THE PHYLOGENY OF THE CHIMAEROIDS

By C. PATTERSON
British Museum (Natural History)

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[Plates 22 to 28]

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The purpose of this paper is to examine the evidence afforded by the chimaeroids and fossil holocephalans on the origin and evolution of the Holocephali, and, in particular, on the hypothesis recently proposed by Ørvig of a relationship between chimaeroids and ptyctodont arthrodires.

Members of all the fossil holocephalan groups which are known by moderately complete specimens except the petalodonts and edestids are described, particular attention being paid to the histology of the dermal skeleton. Three species from the English Lower Lias, *Squaloraja polyspondyla* Agassiz, *Myriacanthus paradoxus* Agassiz and *Metopacanthus granulatus* (Agassiz) (a species previously placed in *Myriacanthus*) are described in detail. From the British Lower Carboniferous *Deltoptychius armigerus* (Traquair), previously placed in *Oracanthus*, is described in detail and two new species, *Deltoptychius moythomasi* sp.nov. and *Menaspacanthus armaghensis* gen. and sp.nov., are described on fragmentary material. The genus *Oracanthus* Agassiz is reviewed: it is shown that the type species is probably acanthodian but that many species have been wrongly included in the genus.

There is found to be strong evidence that the chimaeroids are derived, through the Jurassic myriacanthids and allied forms, from a Palaeozoic group which includes the Permian *Menaspis* and whose most primitive known genus is *Deltoptychius*. The most striking feature of *Deltoptychius* is the dermal armour of dentine-like tissue on the head which includes a complete head shield bearing a pair of sensory canals. This armour is of a peculiar type which is not homologous with the armour of the arthrodires, and appears to be confined to the Chimaeriformes. It is suggested that *Helodus* is not directly related to the Chimaeriformes. These conclusions are embodied in a new classification of the Holocephali in which *Helodus* is made the type of a new order Helodontiformes and in which the Chimaeriformes is divided into four sub-orders, Chimaeroidei, Squalorajoidei, Myriacanthoidei and Menaspoidei, with new families being made in the last two sub-orders.

On the basis of the information obtained from the systematic part, the origin and evolution of the various characters of chimaeroids are discussed. The ethmoid canal appears to be a recent acquisition which occurs only in Chimaeroidei. The tritors on chimaeroid tooth plates are another recent adaptation. There is no convincing evidence that the teeth of Holocephali were primitively numerous, as they are in *Helodus*, petalodonts and edestids: this 'selachian' type of dentition is quite possibly secondarily derived from a 'chimaeroid' type of dentition. The dorsal fin spine of the chimaeroids appears to be a recent adaptation which first appears in the myriacanthoids and has arisen independently, being unrelated to the fin spine of *Helodus*. A series of changes has taken place in the structure of the fin spine in Chimaeriformes which is similar to the changes which have occurred in the fin spines of sharks. The scales of *Deltoptychius* are cyclomorial: the change from a cyclomorial to a placoid (synchronomorial) scale has taken place independently among elasmobranchs at least three times: in the selachians, in the edestids, and in the Chimaeriformes. The scales of *Helodus* are synchronomorial: this is the only Palaeozoic elasmobranch in which this condition has yet been found. The crescentic calcifications surrounding the sensory canals of chimaeroids are shown to be modified scales. The pre-pelvic tenacula of male chimaeroids have evolved from groups of enlarged scales without skeletal support which occur in myriacanthoids. It is suggested that the frontal clasper of male chimaeroids has evolved from paired structures, defensive in function, which occurred in both sexes in Palaeozoic Chimaeriformes. The dermal armour of Chimaeriformes is formed by fusion of scales. It has undergone a series of changes in histological structure which is similar to that undergone by the dorsal fin spine, but which took place much earlier in time.

The evidence for a relationship between Holocephali and the selachians or arthrodires is reviewed. It is concluded that there is evidence of relationship between holocephalans and arthrodires, but that the resemblances between the two groups are in general features only. Mainly because of the structure of the exoskeleton in *Deltoptychius*, a relationship with the ptyctodonts is very unlikely. The holocephalans seem to be closest to the most primitive arthrodires (rhenanids and stensioellids), suggesting that the two groups share a common ancestor but are not directly related.

I. INTRODUCTION

The chimaeroids, the only living holocephalans, are a small group of marine fishes which appear to be the specialized survivors of a large and varied group, marine throughout its history, which in late Palaeozoic times contained the dominant durophagous fishes, replacing the arthrodires in this role, and in turn being replaced by the rays and by specialized actinopterygians. Studies on the phylogeny of the holocephalans are limited by two factors, difficulty in obtaining embryological material of living forms and the great rarity of fossils in which more than tooth plates is preserved. For these reasons, ideas on the ancestry of the chimaeroids have been varied and largely hypothetical. But recently new information on possible arthrodire ancestors of the holocephalans has been published: this new information suggested that a re-examination of the known fossil holocephalans might be of value.

In 1935 de Beer & Moy-Thomas (p. 295) confirmed Schauinsland's (1903, p. 10) observation that in the living chimaeroid *Callorhynchus* the hyoid arch is complete and unmodified, with a pharyngohyal,* and is similar in shape to the branchial arches. From this it follows that the Holocephali were never hyostylic or amphistylic, and cannot be derived from a shark-like ancestor, as many earlier authors, especially Dean (1906), had believed. Any similarities between Holocephali and Selachii must either have evolved independently in the two groups, or must be retained from ancestors in which the palatoquadrate was neither supported by the hyomandibular nor fused with the braincase (autodiastylic, de Beer & Moy-Thomas, 1935, p. 307). De Beer & Moy-Thomas held the view that the Holocephali are related to the arthrodires, a hypothesis first suggested by Stensiö (1925, p. 189). Holmgren (1942, p. 187) carried this idea further and showed that there were grounds for regarding the holocephalans as derived from the neighbourhood of the Ptyctodontida, a group of Middle and Upper Devonian arthrodires of which only *Rhamphodopsis* Watson (1938) was then well known. Recently, Ørvig (1960, 1962) has given a detailed description of a second ptyctodont, *Ctenurella gladbachensis* Ørvig, and has produced additional evidence in support of a relationship between Holocephali and Ptyctodontida. Ørvig believes that the ptyctodonts are related only to the chimaeroids, not to the bradyodonts. Moy-Thomas (1939, p. 11), on the other hand, believed that there was a close relationship between the bradyodonts and the chimaeroids. The results of the present work strongly support Moy-Thomas's view.

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* Watson (1937, p. 141) has criticized de Beer & Moy-Thomas's interpretation of the pharyngohyal, because in their figure of a reconstructed embryo of *Callorhynchus* the tip of the pharyngohyal lies lateral to the efferent hyoidean artery while the pharyngobranchials lie medial to their efferent arteries, and that it is by just such a variation in position relative to the artery that de Beer (1932, p. 310) recognized the pseudohyal in rays. To my knowledge this criticism has not yet been answered, and Moy-Thomas (1939, p. 4) seems to have accepted it in suggesting that the non-suspensory hyoid of holocephalans is secondary. Stensiö (1963, p. 377) also finds the condition of the hyoid arch to be secondary, basing this conclusion on his interpretation of the hyomandibular in ptyctodonts and more generalized arthrodires.

The method employed here is to list the peculiar characters of living chimaeroids and then to pass back in time reviewing each fossil group and comparing it with chimaeroids. Throughout this work the term 'chimaeroid' refers to the sub-order Chimaeroidei as defined on p. 109. The material used is mainly in the British Museum (Natural History), referred to as BMNH, and where a specimen is cited by a number without prefix or with the prefix 'P' it is in this collection. Specimens from the Royal Scottish Museum, Edinburgh, are cited with the prefix RSM, and from the collection of H.M. Geological Survey, London, with the prefix GSM.

II. CLASSIFICATION

In 1921 Smith Woodward (p. 34) proposed that the four Palaeozoic elasmobranch families Petalodontidae, Cochliodontidae, Psammodontidae and Copodontidae should be united in an order Bradyodonti, characterized by slowness of tooth replacement, with not more than seven or eight successional teeth during the life of the individual. Smith Woodward suggested that the bradyodonts were intermediate between the primitive elasmobranchs and the chimaeroids.

