each visceral arch from the mandibular to the fourth branchial. The backward extension of the palato-quadrate and Meckel's cartilages, necessary for the formation of the mouth and the attachment of a powerful jaw musculature, brought the hinder end of these elements over the lateral surface of the hyoidean arch and enabled the mandibular operculum to extend backward for a great distance, until in fact its ventral part came to rest on the front margin of the lower part of the shoulder girdle. This operculum, however, left uncovered a large triangular area above its dorsal margin. It is necessary for the functioning of the gill apparatus that the gill slits so left exposed should be provided with an opercular apparatus. This is done by the retention as functional structures of the dorsal parts of the small opercula (the homologues of the flaps in *Scyllium*, which become the frills of *Clamydoselache*) on the hyoidean and branchial arches. Each of these structures is provided with a bony skeleton, which ceases abruptly where it is overlapped by the main mandibular operculum. In fact *Climatius reticulatus* gives us for the first time a stage in the evolution of an operculate fish in which a relic of the Elasmobranch condition of the gill slits is still preserved.

The lateral-line of the body is represented by a groove which runs between two opposed rows of scales. This line continues along the free margin of the scaled area above the gill chamber and extends forward over the gill region to the patch of enlarged bones above and behind the eye. Above the upper ends of the second and third branchial arches short side branches of the lateral-line system are shown in B.M.N.H. 38596 to arise from the main "canal". The remainder of the lateral-line system is very incompletely shown, but it is evident that the arrangement agrees with that perfectly shown in *Climatius uncinatus* and *Euthacanthus macnicoli*. The greater part of the lateral-line system seems to have lain quite superficially above the exoskeleton, but in the anterior part of the main canal and the posterior part at any rate of the supra-orbital canal it lay deeper, the pores connecting it with the surface passing through circular holes made by a coincidence of notches in the borders of neighbouring bones.

Body—The most complete specimen of *Climatius reticulatus* is No. L. 12096, A and B, in the Manchester Museum, in which the anterior end is dorso-ventrally compressed and the hinder part of the body seen in side view, the tail being complete. A restoration made from this specimen shows an unexpectedly slender, fusiform fish, narrower at the pedicel of the caudal fin than most Acanthodians, with a long, very delicate upper caudal lobe directed only very slightly dorsally. No. 202, Powrie Collection, a laterally compressed fish, gives independent confirmation of this restoration. The squamation varies little in its character in different regions of the body; essentially the whole fish is covered with the customary square, Acanthodian scales which become smaller and lose their angles in the lower lobe of the caudal fin. The middle dorsal line of the body between the two dorsal fins bears a narrow strip, about six (?) scales wide, of rather larger scales, and similar rows lie along the upper and lower margins of the tail pedicel.

Median Fins—The anterior dorsal fin is supported by a spine of enormous antero-posterior length. This spine is laterally compressed, but is in all cases so crushed that its width cannot be determined. The outer surface bears an ornament of sharp-edged continuous ridges which at the base of attachment may number more than twenty, the

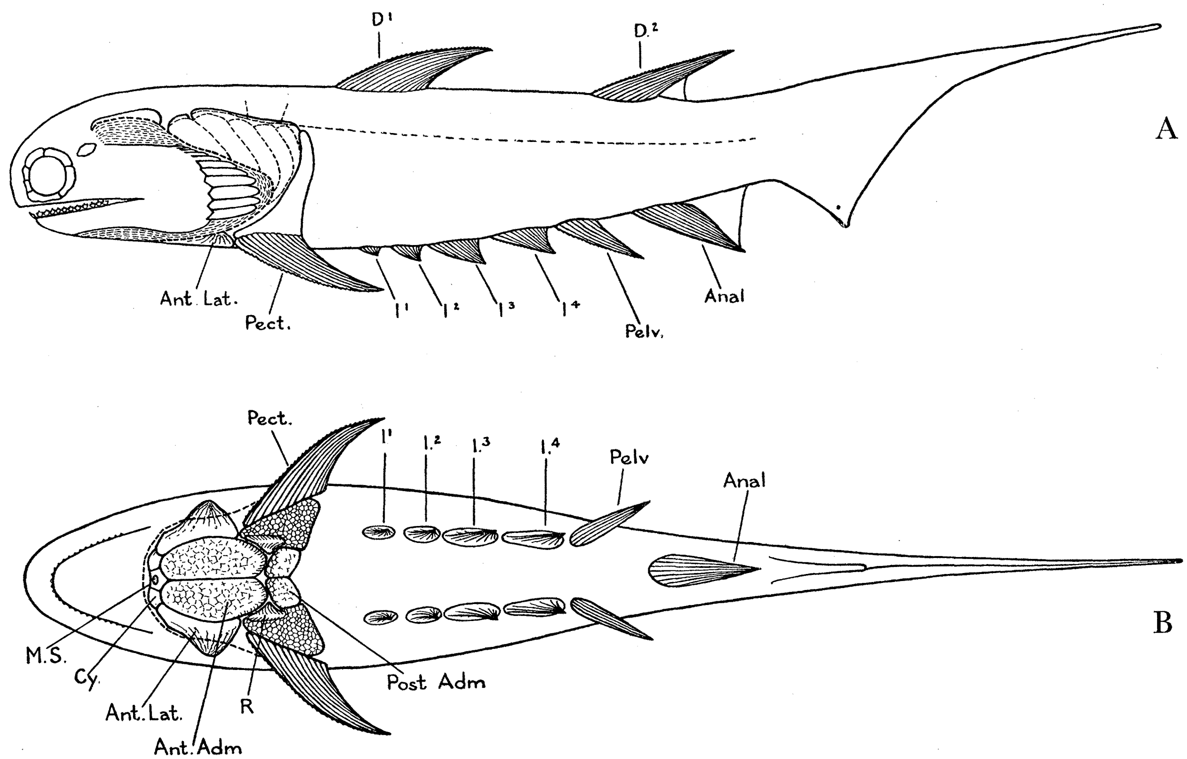


FIG. 2—*Climatius reticulatus* AG. × 1·0. Reconstruction of fish in left lateral view, A; ventral view, B. *Anal*, anal fin; *Ant.Adm.* anterior admedian dermal bone of shoulder girdle; *Ant.Lat.* anterior lateral of shoulder girdle; *Cy.* cylindrical dermal bone of shoulder girdle; D^1 and D^2, dorsal fins; I^1-I^4, intermediate spines; *M.S.* median dermal bone of shoulder girdle; *Pect.* pectoral fin spine; *Pelv.* pelvic fin spine; *Post.Adm.* posterior admedian of shoulder girdle; *R.* ridged dermal bone of shoulder girdle.

number being gradually reduced by the termination of individual ridges until toward the tip of the spine only about four or five remain. The spine is inserted very obliquely into the back and has no inserted base whatsoever, so that its attached margin fits into the ordinary squamation of the body, coming in contact with the lateral margins of scales in exactly the same way as each scale touches its neighbours. The basal two-thirds of the spine contain a very large conical cavity surrounded by thin walls; distally the whole becomes "solid". It is uncertain how far, if at all, the cavity of the spine opens posteriorly into the space within the fin membrane, no trace of which is ever to be seen. The second dorsal and anal fins have exactly the same structures as the first dorsal, except that in them the spine is a narrower structure and stands more vertically. Powrie 1891, 92, 206 shows a series of short ceratotrichia in the base of the anal fin.

The caudal fin includes the very prolonged and slender end of the body, and a small triangular hypocaudal expansion.

Paired Fins—The pectoral fin spines are long, well curved and very wide at their oblique base of insertion. The spine has an anterior ridge which bears a series of low, rounded points, the whole suggesting a series of overlapping scales. The ridges, about twelve in number, ornamenting the flat dorsal and ventral surfaces, bear similar but much lower projections. These spines, like that of the first dorsal which they greatly resemble, are hollow for a great part of their length. The spine is supported by a scapula which is certainly of subdermal origin. It stands vertically following the curve of the posterior end of the gill chamber and can be displaced without affecting at all the squamation lying in the skin over the pectoral region. The scapula rests with its lower border tightly attached to the basal edge of the dorsal surface of the spine, the two structures being so firmly attached to one another that they can be displaced and crushed without dislocation. The ventral surface of this region is covered by a series of powerful dermal bones which are functionally part of the shoulder girdle.

It is evident from the account of the structure of the pharyngeal region given above that the continuous part of the body below the gill slits was narrow and that in front of the pectoral fins there lies a triangular but rounded part of the ventral surface whose margins form the lower borders of the gill chambers. The margin of this area seems to have borne a series of dermal ossicles including anteriorly a low median spine (*M.S.*), to whose lateral border was attached a short, cylindrical bone (*Cy.*). Immediately in front of the pectoral spine there is another bone of a triangular shape forming part of a cylinder resting on the lateral and lower surfaces of the ventral part of the body and extending upward toward the gill slits, so that it is largely concealed by the operculum in lateral view (*Ant.Lat.*). The whole arrangement is completed by a bone, bearing a high, hollow, antero-posteriorly running ridge (*R.*) which is connected to the basal border of the ventral side of the pectoral spine by an area of tightly interlocked small bones, and by a flat dermal one (the anterior admedian) attached to the admedian edges of this bone and that which lies in front of it (the anterior lateral). This element meets its fellow in the middle line. Each anterior admedian lies in front of a small post-admedian which forms part of the posterior border of the shoulder girdle. The whole very complex arrangement can only be made out by careful comparisons of all the existing materials, especially specimens No. B.M.N.H. 38596; Manchester Museum L. 12096 A and B; Edinburgh 1887, 355 and 8*a*; Powrie 206, 204, 203 and 198. It is clear that there are minor differences between the conditions found in these specimens, but the bones are all recognizable as individuals.

There are usually three pairs of intermediate spines, but four may occur. Each is a mere conical cap attached to the ventro-lateral surface of the body by an oblique base. The outer surface is ornamented distally by longitudinal ribs which break up into points basally. The central cavity extends nearly to the tip of the spine. The distribution of these spines is shown in the restored figures.

The pelvic fin spines are similar to, though shorter than, the anal fin spine, and they have essentially the same structure. No supporting elements are to be seen at their base.

EUTHACANTHUS MACNICOLI

Euthacanthus macnicoli Powrie. The fish called *Euthacanthus macnicoli* by Powrie was subsequently referred by Smith Woodward to the genus *Climatius* and is unquestionably nearly related to that animal.

It is found rarely at Turin Hill, so it is fortunate that several specimens, the type Powrie 1891, 92, 231, Edinburgh; its counterpart No. P. 1337, B.M.N.H.; Powrie 236 and another unnumbered specimen in Edinburgh; No. 3329, the Museum of Practical Geology; and P. 295 in my own collection, are very well preserved and between them show all the more important features of the animal.

The fish, which is about 18 cm. in length, has a short rounded head, with rather large orbits placed quite anteriorly; its body is fusiform and apparently nearly circular in cross-section. The tail pedicel is deep and the caudal fin heterocercal. There are two dorsal fins and an anal fin, pairs of pectoral and pelvic fins and a series of five pairs of intermediate fins, all having anterior spines.

The head is similar in general morphology to that of *Climatius reticulatus*, but differs not only in proportions but in many important structural characters. No traces of the neural cranium nor of the endoskeleton of the visceral arches are present, and it is certain that they were entirely unossified. The dorsal surface of the head is covered with the normal body scaling of very small (0·3 mm. square) regularly arranged scales as far forward as an irregular transverse band at about the level of the upper end of the hyoid arch. At this level the scales increase in size a little and become polygonal, losing their very regular arrangement and becoming massed into irregular longitudinal rows.

The main lateral-line of the body passes forward over the gill chamber along the marginal row of scales and then continues along the larger scales which border the dorsal surface of the head to pass mesially of the dorsal orbital bone. The scaling of the head seems to end abruptly at a point above and a little in front of the middle of the orbit, the anterior extremity of the head being naked.

The hinder ends of the supra-orbital canals are clearly shown to pass backward on the inter-orbital surface, each lying between two parallel rows of dermal bones; they end some distance behind the orbit.

In the posterior part of the dorsal head scaling are two pairs of lateral-line grooves;

the posterior arises from the main canal at the point where the body scaling ends and passes inward and forward at about 45 degrees to the middle line. The more anterior one begins in the immediate vicinity of the termination of this groove, and may actually join it. It then passes directly laterally to join the main canal.

The orbit is surrounded by a ring of plates of very delicate structure agreeing in their general character with those of *Climatius* and, like them, being part of the dermal head skeleton. It is unfortunately impossible to determine their detailed arrangement, but

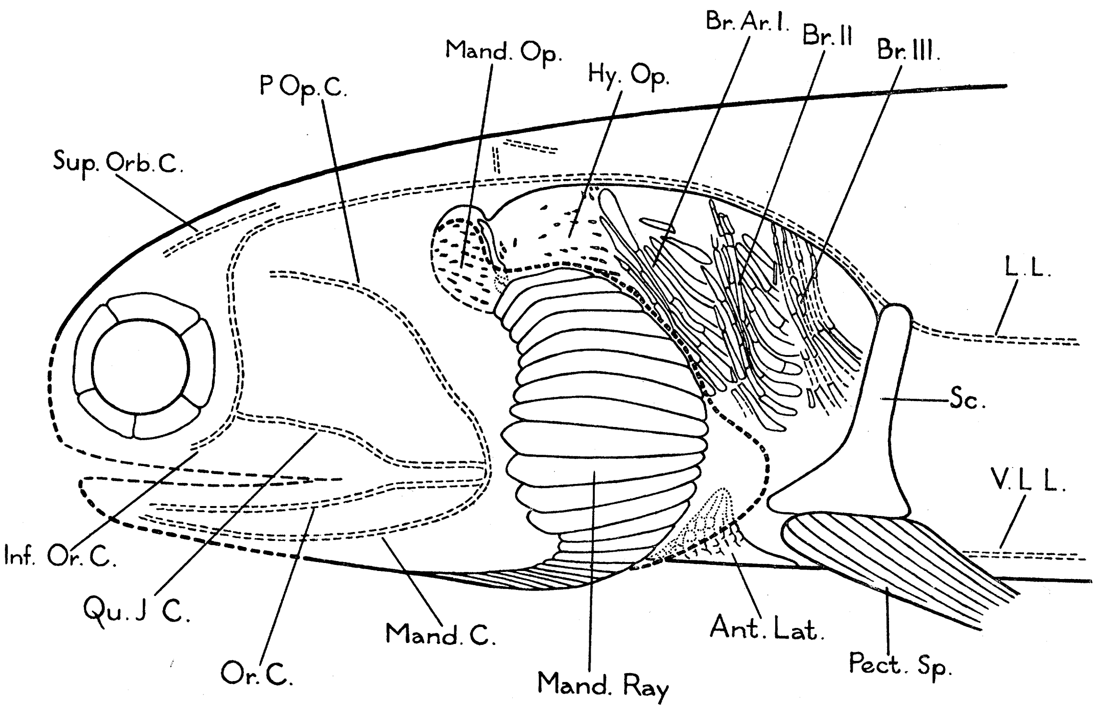


FIG. 3—*Euthacanthus macnicoli* POWRIE. L.O.R.S. Turin Hill. Reconstruction of the head entirely from the type specimen. ×3·0. *Ant.Lat.* antero-lateral bone of shoulder girdle; *Br.Ar.* I, *Br.* II, etc., the dermal bones of the branchial arches; *Hy.Op.* hyoidean operculum; *Inf.Or.C.* infra-orbital canal; *L.L.* lateral-line; *Mand.C.* mandibular canal; *Mand.Op.* upper end of the mandibular operculum; *Mand.Ray*, a ray in the mandibular operculum; *Or.C.* oral canal; *P.Op.C.* preopercular canal; *Pect.Sp.* pectoral spine; *Qu.J.C.* quadrato-jugal canal; *Sc.* scapula; *Sup.Orb.C.* supra-orbital canal; *V.L.L.* ventral lateral-line.

it is evident that two lie dorsal to the eye and that there are at least three others, and probably more.

Behind the orbit lies the cheek whose bony covering is connected with that of the dorsal surface of the head by a patch of unusually large bones, forming a narrow neck in front of the spiracular cleft, over which passes the upper end of the infra-orbital lateral-line canal. This lies considerably behind the orbital ring of bones and can be traced downward between two regular rows of very small bones nearly to the border of the mouth. Behind this groove the cheek passes upward, without any sudden break in its squamation, into the mandibular operculum which covers the upper end of the spiracular gill slit. This structure is covered toward its free margin by exceedingly small and delicate scales. Posteriorly the cheek contains a belt of relatively very large bones mapping out the course of the pre-opercular canal from its origin from the upper end of the infra-orbital canal to its termination at the articulation of the lower jaw. A lateral-line groove, the quadrato-jugal canal, passes forward from the lower end of the pre-opercular canal to join the infra-orbital canal at its lower end. Behind the canal the cheek extends backward with its normal scaling until it passes abruptly into the main part of the mandibular operculum.

The lower jaw is toothless and is represented solely by the two rows of small narrow bones which support the lateral-line grooves, and by an excessively delicate squamation of very small isolated scales. There are two lateral-lines, one near the ventral border of the jaw, the mandibular canal, the other, the oral canal, which is shorter, joining the main canal posteriorly and lying near to the probable dorsal margin of the jaw; both arise from the lower end of the pre-opercular canal.

The first operculum, which on the evidence of the conditions obtaining in *Climatius reticulatus*, *Brachyacanthus scutiger* and later Acanthodians is presumably of mandibular arch origin, is supported by a very extensive series of twenty-five powerful, elongated bones. This series extends from a point about on the level of the horizontal part of the pre-opercular canal to one which must lie toward the middle line between the lower jaws. The most dorsal element has its anterior part directed upward and backward from its attached extremity, it then turns horizontally backward. The five rods immediately below also retain their downturned attached ends, but their distal parts widen rapidly so that by the eighth the whole bone is sensibly straight. The ninth to twelfth rods have wide attached ends and narrow distally, the anterior ends gradually turning upward below the level of the articulation of the jaw. This fan-shaped arrangement is extremely characteristic and is preserved in such more advanced forms as *Mesacanthus*, *Cheiracanthus* and *Acanthodes* itself. The thirteenth rod is narrow from top to bottom but of considerable length. The remaining twelve are slender and shorten gradually. The type specimen shows a small series of fine, slender long rods, lying out of series with the elements of the ventral ends of the right and left opercular folds. These presumably represent the skeleton of the median part of the continuous opercular fold, and parallels to them can be found in *Mesacanthus* and *Acanthodes*.

The hyoidean arch is shown on each side of the type specimen. There is only a very slight indication of a scale-covered area on the upper end of the gill septum; this is followed directly by two long, slender ossicles which stand vertically, the lower lying in front of the more dorsal. The ventral end of the upper bone is turned backward, and the lower bone in the specimen comes into contact with the upper bone of the large mandibular opercular rays, the direction of the two bones being totally different. The hyoidean operculum is seen as a structure supported by delicate oat-shaped ossicles lying horizontally, well separated from one another. The free margin contains a single series of large bones which reach, and presumably rested on, the first branchial arch.

The first branchial arch is similar in its general structure to that of *Climatius*. The outer surface of the narrow gill septum is covered by a series of fine, long, slender rods, similar to the two at the summit of the hyoid arch. Each of these is turned backward horizontally at its widened lower extremity, and additional rays of exactly the same character are inserted between some of these backturned ends, so that there are actually eight visible. The whole structure ends abruptly at the level of the articulation of the upper and lower jaws, that is, the level of the longest mandibular opercular ray.

The second branchial arch has the same structure as the first, but seems to possess six rods and eight rays and to extend to a slightly more ventral point.

The third branchial arch is again similar, but the rods are more sharply bent where they turn backward as rays, and the structure is hidden by scales before its natural end. No trace of any fourth arch is visible.

It will be noticed that the abrupt ventral termination of all the ossifications in the hyoid and branchial arches, which themselves evidently extended downward toward the mid-ventral line, can only be explained by the presence of a large posterior extension ventrally of the mandibular operculum.

The body as a whole is covered continuously with normal, square Acanthodian scales. These are uniform in size and arrangement, the only noticeable variation being the presence of a strip of rather larger scales along the mid-dorsal line, which with a similar ventral strip forms a stiffening to the caudal pedicel. There is also a patch of similar scales at the attachment of the pectoral fin spines.

The anterior dorsal fin spine is straight and sharp pointed with a very oblique insertion on the body. It has a large cavity extending nearly to the tip and no inserted region, the base lying in the squamation. The spine is ornamented by a series of ridges and deep grooves, none of which bears denticles, nor does the posterior margin. A brown stain in the type specimen may represent the fin web, which has no visible scaling.

The second dorsal fin spine is similar to the first, but is longer and inserted at a more open angle. The web of the fin is covered with square scales of exceedingly minute size, which distally are arranged in rows.

The caudal fin is of great interest; it is typically heterocercal, the hypocaudal lobe being, however, small and long based so that the hinder margin of the whole fin is nearly straight. The strip of enlarged scales along the dorsal surface of the deep pedicel ceases abruptly about a third of the length of the fin in front of the posterior end. It here forms a definite free projection behind which the upper border of the tail is covered by minute scales, the continuation of a strip which extends forward for some distance. Ventrally these pass into the pointed hinder end of the body covered with the normal squamation. The hypocaudal lobe has a thickened antero-ventral margin and is otherwise covered with small scales arranged in rows.

The pectoral fins are remarkable in that only the scapula, and that triangular element which contributes to the lateral surface of the ventral part of the body below the gill slits, are present as large bones in addition to the spine. The web of the pectoral fin is often visible as an area covered with very small square scales. The intermediate pairs of spines form a close-packed series beginning a little behind the pectoral fin and ending the length of a spine in front of the pelvics. There are usually five pairs, but the type specimen has an additional spine at the anterior end on one

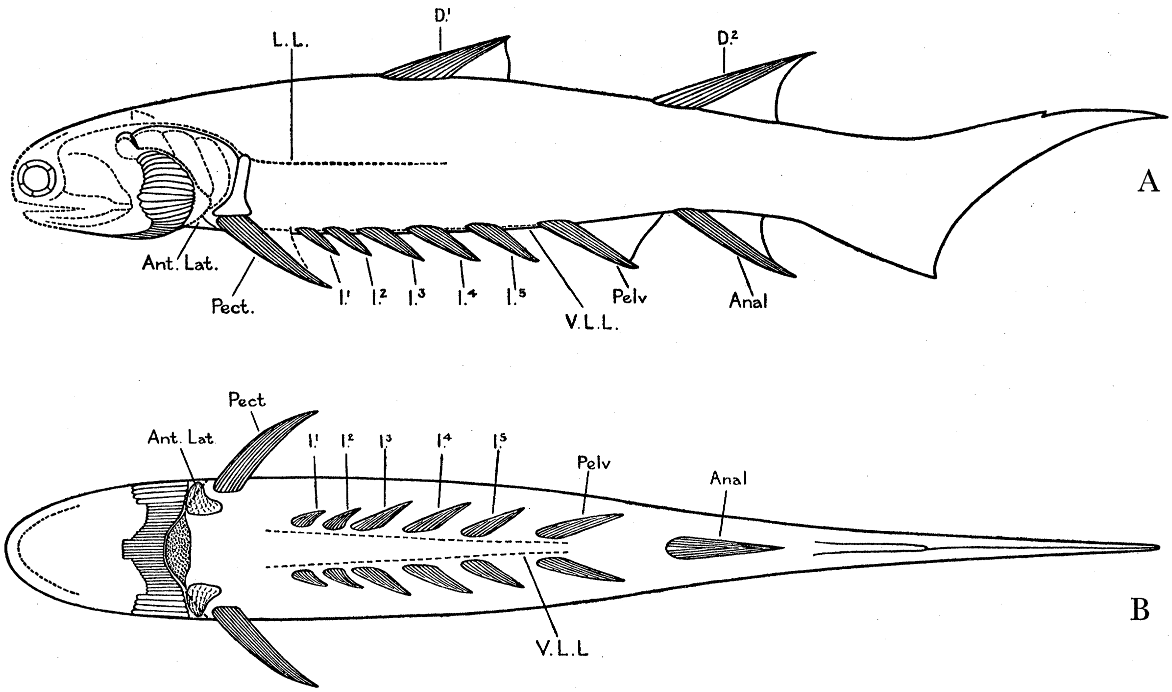


FIG. 4—*Euthacanthus macnicoli* POWRIE. A, lateral and B, ventral reconstructions. × 0·9. *Anal*, anal fin; *Ant.Lat.* antero-lateral pectoral dermal bone; D^1 and D^2, the dorsal fins; I^1–I^5, the intermediate paired spines; *L.L.* lateral-line; *Pect.* pectoral fin; *Pelv.* pelvic fin; *V.L.L.* ventral lateral-line.

side only. These spines have exactly the same structure as the normal fin spines. The series increases in size from first to last, the posterior spine being only very slightly shorter than those of the pelvic fins. I have never seen any trace of fin web, probably because the spines overlap one another closely and never stand out freely beyond the body, the only condition under which the web is ever to be seen.

BRACHYACANTHUS SCUTIGER EG.

The fish described as *Brachyacanthus scutiger* by EGERTON was soon referred by him to *Climatius* AGASSIZ, and has since remained in that genus. It is, however, though a close relation, so different structurally from *C. reticulatus* that it is necessary to revive its original generic name.

Brachyacanthus seems to have been a common fish at Farnell, and has also occurred, though rarely, at Tealing and Duntrune near Dundee; it is doubtful if it really occurs at Turin Hill. It is small, about 7 cm. in maximum length, and appears to have been less slender than *Climatius reticulatus*, the anterior dorsal fin spine being inserted on the summit of an arched back. The tail is long and very slender. All the fin spines are short and exceedingly broad at their bases.

The more important specimens on which the following account is based are: Powrie 1891, 92, 220, from Farnell. This is a mould of the external surface of the left side of the head and anterior part of the body of a large fish. It shows very perfectly the structure of the pharynx, but is at first difficult to interpret, especially in photographs, because fragments of black bone remain in the centre of each individual bone impression and at first appear to be sutures between the individual elements of the skeleton. Powrie 1891, 92, 213, from Tealing, shows the inner surface of the bones covering the top of the head very well. Powrie 214 is a nearly complete fish in lateral aspect, important because it shows from their inner surfaces the large bones of the mandibular operculum. B.M.N.H. P. 9596, which is said to be from Turin Hill, shows well the inner surface of the upper part of the head and, misplaced, the lower jaws and intergular part of the operculum and the cheek and opercular rays of one side.

The Head—There is no evidence of any calcification in the neural cranium, but the palato-quadrate and Meckel's cartilages may be well "ossified"; they are, however, never sufficiently well exposed to be described. There is no evidence of any calcification in other parts of the visceral arches.

Dorsal Surface of the Head—*Brachyacanthus* differs from all other Acanthodians in the presence of a series of large hexagonal median scutes forming a continuous series from the first dorsal fin spine to the back of the head. The normal squamation of very small square scales usually passes into this median series through the intervention of small, rather irregular scutes which form a vague belt on each side. The most anterior and largest of these median bones lies on the level of the first branchial arch; it may be regarded as the hinder end of the dermal skull roof. From its lateral borders series of small bones pass out laterally forming a transition region between the scaling of the body and those large bones which cover the head. The head plating is irregular, varying not only between individuals but also between sides of the same specimen. The median series may be broken occasionally by pairs of bones. A lateral series of bones with a deeply grooved lower surface is evidently related to the main lateral-line canal and can always be traced. This series is separated from the border of the gill chamber by another series which ends in a patch of bones behind the circlet surrounding the eye. One bone of the patch is always recognizable because its inner surface has a deep rounded pit, and its outer surface is raised into a low pyramidal point. The orbital margin is formed by a series of five large ornamented bones of massive construction. The space between the orbits is covered by two pairs of long bones, the anterior end of the head being undescribable. The ventral orbital bone appears to form part of the margin of the mouth, which posteriorly lies on a chain of three large bones. These form the lower part of the covering of the cheek which ends dorsally and posteriorly in a continuous chain of bones, associated with the "hyomandibular" lateral line canal, the rest of its area being covered by an irregular mosaic of polygonal bones extending

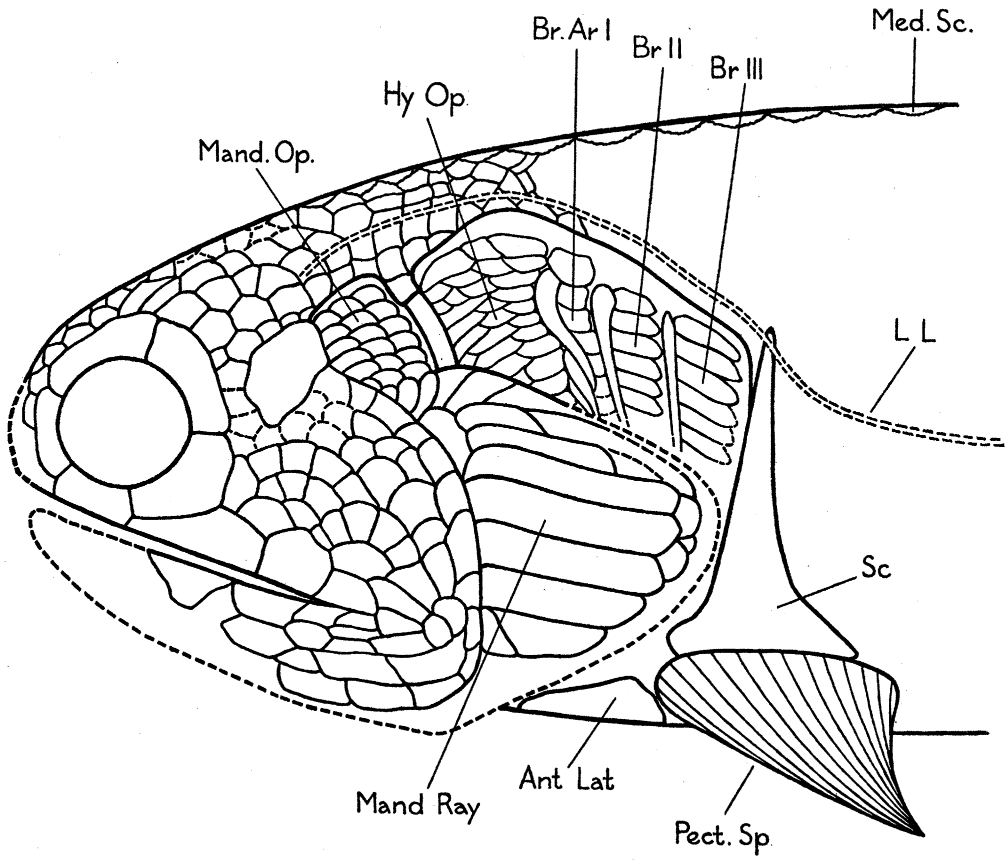


FIG. 5—Head of *Brachyacanthus scutiger* EG. × 6·0. Lower Old Red Sandstone, Farnell. Reconstructed mainly from specimen, Powrie 1891, 92, 220, Royal Scottish Museum. *Ant.Lat.* antero-lateral dermal bone of the shoulder girdle; *Br.Ar.* I, *Br.* II, etc., the branchial arches and their opercula; *Hy.Op.* hyoidean operculum; *L.L.* lateral-line; *Mand.Op.* the upper part of the mandibular operculum; *Mand.Ray*, one of the rays of the mandibular operculum; *Med.Sc.* median scute; *Pect.Sp.* spine of the pectoral fin; *Sc.* scapula.

forward to the circum-orbital series. The posterior part of the lower jaw is covered externally by four irregular longitudinal rows of bones.

The mandibular operculum agrees in principle, and even largely in detail, with that of *Climatius reticulatus*. The small anterior portion which lies immediately in front of the upper portion of the hyoid arch, on which its posterior border rests, is supported by horizontally arranged rows of small bones. These extend down to the upper border of the cheek plating whence the main portion of the operculum begins with a radiating series of relatively large bones whose lower borders eventually become horizontal and rest on the uppermost of the series of five long rays. These rays articulate with the hinder border of the cheek and extend backward to join an irregular series of polygonal bones which form the actual hinder border of the operculum, representing a group of very small ossicles in a homologous position in *Climatius*. The specimen Powrie 220 is of very great importance, because in it the upper border of the mandibular operculum as it crosses the hyoidean operculum is clearly defined, and it is quite obviously an independent and more superficial structure. Specimen P. 9596 shows the whole series of opercular rays of the left side in position behind the cheek, the lower jaws retaining their original position with respect to these structures, the whole being seen partly as an impression from within. The transition from the lateral part of the operculum, through a region which is very short because it is placed between the lower jaw and the shoulder girdle, to the large gular part of the fold which is continuous and free across the middle line, is very well shown in this specimen. The gular part of the operculum, as in *Climatius*, is beset with longitudinally arranged rows of narrow but elongated bones.

The upper end of the hyoidean arch is covered by two bones, articulated with the head plates and projecting beyond the border of the gill chamber, exactly as does the corresponding structure in *Climatius*. Below these the lateral surface of the gill septum is covered by what is apparently a single vertically placed element whose lower end is covered by the mandibular operculum. The hyoidean operculum is an extensive structure with free upper and posterior margins. It contains ten horizontal rows of shallow elongated bones.

The outer surface of the first branchial arch contains, towards its upper end but not in contact with the margin of the gill chamber, a single isodiametric bone below which lie three narrow splints each overlapping the one below and in front of it. In the actual specimen this arch lies very near the second branchial, and its operculum is in consequence not very clearly shown.

The second and third arches have only a single long splint, and each supports a short deep operculum containing horizontal rays which seem to be continuous throughout their length.

The whole structure of the branchial region in *Brachyacanthus* thus agrees with that in *Climatius*, differing only in the general proportions and especially in the fact that all the "bones" in the various opercular folds are very much bigger and more massive. It is of importance because it gives independent and very satisfactory evidence that the first and largest operculum is actually a structure arising from the mandibular arch and is quite independent of the hyoid.

Median Fins—The first dorsal fin spine arises from the most dorsal part of the body. It has a very widely expanded base whose border meets the last of the median scutes in front, and for the rest of its extent is directly in contact with the ordinary squamation.

The whole structure contains a very large cavity which extends nearly to the tip, the wall of the spine being exceedingly thin. In profile it is evident that both the anterior and posterior surfaces are concave, so that the tip is sharply pointed whilst the base is enormous, actually as long as the height of the spine. The lateral surface of the spine is ridged, the number of ridges at the base being about twelve, of which some three only reach the tip, the others dying out. The fin web is often preserved. It is covered with very small quadrangular scales without a very definite arrangement.

The second dorsal spine is longer and more slender than the first, but is otherwise similar. The fin itself differs in that its scales are very regularly arranged in rows which radiate out like the ribs of a fan from an area covered with less regularly arranged scales at the base of the posterior edge of the spine.

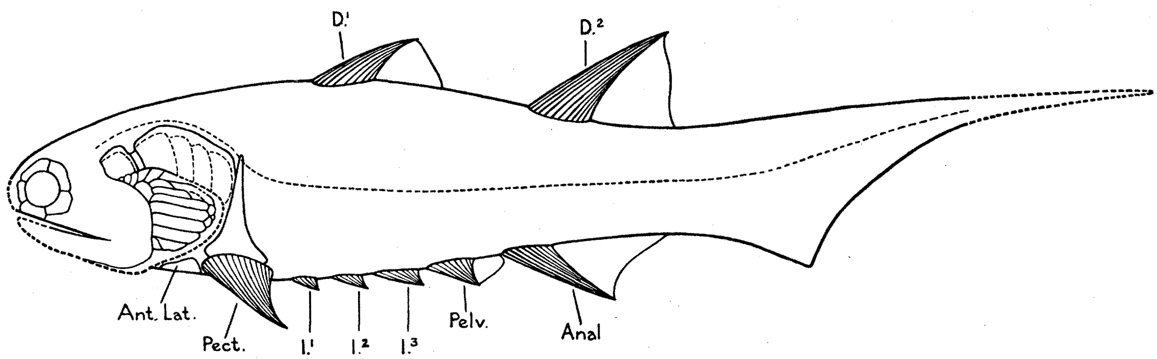


FIG. 6—*Brachyacanthus scutiger* EG. × 1·8. Reconstruction of the fish from material from the Lower Old Red Sandstone of Farnell and Duntrune. *Anal*, the anal fin; *Ant.Lat.* antero-lateral dermal bone of the shoulder girdle; D^1 and D^2, the dorsal fin spines; I^1, I^2, I^3, the intermediate paired fin spines; *Pect.* pectoral fin; *Pelv.* pelvic fin.

The caudal fin was well figured by EGERTON; it is remarkable for the extreme length of the upper lobe, perhaps even exceeding the condition in *Climatius*.

The anal fin spine is very like that of the second dorsal, but the fin itself differs in that the rows of scales on it lie parallel to one another and end on the body and not at the point of insertion of the spine.

The pectoral girdle is not well displayed in any specimen, and I am uncertain of its structure. The scapula is always visible. It differs considerably from that of any other Acanthodian because its shaft is a narrow rod ending dorsally in a point and widening abruptly at its lower extremity to form a hollow plate-like structure which is in some way attached to the margin of the widely open base of the spine. The spine is a hollow conical cap of dentine with very thin walls; its attached margin is oval, nearly as deep dorso-ventrally as it is long, and the spine from base to point along its posterior margin is no longer than the length of its attachment to the body. The outer surface bears a series of longitudinal ribs which proximally bear low points in regular series. There are about twelve rows of ribs on each surface at the base and three distally.

There appears to be one pair of large bones on the ventral surface between the pectoral spines and the hinder border of the operculum.

The three pairs of intermediate spines and the pelvics form a close-set series, each almost in contact with its neighbours. The most anterior, which lies about its own length behind the pectoral spine, is little more than a large oval scale with a horizontal hollow rib having a free extremity. The pelvic spine differs only in being much larger, the attached base being about twice as long, though of nearly the same width, and in having a much more pronounced rib with a definite spine posteriorly. The intermediate spines are exactly intermediate in structure.

It is important that specimen Powrie 214 shows a well-preserved pelvic fin web extending back from this spine to that of the anal fin. In Powrie 213 an enlarged scale lies immediately in front of the first intermediate spine, resembling it in outline but lacking any trace of rib or spine.

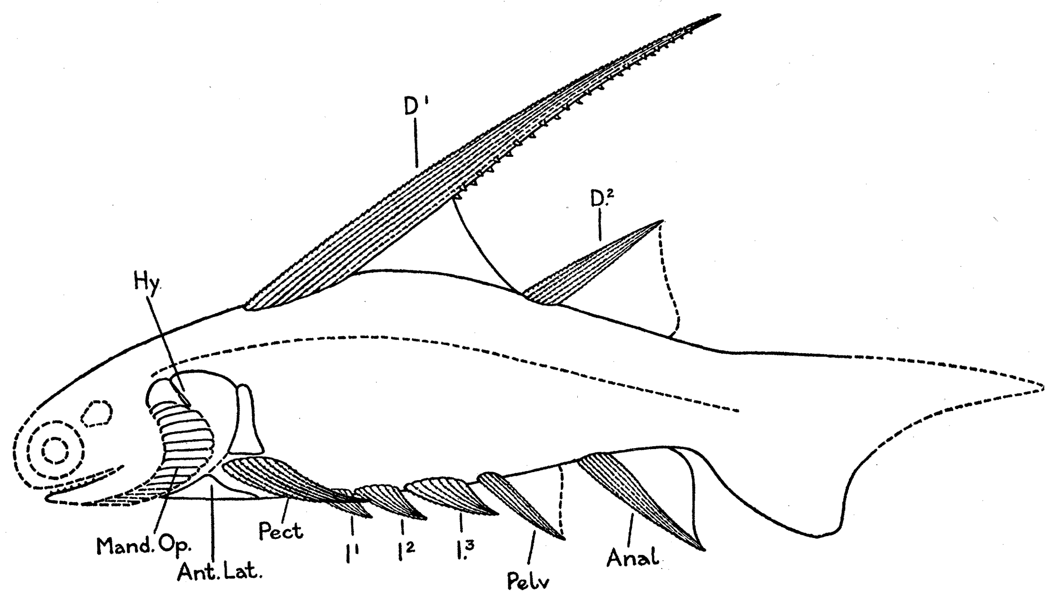


FIG. 7—*Parexus incurvus* AG. × 1·2. Restoration of the fish from specimen L. 12097 B, Manchester Museum. *Anal*, anal fin; *Ant.Lat.* antero-lateral dermal bone of shoulder girdle; D^1 and D^2, dorsal fins; *Hy.* upper end of the hyoid arch; I^1, I^2, I^3, the intermediate paired spines; *Mand.Op.* the mandibular operculum; *Pect.* pectoral fin; *Pelv.* pelvic fin.

PAREXUS INCURVUS AG.

Agassiz, L. 1845.
Powrie, J. 1864, pl. XX, fig. 1.
Powrie, J. 1870, pl. XII, fig. 8.
Woodward, A. S. 1891, fig. 4.

Parexus incurvus and its larger ally *P. falcatus* are rare fish at Turin Hill, and the material available does not allow me to give so complete a description of either as of the other species dealt with in this paper.

In fig. 7 I give a reconstruction founded on the specimen L. 12097 A and B, Manchester Museum. This shows the extraordinary build of the fish which depends on the exaggerated spine of the first dorsal fin.

The head agrees in its general structure with that of *Climatius*, having a very similar dermal skull roof and cheek, but the mandibular operculum, like that of *Euthacanthus*, contains a long continuous series of rays. The hyoid and branchial arches are very similar to those of *Euthacanthus*.

The dermal shoulder girdle is well developed but contains only a single pair of very large bones on the ventral surface, described by SMITH WOODWARD as clavicles.

The first dorsal spine is peculiar in possessing two rows of distally directed denticles on its posterior surface, the denticles on the right and left sides of the spine alternating regularly.

The lower jaw has a dentition resembling that of *Climatius* but in which the individual teeth have narrower cusps.

The head mentioned by TRAQUAIR, and described by SMITH WOODWARD (1915) as *Protodus scoticus*, is clearly that of an Acanthodian, and in all probability of *Parexus*.

MESACANTHUS MITCHELLI

Mesacanthus mitchelli is found abundantly at Turin Hill and Farnell in the well-known, very finely bedded calcareous and micaceous shales which there form rich fish beds. It has also been found very rarely as isolated individuals in small pockets of shale included in the sandstones at Carmylie and Ley's Mill in Forfarshire, all these localities being very nearly the same horizon in the lower Old Red Sandstone. Individuals are usually preserved in exact profile, but two of my series of fifteen were dorso-ventrally compressed, so far as their anterior extremity is concerned. It therefore appears that the fish, though in the main laterally compressed, had a head which may have been nearly circular in section. It is clear that the snout was rounded and blunt, and the relatively very large orbit lies so far forward as to show that the olfactory organs must have been small. The mouth is a little underhung, the lower jaw ending under the anterior border of the orbit and not extending quite so far as the extremity of the snout. The head is small, about two-elevenths of the total length. The fish as a whole is well stream-lined, though the root of the tail is deep, about half the maximum total depth of the fish in the region of the pectoral fins. The caudal fin is clearly heterocercal, but its upper lobe is only very slightly upturned. The hypocaudal lobe is small and triangular but with a short and stiff recurved point. The two unpaired fins lie with the dorsal a little behind the anal, which is almost accurately in the middle of the length of the fish. The dorsal fin spine is about four-fifths of the maximum depth of the body, the anal spine is slightly shorter, each is inserted at an angle of about 45° to the body outline. The dorsal spine is ribbed, or rather grooved, there being one rather deeper and wider groove extending the full length of the spine and smaller but parallel grooves, some of which do not continue to the tip. The web of the fin is only very rarely indicated by slight traces of scales which do not enable one to decide how nearly it extended to the tip of the spine.

The paired fins are three in number, each supported by an anterior spine similar in its general character to those of the dorsal and anal fins, but apparently asymmetrical. The pectoral fin spine is of about the same length as the dorsal but is considerably stouter; its outer dorsal surface bears an irregular and rather shallow groove; its inner ventral surface, on the other hand, has an anterior deep and wide furrow extending the whole of its length, and bears two or three much less well-defined grooves only on its basal half. No trace of the fin membrane is preserved.

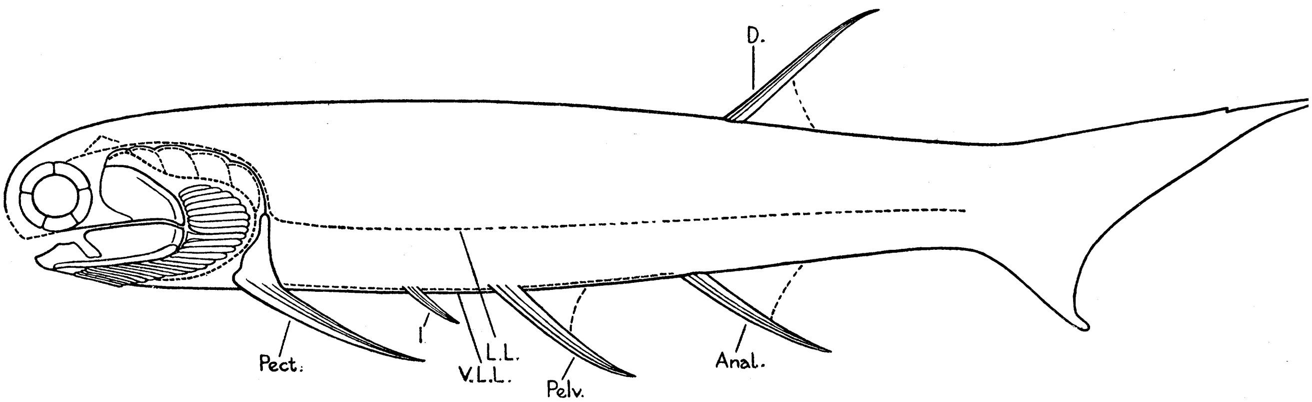


FIG. 8—*Mesacanthus mitchelli* EG. × 3·0. Reconstruction of the fish founded on material from the Lower Old Red Sandstone of Turin Hill. *Anal*, anal fin; *D.* dorsal fin; *I.* intermediate pair of spines; *L.L.* lateral-line; *Pect.* pectoral fin; *Pelv.* pelvic fin; *V.L.L.* ventral lateral-line.

The intermediate fin spines are short, rather broad, and to some extent grooved. They lie close together on the ventral surface of the fish, seemingly parallel to the principal plane.

The pelvic fin spines are relatively more slender and much longer, being indeed about two-thirds the length of the pectoral spines. Each of them, apparently on its lateral surface, has one deep continuous groove behind which lie several much smaller ridges and furrows forming little more than a striation. Slight traces of the web of these fins can be seen.

The fin spines of *Mesacanthus* are purely superficial structures inserted entirely into the skin amongst the scales, and not penetrating into the body between muscles as do those of Elasmobranchs and later Acanthodians. The individual spine has a cavity which extends nearly to its tip and communicates by a wide opening with the sub-dermal tissues of the animal. The bone which forms the border of this opening lies on the same level as the body scales, whose free extremities may overlap the base of the spine.

The greater part of the external surface of the fish is covered with a very close-fitting squamation composed of extraordinarily small scales. The scales measure about onesixteenth of a millimetre across, are almost accurately square, and overlap from before backwards. They are disposed in rows running obliquely at an angle of 45° to the length of the fish, the rows cutting one another at right angles. This very regular squamation alters its character a little in certain regions. The lateral-lines are clearly marked by a slight local enlargement of the scales, leading to a disorganization of their very regular arrangement. Laterally, in the region between the pectoral and pelvic fins, the scales become markedly larger and less square-cut in outline, and the base of the pelvic fin spines is surrounded by somewhat rounded scales, some of which are three times as big as those which cover the flank. Similar enlarged scales occur in front of the dorsal and anal fin spines, but behind these the marginal scales of the body are exceptionally small and lose their regular tessellated pavement arrangement.

The upper lobe of the tail is covered with scales which tend to become elongated, overlapping one another more deeply than those of the trunk; they suggest indeed the rhomboidal scales which occur in this position in Osteolepid fishes. The mid-dorsal line of the caudal fin is specially protected by a series of particularly enlarged scales, apparently paired, which overlap one another and form a definitely thickened margin. This suddenly stops at a point about a quarter of the whole length in front of the hinder end of the fin, forming in three specimens a point of marked break in its outline, indeed almost a small definite lobe. The hypocaudal lobe of the caudal fin has its anterior margin protected by a similar row of enlarged scales which continue on behind the termination of its web to form a curious little recurved point. The scaling of the web of this part of the caudal fin is deeply overlapping, and much less regular and massive than that of the upper lobe. In adult specimens, e.g. P. 472, the squamation is as I have just described it, but in young individuals (Powrie 1891, 92, 275) there is a triangular area of the trunk which is free from scales and lies below the main lateral-line and dorsally to the ventral lateral-line over the shoulder girdle. As the fish grows older this region is gradually reduced in size by addition of scales to its dorsal, and perhaps to its ventral margin.

No trace of any ossification in the neural cranium is visible but the specimen Powrie 1891, 92, 275 retains three small dense rounded calcareous elements lying just behind the orbit at a level which must be nearly that of the basis cranii. These can be seen, less well, in other specimens. I am indebted to Miss Townend for the obviously correct interpretation of these very puzzling structures as otoliths.

The only parts of the endoskeletal structures visible in the head of *Mesacanthus* are Meckel's cartilage and the palato-quadrate cartilage. These are displayed in very many specimens as calcified elements, clearly not of the nature of ordinary calcified cartilage. I propose to refer to them as bone, and shall at a later stage of this paper give some justification for using the term. The palato-quadrate bone recalls very vividly that of *Notidanus*. It has a short and slender suborbital part and a very deep post-orbital region rising to a high otic process, which cannot be shown to have touched the neural cranium and in any case presents no evidence of an articular facet.

There is some evidence that the palato-quadrate bone actually consists of a short anterior suborbital bone and a much longer posterior portion. The anterior bone agrees in its general character with that of *Acanthodes*, having in its admesial border a deep rounded notch whose anterior edge forms a facet for articulation with the basis cranii, behind the orbit. The lower jaw bone equally recalls Meckel's cartilage of the

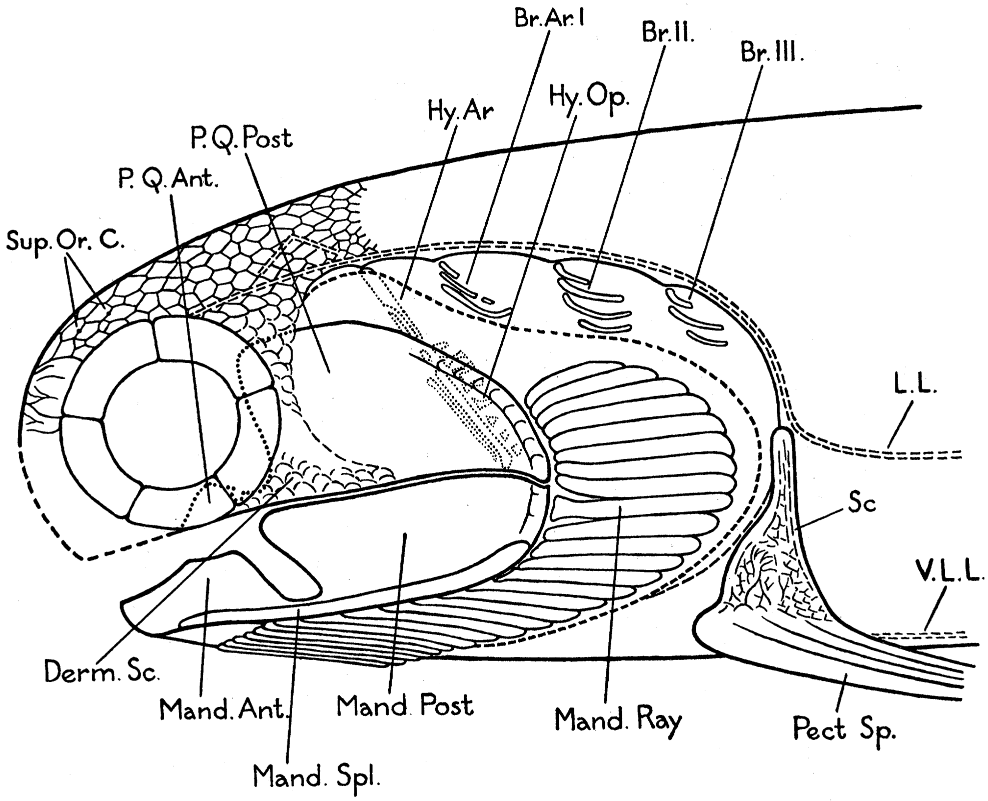


FIG. 9—*Mesacanthus mitchelli* EG. Reconstruction of head. × 9·0. The hyoid and branchial arches mainly from Powrie, 1891, 92, 275, Royal Scottish Museum. *Br.Ar.* I, *Br.* II and III, the dermal bones of the branchial arches; *Derm.Sc.* dermal bones of the cheek; *Hy.Ar.* upper end of the hyoid arch; *Hy.Op.* the hyoidean operculum; *L.L.* lateral-line; *Mand.Ant.* the anterior ossification in Meckel's cartilage; *Mand.Post.* posterior bone in Meckel's cartilage; *Mand.Ray,* a ray in the mandibular operculum; *Mand.Spl.* the mandibular splint; *P.Q.Ant., P.Q.Post.* the anterior and posterior bones in the palato-quadrate cartilage; *Pect.Sp.* pectoral fin spine; *Sc.* scapula; *Sup.Or.C.* supra orbital canal; *V.L.L.* ventral lateral-line.

dogfish; it is shallow anteriorly, deep posteriorly, and bears a concavity which articulates with the posterior and lower corner of the palato-quadrate bone. Neither element bears the slightest trace of teeth. Like the palato-quadrate, the ossified lower jaw consists of two elements, anterior and posterior, which in young individuals are widely separated but fuse completely later in life. A long "bony" splint articulates with the lower border of the jaw throughout its length.

The exoskeleton of the head is very well shown in my series of specimens. The whole dorsal surface, from the anterior end to the region of the gills, is covered with a series of relatively large irregular scales, which, from a point about a quarter of its diameter behind the orbit, pass backwards gradually into the normal squamation of the dorsal surface of the trunk. These scales tend to be longer than they are wide and fall somewhat irregularly into fifteen longitudinal rows. More anteriorly, forming indeed the blunt anterior end of the head, the scales are transversely widened, about four or five covering the inter-orbital space; these may fuse into large plates. The elements which surround the nostrils are sometimes recognizable by their concave rounded borders. It is evident that the nostrils lay on the rounded anterior end of the head between the supra-orbital lateral lines and some way above the border of the mouth. The elements which build up this shield are not rigidly fixed and the whole region has some flexibility, though it is coherent and may be displaced as a whole. At the sides the dorsal shield passes abruptly into the two dorsal elements of the ring of five surrounding the orbit. Their mutual relations are such as to show that these plates, which it is natural to regard as ossifications of the sclerotic capsule of the eye, are actually external dermal elements of the head armour, a view which is confirmed by the ornamentation of the external surface of at least the more dorsally placed elements. The complete series builds up a rather irregular ring, wider dorsally than ventrally. Behind and below the orbit there is little trace of exoskeleton, the greater part of the palato-quadrate and Meckel's cartilage ossifications being visible. A small triangular area, dorsal and posterior to the orbit, is covered with a series of rather large thick scales in five or six irregular horizontal rows, and the mouth below the hinder part of the orbit seems to be bordered by a large ornamented ossification perhaps associated with smaller scales.

The dorsal surface of the head displays the course of the lateral-line canals with clearness. They are visible because of the small perforations, usually lying between two scales, by which their tubuli came out to the surface. They form four parallel series: an inner pair which begins in close contact with the anterior border of the orbit and extends straight backwards along a more or less continuous line of scales for some distance, and another pair which begins above the centre of the orbit, gives origin apparently to an infra-orbital branch, and then passes backward through a continuous line of larger scales to the region of the pectoral girdle and on into the main canal on the body of the fish. In addition the dermal bones of the roof of the head show short lateral-line canals arranged in a V over each ear region. The line of large scales is the most ventral trace of exoskeleton in the body in the gill region, and with the ventral part of the shoulder girdle and a series of enlarged scales extending forward on the ventral surface in front of the pectoral fins, marks out the margins of a well-defined gill chamber.

The only remaining scales in the head are the series of long, powerful rays which clearly have the structure of scales and lie in an opercular fold, so that in the living fish their free posterior extremities must have rested on the ventral portion of the margins of the gill chamber described above. The arrangement of the opercular bones is very remarkable. On the ventral surface between the lower jaws they lie parallel to one another and to the middle line, the complete series being at least sixteen in number. They do not here overlap the lower jaw, with which indeed they lie parallel, nor do they appear to be related in any intelligible way to the hyoid arch. They are quite long so that the posterior margin formed by the entire series is a wide V-shaped notch, it being impossible to say whether the opercular fold was continuous across the mid-ventral line or not. Posteriorly these opercular rays pass farther and farther backwards until they come to rest on the posterior margin and indeed apparently on the outer surface of Meckel's cartilage and the palato-quadrate. Individually they terminate behind in rather blunt points. The entire series makes a rounded posterior edge to the operculum, which extends backward to the shoulder girdle but leaves the upper part of the gill chamber freely visible. The opercular rays just described are obviously the homologues of those in *Euthacanthus*, and indeed resemble them even in detail. For example, the arrangement designed to secure dorso-lateral flexibility at the point of articulation of the jaw, whereby the attached ends of the rays overlapping Meckel's cartilage are directed downward whilst those on the palato-quadrate are upwardly directed, is the same in the two fish. I have shown reasons for believing that this operculum is part of the mandibular arch and that there was a full-sized normally functional hyoidean gill slit. One specimen of *Mesacanthus* (Powrie 1891, 92, 275) gives very important confirmation of this view. It is a young individual very perfectly preserved, the palato-quadrate and Meckel's cartilages are unossified, but the splint along the lower border of the latter and the entire series of opercular rays are present in their natural positions undisplaced. The dermal ossifications in the upper end of the hyoid arch are present in a normal manner, but below them, in a place usually concealed by the more laterally placed jaw elements, lie two superficial bones in the arch and a series of very short widely spaced opercular raylets. No other interpretation of these structures seems possible, and their presence affords conclusive evidence that the main operculum does not include the hyoid arch. Three branchial arches are represented each by a series of three or four slender rods concave upward so that their anterior extremities lay in the gill septum and their lower ends extended into the opercular fold.

The shoulder girdle contains a single element on each side. This is a bar of bone standing vertically on the side of the fish, with a narrow cylindrical upper end covered by the normal body scaling. Ventrally the bone expands into a powerful triangular structure whose ventral edge is rigidly articulated to the base of the pectoral fin spine on its inner and upper aspect. The lower part of the bone has an ornamented surface as if it had a series of large overlapping scales fused on to it; this surface was exposed freely on the flank of the fish. No supporting structures are to be seen associated with the spines of the other paired fins.

The main lateral-line passes along the flank, below the middle of its height, from the shoulder girdle to the tail. The ventral lateral-line is very well shown in C. 18 Zoo. Dept. Univ. Coll. It runs along the ventral surface from a point just mesial of the head of the pectoral spine to pass ventrally to the insertion of the intermediate spine.

Ischnacanthus gracilis

Ischnacanthus gracilis is a common fish in the Lower Old Red Sandstone of Turin Hill. It is supposed to be immediately recognizable because it is the only Acanthodian fish in these deposits in which the jaws are beset with conspicuous teeth. The character of these teeth has been repeatedly described, among others by Smith Woodward and Bashford Dean. Smith Woodward (1915) records that the dentition of *Ischnacanthus* is remarkable in that it includes at least one whorl of fused teeth at the anterior end of the mouth.

So far as I can make out the structure of *Ischnacanthus* in the true sense is as follows. The fish is fusiform and probably a little laterally compressed. Its deepest point lies at some distance behind the head in the region of the first dorsal fin where it is, perhaps, in a large specimen about a sixth of the total length. Smaller individuals appear to be more slender. The head ends in a bluntly rounded snout which projects little if at all beyond the extremity of the lower jaw. The orbit is of medium size and lies very anteriorly so that, as in *Mesacanthus*, the olfactory organ must have been exceedingly small.

The two dorsal fins lie, one rather anteriorly and somewhat in front of the pelvic fins, the other posteriorly and a little behind the anal. Each is supported by an anterior spine, that of the anterior fin usually being somewhat shorter than the spine of the posterior fin, and more distinctly curved. It is deeply grooved and ridged, the deepest groove lies anteriorly, the anterior margin forms a rounded ridge followed by a series of two or three more, less deeply impressed. The ridges separating these grooves have a smoothly rounded cylindrical surface. The spines are deeply inserted into the body in contrast to the entirely superficial attachment in more primitive Acanthodians.

The caudal pedicel is comparatively deep, at its smallest point about half the maximum depth of the fish. The dorsal border of the caudal region is only slightly raised dorsally and extends to a very narrow elongated point. The lower lobe of the caudal fin forms a large triangle terminating, as does that of *Mesacanthus*, in a peculiar recurved hook covered by a double row of large scales.

The anal fin is almost a duplicate of the second dorsal, possessing a similar nearly straight anterior spine. The pectoral fin spines are the largest in the fish and they are quite markedly curved. Structurally they greatly resemble those of the median fins, and are remarkable because of their hollowness. They contain a cavity which is relatively very large and extends along them for at any rate three-quarters of their total length. There are no intermediate fin spines. The pelvic fin spines are short, nearly straight, broad in proportion to their length, and lie close together a little behind the point of insertion of the first dorsal fin.

Only traces of the fin membrane are to be seen, and they are found commonly only in the case of the anal and second dorsal fins, though I have seen fragments associated with the pectoral and pelvic fins. In the great majority of specimens there are no traces whatsoever of normal fin rays, the whole membrane being covered with exceedingly small square scales, similar to those covering the whole body, and arranged in lines parallel to the anterior spine. But Powrie 1891, 92, 254, a rather small fish, is unique in that both pectoral fins are supported by long straight unjointed fin rays, arranged apparently in two layers. These end some distance away from the

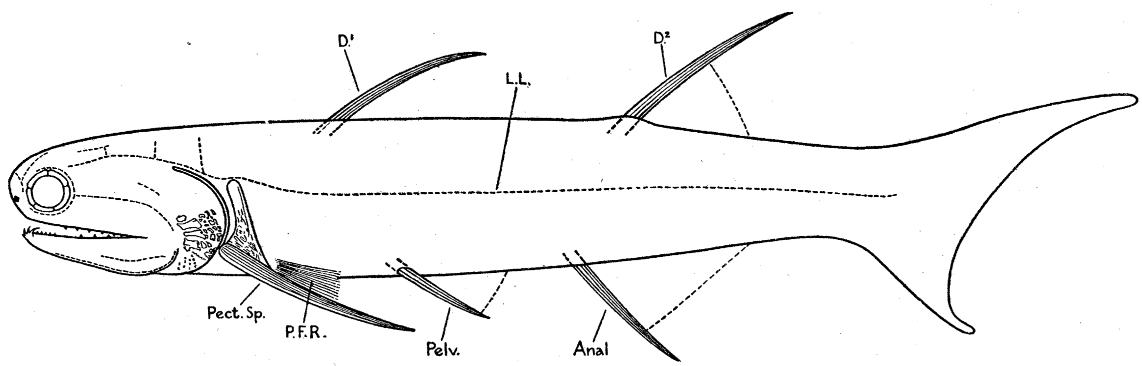


FIG. 10—*Ischnacanthus gracilis* EG. × 1·5 approx. Reconstruction of the fish founded on medium-sized individuals from the L.O.R.S. of Turin Hill. *Anal*, anal fin; D^1, D^2, the dorsal fins; *L.L.* lateral-line; *P.F.R.* pectoral fin rays; *Pect.Sp.* pectoral fin spine; *Pelv.* pelvic fin.

scapula and are about as long as that bone. They are "bony" very slender rods, apparently of oval cross-section, and exactly resemble the corresponding structures of *Acanthodes*.

The body of *Ischnacanthus*, like that of every other Acanthodian, is covered with a continuous pavement of exceedingly small, square ganoid scales. These are proportionately smaller in *Ischnacanthus* than in *Mesacanthus*, being just under a quarter of a millimetre square in a fish whose total length is at least 4 cm. There is no evidence of the occurrence of enlarged scales at the point of insertion of any unpaired or pelvic fin. But the dorsal and ventral borders of the caudal fin are strengthened by a series apparently of one median and two lateral rows of enlarged scales, which are about twice as wide as those covering the body, and which seem to end abruptly a little in front of its termination. The anterior portion of the hypocaudal lobe of the caudal fin has a small area of square scales of similar size, the only considerable occurrence of such scales in the entire fish. The rest of the hypocaudal lobe is covered with scales varying in size from one-sixth of a millimetre down to about one-eleventh. The fin membranes are covered, wherever they can be seen, with square scales which usually, even at the base, are distinctly smaller than those covering the body, and which exhibit a steady diminution in size toward the margin of the fin, ending in mere granulations whose characters can scarcely be seen. It is impossible to be certain whether the fin web extended to the extreme tip of the spine. In the case of the pelvic fin it seems to have done so, in the second dorsal and the anal fin it does not. All the fins are long-based, the margin of the web subsiding quite gradually into the trunk.

No trace of the neural cranium is to be seen in any specimen, but the powerful ossifications associated with the palato-quadrate and Meckel's cartilage are always conspicuous. In one specimen these bones had become disarticulated and are now preserved as exquisitely sharp moulds, squeezes from which display their structure to perfection. The lower jaw, as shown in this material and seen from its inner surface, has the normal outline of a shark's Meckel's cartilage. The articular surface for the quadrate is convex and placed obliquely so that its outer end lies posterior to its inner. The jaw is deep behind, with a rounded lower margin which is not turned outward, and tapers gradually anteriorly, terminating in an irregular and badly preserved expansion which shows some evidence of a pit which served, presumably, for the attachment of a ligament. It is quite clear that the anterior part of the lower jaw was ossified as a separate element from the posterior, but that in the relatively large specimen on which the present account is based, the two portions had become connected by a continuity of ossification along the lower border. The inner surface of the jaw, which alone is shown, has toward its upper margin a smooth and polished surface carried on a thickened rib, readily separable for the greater part of its extent. This surface bears a quite irregularly distributed series of denticles arising from it without any indication of a separately fused base. The upper surface of the lower jaw forms a flat shelf from whose labial edge arises an extremely deep ridge, which must be on the outer surface of whole bone. This ridge bears a series of small denticles some of which seem to be inserted in special depressed areas, recalling those within which the teeth of Osteolepid fishes and Labyrinthodont Amphibia are placed. Lying to the lingual side of the ridge, but completely confluent with it in the lower part at any rate, there is a series of relatively large, massive teeth with smooth pointed crowns. These stand on the flattened upper surface of the jaw, are perfectly continuous with the mass of the bone, and cannot be recognized as independent denticles. They are clearly unprovided with any mechanism for replacement. The dentition so described is restricted to the posterior element of the lower jaw and does not extend beyond it. This condition is recognizable not only in my perfectly preserved isolated jaws but also in complete heads. At the point where the two main elements of the lower jaw come into contact with one another there is a small triangular bone raised above the general level of the upper surface of the jaw, which may be a separate third element, but appears to be continuous with the ridge on the labial side of the jaw, to which the teeth are attached. I have not seen a satisfactory display of the outer surface of the jaw so that I cannot say with certainty whether or no its lower margin was turned outward in the manner commonly found in Elasmobranch Meckel's cartilage, but I do not think that it was.

The palato-quadrate bones of the disarticulated skeleton are perfectly preserved and fortunately display both inner and outer surfaces. This bone is much shorter than the lower jaw, an indication that the palato-quadrate, like Meckel's cartilage, was ossified from more than one centre. This conclusion is drawn from the fact that the part of the palato-quadrate preserved corresponds quite accurately in length to the posterior portion of the lower jaw. The palato-quadrate bone so far as it is shown consists of a very deep post-orbital ramus formed of a thin film of bone which stood vertically in the whole skull, and an exceedingly short abruptly truncated palatal portion lying quite horizontally and very thin dorso-ventrally. The posterior part of the bone toward its anterior end bears at its lower margin a ridge projecting labially which is the palatal ramus, this subsides on to the outer surface of the ventral plate so as to leave space for masticatory muscles. The hinder margin of the bone turns out, the lower border of the everted portion being thickened to form the quadrate articular surface. From the quadrate forward the upper part of the bone forms part of a circle until it ends at a nearly vertical but somewhat irregular anterior border, which passes down to the palatal part of the bone. The tooth-bearing border of the palato-quadrate forms a narrow, wedge-shaped area, widest anteriorly where it forms a strong rod-like lower border to the bone, decreasing in width as it goes back. On the outer surface this area is bounded by a high band of bone, exactly similar to that occurring in the lower jaw. This bears a series of small teeth on its summit, the series being interrupted by the large teeth which are rooted on the surface of the jaw and rise from it with their outer surfaces in complete continuity with the labial flange. The ventral portion of the admedian surface of the palato-quadrate bone, like the corresponding strip of the lower jaw, is beset with tiny denticles, completely fused with it, which exhibit an irregular arrangement in rows parallel to the borders of the mouth, the teeth being ranged in threes, a larger between two considerably smaller denticles.

Many specimens of *Ischnacanthus* show a single whorl of large teeth placed quite anteriorly in the symphysis of the lower jaw. The largest tooth usually points almost directly backward into the mouth, and one or two lie in front of it. In B.M.N.H. 46305 a number of unattached sharp-pointed tooth crowns lie immediately behind the median whorl, the firmly attached teeth of the lower jaw only beginning much farther back. No similar teeth are to be found in the upper jaw. In the very large specimen Edinburgh 1887, 35, 2 a similar whorl consisting of four teeth of which the posterior is much the biggest is very well preserved, but there is not very satisfactory evidence of another similar whorl. In P. 311 of my own collection, a large fish which differs from *Ischnacanthus gracilis* in that the well-ossified jaw elements support only a very few small teeth, there are four independent tooth whorls, all displaced so that their original positions cannot be determined. The anterior part of the mouth in

1887, 35, 2 contains a vast number of exceedingly small toothlets about a quarter of a millimetre high. Each of these is like a *Diplodus* tooth with the middle cusp as long as the lateral ones, the three needle-like spines fanning out from a small base. The individual teeth are tightly packed together. These elements may be compared with those from Campbellton, New Brunswick, called *Doliodus* by TRAQUAIR (1893). These teeth are also shown in the normal-sized specimen B.M.N.H. 46305.

No trace of the hyoid arch is visible, but there is evidence in many specimens of ossifications associated with the branchial arches. These are best shown in P. 481 and P. 298 of my own collection. They are exceedingly slender, elongated, bony splints, attached to one another by their edges and extending from the upper part of the gill chamber downward and backward, at least to the level of the jaw articulation. Three branchial arches are recognizable. There is no doubt that these elements are homologous with those which, in the more primitive Acanthodians, *Climatius*, etc., lie in the skin of the outer surface of the gill septa and support the small opercula. In *Ischnacanthus* they are completely concealed by the mandibular operculum.

The shoulder girdle is represented by a single element on each side which seems to be, in part at least, of the nature of a membrane bone. It lies on the flank of the fish and bears no ornament. It is covered, at any rate for the greater part of its external surface, by the ordinary body squamation. The outer surface widens abruptly at its lower end, where it comes into contact with the upper and admesial surfaces of the pectoral fin spine, whose root, obliquely truncated and rounded, extends forward for a small distance in front of the shoulder girdle. The outer surface of the shoulder girdle turns inward at a line which is sometimes marked by a low outstanding ridge in such a way that it forms a narrow posterior surface to a gill chamber. The inner surface of the shoulder girdle is perfectly smooth and forms a cylindroid hollow, which must have lain in contact with the outer surface of a cartilaginous scapula. In one case, P. 298, there is present a mass of cartilage which lies in contact with the pectoral fin spine and with the inner surface of the shoulder girdle extending posteriorly to that element as a comparatively deep structure, which can only represent a mass of fused cartilaginous basals. The unusual specimen of *Ischnacanthus*, Edinburgh, Powrie 1891, 92, 258, shows a series of ossified basals in the right pectoral fin. These radiate from the point of attachment of the pectoral spine to the shoulder girdle and seem to be four in number; but none the less they present a remarkable resemblance to the basals of an Elasmobranch tribasal fin. The basals terminate at the proximal ends of the ossified fin rays. In another specimen, C. 4, there is some evidence of a calcified, cartilaginous pelvic girdle, associated with the base of the pelvic fin spine, but no details of structure can be given.

The outer surface of the head of *Ischnacanthus* differs somewhat in small (10 cm.) and large (25 cm.) individuals because the development of the ossicles on the cheek takes place late in life. The dorsal surface of the head has the normal Acanthodian structure, the typical body squamation of very small, square scales passing through a very short transition region into the somewhat larger head scaling at a point about midway between the hinder border of the orbit and the articulation of the jaws.

The upper border of the gill chamber is formed by a double row of rather large oval overlapping scales, between which the main lateral-line runs forward from the body to pass above the orbit. Three incomplete commissures arise dorsally from this canal, one (B.M.N.H. 46305 and D.M.S.W. P. 481) just anterior to the posterior end of the gill

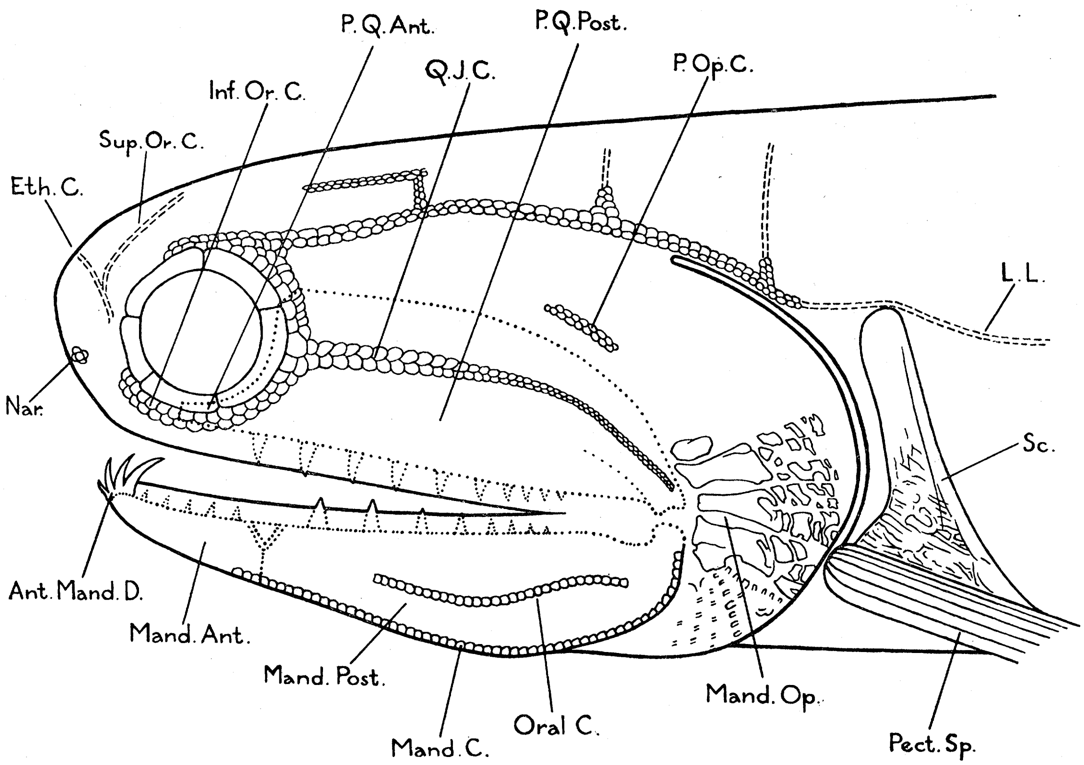


FIG. 11—*Ischnacanthus gracilis* EG. × 4·9. Reconstruction of head of a medium-sized individual from Turin Hill. *Ant.Mand.D.* the median whorl of teeth in the mandible; *Eth.C.* ethmoidal commissure; *Inf.Or.C.* infra-orbital canal; *L.L.* lateral-line; *Mand.Ant.* anterior bone in Meckel's cartilage; *Mand.C.* mandibular canal; *Mand.Op.* mandibular operculum; *Mand.Post.* the posterior mandibular bone; *Nar.* nostril; *Oral.C.* oral canal; *P.Q.Ant.* and *P.Q.Post.* the two ossifications in the palato-quadrate cartilage; *P.Op.C.* pre-opercular canal; *Pect.Sp.* pectoral spine; *Q.J.C.* quadrato-jugal canal; *Sc.* scapula; *Sup.Or.C.* supra-orbital canal.

chamber, the second (Edinburgh 1887, 35, 2), just in front of the articulation of the jaws, is bordered by typical oval scales, whilst the third lies about half-way between the posterior border of the orbit and the articulation of the jaws and is shown as a deep groove between the small thick bones of the skull roof in the transition region from the body squamation. There is some indication of a pair of lateral-line grooves passing forward from the inner ends of these commissural grooves. The bones of the top of the head are small irregular elements arranged in rough antero-posterior rows as far forward as a deep transverse lateral-line groove which crosses the head at the anterior border of the orbit, connecting the anterior ends of the main canals. From the points of junction a pair of badly marked grooves runs backward and inward, approaching one another above the posterior border of the orbit. The rounded anterior end of the head is covered by small thick scales, amongst which are some with rounded margins surrounding the nostrils, which lay probably close together and directed forward at the level of the centre of the orbit. The nostril is perfectly shown in a specimen belonging to the Dundee Natural History Society. It is a small circular hole placed far above the border of the mouth and forms the centre of a series of concentric rings of dermal bones.

The orbit is surrounded by the customary ring of very delicate though ornamented circum-orbitals, whose number appears to be five. This ring is itself framed by a double series of oval lateral-line scales arising from the main canal and extending continuously round the posterior and lower borders of the orbit. Its anterior end is not certainly determinable though it seems to cross the snout below the nostril.

The cheek is comparatively little ossified in small individuals but becomes completely scaled in large ones. It contains a typical double row of oval lateral-line scales arising from the post-orbital canal at about the level of the middle of the orbit, and extending backward to the jaw articulation. The rest of the cheek is when fully ossified completely covered by irregular elongated ornamented scales forming rough ridges and grooves. These in turn pass upward and backward, with no break whatsoever, into the mandibular operculum. The scaling of the cheek in front of the jaw articulation is feeble, but that of the lower jaw, composed of thick ornamented scales, is sometimes well shown. The ventral margin of the lower jaw is formed of a double row of scales bordering its main lateral-line, which is continuous over the articulation with the "pre-opercular" canal, and extends forward apparently to the symphysis. The more dorsally placed "oral" canal passes forward over a series of oval lateral-line scales toward, but not as far as, the anterior end. It appears to arise from the main canal.

The mandibular operculum, unlike that of the fish previously discussed, covers the whole gill chamber. The dorsal part is supported only by a series of very small elongated scales, of extreme tenuity in the small individuals, but becoming quite massive in the large specimens. These are arranged in irregular rows passing downward and backward. A group of short more massive bones, representing the opercular rays of other forms, lies just behind the jaw articulation. Immediately ventral to these, that part of the operculum which lies against the base of the scapula contains a relatively massive group of polygonal scales. The intergular part of the operculum has small isolated scales posteriorly, and seems to be naked in front.

The main lateral-line canal can be traced along the flank as a ridge rather above the middle line on the outer surface of the squamation running into the tail, where it continues along the dorsal lobe close to the lower margin, becoming less and less definite as it approaches the tip. The squamation seems to show extremely little change of character over the lateral-line canal, which is in fact only recognizable along the flank by the presence of this well-defined ridge. This condition can only imply that the actual canal ran in a series of special ossifications lying below the scales and perhaps fixed to their lower surfaces. It is quite clear that the normal Acanthodian condition of the canal running between rows of scales does not apply to *Ischnacanthus*, even though it does to *Acanthodes*. There is a ventral line on the trunk which can usually be seen running backward just mesial of the base of the pectoral fin spine.

Cheiracanthus

Individual fish belonging to the genus *Cheiracanthus* are very common in all the well-known Middle Old Red Sandstone nodule localities in the Moray Firth, at Achanarras, and in Orkney. Two species, *C. murchisoni* Ag. and *C. latus* Eg., are to be distinguished in the Moray Firth materials; they are identical in their morphology but differ in proportion and in some details. The following account distinguishes between them where necessary.

The fish are usually complete, but the scales on the body, unlike those on the fins, are usually displaced, and the exoskeleton of the head is always confused. The fins are very unusual amongst Acanthodians because the outline of the web is usually well preserved. It seems clear that the fish were round bodied and very heavily built. Evidently the head was wide from side to side and the pre-orbital part exceedingly short. The branchial region is short and deep. The body is deep in *C. murchisoni* and even deeper in *C. latus*. There is a single dorsal fin. The fin spines are always deeply inserted into the body. The caudal fin is very large, the upper lobe being upturned whilst the triangular lower lobe has a considerably deflected anterior margin. The caudal pedicel is deep. In *C. latus* the tail is enormous. The anal fin is like the dorsal but lies a little behind it. The pectorals are large and the pelvics also of great size, as large as the dorsal and anal.

The body is completely covered with a normal very fine squamation of very small square scales ornamented by longitudinally running ridges. There are no enlarged lateral-line scales, and none elsewhere on the body. The scales on the webs of the fins are arranged in rows and may be less than one-tenth of a millimetre square.

Many specimens of *Cheiracanthus* preserve an ossified chondrocranium. The ossification appears to have been continuous throughout the neural cranium, merely a thin film over the outer surface of the persisting cartilage as in the homologous structure in *Acanthodes*. The brain case is thus always crushed flat, and little beyond its main outline can be distinguished. It is evident that in general morphology it agreed closely with that of *A. bronnii* described later in this paper. The region of the olfactory chambers is entirely unossified, as is the supra-orbital region above and in front of the orbit. The trabecular region forms a narrow bar, showing that the skull was tropibasic. This bar suddenly widens laterally at the anterior end of the otic region, where it is probable that it had facets directed forward for articulation with the anterior part of the palato-quadrate. The otic region is very broad, and like that of an Actinopterygian has nearly parallel lateral margins forming strong ridges over the horizontal semi-circular canals. These extend backward from a post-orbital process for a long distance. It is probable that the otic process of the palato-quadrate articulated with the hinder surface of the post-orbital process. The character of the occipital region is not shown.

The palato-quadrate cartilage is completely ossified and shows no sign of origin from independent centres. The very long paraotic part of the bone is high, its upper border, which is segmental, being turned outward for the attachment of the masticatory muscles. The hinder end of this ridge is thickened and transversely widened at its

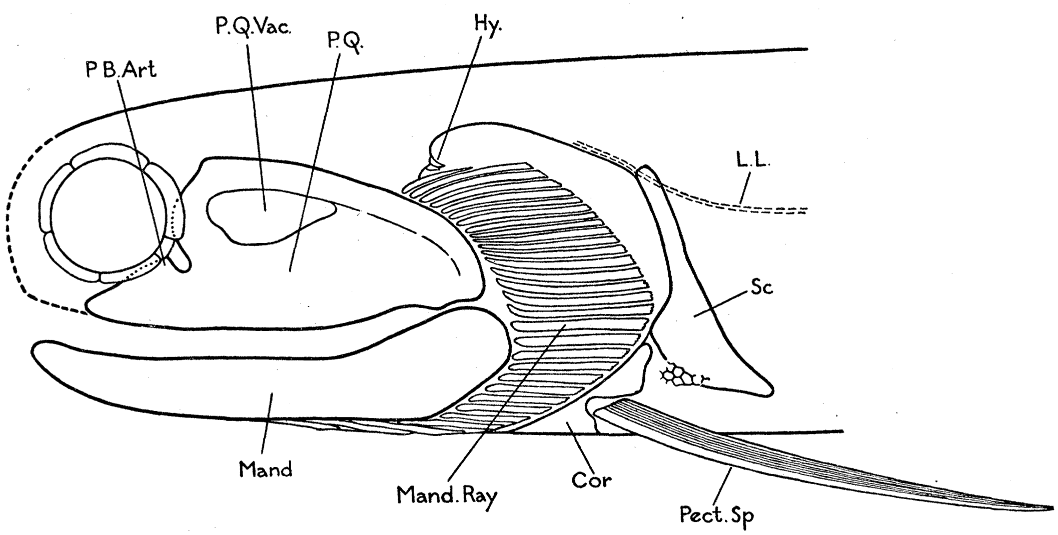


FIG. 12—*Cheiracanthus murchisoni* AG. × 3·4. Reconstruction of head, mainly from specimens from the M.O.R.S. of Gamrie. *Cor.* coracoid; *Hy.* upper end of the hyoid arch; *L.L.* lateral-line; *Mand.* lower jaw; *Mand.Ray*, a ray of the mandibular operculum; *P.B.Art.* palato-basal articulation of the palato-quadrate; *P.Q.* palato-quadrate; *P.Q.Vac.* vacuity in the palato-quadrate; *Pect.Sp.* pectoral fin spine; *Sc.* scapula.

lower end to form a condyle for articulation of the lower jaw. The paraotic ramus ends anteriorly in a generally vertical everted border which finishes abruptly by forming the hinder margin of a deep notch on the admesial edge of the palatal ramus. The upper part of the anterior border of the paraotic plate slopes a little backward and ends in a small rounded anterior otic process which seems to have articulated with the post-orbital process of the neural cranium. The paraotic plate is perforated by a large, usually pear-shaped vacuity (originally found by JAEKEL) lying just within the thickened and everted border.

The short and wide palatal ramus lies nearly at right angles to the paraotic plate and has a blunt anterior point. Its lateral margin is continued backward on the outturned lower margin of the paraotic plate so as to leave only a very shallow bay for the masticatory muscle. The inner border of the palatal ramus ends abruptly in a backwardly facing knob, which lies mesial of the root of the anterior edge of the paraotic plate, and by comparison with *Acanthodes* appears to have articulated with the basis cranii. It is evident that the palato-pterygoids of the two sides were rather widely separated in front. The palato-quadrate of *Cheiracanthus latus* is much deeper than that of *C. murchisoni* but otherwise agrees with it.

Meckel's cartilage is elasmobranch-like in its general character. It is ossified as a single continuous bone. It is very slender in small specimens, becoming deeper in larger individuals, and has a very gently concave oral border. The anterior end is shallow and meets its fellow in symphysis. The articular surface lies on the upper side quite posteriorly, and has a small "coronoid" elevation immediately in front of it. The lower border of the posterior part of the structure is turned outward. It is evident from many specimens (P. 486, D.M.S.W. etc.) that the lower jaw is considerably longer than the palato-quadrate.

The cerato-hyal (figured by JAEKEL 1925) is usually visible as a straight cylindrical rod with an inturned anterior end which approaches nearly to that of its fellow, there being in my material no trace of hypo- or basi-hyals. The small specimen, Edinburgh 1884, 60, 3, suggests the presence of at least two pairs of ossified cerato-branchials. I have seen no evidence of ossified epi-hyals in any specimen.

The opercular fold is supported by a wonderful series of rays. On the ventral surface between the lower jaws there are two groups, each containing about eight very slender elements of great length, the longest of them being probably nearly half the entire length of the lower jaw. These all end anteriorly in a transverse plane or nearly so, and their posterior ends form part of a segment of a circle extending back to a point rather behind that of the articulation of the lower jaw. They lie parallel to one another and to the lower border of the jaw, and pass apparently without interruption into the more flattened rays attached to the lower jaw posteriorly. The rays, seven or eight in number, continue uninterruptedly into a series of some seventeen, which lie like a fringe attached to the hinder border of the palato-quadrate. These opercular rays are massive structures, each with a flat internal surface, and at any rate in the central part of the series each bears a strong longitudinal ridge which bifurcates before it reaches the distal end of the bone. The individual rays have nearly parallel margins by which they are in contact. The attached anterior ends of those rays which belong to the mandible are deflected, a single ray at the articulation of the jaws is straight and widened, whilst the pointed ends of the ventral rays of the palato-quadrate point upward. In *C. murchisoni* the rays are massive and in contact with one another to the dorsal end of the series, in *C. latus* the upper rays are slender and their anterior ends turn sharply downward. The series extends very far up the dorsal border of the palato-quadrate and at first it seemed probable that the whole of the regularly curved hinder end of the series rested on the border of the gill chamber. When, however, the head is reconstructed it becomes evident that only the lower part of the series up to the level of the articulation of the lower jaw can have done so, and that there remains a narrow but deep area which cannot have been covered by the ossified portion of the mandibular operculum.

In several specimens (D.M.S.W. P. 492, B.M.N.H. 43273, P. 3203, 36010, and others) belonging to both species, the mandibular operculum has been dragged a little downward and there is shown a series of dermal ossifications belonging to the branchial arches. These individual bones are long slender rods which overlap one another and clearly lay in the skin on the outer side of the gill septum. They are always a little displaced but three independent arches are recognizable. It is most probable that they are the first three branchial arches, the hyoid arch being without ossification. In B.M.N.H. 43273, where the upper border of the gill chamber is unusually well shown, two small sickle-shaped bones projecting down from it correspond very well with the bones which lie in the upper end of the hyoid arch in *Climatius*.

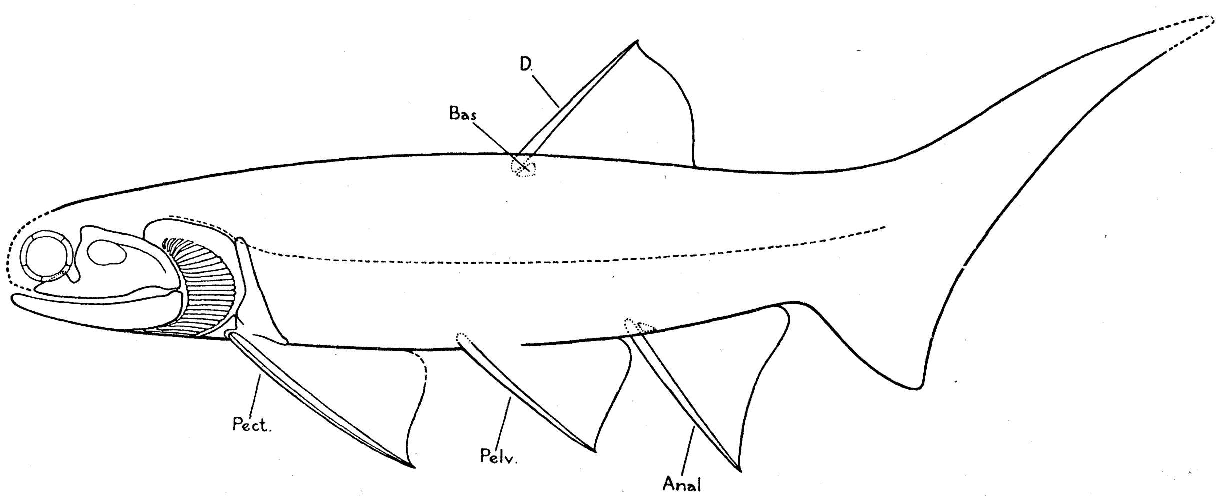


FIG. 13—*Cheiracanthus latus* EG. × 1·0. Reconstruction of fish from specimens from the M.O.R.S. of Tynet Burn and Gamrie. *Anal*, anal fin; *Bas.* basal of dorsal fin *D*; *Pect.* pectoral fin; *Pelv.* pelvic fin.

The exoskeleton of the head is very badly shown. The circum-orbital ring of plates though ornamented is feeble, the individual bones being narrow and thin. They seem in D.M.S.W. P. 485 to be six in number, but can seldom be counted. The upper surface and snout are completely covered by a mosaic of small polygonal scales whose arrangement cannot be determined. There is some evidence of a small nostril lying rather high up on the front of the head. It is probable that the cheek and lower jaw lacked ossification, though there is a series of small scales below the eye.

The main lateral-line is sometimes shown on the flank, but no other parts of the apparatus can be seen.

The shoulder girdle consists of two bones on each side, neither of which bears any ornament but lies underneath the scale-containing skin. The upper bone, the scapula, has a narrow upstanding process containing an hour-glass-shaped cavity formerly filled with cartilage. Ventrally this bone widens, its cavity becoming very large so that the bone is always crushed. It seems, however, to have been flattened in life. The ventral bone is also hollow, a shell of dense bone surrounding a clear calcite infilling which was no doubt cartilage during life. It lies anterior to and below the scapula and may be called coracoid. Its outer surface is deeply grooved for the reception of the base of the spine and its lower edge is turned outward.

The spine is slightly curved, and has a smooth anterior edge separated from the flat surfaces by grooves on each side so deep that the whole front of the spine looks like an independent cylindrical thread. The spine contains a cavity reaching nearly to its tip.

The dorsal fin of *Cheiracanthus latus* commonly, and its anal fin occasionally, possess small basal bones, single elements tightly attached to the extreme base of the fin spine on its posterior surface.

Diplacanthus striatus

Diplacanthus striatus is a fish found frequently in all the Middle Old Red Sandstone nodule localities surrounding the Moray Firth, but is especially common and well preserved at Tynet Burn and Gamrie. It also occurs in abundance at Achanarras in Caithness, and in the Stromness Beds in Orkney.

One single specimen, Powrie 1891, 92, 334, Royal Scottish Museum, which is certainly determinable from the character of its fin spines, shoulder girdle, scales and mandibular splints, differs from all other specimens of *D. striatus* in that it has very massive ossifications in the head skeleton, vertebral column and basals of the fins, and possesses well-preserved dermal fin rays. Other specimens show slight traces of ossification of the same nature in the branchial arches, thus confirming the identification. The causes of this very extensive ossification in this individual are quite unknown. The specimen is not of exceptionally large size.

The normal length is about 9 cm. The dozen specimens before me are preserved dorso-ventrally flattened or in profile in almost equal numbers. This arrangement may depend more on the fact that both the dorsal and ventral fin spines are very long than on the real shape of the body of the fish, but when taken in conjunction with other evidence derived from the shoulder girdle it goes to show that the height and width of the fish at the shoulder were about equal, and that the animal possessed a flattened ventral surface.

It is clear that the fish was rather abruptly truncated in front, the snout being rounded from side to side and probably somewhat wedge-shaped dorso-ventrally; the exact profile is, however, impossible to determine. When allowance is made for the widening due to crushing the fish is comparatively slender and stream-lined, though the caudal pedicel is deep.

The caudal fin is heterocercal, its upper lobe appearing to turn upward somewhat more than in the Lower Devonian Acanthodians and the lower lobe forming a less sharply marked triangle than in those fishes. The posterior border of the web of the caudal fin forms only a very shallow bay.

The dorsal fins of typical Acanthodian pattern are supported by enormously tall fin spines, of which the anterior is curved and the second, somewhat shorter than the first, is inserted at an angle of about 60° with the body surface and is nearly straight. The anal fin has a straight very long and slender spine about the length of the second dorsal, and lies posteriorly to it. The web of the dorsal fins is occasionally preserved, at

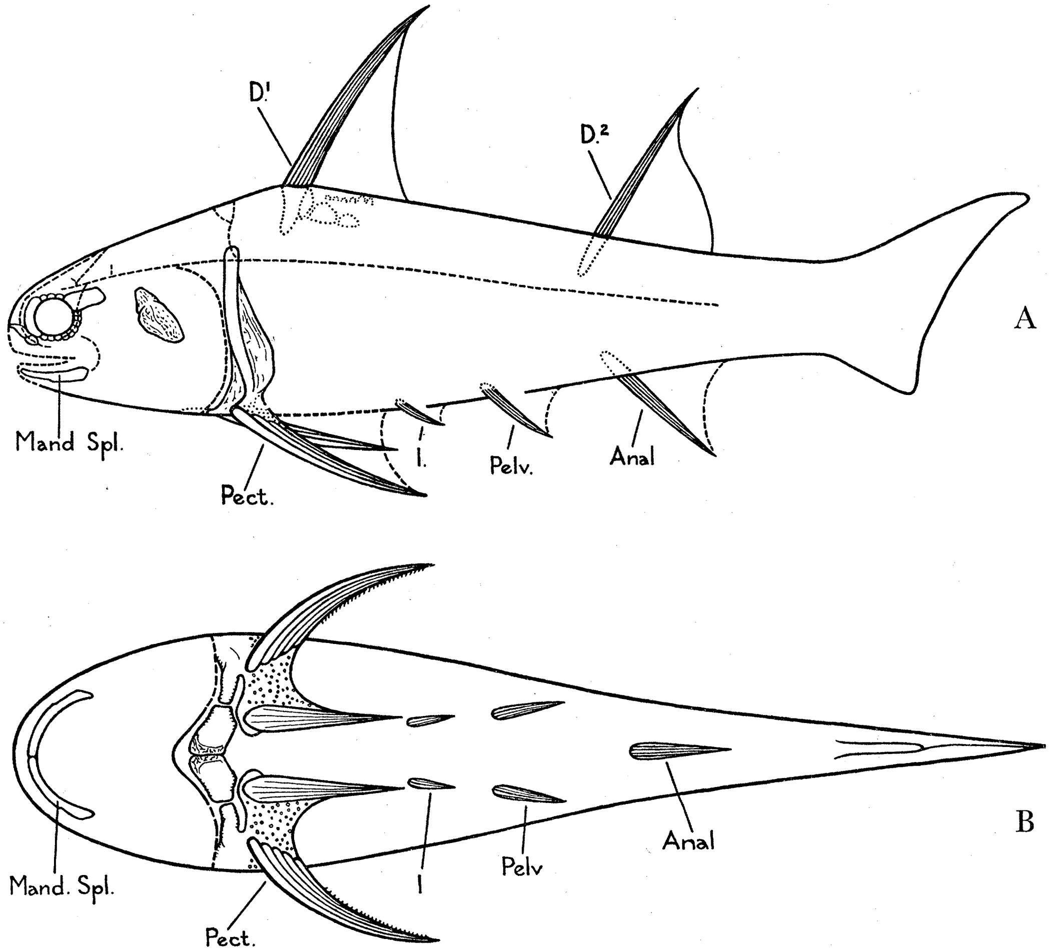


Fig. 14—*Diplacanthus striatus* Ag. × 1·5. Reconstructions of (A) left lateral and (B) ventral surface, founded on specimens from Tynet Burn and Gamrie, M.O.R.S. *Anal*, anal fin; D^1 and D^2, dorsal fins; *I.* intermediate spine; *Mand.Spl.* mandibular splint; *Pect.* pectoral apparatus; *Pelv.* pelvic fin.

any rate in part, and seems to have a very short attachment along the body and not to extend to the extreme tip of the spine. The spines of the dorsal fins are remarkable in that, unlike those of *Mesacanthus* and *Ischnacanthus*, they have a long inserted portion. The exserted part bears an ornamentation of coarse longitudinal ribs parallel to its anterior margin, the insert part narrows rapidly and is longitudinally striated. Each spine is hollow, the cavity extending almost to its tip and lying rather posteriorly in the spine.

The unique specimen, Edinburgh, Powrie 1891, 92, 334, shows a series of three well-ossified basals in the first dorsal fin. Of these the first has its anterior margin clasped by the split hinder surface of the spine, the second is larger, and the third of considerable size. There is definite evidence of the existence of a uniform row of small cylindrical radials in the base of the fin, and some indication of additional bones between these and the three basals. This fin is supported throughout its visible extent by cerato-trichia, delicate cylindrical rods of uniform diameter which are obscurely grouped into bundles ending at the level of the dorsal ends of the radials. This specimen and others show that the surface of the fin web is coated with a mosaic of normal square scales of very small size.

There are three pairs of fins. The pectoral, which in normal specimens never shows any trace of a web, possesses two spines and an elaborate shoulder girdle which will be described later. The lateral spine is long, somewhat curved and widening at its base and shows a marked distinction between exserted and inserted regions, like the dorsal-fin spine. The admedian spine lying parallel to the principal plane of the animal is of such a length that its tip lies a little anterior to that of the lateral spine; it is powerful and deeply ridged and grooved. The very short and delicate spines of the intermediate fins lie immediately behind the posterior ends of the admedian spines of the pectoral fins. The pelvic-fin spines, which lie a short distance behind those of the intermediate fins, are twice as long as the pair in front of them. They are relatively wide and powerful. In C. 15, and in Powrie 1891, 92, 334, there is a trace of the web of the pelvic fins, but it is not sufficiently well preserved to show any details.

The whole body behind the head region is covered with normal square Acanthodian scales, about a quarter of a millimetre across. The fin webs sometimes possess similar squarish scales of much smaller dimensions. The lateral-line runs between two rows of somewhat enlarged scales, the straight obliquely set rows of scales being broken at its level. It lies nearer to dorsal than the ventral margin of the fish, but is often very difficult to follow in the material. The mid-dorsal region of the body immediately in front of the first dorsal fin is covered with a development of rather large irregular scales similar to those covering the top of the head, but separated from them by an area of normal small square body scales.

The endoskeleton of the head is usually completely unossified but traces of the branchial arches are sometimes visible as bone, and Powrie 1891, 92, 334 shows the whole fully ossified but so crushed as to be almost incapable of interpretation. The neural cranium shows no intelligible features, but a deep palato-quadrate ossified in two sections—a small palatal part and a very deep quadrate region—and a similarly double Meckel's cartilage are visible. The other elements of the visceral skeleton are a series of extraordinarily massive rods which may be a cerato-hyal and cerato-branchials. Without the counterpart this specimen cannot be further discussed.

The vertebral column is ossified in Powrie 1891, 92, 334, but its elements are so involved with scales that it is not possible to give a detailed description. The structure was notochordal throughout, but there is a series of rather wide-spaced neural arches. The corresponding subnotochordal bones seem, at any rate in the space between the pelvic and anal fins, to have been continuous across the middle line. There is no evidence of ossified ribs.

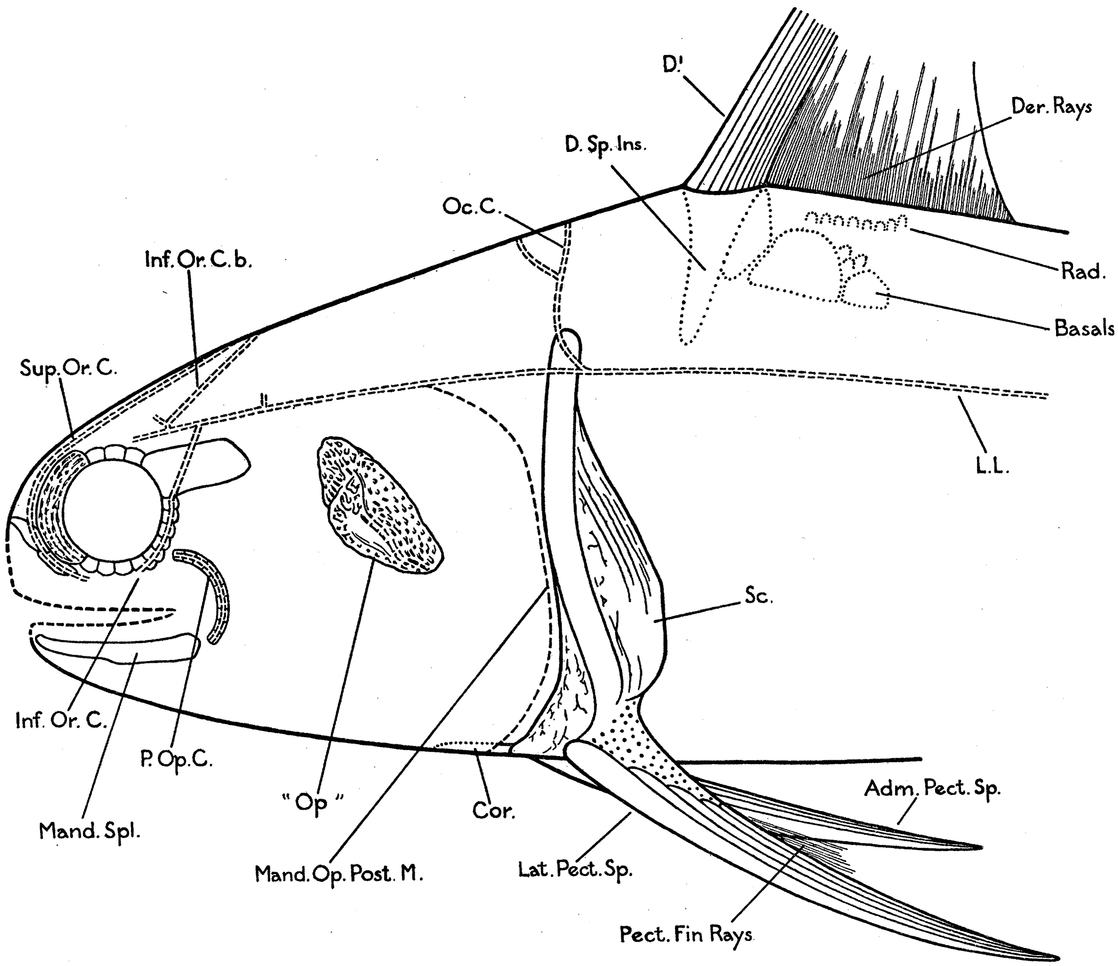


FIG. 15—*Diplacanthus striatus* AG. × 3·8. Reconstruction of anterior part of body on the basis of specimens from the M.O.R.S. of Tynet Burn. *Adm.Pect.Sp.* admedian pectoral spine; *Basals*, of first dorsal fin; *Cor.* coracoid; D^1, spine of first dorsal fin; *D.Sp.Ins.* its inserted part dotted; *Der.Rays*, dermal rays, ceratotrichia, of first dorsal fin; *Inf.Or.C.* infra-orbital canal; *Inf.Or.C.b.* postero-median branch of the infra-orbital canal (STENSIO); *L.L.* lateral-line; *Lat.Pect.Sp.* lateral pectoral spine; *Mand.Op.Post.M.* posterior border of the mandibular operculum; *Mand.Spl.* mandibular splint; *Oc.C.* occipital commissure; "*Op.*" large bone in the operculum; *P.Op.C.* pre-opercular canal; *Pect.Fin Rays*, ceratotrichia of the pectoral fin; *Rad.* radials of first dorsal fin; *Sc.* scapula; *Sup.Or.C.* supra-orbital canal.

The exoskeleton of the head is exceedingly well shown in D.M.S.W. P. 300. The normal regular squamation of the trunk is continued forward to the occiput where it passes into a transition region in which the individual scales become larger and are quite irregularly arranged. As they are traced forward these dermal bones become larger and are arranged in irregular longitudinal rows of which there are about twelve in the orbital region. This coherent dorsal shield ends abruptly in front at a pair of large transversely placed bones, whose lateral and anterior corners are turned downward in front of the circum-orbitals. There is some evidence that another somewhat smaller bone continues the process downward.

The position of the nostril cannot be determined, but it certainly lies below and in front of this head shield in a region which has either no dermal bones or at most a sparse covering.

The whole structure of the circum-orbital chain can be made out from a comparison of many specimens. The orbit is circular, the postero-dorsal part of its border being carried on a large bone which is always recognizable because it is crossed by the upper end of the infra-orbital lateral-line canal. Below this bone the posterior and ventral border of the orbit is borne by a series of about nine small bones forming a continuous chain, which is in part enclosed by a similar external series, the lateral-line running between the two. The anterior border of the orbit lies in a large well-ornamented bone which is in contact, by its non-orbital margin, with the lateral border of the coherent head shield. The orbit is completed by a chain of three small bones lying lateral to the head shield.

The mouth is very short, and the lateral surface of the head below and behind the orbit is continuous with the outer surface of the large mandibular operculum from which it is indistinguishable. This surface in the middle of its height and length contains a single very large highly ornamented bony plate, but is otherwise covered with smal rounded scales which in the region before the large plate and behind the corner of the mouth are vertically elongated and arranged roughly in vertical rows. In a single specimen (P. 299) a short chain of bones, of the kind always associated with a lateral-line canal, runs in a semicircle from the posterior side of the circum-orbital ring toward the hinder end of the lower jaw.

The free border of the mandibular operculum is sometimes shown, visible merely by the disappearance of the squamation, there being no series of bones defining it. These traces are, however, quite consistent and show that the operculum covered the whole gill chamber, its margins resting on the lowest row of the body scaling, on the shoulder girdle, and on the anterior border of a small triangular patch of large scales which extends forward from the shoulder girdle on to the ventral surface of the pharyngeal region. The operculum seems to be continuous across the mid-ventral line and its small squamation merges into that of the intergular space. The only individually recognizable bones in this region are the pair of mandibular splints which are shown in Powrie 1891, 92, 334 to be attached to the ventral border of Meckel's cartilage. They are extremely smooth dense bones of characteristic shape, their shallow anterior ends meeting in a symphysis; they deepen posteriorly and terminate in a blunt point.

The lateral-line of the head is in part shown to perfection in D.M.S.W. P. 300. As in many other Acanthodians the anterior part of the system is peculiar in that the actual canal runs through a chain of short bony cylinders. These may be, and probably are, independent of the normal dermal bones. Usually the canal surrounded by the apparently single cylinder lies between two rows of dermal bones. Posteriorly these cylinders are absent and the course of the canal can only be determined from the two rows of scales, a matter of difficulty especially on the body.

The main canal lies on the flank, rather above its mid-line. It passes forward over the upper part of the scapula on which it leaves no impression and descends on to the margin of the gill chamber. There it continues, becoming surrounded by bony cylinders, immediately mesial of the large circum-orbital plate, until it ends above the

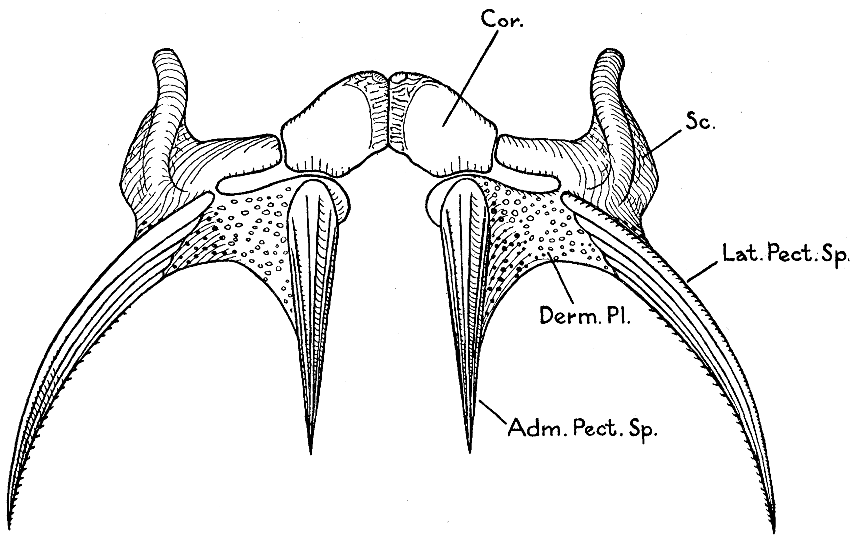


FIG. 16—*Diplacanthus striatus* AG. × 3·6. Reconstruction of the ventral aspect of the pectoral girdle. From Tynet specimens. *Adm.Pect.Sp.* admedian pectoral spine; *Cor.* coracoid; *Derm.Pl.* dermal plate connecting the pectoral spines; *Lat.Pect.Sp.* lateral pectoral spine; *Sc.* scapula.

middle of the orbit. Three dorsal branches arise from this canal, one lies in the region of the shoulder girdle crossing the middle line in front of the spine of the first dorsal fin and having an M-shaped course. The next lies above the hinder border of the large circum-orbital and passes directly inward for a short distance. The most anterior, the posterior branch of the infra-orbital canal, arises above the back of the orbit and passes inward and backward to meet, or nearly to meet, its fellow immediately behind the junction of the supra-orbital canals. The infra-orbital canal arises from the main canal some distance behind its anterior end. It then crosses the large posterior circum-orbital and continues downward below the orbit immediately external to the ring of small circum-orbitals. It cannot be seen to join the anterior end of the supra-orbital canal, but probably does so. A short canal appears to have arisen from the infra-orbital canal at about the level of the lower border of the orbit and proceeds over the cheek to the lower jaw. The supra-orbital canal begins posteriorly in a junction with its fellow in the middle line; the two then separate, pursuing nearly straight courses, until each plunges downward immediately lateral to the large bone which forms the anterior end of the dorsal shield and mesial to the large anterior circum-orbital. It there continues, perhaps to join the anterior end of the infra-orbital canal. There is a slight indication of a ventral line on the body, running on the mesial side of the inner fin spines of the shoulder complex and the intermediate fin spines.

The shoulder girdle of *Diplacanthus* was first described by SMITH WOODWARD (1891), to whose account I can add little. It consists of an element standing vertically, parallel to the flank and about on the posterior border of the gill chamber. This bone, the scapula, is perforated from top to bottom by a cavity, which widens posteriorly at the place where the lateral pectoral spine is inserted. The analogy of all other similar structures in Acanthodians shows that this cavity, which is filled with clear transparent calcite in the fossils, represents a cartilage, and it is completely surrounded by bone. Posteriorly this bone forms a wide lappet which extends down to the insertion of the spine and is ornamented with a series of shallow grooves parallel to its posterior margin. It certainly lay in the skin of the flank. The ventral end of the bone widens in an antero-posterior direction and is attached to the lateral pectoral fin spine for a long distance, fitting on to it by a flat surface which rests on a definite close-fitting and grooved rabbet. The anterior border of the ventral part of the bone turns inwards at right angles to the length of the fish, and quite clearly forms part of the posterior wall of the gill chamber. Here it is smooth, in contra-distinction to the ornamented outer surface of the bone. The wide base of the lateral fin spine is held on its dorsal surface by the expanded lower end of the dorsal shoulder-girdle bone. Its ventral surface exhibits a sudden transition from the coarsely ribbed exsert to a finely striated insert region, which was in life covered by a V-shaped dermal bone (*Derm.Pl.*), connecting together the lateral and admedian spines. This bone bears a well-defined ornament of tubercles. The admedian spine, exceedingly wide and powerful, is firmly held for three-quarters of its length by this dermal bone, and its admedian border also is surrounded by dermal bone which appears to be continuous with that which is interposed between the two spines. Finally, the shoulder girdle is completed by a pair of elements which seem to articulate both with the dorsal shoulder girdle and with the ventral dermal element surrounding the base of the admedian spine, and are themselves connected by some form of sutural union. It seems probable that these bones lay on the ventral surface because in specimen P. 299 they are continued forward by a triangular patch of large scales. These anterior elements which meet in the middle line are hollow and filled with clear crystalline calcite; in other words they are presumably perichondral bone laid down round a coracoid cartilage. The whole arrangement is unique and extraordinarily difficult to determine. The essential facts, however, are that the lateral-fin spine is firmly clasped between two independent bones; the admedian spine is inserted into a slot in one of these; and there is a third ventral element which articulates with the other two. No supporting elements are to be seen in association with any of the other paired fins. The specimen Powrie 1891, 92, 334 shows a series of ceratotrichia associated with the pectoral fin.

Acanthodes

The ironstone nodules from the Lebach shales contain a considerable number of specimens of *Acanthodes*. These are often exceedingly well preserved and our knowledge of the endoskeleton of Acanthodians has been based almost entirely upon them.

Agassiz in 1835 founded the genus *Acanthodes* on such materials, two poor specimens being figured as *A. bronnii*. In 1848 Beyrich described a fish from the Rothliegende of Klein Neundorf as *Holacanthodes gracilis* and this was well described and figured by Roemer in 1857 as *Acanthodes gracilis*. In the same year Troschel published the first characteristic figures of *A. bronnii* Ag., and in 1868 Kner gave further excellent figures of Lebach specimens, referring them to *A. gracilis*.

In the British Museum Catalogue Smith Woodward (1891) groups all the Lebach and Rothliegende *Acanthodes* together under *A. bronnii*, and his views have been accepted by all subsequent authors.

It was therefore with considerable surprise that I found the numerous Lebach specimens forming the basis of the following account to differ very widely from one another in the proportionate sizes of their parts, and that the variations in, for example, the ratio of the length of the mandibular splint to that of the pectoral fin spine, may be 100 %, and cannot be accounted for by growth (see Table I).

Table I—List of Specimens of *Acanthodes* from Lebach used in this Account

No. of specimen	Length in mm. of mandibular splint	Length in mm. of pectoral spine
B.M.N.H. P. 6192	15·0	15·5
B.M.N.H. 40050	13·0 plus	19·5
Berlin (unnumbered)	20·5	32·0
D.M.S.W. P. 496	24·0	40·0
D.M.S.W. P. 498	19·0 plus (< 28)	50·0 plus
D.M.S.W. P. 494	28·5	49·0 plus
Berlin (unnumbered)	29·5	29·0
B.M.N.H. P. 4477 *a*	29·5 (?)	50·0
Edinburgh 1891, 42, 3	32·0	—
Edinburgh (unnumbered)	35·0	45·0
B.M.N.H. 22658 *a* and *b*	37·0	35·5
B.M.N.H. 40049	52·0	61·0 plus
D.M.S.W. P. 493	60·0	—
D.M.S.W. P. 323	65·0	73·0 plus
Pollichia II	71·0	—

Miss Townend has therefore made a series of very careful restorations of the anterior ends of several individual fishes, four of which are reproduced in fig. 20. It is evident that these individuals must belong to different species in that they differ not only in proportion, but very strikingly in the extent to which ossification of the lower jaw has gone at a given size.

Except for the series of forms from the Gas Coal of Nyran described by FRITSCH, and for *A. rouvillei* SAUVAGE, no other names have been given to European Upper Coal Measure or Lower Permian Acanthodians.

It is obvious that AGASSIZ's two type specimens of *A. bronnii* will never be capable of determination, and for the purposes of this paper it is unnecessary to introduce a number of new specific names for these fish. Therefore I shall simply refer when necessary to individual specimens, without specific attributions.

The smaller fish in these nodules are usually preserved complete except for the tail. They are, however, twisted, the anterior end of the body often forming a loop from which the hinder end stretches straight backward. The long cylindrical head is crushed into a plane usually in such a way that the flattened dorsal surface and the intergular space retain their full widths, the sides of the head being superimposed, one dorsal of the other by a distance equal to the width of the dorsal surface. This arrangement allows restorations of the head to be made easily and accurately, but results in a compression of the rounded anterior end of the head of such a kind that the structure in front of the orbits can never be understood.

The larger specimens are always represented by isolated portions, head, body and tail being in separate nodules. In my experience these heads are usually seen in lateral aspect, but REIS has figured a considerable number which are dorso-ventrally compressed. The appearance of these heads suggests that the skin, cartilages and ligaments were all intact at the time of burial whilst all other tissues had been destroyed, so that in dorso-ventrally flattened specimens the pharyngo-branchials rest directly on the cerato-branchials, a disposition which adds greatly to the difficulties of interpretation. The structures are, however, quite perfectly preserved, chiefly as moulds from which the remaining fragments of bone can be removed by treatment with dilute hydrochloric acid.

REIS in his elaborate description of *Acanthodes* gave an account of the neural cranium based on such part of it as could be seen in complete heads. According to his description it was composed essentially of two bony elements, a large thin shield dorsally and a remarkable T-shaped bone perforated by a large foramen lying on the ventral surface in the orbital region; this he called the trabecular. I am fortunate in that a single specimen, P. 495, shows the entire isolated neural cranium so far as it was ossified. Owing to the fact that a great deal of the side wall remained as cartilage, the ventral elements of this brain case sank down until they came into contact with its dorsal bones, but they are not otherwise displaced. The individual elements all consist of thin sheets of bone surrounding cavities which still exist as such and were in life certainly occupied by cartilage. The account that I give of them pays no attention to the cartilaginous hollow, the whole bone being described as though it were solid, or as if the description applied to the cast.