Nielsen (1932, p. 20) described well-preserved material of the edestids *Agassizodus* and *Fadenia*, and proposed that the Edestidae should be included in the Bradyodonti because of the bradyodont-like arrangement and microstructure of their teeth. Nielsen also held that the Carboniferous genus *Orodus*, known only by isolated teeth, should be placed in the Bradyodonti as the only member of a family Orodontidae, because of the similarity of its teeth in shape and microstructure to the lateral teeth of edestids. Moy-Thomas (1936*b*) showed that the Upper Carboniferous cochliodont *Helodus simplex* (in which only one or two of the successional tooth rows are fused into tooth plates) resembles the chimaeroids in its holostylic suspension, the shape and general structure of its skull, the anatomy of its pectoral fin, the separation of the two halves of its pelvic girdle, and the presence of a single spine in front of the first dorsal fin. Moy-Thomas (1936*a*, p. 500) therefore proposed that the bradyodonts as defined by Nielsen, the chimaeroids and the chondrenchelyids (Moy-Thomas, 1935*b*, p. 402) form a natural group characterized by the microstructure of their teeth and possibly also by holostylic jaw suspension. In 1939 Moy-Thomas expanded these ideas, and proposed the following classification:

Sub-class Elasmobranchii
  Division Bradyodonti
    Order 1 Eubradyodonti
      Sub-order 1 Cochliodonti
      Sub-order 2 Holocephali
      Sub-order 3 Petalodonti
      Sub-order 4 Psammodonti
      Sub-order 5 Copodonti
      Sub-order 6 Edestidi
    Order 2 Chondrenchelyidi

Moy-Thomas considered that the Holocephali are the direct descendants of the Cochliodonti. The edestids he thought might be a heterogeneous group, some being bradyodont (in the sense of tooth structure), others selachian. Similarly, he agreed with Nielsen that *Orodus ramosus* should be placed in the bradyodonts on account of its tooth structure, but thought that some forms described as *Orodus* might in fact be selachians. Nielsen (1952, p. 19) has since shown that the edestid *Sarcoprion* is holostylic, and has confirmed the position of the edestids.

Since 1939 three other classifications of the bradyodont group have been published, by Berg (1940, p. 139, modified in 1955, p. 74), by Arambourg & Bertin (1958, p. 2057), these two classifications being part of general classifications of fishes, and by Obruchev (1953, p. 57) in a work on the edestids. These classifications are set out below.

Berg (1955)

- class Holocephali
  - sub-class Chondrenchelyes
  - sub-class Chimaerae
    - order Chimaeriformes
      - family Cochliodontidae
      - family Menaspidae
      - family Petalodontidae
      - family Janassidae
      - family Psammodontidae
      - family Copodontidae
      - family Myriacanthidae
      - family Squalorajidae
      - family Chimaeridae, etc.
      - family *incertae sedis*:
      - Edestidae
      - Helicoprionidae
      - Radamantidae

Arambourg & Bertin

- class Chondrichthyes
  - sub-class Bradyodonti
    - super-order Eubradyodonti
      - family Cochliodontidae
      - family Petalodontidae
      - family Psammodontidae
      - family Copodontidae
      - family Edestidae
      - family Chondrenchelyidae
    - super-order Holocephali
      - family Myriacanthidae
      - family Squalorajidae
      - family Chimaeridae, etc.

Obruchev

- sub-class Holocephali
  - super-order Chondrenchelyes
  - super-order Chimaerae
    - order Cochliodontiformes
    - order Janassiformes
    - order Psammodontiformes
    - order Copodontiformes
    - order Menaspiformes
    - order Edestiformes
    - order Chimaeriformes

Arambourg & Bertin still include the bradyodonts with the selachians as sub-classes of the Chondrichthyes, but Berg makes the holocephalans and selachians separate classes. Since there is no evidence that the two groups are directly related (see p. 206), there is no valid reason for associating them in opposition to the arthrodires. Stensiö (1936, p. 30) has proposed a 'branch' Elasmobranchii to include four 'sub-branches', the arthrodires, acanthodians, selachians and holocephalans: the less ambiguous term Elasmobranchiomorphi (Jarvik 1960, p. 20) is to be preferred for this group. More recently Stensiö (1963, p. 410) has radically revised his grouping in the Elasmobranchiomorphi. He now places the acanthodians in a separate class, an opinion endorsed by Miles (1964, p. 459), and divides the Elasmobranchiomorphi as follows:

- sub-class 1 Elasmobranchii
  - Cratoselachii, Cladoselachii, Ichthyotomi, Bradyodonti, Selachii, Rajiformes
- sub-class 2 Placodermata
  - super-order Arthrodira
  - super-order Holocephali

This wide separation of the holocephalans and bradyodonts is not supported by the material described below. In this paper the Elasmobranchiomorphi will be regarded as comprising the three classes Arthrodira, Holocephali and Selachii.

Whether the group containing the bradyodonts and chimaeroids should be called the Bradyodonti or Holocephali is not yet fixed. Of the two names, Holocephali is certainly the older, and as Nielsen (1932, p. 20) notes, the name Bradyodonti is unsuitable for a group containing the edestids, in which tooth replacement was often very rapid. In the absence of evidence that any member of the group is not holostylic, Berg's and Obruchev's use of the name Holocephali is preferable. Within the Holocephali, again the classifications of Berg and Obruchev appear more logical, since they combine the typical bradyodonts and the chimaeroids in the same group, rather than separating them as do Arambourg & Bertin. The old family groups of the bradyodonts, which Moy-Thomas raised to sub-ordinal rank, are retained as families by Berg and by Arambourg & Bertin but are made orders by Obruchev. Obruchev's procedure has three advantages, it brings the classification of the Holocephali into line with that of other classes of fishes, it allows families to be recognized within the groups, as has already been done within the Chimaeriformes, and as is done in the Edestiformes by Obruchev, and it recognizes that in those cases where much of the anatomy is known ordinal status appears justified.

The present study suggests that the relationships between the holocephalans is expressed more precisely in the following new classification.

Super-class Elasmobranchiomorphi

- Class Holocephali
  - Order 1 Chimaeriformes (definition see p. 109)
    - Sub-order Chimaeroidei (definition see p. 109)
    - Sub-order Squalorajoidei (definition see p. 116)
    - Sub-order Myriacanthoidei (definition see p. 127)
    - Sub-order Menaspoidei (definition see p. 148)
      - *incertae sedis* Family Cochliodontidae
  - Order 2 Copodontiformes
  - Order 3 Psammodontiformes
  - Order 4 Helodontiformes (definition see p. 177)
  - Order 5 Petalodontiformes
  - Order 6 Edestiformes
  - Order 7 Chondrenchelyiformes (definition see p. 184)

The cochliodontids (*Cochliodus*, *Deltodus*, *Sandalodus*, etc.) are placed as Chimaeriformes *incertae sedis* since they are known only by tooth plates, and only in *Cochliodus* is the dentition known more or less completely. The dentition of cochliodonts agrees with the Chimaeriformes, but until more of the anatomy is known, particularly whether they bore armour on the head, their precise position and rank within the Chimaeriformes will not be known.

The Copodontiformes and Psammodontiformes are each known only by isolated teeth and are of doubtful position. The Petalodontiformes and Edestiformes are known by more or less complete specimens: they are not dealt with here but are to be treated in a forthcoming publication by Dr S. E. Bendix-Almgreen of Copenhagen.

III. TOOTH STRUCTURE

Both Nielsen (1932, p. 27) and Moy-Thomas (1939, p. 2) held that the microstructure of the teeth was the major character of the Bradyodonti. Ørvig (1951, p. 342) refers to the tissue of the crown of the tooth in bradyodonts and dipnoans as tubular dentine. In tubular dentine there are many parallel vascular canals which run towards the grinding surface of the tooth, ending just below this surface in unworn teeth. Each vascular canal is surrounded by a dentinal osteon, and the osteons are separated from each other by a tissue which Nielsen (1932, p. 33) calls enamel (in bradyodonts) and which Lison (1941, p. 286) calls petrodentine in dipnoans.

Radinsky (1961, p. 80) has recently criticized this concept of a special dental structure in bradyodonts. He suggests that the development of tubular dentine is an adaptive feature which has occurred independently in several groups where crushing teeth are present (*Asteracanthus*, *Ptychodus*, rays, etc.), and that the term bradyodont should only be applied in Smith Woodward's original sense, to groups in which tooth replacement is slow. That tubular dentine is an adaptive feature in a crushing or grinding dentition is certainly true. This is well shown in the bradyodonts, where the layer of tubular dentine becomes thin in acuminate teeth like those of the petalodonts. But the question is whether there is any constant histological feature by which the teeth of bradyodonts in the sense of Nielsen and Moy-Thomas may be distinguished from the teeth of durophagous selachians like *Asteracanthus*, *Ptychodus* and the rays. There seems no doubt that the osteodentine of the root and the vertical vascular canals lined with dentinal osteons of the crown are identical in the two types of tooth. The two parts of the tooth which might be distinguishable are the tissue separating the dentinal osteons of the crown, and the tissue at the surface of the crown in unworn teeth.

(*a*) *The interosteonal tissue of the crown*

Ørvig (1951, p. 342) is in no doubt that there is a difference between the interosteonal tissue in the crowns of bradyodont and ray teeth. In rays and *Ptychodus* he finds the interosteonal tissue of the crown to be the same as the interosteonal tissue in the osteodentine of the root. He defines this tissue (1951, p. 337) as 'bone without cells', and finds that it differs from osteonal dentine in (i) containing fairly coarse fibres, (ii) in being penetrated by short cell processes, not long ones as in dentine, and (iii) in being secreted by cells which are osteoblast-like in shape. Ørvig contrasts the interosteonal tissue of the crowns of bradyodont teeth with this 'bone without cells', and calls it 'a special kind of hard tissue', saying 'the true nature of this hard tissue is still unknown'. Ørvig does not say how this tissue differs from acellular bone, but proposes to discuss this in detail in Part II of his 'Histologic studies of placoderms and fossil elasmobranchs'.