The base of the skull is composed of a series of three bones, the anterior and posterior of which are much more massive than that which lies between them, and are to be seen in other specimens. Seen from its ventral surface the posterior bone has a wide anterior and very narrow posterior end, its lower surface being gently convex and its lateral surfaces in the posterior three-quarters of the bone curving upwards almost at right angles to the ventral surface, indeed in the middle of its length being inrolled above it. Quite anteriorly the lateral surface flares somewhat outward and is deep. In

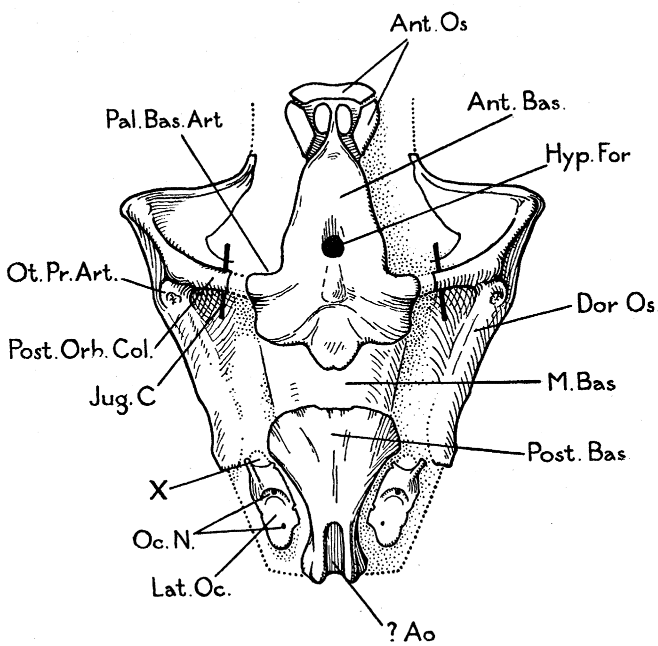


FIG. 17—*Acanthodes* sp. Lebach ironstones, P. 495, D.M.S.W. collection. Ventral aspect. × 1·2. Parts shaded in line direct drawings, stippled areas restored. *Ant.Bas.* anterior basal; *Ant.Os.* anterior ossicles; ? *Ao.* groove for dorsal aorta?; *Dor.Os.* dorsal bone; *Hyp.For.* hypophysial foramen; *Jug.C.* jugular canal; *Lat.Oc.* lateral occipital; *M.Bas.* middle basal; *Oc.N.* foramina for occipital nerves; *Ot.Pr.Art.* articulation for the otic process; *Pal.Bas.Art.* articulation for the palato-basal process; *Post.Bas.* posterior basal; *Post.Orb.Col.* post orbital column; *X*, notch for the vagus nerve.

the middle of the length it seems certain that the upper surface of the bone was carved out into a notch forming the lower part of a foramen and continued posteriorly by a shallow groove on the side of the bone. The posterior margin of the bone is deeply notched in the middle line, and a very well-defined groove, presumably for the anterior end of the dorsal aorta, runs forward from the notch until it suddenly ends, the bone in front of it descending abruptly to the ordinary level of the lower surface. The middle bone is a featureless structure shown to be exceedingly thin, but the anterior bone is very massive and has a most characteristic and recognizable shape. The large foramen which perforates it lies in the middle of its length and occupies one-quarter of the total width of the nearly flat lower surface at this point. Forward from here the bone

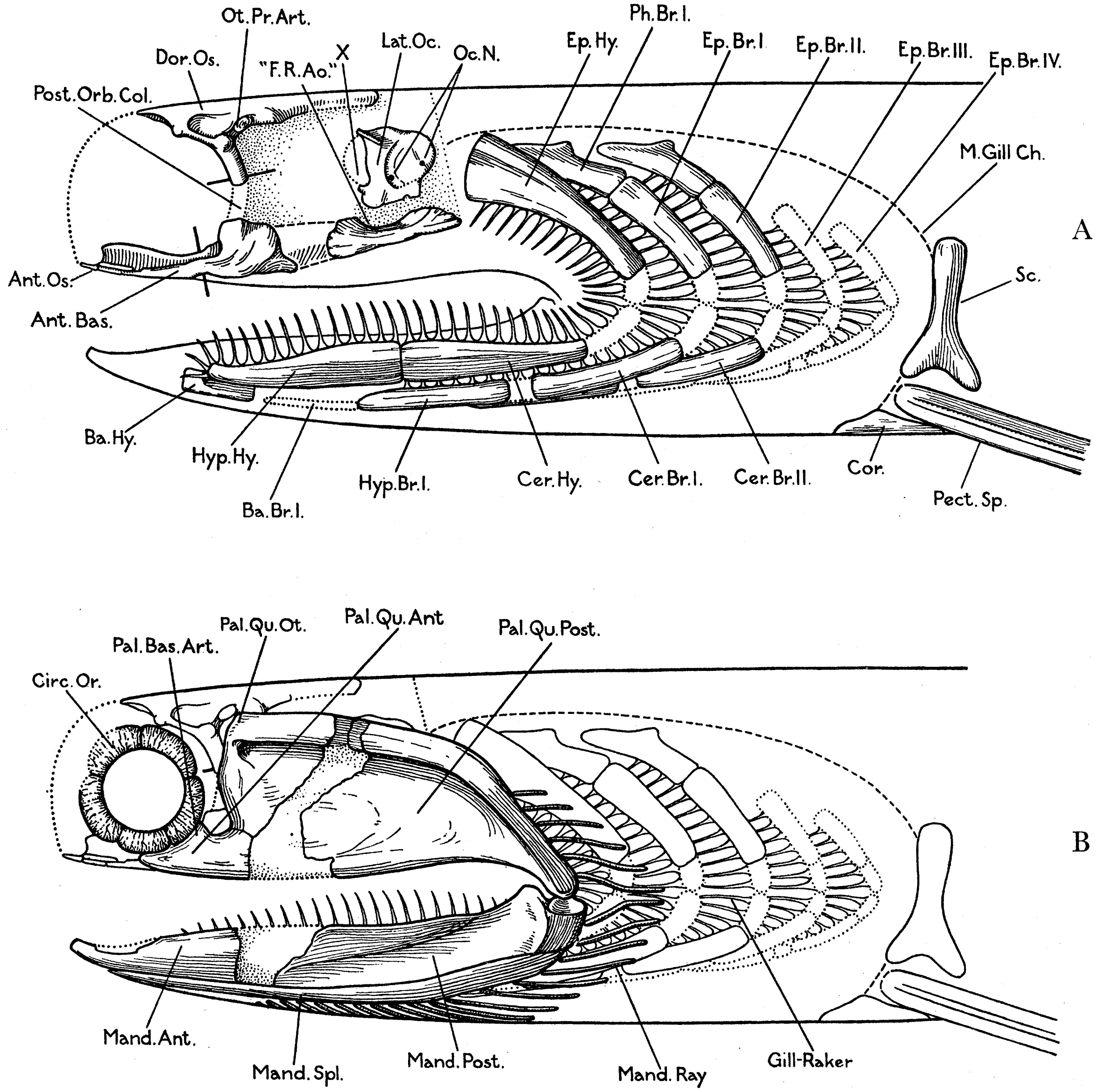


FIG. 18—*Acanthodes* sp. Reconstructions of the head, from specimens from the Lebach ironstones, especially P. 495, P. 493, P. 323, D.M.S.W. collection; B.M.N.H. 40049, and Pollichia II. × 1·1. A, with the mandible and palato-quadrate removed. B, complete except for the squamation. *Ant.Bas.* anterior basal; *Ant.Os.* anterior ossification in the basis cranii; *Ba.Br.* I, basi-branchial I; *Ba.Hy.* basi-hyal; *Cer.Br.* I, II, cerato-branchials I, II, etc.; *Cer.Hy.* cerato-hyal; *Circ.Or.* circum-orbital bones; *Cor.* coracoid; *Dor.Os.* dorsal bone in the neural cranium; *Ep.Br.* I, II, III, IV, epi-branchials I, II, etc.; *Ep.Hy.* epi-hyal; "*F.R.Ao.*" foramen for the radix aortae; *Gill-Raker*; *Hyp.Br.* I, hypo-branchial; *Hyp.Hy.* hypo-hyal; *Lat.Oc.* lateral ossification in the neural cranium; *M.Gill Ch.* margin of the gill chamber; *Mand.Ant.* anterior ossification in Meckel's cartilage; *Mand.Post.* posterior ossification in Meckel's cartilage; *Mand.Ray*, ray of the mandibular operculum; *Mand.Spl.* mandibular splint; *Oc.N.* foramina for the occipital nerves; *Ot.Pr.Art.* articular facet for the otic process;

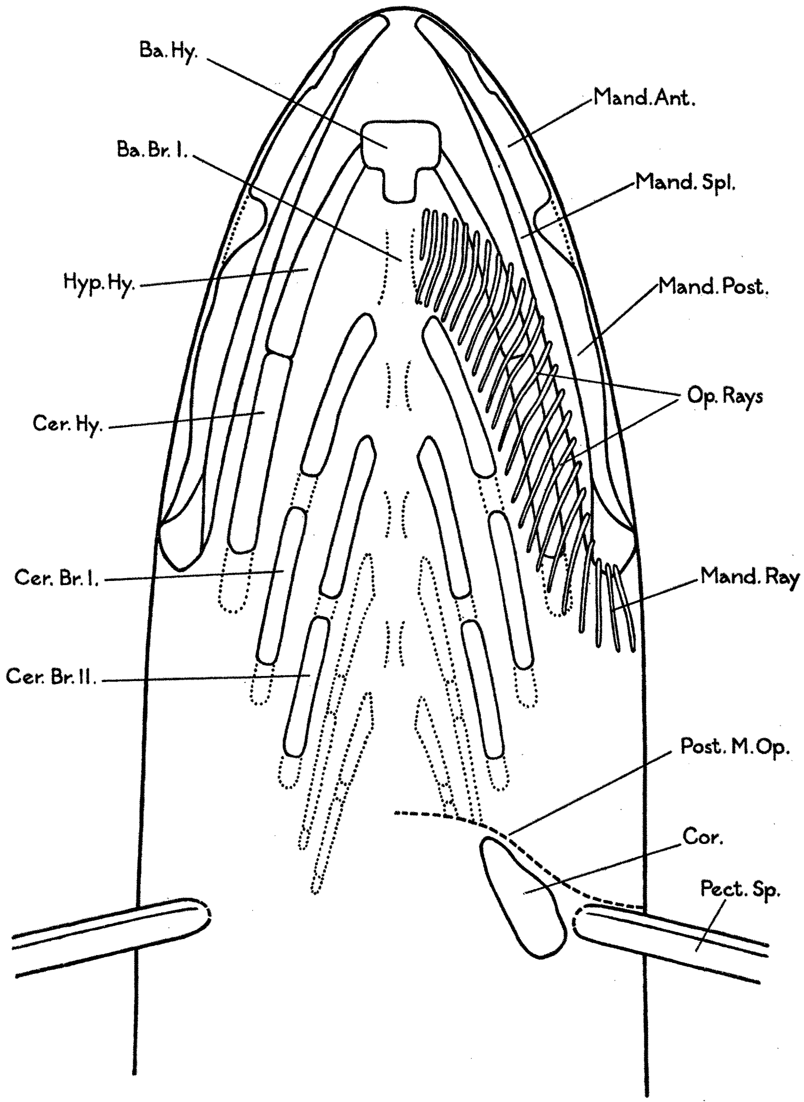


FIG. 19—*Acanthodes* sp. Lebach ironstones, reconstruction of the head, × 1·1, from the same material as fig. 18. Ventral aspect with the squamation not shown, and the gill-rakers omitted. *Ba.Br.* I, basi-branchial I; *Ba.Hy.* basi-hyal; *Cer.Br.* I and II, cerato-branchials I, II, etc.; *Cer.Hy.* cerato-hyal; *Cor.* coracoid; *Hyp.Hy.* hypo-hyal; *Mand.Ant.* anterior bone in Meckel's cartilage; *Mand.Post.* posterior bone in Meckel's cartilage; *Mand.Ray*, ray in the mandibular operculum; *Mand.Spl.* mandibular splint; *Op.Rays*, rays in the mandibular operculum; *Pect.Sp.* pectoral fin spine; *Post.M.Op.* posterior margin of the operculum.

Pal.Bas.Art. palato-basal articulation; *Pal.Qu.Ant.* anterior bone in the palato-quadrate cartilage; *Pal.Qu.Ot.* otic process of the palato-quadrate; *Pal.Qu.Post.* posterior bone in the palato-quadrate cartilage; *Pect.Sp.* spine of the pectoral fin; *Ph.Br.* I, pharyngo-branchial I; *Post.Orb.Col.* post-orbital column; *Sc.* scapula; *X*, foramen for the vagus nerve.

narrows gently until its lateral margins suddenly turn in to meet anteriorly in a blunt point. The foramen lies at the hinder end of a short shallow groove which travels forward in the middle line of the under-surface of the bone, and is for a persistent hypophysial duct. Immediately behind the foramen the lateral margins suddenly turn outward and pass upward as powerful bony transverse flanges. The flanges end abruptly, their lateral surfaces forming rounded ridges anteriorly which were obviously continued upward by cartilage in the complete neural cranium to meet a large process lying behind the post-orbital process on the dorso-lateral bone. Behind this ridge the surface of the flange is depressed and slopes dorsally at a somewhat higher angle than the ridge itself. On its upper surface this bone has a deep rounded ridge along the middle line, which runs forward from the anterior border of the foramen to the extreme anterior end where it is truncated abruptly for a cartilaginous extension. There seems no doubt that this ridge gave attachment to a membranous inter-orbital septum which must have risen for a considerable distance before it divided to surround the anterior end of the brain. The transverse flanges are shown to be very deep and to bear articular facets facing directly anteriorly, with which a special process of the anterior bone of the palato-quadrate cartilage articulated. Mesially of these facets the dorsal surface of the bone bears a pair of grooves which begin at shallow notches on the lateral borders of the ventral surface of the bone and pass upward and toward the mid-line behind the border of the foramen. These grooves were presumably associated with the internal carotid arteries. They end at a margin which maps out a triangular area, within which lies a small apparently independent bone with no features other than a small circular pit which passes down into its substance and ends in a rounded surface. Behind this bone and lateral to it the transverse flanges are thin and their upper surface featureless. When seen from its dorsal surface the anterior basi-cranial element is wide anteriorly, but ventrally it is hidden by four independent ossicles—a smaller pair lying adjacent to one another and immediately anterior to the pointed front end of the basi-cranial bone, and a larger pair which lie laterally and are indeed independent because one of them is slightly misplaced in the specimen. Finally the whole structure ends with a very thin transversely expanded plate of bone which crosses and lies in contact with the anterior margin of these four small elements.

The dorsal surface of the temporal region of the brain case is formed in large part by a pair of very big bones which may in extremely old individuals have become co-ossified across the middle line, but which in younger though still large specimens were certainly separate. Anteriorly they remain distinct, even in my isolated neural cranium. At the extreme anterior end each forms a narrow and sharp point, lying in the orbital margin, whose inner border seems to be continued directly backward parallel to the mid-line perhaps throughout the entire length of the bone. On its dorsal surface the bone forms a convex surface which descends laterally and extends out to the almost transversely placed orbital margin which ends abruptly at a massive post-orbital process. The hinder wall of the orbit is in part ossified as a spheroidal surface extending down from this margin; it is shown to be perforated by a rather small canal passing directly backward from a point some distance below the dorsal surface and mesially of the post-orbital process. Immediately below this foramen the bone forms a very massive pillar nearly circular in horizontal section, separating the orbit from a deep depression in the otic region within which lies the facet for the articulation of the otic process of the palato-quadrate. It is perfectly clear that this column was formerly connected by cartilage with the summit of the transverse ramus of the anterior basi-cranial bone. It is possible to determine the distance which separated these two bony surfaces by continuing the transverse rami dorsally until they become so far separated that they meet the proper spots on the dorsal bones; the height so determined can be checked because the depth of the palato-quadrate between the articulation of its otic process with the dorsal bone, and its basi-cranial articulation, is known. Both methods give the same height for the neural cranium in this region, and the diameter of the eye, determinable from the orbital plates surrounding it, is entirely appropriate to the orbital cavity so reconstructed. The lateral surface of the dorsal bone immediately above this descending column is concave, but soon shows a well-defined convexity marking the outer end of a concave face on its under surface, which is clearly the point of articulation of the otic process of the palato-quadrate. Posteriorly to the wide ventral expansion the bone is only represented by the ventral edge of its thin lateral surface, which stands more or less vertically in the skull. The dorsal surface of the bone in this region seems to be a direct continuation of that overhanging the orbit, and the bone terminates at a transversely placed margin. Trial with a plasticene model and general probability suggest that in the region immediately behind the column descending from the dorsal bone, the cartilaginous side wall of the brain case stood almost exactly vertically, but inclined a little outwards toward the dorsal surface. It seems to be certain that anteriorly it formed a deeply overhung depression like the corresponding region in a Palaeoniscid brain case.

One additional pair of elements lies posteriorly, each of which is a squarish bone now displaced in the specimen but apparently lying in the side wall of the occipital region. The anterior margin is a thick smoothly rounded column, with a well-defined notch toward its lower end below which the bone is produced to a point. The inner surface of the bone here is smooth and forms part of a cylinder with a horizontal axis. Unquestionably it formed part of the side wall of the actual brain cavity. The outer surface behind the anterior margin is at its upper edge produced into a short outstanding process which must have been in contact, or nearly so, with the cranial roof. Behind and below this process the outer surface bears a shallow groove which forms a quadrant extending from the posterior upper corner of the bone toward the posterior lower corner. This groove at about one-third of its length from the ventral end is entered by a small foramen, which is shown to pass through into the cranial cavity. Still more posteriorly but at the same general level there is another small foramen, also shown on both surfaces, which itself opens into the lower end of a much more shallow groove passing dorsally and appearing to join that just described. It seems certain that the antero-ventral corner of this bone was in contact with the lateral flange of the anterior end of the posterior basi-cranial bone, and that the whole lay nearly vertically but inclined somewhat outward dorsally, in the side wall of the occipital region. If this were so then the notch in the anterior border must have been for the vagus nerve, and the two posteriorly placed foramina for spinal-occipital nerves whose dorsal rami passed up the grooves, the ventral ramus of the more anterior lying in the ventral part of its groove. The posteriorly and laterally directed foramen, which seems to have existed between the ventral border of the posterior basi-cranial bone and this lateral-occipital element, remains without explanation. I am acquainted with nothing in fish which will account for it, although it is conceivable, and no more, that the jugular vein comes out through it. An apparently homologous foramen in the Arthrodeir *Leiosteus* is believed by STENSIO to have transmitted the radix aortae.

Several specimens show that the first ossifications to appear in the neural cranium are cylinders of bone surrounding the anterior and posterior vertical semi-circular canals. These were first figured and recognized by BASHFORD DEAN (1907, fig. 29). In D.M.S.W. P. 470 these are in contact by their upper ends and do not extend down to the ampullae; there is no trace of utriculus nor of the horizontal canal. An Edinburgh specimen shows an extension of ossification to surround the ampullae of the vertical canals and to enclose part of the horizontal semicircular canal. There is still no sign of the utriculus or sacculus. The only other ossification in the neural cranium of this specimen is in the anterior part (to the hinder border of the foramen) of the anterior basi-cranial bone. These specimens show the position and size of the ear which lies, as might be expected, in the side wall of the neural cranium above the middle basi-cranial bone. The general structure of the semicircular canals, their length and slenderness, is comparable with that of the Elasmobranchs, and stands in marked contrast to that of the corresponding structures in Osteolepis and Palaeoniscids. There is, however, no visible trace of the complexities which are commonly found in modern Elasmobranch labyrinths.

Visceral Skeleton—As REIS originally discovered and as JAEKEL and BASHFORD DEAN have confirmed, the palato-quadrate cartilage in *Acanthodes bronnii* is ossified as three independent structures. It is quite clear from the character of the material that these bones during life surrounded parts of a continuous cartilaginous palato-quadrate. The whole palato-quadrate cartilage so restored resembles that of an Elasmobranch in its general character except for the wide separation of the anterior end from that of its fellow. It has a very short palatal portion and a greatly elongated deep paraotic region whose dorsal margin is everted so as to form a thick and powerful ridge projecting laterally above the recessed surface of the rest of the bone. This ridge becomes somewhat deeper as it is traced posteriorly and ultimately terminates at the quadrate condyle, which lies a little obliquely to the general length of the bone and is comparatively narrow from side to side. The hinder half of the cartilage is sheathed by a single bone, whose lower margin for the anterior half of its length is turned outward, so that the structure forms a nearly horizontal surface on the palate. Behind this there is a well-marked semi-elliptical notch for the masticatory muscle. The dorsal element, which bears the otic process and unquestionably articulated with the dorsal bone of the neural cranium, has a marked vertical ridge along its anterior margin which lies immediately behind that post-orbital bar of the neural cranium whose lower end is the transverse flange of the anterior basi-cranial bone. The bone is perforated by a foramen which passes dorsally through its anterior and upper corner; the significance of this foramen is obscure. The anterior bone of the palato-quadrate forms a shallowly concave shell which continues the everted anterior end of the posterior bone and lies at a low angle with the horizontal in the palate. The bone terminates anteriorly in a point lying under the middle of the orbit. From this point backwards the inner edge is gently concave until it ends abruptly at a backward-facing facet, which is shown in several specimens to articulate with the front face of the transverse flange of the anterior basi-cranial bone. Behind this facet the bone is cut out into a deep rounded notch and then comes into contact with the dorsal element in the palato-quadrate, with which it may in old individuals be continuous. The upper jaw is thus well supported by two articulations with the neural cranium lying almost in the same transverse plane. It is certain that the palato-quadrates of the two sides did not meet in the middle line anteriorly as they do in Elasmobranchs and in the sturgeon.

The lower jaw is ossified as two independent bones which, even in the largest specimens, were separated by a considerable mass of cartilage. The whole structure has much the appearance of Meckel's cartilage of an Elasmobranch. The lower margin of the hinder half is turned out to form an outstanding ridge which posteriorly passes upward to form the labial side of the articular region, the latter bearing a concave facet for articulation with the quadrate. Posteriorly the structure is thin from side to side, but anteriorly it widens so that the oral surface is nearly flat and it is roughly triangular in section. It narrows very rapidly and becomes extremely slender anteriorly, where it is slightly turned inward and bears a very small pit, presumably for the short ligament by which it was attached to its fellow of the opposite side.

The structures so far described consist of a thin film of bone surrounding the still persistent cartilages, but the lower jaw includes also a structure, Reis's extra-mandibular spine, which is clearly of a different nature. It is completely formed even in such very small specimens as B.M.N.H. P. 6192, where there are no cartilage bones whatsoever in the head. The extra-mandibular spine is a massive and nearly straight splint firmly attached to the lower and outer surfaces of the lower jaw; it lies indeed in a groove in that structure and extends continuously from a point near its anterior end to the middle of the articular surface. The morphological significance of this structure is uncertain but it clearly belongs to the mandibular arch. As Reis has already recognized it is associated with a series of delicate bony rods, called by him the extra-mandibular rays. Many specimens (that in Pollichia being especially useful) show that these rays are definitely related to the mandible and retain their positions even where the hyoid arch is misplaced. Young individuals as a whole confirm this arrangement. The rays indeed seem to have been attached to the lower surface of the extra-mandibular spine and are constantly seen crossing it in many specimens. They begin with one or two pairs which are short, lie parallel to the middle line, and are far removed from the lower jaws. These are followed by about twenty more of which the anterior are S-shaped bones, the outer ends tending to lie parallel to the middle line, the middle portion transversely, and the inner ends being directed backward (B.M.N.H. 22658 has twenty-four pairs). Posteriorly these rods become straighter and project backward as a fringe from the outer surface of the hinder end of the mandible; towards the articulation of the upper and lower jaws the attached ends of these bones are turned downward. A sudden break occurs at the articulation, the three or four rays lodged on the posterior edge of the palato-quadrate having an upturned articular end. A comparison of this account with that which I have given for the opercular rays of *Mesacanthus* and *Cheiracanthus* will show that it is beyond question that the extra-mandibular rays in *Acanthodes* lay in the operculum, the greater part of which was unsupported by skeletal structures and not even protected by a scaly covering, its existence and extent being shown only by the lateral line crossing it. It is, I think, abundantly clear from the whole character of this material, and especially from those specimens in which the hyoid arch, as represented by its continuous series of gill-rakers, has undergone some displacement, that the whole opercular skeleton was supported by the lower jaw and the palato-quadrate cartilage and had no connexion with the hyoid arch. This series of opercular rays is found early in development; nineteen pairs are present in P. 6192.

The hyoid arch is very well displayed in many specimens, especially Pollichia and P. 323, P. 493 and P. 494 in my own collection. It is angulated, forming a horizontally placed V, the joint along which it was movable lying in the same horizontal plane as the articulation of the lower jaw, though its articulation lay between residual cartilages, the bones (epi-hyal and cerato-hyal) not nearly reaching one another. The epi-hyal or hyo-mandibular lies mesially of the posterior bone in the palato-quadrate when in its natural position. Its widened upper end lies almost on the same level as the upper margin of that bone but the narrower lower extremity projects some distance behind it. It is clear that the upper end of the bone lies high in the head and might be expected to articulate with the dorsal bone of the neural cranium, which, however, shows no sign whatsoever of any facet for such a contact. REIS, JAEKEL and BASHFORD DEAN are in agreement that there is another element in the hyoid arch which would represent a pharyngo-hyal and lie dorsally to the epi-hyal. None of the materials at my disposal show a trace of such a bone and some of these are so well preserved and satisfactorily displayed as to make me doubtful of its actual existence, although in face of the concensus of opinion of the authors I have mentioned I should be very sorry to deny its presence. The ventral portion of the hyoid arch is formed by two bones, the cerato- and hypo-hyals, which meet one another. At their point of contact each is very deep dorso-ventrally and each is reduced in height as it leaves this region until both anteriorly and posteriorly the structure is quite shallow. The posterior bone is nearly straight, the anterior turned a little inward toward the middle line and ending in an enlarged knob for articulation with the basi-hyal. The ventral surface of the two bones in the middle of their length bears a shallow longitudinal groove which passes out on to the lateral surface posteriorly and dies away anteriorly. The basi-hyal is a T-shaped bone, the hypo-hyals articulating in the angles between the leg and the cross-stroke. It possesses a short not very deep posterior extension in the middle line, and was in all probability in contact with the first of a series of cartilaginous basi-branchials, of whose existence my material gives no satisfactory evidence. The complete hyoid arch, from the dorsal end of the epi-hyal to the basi-hyal, supports a series of gill-rakers of very characteristic and remarkable structure. Each one consists of a blade, relatively wide from side to side, widening greatly at the middle of its length but extremely narrow from back to front. It has a lenticular transverse section and its free extremity is pointed. The surface bears a series of irregular low longitudinal ridges and furrows which lie in the main parallel to its length. The blade of the gill-raker is a little narrowed just above its base. The base itself is a hollow bone expanded in a plane at right angles to the breadth of the whole element. It is thick so that its cavity is nearly circular in section. The attached surface, which lies in very close contact with the underlying bone of the hyoid arch, is a hollow half-cylinder placed transversely to the length of the hyoid arch. In consequence the visceral surfaces of all the bones of the hyoid and branchial arches which bear gill-rakers are crossed by low ridges on to which the bases of the gill-rakers fit. The dorsal part of the hyoid arch bears about thirteen gill-rakers, the ventral part about thirty-two in a large specimen. The whole arrangement of the gill-rakers on the ventral portion of the hyoid arch is exceptionally well shown in a specimen of the Coal Measure, *Acanthodes wardi* from the Knowles Ironstone, which is number LL. 181 in the Manchester Museum. Here it is shown that anteriorly the gill-rakers of the two sides come together so that their bases were inserted side by side, presumably on the oral surface of the basi-hyoid bone. Whether this arrangement occurs in precisely the same form in *A. bronnii* is uncertain. In young individuals at least it apparently did not, the series of gill-rakers terminating whilst the hyoid arches are still separated. There is, however, in the Pollichia specimen evidence of certain small structures seen only in broken section which have not the appearance of bone but rather that of gill-rakers. They lie laterally to, and also immediately in front of the wide anterior end of the basi-hyoid bone. It is thus clear that the whole hyoid arch, from end to end, was coated with a single series of extremely powerful bony spikes. In young specimens the gill-rakers are only developed over the hypo- and cerato-hyals, those supported by the epi-hyal only appearing after ossification in the palato-quadrate is well advanced.

The relationship of the hyoid to the mandibular arch is difficult to establish. In certain cases, the Pollichia specimen for example, where the palato-quadrate has been rotated outward it has carried the epi-hyal with it, an indication of a close relationship and some attachment by soft tissues. But in other cases, the original of REIS's 1895, Plate V for example, where all the visceral arches have been dragged sideways and have rotated about the articulations of the palato-quadrate with the neural cranium, the hyoid arch has been separated from the mandibular arch and now leaves a space about as great as that separating the hyoid from the first branchial arch. In the specimen P. 495, which shows the neural cranium, the epi-hyal, pharyngo-branchial and epi-branchial of the first branchial arch have almost retained their natural relationship to one another, although they are scattered and no trace of the mandibular arch remains. It seems therefore that the attachment of the hyoid arch to the mandibular arch was no closer than its association with the first branchial.

The first structures associated with the branchial arches to be calcified are the gill-rakers. These first appear at the point of angulation of each arch between the epi- and cerato-branchial, and form a short series with a very characteristic festoon appearance, the attached bases of the denticles making a narrow U. It seems certain that the development of these structures began on the first arch, the others following in turn, the gill-rakers on the fifth arch only appearing in really large fish in which the ossification of the mandibular arch is complete.

The fact of the existence of so many different species in Lebach makes it impossible to trace the course of this calcification in detail. When fully developed in the largest heads, e.g. D.M.S.W. P. 323, and Pollichia II, the first branchial arch contains four bones. The pharyngo-branchial is a bone of characteristic shape which, in contrast to the equivalent cartilage in all Elasmobranchs, is directed forward, its ventral border continuing the curve of the epi-branchial. Its upper border has a small roughened projection, relatively thin from side to side. The posterior end of this bone in the largest specimens approaches the anterior end of the epi-branchial, which is a laterally flattened cylinder of bone. The angulation of the arch lies in the wide space between the epi- and cerato-branchials. The laterally flattened cerato-branchial is a bone of considerable length whose anterior end lies about in the plane of the hinder end of the lower jaw. The arch then contains a long slender hypo-branchial bone which directly continues the line of the cerato-branchial and anteriorly ends in a slender rounded point behind which its admesial border forms a low process associated with the attachment to the unossified basi-branchial. In the largest specimens the whole of the inner surface of the first branchial arch, at least from the upper end of the epi-branchial to the anterior extremity of the hypo-branchial, is covered by a series of gill-rakers identical in structure with those on the hyoid arch. In the small but exceptionally completely ossified P. 494 the dorsal part of this series is perfectly shown, the tips of the gill-rakers overlapping and resting upon the inner surface of the epi-hyal.

The second branchial arch seems to be identical in its general character with the first, but ossification begins later and seldom if ever becomes so complete.

The third arch has an ossified hypo-branchial in the Pollichia specimen, and has only doubtful traces of bone in other specimens. It possesses, however, a fully developed series of gill-rakers.

The fourth arch does not contain any bone in any specimen I have seen, though in the very large specimen figured by Reis 1895, Plate V, it seems to be well ossified. In normal specimens its series of gill-rakers is short.

Some specimens, the one from Pollichia and one in Edinburgh for example, show a short series of gill-rakers belonging to the fifth arch, but the majority of specimens do not. Probably the arch and a gill slit before it are constantly present, but the gill-rakers only develop in extreme old age.

Consideration of the whole series of specimens makes it evident that the gill-rakers of each arch guarded the gill slit before that arch and their tips overlapped the arch in front. The arrangement was in all likelihood comparable with that in *Polyodon* or a herring, the V-shaped arches being separated by very long gill slits each converted into a sieve by this gill-raker series, the whole allowing the animal to feed on very small food. It seems probable that *Acanthodes* had already developed long gill filaments projecting freely into the gill chamber below the operculum as in bony fishes, and it is certain that it cannot have possessed the ordinary Elasmobranch type of gill.

The structure of the hyoid arch with its very extensive series of gill-rakers is so similar to that of the first branchial arch as to make it certain that the gill slit in front of the hyoid arch was as long dorso-ventrally as the one behind it. Hence the operculum must have been entirely of mandibular origin and a spiracle of normal fish pattern not developed.

The Exoskeleton of the Head—The younger specimens of *Acanthodes* in which ossification of the visceral arches and neuro-cranium is either non-existent or slight show the exoskeleton of the head extremely well; the different species vary considerably in the extent to which it is developed. In all the body is covered incompletely with a continuous coat of normal small square scales, which may become extremely tiny toward the dorsal and ventral margins. In most individuals, e.g. D.M.S.W. P. 490 and P. 494, and Edinburgh unnumbered, these scales die out behind the shoulder girdle leaving a naked triangular area bounded by short forward extensions of squamation round the main and ventral lateral lines. In these fish there is a complete absence of normal squamation and of dermal bones in the head, except for the ring of circum-orbital bones and for the rows of enlarged scales bordering the lateral-line grooves and canals. In older and more fully ossified specimens, e.g. D.M.S.W. P. 493, the anterior parts of the lateral-line apparatus are actually very slender canals supported by rows of bony cylinders. In a rarer type of *Acanthodes* from Lebach, B.M.N.H. 22658, B.M.N.H. P. 4477, and B.M.N.H. 40049, the squamation extends forward on to the head, passing into a continuous shield of very thin polygonal bones just as it does in the earlier Acanthodians, *Climatius*, *Mesacanthus* and *Diplacanthus*. This region lies entirely dorsal to the main lateral line and orbit and does not continue over the snout. These dermal bones differ entirely from normal scales in that they are excessively thin, with convex external and concave internal surfaces, whilst they are no larger than the ordinary body scales. REIS, 1896, fig. 2 is a good representative of this type.

The only individually recognizable dermal bones are thus those surrounding the orbit. On the justifiable assumption that the orbital margin was circular these can be restored to their natural position and then prove to form part of a sphere. The series usually includes five bones (the commonest number in Acanthodians in general) but sometimes only four are present. Each bone has a smooth concave inner surface and an ornamented convex outer aspect. The width of the individual bones in the ring varies considerably and it is not clear that the widest plate is always in the same position. Their ornamented surface when taken in connexion with the character of the obviously homologous bones in other Acanthodians shows conclusively that these plates are circum-orbitals, and not as it is natural to suppose sclerotics. The eyes are always large, sometimes very large, and lie quite anteriorly, the snout being no more than a rounded surface connecting the anterior circum-orbitals of the two sides. Its surface passes back smoothly into the flattened wide inter-orbital part of the dorsal surface, which itself extends backward into the occipital surface and the trunk.

The main lateral-line lies rather above the mid-line of the flank and passes forward above the gill chamber over the eye, dorsal to the circum-orbitals, at least to a point half-way down the front of the orbit. From the main lateral line a variable number of side branches pass dorsally toward the mid-dorsal line. Specimens figured by Troschel show five and four, and by BASHFORD DEAN, five of such incomplete commissures in the anterior part of the trunk behind the shoulder girdle. P. 494 shows two, and many other specimens give similar evidence. Anteriorly to the shoulder girdle D.M.S.W. 490 shows two short branches, one above the angulation of the fourth branchial arch, the next above that of the second arch. From a point immediately in front of this latter a long branch passes inward and forward at an angle of about 45° to the main canal until it closely approaches, and may have coalesced with, the admesial end of another branch which arises from the main canal at right angles at a point a little in front of the jaw articulation. From the main canal the infra-orbital canal arises at a point some distance behind the posterior border of the circum-orbital ring and extends downward and then forward below the circum-orbitals at least to the level of the centre of the orbit. A mainly horizontal canal (the quadrato-jugal canal) takes its origin from the infra-orbital a little below the mid-point of its height and can, with certain interruptions by other structures of the head, be traced backward to the hinder end of the jaw, where it joins a more or less vertical canal (the pre-opercular canal). This arises from the main canal at the level of the hinder end of the posterior vertical semicircular canal, and, though interrupted by being lost amongst gill-rakers, can be traced downward to its junction with

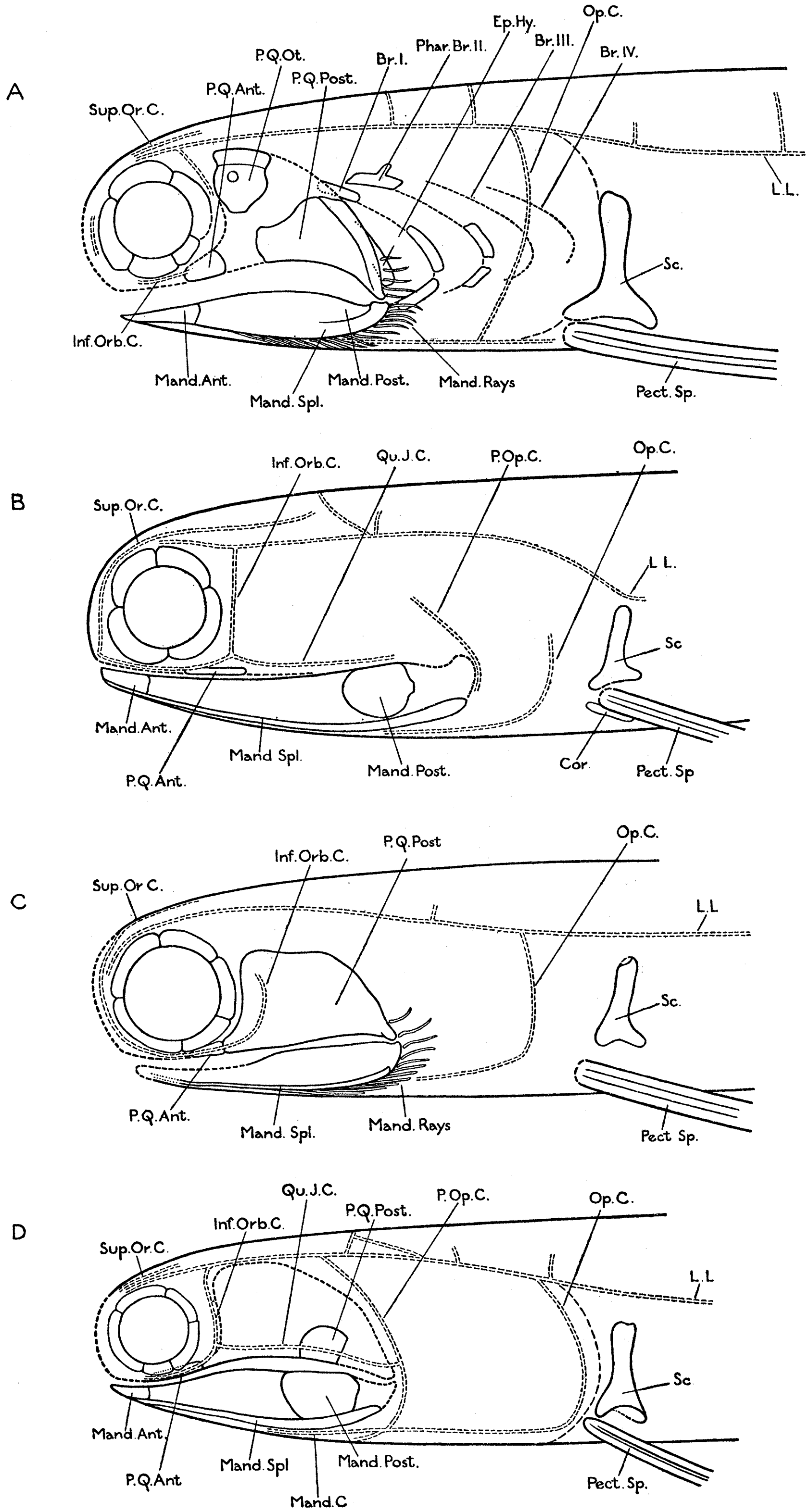


FIG. 20—*Acanthodes*. Partial reconstructions of the anterior ends of four individual specimens from the Lebach ironstones, various magnifications. A, D.M.S.W. P. 494 × 1·05; B, B.M.N.H. 22658*a* and *b* × 1·27; C, D.M.S.W. P. 498 × 1·23; D, D.M.S.W. P. 496 × 1·43. *Br.* I, III, IV, branchial arches, I, III, etc.; *Cor.* coracoid; *Ep.Hy.* epihyal; *Inf.Orb.C.* infra-orbital canal, of the lateralis system; *L.L.* main lateral-line canal; *Mand.Ant.* anterior ossification in Meckel's cartilage; *Mand.C.* mandibular canal; *Mand.Post.* posterior ossification in Meckel's cartilage; *Mand.Rays*, rays in the mandibular operculum; *Mand.Spl.* mandibular splint; *Op.C.* opercular canal of the lateralis system; *P.Op.C.* preopercular canal; *P.Q.Ant.* anterior bone in the palato-quadrate; *P.Q.Ot.* otic process of the palato-quadrate cartilage; *P.Q.Post.* posterior bone in the palato-quadrate; *Pect.Sp.* pectoral fin spine; *Phar.Br.* II, pharyngo-branchial II; *Qu.J.C.* quadrato-jugal canal; *Sc.* scapula; *Sup.Or.C.* supra-orbital canal.

the quadrato-jugal canal just above and behind the jaw articulation. The preopercular canal extends downward below this point, and its anterior prolongation is shown just ventral to the mandibular splint in the region anterior to the opercular rays. There is some evidence that the preopercular canal actually extends into the intergular space.

The main canal gives off one further ventral branch. The origin of this is not shown but its course is nearly vertical, parallel to the posterior margin of the gill chamber as far as the level of the ventral border of the lower jaw. It then turns abruptly and extends forward apparently to join the preopercular canal and form the canal of the lower jaw. The vertical part of this canal crosses the festoon of gill-rakers of the fourth branchial arch unaffected by them. It is thus evident that it was carried on the operculum. The presence of this opercular canal is confirmed by several other specimens, e.g. D.M.S.W. P. 498, and P. 494, where it crosses between the angulations of the second and third arches without conforming to them. An unnumbered specimen from Berlin is important because it is the only one in addition to P. 490 which shows with perfect clearness the infra-orbital, preopercular and opercular lateral-line canals.

The supra-orbital canal in D.M.S.W. P. 490 begins at the level of the front of the ear and extends forward parallel to, and mesial of the main canal until it turns down on to the snout in front of the orbit, its further course being incapable of determination. Consideration of the whole material seems to show that the infra-orbital canal passes round the eye until it terminates dorsal to the orbit, not far in front of the anterior end of the main lateral line. A branch arising from this canal passes downward and inward over the snout, turning up again to meet the anterior end of the supra-orbital canal, which at this point is connected to its fellow by a V-shaped commissure. It is unfortunately impossible to be certain of these connexions, which indeed may vary a little from specimen to specimen. B.M.N.H. P. 4477 is important because Miss Townend found in it a circular space, free from all trace of bone, and in part bounded by a definite small plate which may plausibly be interpreted as a nostril. This lies near the middle line, dorsal to the lateral-line commissure, and mesial of the supra-orbital canal.

Body and Fins—The contorted position of most specimens of *Acanthodes* from Lebach makes it difficult to draw accurate reconstructions of the whole fish, but in some cases it is possible by following the main or the ventral lateral lines to determine the proportions with reasonable certainty. It is, however, unfortunate that the tail is almost always missing, though the anterior margin of its ventral lobe is often included in the nodules. In Table II I give the head length, depth of body and length to the dorsal fin in mm. for a series of specimens, determined from restorations so made.

The general shape of *Acanthodes* was quite well illustrated by Roemer. It is a very slender eel-like fish with a heterocercal tail, whose hypocaudal lobe is shorter than the extension of the body and projects downward. The single dorsal and the anal fin are placed very far back, the anal being larger than the dorsal and a little in front of it. The pectoral fins are "enormous" and the pelvics small.

TABLE II

	Head length mm.	Depth mm.	Length to dorsal mm.	Length / Head length mm.	Length / Depth mm.
B.M.N.H. P. 6192	20	12	76	3·8	6·3
40050	31	14	131	4·2	9·3
D.M.S.W. P. 490	49	32	198	4·0	6·2
P. 498	58	31	213	3·7	6·8
P. 494	69	39	305	4·4	7·7
B.M.N.H. 40049	100	—	440?	—	6·6

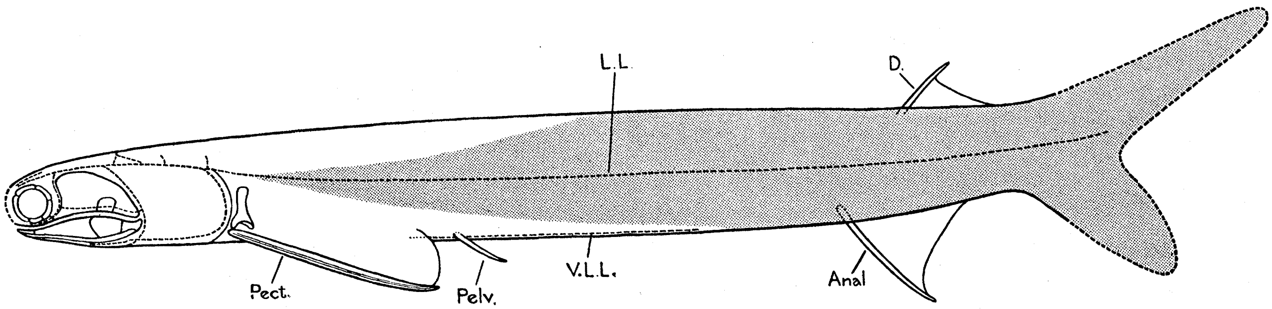


FIG. 21—*Acanthodes* sp. Lebach ironstone. Reconstruction of specimen P. 496, D.M.S.W. collection. × 0·6. The area covered with mechanical tint represents the extent of the squamation. *Anal.* anal fin; *D.* dorsal fin; *L.L.* main lateral-line; *Pect.* pectoral fin; *Pelv.* pelvic fin; *V.L.L.* ventral lateral-line.

The development of scales on the body can be determined in outline. The first scales to appear are those which border the main lateral-line canal in the hinder part of the body, new scales being added both above and below the lateral line and at its anterior end. In B.M.N.H. P. 6192 (76·0 mm. long) both lobes of the caudal fin are completely scaled, though the fin is here much more deeply cleft than it would ultimately become. That part of the body behind the median fins is covered with scales throughout its height, though the dorsal and ventral surfaces seem to be scaleless. There are no scales on the fin webs. In front of the median fins the squamation covers a decreasing depth of the flank, the lateral-line scales alone remaining at a point about half-way between the pectoral and anal fins, and no traces of lateral-line bones being visible in the anterior part of the trunk or on the head. In B.M.N.H. 40050 the main lateral-line can be traced forward on to the head, and the patch of flank scales associated with it has extended farther forward and posteriorly is deeper. In addition a new ventral strip of squamation has appeared. This is associated with the pair of ventral lateral-line canals which arise quite anteriorly between the pectoral fins and extend backward to the anal fin. In the anterior part of their course the two lines are separated by a small space, the width of about six scales, but posteriorly they come together, the admesial edges of the ventral rows of enlarged scales bounding them being in contact or nearly so. This arrangement was well figured by TROSCHEL (1857, Taf. I, figs. 1 and 3), but has escaped the notice of all subsequent writers. The ventral lateral-line area of scales is certainly discontinuous with the flank series from its anterior end as far back as the anal fin, but appears to join them in that region, an indication that the hinder part of the body was already completely scaled. No scales occur on the webs of any of the fins other than the caudal.

In larger specimens, e.g. D.M.S.W. P. 490, the spread of the scaled areas continues, the mid-ventral strip remaining separate and a long triangular area behind the shoulder girdle being still free from scales. The main trunk scaling now continues forward as a slender triangular area to the region of the shoulder girdle. The body seems to have been essentially completely scaled behind a point about one-third of the distance from the dorsal fin to the pectoral fins. In this fish a considerable area of the base of the web of the anal fin and a small part of that of the dorsal fin are scale covered, but the pelvic and pectoral fins are scaleless. In B.M.N.H. 40049, the anterior third of a large fish with a lower jaw length of 6·6 cm. and a total length to the dorsal fin of presumably about 450 mm., the scales continue uninterruptedly over the dorsal surface and extend forward to the ear. A scanty ventral strip of scales can be traced to the hinder end of the lower jaw, but the triangular area behind the shoulder girdle still remains free from scales. The size of the scales is on the whole similar over the whole flank of a fish, but they decrease a little toward the dorsal and ventral surfaces. The scales on the fin webs are often extremely small. This mode of development of the squamation gives the explanation of the remarkable fact that the scales of large specimens of *Acanthodes* may be no larger than those of small individuals. The scales of the specimens last considered are of the same size within the necessarily wide limits of measurement. Those of the Edinburgh specimen, about 230 mm. in length, are about twice as wide as those of the series above described.

The caudal fin is very seldom well preserved; that of a small specimen belonging to Berlin is illustrated in fig. 6, Plate 13. In this the interesting features are the extension of the main lateral line to a termination just in front of the fork of the tail and the absence of any upturning of its posterior end; the presence of a narrow mid-dorsal strip of scales with a free posterior end identical with a similar arrangement in *Euthacanthus* and *Mesacanthus*; and the occurrence of a sharply differentiated strip of scaling parallel to the dorsal margin of the upper lobe of the fin, again a parallel to the two genera last mentioned. The lower lobe has a rounded termination lacking the peak of certain genera. I can add nothing to the account and figures of the tails of full-grown specimens of "*Acanthodes bronnii*" given by KNER (1868, pl. V, fig. 2, and pl. VII, fig. 1). These specimens show the presence of ossified neural and haemal arches in the tail and of a series of long radials, extending about two-fifths of the distance to the tip of the ventral lobe, unjointed and each corresponding to a haemal arch.

The structure of the other fins of *Acanthodes* is best shown by specimen D.M.S.W. P. 498. Here the dorsal fin spine has the normal structure. It is a nearly straight rod with flattened lateral surfaces. The rounded anterior margin is marked off by a well-defined groove on each side of the spine. There is a cavity in the lower part of the spine which is open toward the web of the fin, and the spine has an inserted base of considerable length. A single basal bone extending backward from the spine is indicated by a rather obscure impression. Dorsal to this bone is a series of delicate bony fin rays, very short and no doubt paired. Surrounding these and passing farther out into the web is a small patch of normal square scales.

The anal fin of this specimen, though larger, is similar to the dorsal fin. No trace of a basal can be seen nor are the fin rays visible, but a large area of the fin web is covered

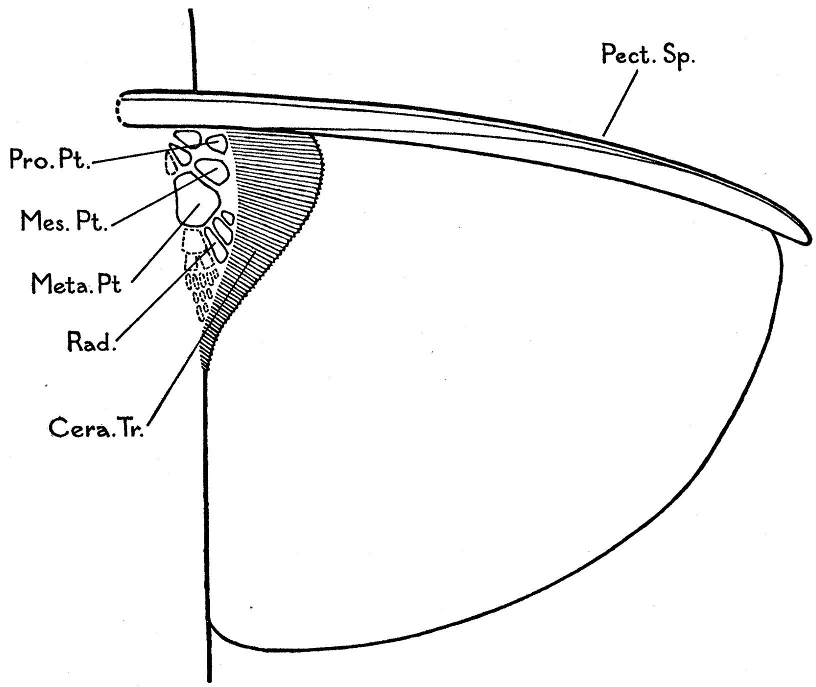


FIG. 22—*Acanthodes* sp. Reconstruction of a pectoral fin, the skeleton from P. 498, and the outline from P. 490, D.M.S.W. collection; both are from Lebach. × 1·6. *Cera.Tr.* cerato-trichia; *Mes.Pt.* meso-pterygium; *Meta.Pt.* meta-pterygium; *Pect.Sp.* pectoral spine; *Pro.Pt.* propterygium; *Rad.* radials.

with square scales whose sides lie respectively parallel and at right angles to the ventral line of the body. These scales become smaller as they are traced toward the margin of the fin. In P. 490 the anal fin is represented by its spine, by a low scaled area extending far posteriorly toward the caudal fin, and by a carbonaceous film which is part of the delicate unscaled distal area of the web.

The pectoral fins are well shown in P. 498, in which the shoulder girdle has its normal structure. It is a bony cylinder, very nearly circular in transverse section and standing vertically in the body, its slightly expanded upper end reaching only to about half-way up the flank. The lower end is widened antero-posteriorly and is produced downward into lappets, that on the inner surface lying anteriorly, and that on the outer surface at the hinder end. The bone contains an hour-glass-shaped cavity. The shape and character of this bone, apart from its evident relationship to the homologous structures in other Acanthodians, show that it was laid down round a cartilage, and I call this bone the scapula. No other bone is to be seen in the shoulder girdle in most specimens, but in B.M.N.H. 22658 and 40049 another small rounded but flattened bone lies ventral to the scapula. The homology of this bone is uncertain; it may be a cartilage bone, a coracoid, or it might be of ultimate dermal derivation. Its homologue is known in *Cheiracanthus*.

Even in large specimens the pectoral fin usually has no ossifications in its cartilage, but in D.M.S.W. P. 498 there are well-developed basal and radial elements. It is evident that these are radially arranged, the basals being concentrated. In the absence of any certainty as to the position of the articulation between the shoulder girdle and the fin skeleton it is not possible to be sure of the structure, but the most reasonable interpretation is to regard the fin as tribasal, of general Elasmobranch character. At any rate the proximal row represented consists of a short and small pro-pterygium supporting a single radial, a small meso-pterygial with a long and stout radial and a large meta-pterygial with a narrow base widening greatly as it is followed distally. This bone supports two slender radials which are in contact with one another, and extends admesially of them leaving space for further radials and probably for an extension of a meta-pterygial axis, of which no trace remains. The base of the fin web is supported by two series, dorsal and ventral, of short, massive, closely set dermotrichia. These are straight rods ossifying very early in the life of the animal. They form a graded series, the longest on the outer side of the fin just within the fin spine, those lying toward the inner margin being very short. The proximal ends of these rods lie on a smooth curve which sweeps inward from a point little removed from the shoulder girdle to one at a considerable distance from the base on the inner side of the fin. Distal to this series lies another, similar in general character but usually of more slender and less closely set rods. In the great majority of specimens these are short, but in D.M.S.W. P. 494 some of them are extraordinarily long, extending out nearly, but not quite, to the margin of the fin. The fin web is beautifully shown as a carbonaceous film in D.M.S.W. P. 490 and P. 494. The fin is of extraordinary width; the fin spines can be erected so that the two make an angle of 130° with one another (in P. 490), and the fins, though fully extended, are not then torn away from the body. The evidence of this specimen seems to show that the tip of the spine projected beyond the margin of the fin, and there is evidence of non-ossified dermotrichia reaching the fin border. In laterally compressed specimens the series of dermotrichia is usually folded on itself in such a way as to suggest that the inner margin of the fin was attached to the body near the ventral surface for a long distance. The whole fin is usually devoid of scales, but D.M.S.W. P. 321 shows a small patch of small square scales which become rounded and radially arranged distally, covering the region of the radials and proximal dermotrichia.

The pelvic fin is represented only by its spine in all specimens seen.

Professor Kner (1868, pl. V, fig. 2) figured a specimen of *Acanthodes* which contained a mass of *Estheria* in the region of the abdominal cavity. I have occasionally seen single specimens of *Estheria* within *Acanthodes*, and the crustacean is commonly seen in the ironstone nodules containing that animal. There is, however, in the Edinburgh Museum a specimen (1891, 16, 3) of *Acanthodes sulcatus* from the Straiton Ironstone (Lower Carboniferous) which contains within its body cavity the disorganized remains of a specimen of the Palaeoniscid fish *Cryphiolepis*. These remains occupy a length of some 12 cm., the *Acanthodes* has pectoral spines of about 5 cm. and its length from snout to anal fin may be estimated at 30 cm. Thus the food of *Acanthodes* was more varied than its toothless condition and elaborate filter apparatus of gill-rakers might suggest. But it is probable that it did in general live on small animals which, as in the case of *Estheria*, need not necessarily have been plankton.

On the Nature of the Hard Parts of Acanthodians

I have not made any extensive investigation of the histology of the bones and scales of Acanthodians because I am doubtful whether the materials from Turin Hill, which are the most abundant and interesting of those at my disposal, give a true picture of the structure. In the absence of sections of some animal from those rocks, known to be bony, it must remain uncertain whether the absence of cell spaces in the jaw bones and scales of *Ischnacanthus* is primary or results from unsuitable preservation.

I have never myself seen unquestionable lacunae in any Acanthodian material, but a section, which Professor A. Karpinsky was kind enough to send me, through some very large scales presumably of *Acanthodes* from the Upper Devonian or Lower Carboniferous of the North Ural, shows very rarely bipolar spaces which may have contained bone cells. These lie scattered amongst the fine canals which penetrate the whole thick rounded root of the scale, below its "ganoine" surface, and in one case form a continuous though widely spaced layer. More generally only about half a dozen are to be seen in a section of a scale about 1 mm. sq. With this exception the structure of these scales is exactly as Goodrich (1909, p. 188) describes it, the base of the scale being perforated by immense numbers of minute little branched canaliculi. I am thus very doubtful whether the scales described by Brotzen (1934*a* and *b*) are all rightly referred to the Acanthodii. In any case I am sure that it is impossible to determine isolated Acanthodian scales generically.

The calcified material associated with the cartilaginous skeleton of Acanthodians has been examined in section by Reis (1896), Smith Woodward (1917) and by Hancock and Atthey (1869). I have cut sections of jaw elements of *Ischnacanthus* and *Acanthodes*, and of the scapula of *Acanthodes*. Smith Woodward describes the structure of a very large Acanthodian jaw (*Plectrodus*) as follows: "The hard base to which the teeth are affixed proves to consist of almost structureless translucent calcified tissue in which there are occasional streams of elongated cellular spaces, irregular in shape, and sometimes with traces of ramifying canaliculi. It thus agrees exactly with the corresponding tissue in *Ischnacanthus*." HANCOCK and ATTHEY (1869) say of *Acanthodopsis*: "The jaw itself is composed of very dense bone on the surface, in which the Haversian canals are well defined, and the radiating cells are very numerous and minute; they are elongated fusiform, with the canaliculi (when observable) sufficiently abundant, and arranged for the most part at right angles to the long axis of the cells.... In the superficial and denser portions of the tissue, the cells and tubules are the most minute; in the deeper portions they are larger and less regular in form and the bone becomes riddled with medullary cavities, until at length it is entirely reduced to a sort of cellular structure." It is evident that this account, founded on very well-preserved material, is comparable with REIS's description and fig. (1896, pl. VII, fig. 1) of the jaw of *Acanthodes*, which is derived from much less well-preserved material.

Taken together these descriptions leave no real doubt that true bone does occur in the visceral ossifications of Acanthodians. But if no bone cells could be observed or even if they had never existed, it is evident from the fact that some portions of them must be resorbed during the growth of the animal that the jaw bones of *A. bronnii* agree with true bone and differ from all other vertebrate hard parts.

SUMMARY OF THE STRUCTURE OF ACANTHODIANS IN GENERAL

The Acanthodians are fish-like gnathostomes whose general build is fusiform, with a body which may be rather deep (*Cheiracanthus*) but which is generally slender, ultimately becoming eel-like (*Acanthodes*).

General Shape

Fins—There are one or two dorsal, an anal and a caudal fin. The tail is always heterocercal, the muscular upper lobe being only slightly turned up, whilst the lower lobe is triangular. There are no ridge scales associated with the tail, but the upper edge of the upper lobe may have a special squamation ending in a fine point, perhaps a relic of a former third dorsal fin. The anterior border of the ventral lobe may be strengthened by a paired row of enlarged scales which extend backward as a hook.

The other median fins are supported by an anterior fin spine. In primitive forms (*Brachyacanthus*) this is extremely wide from side to side and contains a great cavity opening backward to the fin web; it is indeed nothing more than a thin scale-like plate bent round the anterior margin of the fin. In consonance with this structure the spine is restricted to the skin, its proximal margin being joined by ordinary body scales. In later forms the fin spine becomes laterally flattened, its very narrow cavity opening only within the body, and gains a definite root inserted between the myotomes.

In the primitive forms there is a long series of paired fins, usually represented only by their anterior spines. There may be as many as seven pairs; of these the first, the pectoral fins, are the largest, the remainder increasing regularly in size to the last, the pelvic fins. The fin spines of the paired fins agree exactly in their structure with those of the median fins of the same fish.

Head—The head is very variable in its proportions; the mouth may be very short (*Diplacanthus*), or very long (*Acanthodes*), or of any intermediate length. The orbits always lie very far forward, so that the snout is short, merely a rounded anterior surface connecting them. A nostril is very seldom visible, and in all known cases (*Ischnacanthus*, *Cheiracanthus* and *Acanthodes*) lies high up, well removed from the mouth, and not far from the middle line.

Squamation—The body is covered with a very characteristic coating of extremely small square thick ganoid scales which lie close packed in contact with one another. Except in *Brachyacanthus*, where there is a row of large mid-dorsal scutes behind the head, there are never any enlarged mid-dorsal or mid-ventral scales. The size of the scales varies somewhat over the body. In many forms, though not in all, the lateral lines are bordered by enlarged scales.

In *Mesacanthus* and *Acanthodes* it can be shown that the squamation begins round the main and ventral lateral lines in the posterior part of the body, new scales being added dorsally and ventrally, the scale-clad area gradually extending forward toward the shoulder. The scales seem to reach their maximum size early in the life of the fish and growth takes place by the addition of new scales. In many forms the cheeks and ventral parts of the head remain without any covering of bony elements.

Structure of Head—The neural cranium is known at all completely only in *Acanthodes*, but *Cheiracanthus* seems to agree with that genus. The skull is tropibasic, there being a narrow inter-orbital septum with a brain cavity contained within its dorsal part. No trace of the nasal capsules or ethmoidal region can be seen. The orbito-temporal region is floored by a median T-shaped bone, whose anteriorly directed stem ends at a series of five small independent bones. The widened hinder end of the bone lies at the back of the eye, and its limbs are directed upward and outward towards the post-orbital processes of the paired dorsal bones. The anterior faces of the transverse flanges of this bone bear articular facets for the palato-quadrates. The ventral surface of the stem of the T-shaped bone has a groove which at its hinder end becomes a foramen for a persistent hypophysial duct.

The upper border of the orbit is ossified and ends in an outstanding post-orbital process. Behind and a little within this is a massive column formerly connected to the transverse wings of the T-shaped bone by cartilage. This is perforated by a horizontal jugular canal and its posterior face has a facet for the otic process of the palato-quadrate. The skull is narrow in the lower part of the otic region but it widens suddenly to a thick horizontal flange (?over the horizontal canal) toward the dorsal surface of the head.

The ventral surface of the skull in the otic region is made by a thin, formless sheet of bone which connects the T-shaped bone with the "basi-occipital". This latter has a widened anterior end and then becomes very narrow, its lateral surfaces bearing deep grooves, which lead to large foramina anteriorly. They rise posteriorly to support the exoccipitals. The ventral surface of the basi-occipital bears a groove presumably for the dorsal aorta. The anterior border of the exoccipital is notched for the vagus and the bone is pierced by two foramina for occipital nerves.

Visceral Arches—The mandibular arch forms the upper and lower jaws. The palato-quadrate has a deep vertical paraotic portion whose nearly vertical anterior border lies behind the orbit and descends to a short more nearly horizontal palatal part. The palato-quadrates of the two sides of the head do not meet in symphysis. In *Climatius* they seem to have no contact with the neural cranium. In *Mesacanthus*, *Cheiracanthus* and *Acanthodes* the summit of the paraotic flange bears a definite otic process which articulates with the skull behind the post-orbital process, and the palatal part of the bone has a special basal articulation. In *Climatius* and *Cheiracanthus* the whole palato-quadrate in the adult forms a single bone, which is perforated by a vacuity in the paraotic region in the latter. In *Mesacanthus*, *Ischnacanthus* and *Acanthodes* the palatal ramus is an independent ossification, and in *Acanthodes* the otic portion is also independent.

Meckel's cartilage is always longer than the palato-quadrate, so that its symphysis lies in front of the anterior end of the palatal process. In *Climatius* and *Cheiracanthus* the lower jaw is in adults a single bone. In *Mesacanthus*, *Ischnacanthus* and *Acanthodes* it ossifies in two parts, an anterior and a posterior.

Teeth are present in the lower jaws of *Climatius* and *Parexus*; each tooth has a flat plate-like lower portion whose upper edge is cleft into small sharp-pointed cusps, usually a central large cusp and one or two smaller cusps both before and behind it. Three or four teeth of a single family are present simultaneously, forming a whorl. In *Ischnacanthus* there is a symphysial whorl of large simple teeth, and the palato-quadrate and Meckel's cartilage support a remarkable dentition of large and small teeth ankylosed to the bone, and a granulation on the lingual surface. In *Ischnacanthus* the anterior part of the buccal cavity is beset with a multitude of minute tricuspidate denticles. All other Acanthodians seem to be devoid of teeth.

The mandibular arch supports an operculum which stretches backward from the whole of the posterior border over the other visceral arches. In *Climatius*, *Parexus* and *Brachyacanthus* the greater part of this operculum, both between the lower jaws and also the whole periphery, is strengthened by a series of very small oat-like scales, but that part of the structure lying behind the articulation of the jaws contains a series of long opercular rays which merge into the scales covering the cheek. This operculum meets the ventral part of the shoulder girdle but does not cover the whole of the gill chamber. In *Euthacanthus* the series of opercular rays is much larger, extending downward to the middle line between the lower jaws; it is, however, short, covering only a small part of the side of the gill chamber. In *Mesacanthus* the series becomes even more extensive, and the attached ends of the rays round the jaw articulation have a very characteristic structure. In *Cheiracanthus* the series of opercular rays reaches its maximum size, but retains the structure it has in *Mesacanthus* and still leaves part of the gill chamber uncovered. Finally in *Acanthodes* the opercular rays whilst still retaining their structure become reduced to very delicate short rods, the great operculum covering the entire gill chamber possessing only double rows of scales surrounding lateral-line canals. *Ischnacanthus* has a complete operculum covered by small scales but retaining small irregular series of rays, and *Diplacanthus*, which also seems to have a complete operculum, has a single very large bone in its proximal region.