Nielsen (1932, p. 30) describes the interosteonal tissue of the crown in edestid teeth as being light in colour, penetrated by the terminal parts of the dentinal tubules of the adjacent osteons (these tubules occasionally anastomosing within the tissue with tubules from other osteons), the tissue differs from dentine in its reaction in polarized light, and it is formed earlier than and independently of the dentine of the root. Nielsen's photographs of thin sections of edestid teeth (1932, pl. 9, fig. 1; pl. 10, figs. 1, 2; pl. 11, figs. 2, 3) show clearly that there is a marked contrast between the interosteonal tissue of the crown and the much less abundant interosteonal tissue of the root, and that the two tissues are everywhere separated by a layer of osteonal dentine. All these features are also to be seen in sections in the British Museum (Natural History) of teeth of *Helodus simplex* (P 40126), and the chimaeroid *Ischyodus* (P 33823). In sections of teeth of *Psammodus rugosus* (P 31742, P 31899) the contrast between the interosteonal tissue of the crown and root is less obvious, but under polarized light there is a marked difference between the very active tissue of the crown and the almost inactive tissue of the root, and there are traces of a layer of osteonal dentine along the line of junction of the two. In sections of teeth of *Asteracanthus* (P 5301) and *Ptychodus* (P 5302) the interosteonal tissue of the crown seems to agree exactly with that of the bradyodonts mentioned above except that as the substance is traced downwards from the grinding surface of the tooth, it changes gradually as the junction of root and crown is approached, the dentine tubules becoming coarser and more obvious and the activity in polarized light decreasing. The only difference that I can detect between the interosteonal tissue of the crown in the teeth of bradyodonts and durophagous selachians is that in selachians, though near the surface of the tooth the tissue may simulate exactly that of the bradyodonts, the nature of the tissue changes as the root/crown junction is approached, while in bradyodonts the tissue is homogeneous throughout its depth.

(ii) *The surface tissue of the crown*

Radinsky (1961, p. 80) was unable to find an external layer of pallial dentine (Ørvig, 1951, p. 332) or enamel in any of the bradyodont teeth he examined (*Helodus*, *Streblodus*, *Sandalodus*, *Psammodus*, *Petalodus*, *Polyrhizodus*, *Orodus*), while in the selachians *Asteracanthus*, *Heterodontus*, *Myliobatis* and *Ptychodus*, he found that although enamel may be absent, there is always a layer of pallial dentine in unworn teeth. Radinsky thinks this difference is of little importance, since as pallial dentine may be very thin in some selachians (*Myliobatis*), its absence in others would not be surprising. Nevertheless, until a selachian without pallial dentine or a bradyodont with pallial dentine is found, it appears to be a real difference between the two groups. The only bradyodont in which enamel has been described is *Helicoprion* (Karpinsky 1899, p. 417), where, as Teichert (1940, p. 146) notes, Karpinsky's description and figures indicate that a layer apparently identical with the enamel of selachians is present. But *Helicoprion* is clearly linked with more generalized forms like the edestids described by Nielsen (1932), in which the tooth structure agrees with other bradyodonts in the absence of enamel and pallial dentine. Below the enamel in *Helicoprion* there is a layer of tissue which Karpinsky called 'Röhrchen-Vasodentin'. Teichert (1940, p. 146) interprets this tissue as what is now called pallial dentine, since he refers to the parallel canals in the tissue as dentinal tubes, and compares the tissue to the outer layer of a pike's tooth. But Karpinsky's figs. 45 and 46 show clearly that the parallel canals are vascular, and the 'Röhrchen-Vasodentin' is in fact a poorly developed layer of tubular dentine. No histological investigation of *Helicoprion* has been made since Karpinsky's work, and a decision on the nature of the enamel layer must await such an investigation. At present, leaving the symphysial teeth of *Helicoprion* aside, the tooth structure of bradyodonts can be defined as: no pallial dentine, no enamel, the crown made up partially or wholly of vertical, roughly parallel vascular canals surrounded by dentinal osteons, the osteons separated by abundant, homogeneous, optically active interosteonal tissue which is sharply marked off from the interosteonal tissue of the root.

In durophagous selachians there is always a layer of pallial dentine at the coronal surface, and the interosteonal tissue of the crown is not homogeneous throughout its depth.

IV. SYSTEMATIC DESCRIPTIONS

Class Holocephali

Elasmobranchiomorph fishes in which the jaw suspension is holostylic, with the palatoquadrate completely fused to the neurocranium; hyoid arch complete and unmodified; teeth with a superficial layer of tubular dentine; branchial arches lying below the neurocranium; endoskeleton of cartilage, normally calcified in prisms; exoskeleton of dentine or dentine-like tissue, without cellular bone.

Order Chimaeriformes

Amended diagnosis: Holocephali in which the dentition consists of a few large tooth plates, normally in a single series along the length of each ramus of the jaws, and with three or less pairs of tooth plates in the upper jaw and a single pair in the lower jaw; tritors present on tooth plates only in advanced forms; dermal armour commonly present on the head; frontal clasper present in all but the most primitive forms; notochord uncalcified or with calcifications which are more numerous than the trunk segments, synarcual present(?); a dorsal fin spine in more advanced forms; pectoral fin dibasal, pelvic with a single basal; pelvic claspers present; pre-pelvic tenacula present in advanced forms; squamation complete except in advanced forms, specialized scales surrounding the sensory canals.

Sub-order Chimaeroidei

Amended diagnosis: Chimaeriformes in which the head and trunk are laterally compressed; two pairs of tooth plates in the upper jaw, one pair in the lower jaw, tritors present on all tooth plates, tooth plates thick and massive; rostrum large or small, frontal clasper small and present only in males, ethmoid canal present; no dermal plates on the head; calcified rings normally present in the sheath of the notochord; dorsal fin spine present, spine smooth, with a narrow outer zone of osteodentine; tenacula present with independent cartilagenous skeleton; scales placoid (synchronomorial), squamation much reduced.

The six known genera of living chimaeroids are placed in three families, the Chimaeridae Rhinochimaeridae and Callorhynchidae. These families differ from each other only in the form of the snout and tooth plates, in the absence of notochordal calcifications in Callorhynchidae, and in a few other details. Descriptions of living chimaeroids are given by Garman (1904), Dean (1906) and Bigelow & Schroeder (1953).

The Chimaeridae contains the living genera *Chimaera* and *Hydrolagus*, the first known since the Lower Eocene, and several fossil genera (*Ischyodus*, *Ganodus*, *Edaphodon*, *Brachymylus*, *Pachymylus*) ranging back to the Middle Jurassic.

The Rhinochimaeridae contains the living genera *Rhinochimaera* (figure 1), *Harriota* and *Neoharriota*. These genera are unknown as fossils, but Smith Woodward (1932, p. 97) says

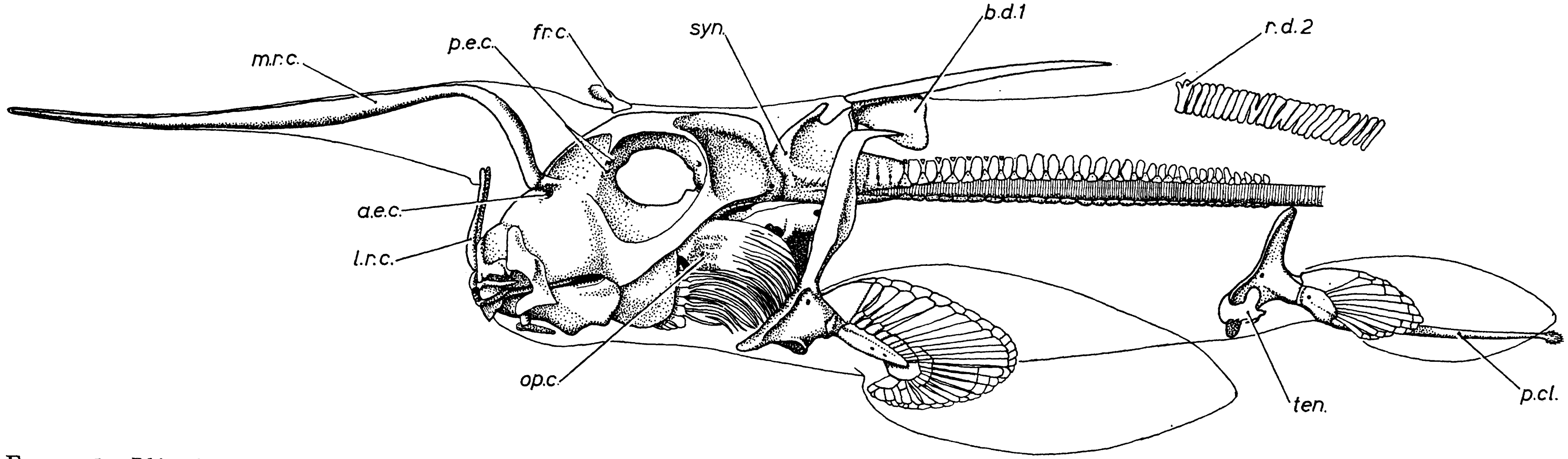

FIGURE 1. *Rhinochimaera pacifica* (Mitsukuri). Skeleton of the head and anterior part of the trunk in a male individual, with outline of body and fins (× $\frac{1}{2}$ approx.). After Garman (1904). *a.e.c.*, Anterior opening of ethmoid canal; *b.d.*1, basal cartilage of first dorsal fin; *fr.c.*, frontal clasper; *l.r.c.*, *m.r.c.*, lateral and median rostral cartilages; *op.c.*, opercular cartilage; *p.cl.*, pelvic clasper; *p.e.c.*, posterior opening of ethmoid canal; *r.d.*2, radials of second dorsal fin; *syn.*, synarcual; *ten.*, tenaculum.