Hyoid Arch—The hyoid arch cartilages are seldom ossified, but dermal ossifications are often to be found associated with it. The hyoid arch in Acanthodians is separated from the mandibular arch by a greatly elongated gill slit, as long as that which lies between the hyoid and first branchial arches. In all forms the hyoid arch is sharply bent, a ventral moiety articulating with a dorsal part at the level of the jaw articulation. In *Climatius* and *Cheiracanthus* the ventral part is composed of a single bone articulating in front with a median basi-hyal, whilst the dorsal part is unossified. In *Acanthodes* the dorsal part of the hyoid cartilage is surrounded by a single epi-hyal bone, perhaps developing an ossified pharyngo-hyal late in life. The ventral part is formed by well-ossified cerato- and hypo-hyals, the latter articulating with an ossified basi-hyal. In *Climatius*, *Brachyacanthus* and *Euthacanthus* the upper end of the hyoid arch has a series of longitudinal dermal bony splints. From these a hyoidean operculum extends backward to rest on the first branchial arch. The lower part of the arch is concealed by the mandibular arch and its operculum. In *Mesacanthus* similar dermal splints protect the upper edge of the hyoid arch, the operculum not containing any ossifications in this region, although on the level of the jaw articulation it possesses a series of short opercular rays, the serial homologues of those in the mandibular operculum. In *Cheiracanthus* the upper end of the hyoid arch is marked by two hook-like scales, but no dermal ossifications occur in connexion with it in *Ischnacanthus* or *Diplacanthus*. In *Acanthodes* the hyoid arch has no external dermal bones, but the visceral side of the whole structure is beset with a single series of very massive, close-set gill-rakers.

Branchial Arches—Four branchial arches of similar structure occur in *Climatius*. In them the skin contains a series of bony splints, lying parallel to the length of the arch, whose lower extremities are turned backward into an operculum the distal part of which is supported by small lineal splints lying horizontally. The series of opercula so formed overlap one another and cease, in the sense that they contain no more bones, at the free margin of the mandibular operculum. *Brachyacanthus* and *Euthacanthus* have an essentially similar structure, but show only three branchial arches. *Mesacanthus* shows a series of three or four curved opercular rodlets in each of its three branchial arches. In *Cheiracanthus* only longitudinally arranged splints without any sign of opercular projection can be seen. In *Ischnacanthus* such longitudinal splints extend down to the level of the jaw articulation within the complete mandibular operculum. In *Acanthodes* there are no external dermal bones associated with the branchial arches, but the cartilages themselves are ossified. The first branchial arch in adults consists of four bones, a pharyngo-branchial directed forward continuing the course of the epibranchial, which extends downward nearly to the point of sharp angulation of the arch. The ventral part of the arch contains a cerato- and a hypo-branchial bone, the latter reaching a basi-branchial. The whole inner surface of the arch bears a single series of gill-rakers identical with that on the hyoid. The posterior arches only differ in that ossification begins in them progressively later and seldom goes so far. Four branchial arches can usually be seen, a fifth rarely.

The Acanthodians thus form a series showing how the mandibular operculum, at first merely the largest of a series (one from the anterior margin of each gill slit), gradually extends backward until it covers the whole gill region, the smaller posterior opercula becoming functionless and disappearing *pari passu* with its development. It is evident that ultimately a Teleostome-like arrangement of V-shaped gill arches, separated by extremely long gill slits and bearing long gill filaments projecting outward into a gill chamber covered by an operculum, is achieved.

Lateral-Line System—A large part of the lateral-line system of Acanthodians remains in the condition of pit lines, although in the anterior part of the head some portion of the system sank down into true canals connected with the surface by small "primary" pores. The character of the material and nature of the system make it difficult to work out the distribution completely; the accounts given in this paper are incomplete but I hope accurate.

The body of all Acanthodians is traversed for a long distance (usually from the point of upturning of the ventral border of the muscular lobe of the tail) by a main (middle) lateral-line, which passes forward along the upper border of the gill chamber to the dorsal surface of the head. It extends onward in an essentially straight course above the orbit in *Ischnacanthus* and *Acanthodes* to, or nearly to, the level of the anterior edge of the orbital margin.

From this canal behind the head a very varied series of dorsally directed (commissural) branches pass upward toward the mid-dorsal line, but seldom reach it. In *Acanthodes*, two in my material, four or more in figures by Troschel and Bashford Dean, of these branches may lie behind the shoulder girdle. In *Diplacanthus* a single commissure lies immediately in front of the dorsal fin spine; the commissural branches which lie in the head region in front of the shoulder girdle are most variable. In *Euthacanthus* just posterior to the upper end of the hyoid arch there is a branch, inclined forward at 45° to the middle line, whose anterior end nearly joins a short transverse groove passing out toward the main canal. In *Mesacanthus* the apparently homologous grooves are directed forward and backward at 45°. In *Diplacanthus* the anterior groove is transverse and the posterior absent. In *Ischnacanthus* there are three transverse grooves, the anterior joining the hinder end of a longitudinal canal. In *Acanthodes* the number of grooves visible ranges from two to four, one of the anterior members of the series often inclining inward and forward at 45°.

It seems impossible to homologize these canals individually through the series, but they clearly form a group from which the middle pit line and occipital commissure of ordinary fish could be derived.

The supra-orbital canal is never continuous with the main canal. It usually begins well behind the orbit and runs forward parallel to the main canal, ultimately passing down on to the rounded snout in front of the eye and apparently becoming continuous with the anterior end of the infra-orbital canal. In *Diplacanthus* the supra-orbital canals arise together in the mid-dorsal line far behind the orbit, and a pair of canals, starting from a spot just behind this point, pass outward and forward to join the main canal above the orbit in front of the point of departure of the infra-orbital canal. No homologue of these canals occurs in any normal fish, but they are exactly paralleled in Arthrodeirs. There is evidence of an ethmoidal cross-commissure in *Ischnacanthus* and *Acanthodes*, and it is probably of general occurrence.

The infra-orbital canal has its usual course round the orbit and seems to have been continuous with the supra-orbital canal. In *Euthacanthus* two posteriorly running canals arise from the infra-orbital canal behind the eye. The more ventral extends backward toward the jaw articulation, parallel to the mouth. It is the oral canal, the homologue of the quadrato-jugal pit line or vertical pit line of the cheek of *Osteolepis*. It seems to be continued by the oral mandibular canal which runs forward for some distance, and is the homologue of the mandibular pit line of *Osteolepis*. The dorsal branch from the infra-orbital canal runs backward to the jaw articulation following the general line of the upper border of the palato-quadrate and is continued as the ventral canal on the lower jaw. This is the homologue of the jugal, pre-opercular and mandibular canal of *Osteolepis*. In *Ischnacanthus* there is a canal on the cheek, presumably the jugal; it arises low down from the infra-orbital. Both mandibular canals are present. In *Acanthodes* the oral or quadrato-jugal canal runs parallel to the mouth from the infra-orbital to the pre-opercular canals. The jugal pre-opercular canal arises, not from the infra-orbital canal, but quite dorsally from the main canal. It passes downward, parallel to the hinder border of the palato-quadrate cartilage, to the jaw articulation and is continued as the mandibular canal. This animal, however, has an entirely new canal which arises from the main lateral canal quite posteriorly, passes downward over the operculum not far in front of its hinder margin, and then turns forward, ultimately passing into the mandibular canal. For this, the opercular canal, no homologue can be found.

Most Acanthodians have a ventral lateral line running below the paired fins from the pectoral to the pelvics. I have seen no certain evidence of the occurrence of a dorsal lateral line in any Acanthodian.

Fin Skeleton—The pectoral girdle always has as its chief element a bone associated with the scapular portion of the primary cartilaginous shoulder girdle. This bone in most forms lies so deep that it can be displaced without disturbing the scales which lie above it, but occasionally (*Mesacanthus*, *Diplacanthus*, for example) its outer surface becomes ornamented and it appears to reach out into the skin. The lower portion of the shoulder girdle may be ossified as a coracoid in *Cheiracanthus* and *Acanthodes*, and perhaps other earlier forms.

In *Climatius*, *Euthacanthus*, *Brachyacanthus* and *Parexus* the ventral part of the body in the shoulder region, so far as it is exposed behind the operculum, contains a very variable series of bones. Some of these are certainly of dermal origin whilst all of them may be so. They form in effect a secondary shoulder girdle.

In *Diplacanthus* Mr. GRAHAM SMITH has pointed out to me that the anterior pair of intermediate fin spines has become involved with the ventral part of the shoulder girdle. The chief interest of the animal lies in the way in which the lower end of the scapular and the outer end of the large ventral dermal bone hold the pectoral fin spine firmly, each being attached to a special recessed area on the base of the spine.

The cartilages of the pectoral fin are well shown in *Acanthodes*, with which a less satisfactory specimen of *Ischnacanthus* agrees. In each case the cartilages radiate from a point at the base of the fin. In *Acanthodes* it seems clear that the fin is tribasal. The pro-pterygium supports a single radial and the meso-pterygium another, whilst the small meta-pterygial basal gives attachment to a large bone, the first of a short axis which supports three or four preaxial radials. Immediately distal to the radials lies a double series of dermotrichia which may be ossified in *Ischnacanthus*, *Diplacanthus* and *Acanthodes*. In *Acanthodes* these end whilst still in the basal part of the fin, and another series of dermotrichia which extend out to the fin margin is occasionally preserved.

In all Acanthodians, including rare individuals of *Acanthodes*, it is clear that the fin webs may be coated in part or completely by a regular squamation of extremely small square scales. It thus appears that the dermotrichia may be regarded as ceratotrichia. Nothing is known of the cartilaginous skeleton of the pelvic fin; it possesses ceratotrichia and scales as do the other fins.

The first dorsal fin of *Diplacanthus* is supported by a series of three large basals which support other large bones; these give attachment at any rate for part of their length to a series of short radials. The web of the fin is strengthened by bony ceratotrichia. A similar concentrated basal occurs at the base of the dorsal and of the anal fin in *Acanthodes*.

Thus the general structure of the cartilaginous and dermal skeleton of the fins of Acanthodians resembles that of *modern* sharks in the concentration of the basal elements and the presence of ceratotrichia.

Vertebral Column—In *Diplacanthus* and *Acanthodes* well-developed bony vertebrae were present, but are not well enough preserved to yield detailed information.

Systematic Position of Acanthodians

The studies of many embryologists, from Balfour to the present day, have shown that the vertebrate head is in the main a segmental structure, each segment possessing pairs of dorsal and ventral nerves, homologous with the dorsal and ventral roots of spinal nerves. This segmentation, which is in origin restricted to the paraxial mesoderm from which the somites are cut off, is designed to allow of lateral flexures of the body and of the mode of swimming based on that possibility. It now seems certain that the earliest vertebrates were microphagous, sieving their food from a water stream, taken in at the mouth and expelled through gill slits, which necessarily passed out from the pharynx between the myotomes arising from the segmental part of the mesoderm. This secondary segmental arrangement of the gill slits thus conforms to the primary segmentation of the somites.

As the gill slits pierce the wall of the gut they necessarily impose a secondary segmentation on the anterior part of the wall of the alimentary canal, which is of lateral-plate mesoderm origin. Thus the primarily unsegmented mesoderm of the head becomes divided into visceral arches, whose segmental arrangement corresponds with that of the somites. Continuation of this reasoning leads to the conclusion that the original mouth lay in front of the segmented part of the body and that it was overhung by a non-segmented prostomial region. Thus a primitive vertebrate should possess a small mouth, followed immediately by a pair of gill slits related to the ophthalmicus profundus nerves. This pair of gill slits is followed by a series similarly supplied by the trigeminus, facialis, glossopharyngeus and the various branchiomeric elements of the vagus nerves. Stensio (1927) has shown that this condition actually existed in the Cephalaspids, and that these animals are directly related to the living lampreys. In these animals the respiratory, or in larvae, the feeding current of water was pumped by the muscles of gill pouches, the pharynx being supported by a skeleton of which the dorsal part was a single continuous bony structure, and the ventral portion though probably stiff was not entirely inflexible. At some stage of vertebrate evolution it became the practice to pump this respiratory stream by volume changes of the pharynx as a whole, brought about by muscles acting on a skeleton which consisted of a series of segmental rods anchored to the vertebral column or basis cranii above and to median elements in the body wall below the gill slits. This visceral arch skeleton and musculature had necessarily a segmentation corresponding to that of the somites of the head, and lay in the gill septa separating the gill slits.

Probably concurrently with these changes, or immediately succeeding them, the vertebrates became macrophagous, eating large prey, presumably still sucking them in and passing the mass backward by muscular movements of the visceral skeleton. The small original mouth proved inadequate and its corners migrated backward, crushing out of existence or absorbing the profundus gill slit, and ultimately settling down at the trigeminal gill slit. The skeleton of the gill septum lying between the trigeminal and facial gill slits, which consisted of a single chain of four elements, the pharyngo-, epi-, cerato- and hypo-branchial cartilages or bones, thus came to be related to the mouth, and its musculature enabled it to be used as a jaw. In fact it becomes the palato-quadrate and Meckel's cartilage. At this stage the facialis or hyoid gill slit obviously remains of its original size and structure; it was identical in all its important features with the glossopharyngeal gill slit. This is the primitive Gnathostome condition. Continuation of the process of lengthening the mouth, subsequent to the establishment of a definite jaw skeleton, will clearly tend to occlude the middle of the hyoid gill slit by bringing the articular region of the jaws into contact with the main articular region of the hyoid arch. If this contact be established the hinder end of the long jaw will gain a much-needed support through the upper part of the hyoid arch skeleton, a hyomandibular being established and a small relic of the dorsal extremity of the hyoid gill slit surviving as the spiracle. The ventral part of this gill slit would vanish entirely, probably for some reason depending on the time rates of development of the structures involved. This condition is that found in all living fish, Chondrichthyes and Osteichthyes alike, with the possible, though I think highly improbable, exception of the Holocephali.

That the Acanthodians are Gnathostomes is obvious; they all possess well-developed jaws which clearly belong to the trigeminal segment. As in all of them the hyoid gill cleft remains of full size, having indeed a very great dorso-ventral extent, and the hyoid arch cannot in consequence assist at all in supporting the articular region of the jaw, it is evident that they may be very primitive Gnathostomes, ante-dating the development of the spiracle and hyomandibular; the only alternative is to make the gratuitous assumption that the full-sized gill slit has been secondarily reacquired. Which view be correct can be judged from a wider analysis of their structure.

The Acanthodians are the oldest group of Gnathostomes of which there is any record, unless some of the Polish Arthrodeirs be actually of Downtonian age. In any case their acme was in the Lower Old Red Sandstone and they declined from that time onward.

The cartilage ossifications of Acanthodians resemble those of Cephalaspids and Arthrodeirs in being entirely perichondral, the cartilage remaining complete within a thin bony shell. It seems evident that this is the most primitive arrangement known.

The unique neural cranium of *Acanthodes* is very difficult to interpret. The anterior basicranial bone surrounds the hypophysial duct and extends for some distance behind it; this bone must therefore represent the trabeculars. The small bones attached to its anterior end have no obvious homologues in other vertebrates. The posterior basicranial bone must be of parachordal origin. There remains the middle basicranial element. This lies too far back to represent polar cartilages. It is conceivable that it is of acrochordal origin, but the structure seems to lie too ventral to be reasonably interpreted in this way. It is therefore possible that it really represents a detached anterior part of the parachordal, analogous to that found transiently in birds, and may be a relique of an original segmentation of the parachordal cartilage.

The jaws of Acanthodians are remarkable for the fact that in all of them the lower jaw is longer than the upper, exactly as the ventral part of each of the other visceral arches is longer than its dorsal end. The jaws are also remarkable because both upper and lower may be, and presumably at some stage of development always were, formed of two cartilages which, as Reis and Jaekel have shown, are directly comparable with the corresponding elements of the branchial arches. (The bone supporting the otic process of the palato-quadrate in *Acanthodes* is probably a neomorph.) It is improbable that the palato-quadrate of *Climatius* had any articulation with the neural cranium, but a palato-basal and an otic articulation exist in later forms.

The branchial arches have the primitive gnathostome four-part structure.

The teeth in primitive forms have what is no doubt a primitive Elasmobranch type of replacement and are in some forms extremely scale-like in appearance.

The gill slits open independently to the exterior in early Acanthodians, each gill slit being covered by an operculum arising from its anterior border. Subsequently the mandibular operculum grows back to cover the whole series. Thus the group shows the gradual suppression of a primitive condition.

It has long been recognized that the occurrence of a long series of paired fin spines in the more primitive Acanthodians is a primitive feature. It is explicable on the finfold theory of paired fins, and provides an immediate point of comparison with Anaspids and Cephalaspids, where Kiaer has shown that a series of spines or a ridge of enlarged scales can be interpreted in the same way. The fin spines of *Brachyacanthus*, mere bony plates bent round the front margin of the thick fold which constitutes the fin, are directly comparable with the dorsal-fin spine of Hemicyclaspis and are clearly very primitive structures. The presence of ceratotrichia and absence of lepidotrichia is another primitive character, not achieved by the Cyclostomes.

It is thus justifiable to regard the Acanthodians as most primitive gnathostomes, belonging to a division of that group characterized by the retention of a full-sized hyoid gill slit. As all other well-known Gnathostomes have this slit reduced to a spiracle, or closed altogether, it is clearly necessary to introduce a new class of vertebrates of a rank equivalent to the Cyclostomata or Pisces for their reception. This new class, which may be termed the Aphetohyoidea (ἄφετος, free; ὑο-ειδής, hyoid bone), falls into an intermediate position between the Cyclostomata and the Pisces. It may be assumed to be of ultimate Cyclostome (Ostracoderm) origin, and its possible relationships to true fishes must now be considered.

Comparison of Acanthodians with Elasmobranchs

A group of the grade here attributed to the Aphetohyoidea would, on the analogy of the Ostracodermi and the Pisces, be of complex constitution, exhibiting a wide adaptive radiation, and it would necessarily include the ancestors of the true fish, the Pisces. The following discussion is directed to the elucidation of the relationship which the presumed Aphetohyoidean ancestors of the Chondrichthyes bore to the

Acanthodii. The group of Chondrichthyes includes essentially the Elasmobranchii and the Holocephali. I deal with the latter independently and restrict the present section to the true Elasmobranchs.

It is clear that the Upper Devonian fish *Cladoselache*, *Cladodus wildungensis* and *Ctenacanthus clarki* are true Elasmobranchs and that no fish of earlier date, represented by adequate material, can be referred to that class. The Middle Devonian fossils which have been regarded as Elasmobranchs are the spines *Machaeracanthus*, *Gyracanthus* and *Onchus* which are in all probability Acanthodians; *Eczematolepis* which is a Ptyctodont; *Cyrtacanthus* and *Gamphacanthus* which do not at all resemble any known Elasmobranch spines; and a few spines referred to the form genus *Ctenacanthus*, whose relationships are uncertain. In addition there are teeth referred to *Diplodus* which may be the Acanthodian *Doliodus*, and two individual teeth referred perhaps correctly to *Cladodus* but probably incapable of real determination. The Lower Devonian fish remains sometimes regarded as Elasmobranchs are the spines *Onchus*, *Gyracanthus*, *Homacanthus*, *Pinnacanthus*, *Helenacanthus* and *Bulbacanthus*, of which the first three may well be Acanthodians whilst the remainder present no resemblance to any Elasmobranch structure. It thus follows that the earliest known Elasmobranchs are from the Upper Devonian, the group appearing much later than the Osteichthyes.

The early history of the Elasmobranchs though little known was clearly complex; an attempt to discuss it must be founded on the fin structure. *Cladoselache* is a fish apart, characterized by the fact that all the fins, both median and paired, are supported by a single series of parallel radials which extend outward very nearly to their margins and leave unsupported only a very small expanse of fin web, strengthened by ceratotrichia which have not been preserved. All the fins are attached to the body by a very long base, but some concentration of the base of the fin is shown by the occurrence of certain radials which extend in only half-way to the base, and by a fusion of the more posterior basal cartilages of the pectoral fin, each anterior basal supporting its own radial. There are no fin spines. *Ctenacanthus clarki*, a contemporary of *Cladoselache*, is remarkable because it possesses at least one dorsal fin spine. The pectoral fin resembles that of *Cladoselache* in the long extension of its radials all of which extend inward to the base so that there is no evidence of concentration. The fin was interpreted by Bashford Dean as showing a continuous series of basals, one to each radial, but this reading of its structure leaves unexplained the apparent basals attached to the misplaced shoulder girdle, and certain other structures shown in the photograph. Mr Moy-Thomas has suggested to me that the so-called basals are really the detached basal parts of the radials, and that a still deeper series of largely fused basals may have occurred.

Those Lower Carboniferous Elasmobranchs sufficiently well preserved to be usable are *Sphenacanthus costellatus*, *Tristychius armatus*, *Chondrenchelys problematica* and *Cladodus neilsoni*. It should be remembered that *Pleuracanthus* occurs in the Lower Carboniferous although the well-preserved complete skeletons are Upper Coal Measures, Permian or

Triassic in age. *Cladodus neilsoni* has every appearance of being a direct successor of *Cladoselache*. It is devoid of fin spines, and the pectoral fin differs only by the backward growth of a long metapterygial axis from the group of posterior fused basals which occurs in the latter. The long radials extending nearly to the fin margin are the same in the two fish. *Sphenacanthus costellatus* is a most interesting fish. As SMITH WOODWARD has pointed out, it resembles *Cladoselache* in the extension of parallel radials nearly to the fin margin in all the fins except the first dorsal; but as BROUGH (1935) and MOY-THOMAS (1935 *b*) have shown, the pectoral fin is tribasal, three elements articulating with the shoulder girdle; the posterior of these seems to me to support a short metapterygial axis. The radials, unlike those of *Cladoselache*, are divided into proximal and distal moieties. I think that BROUGH is correct in holding that this fish is a Hybodont. In later Hybodonts the radials become much shorter, they are indeed restricted to the base of the fin, and those of the pectoral fin are further subdivided. *Tristychius* is of interest because its dibasal pectoral fin still retains radial cartilages, perhaps jointed, which extend out nearly to the margin of the fin and are parallel to one another, agreeing in these respects with *Cladoselache*, *Cladodus* and *Sphenacanthus costellatus*. It seems to me probable that the long metapterygial axis of *Cladodus neilsoni* projected from the body and would thus serve as a morphological ancestor of the "biserial archipterygia" of *Pleuracanthus* and *Chondrenchelys*.

The Coal Measure Elasmobranchs are *Symmorium reniforme* and *Petrodus patelliformis*. Of these the first may readily be interpreted as a Cladodont with an elongated but not subdivided metapterygium. *Petrodus* is more interesting because it is typically tribasal, there being no extended metapterygial axis, and the straight parallel radials are short and jointed, a definite advance on the Lower Carboniferous *Sphenacanthus* and *Tristychius*.

It follows from this analysis that the most primitive known Elasmobranch pectoral fin, from which all others can be derived, is that of *Cladoselache*, and that the most striking of its characters are the parallelism, extension nearly to the fin margin, and unjointed nature of the radials, and the parallel series of short basals.

I have shown that the best known Acanthodian pectoral fin (that of *Acanthodes*) is tribasal and has extremely short jointed radials. In fact it resembles a type of fin, found only in Mesozoic or still later Elasmobranchs, which is the result of a long evolutionary process. The pectoral fin of the Lower Devonian *Ischnacanthus* clearly agrees in its general structure with that of *Acanthodes*. So that even the earlier Acanthodians cannot be compared with the very much more recent primitive Elasmobranchs.

The oldest known Elasmobranch neural cranium is *Cladodus wildungensis*, the only other reasonably well-known Palaeozoic form being *Diacranodus* (*Pleuracanthus*) *texensis*. These two agree very closely indeed with modern Elasmobranchs like *Notidanus* or *Chlamydoselache*. The Elasmobranch neural cranium from the earliest times onward has thus the following qualities: It is composed of cartilage with a characteristic superficial calcification of a single layer of prismatic granules. (No fragment of any Palaeozoic fish of certain Elasmobranch nature shows any other type of calcification, the known forms are *Cladoselache*, *Ctenacanthus*, *Cladodus*, *Sphenacanthus* and all Hybodonts, *Petrodus*, *Pleuracanthus*, Cochliodonts, Petalodonts and Edestids.) The neural cranium is platybasic, the occipital region being very short and ending abruptly at a nearly transversely placed posterior surface of the otic capsules. The otic capsules are square-cut masses of cartilage confluent with the post-orbital process, forming the transversely placed hinder wall of the orbit. They are deep at their outer surface, and their lateral surface is nearly at right angles to their ventral surface. There is a hyomandibular facet on the outer surface of the otic capsule below the level of the horizontal semicircular canal and often very ventrally placed. The orbits are separated by the relatively wide brain cavity which extends down between them. Each is overhung by well-developed crista supraorbitales and floored by a suborbital shelf which was broad in the primitive forms but becomes reduced when it is cut into by the orbital process of the palato-quadrate. *Pari passu* with this lateral embayment of the suborbital shelf proceeds the appearance and development of the "basal-angle" (Basalecke, GEGENBAUR). The large spheroidal olfactory capsules are separated, often very widely, by the extension forward of the brain cavity as the precerebral cavity, the walls of which support the rostrum and may be reduced to rods of cartilage. The nasal openings are directed ventrally or ventrolaterally, never forward.

Comparison of this account of the fundamental type of Elasmobranch neural cranium with that of *Acanthodes* on pp. 97–102 (with which *Cheiracanthus* is known to agree in essence) will show that the two structures differ as completely as is possible. The Acanthodian neural cranium is bony. The Acanthodian neural cranium is tropibasic. The occipital region of *Acanthodes* is long and passes directly into the otic region. The lateral surface of the otic region bears a horizontal crest, below which it is excavated, passing smoothly into the ventral surface. The post-orbital process is independent of the otic capsule and is connected with the basis cranii by powerful sloping columns of cartilage, perforated by the jugular canal (and in so far agreeing with the post-orbital processes of *Cladodus wildungensis*), which abruptly end the recess on the lateral surface of the otic capsule exactly as do the homologous structures in Palaeoniscids. There are well-developed basipterygoid facets, and a complete absence of the clearly non-homologous articular faces for the intra-orbital processes of the palatoquadrate and the basal angle associated with them. There is an inter-orbital septum, whose slightly expanded lower edge can scarcely be called a suboccular shelf. The shape of the snout of all Acanthodians, and the known position of the nostrils in some, show that the olfactory capsules must have been small, in contact with one another, and have had anteriorly directed nostrils.

These differences in the neural cranium reflect a corresponding difference in the brain and in the whole behaviour of the animals. Elasmobranchs are fish in which smell is the dominating sense of distant perception, sight being of minor importance. Acanthodians were clearly creatures in which sight was highly developed and smell of correspondingly less importance.

The Elasmobranch mandibular arch consists of a single palato-quadrate cartilage which anteriorly meets its fellow in the middle line below the neural cranium. It articulates with the suborbital shelf by an orbital process, has no palato-basal articulation, its deepened hinder end does not usually articulate with the post-orbital process by an otic process, and the whole is usually longer than the lower jaw. The lower jaw is a single Meckel's cartilage. (Note: VAN WIJHE has reported the occurrence of two centres of chondrification in the lower jaw of *Squalus*.) The Acanthodian jaw cartilages are superficially very similar to those of Elasmobranchs, but differ in the following ways: The palato-quadrate is composed of two independent bones (presumably representing independent cartilages). The anterior of these is widely separated from its fellow by the ventral edge of the inter-orbital septum; it articulates, if at all, by a basi-cranial facet with the hinder end of the orbito-temporal region, there being no orbital process. There is no otic articulation in the more primitive forms though one appears later. The whole is always markedly shorter than the lower jaw. The lower jaw is ossified in two segments.

In Elasmobranchs the upper element of the hyoid arch is always a hyomandibular. In Acanthodians it is not. In Elasmobranchs the skeleton of each branchial arch is $\leqslant$ shaped, the pharyngo- and hypo-branchials having their tips directed backward. In Acanthodians it is $>$ shaped, the dorsal and ventral elements having exactly the opposite direction. Typical Elasmobranchs have the hyoid cleft reduced to an inhalant spiracle, and the gill slits opening independently to the exterior. In Acanthodians the hyoid cleft is a full-sized gill slit and with those lying behind comes eventually to open into a gill chamber covered by a mandibular operculum.

The above comparisons, which might be greatly extended, are I think sufficient to show that the Acanthodians cannot bear any close relationship to the ancestral Elasmobranchs. It follows that no characters which are common to both Elasmobranchs and Acanthodians can be used as evidence of Elasmobranch affinities of a Palaeozoic and especially of a Devonian fish.

Comparison of Acanthodians with Arthrodeirs

The group which may be called the Arthrodeirs for my present purpose is composed of the Acanthaspids, Coccosteomorphi and Ptyctodonts. Our knowledge of the neural cranium of these forms depends entirely on the work of STENSIO (1934). In all known cases the cartilaginous neural cranium remained intact, sheathed for part of its surface by a thin layer of perichondral bone exactly as in Acanthodians. In *Leiosteus* the occipital region is wide and shallow, a condition imposed on it by the general head shape. It is short antero-posteriorly, a condition obviously variable in Arthrodeirs. In *Homosteus* for example it is evident from the specimen figured by HEINTZ (1934, pl. III, fig. 1) that the normal myotomes extended very far forward under the skull roof and that the occipital region must have been very long and slender, transmitting about ten spino-occipital nerves. In *Leiosteus* the notochord was persistent, its sheath being clasped laterally by the lower ends of the large posterior occipital bone which surrounded the foramen magnum and roofed the hind brain for some distance. This bone is perforated probably for the exit of occipital nerves, its relationship to the vagus is not shown. It may be compared directly with the basi-occipital and ex-occipitals of *Acanthodes* taken together. Apart from proportions the two agree well, indeed very strikingly, in the identical character of the great backwardly opening foramen which is interpreted by STENSIO as the course of the radix aortae. The anterior occipital described by STENSIO (1934) in *Leiosteus* is clearly the homologue of the featureless ventral bone below the otic region of *Acanthodes*.

The only representative of the otic region is a small isolated bone perforated by a jugular canal and a hyoid vein in *Pholidosteus friedeli*. The position of this fragment cannot be fixed and I believe that STENSIO has placed it a good deal too far from the middle line. I base this view on the fact that STENSIO's suggested restoration of the relation of the neural cranium to the dermal roof (STENSIO 1934, text-fig. 15) cannot be right because it makes no allowance for the thickness of the dermal bones.

In *Deinichthys* (HEINTZ 1932, text-fig. 13) the position and possible lateral extension of the neural cranium in front of the occipital region are defined by deep flanges descending from the dermal roof. The similar structures in *Coccosteus* have the same distribution and in addition show entirely different surface features in the regions in contact with the neural cranium and in the rest of the visceral surface of the skull roof. Consideration of this evidence suggests that the "neural process" of HEINTZ in *Deinichthys* abutted against the outer end of a post-orbital ridge which is the most anterior part of the otic region in *Pholidosteus*.

The extent of the dorsal surface of the neural cranium is very clearly defined in *Coccosteus* (cf. HEINTZ 1931, fig. 7) and *Deinichthys*. In the former the position, size and approximately spherical shape of the olfactory capsules are evident from impressions in the dermal roof, and the position of the nostril is shown by the notch in the post-nasal. I have shown that there was a cartilaginous ectethmoid, or preorbital process underlying the latter bones. The diameter and position of the eye can be determined, and the general size, shape and position of the palatal part of the palato-quadrate are fixed by the supra-gnathals which lie attached to its lower surface. The lower surface of the anterior part of the neural cranium can thus be restored with considerable probability; it agrees remarkably with the conditions actually found by STENSIO in *Pholidosteus*. STENSIO's Acanthaspid suggests that a pituitary foramen existed posteriorly. I thus arrive at fig. 23 as a possible neural cranium in *Coccosteus*. In it all the stippled regions represent areas slightly modified from the bones figured by STENSIO. That the brain case so restored presents a very remarkable resemblance to that of *Acanthodes* is obvious and requires no elaborate discussion. It should however be pointed out that the resemblances would remain even if the proportions of the whole structure were changed, and that they are visible in such parts of the structure as are preserved in

STENSIO's materials. It is therefore interesting to look for further evidence to confirm the relationship so suggested.

In *Pholidosteus* the palato-quadrate is surrounded by two perichondral bones, an anterior which articulates with the ventral part of the neural cranium just behind the olfactory capsules, and a posterior quadrate. This condition is directly comparable with that occurring in several Acanthodians. Meckel's cartilage in *Pholidosteus* and

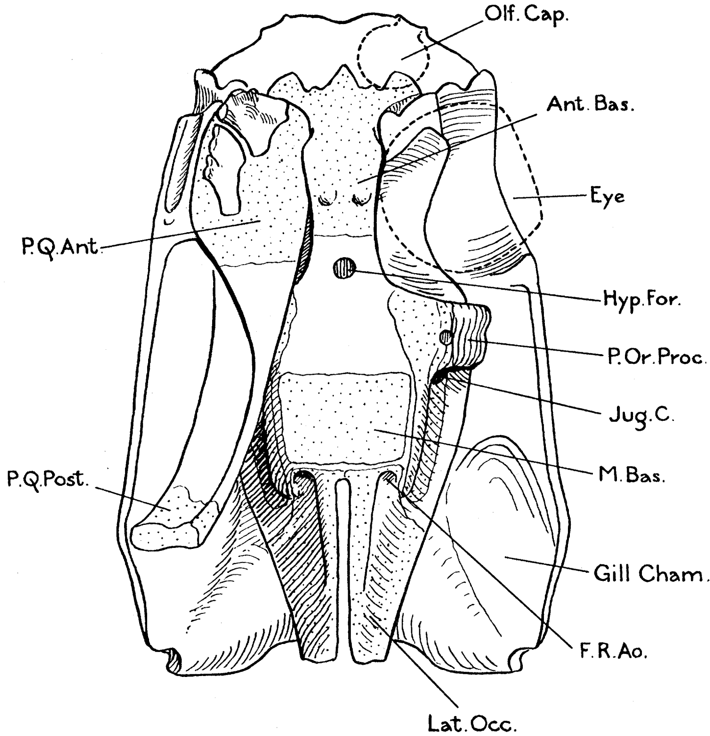


FIG. 23—An attempt to restore the brain case and palato-quadrate of an Arthrodeir by modifying the bones of *Leiosteus* and *Pholidosteus* figured by STENSIO to fit the dermal skull roof and "gnathals" of *Coccosteus decipiens*. × 1·0. *Ant.Bas.* anterior basal; *Eye*, eyeball; *F.R.Ao.* foramen for the radix aortae; *Gill Cham.* the depression on the skull roof which is the roof of the gill chamber; *Hyp.For.* foramen for the hypophysis; *Jug.C.* jugular canal; *Lat.Occ.* lateral occipital; *M.Bas.* median basal; *Olf.Cap.* the olfactory capsule; *P.Or.Proc.* post-orbital bar of the neural cranium; *P.Q.Ant.* and *P.Q.Post.* the two ossifications in the palato-quadrate cartilage.

Leiosteus is also ossified as anterior and posterior bones, again agreeing with many Acanthodians. These conditions do not exist in any Elasmobranch, though a parallel may be found in Palaeoniscids. I have shown that there is evidence in *Coccosteus* that the teeth were arranged in more than one row, a condition which suggests derivation from a dentition comparable to that of early Acanthodians and especially to *Ischnacanthus*.

Gills—It has been shown (WATSON 1934, p. 459) that the Arthrodeirs, especially the Ptyctodonts, were operculate fish with the gill slits opening into an extensive gill chamber. This was covered externally by an unossified operculum which was attached to the hinder border of the post-suborbital and lower jaw, and carried the lower part of the pre-opercular canal. That this gill cavity extended far up into the head is obvious from the character of the anterior lateral of Ptyctodonts, and there is no real doubt that in *Coccosteus* and *Deinichthys* its upper surface lay immediately below the skull roof on which it leaves a smooth rounded depression. This depression was supposed by STENSIO (1925) to have housed a lateral extension of the otic region of the neural cranium, a view which is obviously at variance with the whole nature of the groove and its inner termination and is not supported by the character of such parts of the neural cranium as are actually known in Coccosteomorphs. HEINTZ, on the other hand, regards it as overlying his "musculus depressor capitis" which I have shown (1934) to have had no existence.

It is clear from examination of actual materials that this depression in *Deinichthys* leads down directly to the gill chamber. Furthermore in *Homosteus* (*vide* HEINTZ 1934, pl. III, fig. 1) the homologous area was bounded both in front and above by the anterior end of the body musculature, as a gill chamber should be. Thus the gill slits of Arthrodeirs must have had a great vertical extension. Consideration of the extreme antero-posterior compression of the whole gill region in the enormous *Deinichthys* suggests that very long gill slits were necessary to provide an adequate area of respiratory surface. Thus the whole arrangement of the branchial apparatus in Arthrodeirs must have greatly resembled that in Acanthodians.

The most striking feature of the more primitive Arthrodeirs, the Acanthaspids, is the occurrence in them of a long dermal armour over the anterior part of the trunk, and the existence of a long spine projecting laterally from the anterior latero-ventral part of this armour. This spine occupies the position of the anterior margin of a non-existent pectoral fin and is rigidly held by two dermal bones, the antero-lateral and the anterior ventro-lateral, which fit into rabbets on its base. The spine is hollow and variously ornamented with longitudinal ridges, and points or hooks along its inner and outer margins. It is evident from the conditions in Ptyctodonts that the anterior part of the body armour fulfils the functions of a dermal shoulder girdle and is in many ways comparable with the elaborate structures existing in *Climatius* and other primitive Acanthodians. The way in which the large spine of the Middle Old Red Sandstone Ptyctodont *Rhamphodopsis* is held between the antero-lateral and inter-lateral plates is identical, even in the surface detail of the attachments, with that in which the pectoral spine of *Diplacanthus* is held in place. If the spinale of Arthrodeirs be really a pectoral fin spine, and no other explanation of it has ever been suggested, then we should expect to find other fin spines within the group. BROILI has shown (1930*a*) that in *Lunaspis* there is a spine arising from the anterior median dorsal which is perhaps only a part of that plate and was never related to a fin, and that on the mid dorsal ridge of the body there were two enlarged scales or "stachel-artige Bildungen" which may have been associated with dorsal fins. In *Rhamphodopsis* the median dorsal clasps the root of a spine which stands up dorsally and is comparable with a fin spine.

Thus it is not impossible that the ancestral Arthrodeirs may have possessed Acanthodian-like fins, with anterior spines. Confirmatory evidence may be afforded by the fact that in *Pterychthiodes*, which STENSIO has shown to be related to the Arthrodeirs, the single dorsal fin has its anterior edge surrounded by a spine which is exactly similar to a fin spine of *Brachyacanthus*. The idea held by TRAQUAIR that this spine was composed of more than one element seems to be erroneous. It is difficult to carry the comparison much further because of the incompleteness of our knowledge, but it may be pointed out that the lateral-line system of the head of *Diplacanthus* is in some ways very reminiscent of that of Arthrodeirs.

In general body form the Arthrodeirs with their macruriform appearance do not recall Acanthodians, the row of ridge scales along the dorsal border of the tail of *Rhamphodopsis*, and the character of the squamation of *Lunaspis* are definite points of difference. It is none the less reasonable to suggest that the two groups possess the same grade of structure and may legitimately be grouped as "Aphetohyoidea". Such reference would not of course preclude a relationship between the Arthrodeirs and the Elasmobranchs or Chimaeroids. The current belief in such an association depends on Dr. STENSIO's comparison of *Macropetalichthys* with the Elasmobranchs, and it is therefore necessary to discuss this fish.

COMPARISON OF ACANTHODIANS WITH MACROPETALICHTHYS

Macropetalichthys is known from STENSIO's classical account (1925) of the structure of the neural cranium, and BROILI's (1933 *b*) excellent description of the whole skeleton. It may be pointed out that the extreme similarity between the neural crania of *Macropetalichthys* and an Acanthaspid seems to establish the existence of a real relationship between the groups to which they belong, despite the very great differences in other parts of the skeleton.

STENSIO compares the Macropetalichthid and Elasmobranch neural crania in the following words: "(1) The general shape of the primordial neuro-cranium, especially the tendency to broadening of the ventral surface, partly at the expense of the lateral surfaces. (This is especially the case in the labyrinth region in which the sacculus and perhaps the canalis semicircularis externus had about the same relation to the ventral surface as in *Chlamydoselachus* and most other Selachians.) (2) The position and relations of the olfactory capsule. (3) The presence of a nasal fontanelle on the lower side of the nasal capsule as in *Chlamydoselachus* and certain other Selachians. (4) The presence of the cavum precerebrale. (5) The general shape of the labyrinth, especially with regard to the position of certain of its main parts, as, for instance, the utriculus. (6) The presence of the ductus endolymphaticus and the fact that there probably was a distinct fossa endolymphatica on the dorsal surface of the primordial neuro-cranium beneath the dermal bones. (7) The fact that the ductus endolymphaticus perforated the dermal cranial roof and had an external opening situated as in certain primitive Selachians (*Chlamydoselachus*). (8) The general shape of the brain as far as this can be restored from the exit of the nerve canals and the shape of the cavum cerebrale. (9) To a certain extent the course and arrangement of the blood vessels and the presence of certain important trunks, as, for instance, the vena hyoidea. (10) The fact that the palato-quadrates as far as can be judged did not articulate with the ethmoid region but must have been suspended below this by ligaments. (11) The probable course of the anterior part of the supraorbital sensory canal. (It should also be mentioned that the sensory canals must have had rather numerous sense organs and that they opened outward with very many tubuli.)"

In 1934 Stensio, on the basis of a comparison with Arthrodeirs, withdrew his account of the ethmoidal region of *Macropetalichthys* and thereby removed Nos. 2, 3 and 4 from this list. No. 8, the general shape of the brain as determined from the cranial cavity, also falls to be modified. In Stensio's fig. 10, representing the cranial cavity, the canals for the olfactory tracts are represented as diverging very greatly, in order to reach what were then presumed to be the nasal capsules. This great divergence is not shown in the photographs on pls. XXVII and XXXIII, and cannot have occurred on the new interpretation of 1934, by which the nasal capsules are brought in towards the middle line. As so modified the cranial cavity would very nearly fit an enlarged brain of *Osteolepis*, and cannot be regarded as showing any special Elasmobranch resemblances. Nos. 5, 6 and 7 are concerned with the labyrinth. No. 5, the general character of the labyrinth in *Macropetalichthys*, is as much that of *Acanthodes* as of an Elasmobranch. No. 7, that the ductus endolymphaticus opened on the top of the head is true of *Climatius* as well as of Elasmobranchs. No. 6, that there may have been an expansion of the ductus endolymphaticus between the cartilaginous cranium and the dermal bone of the skull roof, is of very little significance. No. 9 is of very little importance. No. 11, the relation of the anterior end of the supraorbital canal to the nostril, is of course completely changed by the alteration in the position of the nostril, and is in fact as in Acanthodians, and not as in Elasmobranchs. Nos. 1 and 10 are dealt with below. Professor Broili added to the series of Elasmobranch resemblances of *Macropetalichthys* the following:

(1) The ventral position of the mouth.
(2) The structure of the mandible.
(3) The scales acting as teeth.
(4) The five branchial arches.
(5) The thoroughly Selachian-like shoulder girdle.
(6) The Elasmobranch-like paired fins.

These may be discussed as follows:

(1) *Macropetalichthys* is a flattened, ground living and bottom feeding fish and the ventral position of its mouth may be merely an adaptive character.

(2) The shape and structure of the mandible are related to the feeding habits and may receive the same explanation as (1).

(3) The functional conversion of scales into teeth is merely a primitive feature which is likely to have been practised by the ancestors of all gnathostomes.

(4) The five branchial arches may be paralleled by the five which sometimes occur in *Acanthodes*.

(5) The Selachian-like shoulder girdle is a definite point of resemblance. In some Acanthodians, e.g. *Diplacanthus* and *Cheiracanthus*, there is evidence that in addition to the dorsally directed scapula there was a downwardly and inwardly directed coracoid, which might meet its fellow in a symphysis. In *Climatius* the scapula region is quite like the corresponding structure in *Macropetalichthys*, and a coracoidal extension certainly existed although it is not ossified. The primary shoulder girdle of *Diplacanthus* is in fact like that of *Macropetalichthys*.

(6) The tribasal pectoral fin of *Macropetalichthys* with its short radials is directly comparable, except for the absence of a spine, with that of *Acanthodes* or *Ischnacanthus*. I have already shown that such a fin is not found in the earliest Elasmobranchs and that its occurrence in a Lower Devonian fish is on the whole evidence against Elasmobranch affinities. The very remarkable pelvic fin of *Macropetalichthys* is of course comparable with a primitive Elasmobranch like *Cladoselache*, but it is equally similar to the primitive pelvic fins found in Sturgeons and in *Saurichthys* and Palaeoniscids.

There remain only two of STENSIO's comparisons.

(10) The non-articulation of the palato-quadrate with the ethmoidal region. Even if true this fact would provide no evidence of Elasmobranch affinities; the palato-quadrates of Acanthodians always end in a free anterior border which lies behind the ethmoidal region.

(1) The general shape of the neuro-cranium with its widened ventral surface was by far the most Elasmobranch-like of all the structures of the fish. This resemblance becomes much less striking when critically considered. The very long occipital region is unparalleled in Elasmobranchs, where indeed it is always exceptionally short. The postero-lateral process arising from the occipital region behind the foramen for the vagus and the distance of that opening from the middle line are unparalleled in Elasmobranchs. The presence of a wide suborbital shelf is very shark like, but is obviously to be associated with the general platybasy and with the small dorsally directed eyes of this bottom-living fish. The very Elasmobranch ethmoidal region has now been shown by STENSIO to have been wrongly interpreted. Thus there are no indubitable Elasmobranch qualities to be found in the very well-known skeleton of *Macropetalichthys*.

It is, however, possible to go further than this purely negative conclusion. The skull roof of BROILI's *M.*? *prümiensis* agrees, except that as it is a small young individual the eyes are relatively large, with the specimen from Bundenbach figured by GROSS, and this latter in turn is not dissimilar to *M. rapheidolabis*. Stensio has shown that the incompletely known neural cranium of *Epipetalichthys wildungenensis* agrees in all important features with that of *Macropetalichthys rapheidolabis*. Thus there is no difficulty in making the very slight changes in proportion necessary to fit a neural cranium to the skull of Broili's specimen.

That lateral part of the labyrinth region which is perforated by the jugular canal lies immediately in front of the origin of the pre-opercular lateral line canal and extends forward one-third across the orbit from the posterior margin of that opening.

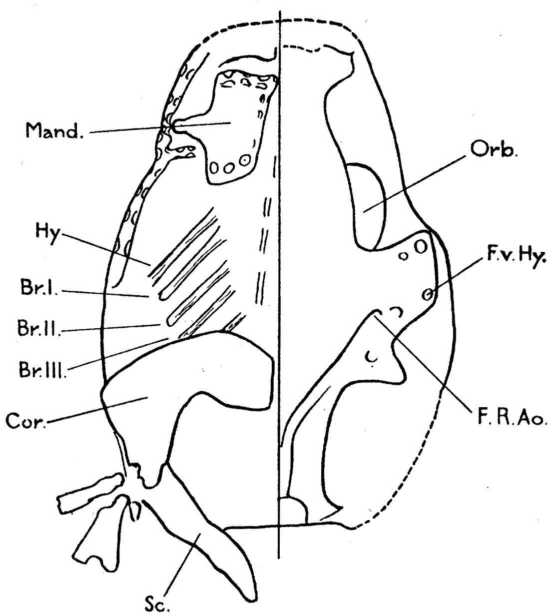


Fig. 24—*Macropetalichthys*. The ventral surface of the head, left side of the figure traced from Broili (1933 *a*), right side, Stensio's figure of the neuro-cranium modified in proportions to fit. × 1·3. *Br*. I–III, the cerato-branchials; *Cor*. coracoid; *Hy*. cerato-hyal; *F.R.Ao*. foramen for the radix aortae; *F.v.Hy*. foramen for the hyoidean vein; *Mand*. mandible; *Orb*. orbit; *Sc*. scapula.

Stensio has shown that the upper end of the hyoid arch must have laid below and toward the front of this process, because of the position of the hyoid vein. Trial will show that the posterior end of the most anterior of the branchial arches of Broili's specimen falls exactly on to this place. It thus seems certain that this is the hyoid arch. It cannot be the first branchial, because if so the upper end of the hyoid arch would be impossibly far forward, especially as the unossified extremity of this arch must also have been directed to some extent forward. We have thus direct evidence that the hyoid arch in *Macropetalichthys* had no suspensory function, but like that of Acanthodians was in function as in homology merely a branchial arch.

In *Macropetalichthys* the pre-opercular lateral line canal passes backward and outward until it is cut off abruptly by the margin of the head shield. In Arthrodeirs it has exactly the same position and was obviously continued on the unossified operculum which covered the gill chamber. It thus seems probable that in *Macropetalichthys* there was present an operculum which must have been borne on the mandibular arch as is that of Acanthodians. The exact similarity of the hyoid to the branchial arches shows that it cannot have supported the operculum, but must have been over-ridden by it. There is thus direct evidence that the *Macropetalichthyes* are Aphetohyoidea.

Comparison of Acanthodians with *Gemündina*

The systematic position of that very interesting Lower Devonian fish *Gemündina*, and its later relatives *Asterosteus* and *Jagorina*, may now be discussed.

The original account by Traquair was exceedingly tentative and a reconstruction by Abel founded on it represents a remarkably successful reinterpretation. In 1930 Professor Broili (1930*b*) published an account founded on much new material and subsequently extended his treatment in a description of two further specimens. He summed up the affinities of *Gemündina* by concluding that it represented a specialized side branch of a subclass of fishes which had a well-developed dermal skeleton, and of which no other representatives were known. The great resemblance to skates and rays is an example of convergence dependent on similar adaptation to a benthonic life. With this view I am in complete agreement, but I believe it possible to go farther with the analysis of the characters of the animal. Professor Broili's description is so clear and objective, and his illustrations from un-retouched photographs (made from specimens which have not been painted in any way) are so good, that with the experience gained by handling two specimens, the type in Edinburgh and P. 501 in my own collection, I feel justified in offering a reinterpretation of *Gemündina*.

It is clear that all specimens from the Hünsruckschiefer have been to some extent deformed by cleavage, and that in general this deformation is a proportionate reduction in all lengths measured in one direction, in comparison with those in a direction at right angles to it. The ratio of head length to width in the nine specimens which are measurable varies from 0·76 in Traquair's type to 1·57 in Münich III. The others cover this great gap reasonably completely and suggest that the variation depends almost entirely on the cleavage. The average 1·01 probably represents the normal condition during life.

Münich III (Broili 1930*b*, pl. II) is in many ways the best preserved specimen, and by making a grid over it and so laterally compressing it in a drawing, I have restored its original shape. It forms the basis of fig. 25 A and B.

It seems to me possible to regard the dorsal and ventral parts of the shoulder girdle, and the Flossenträgerplatte of Broili, as a series of dermal elements quite comparable to the body armour of a Ptyctodont (Watson 1934, figs. 6 and 7). The most obtrusive structure of the dorsal surface is the remarkable trefoil shaped frame which surrounds the posterior and lateral borders of the skull. The giant specimen (Broili 1933*a*, pl. I), that figured by Broili (1930*b*, pl. IV, fig. 1), and the Type, show that the mid-dorsal recess of this frame is bounded behind by a median dorsal bone with a pointed posterior edge. This is connected to the rest of the armour by long unornamented forward projections of its lateral margins, which lie on the line of the widened hinder end of the neural cranium and its dermal plate. Laterally, forming the side of the mid-dorsal recess in the upper part of the frame, is a wedge-shaped area marked out by two ridges which meet anteriorly at a point immediately behind the dermal bone L^3 of Broili, just lateral to the tip of the median dorsal. Appearances in the Type specimen make me suspect that this area is an independent anterior-dorso-lateral bone.

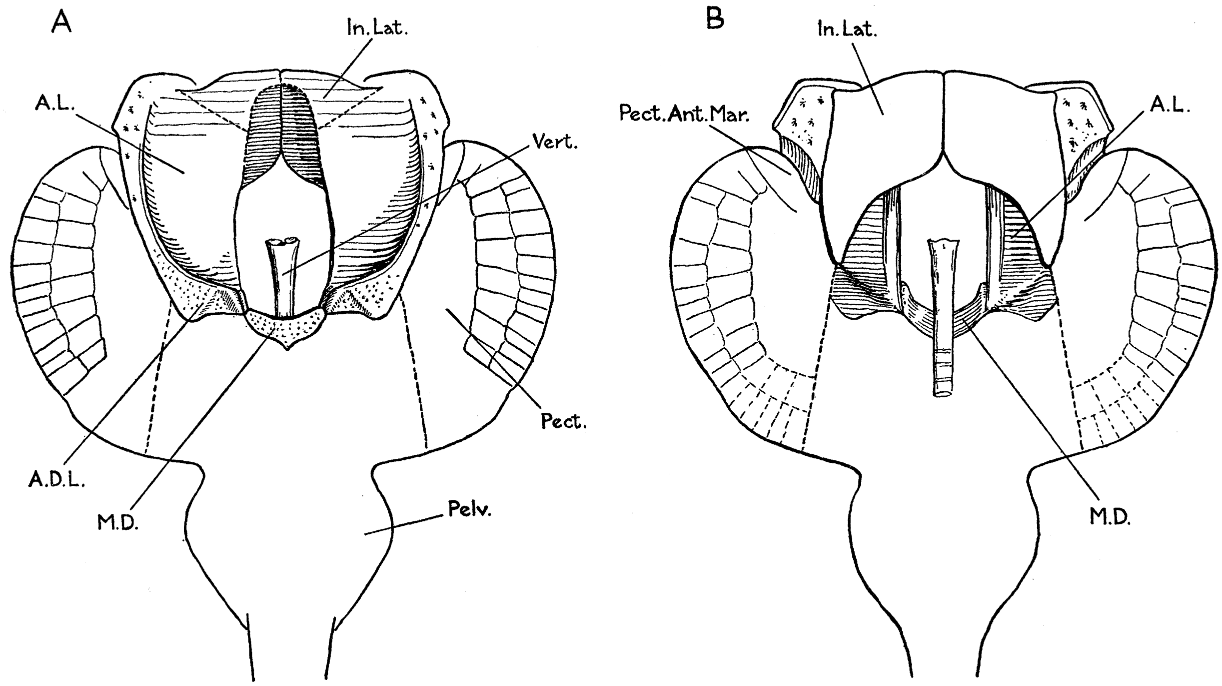


Fig. 25—*Gemündina sturtzi* Traq. × $\frac{2}{3}$. An attempted restoration of the front part of the body with the head removed. A, dorsal; B, ventral surface; *A.D.L.* anterior-dorso-lateral; *A.L.* anterior-lateral; *In.Lat.* inter-lateral; *M.D.* median dorsal; *Pect.* pectoral fin; *Pect.Ant.Mar.* anterior margin of pectoral fin; *Pelv.* pelvic fin; *Vert.* vertebral column.

The remaining part of the armour visible from the dorsal aspect has an ornamented external surface of variable width, ending abruptly at the sharp margin of a recessed smooth area, only a narrow strip of which is seen behind the head. This bone may be called the anterior-lateral. As Broili has recognized, a broad inwardly directed sheet of bone with a thickened admesial edge forms part of the shoulder girdle, it is his ventral part, *c.o.* in the figures. Superposition of tracings of dorsal and ventral views of the same specimen shows that this sheet is part of the same bone (the anterior-lateral) as the ornamented dorsal rim.

The whole arrangement can readily be interpreted on the basis of a comparison with Ptyctodonts, the inwardly directed bone sheet being the hinder wall of a very extensive though flattened gill chamber, the ornamented rim the superficial exposure of the bone. The exposed part of the anterior lateral widens before it ends, the point of expansion being marked by a distinct notch in the lateral border of the bone, well shown in Broili (1933*a*, pl. II, left side; 1930*b*, pl. IV, fig. 2); and the Type specimen. The whole bone ends in a thin transversely placed anterior margin which overlaps the outer end of the anterior margin of the Flossenträgerplatte. This region is best shown in Broili 1930*b*, pl. II, fig. 2, right side; pl. III, fig. 1, left side; and P. 501, D. M. S. Watson collection.

The ventral surface of this dermal armour is almost entirely made by the great Flossenträger, which may be called interlaterals. They meet in the middle line, and probably possessed a dorsally directed back-turned projection which articulated with that sheet of the anterior lateral lying below and behind the gill chamber. The lateral margin is free, but is connected with the lower end of the lateral part of the anterior lateral by an area of skin containing a few large stellate tubercles. This ends abruptly at an embayed edge, best shown in Broili (1930*b*, pl. III, fig. 1), apparently marking a depression for the anterior corner of the pectoral fin, which is shown (P. 501) by the fact that it can be displaced to have been free. It is evident that a space separated the ventral border of the anterior lateral from the hinder part of the lateral border of the interlateral, and allowed the fin skeleton and musculature to pass from the primary shoulder girdle (of which no trace is preserved) to the fin itself. Comparison of this description, and fig. 25 illustrating it, with the shoulder girdle of a Ptyctodont will show that in principle and indeed in many details the two agree.

It follows automatically from this conclusion that *Gemündina* was an operculate fish, and that the operculum is the large lateral area of the head, containing the plates L^2 and L^3 of Broili. The structure of the neural cranium, so far as it is known in *Asterosteus* and *Jagorina*, is consistent with this view. It is impossible to determine how far ventrally the slit behind the operculum extended; it seems however most probable that it terminated immediately behind the anterior border of the anterior lateral, the external surface of the operculum and the shoulder there becoming continuous.

Inspection of the published photographs shows that, apart from proportional changes due to crushing and to those which may depend on growth, the extent to which the head (including the lower jaw) is prolonged in front of the anterior lateral is variable. As Broili has shown the mouth faces dorsally, being in fact most reminiscent of that of an Angler fish *Lophius*. As the centre of the upper jaw is clearly fixed by association with the anterior end of the neural cranium, it is evident that the mouth can only be opened by a protrusion of the lower jaw, and the specimens show that this forward thrust did occur, and that it was associated, as on mechanical grounds it must have been, with a lateral contraction of the mouth. It seems probable that only the "spitz rhombischen Täfelchen" with their stellate tubercles were attached to the lower jaw, and that the "spitzen stachelzähnen" were really carried by the antero-posteriorly widened admesial end of the hyoid.

Broili has shown that the large admedian part of the hyoid is closely attached to the lower jaw, that its lateral extremity is extended into a slender backwardly and outwardly directed process, and that a series of two or three other slender rods are attached to the hyoid and pass back roughly parallel to this process. As Broili has stated these can only be the anterior ends of branchial arches. It is possible that the whole unusual arrangement is associated with the protrusible mouth and represents a device for driving the jaw forward.

One very interesting feature of *Gemündina* is the fact that the whole extent of the large pectoral fin is supported by ossified radials, a condition comparable with that of *Cladoselache* and in sharp contrast to that of the Acanthodians. It is probable that the condition in *Gemündina* represents a secondary lengthening of the radials from a stage in which they were short and restricted to the base of the fin.

Professor Broili's admirable restored figure (1930*b*, fig. 8) represents the animal swimming by causing a series of waves to pass from the anterior to the posterior ends of the pectoral fin. That this conception is correct seems to me altogether probable. But such movements can only be carried out with the necessary power if the intrinsic fin muscles, and the radials to which they are attached, be long. The exactly similar conditions in skates were clearly introduced to subserve the same end. *Gemündina* is also interesting because its single dorsal fin has an anterior spine as in *Pterichthys* or an Acanthodian.

If the foregoing interpretation be true it follows that *Gemündina* is closely related to the Arthrodeira. This conclusion has already been reached by Stensio. The published figures of *Asterosteus* and *Jagorina* show that their neural crania are far more like those of Elasmobranchs than are the brain cases of *Macropetalichthys* and Arthrodeirs. It will be interesting to consider how far these resemblances depend on the skate-like form of the Rhenanida and how far they are evidence of real affinity between the two groups.

Comparison of Acanthodians with Chimaeroids

Very many authors have suggested that the Chimaeroids are the least modified living descendants of the first skull and jaw bearing vertebrates, and that they retain a pre-Elasmobranch condition in the preservation of a complete hyoid arch including an epi- and a pharyngo-hyal. I do not propose to discuss the relationships of this group in any detail, but am compelled to consider the view still held by Stensio, that they are related to the Arthrodeirs, and the suggestions made by de Beer and Moy Thomas (1935) in the following words: "If it could be shown that the jaw suspension of Arthrodira was autodiastylic a good case would have been made out for the existence of an extensive pre-Elasmobranch group from which Acanthodians, Arthrodira, Selachii and Holocephali could be derived. It may be noted that the Holocephali living to-day, with their non-suspensional hyoid arch, are the only survivors of this group to have kept this character, and in spite of their specializations in other directions, they must be regarded as representatives of the most primitive living gnathostomes." That the Chimaeroids are closely related to the Elasmobranchs is certain (DEAN 1906; GOODRICH 1909) and has never been disputed.

The preceding analysis has shown that there is no evidence of close relationship between any of the known Aphetohyoidea—Acanthodii, Arthrodira, Petalichthids and Rhenanida—and the Elasmobranchs, and that it is hence improbable that the Chimaeroids, even if they were still-living Aphetohyoideans, should be at all closely related to them.

The morphology of one of the most remarkable features of the Chimaeroids—the interorbital septum lying dorsal to the brain cavity—has been most lucidly explained by DE BEER on an embryological basis as the result of a series of changes starting from conditions, found only in Elasmobranchs, of a fenestra precerebralis opening forward into a fossa precerebralis whose walls form the skeleton of the rostrum.

The general build of the otic and occipital regions of the neural skull of Chimaeroids is thoroughly Selachian and differs from that of all other vertebrates. Indeed the only character which has been held to prohibit a derivation of the Holocephali from an Elasmobranch stock is the absence of a hyomandibular and the presence of a pharyngohyal. As GOODRICH pointed out (1909, pp. 169–71) there is nothing either in the adult anatomy or in the development to show that the hyomandibular is not fused with the hinder border of the palato-quadrate and with the otic capsule, being indeed the so-called otic process. DE BEER points out that this process lies dorsal to the hyoid vein, instead of being below it as is the head of the hyomandibular in all Selachians. He also identifies a group of ampullae as the spiracular sense organ, and uses them to show that the spiracle lay behind this otic process. I do not think that the identification of this structure is in the least certain or indeed probable, and feel that a migration of the head of the hyomandibular across the vein cannot be excluded.

The branchial arches of Chimaeroids are typically selachian in their backwardly directed pharyngo-branchials, and the hyoid arch agrees entirely with them in its appearance but, according to DE BEER's fig. 1 of a 95 mm. *Callorhynchus*, differs from them in one important respect. Like the opercular cartilage the tip of the "pharyngohyal" lies lateral to the efferent hyoidean artery, whilst the true pharyngo-branchials lie mesial to their efferent branchial arteries. The difference between them is of exactly the same character as that which has been shown by DE BEER (1932) to distinguish the pseudo pharyngo-hyal of the Rays from the hyomandibular and the true pharyngobranchials of these fish. It is thus natural to compare the so-called pharyngo- and epi-hyals of Chimaeroids with the pseudo hyoid arch of Rays, and to regard them as neomorphs fulfilling some functional purpose. That this view is correct is I think shown by the complete disappearance, even in early stages of development, of all traces of the hyoid cleft. Had the Chimaeroids been derived from fish which, like Acanthodians, had a primary complete hyoid arch and a complete pre-hyoidean gill slit, it is very difficult to conceive any reason why the latter structure should have been so completely suppressed.