that the Oligocene *Amylodon* lies very close to *Rhinochimaera*, and Dean (1906, p. 150) suggests that the Cretaceous and Lower Tertiary genera *Elasmodus* and *Elasmodectes* should be placed in the Rhinochimaeridae.

The Callorhynchidae contains the living *Callorhynchus*, known since the Upper Cretaceous.

Of the fossil members of these three families, only the Kimmeridgian *Ischyodus quenstedti* and *I. avitus* (Dean 1909), and the Portlandian *I. schuebleri* (Heimberg 1949) (figure 2) are known by more than isolated tooth plates and fin spines. These three Upper Jurassic species of *Ischyodus* are known by almost complete specimens. They differ from the living forms only in details of the snout and tooth plates, in the broader pectoral girdle, the presence of a series of small cartilages along the distal edge of the basal of the first dorsal fin, the larger frontal clasper, and in the wider zone of osteodentine around the periphery of the dorsal fin spine (figure 4). It is clear that the chimaeroids have changed very little since their appearance in the Middle Jurassic, and that all the holocephalans which survived beyond the Jurassic belong in the Chimaeroidei.

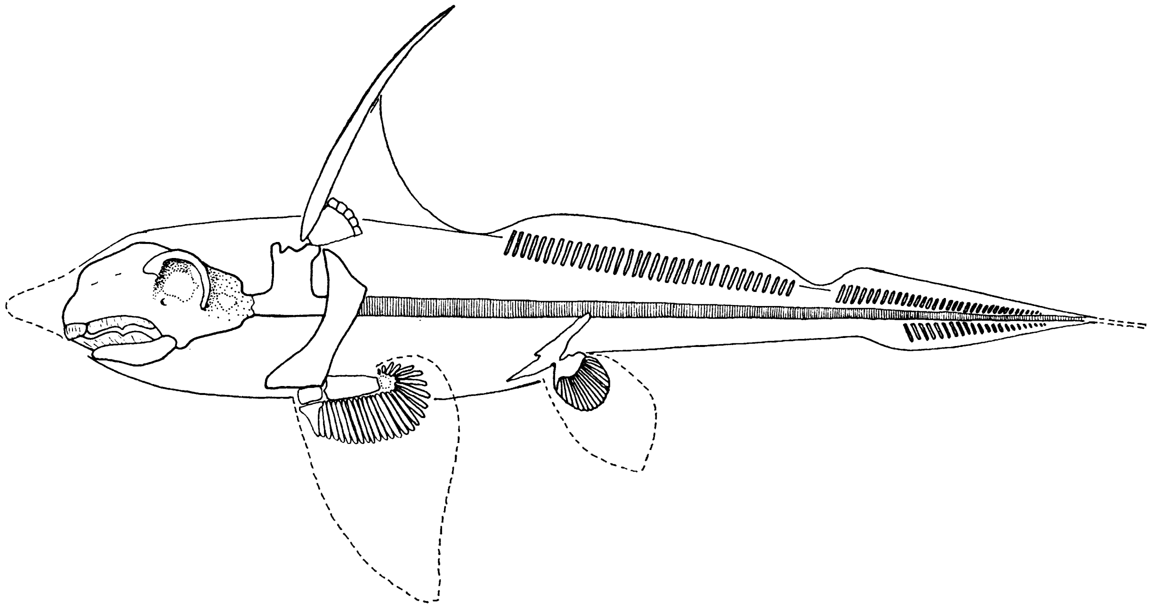

FIGURE 2. *Ischyodus schuebleri* (Quenstedt). Restoration of female in lateral view (× $\frac{1}{7}$ approx.). After Heimberg (1949).

The major characters which are peculiar to the living chimaeroids are the following:

(1) The jaw suspension is holostylic.

(2) There is an ethmoid canal in the neurocranium (*a.e.c.*, figures 1, 3).

(3) There is an interorbital septum lying dorsal to the forebrain.

(4) The dentition consists of two pairs of tooth plates in the upper jaw and one pair in the lower jaw.

(5) The crowns of the tooth plates contain tubular dentine (defined on p. 108).

(6) The tubular dentine is confined to limited areas of the tooth plates, the tritors.

(7) The hyoid arch is complete and unmodified, with a pharyngohyal.

(8) The branchial arches lie below the occipital part of the neurocranium (figure 1), not behind the neurocranium as they do in selachians.

(9) The spiracle closes very early in ontogeny, and is absent in the adult.

(10) The gills are covered by an operculum of soft tissue which is supported by an opercular cartilage (figure 1) borne on the hyoid arch.

(11) There are three well-developed rostral cartilages (figure 1) which in the adult are articulated with the neurocranium. The median rostral cartilage lies dorsal to the paired cartilages.

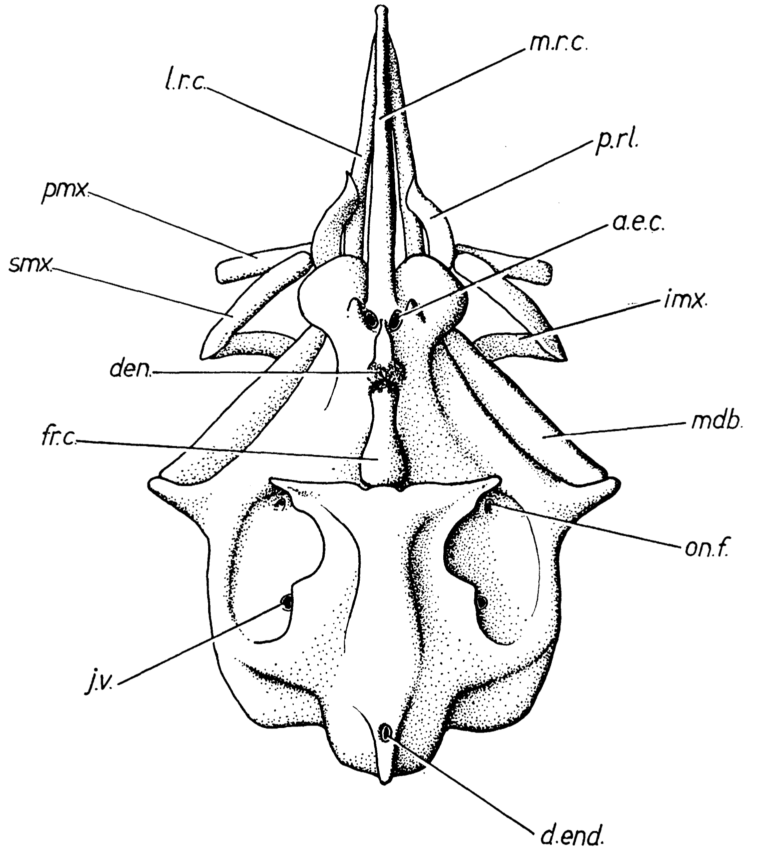

FIGURE 3. *Callorhynchus sp.* Skull of a male individual in dorsal view (× ½ approx.). After de Beer & Moy-Thomas (1935). *a.e.c.*, Anterior opening of ethmoid canal; *den.*, denticles opposing those on the frontal clasper; *d.end.*, opening of ductus endolymphaticus; *fr.c.*, frontal clasper; *imx.*, inframaxillary labial cartilage; *j.v.*, foramen transmitting jugular vein, orbital artery and hyomandibular and palatine nerves; *l.r.c.*, *m.r.c.*, lateral and median rostral cartilages; *mdb.*, mandible; *on.f.*, orbitonasal canal; *pmx.*, *smx.*, premaxillary and supramaxillary labial cartilages; *p.rl.*, prelabial cartilage.

(12) The labial cartilages are large and well developed. In Chimaeridae and Rhinochimaeridae (figure 1) there are four pairs of labials, in Callorhynchidae (figure 3) there are six pairs.

(13) The notochord is not constricted or segmented in the adult. In Chimaeridae and Rhinochimaeridae the sheath of the notochord becomes calcified in rings which are more numerous than the segments of the trunk (figure 1). In Callorhynchidae there are no notochordal calcifications.

(14) The anterior part of the notochord is surrounded by a cartilagenous synarcual (Stensiö 1959, fig. 61), formed by fusion of segmental arcual elements, which bears a

median dorsal crest with which the spine and basal of the first dorsal fin articulate (figure 1).

(15) The pectoral fin is dibasal, with a small propterygium, a large metapterygium, and the anterior radials fused (figure 1).

(16) The halves of the pelvic girdle are not fused in the mid-line.

(17) The first dorsal fin has an erectile spine and a single triangular basal cartilage (figure 1).

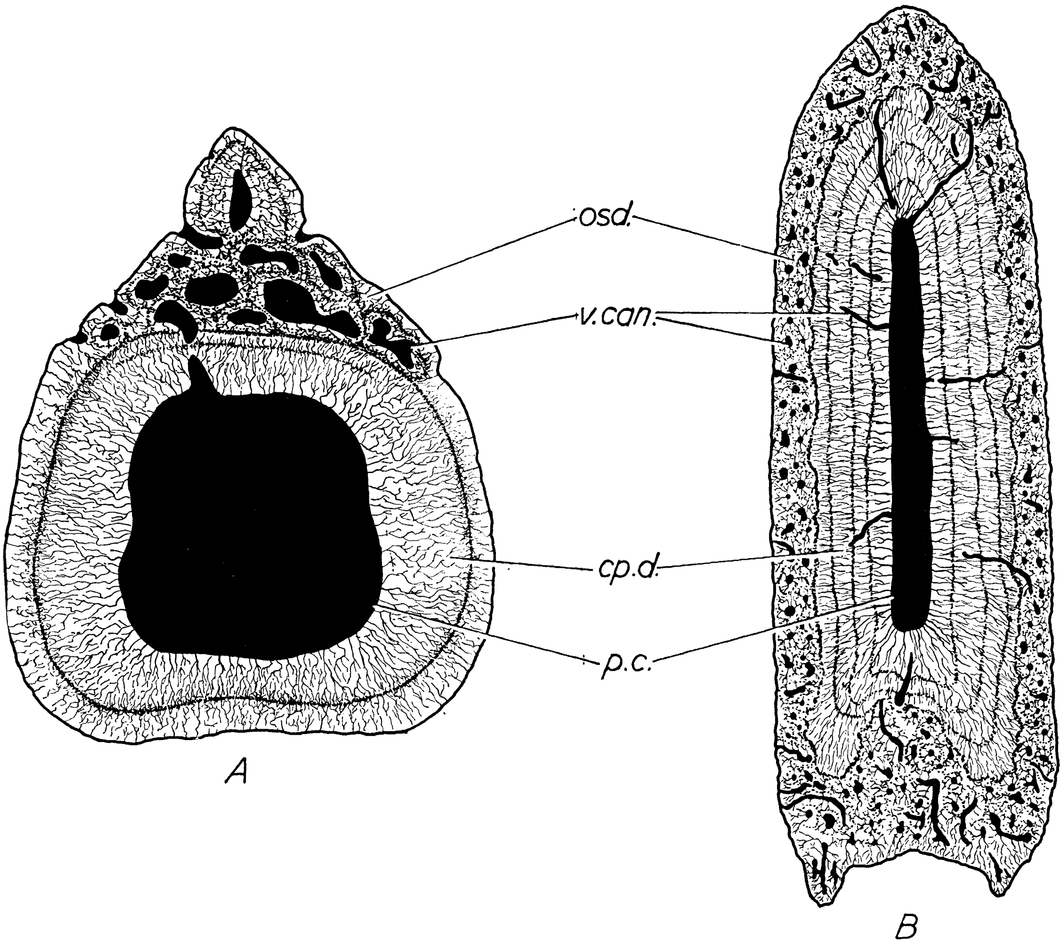

FIGURE 4. Transverse sections cut near the middle of the dorsal fin spine in: *A*, *Chimaera monstrosa* Linné, Recent (× 20 approx.); *B*, *Ischyodus quenstedti* Wagner, Kimmeridgian (× 11 approx.). Both after Stromer (1927). *cp.d.*, lamellar tissue; *osd.*, osteodentine; *p.c.*, pulp cavity; *v.can.*, vascular canals.

(18) The fin spine consists of a narrow and incomplete outer zone of osteodentine and a broad inner zone of tissue laid down in concentric lamellae around the central cavity (figure 4; figure 45, plate 22). This tissue is penetrated by long, sinuous, much-branched tubules which are always described as dentine tubules. The tissue is called 'Pulpadentin' by Stromer (1927), orthodentine by Ørvig (1951, p. 344), Peyer (1957, p. 161) and Bertin (1958, p. 508), and the 'Pulpaosteon' (in acanthodians) by Gross (1957, p. 17). I hope to discuss this tissue at a later date, but it should be noted that in living sharks and chimaeroids (though not in Palaeozoic and most Mesozoic forms) the tissue has an outer layer in which the tubules pass inwards, thus differentiating it clearly from both osteonal

dentine and orthodentine. In this paper the tissue will be referred to by the non-committal term 'lamellar tissue', pending investigation of its true nature (see also p. 133). The spine is smooth, and has a short series of paired denticles on the distal part of the posterior face.

(19) The second dorsal fin has no spine and a single series of parallel, rod-like radials (figure 1).

(20) The scales are placoid and similar to the scales of recent selachians in structure (figure 5).

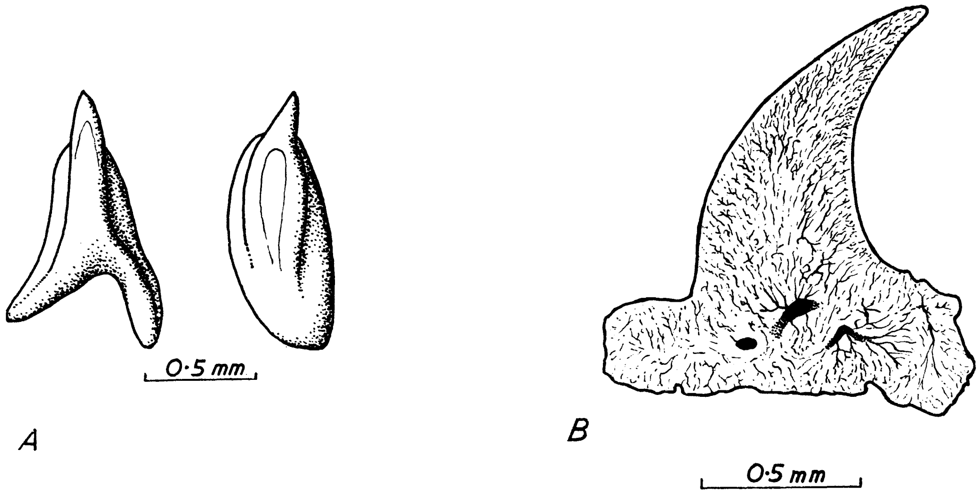

Figure 5. Scales of Recent *Callorhynchus*. *A*, *Callorhynchus sp.*, scales from the head (right) and trunk (left) of an embryo, dorsal view. After Schauinsland (1903). *B*, *Callorhynchus antarcticus* Lacépède, scale from the frontal clasper of a male individual in longitudinal section. P 45954.

(21) The squamation is greatly reduced. There are scales on the secondary sexual organs of the male, and a few scales on the dorsal surface of the trunk in Callorhynchidae and Rhinochimaeridae.

(22) The pattern of the sensory canals on the head (figure 6) is peculiar, and not easily homologized with any other vertebrate group.

(23) The sensory canals lie in open grooves which are lined with crescentic calcified structures (figure 7). These calcifications are referred to by Schauinsland (1903, p. 13) as being calcified and bony, capped with dentine, by Dean (1909, p. 262) as cartilage, by Smith Woodward (1932, p. 94) as calcified cartilage, and by Ørvig (1962, p. 56) as bone. These structures are modified scales (see p. 198).

(24) In males there is a pair of pelvic claspers supported by rods of calcified cartilage which articulate with the basipterygium of the pelvic fin (figure 1).

(25) In males there is a pair of pre-pelvic claspers, the tenacula, armed with enlarged scales, and supported by cartilages articulating with the pelvic girdle (figure 1).

(26) In males there is a frontal clasper armed with enlarged scales and supported by calcified fibro-cartilage (figure 51, plate 23) which articulates with the neurocranium in the mid-dorsal line just in front of the orbit (figures 1 and 3).