I think therefore that all the peculiarities of the Chimaeroids can be accounted for by the view that they represent the secondarily free-swimming descendants of a series of primitive, bottom living, Squatina-like Elasmobranchs, which in association with durophagous habits produced tooth-plates and an autostylic jaw suspension, and in which eyes were carried up as a kind of turret above their flattened heads. As SMITH WOODWARD has shown, the Cochliodonts may be their ancestors.

There remains for consideration the possible relationship between the presumed Aphetohyoidean ancestors of the bony fish and the known members of that group, and the existing evidence showing whether or not the hyostylie and reduced spiracular gill-slit of Elasmobranchs and Osteichthys were independently acquired.

COMPARISON OF ACANTHODIANS WITH BONY FISH

It is evident that the Acanthodians have no close relationship to bony fish. The character of the fins with their concentrated basals and anterior spines is far too advanced to have given origin to those of Palaeoniscids; and it is difficult to relate the dermal skeleton, two members of which clasp the lateral line between them, to that of *Osteichthyes* where the centres of ossification of many important bones lie below neuromast organs. The absence of all dermal ossifications from the palate of Acanthodians is a further important difference.

Nevertheless there is a most curious series of qualities in which the members of the two great groups agree. They are both possessed of replacement and dermal bone. In general build, though not in details of ossification, the neural cranium of Acanthodes is reminiscent of that of Palaeoniscids. The palato-quadrate and Meckel's cartilages are ossified from two independent centres in Acanthodians and in some Palaeoniscids. All the Middle Old Red Sandstone bony fish resemble the Acanthodians in the extremely anterior position of their orbits and the small size of their olfactory organs.

It seems probable that these were characters of the primitive gnathostomes which had been already lost by the ancestors of the Elasmobranchs. If this be the case it seems probable that the *Chondrichthyes* and the *Osteichthyes* were derived from such dissimilar Aphetohyoidean ancestors that the hyostylie and reduced spiracles of each must have been independently acquired and that REGAN is justified in placing the two groups in independent classes or subclasses. If this view be accepted the classification of the lower Craniates will become:

SUMMARY OF CLASSIFICATION

Subphylum.	CRANIATA.
Branch.	AGNATHA.
Order.	Heterostraci.
,,	Anaspida.
,,	Osteostraci.
,,	Cyclostomata.

Branch.	GNATHOSTOMATA.
Grade and Class.	Aphetohyoidea.
Order.	Acanthodii.
,,	Arthrodira.
,,	Antiarchi.
,,	Petalichthyida.
,,	Rhenanida.
Grade.	Pisces.
Class.	Chondrichthyes.
,,	Osteichthyes.

The description in this paper of the structure of several Acanthodians, and the determination of their systematic position on an adequate though still very incomplete knowledge of the anatomy, will enable them to be used in morphological studies. The most important result is however the verification of a prediction, long implicit in all discussions of the morphology of the lower gnathostomes, that there must have existed a group of vertebrates in which the hyoid gill slit and hyoid arch resembled in their structure the homologous gill slits and arches lying behind them. Such a verification of a prediction which rests on a long chain of reasoning helps to establish the validity of the methods and assumptions of morphology as a mode of thought.

I am very much indebted to the following gentlemen who have allowed me to borrow materials from the collections under their control, and have allowed me to retain such specimens often for years:

Dr. W. D. LANG and Dr. E. I. WHITE, British Museum (Natural History);

The late Dr. KITCHIN and Dr. PRINGLE, of the English Geological Survey;

Dr. RITCHIE, Mr. GRIMSHAW and Dr. STEPHEN, of the Royal Scottish Museum, Edinburgh;

Dr. J. W. JACKSON, of the Manchester Museum;

Dr. JANENSCH and Dr. QUENSTEDT, of the Berlin Museum;

Dr. POEVERLEIN and Dr. VOELKER, of the Museum of Pollichia;

Dr. WHITTARD, of the Imperial College of Science;

Mr. C. FORSTER COOPER, the Zoological Museum, Cambridge;

Professor H. G. A. HICKLING, of the Armstrong College, Newcastle-on-Tyne;

Professor PEACOCK, of the University College, Dundee, and the Dundee Natural History Society.

I am also much indebted to Mr. J. THOMAS of the Zoology Department of University College, London for very many admirable photographs, and to Mr. F. J. PITTOCK of the Department of Anatomy of University College, London for the enlargements used in the plates.

Finally my thanks are due to Miss Joyce Townend who has helped me throughout the work in the laborious and very difficult task of making restorations of these fish.

Summary

The Acanthodian fishes are the oldest gnathostomes known and they reached their acme in Lower Devonian times, before any other group.

Their structure has been much less fully described than that of any other group of palaeozic vertebrates, and the present paper is intended to fill this great gap in our knowledge.

The Acanthodians possess both dermal and perichondral bones, of peculiar character.

They have large eyes and the head has only a very small preorbital portion, with very small olfactory organs and anteriorly directed nostrils. The typical ear has long, slender, semicircular canals and a ductus endolymphaticus open to the exterior.

The neural cranium in general shape recalls that of an Actinopterygian fish, but is differently ossified.

The palato-quadrate has usually a palato-basal articulation, and in advanced forms also an otic attachment. It commonly contains an anterior and a posterior ossification. Meckel's cartilage projects farther forward than the palato-quadrate and also has two centres of ossification.

The hyoid arch is separated from the mandibular arch by a full-sized gill slit, and except for the possible absence of a pharyngo-hyal agrees with the branchial arches in having four bone centres. In primitive forms each arch has a small operculum closing the upper part of the gill slit behind it, but the lower parts of all the gill slits are covered by a mandibular operculum; in advanced forms this comes to override all the gill septa and to rest on the shoulder girdle as does the hyoidean operculum of a teleostome.

An analysis of the whole structure shows that the Acanthodians are the most primitive known gnathostomes, distinguished from all others by the complete development of the pre-hyoidean gill slit. On this basis they are referred to a new grade, the Aphetohyoidea, ranking with the Pisces.

It is shown by a detailed analysis and comparison that the Arthrodira, Antiarchi, Petalichthyida and Rhenanida may be regarded as members of the Aphetohyoidea.

References

Agassiz, L. 1832 *Z. Miner.* p. 149.

— 1835 On the fossil fishes of Scotland. *Rep. Brit. Ass. Edin.* 1834, pp. 646, 647.

— 1844(45) "Recherches sur les poissons fossiles," **1**, 32 and 45.

de Beer, G. R. 1932 On the skeleton of the hyoid arch in Rays and Skates. *Quart. J. Micr. Sci.* **75**, 307–20.

de Beer, G. R. and Moy-Thomas, J. A. 1935 On the skull of the Holocephali. *Philos. Trans.* B, **224**, 287–312.

Beyrich, E. 1848 Ueber *Xenacanthus decheni* etc. *S.B. preuss. Akad. Wiss.* pp. 24–33.

Broili, F. 1929 Acanthaspiden aus dem rheinischen Unterdevon. *S.B. bayer. Akad. Wiss.* pp. 143–63.

— 1930*a* Neue Beobachtungen an Lunaspis. *S.B. bayer. Akad. Wiss.* pp. 47–51.

— 1930*b* Über *Gemündina Stürtzi* Traq. *Abh. bayer. Akad. Wiss.* N.F. **6**, 1–24.

— 1933*a* Weitere Fischreste aus den Hunsrückschiefern. *S.B. bayer. Akad. Wiss.* pp. 269–313.

— 1933*b* Ein Macropetalichthyide aus den Hunsrückschiefern. *S.B. bayer. Akad. Wiss.* pp. 417–37.

Brotzen, F. 1934*a* Erster Nachweis von Unterdevon in Ostseegebiete durch Konglomeratgeschiebe mit Fischresten. *Z. Geschiebeforsch.* **10**, 1–65.

— 1934*b*. Die Morphologie und Histologie der Proostea- (Acantodiden) Schuppen. *Ark. Zool.* **26** A, 1–27.

Brough, J. 1935 On the structure and relationships of the Hybodont Sharks. *Manchester Memoirs*, **79**, 35–48.

Davis, J. W. 1895 On the Fossil fish remains of the Coal Measures of the British Isles. Acanthodidae. *Trans. Roy. Dublin Soc.* **5**, 249–58.

Dean, B. 1907 Notes on Acanthodian sharks. *Amer. J. Anat.* **7**, 209–22.

Egerton, P. de M. G. 1860 *Acanthodes mitchelli. Rep. Brit. Ass.* 1859, Trans. Sec. p. 116.

— 1861 *Acanthodes mitchelli, Ischnacanthus gracilis, Brachyacanthus scutiger, Cheiracanthus latus. Mem. Geol. Survey*, **10**.

Eastman, C. R. 1900 Dentition of some Devonian Fishes. *J. Geol.* **8**, 32–41.

Gegenbaur, C. 1872 "Untersuchungen zur Vergleichenden Anatomie der Wirbelthiere", 3. Heft, "Das Kopfskelet der Selachier". Leipzic.

Goodrich, E. S. 1909 "Vertebrata craniata." In Lankester's "Treatise of Zoology". London.

Gross, W. 1933 Die Wirbeltiere des rheinischen Devons. *Abh. preuss. geol. Landesanst.* N.F. Heft 154, pp. 1–84.

Hancock, A. and Atthey, T. 1869 Notes on the remains of some reptiles and fishes from the shales of the Northumberland coal field. *Nat. Hist. Trans. Newcastle*, **3**, pt. I, pp. 66–120 (Acanthodopsis, p. 103).

Heintz, A. 1929 *Skr. Svalb. og Ishavet*, No. 22, pp. 7–81.

— 1931 Revision of the structure of *Coccosteus decipiens* Ag. *Norsk geol. Tidsskr.* **12**, 291–313.

— 1932 "The structure of *Dinichthys*." Bashford Dean Memorial volume. *Amer. Mus. Nat. Hist.* pp. 115–224.

— 1934 Revision of the Esthonian Arthrodira, Pt. 1. Homosteus. *Arch. Naturk. Liv-, Esth- u. Kurl.* (1), **10**, 4–115.

Holmgren, N. and Stensio, E. A. 1936 Kranium und Visceralskelett der Akranier Cyclostomen und Fische. *Handb. Vergl. Anat. von Bolk.* Berlin u. Wien.

Jaekel, O. 1925 Das Mundskelett der Wirbeltiere. *Morph. Jb.* **55**, pp. 402–84.

Kner, R. 1868 Über *Conchopoma* und *Acanthodes* aus dem Rothliegenden von Lebach. *S.B. Akad. Wiss. Wien*, 1. Abt. pp. 3–28.

Moy-Thomas, J. A. 1935*a* The structure and affinities of *Chondrenchelys problematica* Tr. *Proc. Zool. Soc. Lond.* pp. 391–403.

— 1935*b* On the Carboniferous shark *Petrodus patelliformis* M'Coy. *Proc. Leeds Phil. Soc.* **3**, 68–72.

Newberry, J. S. 1889 The Palaeozoic Fishes of North America. *U.S. Geol. Survey Monogr.* **16**.

Powrie, J. 1864 On the fossiliferous rocks of Forfarshire and their contents. *Quart. J. Geol. Soc.* **20**, 413, 429.

— 1870 On the earliest known vestiges of vertebrate life. *Trans. Edinb. Geol. Soc.* **1**, 284–301.

Reis, O. M. 1895 Illustrationen zur Kenntnis des Skeletts von *Acanthodes Bronnii* Ag. *Abh. senckenb. naturf. Ges.* **19**, 49–64.

— 1896 Ueber *Acanthodes Bronnii* Ag. *Morphol. Arb.* von G. Schwalbe, **6**, 143–220.

Roemer, F. 1857 Ueber Fisch- und Pflanzenführende Mergelschiefer des Rothliegenden bei Klein-Neundorf. *Z. dtsch. geol. Ges.* **9**, 51–83.

Romer, A. S. and Grove, B. H. 1935 Environment of the early Vertebrates. *Amer. Midl. Nat.* **16**, 805–62.

Stensio, E. A. 1925 On the head of the *Macropetalichthyids*. *Field Mus. Publ. Geol. Series*, **4**, 87–197.

— 1927 The Downtonian and Devonian Vertebrates of Spitzbergen. Cephalaspidae. *Skr. om Svalb. og Nordishavet.* **12**, Norske Vidensk.-Akad. Oslo.

— 1931 Upper Devonian Vertebrates from East Greenland. *Medd. Grønland*, **86**, 5–212.

— 1934 On the heads of certain Arthrodires. *K. svenska VetenskAkad. Handl.* **13**, 1–79.

Thomson, J. 1870 On a specimen of *Acanthodes Wardi* Eg. from the Lanarkshire Coalfield. *Trans. Glasg. Geol. Soc.* **4**, 57–9.

Traquair, R. H. 1888 Notes on the nomenclature of the fishes of the Old Red Sandstone of Great Britain. *Geol. Mag.* Dec. 3, **5**, 507–17.

— 1893 Notes on the Devonian Fishes of Campbellton and Scaumenac Bay in Canada, No. 2. *Geol. Mag.* Dec. 3, **10**, 145–9.

— 1894 On a new species of *Diplacanthus*, with remarks on the Acanthodian shoulder-girdle. *Geol. Mag.* Dec. 4, **1**, 254–7.

— 1896 The extinct Vertebrata of the Moray Firth area. From J. A. Harvie-Brown and T. E. Buckley. "Vertebrate Fauna of the Moray Basin." Edinburgh.

— 1900 On *Cladodus neilsoni*. *Trans. Geol. Soc. Glasg.* **11**, 41–50.

— 1903 The Lower Devonian fishes of *Gemünden*. *Trans. Roy. Soc. Edinb.* **40**, 723–39.

Troschel, F. H. 1857 Beobachtungen über die Fische in den Eisennieren des Saarbrücker Steinkohlengebirges. *Verh. naturh. Ver. preuss. Rheinl.* N.F. 4th year, pp. 1–19.

Watson, D. M. S. 1934 The interpretation of Arthrodires. *Proc. Zool. Soc. Lond.* pp. 437–64.

Woodward, A. S. 1891 *Cat. Fossil Fishes. Brit. Mus.* (*Nat. Hist.*), Part II.

— 1915 The use of fossil fishes in Stratigraphical geology. *Proc. Geol. Soc.* **71**, lxiii–lxxv.

— 1917 Note on *Plectrodus*, the jaw of an Upper Silurian Fish. *Geol. Mag.* Dec. 6, **4**, 74–5.

— 1921 Observations on some extinct Elasmobranch fishes. *Proc. Linn. Soc. Lond.* pp. 29–39.

— 1924 A Hybodont shark (*Tristychius*). *Quart. J. Geol. Soc.* **80**, 338–42.

— 1935 The affinities of the Acanthodian and Arthrodiran fishes. *Ann. Mag. Nat. Hist.* (10), **15**, 392.

Description of Plates 5–14

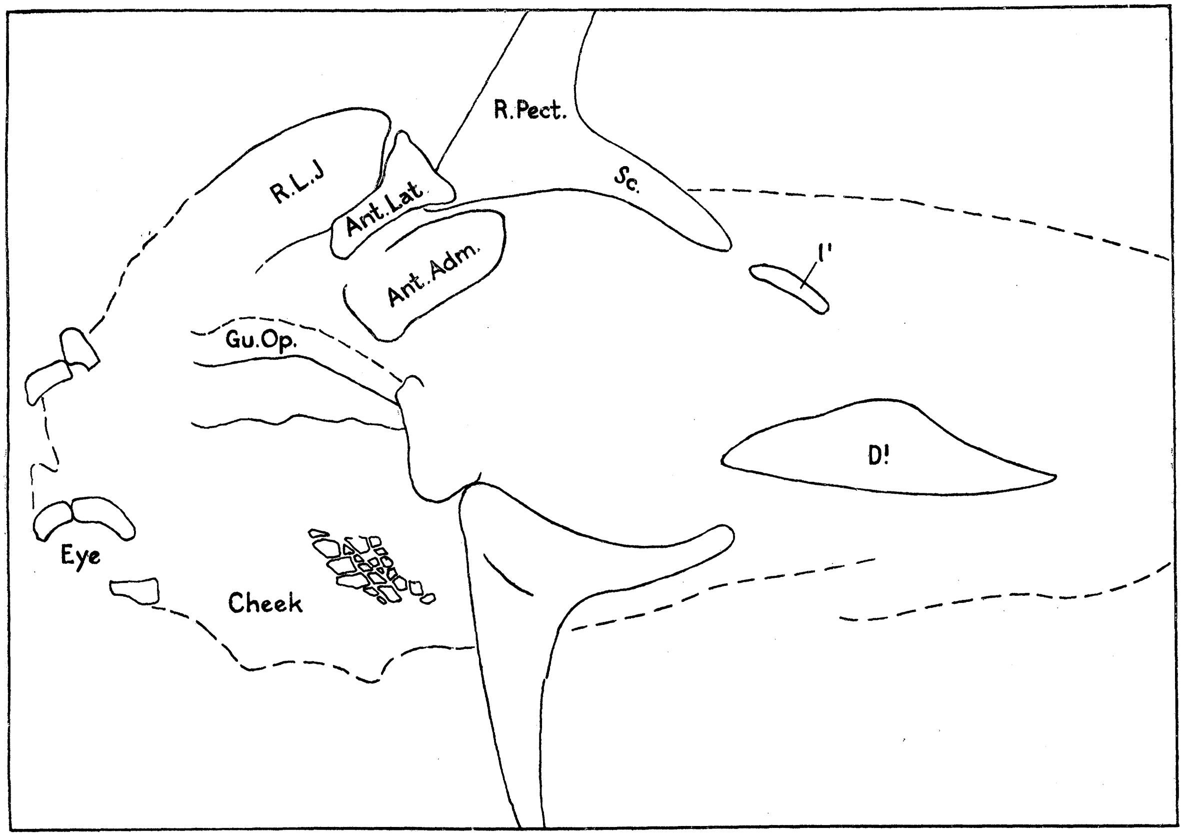
All the photographs reproduced in these plates are unretouched enlargements from negatives taken from specimens which, except in the case of some figures of *Acanthodes*, have had no treatment designed to emphasize structures. They are thus evidence to which reference can be made.

Plate 5

Fig. 1—*Climatius reticulatus* Ag. The head and anterior part of the body, L.O.R.S., Turin Hill. Royal Scottish Museum, Powrie 1891, 92, 198. Ventral surface, the cheek of the left side being exposed. × 1·4.

Fig. 2—*Climatius reticulatus*, the counterpart of the original of fig. 1., B.M.N.H., No. 38596. × 1·4. The dorsal surface of the head, and the cheek, lower jaw and branchial arches of the right side are seen from the inner surface.

Ant.Adm. anterior admedian dermal bone of shoulder girdle; *Ant.Lat.* anterior lateral of shoulder girdle; *Br.Ar.* I, II, etc. the dermal elements of the branchial arches and their opercula; *Circ.Orb.* circum orbital series; *D.Endo Lym.* foramen for the ductus endolymphaticus; D^1, dorsal fin spine; *Eye*, the orbit; *Gu.Op.* gular operculum; *Hy.Op.* hyoid operculum; I^1, first intermediate spine; *L.L.* lateral-line; *L.Pect.* left pectoral spine; *Mand.* mandible; *Mand.Ray*, a "ray" in the mandibular operculum; *R.L.J.* right lower jaw; *R.Pect.* right pectoral spine; *Sc.* scapula.


R.Pect.
R.L.J
Ant.Lat.
Sc.
Ant.Adm.
I'
Gu.Op.
D!
Eye
Cheek

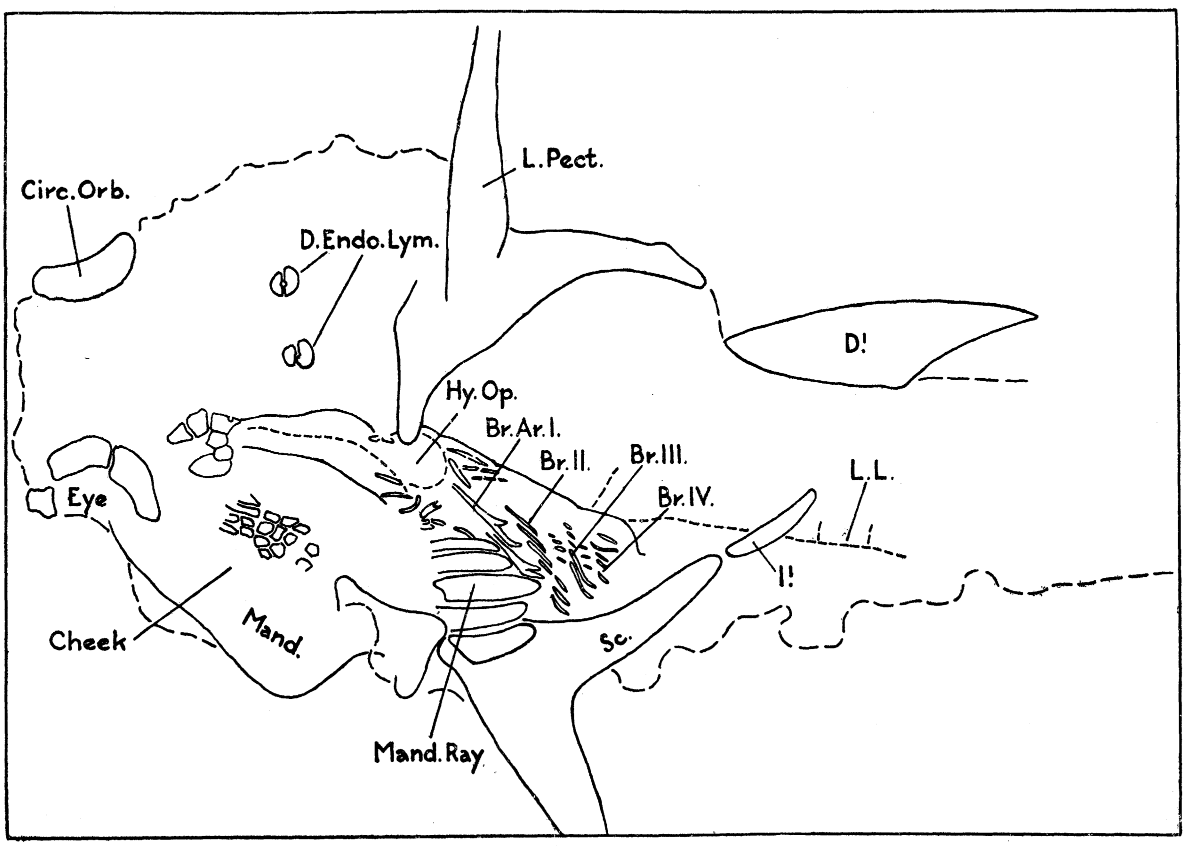

L.Pect.
Circ.Orb.
D.Endo.Lym.
D!
Hy.Op.
Br.Ar.I.
Br.II.
Br.III.
L.L.
Br.IV.
Eye
I!
Cheek
Mand.
Sc.
Mand.Ray

Fig.1.

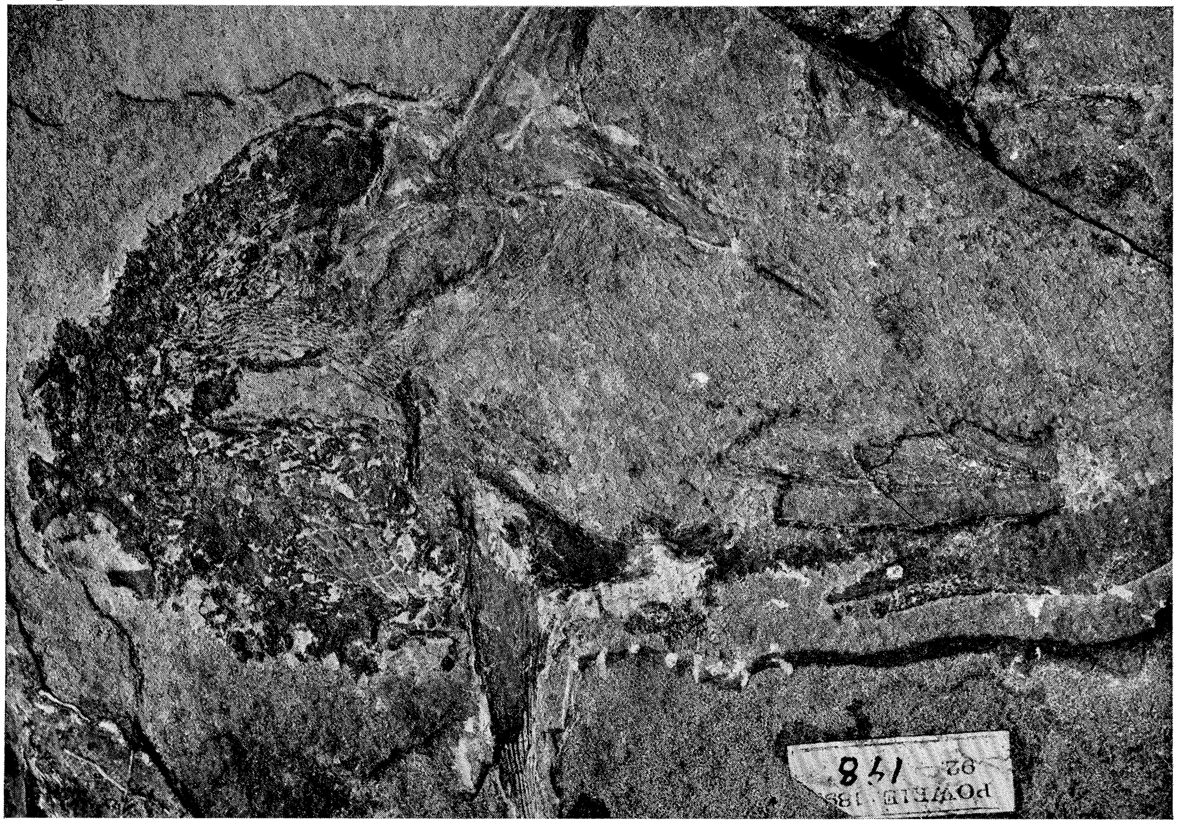


Fig. 2

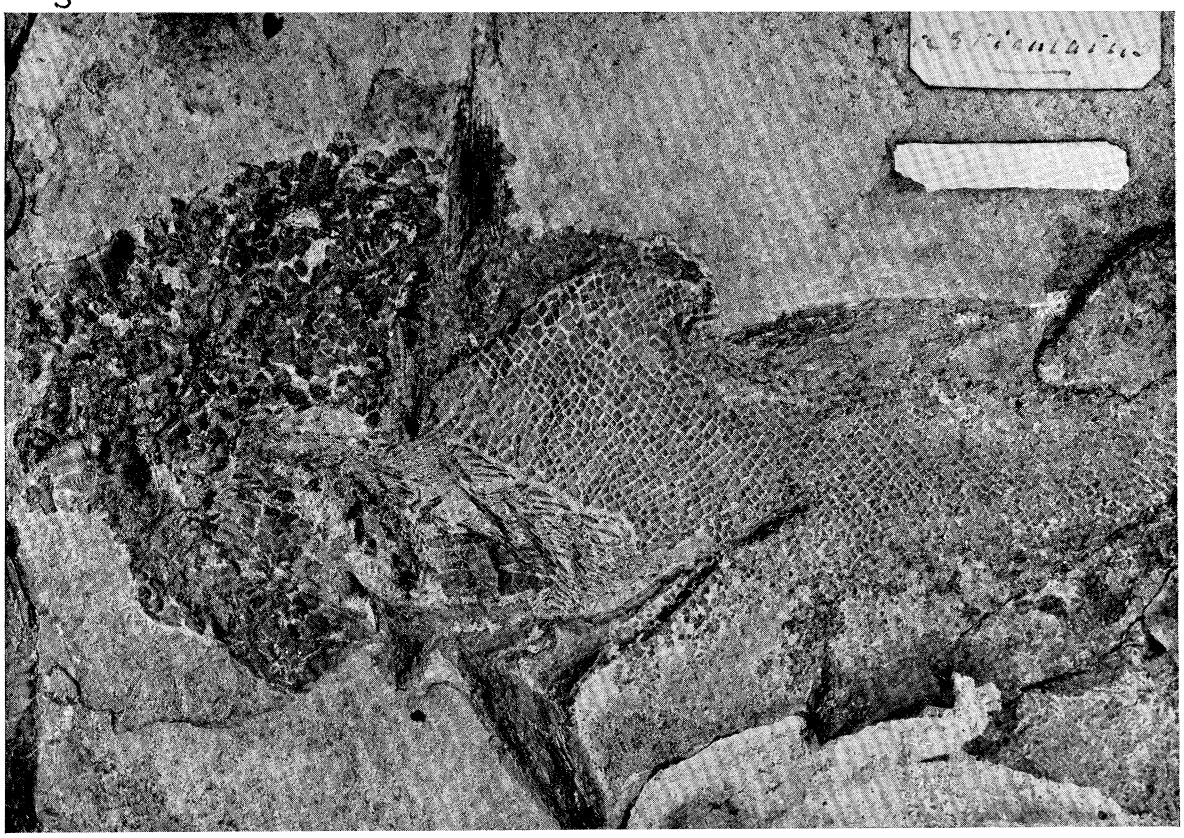


Fig. 1.

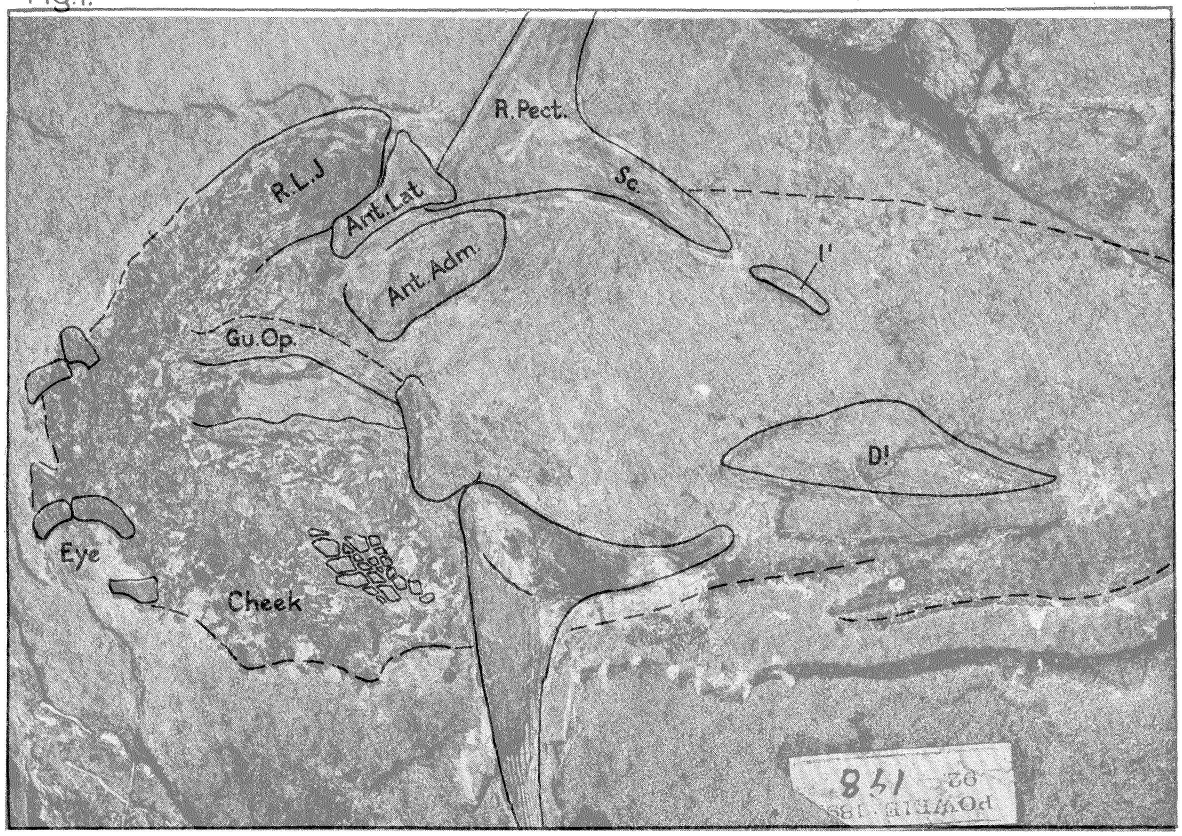

R.Pect.
R.L.J
Ant.Lat.
Sc.
Ant.Adm.
I'
Gu.Op.
D!
Eye
Cheek

Fig. 2

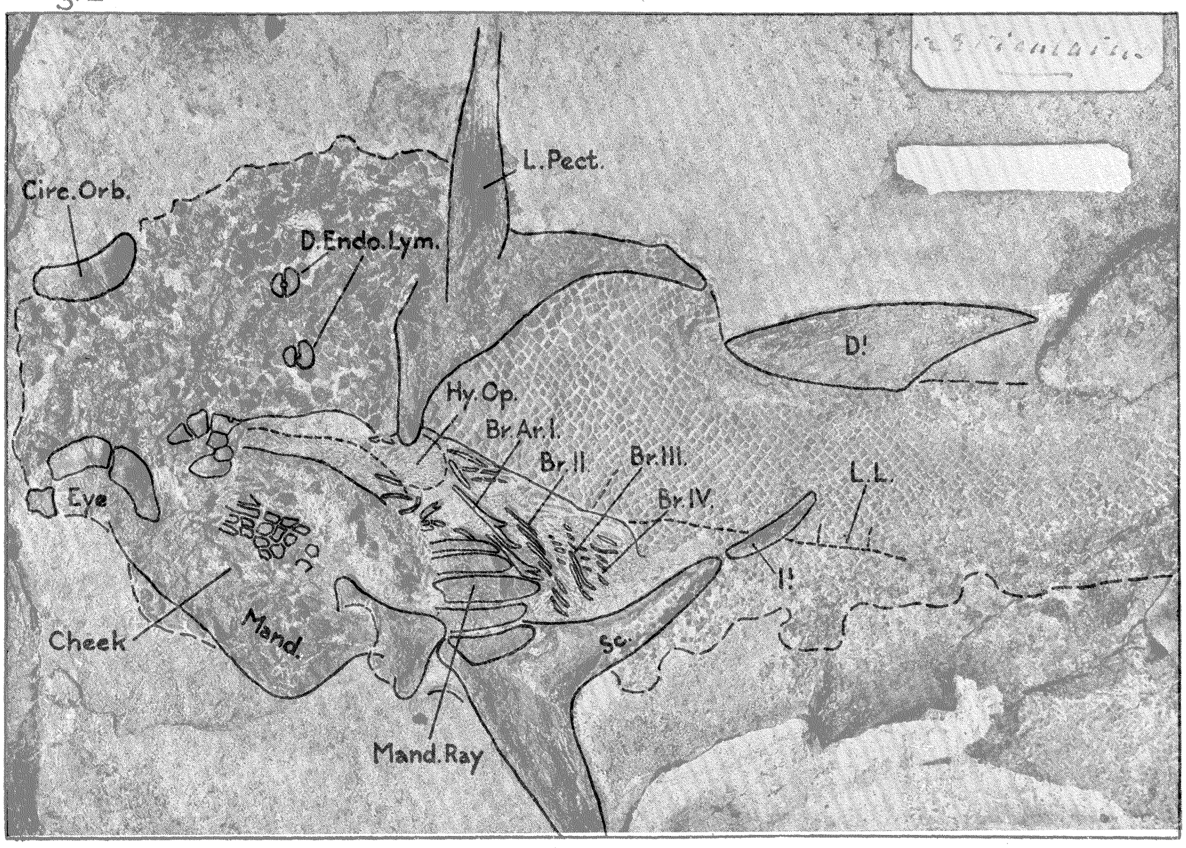

L.Pect.
Circ.Orb.
D.Endo.Lym.
D!
Hy.Op.
Br.Ar.I.
Br.II.
Br.III.
Br.IV.
L.L.
Eye
I!
Cheek
Mand.
Sc.
Mand.Ray

PLATE 6

FIG. 1—*Climatius reticulatus*, L.O.R.S. Turin Hill. Manchester Museum, L. 12096. × 0·75. Complete fish, the head viewed from below, the body in lateral aspect.

FIG. 2—*Climatius reticulatus*, the head of fig. 1, enlarged. × 1·72.

FIG. 3—*Climatius reticulatus*, L.O.R.S. Turin Hill. Royal Scottish Museum, Powrie 1891, 92, 206. × 1·24. The head and shoulder girdle viewed from below. The snout is well shown.

FIG. 4—*Brachyacanthus scutiger* EG., L.O.R.S. Farnell. Royal Scottish Museum, Powrie 1891, 92, 220. × 3·0. Impression of the left side of the anterior part of the fish, with dark fragments of bone left in the deeper hollows.

Anal, anal fin; *Br.* I, II, III, dermal bones of the branchial arches and their opercula; *Caud.* extremity of the tail; D^1, D^2, the dorsal fins; *Eye*, orbit; *Hy.Op.* hyoid operculum; I^1, I^2, etc. intermediate fins; *L.L.* lateral-line; *L.Pect.* left pectoral fin; *M.S.* median dermal bone of shoulder girdle; *Mand.Ray*, a "ray" of the mandibular operculum; *Mand. Teeth*, the whorls of teeth on the mandible; *Med.Sc.* median scutes; *P.Q.* palato-quadrate; *Pect.* pectoral spine; *Pelv.* pelvic fin; *R.* ridged bone of shoulder girdle; *R.Pect.* right pectoral fin; *Sc.* scapula.

Fig. 1.

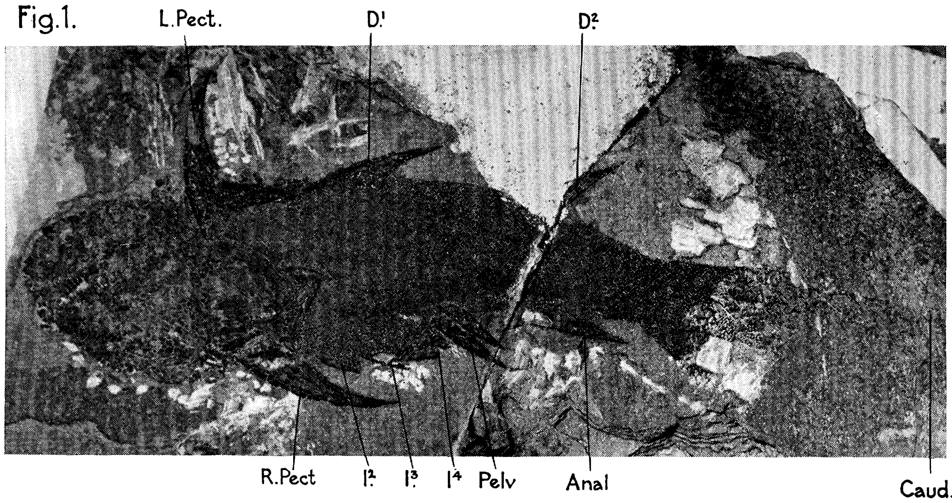


Fig. 3.

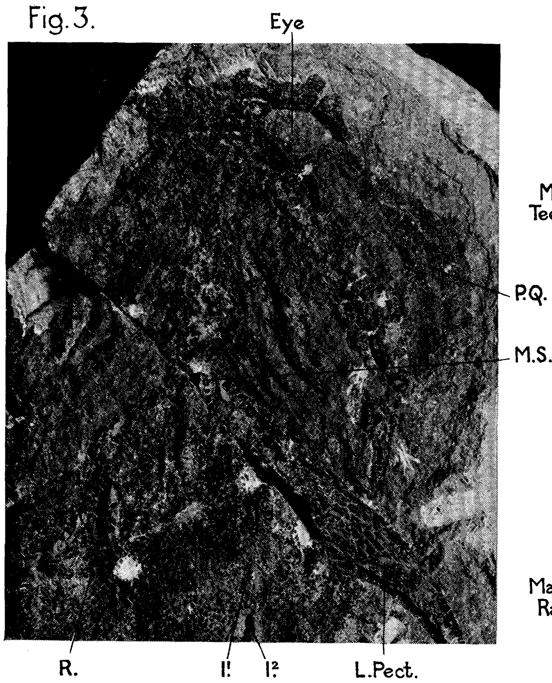


Fig. 2.

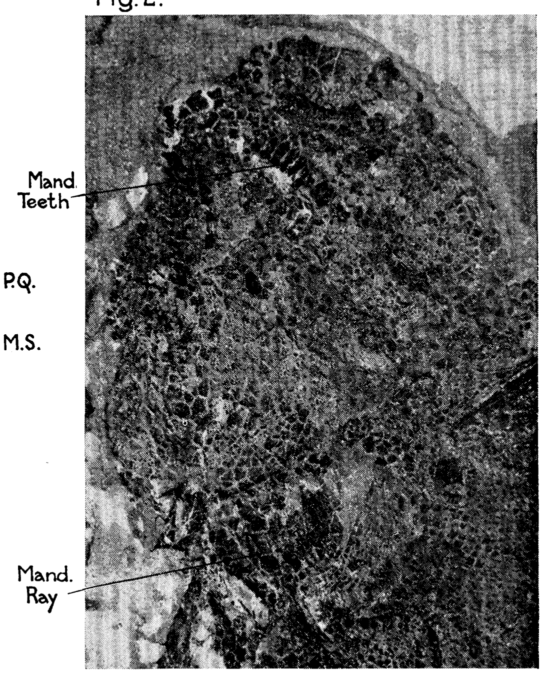


Fig. 4.

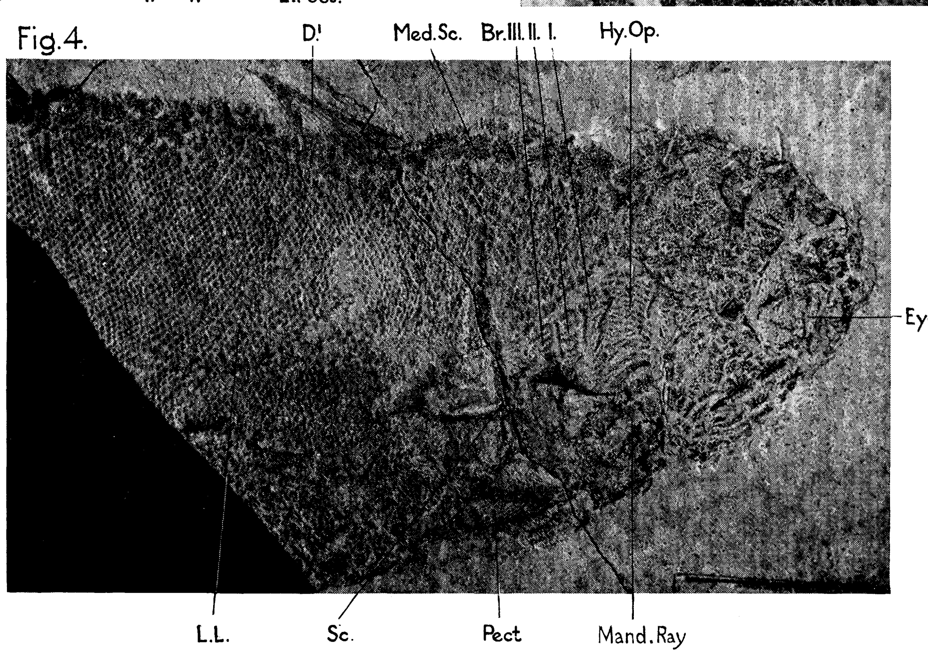


Plate 7

Fig. 1—*Euthacanthus macnicoli* Powrie. Type specimen, L.O.R.S. Turin Hill. Royal Scottish Museum, Powrie 1891, 92, 251. × 1·0. The whole fish seen from the left side.

Fig. 2—*Euthacanthus macnicoli*. The head of fig. 1 enlarged. × 3·45.

Anal. anal fin; *Br.Ar.* I, II, III, the dermal bones in the branchial arches and their opercula; D^1, D^2, the dorsal fin spines; *Eye*, orbit; *Gu.* gular mandibular rays; *Hy.* hyoid; I^1–I^5, the intermediate fin spines; *L.L.* lateral-line; *Mand.C.* mandibular canal; *Mand.Ray*, a "ray" of the mandibular operculum; *Or.C.* oral canal; *P.Op.C.* preopercular canal; *Pect.* pectoral fin; *Pelv.* pelvic fin; *Sc.* scapula.

Fig. 1.

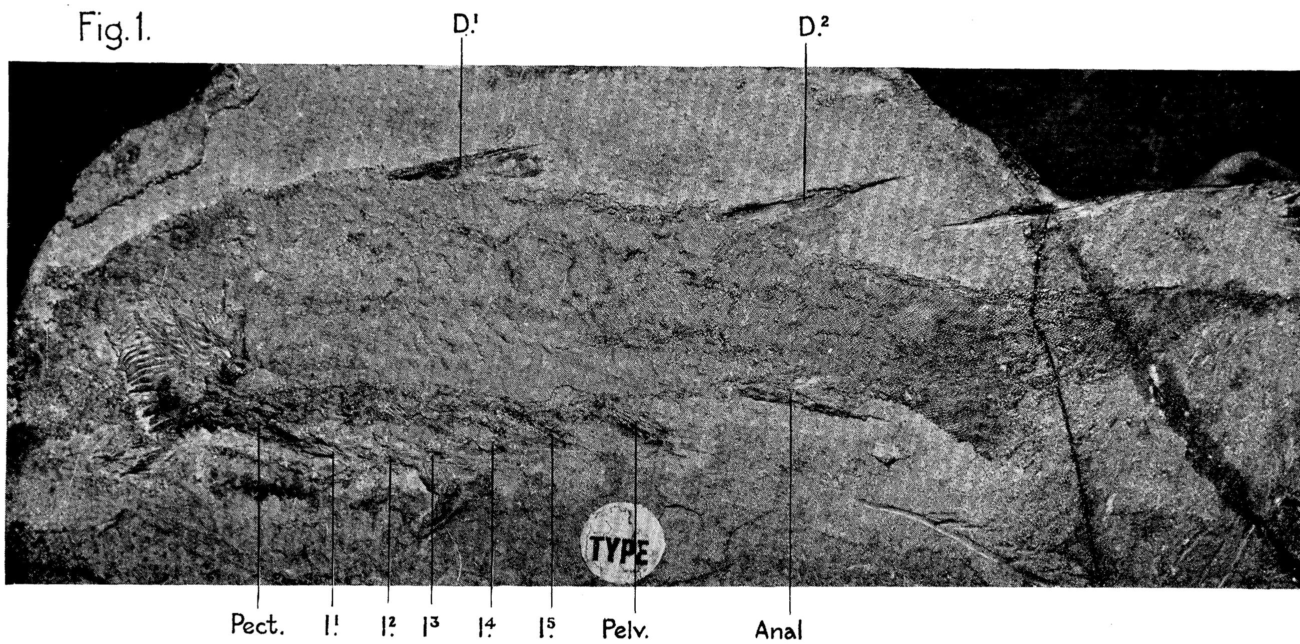

D.[1]
D.[2]
TYPE
Pect.
l.[1]
l.[2]
l[3]
l.[4]
l.[5]
Pelv.
Anal

Fig. 2.

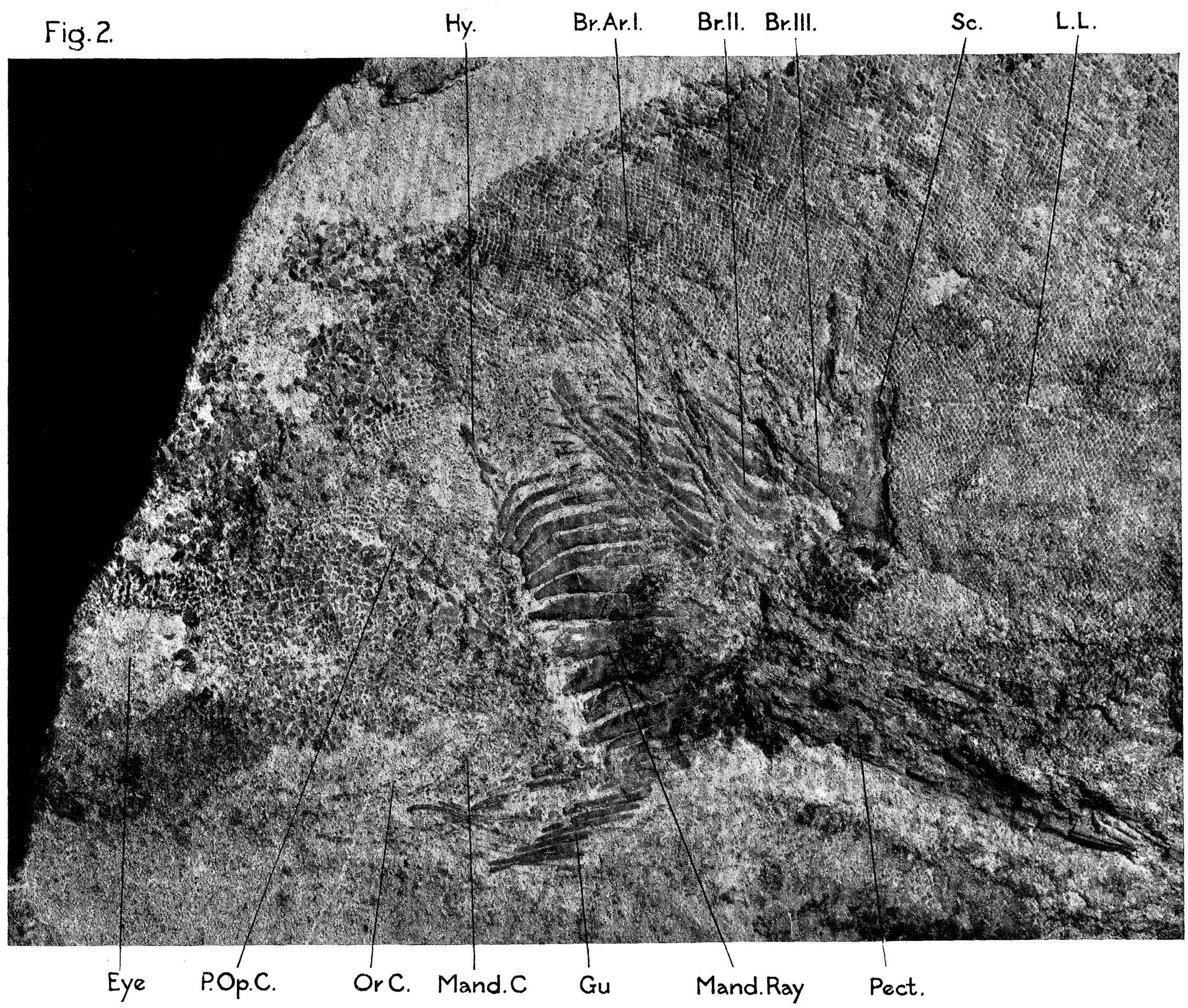

Hy.
Br.Ar.I.
Br.II.
Br.III.
Sc.
L.L.
Eye
P.Op.C.
Or C.
Mand.C
Gu
Mand.Ray
Pect.

PLATE 8

FIG. 1—*Mesacanthus mitchelli* EG., L.O.R.S. Turin Hill. Royal Scottish Museum, Powrie 1891, 92, 275. × 2·5. A complete young individual from its right side.

FIG. 2—*Mesacanthus mitchelli*, L.O.R.S. Turin Hill. D.M.S.W. Coll., P. 473. × 4·7. Left side of the head of an adult.

FIG. 3—*Mesacanthus mitchelli*, L.O.R.S. Turin Hill. Royal Scottish Museum, 1881, 5, 80. × 3·6. Left side of the head, the palato-quadrate, Meckel's cartilage, and the mandibular operculum well shown.

FIG. 4—*Mesacanthus mitchelli*, the head of fig. 1, further enlarged. × 3·8. Shows especially well the hyoid arch and its operculum.

FIG. 5—*Mesacanthus mitchelli*, L.O.R.S. Turin Hill. Royal Scottish Museum, Powrie 1891, 92, 277. × 3·8. Left side of the head.

Anal, anal fin; *Br.* I, II, III, dermal bones in the branchial arches; *Eye*, orbit; *Gu.* gular mandibular ray; *Hy.* hyoid; *Hy.Op.* hyoid operculum; *I.* intermediate fin; *L.L.* lateral-line; *Mand.Ant.* anterior bone in Meckel's cartilage; *Mand.Post.* posterior bone in Meckel's cartilage; *Mand.Ray*, a "ray" in the mandibular operculum; *Mand.Spl.* mandibular splint; *Otolith*; *P.Q.Post.* posterior bone in the palato-quadrate; *Pect.* pectoral fin; *Pelv.* pelvic fin; *Sc.* scapula; *V.L.L.* ventral lateral-line.

Fig.1.

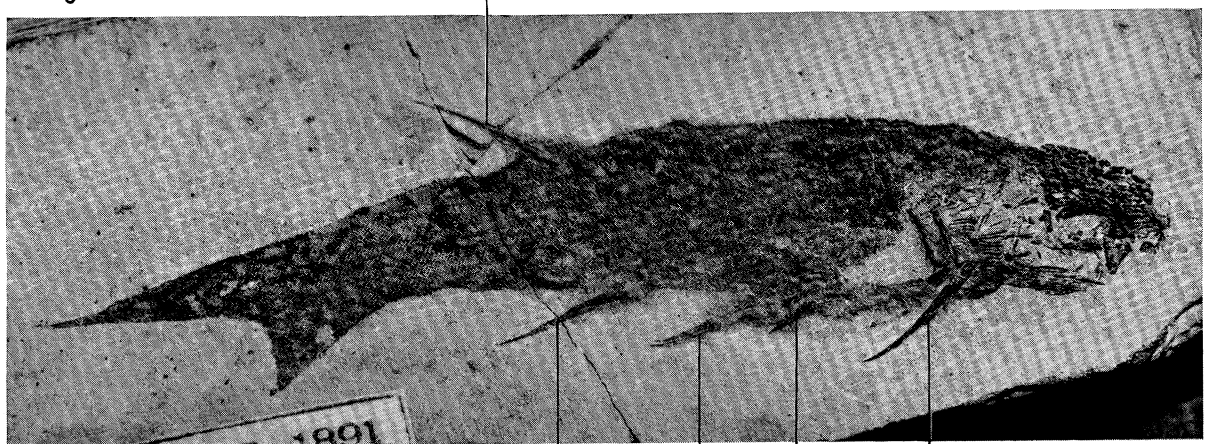


Fig.2.

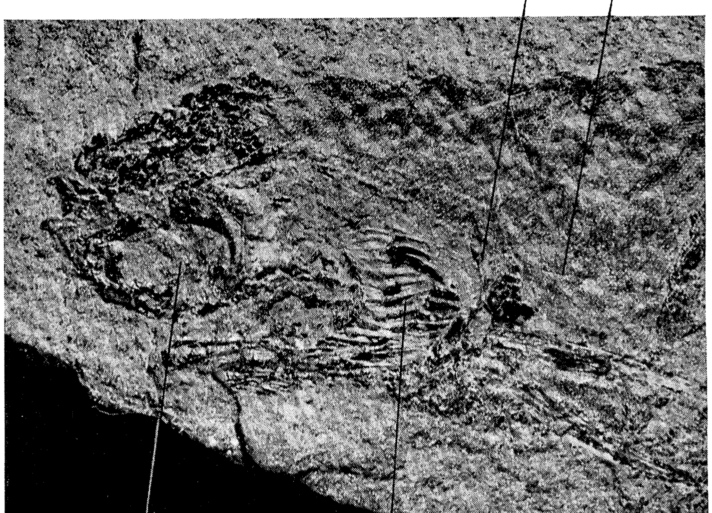


Fig.3.

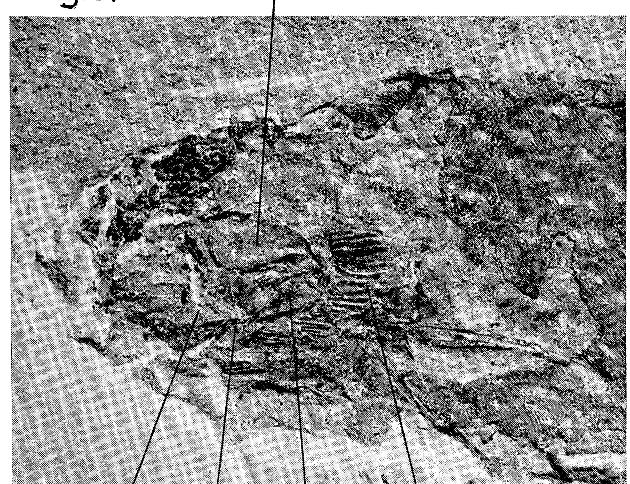


Fig.4

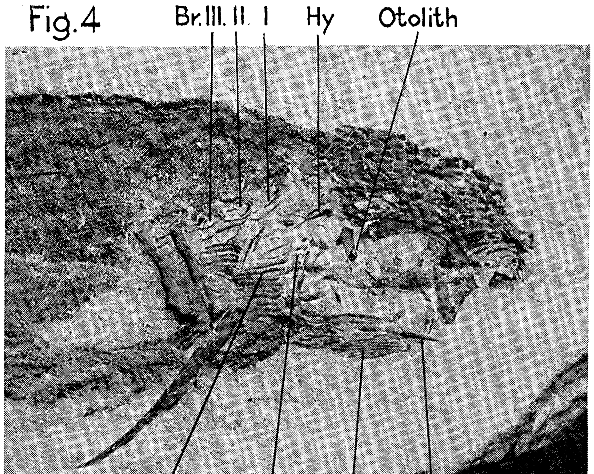


Fig.5.

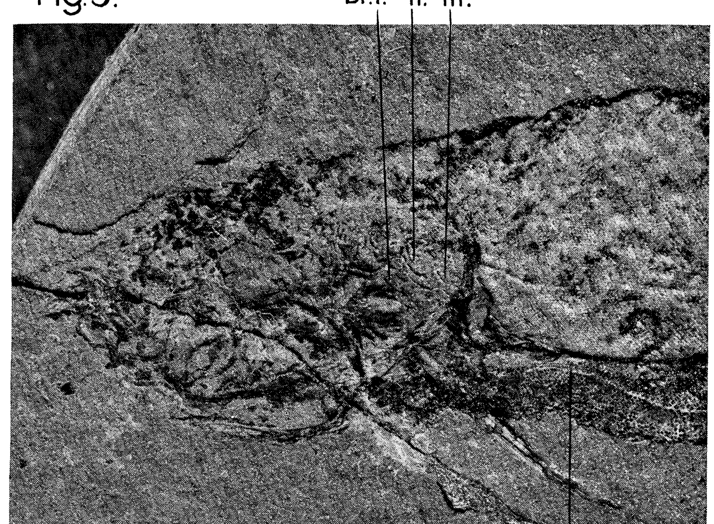


PLATE 9

FIG. 1—*Ischnacanthus gracilis* EG., L.O.R.S. Turin Hill, B.M.N.H. 46305. ×2·0. Left aspect of a small fish lacking the tail.

FIG. 2—*Ischnacanthus gracilis* EG., L.O.R.S. Turin Hill, Royal Scottish Museum, 1887, 35, 2. ×2·4. Left side of the head of a large individual.

FIG. 3*a*—*Ischnacanthus gracilis* EG., L.O.R.S. Turin Hill, D.M.S.W. Coll., P. 478. ×1·4. Isolated lower jaws seen from the lingual sides, and left posterior palato-quadrate from its palatal surface.

FIG. 3*b*—The right posterior palato-quadrate bone of the specimen in Fig. 3*a*, from its outer surface. ×1·4.

FIG. 4—*Ischnacanthus gracilis* EG., L.O.R.S. Turin Hill, D.M.S.W. Coll., P. 481. ×2·6. Right side of the head of a small fish.

FIG. 5—*Ischnacanthus gracilis* EG., L.O.R.S. Turin Hill, D.M.S.W. Coll., P. 297. ×1·15. The tail of a medium-sized individual.

Anal, anal fin; *Ant.Mand.D.* fused whorl of symphysis mandibular teeth; D^1, D^2, the dorsal fin spines; *Eth.C.* ethmoidal commissure; *Eye*, orbit; *L.L.* lateral-line; *L.P.Q.* left posterior palato-quadrate; *Mand.Ant.* anterior mandibular ossification; *Mand.C.* mandibular canal; *Mand.Op.* mandibular operculum; *Mand.Post.* posterior bone in the mandible; *Oral.C.* oral canal; *Pect.* pectoral fin spine; *Pelv.* pelvic fin spine; *Sc.* scapula.

Fig. 1.

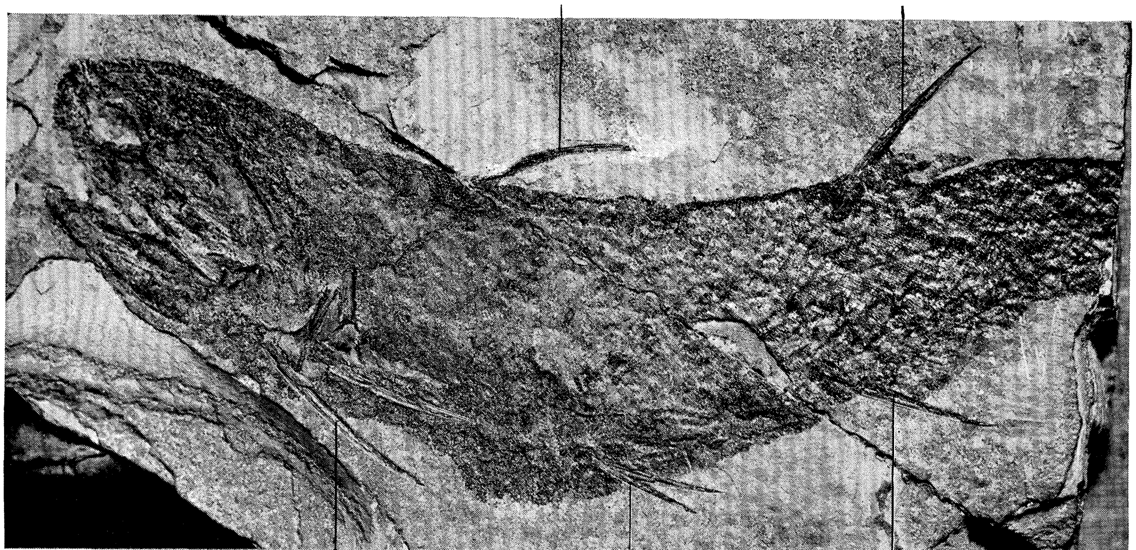


Fig. 2.