Of these 26 characters of living chimaeroids, evidence concerning numbers 7, 9 and 10 is unlikely to be found in fossil forms. Characters numbers 7, 12, 16 and 19 are certainly primitive, the remainder are probably specialized.

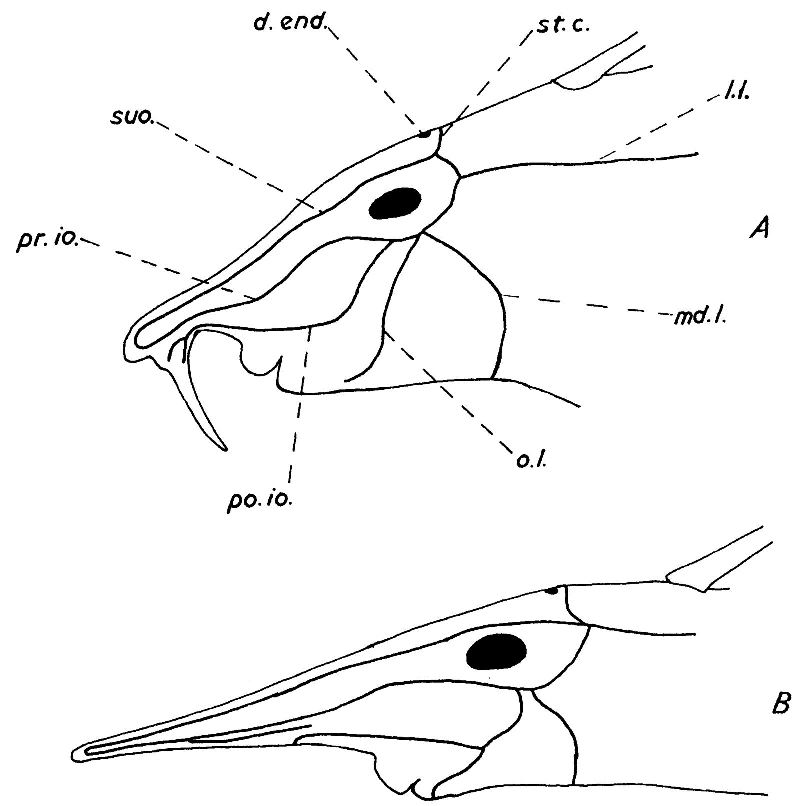

FIGURE 6. The arrangement of the sensory lines on the head in *A*, *Callorhynchus*; *B*, *Rhinochimaera*. After Holmgren & Pehrson (1949). *d.end.*, Opening of ductus endolymphaticus; *l.l.*, lateral line of trunk; *md.l.*, mandibular line; *o.l.*, oral line; *po.io.*, *pr.io.*, postnasal and prenasal divisions of the infraorbital line; *st.c.*, supratemporal commissure; *suo.*, supraorbital line.

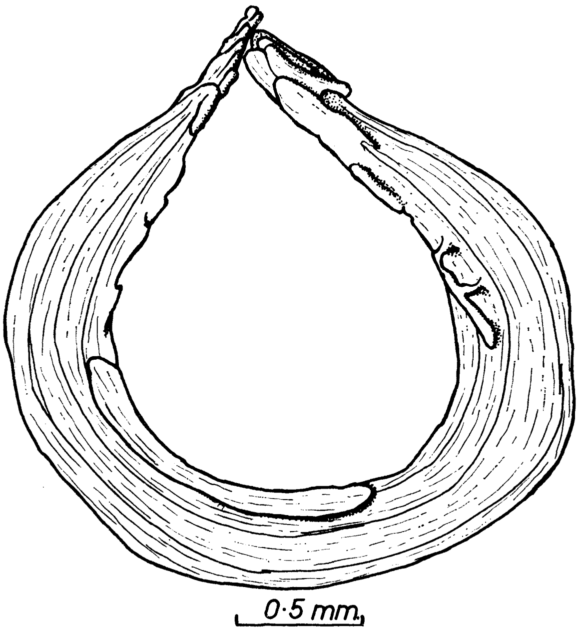

FIGURE 7. *Chimaera monstrosa* Linné, modified scale from the infraorbital sensory canal. P 45955.

SUB-ORDER SQUALORAJOIDEI nov.

Diagnosis: Chimaeriformes in which the head is dorso-ventrally flattened; two pairs of tooth plates in the upper jaw, one pair in the lower jaw, tooth plates without localized tritors but with the crown made up of alternate parallel bands of osteonal and inter-osteonal dentine, tooth plates thin; rostrum and frontal clasper very large, frontal clasper possibly present in all individuals, no ethmoid canal; no dermal plates on the head; synarcual present, notochordal calcifications very thick; no dorsal fin spine, first dorsal fin absent or reduced; tenacula present, supported by an anterior process of the pelvic girdle; scales placoid, squamation not much reduced.

FAMILY SQUALORAJIDAE Smith Woodward (1886, p. 538)

Diagnosis: as sub-order, only family.

The Squalorajidae contains the single genus *Squaloraja* Riley (1833, p. 484), with two species from the Lower Lias of Lyme Regis, Dorset, *S. polyspondyla* Agassiz, the type species, and *S. tenuispina* Smith Woodward (1886, p. 530), the latter known only by a single frontal clasper.

Berg (1955, p. 77) suggests that *Macrodontacanthus kingi* Romer (1942, p. 226, pl. 1, figs. 13, 14), from the Permo-Carboniferous of Texas, should be placed in the Squalorajidae. The holotype and only known specimen of *M. kingi* is an incomplete spine bearing large, symmetrically placed denticles on each side, and with a longitudinal groove on one side. Romer compares the spine with the frontal claspers of *Squaloraja* and *Myriacanthus*, and suggests that it belongs to a bradyodont. The microstructure of the spine is unknown, but only if it consists of calcified fibro-cartilage can it be a holocephalan frontal clasper. The longitudinal groove suggests that the whole of the grooved surface was in contact with the dermis and that the structure did not project freely, as do holocephalan frontal claspers. There seems to be some resemblance, however, to the structure in *Acanthorhina jaekeli* Fraas which is here (p. 146) suggested to be the frontal clasper. Until the microstructure of *M. kingi* is known, it is best left as an ichthyodorulite *incertae sedis*.

Squaloraja polyspondyla Agassiz

Figure 52, plate 23; figures 55, 56, plate 24; figures 8 to 12.

1833 *Squaloraia dolichognathos* Riley, p. 484.
1836 *Spinacorhinus polyspondylus* Agassiz, **3**, pls. 42, 43; Feuill., p. 94.
1890 *Squaloraja polyspondyla* Agassiz; Howes, p. 687.
1891*a* *Squaloraja polyspondyla* Agassiz; Smith Woodward, p. 41, pl. 3, fig. 2; lists earlier references.
1895 *Squaloraja polyspondyla* Agassiz; Reis, p. 385, pl. 12, figs. 1, 2, 4, 5, 6.
1906 *Squaloraja polyspondyla* Agassiz; Dean, p. 141, text-figs. 120, 133, 137, 137A, 138, 139.
1922 *Squaloraja polyspondyla* Agassiz; Leigh-Sharpe, p. 193, text-fig. 3.
1935 *Squaloraja polyspondyla* Agassiz; de Beer & Moy-Thomas, p. 304, text-fig. 19.
1951 *Squaloraja polyspondyla* Agassiz; Ørvig, p. 416, text-fig. 19.

Note: This species was first described by Riley (1833, p. 484) as *S. dolichognathos*; the trivial name was changed to *polyspondyla* by Agassiz because Riley's name is inappropriate, but this does not render a name unavailable. Under the present (1961) edition of the *Code of zoological nomenclature* Riley's trivial name must become a *nomen oblitum* since it has not been used as a senior synonym in primary literature for over fifty years. But if, as seems likely, Article VI of the *Code* is emended by the 1963 International Congress of Zoology, the species must become *S. dolichognathos* Riley.

Diagnosis: *Squaloraja* reaching about 60 cm in length, frontal clasper strongly expanded proximally, bluntly pointed distally.

Holotype: incomplete skeleton in Bristol Museum.

Horizon and locality: Lower Lias, Lyme Regis, Dorset.

Squaloraja polyspondyla is known by about half a dozen almost complete skeletons. The most important descriptions of the species are those by Davies (1872), Smith Woodward (1886, 1891*a*), Reis (1895) and Dean (1906). The pectoral girdle and fin are figured by Leigh-Sharpe (1922), and the skull is restored and described by de Beer & Moy-Thomas (1935).

Description

A restoration of the skeleton in dorsal view is shown in figure 8. With regard to the skull, there is little to add to the description given by de Beer & Moy-Thomas. In de Beer & Moy-Thomas's reconstruction of the skull, the lateral rostral cartilages (*l.r.c.*) are shown passing ventral to the mandible, but in fact they join the neurocranium antero-dorsal to the mandibular symphysis. The three rostral cartilages of *Squaloraja* are fused to the neurocranium. In living chimaeroids there is some confusion as to whether the rostral cartilages are fused with or articulated with the neurocranium, but according to Garman (1904, p. 270) they are articulated in the adult, though they may be fused in the embryo (Schauinsland 1903, p. 8). Allis (1917, p. 134) found that in adult *Chimaera* the median rostral is articulated with the skull but the lateral rostrals are fused. The great length and breadth of the snout in *Squaloraja* seems sufficient explanation for this difference from the living forms. The three labial cartilages of *Squaloraja* are evidently homologous with the premaxillary (*pmx.*), supramaxillary (*smx.*) and inframaxillary (*imx.*) of *Callorhynchus* (Holmgren 1942, p. 244). There is no sign in *Squaloraja* of the prelabial cartilage which in living chimaeroids lies along the proximal part of the lateral rostral cartilage, nor of the premandibular cartilages which occur in living chimaeroids (Holmgren 1942, p. 241). The prelabial cartilage is possibly fused into the very wide base of the lateral rostral cartilage, and the absence of pre-mandibular cartilages is probably due to imperfect preservation.

By comparison with *Callorhynchus*, de Beer & Moy-Thomas identified the anterior of the two foramina in the floor of the orbit (*e.ps.a*) as the orbito-nasal foramen, and the posterior (*j.v.*) as the cranio-quadrate fissure. Holmgren (1942, p. 192) interprets the floor and lateral wall of the orbit in chimaeroids as a subocular shelf, not an otic process as de Beer & Moy-Thomas thought it to be. These different interpretations are based on the same evidence, the descriptions of chimaeroid embryos by Schauinsland (1903), Dean (1906) and de Beer & Moy-Thomas, and the question can only be settled by new information on

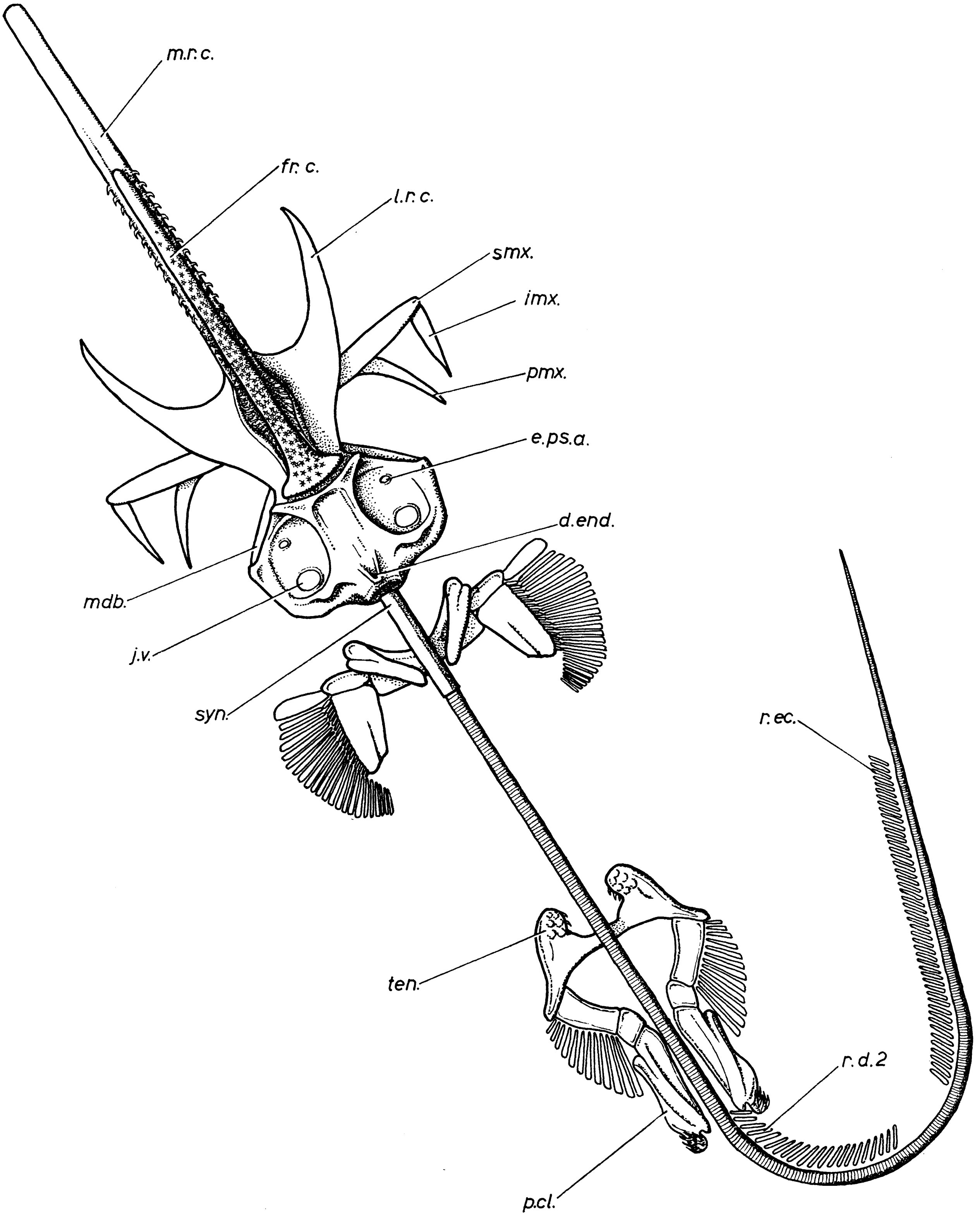

FIGURE 8. *Squaloraja polyspondyla* Agassiz. Restoration of the skeleton in dorsal view, the tail drawn in lateral view (× ½ approx.). *d.end.*, Opening of ductus endolymphaticus; *e.ps.a.*, foramen probably transmitting the efferent pseudobranchial artery; *fr.c.*, frontal clasper; *imx.*, inframaxillary labial cartilage; *j.v.*, foramen transmitting the jugular vein, orbital artery and hyomandibular and palatine nerves; *l.r.c.*, *m.r.c.*, lateral and median rostral cartilages; *mbd.*, mandible; *p.cl.*, pelvic clasper; *pmx.*, *smx.*, premaxillary and supramaxillary labial cartilages; *r.d.* 2, *r.ec.*, radials of the second dorsal fin and the epichordal lobe of the caudal fin respectively; *syn.*, synarcual; *ten.*, pre-pelvic tenaculum.

embryology. In either case, the posterior foramen must have transmitted the hyomandibular nerve, the palatine nerve, the orbital artery and the jugular vein. The anterior foramen, called by de Beer & Moy-Thomas the orbito-nasal foramen, opens on the underside of the neurocranium well behind the sockets of the anterior tooth plates of the upper jaw, and can have had no connexion with the nasal capsule, which lay well in front of these tooth plates in an embayment below the base of the lateral rostral process (41353; figure 9). The foramen possibly transmitted the mandibular branch of the trigeminal nerve, or the efferent pseudobranchial artery, which might lie rather far laterally in a dorso-ventrally flattened form like *Squaloraja*, or both of these structures, since there are no other visible foramina in this region. 41353 and P 3184 show that there was a median hypophysial fenestra on a ridge on the ventral face of the neurocranium at the level of the mandibular articulation. The internal carotids, which are very small in living chimaeroids, probably also entered through this fenestra.

De Beer & Moy-Thomas did not discuss the presence or absence of an ethmoid canal in *Squaloraja*. The ethmoid canal in living chimaeroids is a median cavity lying above the forebrain and in front of the orbits. The superficial ophthalmic nerves and the profundus nerve enter the cavity from the orbit posteriorly, and leave it to pass on to the surface of the snout anteriorly. Interpretations of the canal vary. Allis (1917, p. 113) first held that the canal was formed by the roofing over and subsequent coalescence of the grooves which house the superficial ophthalmic nerves on the roof of the selachian skull, but later (1926, p. 337) he suggested that the ethmoid canal was part of the forebrain cavity, and that it was floored by the trabeculae. De Beer & Moy-Thomas (1935, p. 299) follow Allis's earlier opinion in regarding the canal as an extracranial space, but they consider it to be formed by upgrowth of the lamina orbito-nasalis, as a sequel to the raising of the skull roof caused by the formation of the interorbital septum. Holmgren (1942, p. 196) considers the canal to be an intracranial space secondarily segmented off from the main cranial cavity as a consequence of the formation of the interorbital septum. The variety of these interpretations is again due to the lack of early embryological material of living chimaeroids. The only one of these interpretations to have received any support from palaeontology is that of de Beer & Moy-Thomas: in the Carboniferous *Helodus simplex* Moy-Thomas (1936*b*, p. 501) found that the roof of the ethmoid region is lower than that of the rest of the skull, and that the laminae orbitonasalis are raised up lateral to the ethmoid roof, enclosing the foramina of the superficial ophthalmic nerves between them. This is discussed on p. 187.