Fig. 3a

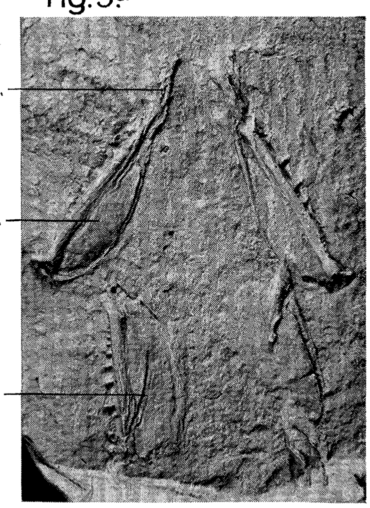


Fig. 3b

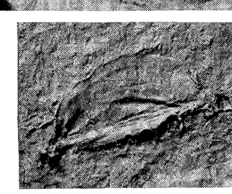


Fig. 4.

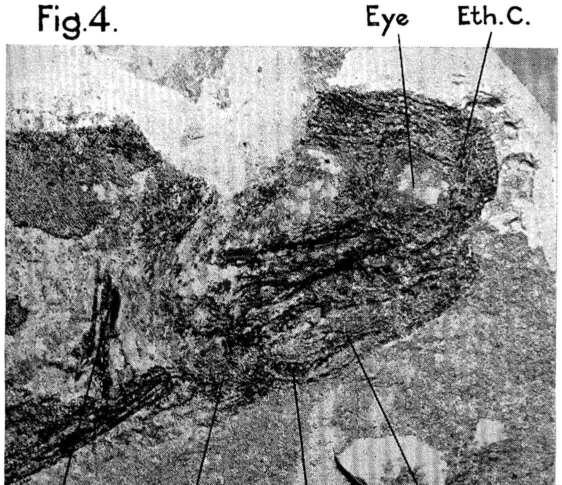


Fig. 5.

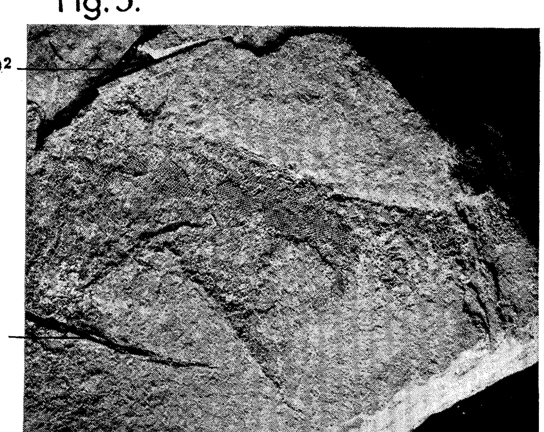


Plate 10

Fig. 1—*Diplacanthus striatus* Ag., M.O.R.S. Tynet Burn, Royal Scottish Museum, Powrie 1891, 92, 334. ×2·2. Left aspect of a fish unique in possessing extensive ossifications in the visceral arches, vertebral column, and basals and radials of the first dorsal fin, and in showing calcified ceratotrichia in the first dorsal and pectoral fins.

Fig. 2—*Diplacanthus striatus* Ag., M.O.R.S. Tynet Burn, D.M.S.W. Coll., P. 299. ×2·3. Complete fish showing the cheek, intergular space, pectoral girdle, fin spines and tail.

Adm.Pect.Sp. admedian pectoral spine; *Anal*, anal fin spine; *Cor.* coracoid; D^1, D^2, the dorsal fin spines; *Eye*, orbit; *I.* intermediate fin spine; *L.L.* lateral-line; *Lat.Pect.Sp.* lateral pectoral spine; *Mand.* ossified Meckel's cartilage; *Mand.Spl.* mandibular splint; *Pelv.* pelvic fin; *Sc.* scapula.

Fig. 1.


D.²
L.L.
D.¹
Anal
Pelv.
I.
Sc.
Mand.
Mand. Spl.

Fig. 2.


D.²
D.¹
Sc.
Eye
Cor.
Mand. Spl.
Anal
Pelv.
I.
Adm. Pect. Sp.
Lat. Pect. Sp.

PLATE 11

FIG. 1—*Diplacanthus striatus*, M.O.R.S. Tynet Burn, D.M.S.W. Coll., P. 300. × 3·0. Anterior part of a fish in which the ventral surface from the lower jaws to the pectoral fins is seen from the outer surface, and the lateral and dorsal surfaces of the head are spread out on the left of the figure, represented mainly by impressions of their inner surfaces. Part of the infilling of the lateral line canals remains.

FIG. 2—*Parexus incurvus* AG., L.O.R.S. Turin Hill, Manchester Museum, L. 12097*b*. × 1·5. A nearly complete fish from the left side.

Adm.Pect.Sp. admedian pectoral spine; *Anal*, anal fin spine; *Cor.* coracoid; D^1, D^2, dorsal fins; *Derm.Pl.* dermal plate of the shoulder girdle; I^1, I^2, I^3, intermediate fin spines; *Inf.Or.C.* infra-orbital canal; *Inf.Or.C.b.* posterior median branch of the infra-orbital canal (STENSIO); *Lat.Pect.Sp.* lateral pectoral fin spine; *Mand.Spl.* mandibular splint; *Oc.C.* occipital cross commissure; "*Op.*" large opercular plate; *P.O.* post-orbital plate; *Pect.* pectoral fin spine; *Pelv.* pelvic fin spine; *Sc.* scapula; *Sup.Or.C.* supra-orbital canal.

Fig. 1.

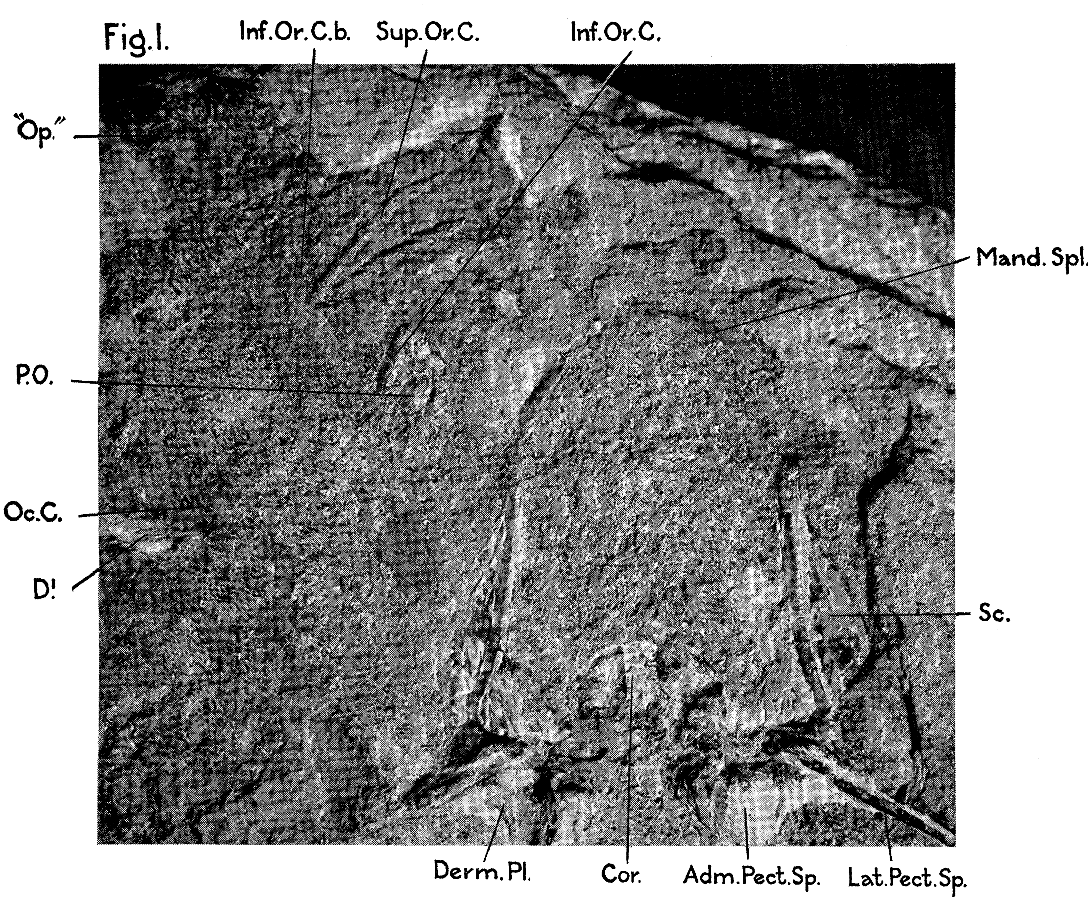

Inf.Or.C.b.
Sup.Or.C.
Inf.Or.C.
"Op."
Mand. Spl.
P.O.
Oc.C.
D!
Sc.
Derm.Pl.
Cor.
Adm.Pect.Sp.
Lat.Pect.Sp.

Fig. 2.

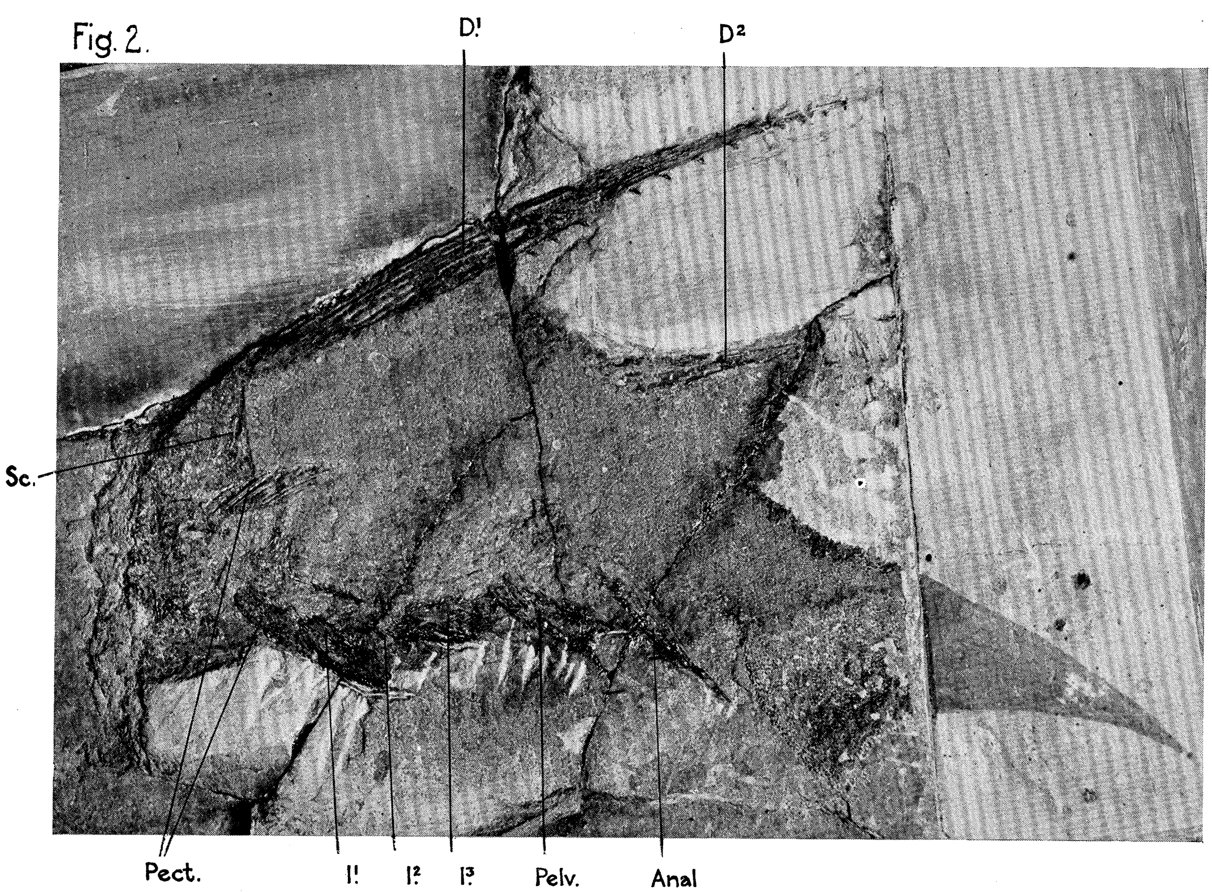

D!
D²
Sc.
Pect.
I!
I²
I³
Pelv.
Anal

PLATE 12

FIG. 1—*Cheiracanthus murchisoni* AG., M.O.R.S. Gamrie, D.M.S.W. Coll., P. 492. ×3·0. Right side of the head showing the mandibular operculum, and lower jaw.

FIG. 2—*Cheiracanthus murchisoni* AG., M.O.R.S. Gamrie, U.C.L. Zoo. Dept., C. 21. ×2·0. Isolated right palato-quadrate from its outer surface.

FIG. 3—*Cheiracanthus murchisoni* AG., M.O.R.S. Tynet Burn, B.M.N.H. 43273*a*. ×2·5. Posterior part of the head to show the mandibular operculum dragged down so as to expose the dorsal end of the hyoid and the slender ossifications in the branchial arches.

FIG. 4—*Cheiracanthus latus* EG., M.O.R.S. Tynet Burn, B.M.N.H., P. 3253. ×1·9. The head, mainly an impression of the right surface.

FIG. 5—*Cheiracanthus latus* EG., M.O.R.S. Tynet Burn, Imperial College, Geol. Dept. ×2·2. The head, mainly an impression of the right surface, showing the row of small bones which forms the border of the mouth, and the jaw elements.

FIG. 6—*Cheiracanthus latus* EG., M.O.R.S. Tynet Burn, D.M.S.W. Coll., P. 509. ×2·4. The right shoulder girdle and pectoral fin spine from without.

Br. I, II, III, dermal bones of the branchial arches; *Circ.Orb.* circumorbital bones; *Cor.* coracoid; *Gu.* gular rays; *Hy.* upper end of the hyoid arch; *L.L.* lateral-line; *Mand.* the ossification in Meckel's cartilage; *Mand.Ray*, a "ray" of the mandibular operculum; *P.B.Art.* palato-basal articulation of the palato-quadrate; *P.Q.* palato-quadrate; *P.Q.Vac.* vacuity in the palato-quadrate; *Pect.* pectoral fin spine; *Sc.* scapula.

Fig. 1.

Fig. 2.

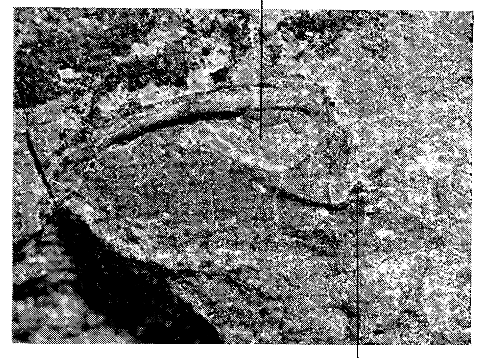


Fig. 3.

Fig. 4.

Fig. 5.

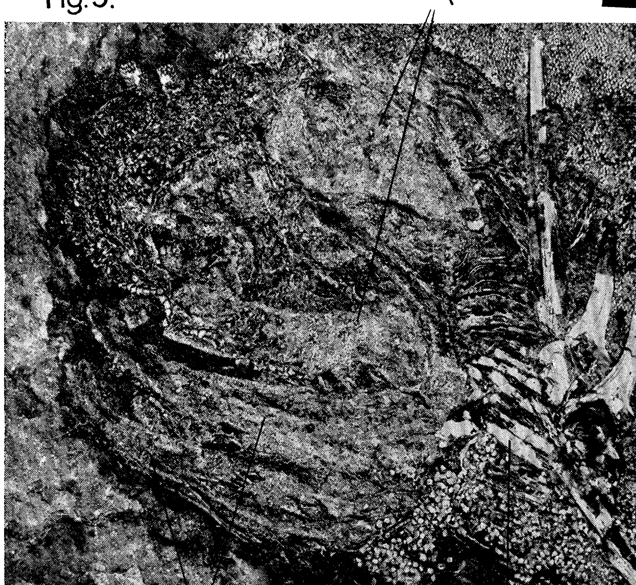


Fig. 6.

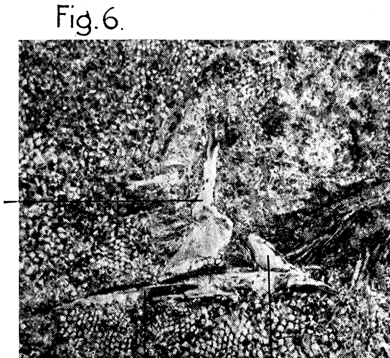


Plate 13

Fig. 1—*Acanthodes Wardi*. M.C.M. Knowles Ironstone, Longton, Staffordshire, Manch. Mus. LL. 181. × 1·4. Fragment of a head showing the series of gill-rakers on the ventral part of the hyoid arch.

Fig. 2—*Acanthodes* sp. Lebach shales. D.M.S.W. Coll., P. 323. × 1·13. Gelatine cast of the head from the left side, showing the left palato-quadrate and lower jaw and other structures.

Fig. 3—*Acanthodes* sp. Lebach shales. D.M.S.W. Coll., P. 495. × 1·25. Gelatine cast of the brain case viewed from below. Cf. text-figs. 17 and 18.

Fig. 4—*Acanthodes* sp. × 1·15. The specimen shown in fig. 3, from the dorsal aspect, a gelatine cast from the counterpart.

Fig. 5—*Acanthodes* sp. Lebach ironstones. D.M.S.W. Coll., P. 498. × 1·42. To show the pectoral fins.

Fig. 6—*Acanthodes* sp. Lebach ironstones. Berlin Museum, unnumbered. × 1·4. The tail of a small individual.

Ant.Bas. anterior basal; *Ant.Os.* anterior bones of the neural cranium; *Dor.Os.* dorsal bone of the neural cranium; *Ep.Hy.* epi-hyoid; *Hy.Gill-raker*, gill-raker on the hyoid arch; *Hyp.For.* hypophysial foramen; *Lat.Oc.* lateral occipital; *Mand.Ant.* anterior bone in Meckel's cartilage; *Mand.Post.* posterior bone in Meckel's cartilage; *Mand.Ray*, a "ray" in the mandibular operculum; *Mand.Spl.* mandibular splint; *M.Bas.* middle basal bone in the neural cranium; *Mes.Pt.* mesopterygium; *Met.Pt.* metapterygium; *Oc.N.* foramina for occipital nerves; *Ot.Pr.Art.* articulation of the otic process; *Pal.Bas.Art.* palato-basal articulation; *Pal.Q.Post.* posterior bone in the palato-quadrate; *Pal.Q.Ot.* otic process of the palato-quadrate; *Ph.Br.* I, first pharyngo-branchial; *Post.Bas.* posterior basal bone in the neural cranium; *Pro.Pt.* propterygium; *Rad.* radial; *X*, notch for the tenth nerve.

Fig. 1.

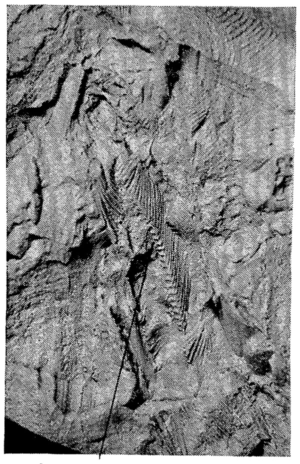


Fig. 2.

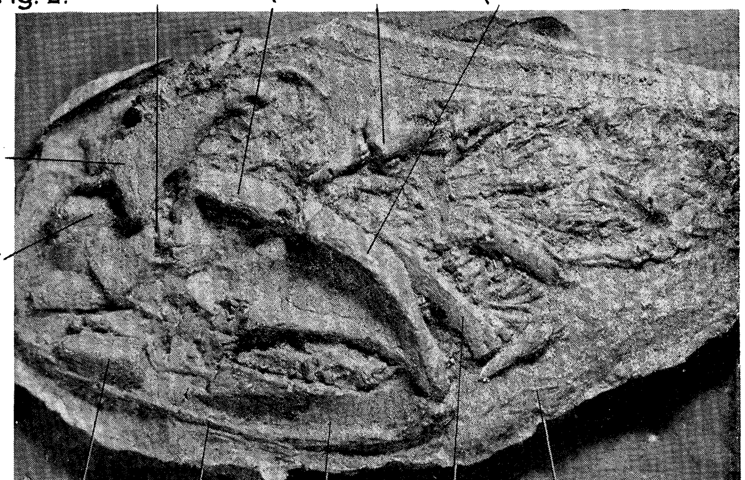


Fig. 3.

Fig. 4.

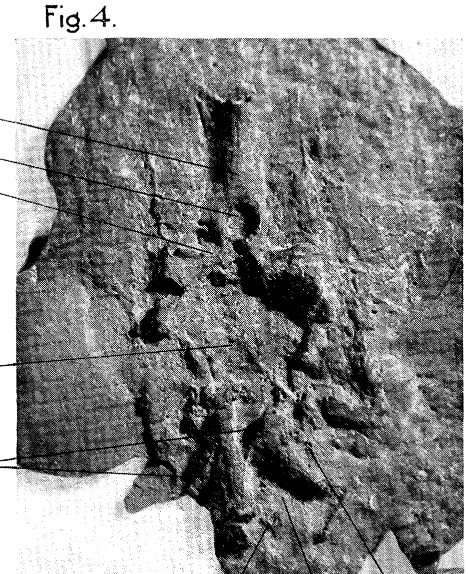


Fig. 5.

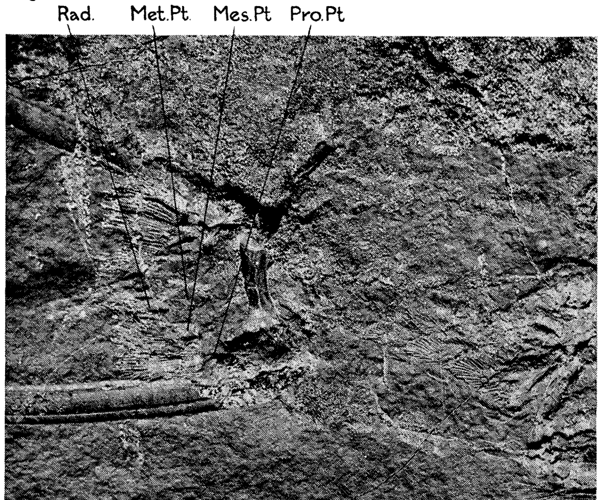


Fig. 6.

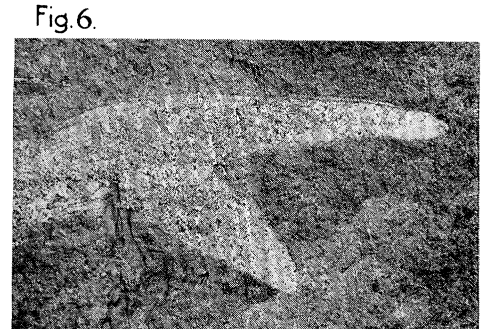


Plate 14

Photographs of medium sized specimens of *Acanthodes* from the Lebach ironstones of the Saar, Lower Permian. It is probable that each specimen is specifically different from the others.

In every figure except 6 some part of the lateral-line system retains in cavities traces of white paint.

Fig. 1—D.M.S.W. Coll., P. 496. ×1·15. Head viewed from the right. Compare text-fig. 20D.

Fig. 2—Royal Scottish Museum 1891, 42, 3. ×1·52. Head viewed from the left.

Fig. 3—D.M.S.W. Coll., P. 498. ×1·2. Head viewed from the right. Compare text-fig. 20C.

Fig. 4—B.M.N.H., No. 22658*a*. ×1·3. Compare text-fig. 20B.

Fig. 5—D.M.S.W. Coll., P. 494. ×1·05. Head viewed from the left. Compare text-fig. 20A.

Fig. 6—Royal Scottish Museum, unnumbered. ×1·08. Head from the left.

Br. I–IV, the branchial arches, usually only represented by the gill-rakers; *Cer.tr.* ceratotrichia; *Cor.* coracoid; *Ear*, the semicircular canals; *Ep.Hy.* epi-hyal; *Eye*; *Gu.* gular rays of the mandibular operculum; *Hy.Gill R.* hyoid gill-raker; *Inf.Or.C.* infra-orbital canal; *L.L.* lateral-line; *L.Sup.Or.C.* left supra-orbital canal; *Mand.Ant.* anterior bone in Meckel's cartilage; *Mand. Post.* posterior bone in Meckel's cartilage; *Mand.Ray*, a "ray" in the mandibular operculum; *Mand.Spl.* mandibular splint; *Op.C.* opercular canal; *P.Op.C.* pre-opercular canal; *P.Q.Ant.* anterior bone in the palato-quadrate; *P.Q.Ot.* otic process of the palato-quadrate; *P.Q.Post.* posterior bone in the palato-quadrate; *Pect.* pectoral fin spine; *Phar.Br.* II, the pharyngobranchial of the second arch; *Sc.* scapula; *Sup.Or.C.* supra-orbital canal; *V.L.L.* ventral lateral-line.

Fig. 1

Fig. 2

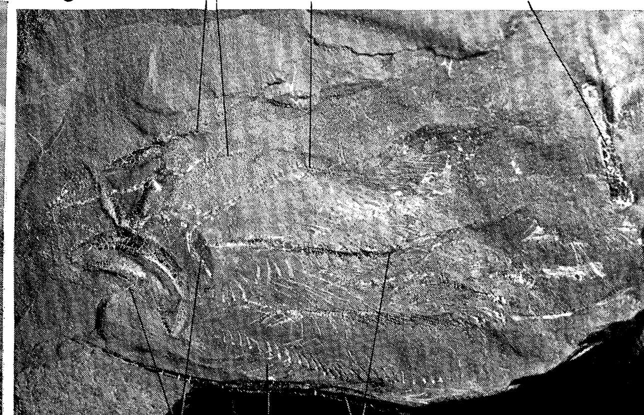


Fig. 3.

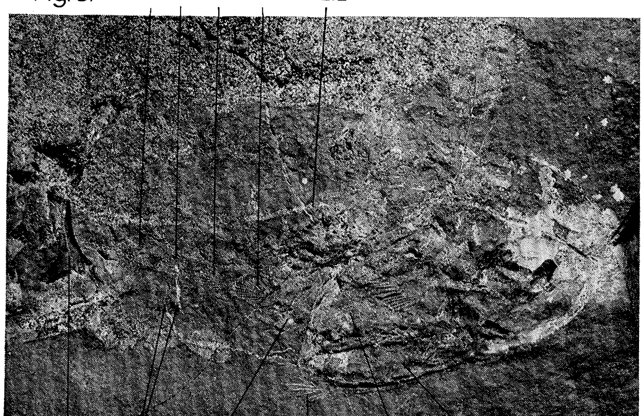


Fig. 4

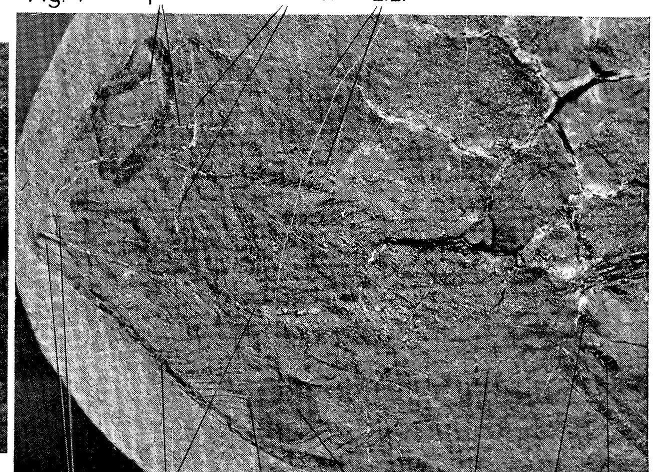


Fig. 5.

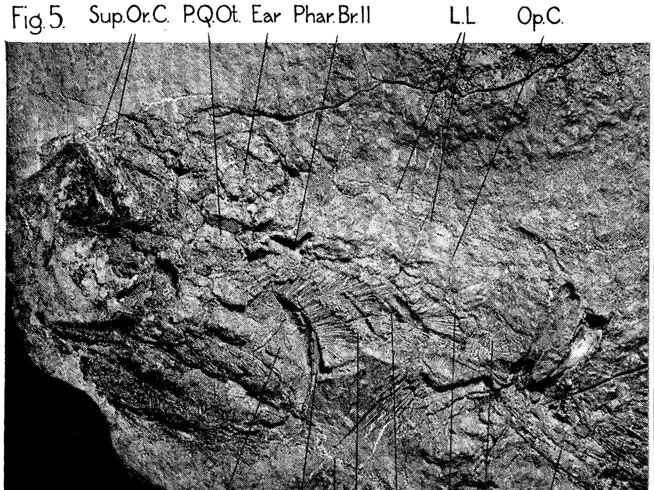


Fig. 6.

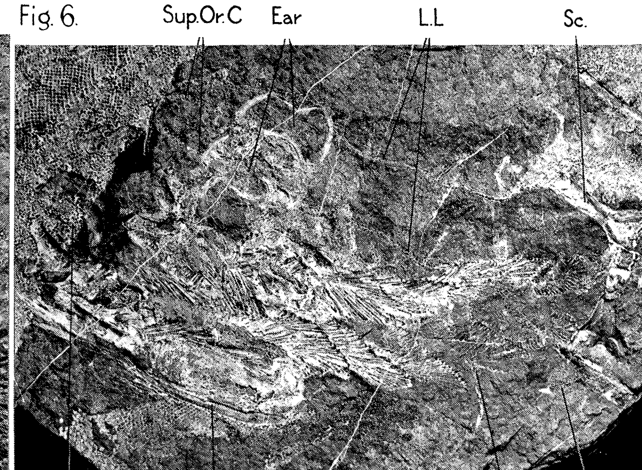


Fig.1.

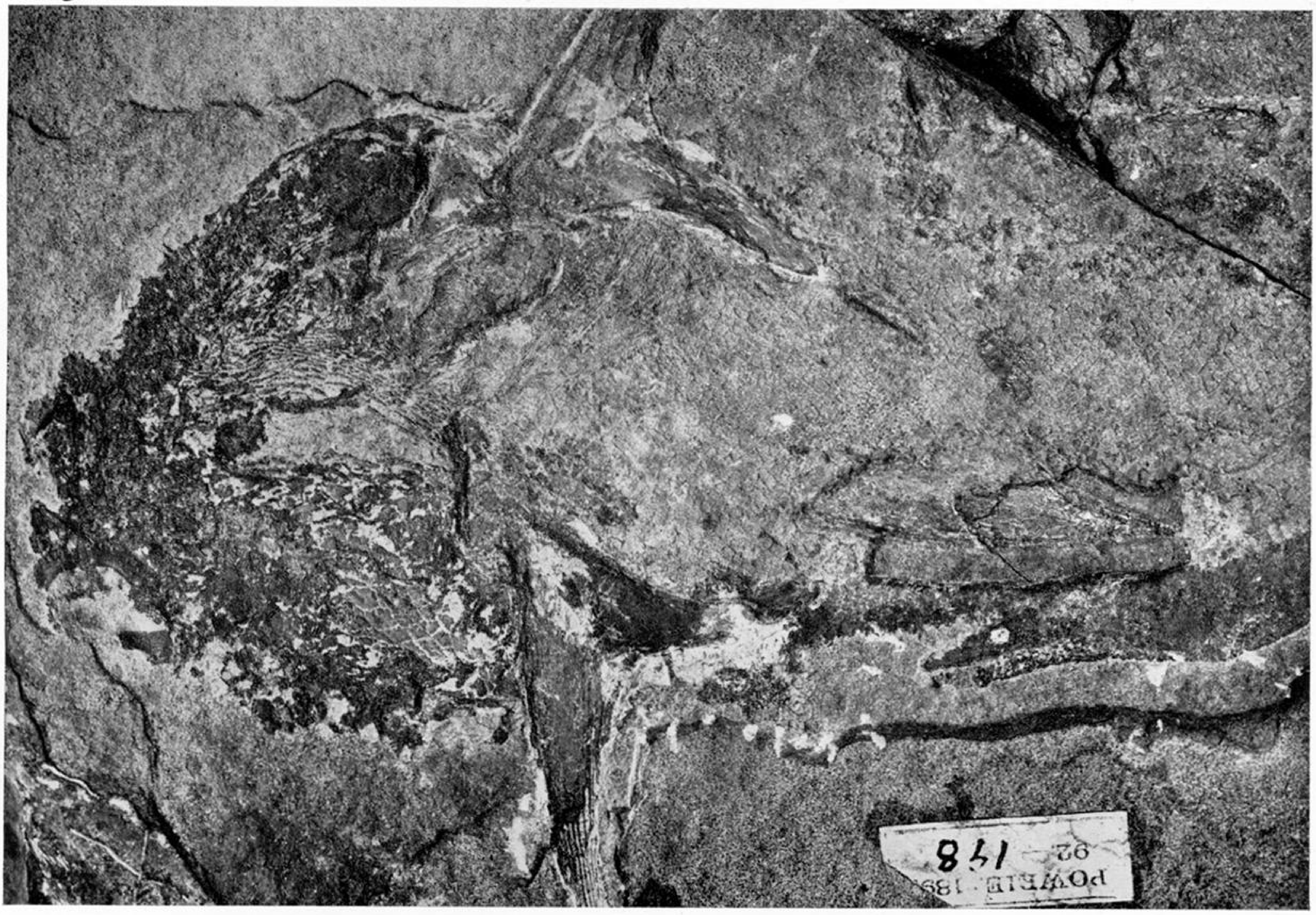


Fig. 2

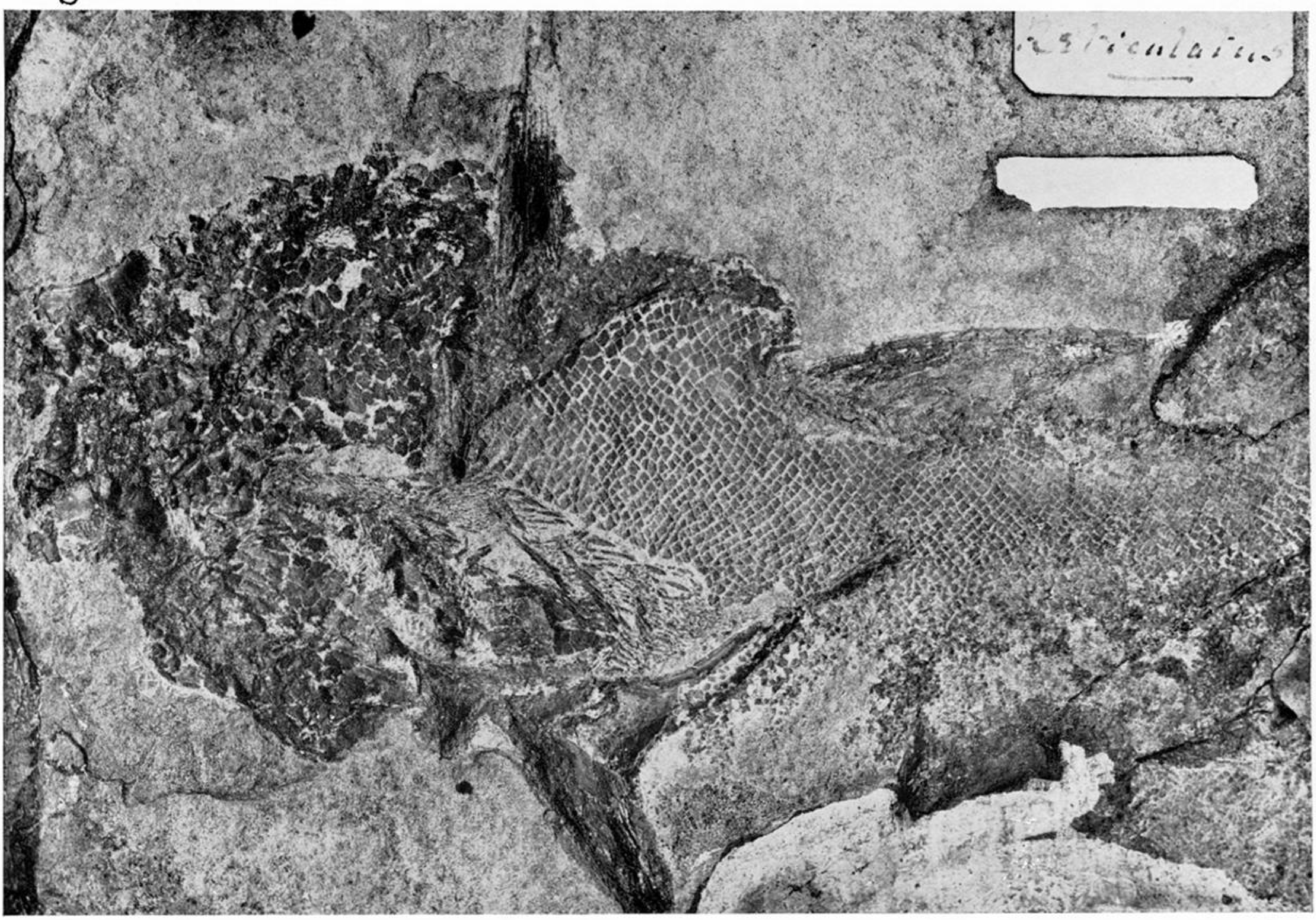


Fig. 1.

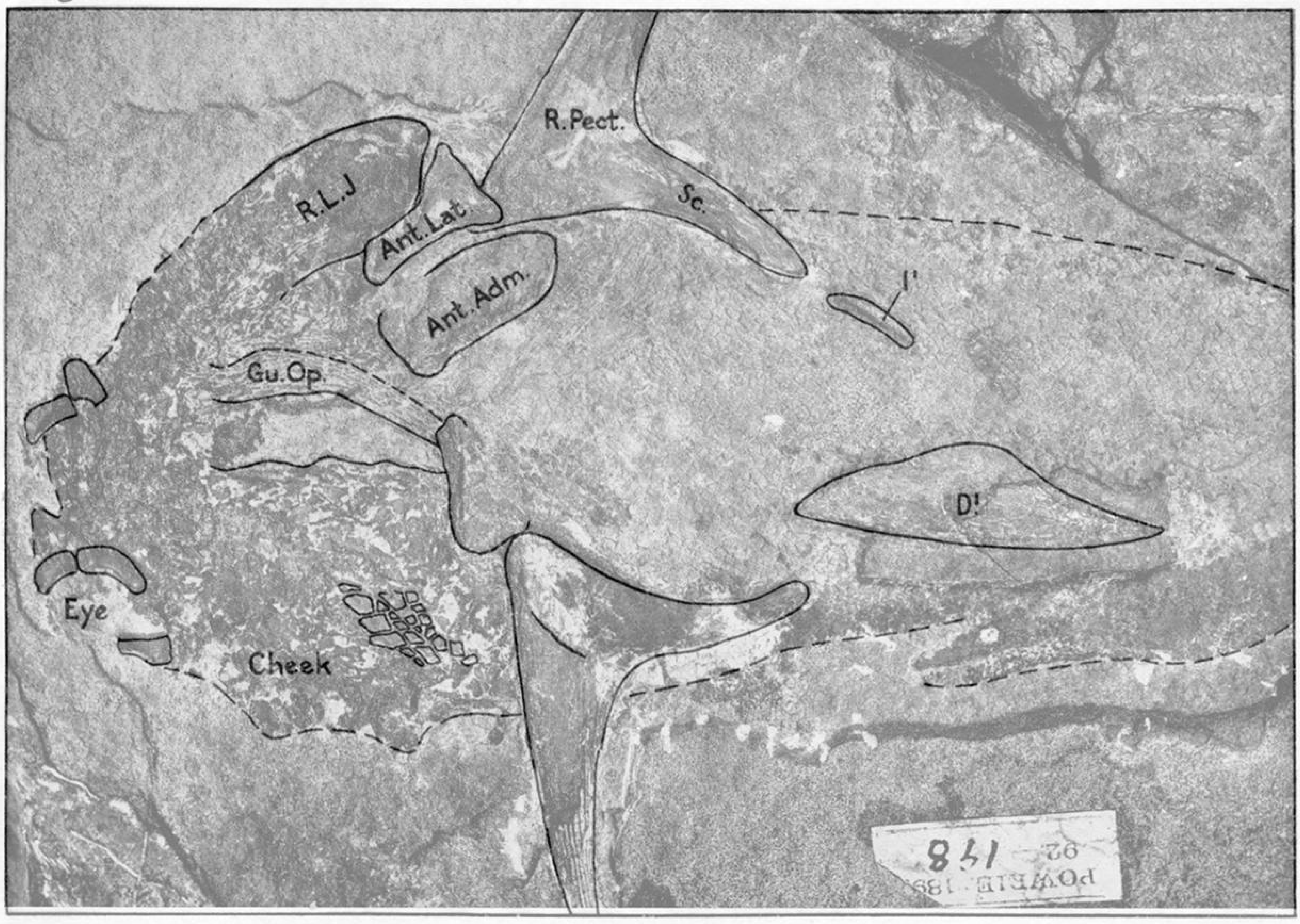


Fig. 2

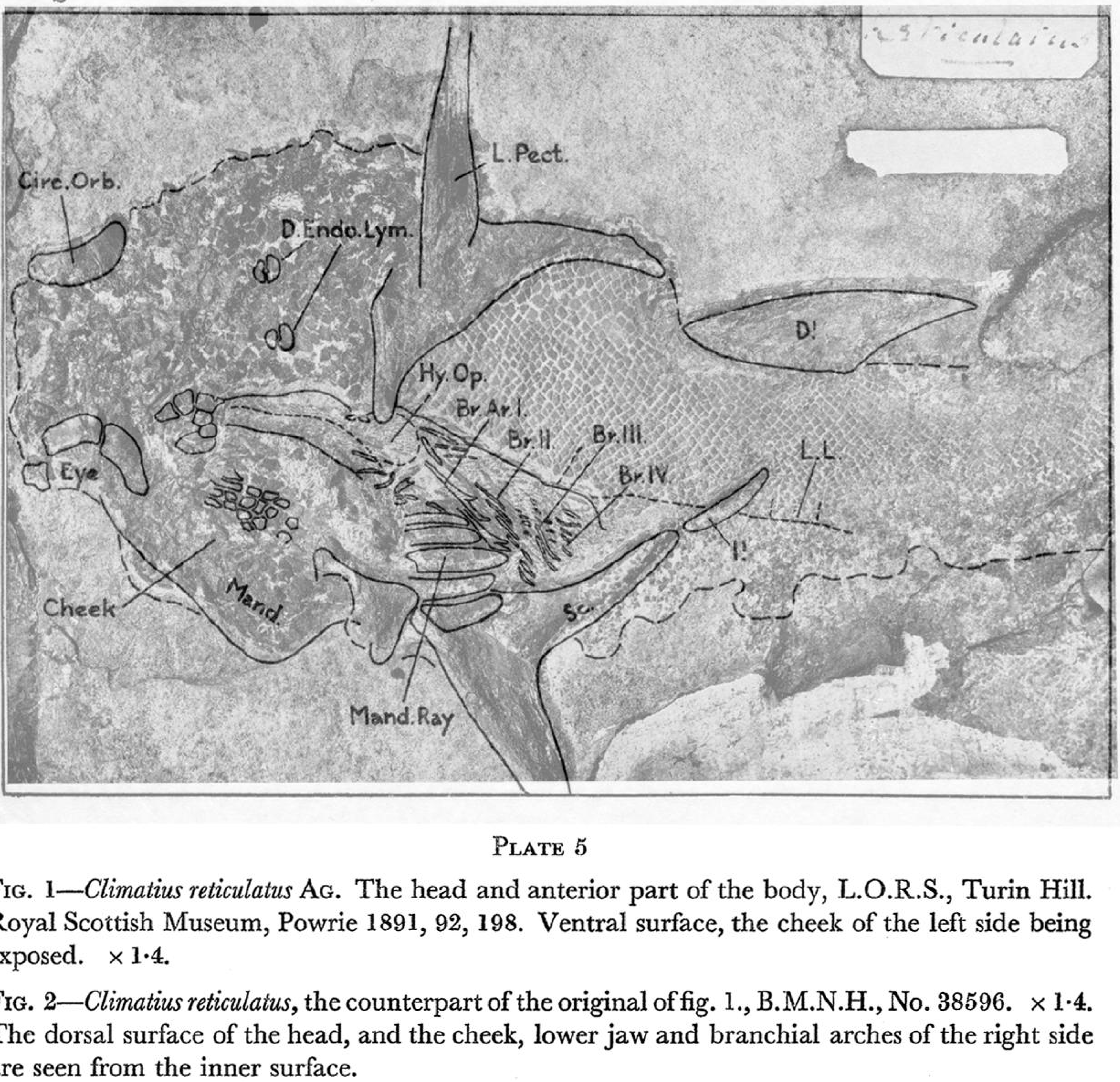


PLATE 5

FIG. 1—*Climatius reticulatus* AG. The head and anterior part of the body, L.O.R.S., Turin Hill. Royal Scottish Museum, Powrie 1891, 92, 198. Ventral surface, the cheek of the left side being exposed. × 1·4.

FIG. 2—*Climatius reticulatus*, the counterpart of the original of fig. 1., B.M.N.H., No. 38596. × 1·4. The dorsal surface of the head, and the cheek, lower jaw and branchial arches of the right side are seen from the inner surface.

Ant.Adm. anterior admedian dermal bone of shoulder girdle; *Ant.Lat.* anterior lateral of shoulder girdle; *Br.Ar.* I, II, etc. the dermal elements of the branchial arches and their opercula; *Circ.Orb.* circum orbital series; *D.Endo Lym.* foramen for the ductus endolymphaticus; D^1, dorsal fin spine; *Eye*, the orbit; *Gu.Op.* gular operculum; *Hy.Op.* hyoid operculum; I^1, first intermediate spine; *L.L.* lateral-line; *L.Pect.* left pectoral spine; *Mand.* mandible; *Mand.Ray*, a "ray" in the mandibular operculum; *R.L.J.* right lower jaw; *R.Pect.* right pectoral spine; *Sc.* scapula.

Fig. 1.

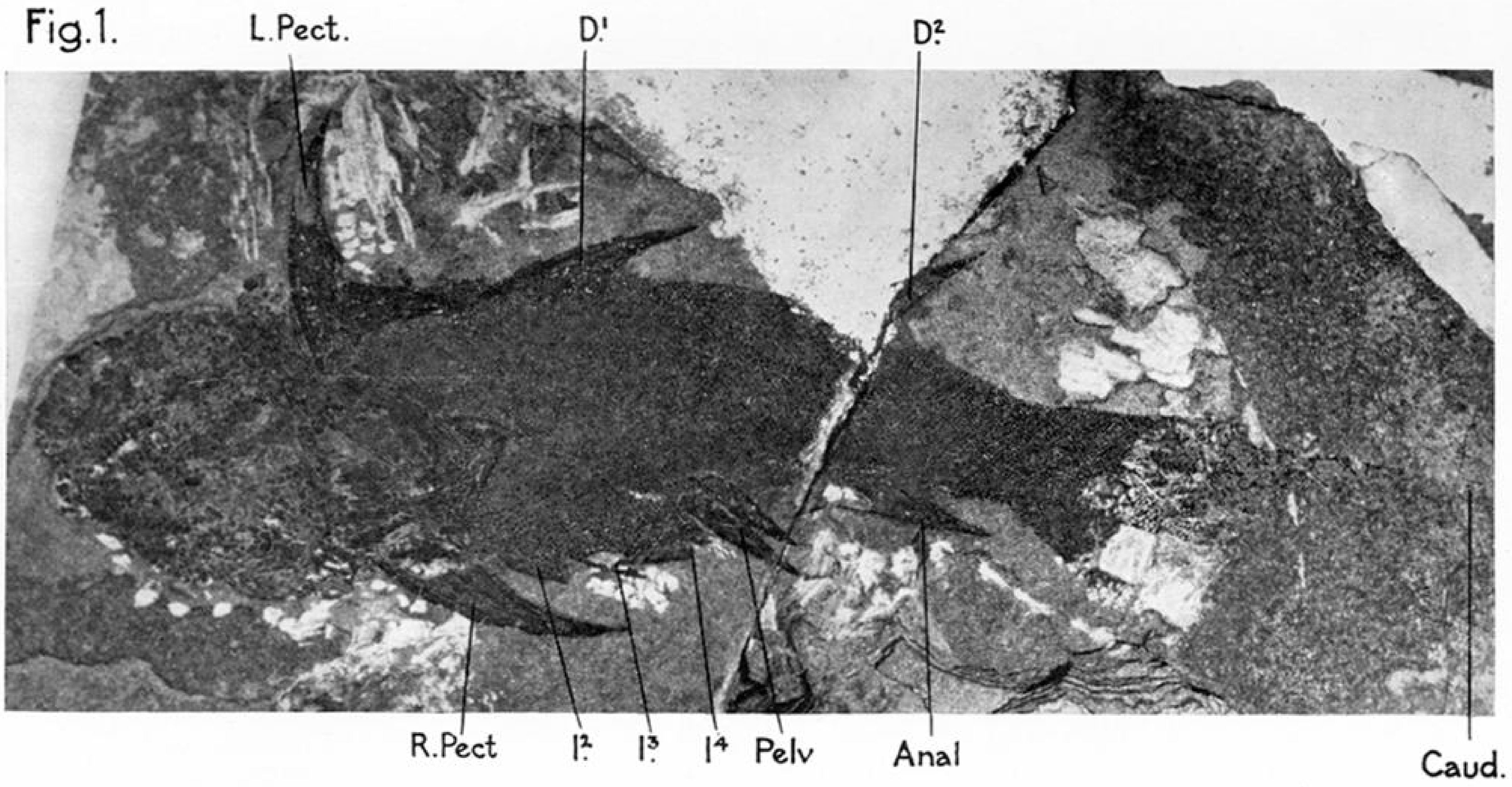


Fig. 3.

Fig. 2.

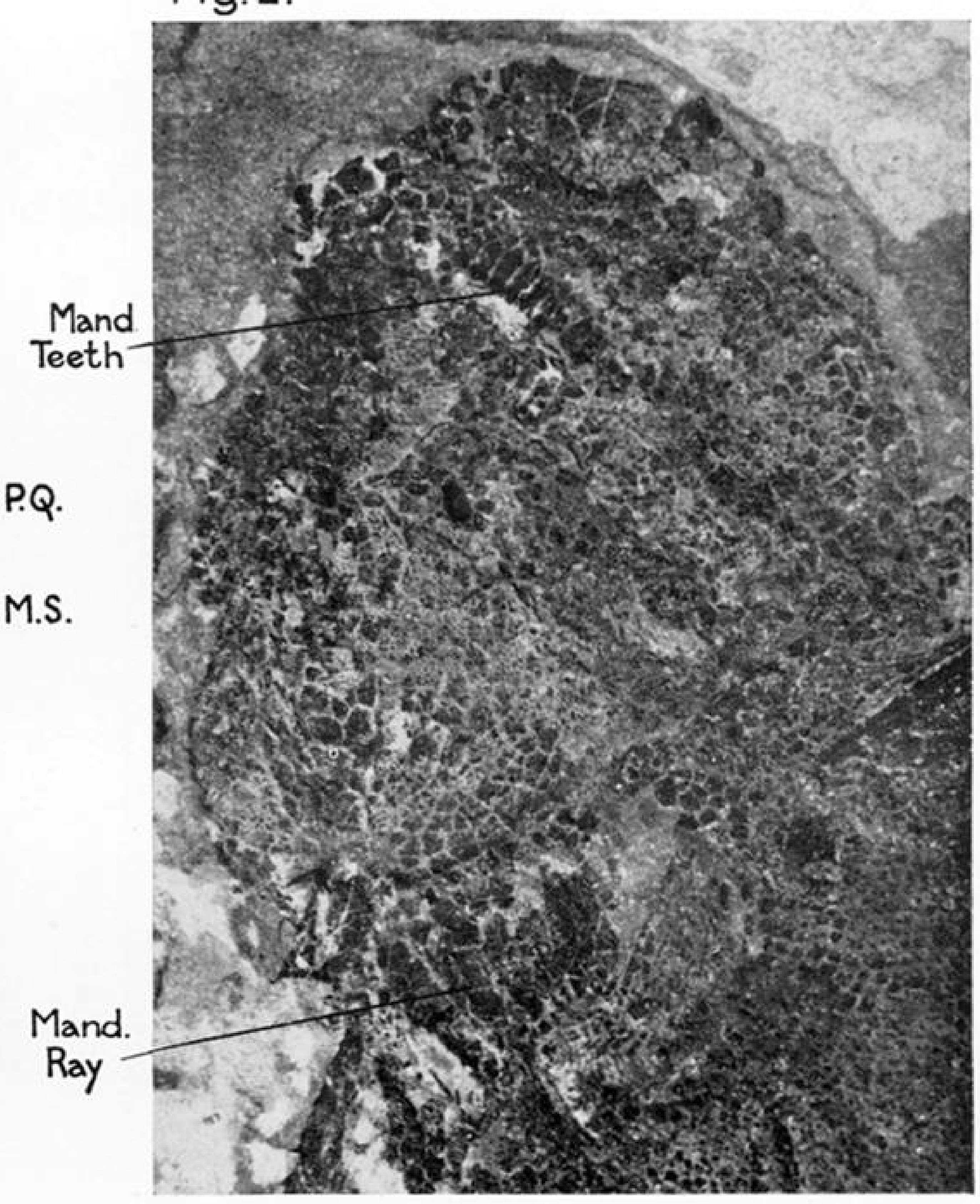


Fig. 4.

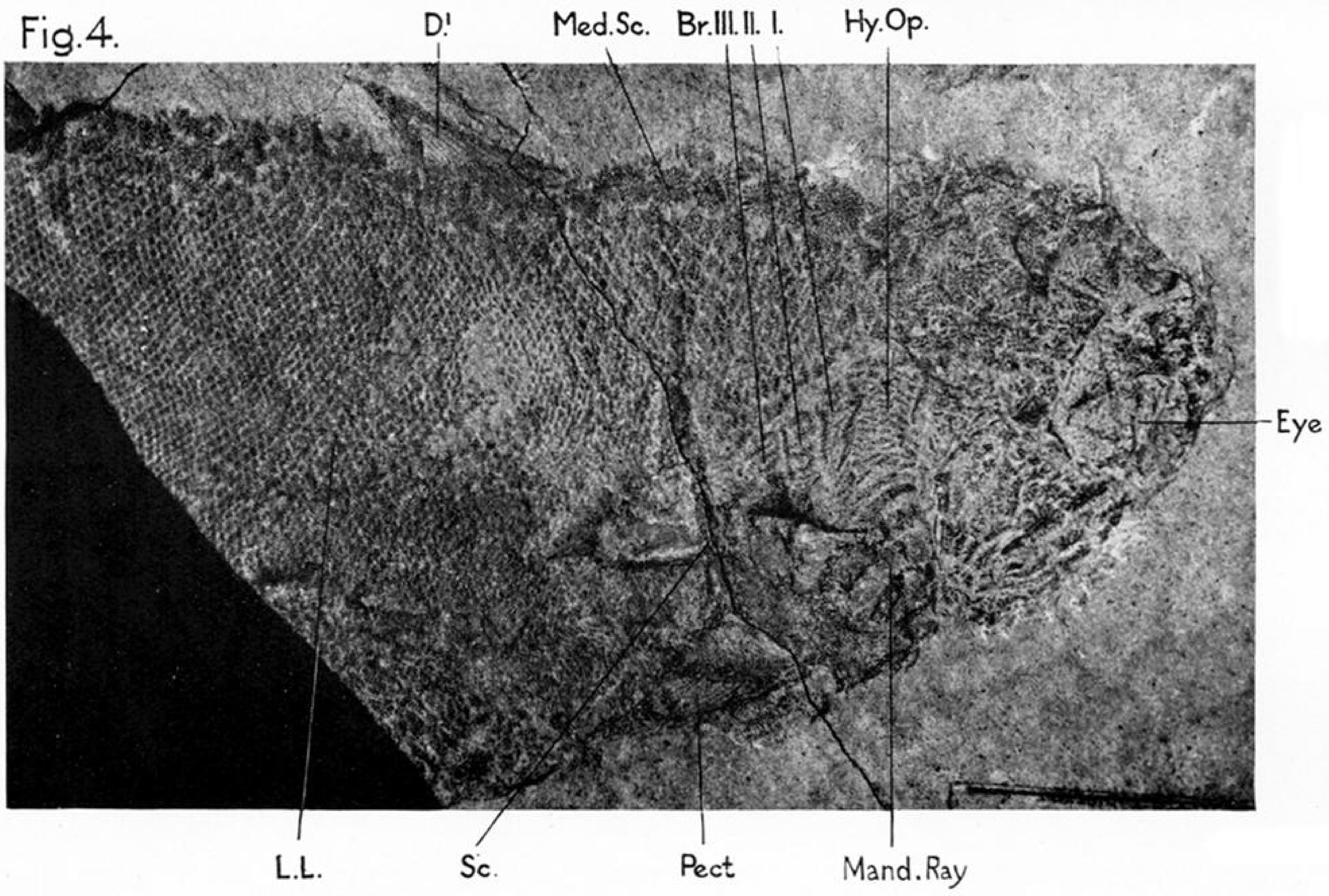


PLATE 6

FIG. 1—*Climatius reticulatus*, L.O.R.S. Turin Hill. Manchester Museum, L. 12096. × 0·75. Complete fish, the head viewed from below, the body in lateral aspect.

FIG. 2—*Climatius reticulatus*, the head of fig. 1, enlarged. × 1·72.

FIG. 3—*Climatius reticulatus*, L.O.R.S. Turin Hill. Royal Scottish Museum, Powrie 1891, 92, 206. × 1·24. The head and shoulder girdle viewed from below. The snout is well shown.

FIG. 4—*Brachyacanthus scutiger* EG., L.O.R.S. Farnell. Royal Scottish Museum, Powrie 1891, 92, 220. × 3·0. Impression of the left side of the anterior part of the fish, with dark fragments of bone left in the deeper hollows.

Anal, anal fin; *Br.* I, II, III, dermal bones of the branchial arches and their opercula; *Caud.* extremity of the tail; D^1, D^2, the dorsal fins; *Eye*, orbit; *Hy.Op.* hyoid operculum; I^1, I^2, etc. intermediate fins; *L.L.* lateral-line; *L.Pect.* left pectoral fin; *M.S.* median dermal bone of shoulder girdle; *Mand.Ray*, a "ray" of the mandibular operculum; *Mand. Teeth*, the whorls of teeth on the mandible; *Med.Sc.* median scutes; *P.Q.* palato-quadrate; *Pect.* pectoral spine; *Pelv.* pelvic fin; *R.* ridged bone of shoulder girdle; *R.Pect.* right pectoral fin; *Sc.* scapula.

Fig. 1.

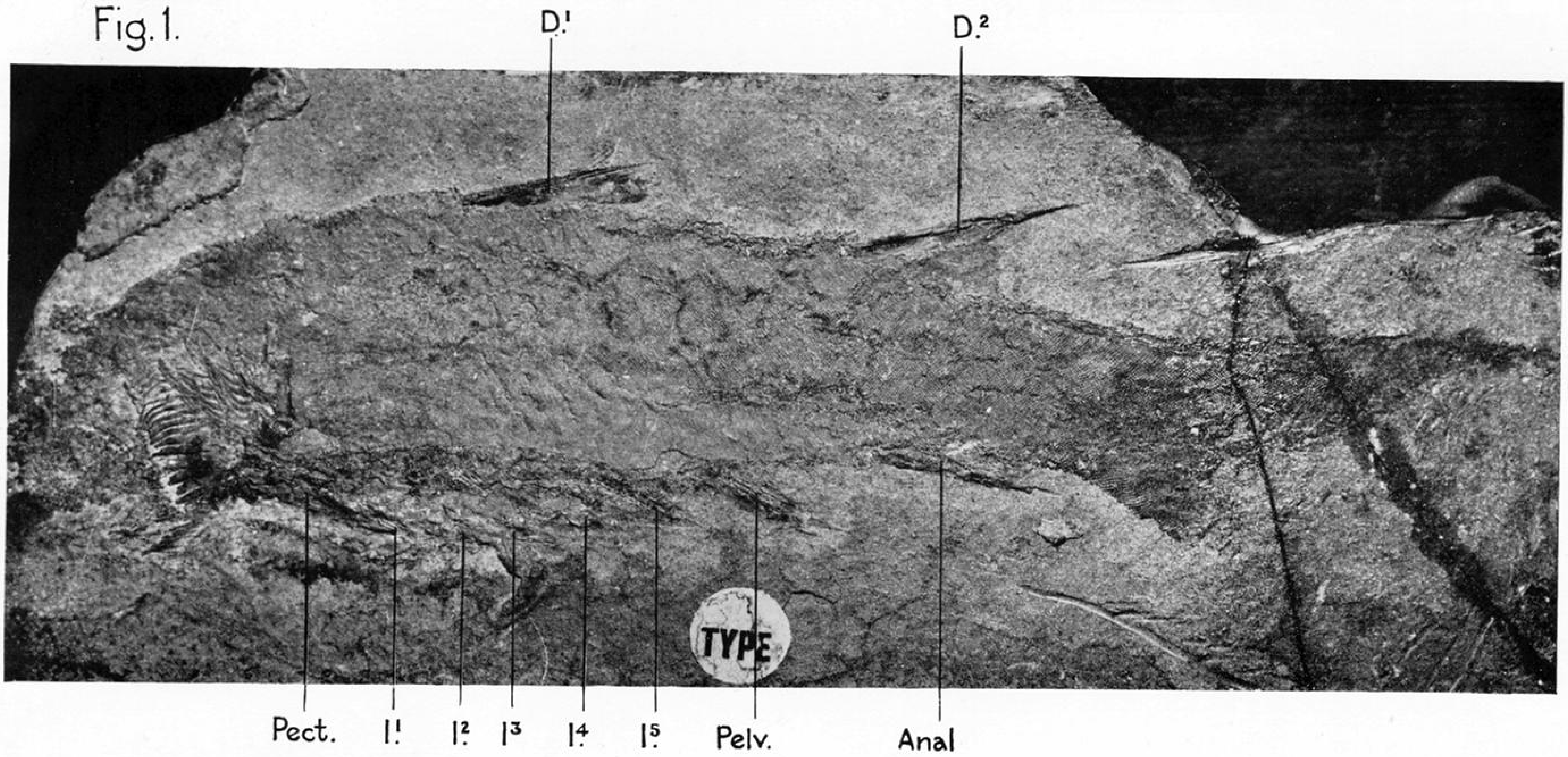


Fig. 2.

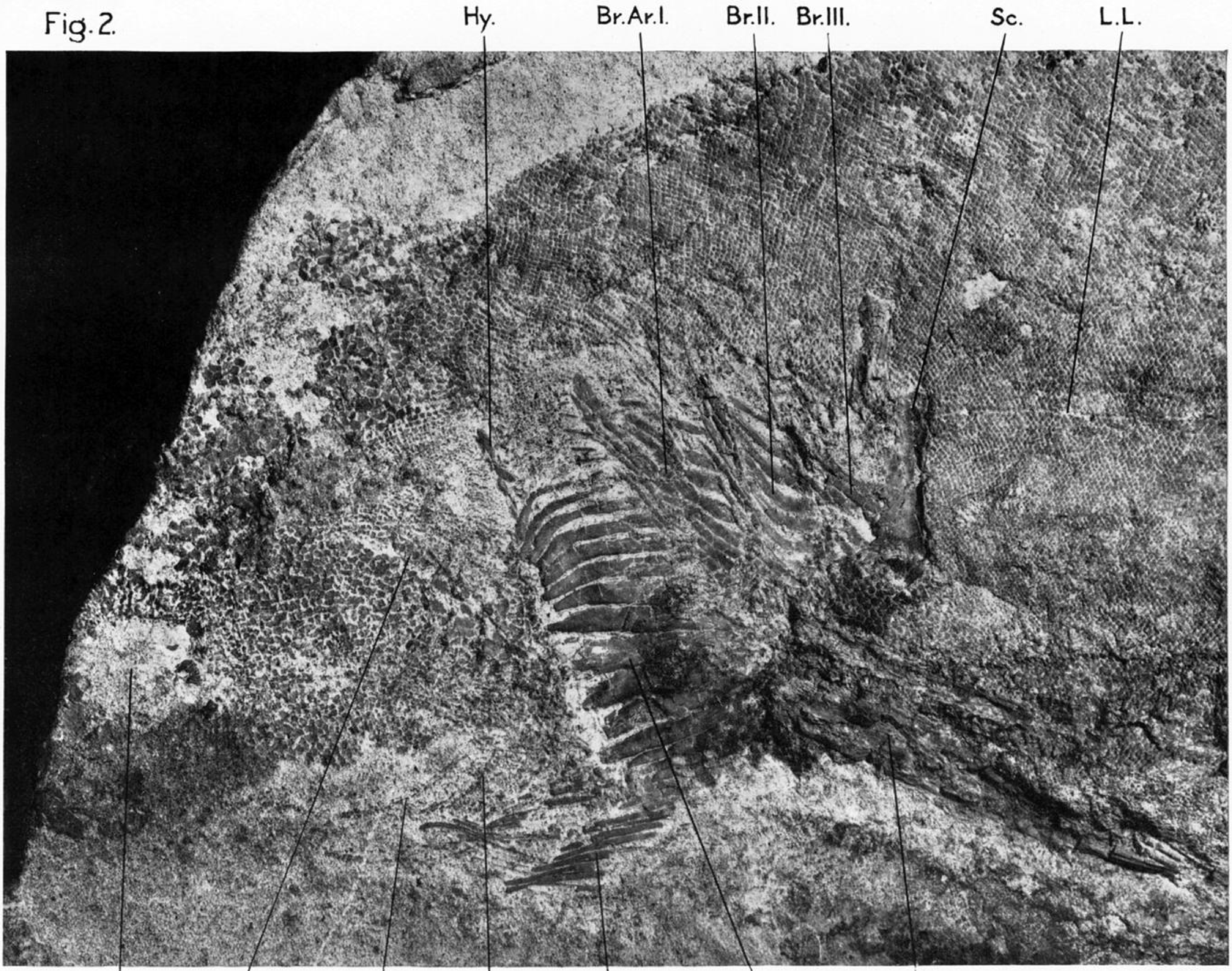


PLATE 7

FIG. 1—*Euthacanthus macnicoli* POWRIE. Type specimen, L.O.R.S. Turin Hill. Royal Scottish Museum, Powrie 1891, 92, 251. ×1·0. The whole fish seen from the left side.

FIG. 2—*Euthacanthus macnicoli*. The head of fig. 1 enlarged. ×3·45.

Anal. anal fin; *Br.Ar.* I, II, III, the dermal bones in the branchial arches and their opercula; D^1, D^2, the dorsal fin spines; *Eye*, orbit; *Gu.* gular mandibular rays; *Hy.* hyoid; I^1–I^5, the intermediate fin spines; *L.L.* lateral-line; *Mand.C.* mandibular canal; *Mand.Ray*, a "ray" of the mandibular operculum; *Or.C.* oral canal; *P.Op.C.* preopercular canal; *Pect.* pectoral fin; *Pelv.* pelvic fin; *Sc.* scapula.

Fig.1.

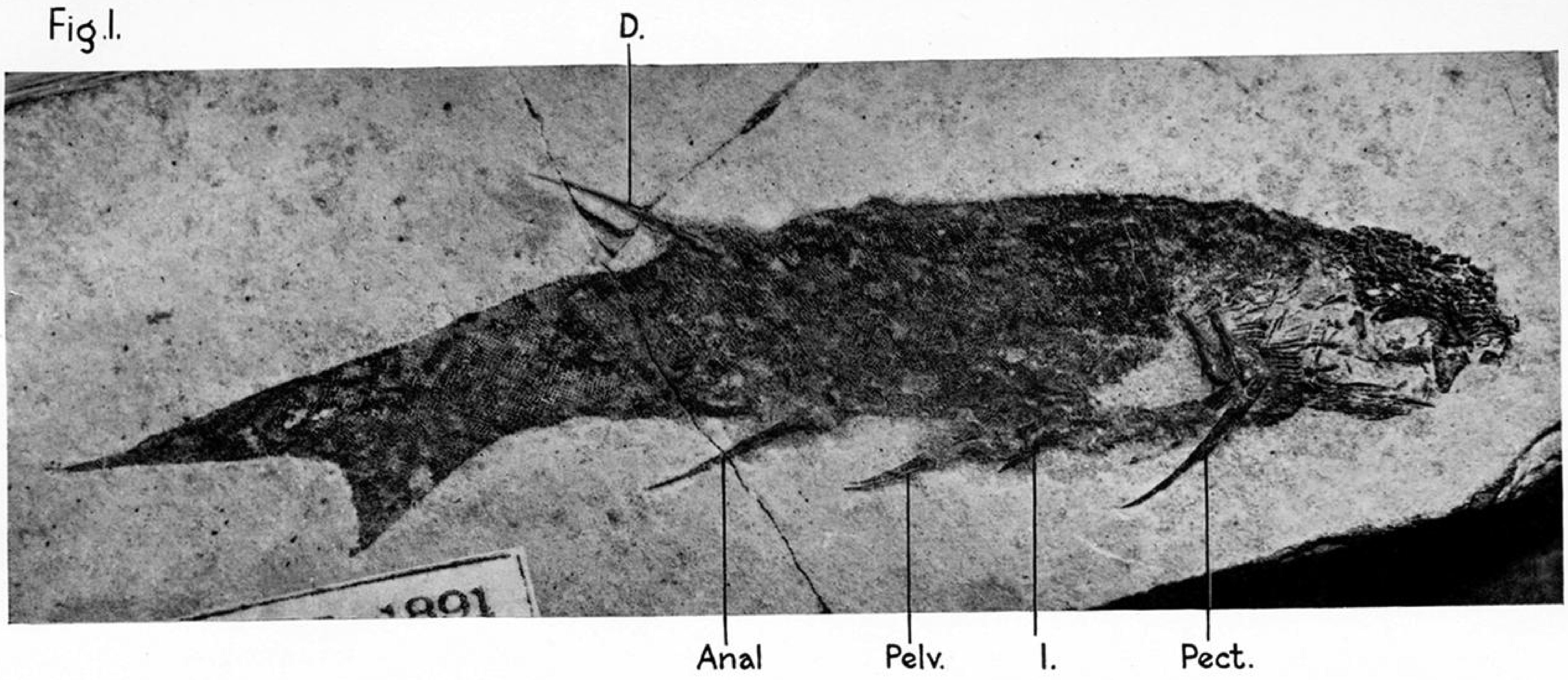


Fig.2.

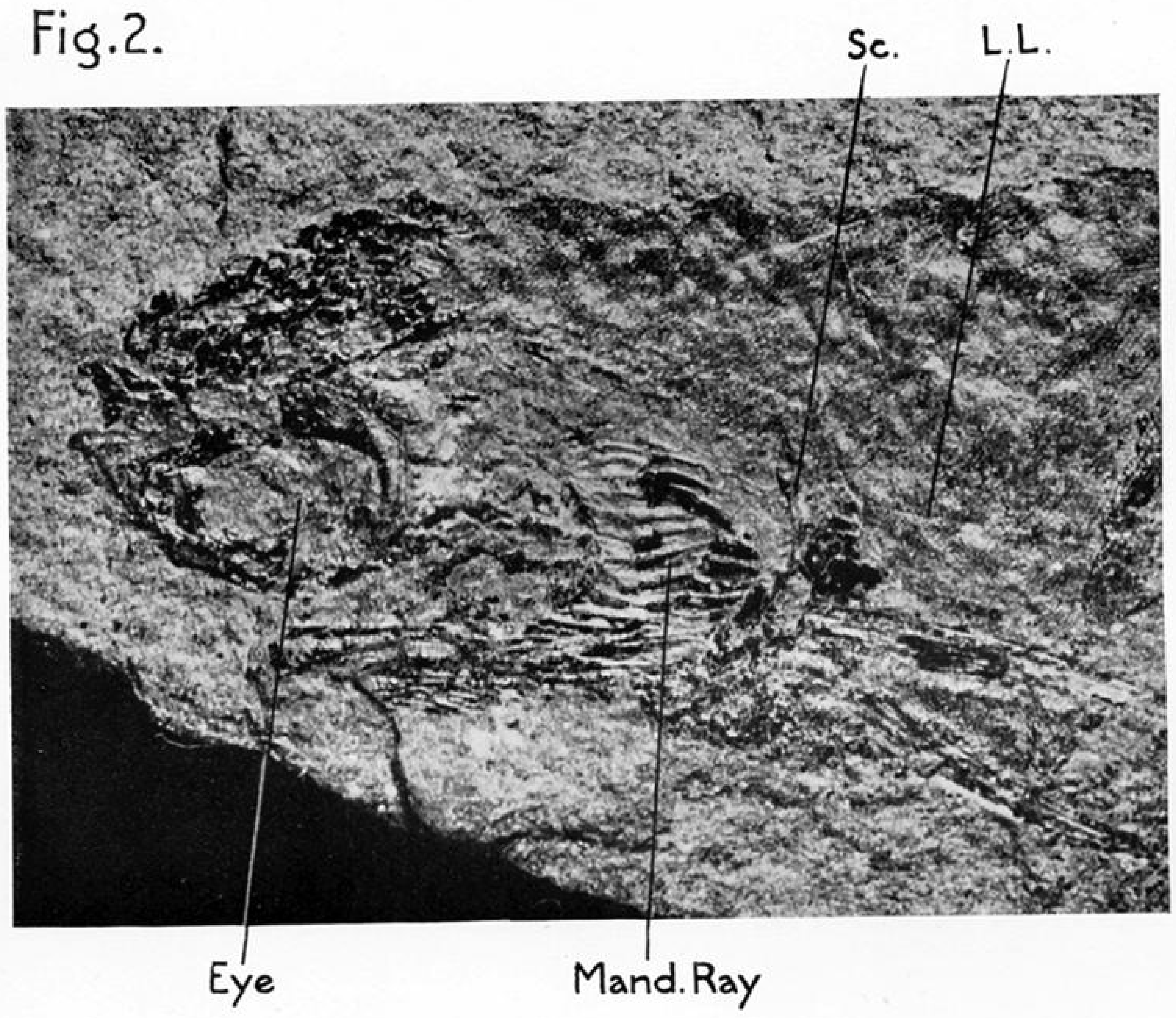


Fig.3.

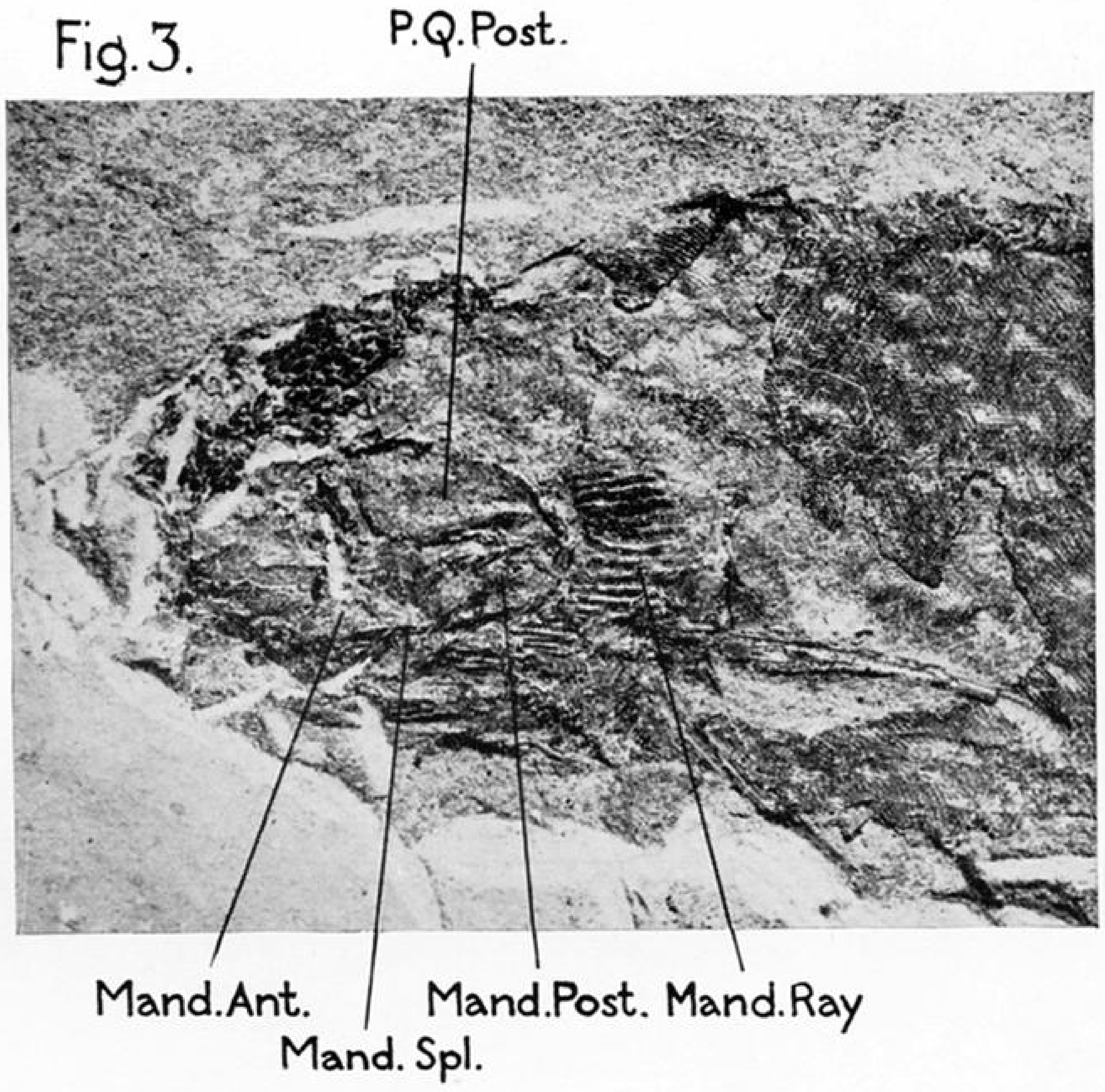


Fig.4

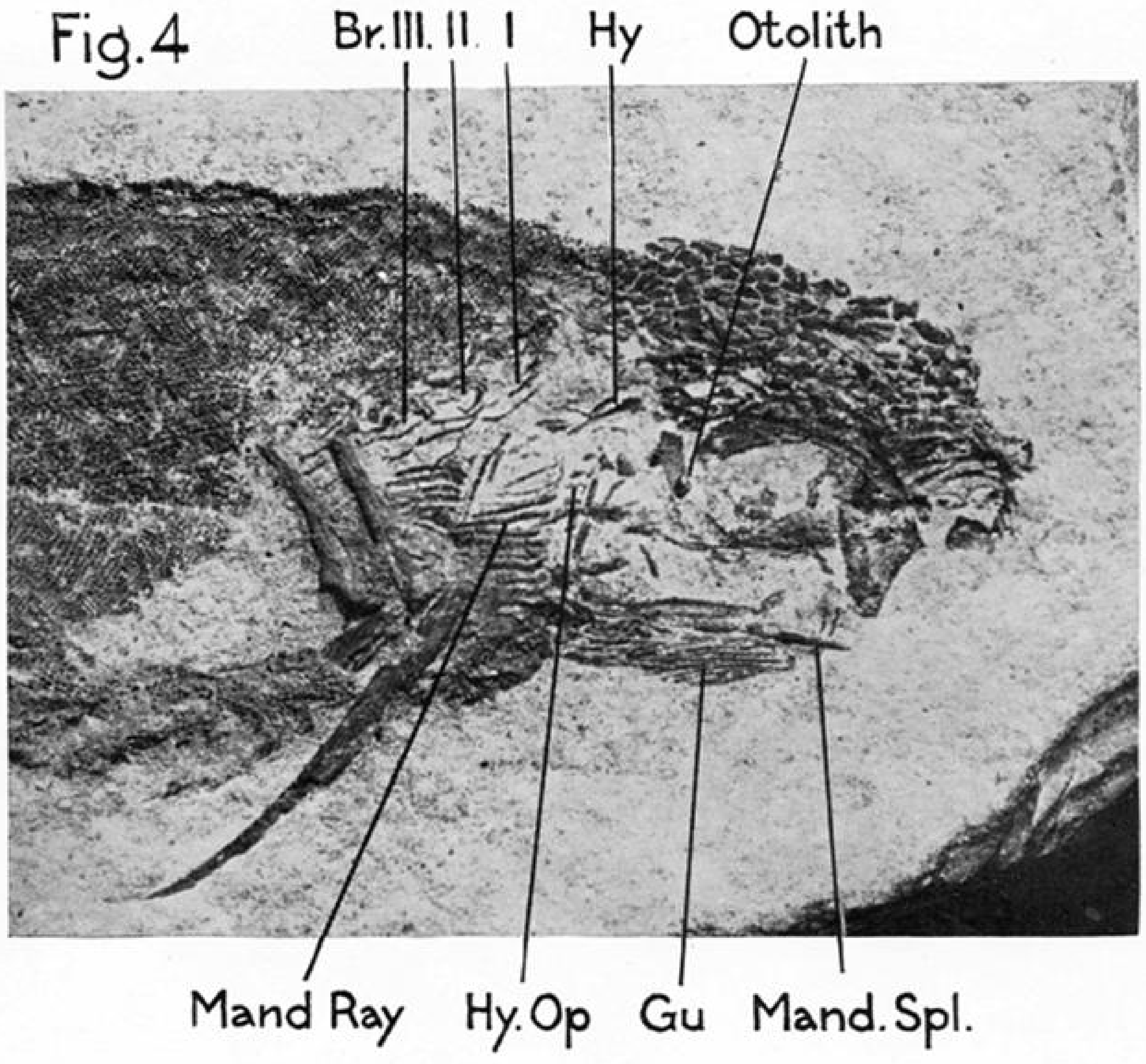


Fig.5.

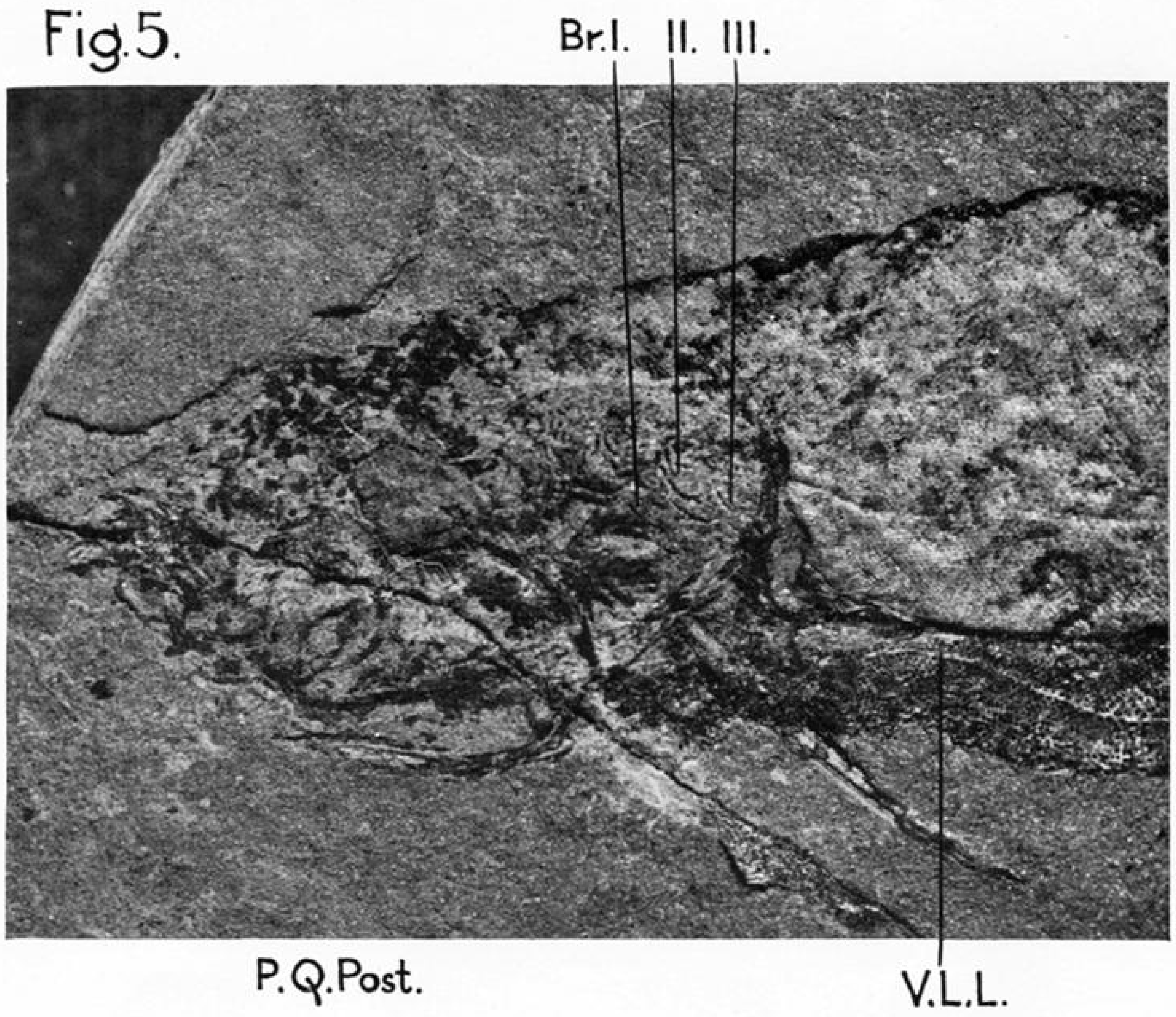


PLATE 8

FIG. 1—*Mesacanthus mitchelli* EG., L.O.R.S. Turin Hill. Royal Scottish Museum, Powrie 1891, 92, 275. ×2·5. A complete young individual from its right side.

FIG. 2—*Mesacanthus mitchelli*, L.O.R.S. Turin Hill. D.M.S.W. Coll., P. 473. ×4·7. Left side of the head of an adult.

FIG. 3—*Mesacanthus mitchelli*, L.O.R.S. Turin Hill. Royal Scottish Museum, 1881, 5, 80. ×3·6. Left side of the head, the palato-quadrate, Meckel's cartilage, and the mandibular operculum well shown.

FIG. 4—*Mesacanthus mitchelli*, the head of fig. 1, further enlarged. ×3·8. Shows especially well the hyoid arch and its operculum.

FIG. 5—*Mesacanthus mitchelli*, L.O.R.S. Turin Hill. Royal Scottish Museum, Powrie 1891, 92, 277. ×3·8. Left side of the head.

Anal, anal fin; *Br.* I, II, III, dermal bones in the branchial arches; *Eye*, orbit; *Gu.* gular mandibular ray; *Hy.* hyoid; *Hy.Op.* hyoid operculum; *I.* intermediate fin; *L.L.* lateral-line; *Mand.Ant.* anterior bone in Meckel's cartilage; *Mand.Post.* posterior bone in Meckel's cartilage; *Mand.Ray*, a "ray" in the mandibular operculum; *Mand.Spl.* mandibular splint; *Otolith*; *P.Q.Post.* posterior bone in the palato-quadrate; *Pect.* pectoral fin; *Pelv.* pelvic fin; *Sc.* scapula; *V.L.L.* ventral lateral-line.

Fig. 1.

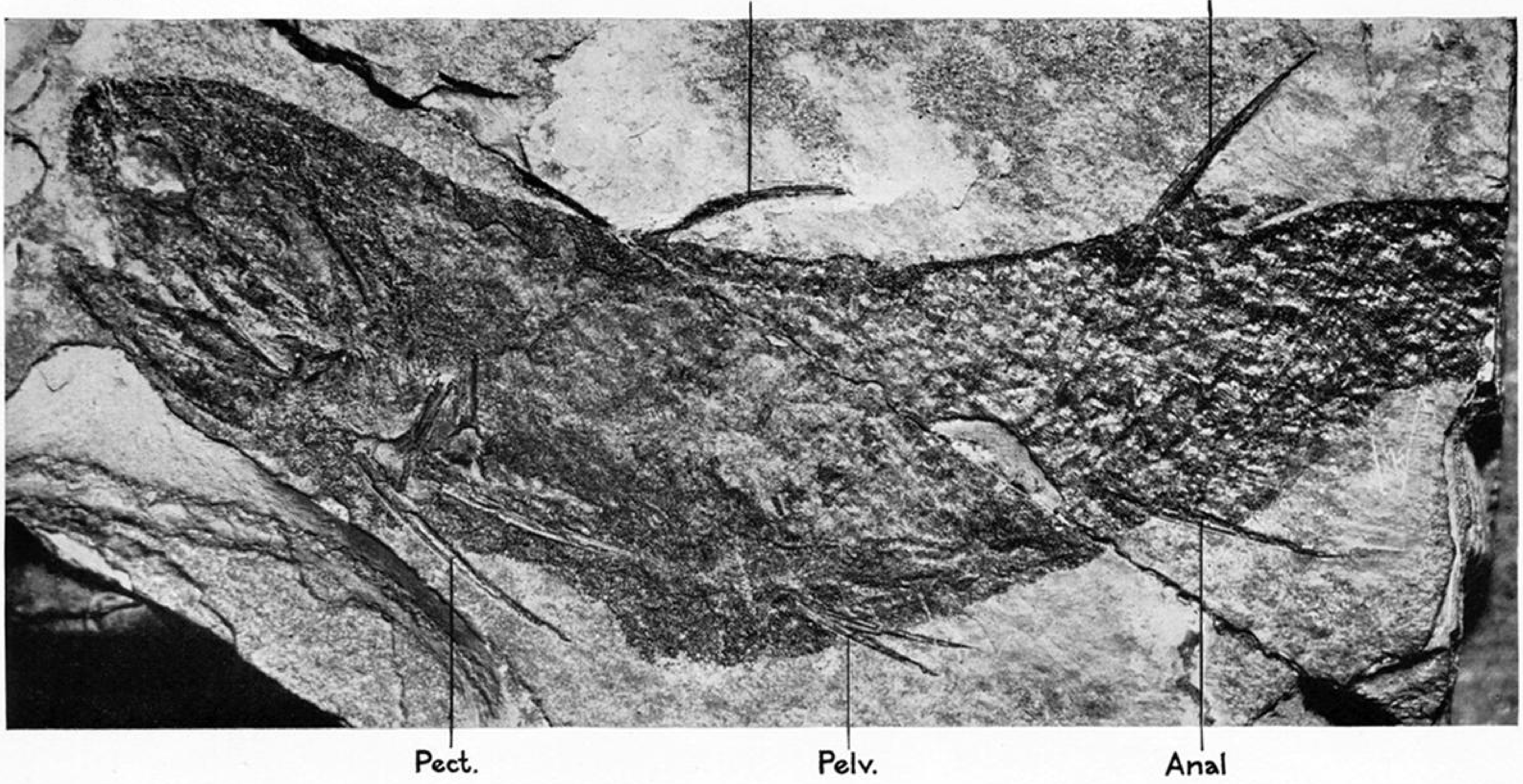


Fig. 2.

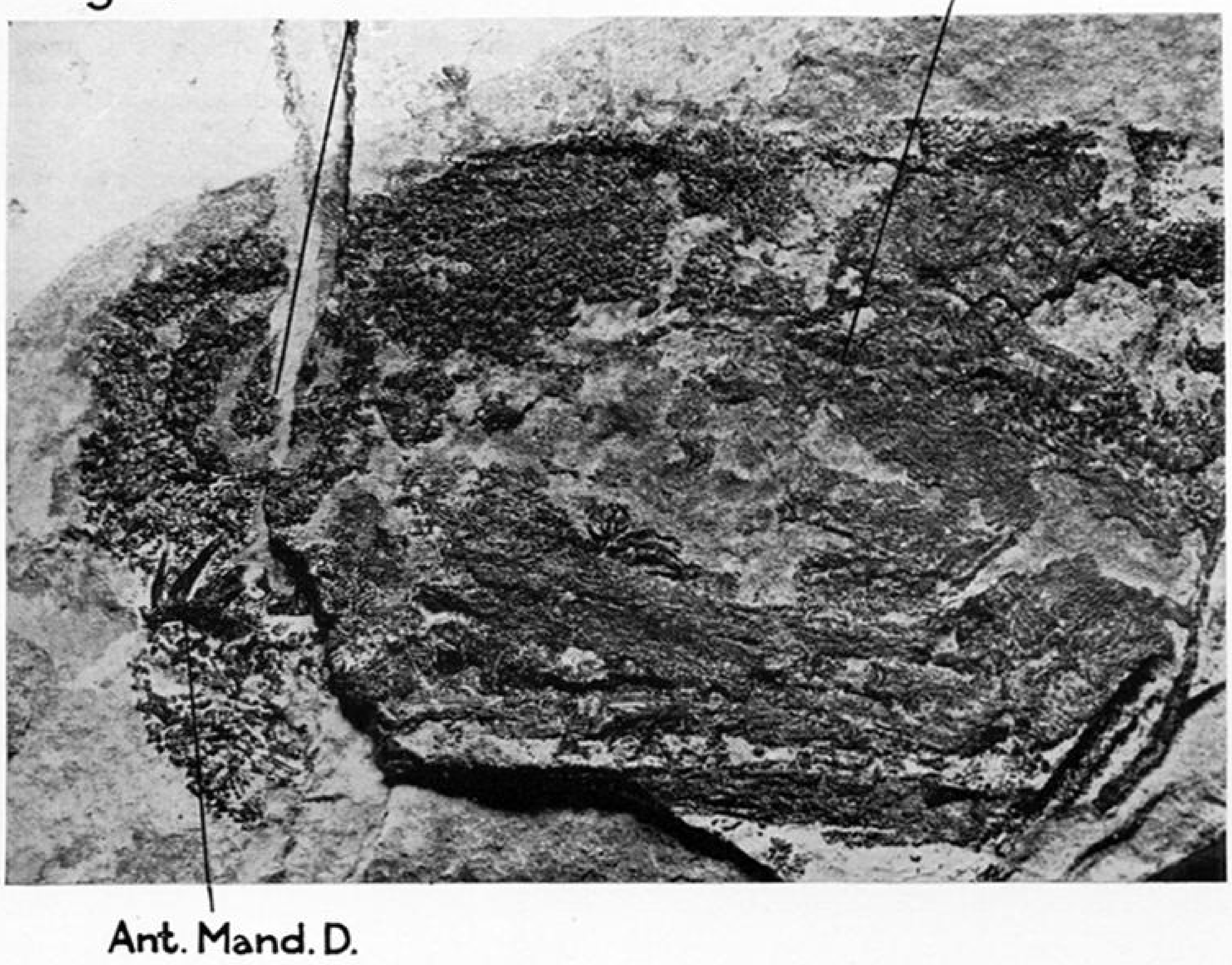


Fig. 3a

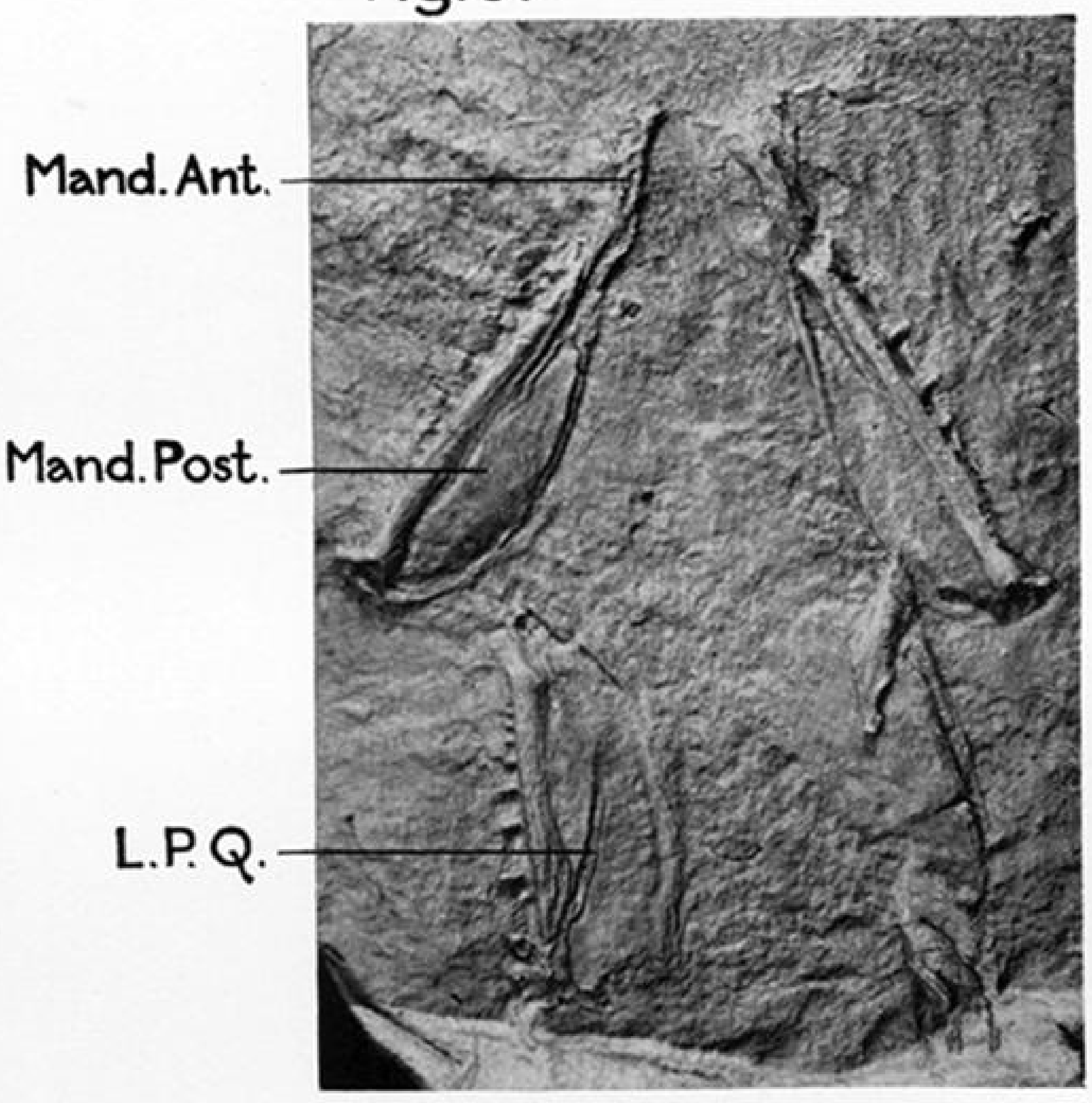


Fig. 3b

Fig. 4.

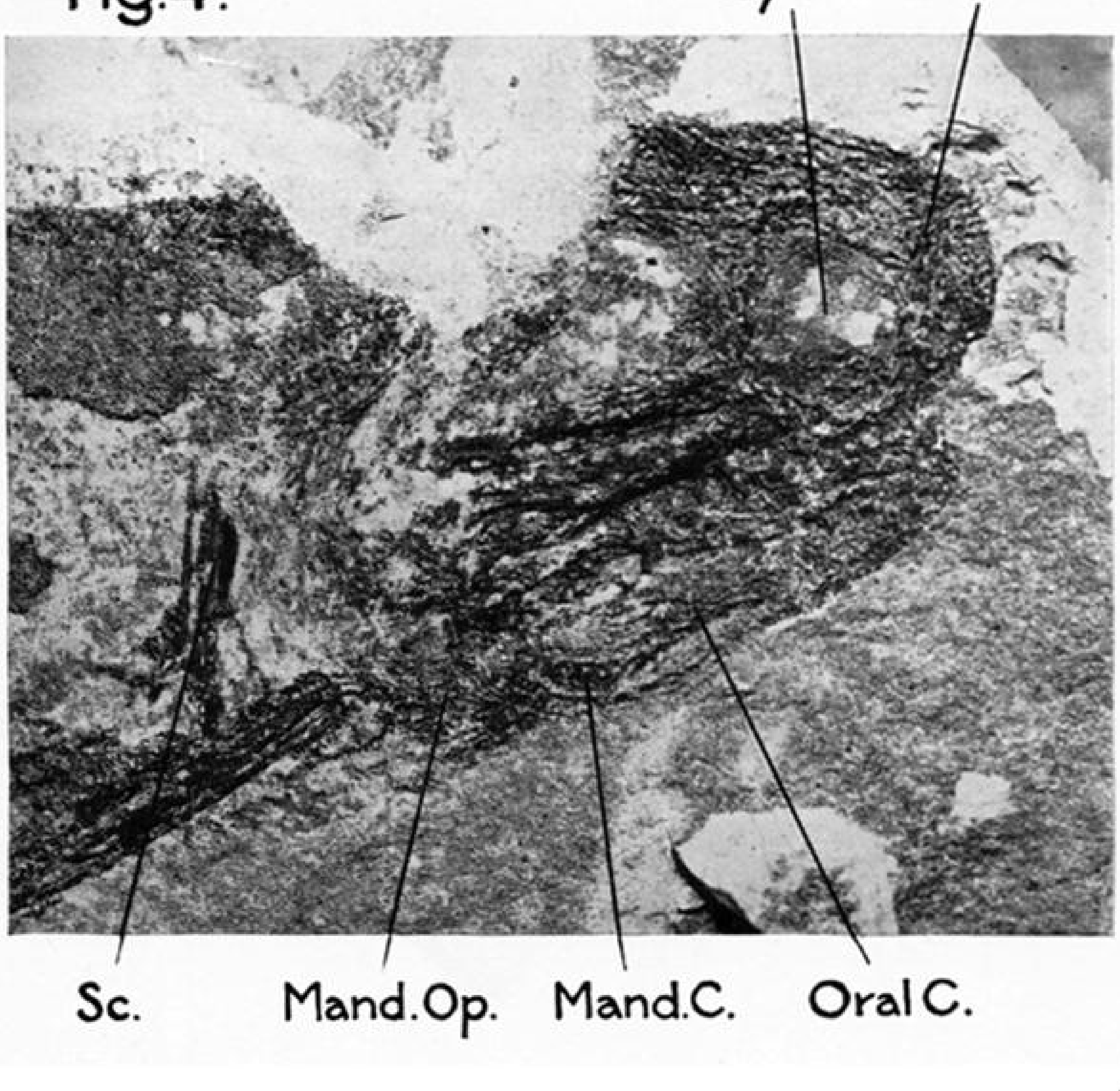


Fig. 5.

PLATE 9

FIG. 1—*Ischnacanthus gracilis* EG., L.O.R.S. Turin Hill, B.M.N.H. 46305. ×2·0. Left aspect of a small fish lacking the tail.

FIG. 2—*Ischnacanthus gracilis* EG., L.O.R.S. Turin Hill, Royal Scottish Museum, 1887, 35, 2. ×2·4. Left side of the head of a large individual.

FIG. 3*a*—*Ischnacanthus gracilis* EG., L.O.R.S. Turin Hill, D.M.S.W. Coll., P. 478. ×1·4. Isolated lower jaws seen from the lingual sides, and left posterior palato-quadrate from its palatal surface.

FIG. 3*b*—The right posterior palato-quadrate bone of the specimen in Fig. 3*a*, from its outer surface. ×1·4.

FIG. 4—*Ischnacanthus gracilis* EG., L.O.R.S. Turin Hill, D.M.S.W. Coll., P. 481. ×2·6. Right side of the head of a small fish.

FIG. 5—*Ischnacanthus gracilis* EG., L.O.R.S. Turin Hill, D.M.S.W. Coll., P. 297. ×1·15. The tail of a medium-sized individual.

Anal, anal fin; *Ant.Mand.D.* fused whorl of symphysis mandibular teeth; D^1, D^2, the dorsal fin spines; *Eth.C.* ethmoidal commissure; *Eye,* orbit; *L.L.* lateral-line; *L.P.Q.* left posterior palato-quadrate; *Mand.Ant.* anterior mandibular ossification; *Mand.C.* mandibular canal; *Mand.Op.* mandibular operculum; *Mand.Post.* posterior bone in the mandible; *Oral.C.* oral canal; *Pect.* pectoral fin spine; *Pelv.* pelvic fin spine; *Sc.* scapula.

Fig. 1.

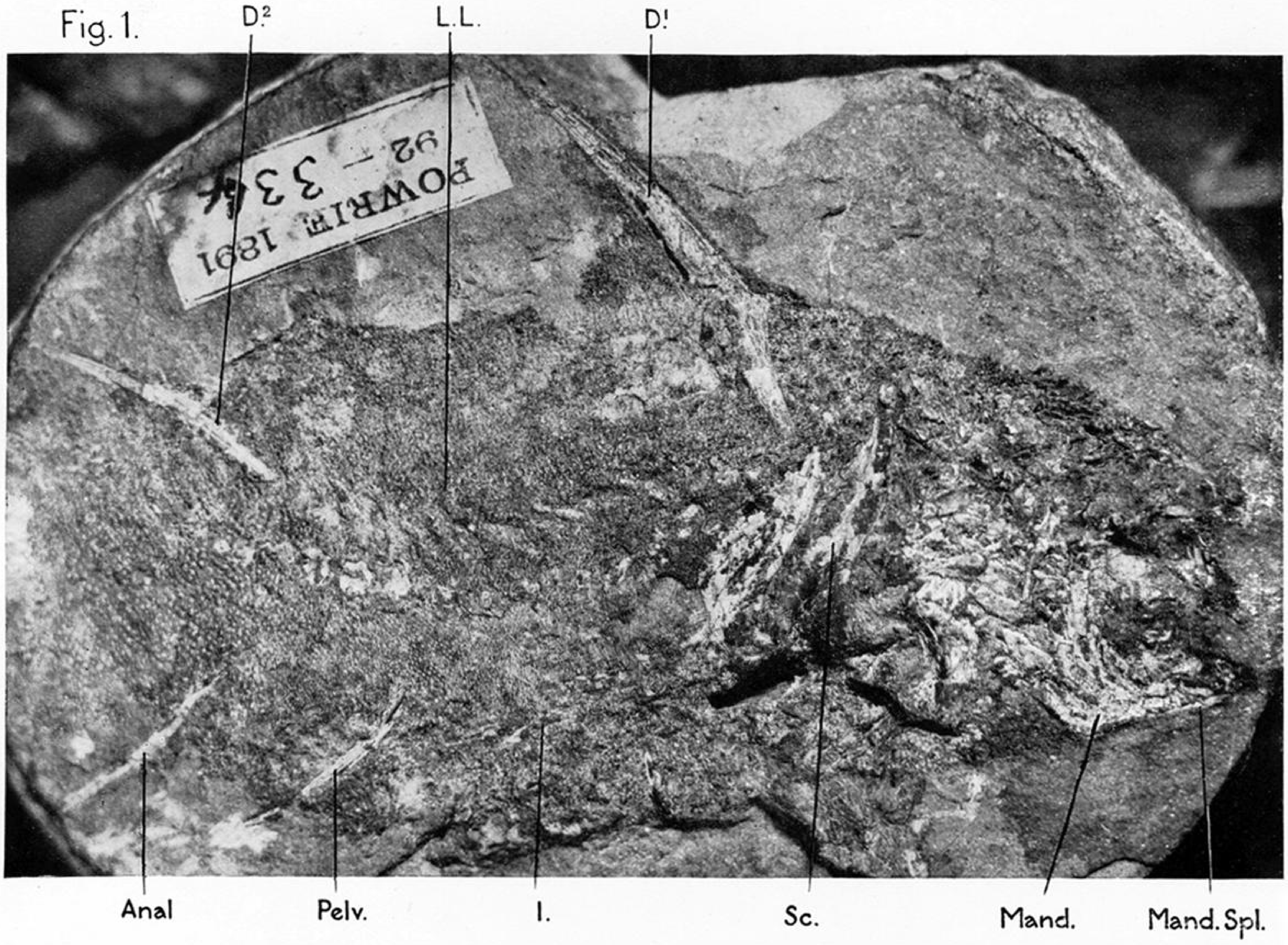


Fig. 2.

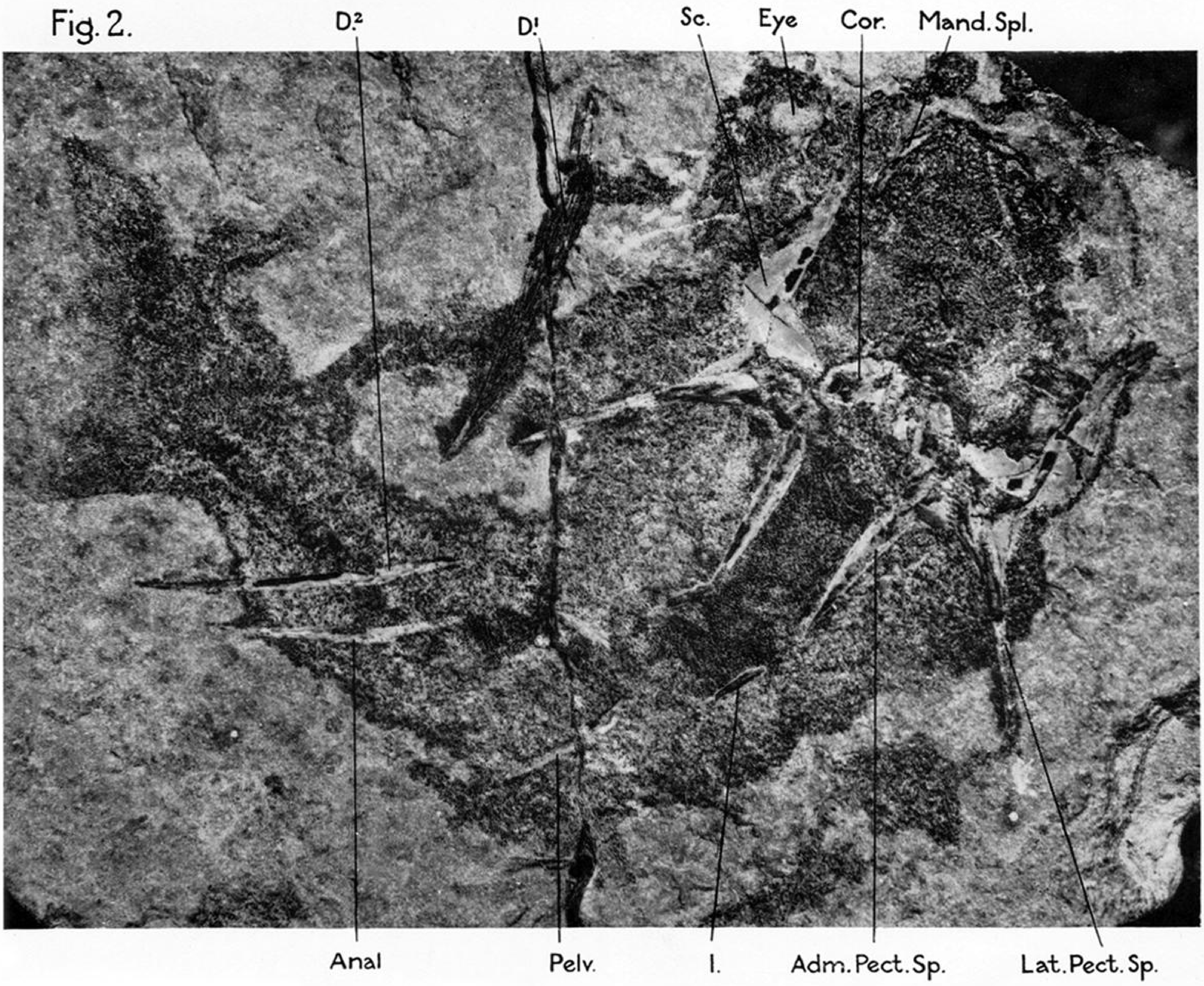
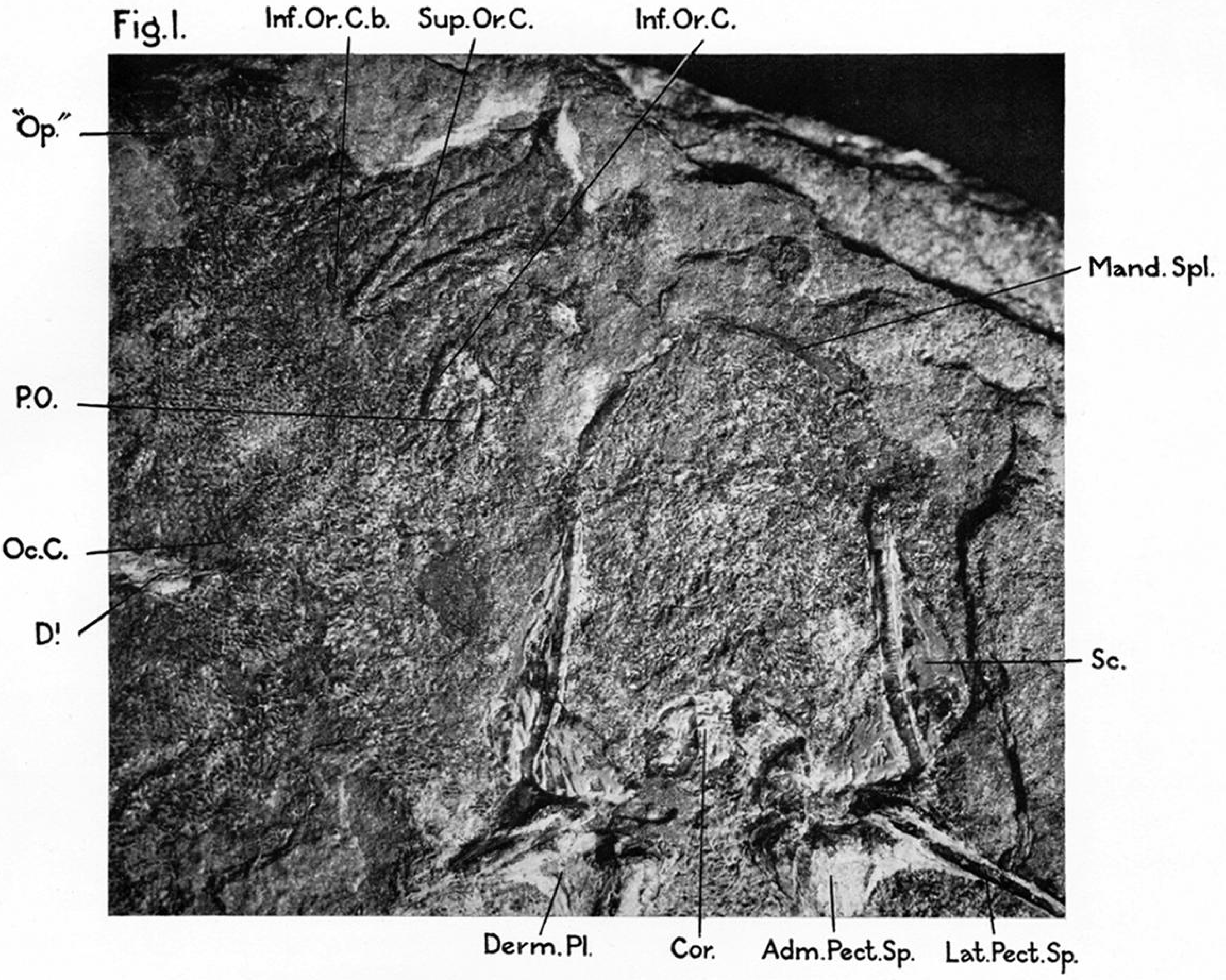


PLATE 10

FIG. 1—*Diplacanthus striatus* AG., M.O.R.S. Tynet Burn, Royal Scottish Museum, Powrie 1891, 92, 334. ×2·2. Left aspect of a fish unique in possessing extensive ossifications in the visceral arches, vertebral column, and basals and radials of the first dorsal fin, and in showing calcified ceratotrichia in the first dorsal and pectoral fins.

FIG. 2—*Diplacanthus striatus* AG., M.O.R.S. Tynet Burn, D.M.S.W. Coll., P. 299. ×2·3. Complete fish showing the cheek, intergular space, pectoral girdle, fin spines and tail.

Adm.Pect.Sp. admedian pectoral spine; *Anal*, anal fin spine; *Cor.* coracoid; D^1, D^2, the dorsal fin spines; *Eye*, orbit; *I.* intermediate fin spine; *L.L.* lateral-line; *Lat.Pect.Sp.* lateral pectoral spine; *Mand.* ossified Meckel's cartilage; *Mand.Spl.* mandibular splint; *Pelv.* pelvic fin; *Sc.* scapula.



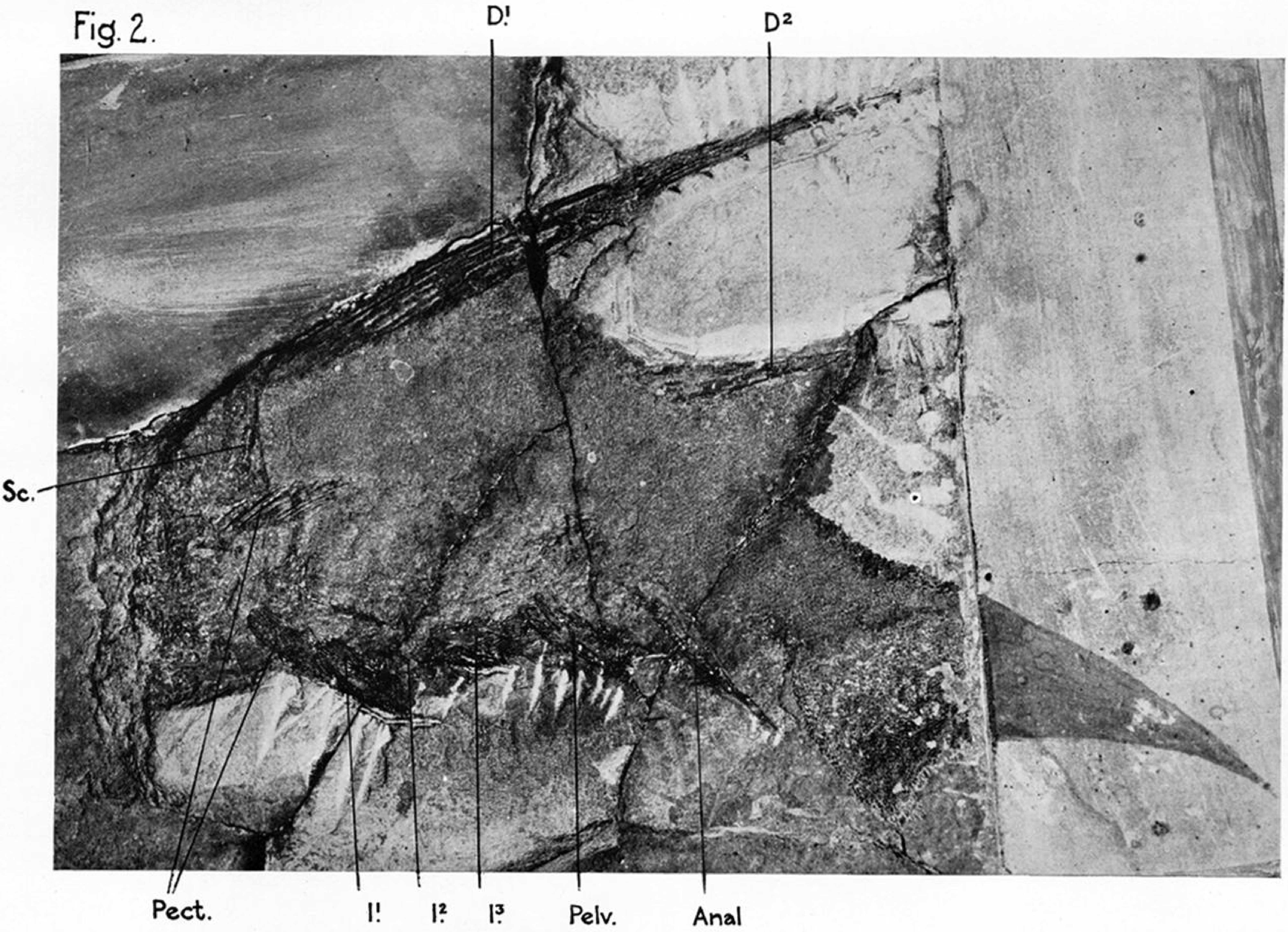


PLATE 11

FIG. 1—*Diplacanthus striatus*, M.O.R.S. Tynet Burn, D.M.S.W. Coll., P. 300. × 3·0. Anterior part of a fish in which the ventral surface from the lower jaws to the pectoral fins is seen from the outer surface, and the lateral and dorsal surfaces of the head are spread out on the left of the figure, represented mainly by impressions of their inner surfaces. Part of the infilling of the lateral line canals remains.

FIG. 2—*Parexus incurvus* AG., L.O.R.S. Turin Hill, Manchester Museum, L. 12097*b*. × 1·5. A nearly complete fish from the left side.

Adm.Pect.Sp. admedian pectoral spine; *Anal*, anal fin spine; *Cor.* coracoid; D^1, D^2, dorsal fins; *Derm.Pl.* dermal plate of the shoulder girdle; I^1, I^2, I^3, intermediate fin spines; *Inf.Or.C.* infra-orbital canal; *Inf.Or.C.b.* posterior median branch of the infra-orbital canal (STENSIO); *Lat.Pect.Sp.* lateral pectoral fin spine; *Mand.Spl.* mandibular splint; *Oc.C.* occipital cross commissure; "*Op.*" large opercular plate; *P.O.* post-orbital plate; *Pect.* pectoral fin spine; *Pelv.* pelvic fin spine; *Sc.* scapula; *Sup.Or.C.* supra-orbital canal.

Fig. 1.

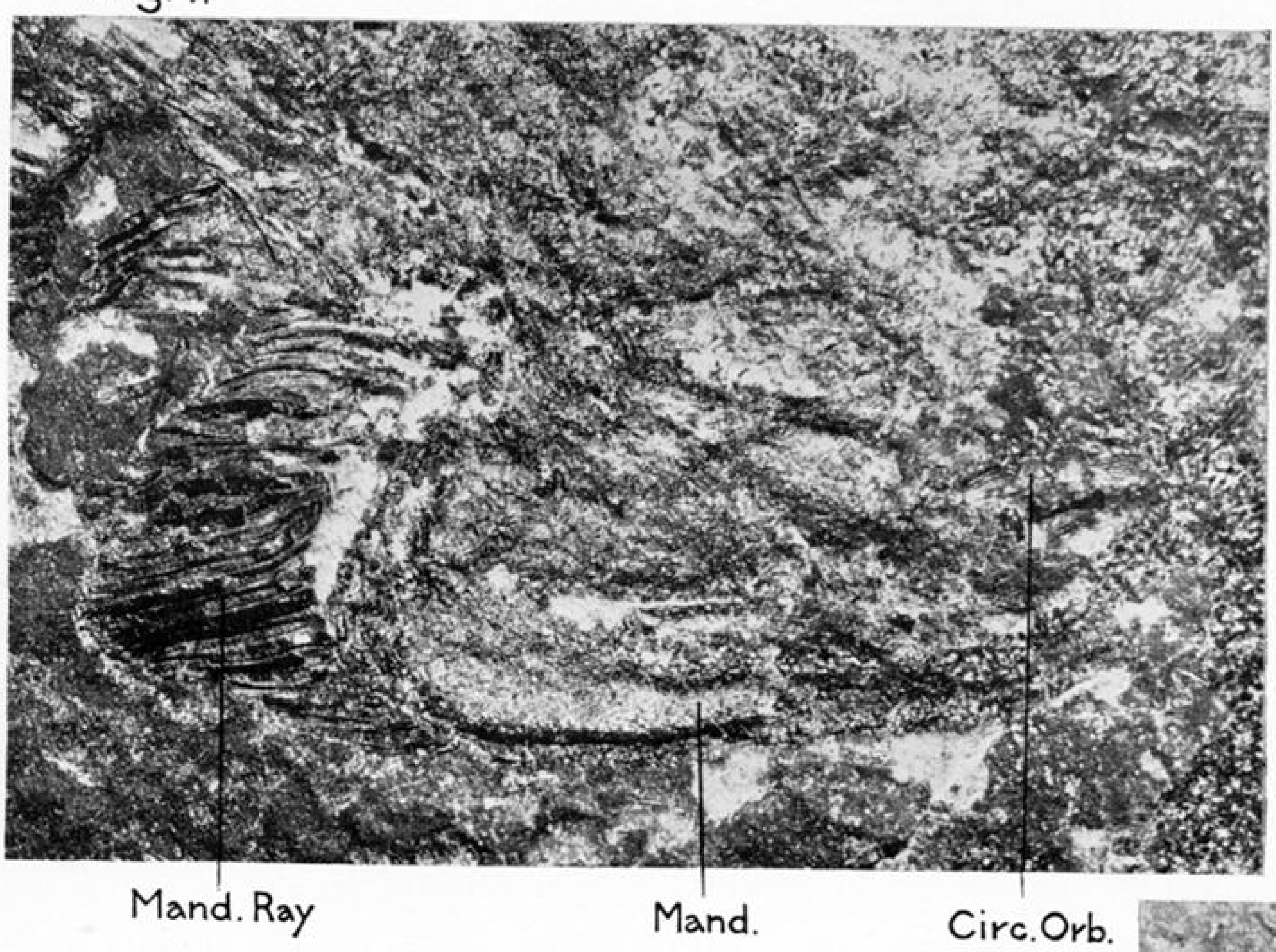


Fig. 2.

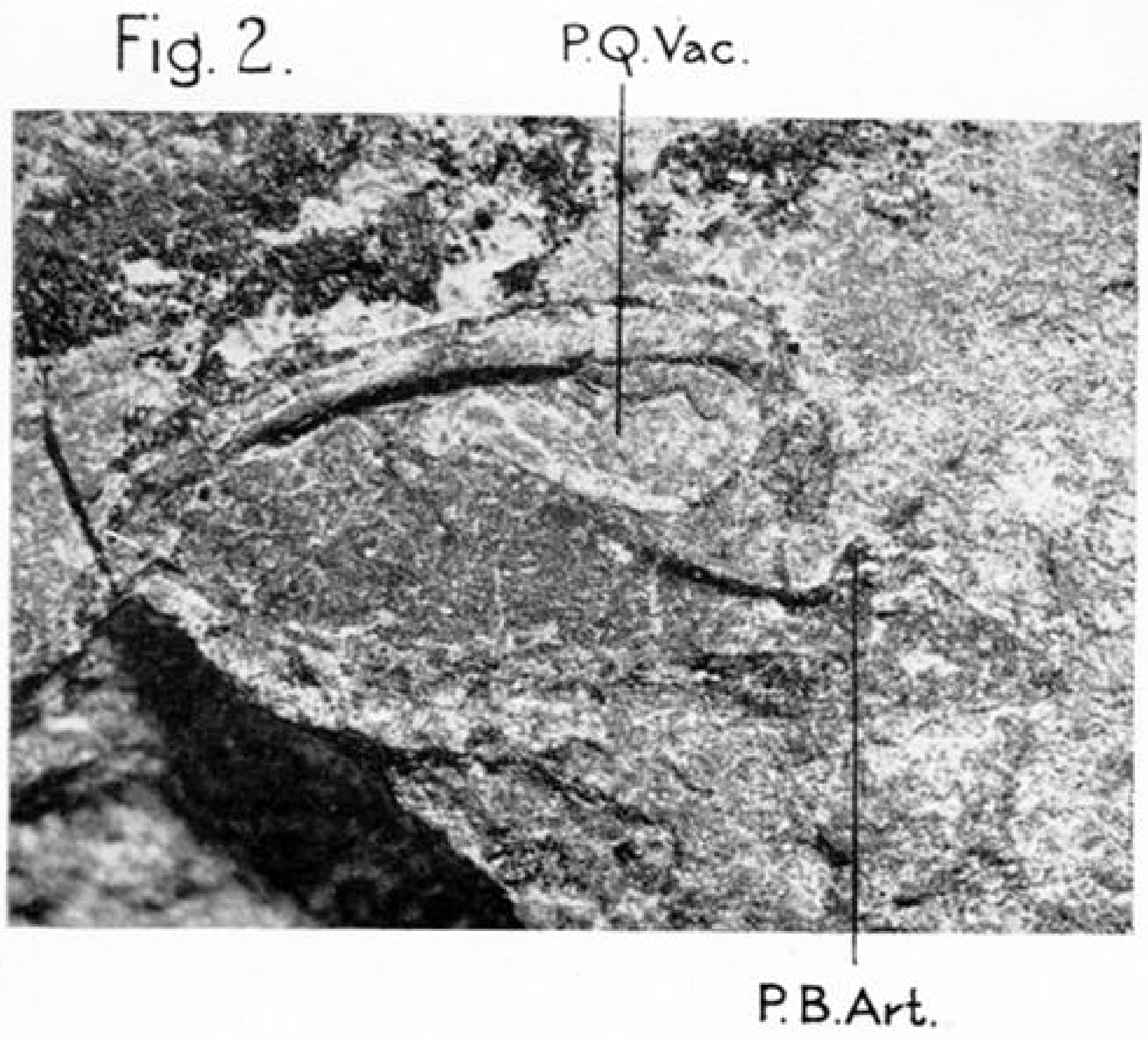


Fig. 3.

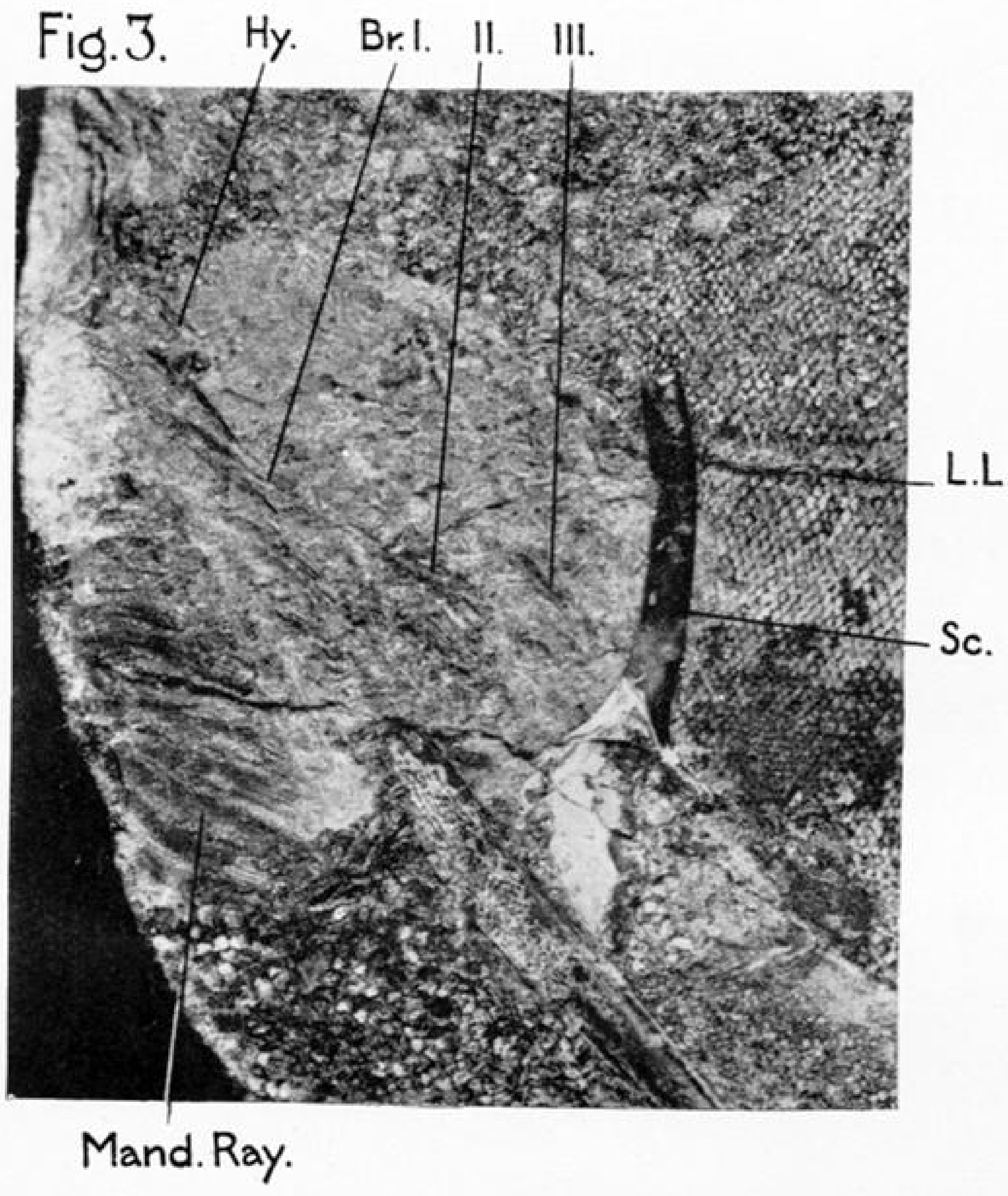


Fig. 4.

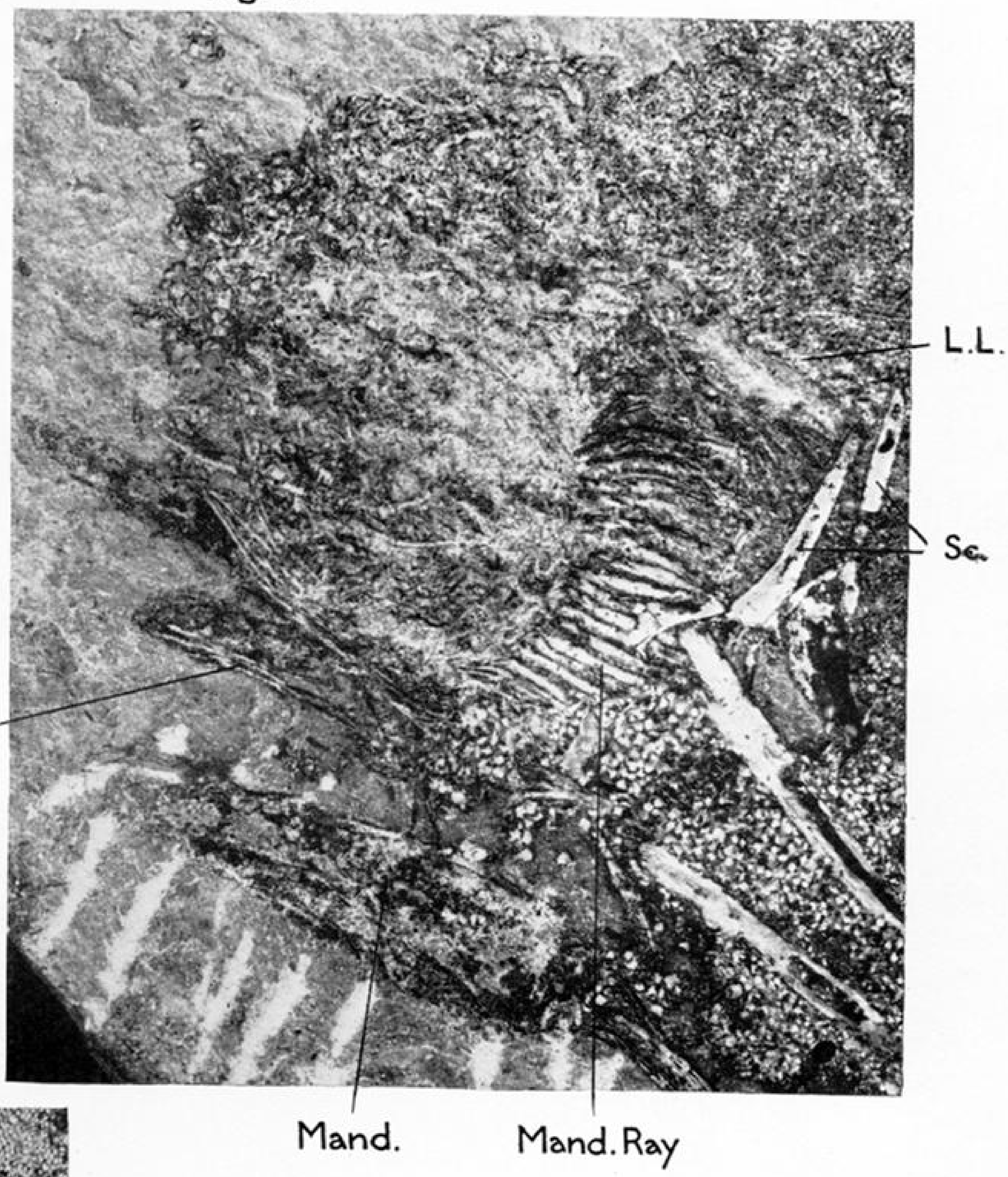


Fig. 5.

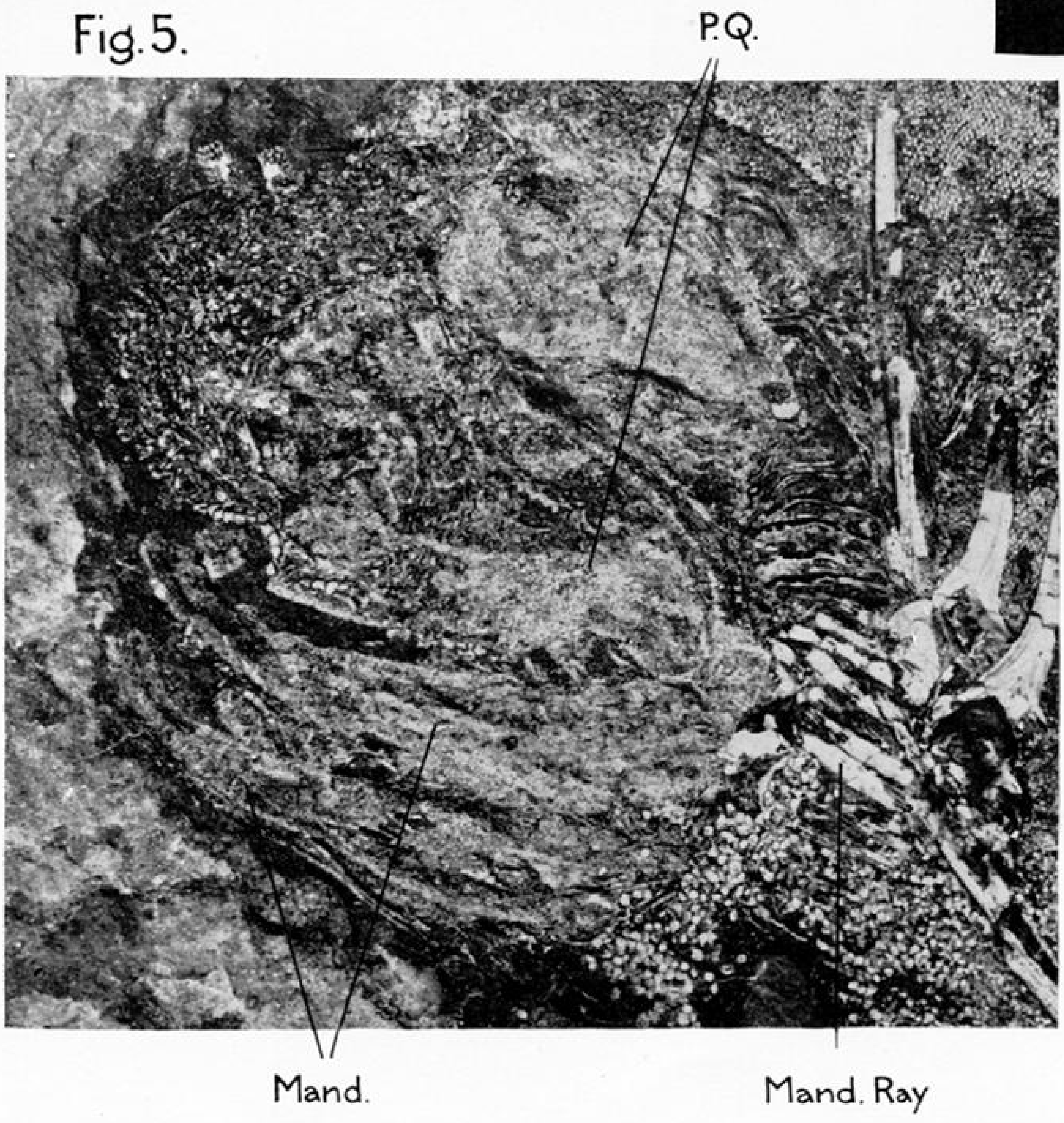


Fig. 6.

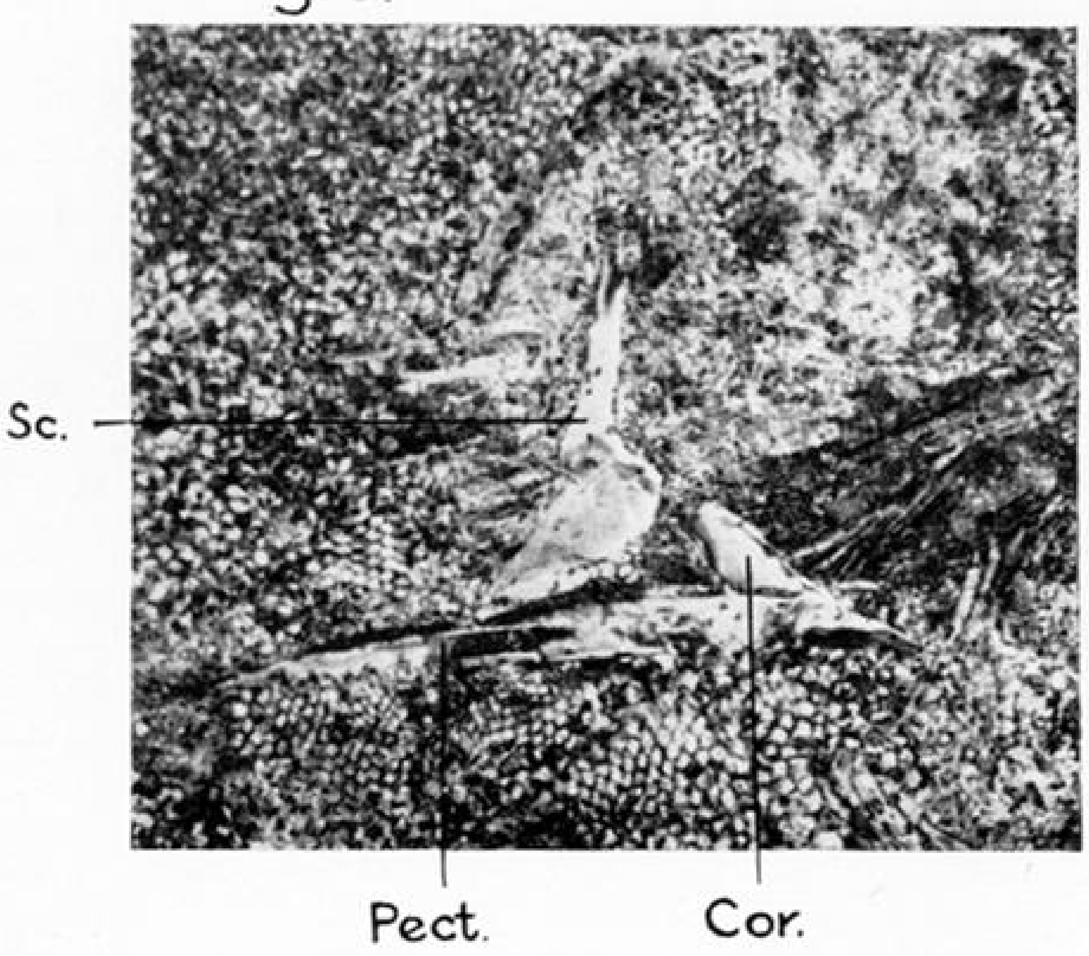


Plate 12

Fig. 1—*Cheiracanthus murchisoni* Ag., M.O.R.S. Gamrie, D.M.S.W. Coll., P. 492. ×3·0. Right side of the head showing the mandibular operculum, and lower jaw.

Fig. 2—*Cheiracanthus murchisoni* Ag., M.O.R.S. Gamrie, U.C.L. Zoo. Dept., C. 21. ×2·0. Isolated right palato-quadrate from its outer surface.

Fig. 3—*Cheiracanthus murchisoni* Ag., M.O.R.S. Tynet Burn, B.M.N.H. 43273*a*. ×2·5. Posterior part of the head to show the mandibular operculum dragged down so as to expose the dorsal end of the hyoid and the slender ossifications in the branchial arches.

Fig. 4—*Cheiracanthus latus* Eg., M.O.R.S. Tynet Burn, B.M.N.H., P. 3253. ×1·9. The head, mainly an impression of the right surface.

Fig. 5—*Cheiracanthus latus* Eg., M.O.R.S. Tynet Burn, Imperial College, Geol. Dept. ×2·2. The head, mainly an impression of the right surface, showing the row of small bones which forms the border of the mouth, and the jaw elements.

Fig. 6—*Cheiracanthus latus* Eg., M.O.R.S. Tynet Burn, D.M.S.W. Coll., P. 509. ×2·4. The right shoulder girdle and pectoral fin spine from without.

Br. I, II, III, dermal bones of the branchial arches; *Circ.Orb.* circumorbital bones; *Cor.* coracoid; *Gu.* gular rays; *Hy.* upper end of the hyoid arch; *L.L.* lateral-line; *Mand.* the ossification in Meckel's cartilage; *Mand.Ray*, a "ray" of the mandibular operculum; *P.B.Art.* palato-basal articulation of the palato-quadrate; *P.Q.* palato-quadrate; *P.Q.Vac.* vacuity in the palato-quadrate; *Pect.* pectoral fin spine; *Sc.* scapula.

Fig. 1.

Fig. 2.

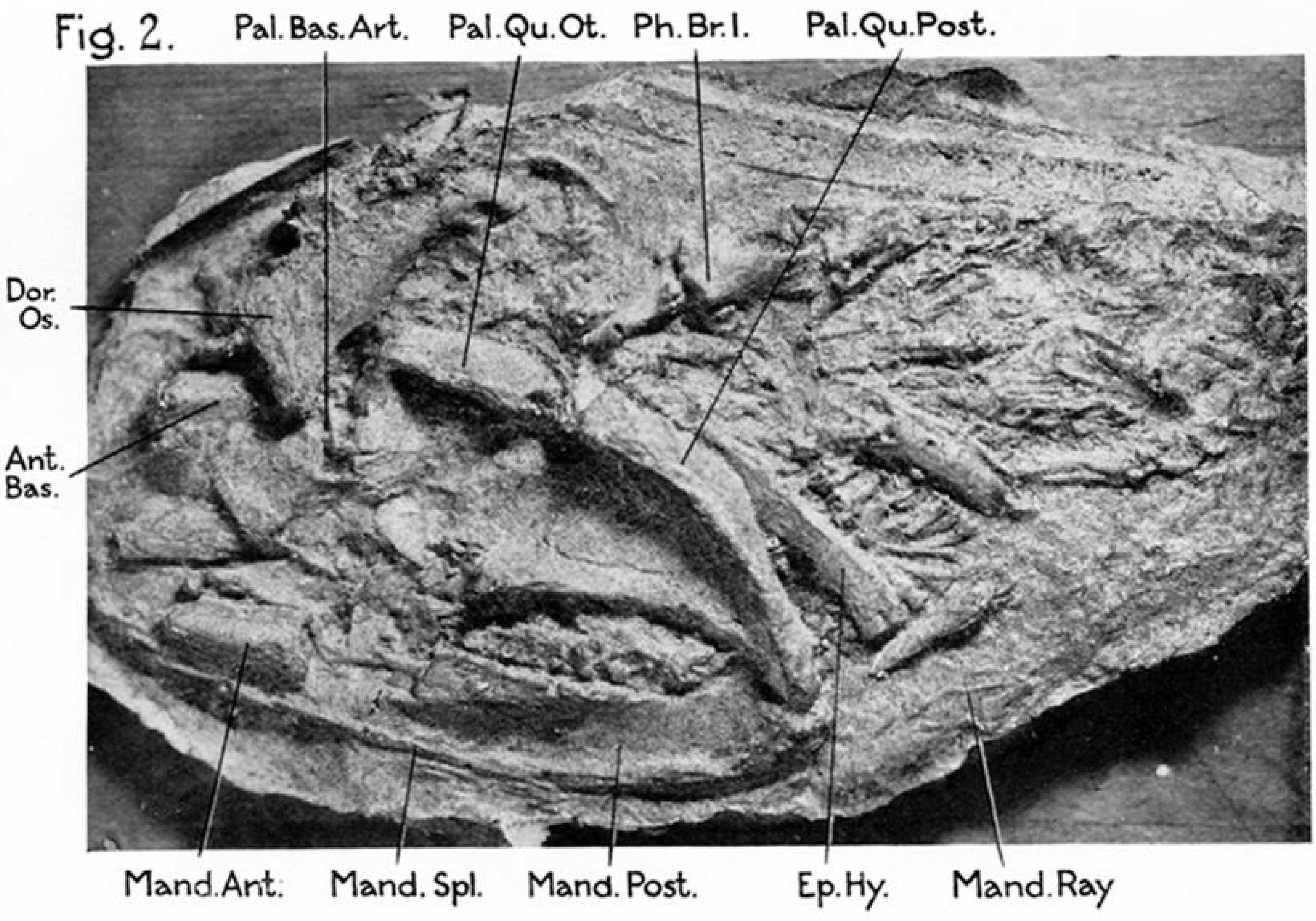


Fig. 3.

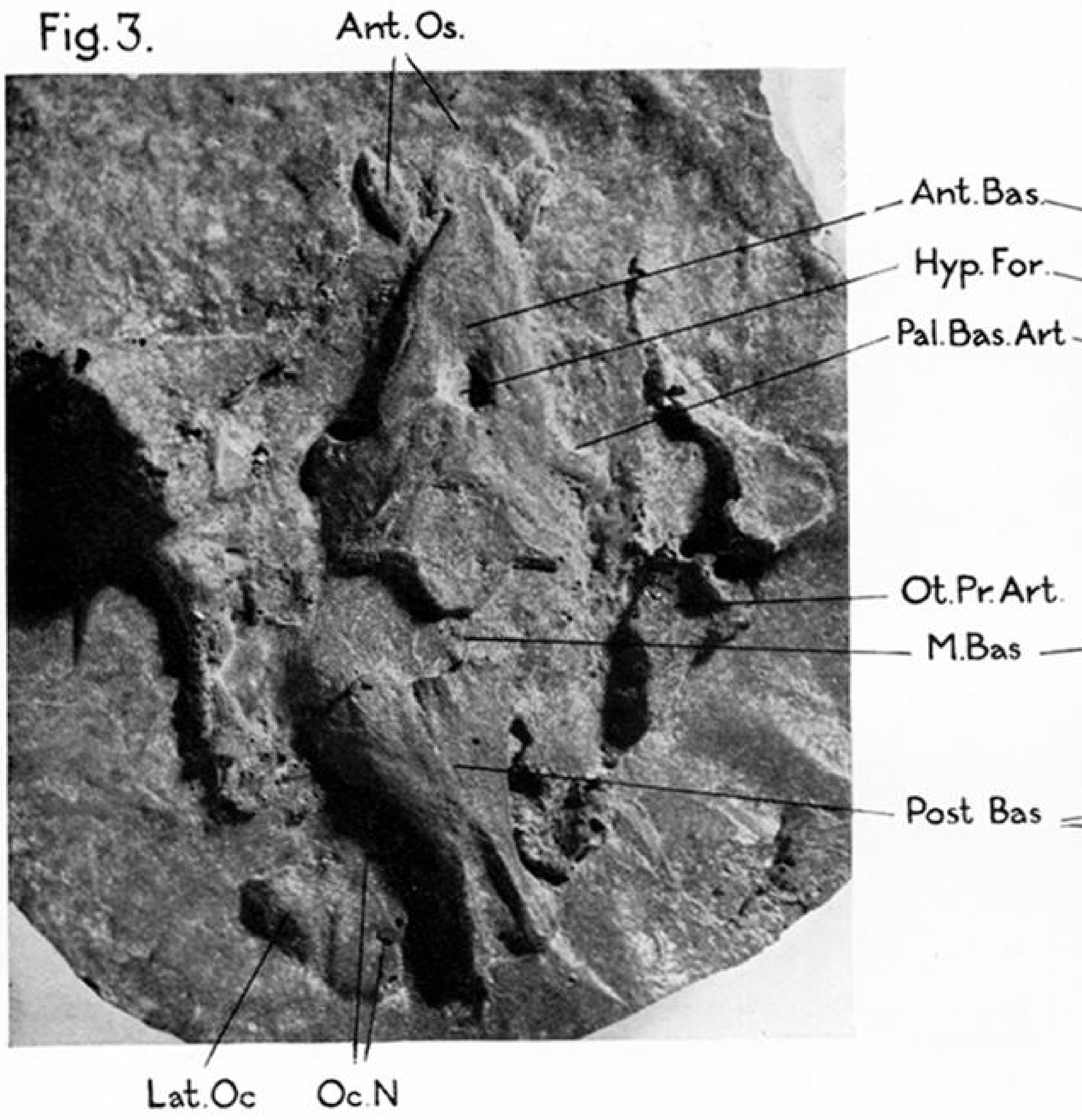


Fig. 4.

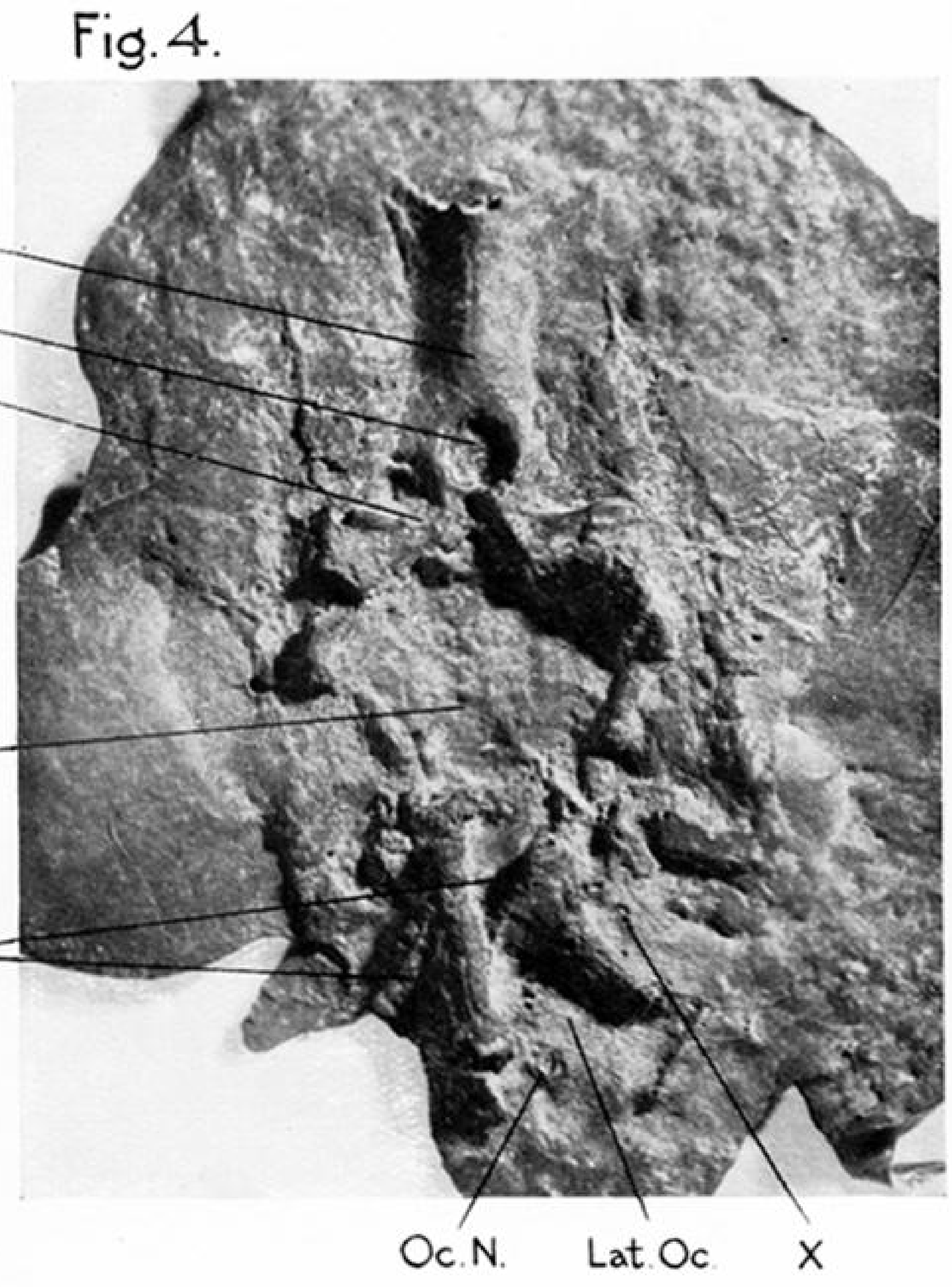


Fig. 5.

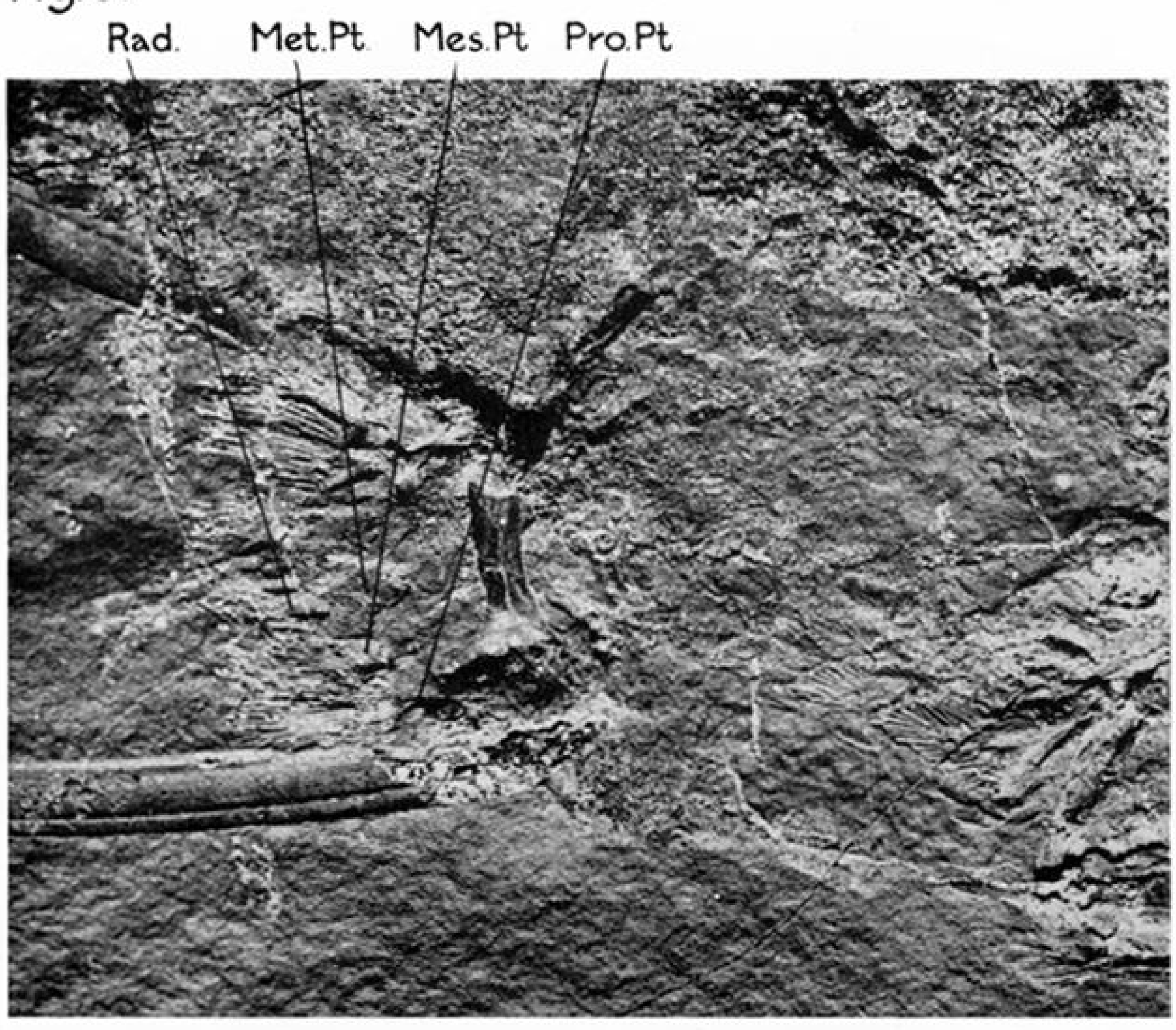


Fig. 6.

PLATE 13

FIG. 1—*Acanthodes Wardi.* M.C.M. Knowles Ironstone, Longton, Staffordshire, Manch. Mus. LL. 181. × 1·4. Fragment of a head showing the series of gill-rakers on the ventral part of the hyoid arch.

FIG. 2—*Acanthodes* sp. Lebach shales. D.M.S.W. Coll., P. 323. × 1·13. Gelatine cast of the head from the left side, showing the left palato-quadrate and lower jaw and other structures.

FIG. 3—*Acanthodes* sp. Lebach shales. D.M.S.W. Coll., P. 495. × 1·25. Gelatine cast of the brain case viewed from below. Cf. text-figs. 17 and 18.

FIG. 4—*Acanthodes* sp. × 1·15. The specimen shown in fig. 3, from the dorsal aspect, a gelatine cast from the counterpart.

FIG. 5—*Acanthodes* sp. Lebach ironstones. D.M.S.W. Coll., P. 498. × 1·42. To show the pectoral fins.

FIG. 6—*Acanthodes* sp. Lebach ironstones. Berlin Museum, unnumbered. × 1·4. The tail of a small individual.

Ant.Bas. anterior basal; *Ant.Os.* anterior bones of the neural cranium; *Dor.Os.* dorsal bone of the neural cranium; *Ep.Hy.* epi-hyoid; *Hy.Gill-raker*, gill-raker on the hyoid arch; *Hyp.For.* hypophysial foramen; *Lat.Oc.* lateral occipital; *Mand.Ant.* anterior bone in Meckel's cartilage; *Mand.Post.* posterior bone in Meckel's cartilage; *Mand.Ray*, a "ray" in the mandibular operculum; *Mand.Spl.* mandibular splint; *M.Bas.* middle basal bone in the neural cranium; *Mes.Pt.* mesopterygium; *Met.Pt.* metapterygium; *Oc.N.* foramina for occipital nerves; *Ot.Pr.Art.* articulation of the otic process; *Pal.Bas.Art.* palato-basal articulation; *Pal.Q.Post.* posterior bone in the palato-quadrate; *Pal.Q.Ot.* otic process of the palato-quadrate; *Ph.Br.* I, first pharyngo-branchial; *Post.Bas.* posterior basal bone in the neural cranium; *Pro.Pt.* propterygium; *Rad.* radial; *X*, notch for the tenth nerve.

Fig. 1

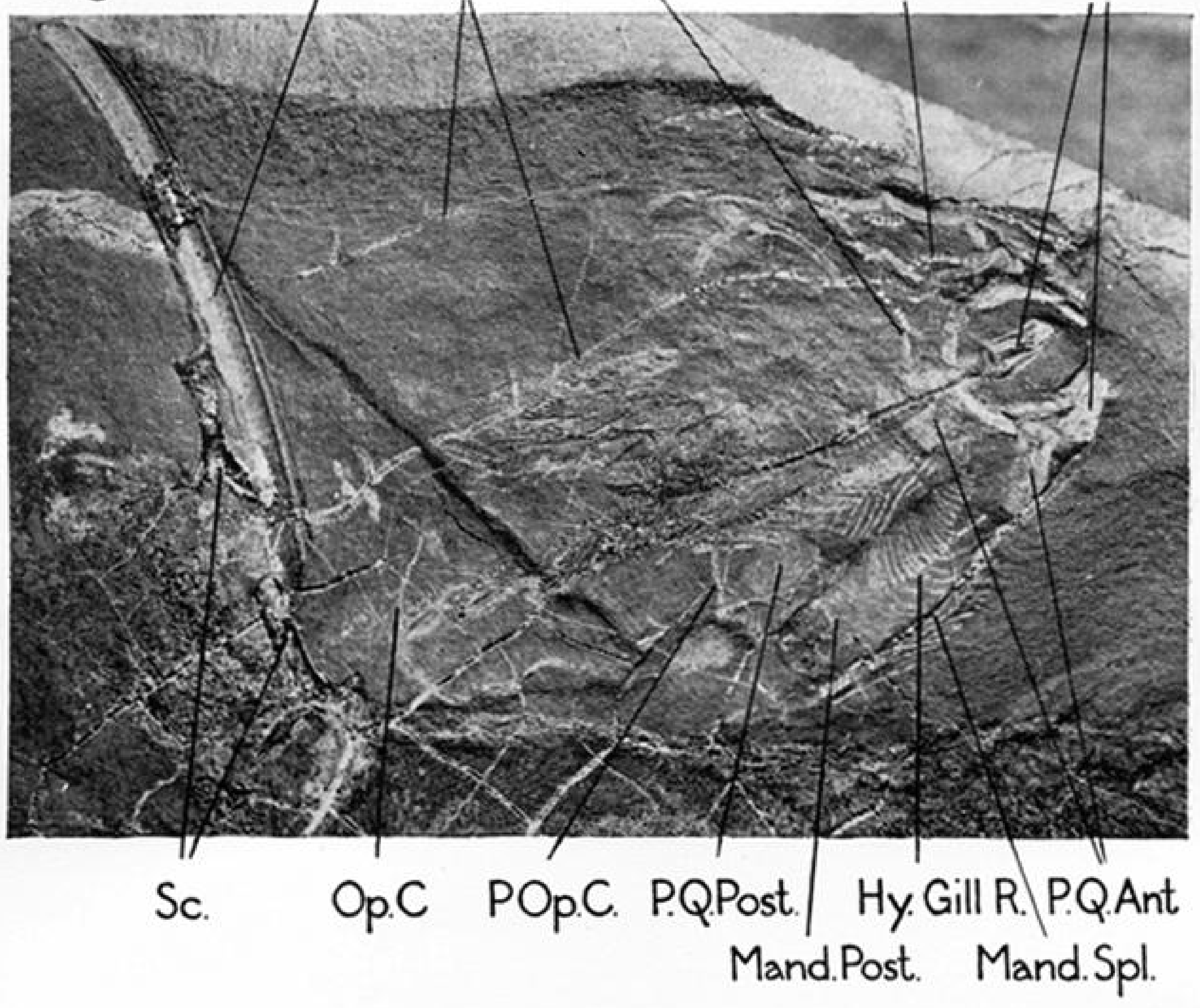


Fig. 2

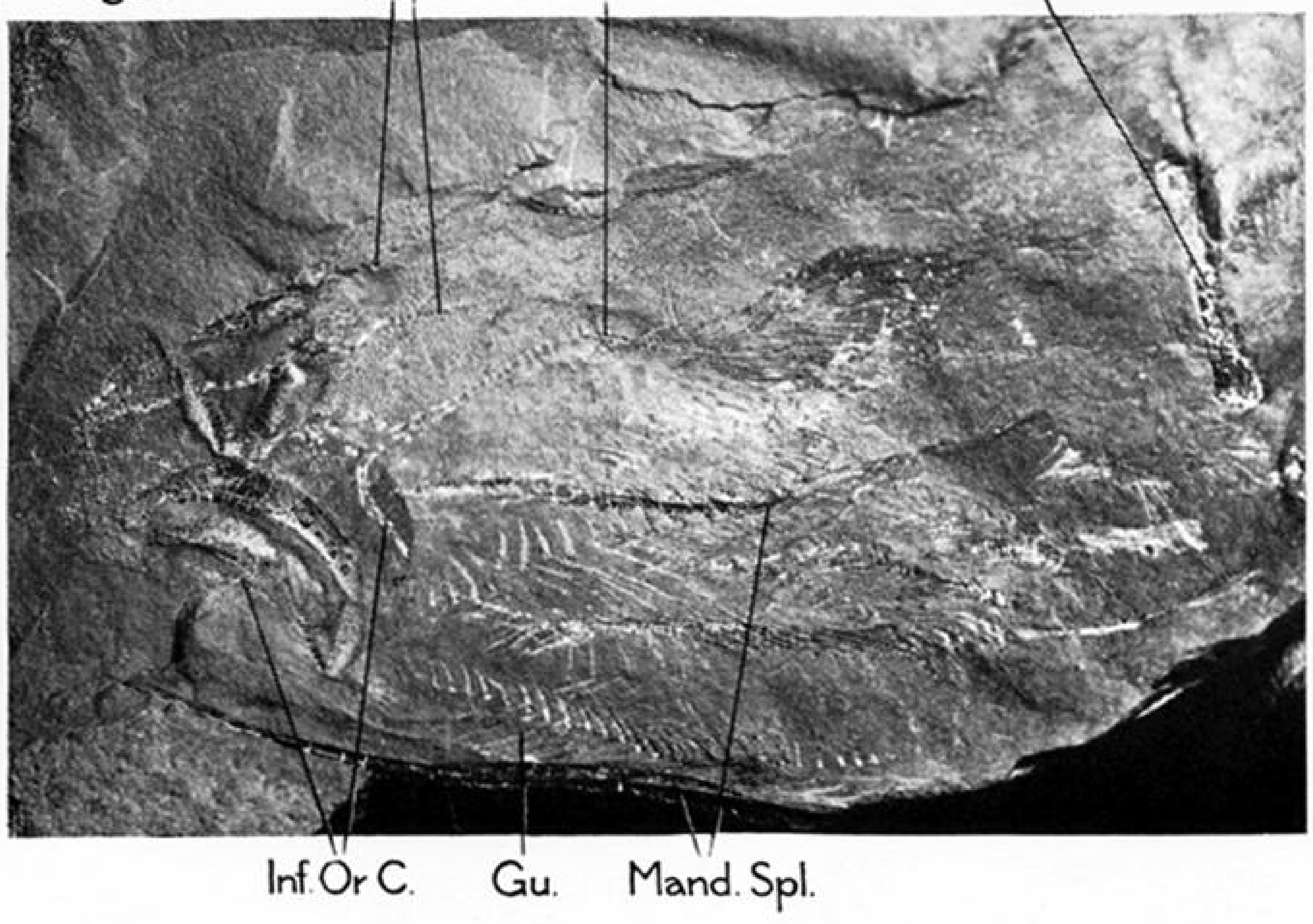


Fig. 3

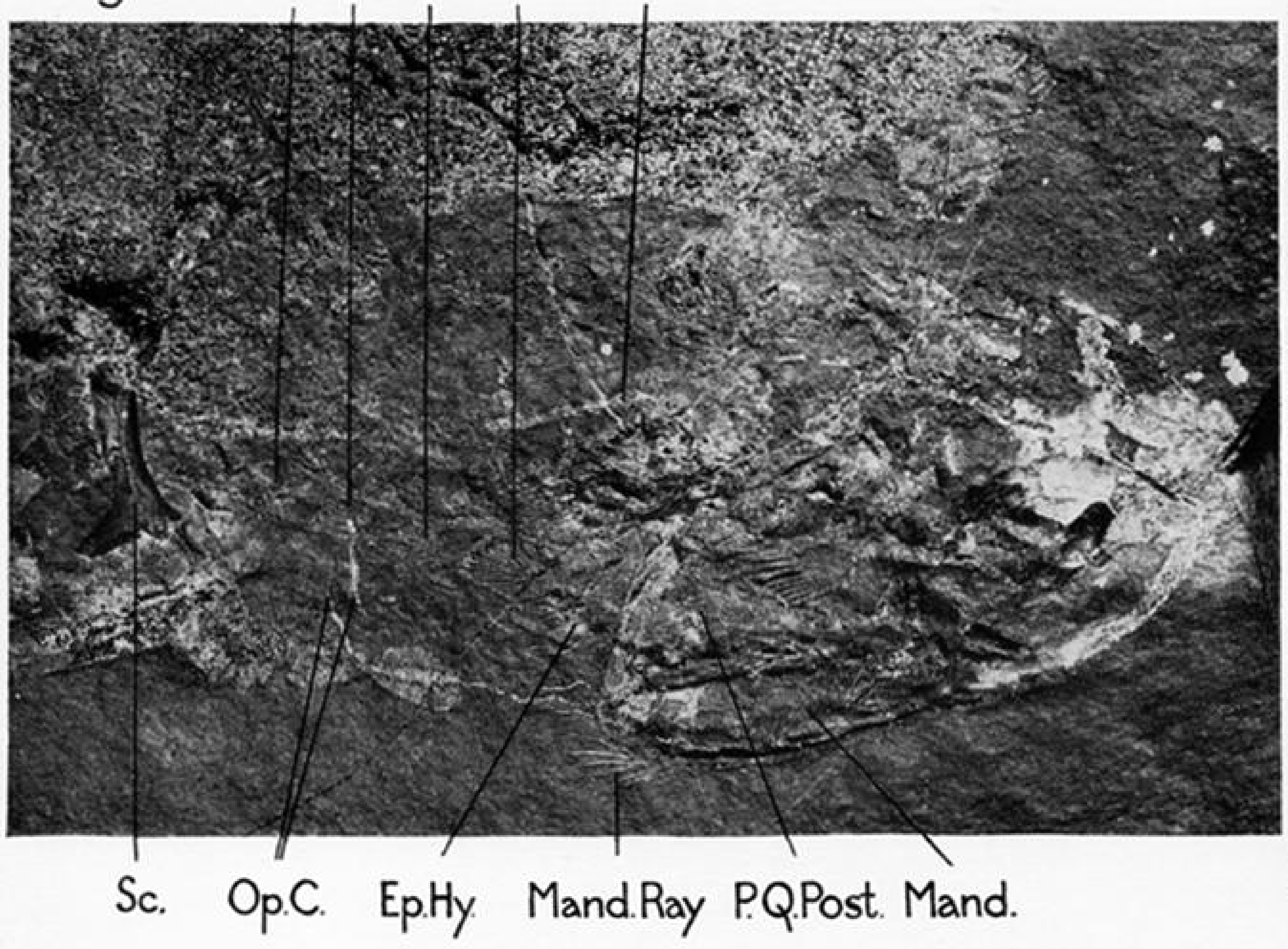


Fig. 4

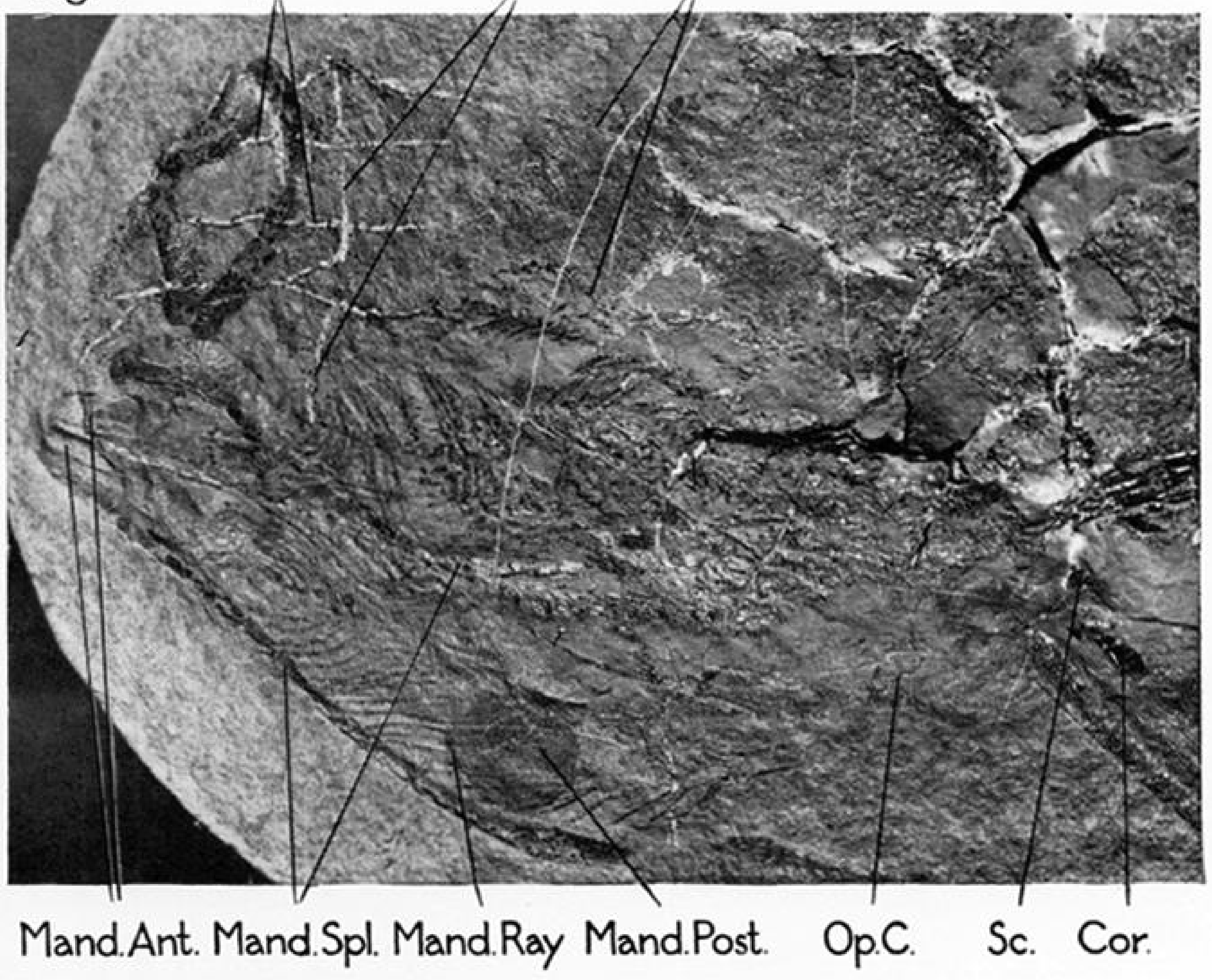


Fig. 5

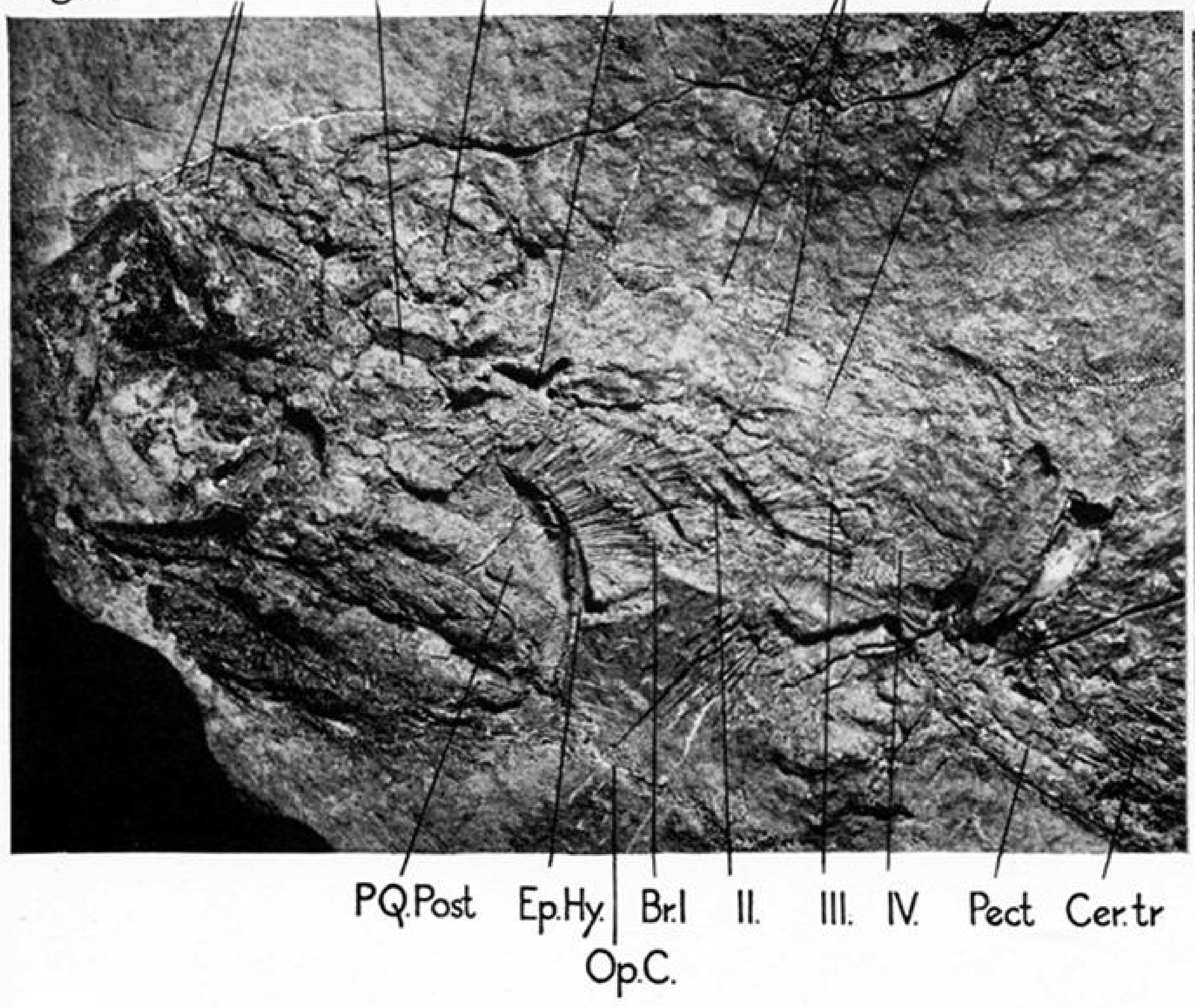


Fig. 6

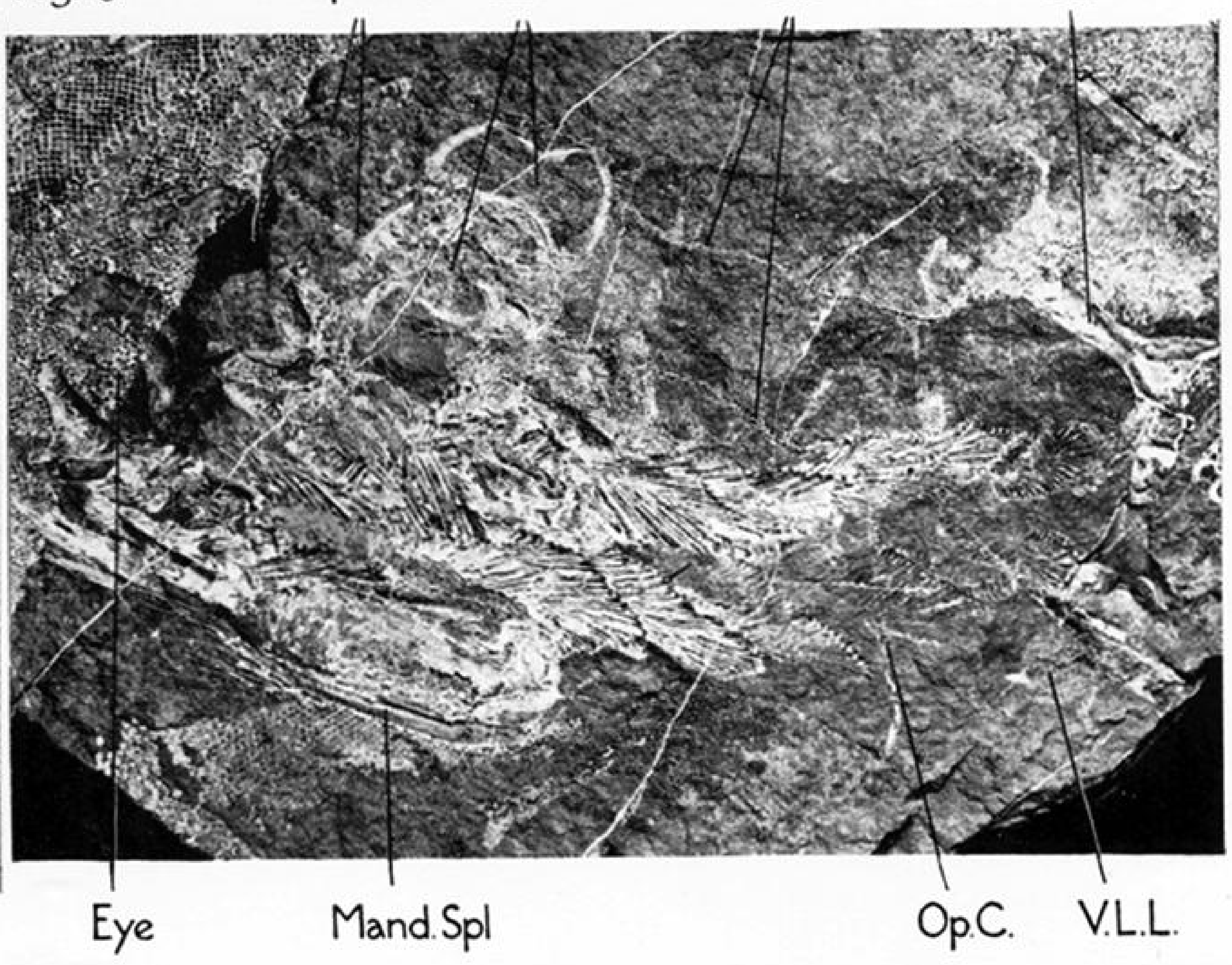


PLATE 14

Photographs of medium sized specimens of *Acanthodes* from the Lebach ironstones of the Saar, Lower Permian. It is probable that each specimen is specifically different from the others.

In every figure except 6 some part of the lateral-line system retains in cavities traces of white paint.

Fig. 1—D.M.S.W. Coll., P. 496. ×1·15. Head viewed from the right. Compare text-fig. 20D.

Fig. 2—Royal Scottish Museum 1891, 42, 3. ×1·52. Head viewed from the left.

Fig. 3—D.M.S.W. Coll., P. 498. ×1·2. Head viewed from the right. Compare text-fig. 20C.

Fig. 4—B.M.N.H., No. 22658*a*. ×1·3. Compare text-fig. 20B.

Fig. 5—D.M.S.W. Coll., P. 494. ×1·05. Head viewed from the left. Compare text-fig. 20A.

Fig. 6—Royal Scottish Museum, unnumbered. ×1·08. Head from the left.

Br. I–IV, the branchial arches, usually only represented by the gill-rakers; *Cer.tr.* ceratotrichia; *Cor.* coracoid; *Ear*, the semicircular canals; *Ep.Hy.* epi-hyal; *Eye*; *Gu.* gular rays of the mandibular operculum; *Hy.Gill R.* hyoid gill-raker; *Inf.Or.C.* infra-orbital canal; *L.L.* lateral-line; *L.Sup.Or.C.* left supra-orbital canal; *Mand.Ant.* anterior bone in Meckel's cartilage; *Mand.Post.* posterior bone in Meckel's cartilage; *Mand.Ray*, a "ray" in the mandibular operculum; *Mand.Spl.* mandibular splint; *Op.C.* opercular canal; *P.Op.C.* pre-opercular canal; *P.Q.Ant.* anterior bone in the palato-quadrate; *P.Q.Ot.* otic process of the palato-quadrate; *P.Q.Post.* posterior bone in the palato-quadrate; *Pect.* pectoral fin spine; *Phar.Br.* II, the pharyngobranchial of the second arch; *Sc.* scapula; *Sup.Or.C.* supra-orbital canal; *V.L.L.* ventral lateral-line.