In living chimaeroids (*Chimaera*, Allis 1917, pl. 2: *Callorhynchus*, de Beer & Moy-Thomas 1935, figs. 1, 18: *Rhinochimaera*, figure 1) the ethmoid canal opens into the orbit just below and behind the point of insertion of the frontal clasper, and opens anteriorly immediately lateral to the base of the median rostral process (figures 1, 3). The size of the anterior opening of the canal varies with the size of the rostrum: the opening is larger in the long snouted *Callorhynchus* and *Rhinochimaera* than it is in *Chimaera*. In *Squaloraja*, where the snout is even longer and broader than it is in *Rhinochimaera*, one would expect the opening to be large. In *Squaloraja* it is difficult to fix the base of the median rostral process since the process is fused with the neurocranium, but the base must have lain at about the posterior limit of the lateral denticles on the process, since behind this level the dorsal surface of the rostrum bore muscles which served in life to depress the frontal clasper

(Davies 1872, p. 147). The dorso-lateral edges of the median rostral process bear a pair of elongated plates of the same densely calcified cartilage as the frontal clasper (Reis 1895, p. 386; Ørvig 1951, text-fig. 19). At the proximal end of the process these plates expand into a concave pad (figure 9) whose edges bear large denticles pointing dorso-medially. Below the hind edge of this pad there is a deep crevice which agrees in position with the

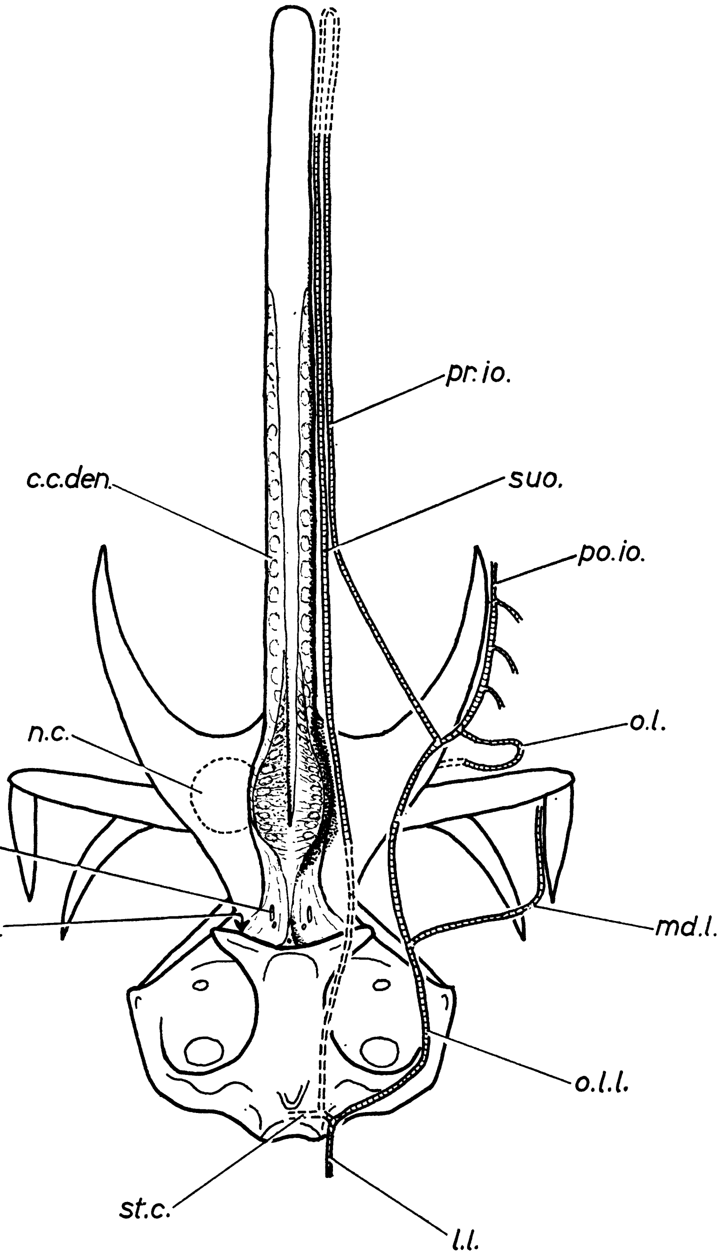

FIGURE 9. *Squaloraja polyspondyla* Agassiz. Restoration of the skull in dorsal view with the frontal clasper removed (× ⅔ approx.). The course of the sensory canals is indicated on the right side. *c.c.den.*, Strip of calcified cartilage bearing denticles which oppose those on the frontal clasper; *f.s.o.n.*, efferent foramen of the superficial ophthalmic nerves; *f.v.*, foramen transmitting nutritive vessels to the depressor muscles of the frontal clasper; *l.l.*, lateral line of the trunk; *md.l.*, mandibular line; *n.c.*, position of nasal capsule; *o.l.*, oral line; *o.l.l.*, otic innervated portion of lateral line; *po.io.*, *pr.io.*, postnasal and prenasal divisions of the infraorbital line; *st.c.*, supratemporal commissure; *suo.*, supraorbital line.

anterior opening of the ethmoid canal in living chimaeroids, but excavation of this crevice in 41354 shows that there is no foramen in it. 41354 (figure 56, plate 24) is the rostrum of an individual which shows the area of insertion of the frontal clasper because the clasper itself is missing. On each side of a median ridge in this area there is a cluster of small foramina (*f.v.*, figure 9), but these are too small to have transmitted the superficial ophthalmic nerves, and must have served for blood vessels to the depressor muscles of the clasper. Behind the base of the clasper there is a strong transverse ridge on the skull roof. At the foot of the lateral part of this ridge (*f.s.o.n.*) there is a deep crevice, and excavation of this has failed to reveal a hind wall; I believe this to be the foramen of the superficial ophthalmic nerves. If this is so, then this foramen is homologous not with the anterior opening of the ethmoid canal in living chimaeroids, but with the foramen for the superficial ophthalmic nerves in *Helodus* (Moy-Thomas 1936*b*, p. 495; figure 38), with which it exactly corresponds in position, and there can have been no ethmoid canal in *Squaloraja*. But whereas in *Helodus* Moy-Thomas found a pair of vertical laminae which suggested that an ethmoid canal was incipient, in *Squaloraja* there is no sign of such upgrowths, and the form of the rostrum and frontal clasper seem to exclude the possibility of them. *Squaloraja* gives support to no one of the theories concerning the origin of the ethmoid canal, but suggests that the canal arose late in holocephalan history.

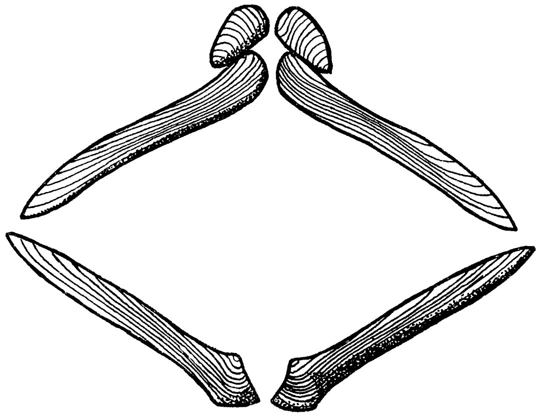

FIGURE 10. *Squaloraja polyspondyla* Agassiz. Dentition restored as if seen from in front with the mouth wide open (× 1 approx.). Modified from Dean (1906).

It is not possible in *Squaloraja* to discover whether an interorbital septum of chimaeroid type was present, but the width and separation of the orbits suggests that the eyes would not have been closely approximated in the mid-line.

The branchial arches of *Squaloraja* are known only by fragments, but from the position of the pectoral girdle close behind the occiput it is clear that the branchial arches lay beneath the neurocranium, as they do in living chimaeroids.

The dentition has been described by Smith Woodward (1891*a*, p. 41) and Dean (1906, p. 140), and is restored in figure 10. As in chimaeroids, there is a single pair of tooth plates in the lower jaw and two pairs in the upper jaw. There are no localized tritors: the 'parallel longitudinal ridges, which represent the tritors' (Smith Woodward) and the 'tritors...in the form of conspicuous lamellae' (Dean) which cover the surface of the tooth plates are not tritors but alternate bands of osteonal and interosteonal dentine. The whole surface of the tooth plate is made up of tubular dentine in which the dentinal osteons surrounding the vertical vascular canals have become united in a series of parallel bands. The same type of tubular dentine occurs in the tritors of some chimaeroids (*Elasmodus*).

In the vertebral column, as in chimaeroids, there are no true centra but ring-like calcifications in the sheath of the notochord which are much more numerous than the segments of the trunk. These calcifications have been described by Hasse (1884, p. 4, pl. 1, figs. 2, 3). That the calcifications are notochordal structures is evident from the fact that they continue into the occipital region of the neurocranium, where the notochord was enclosed (P 2079). In *Squaloraja* the calcifications extend much further into the notochord than they do in living chimaeroids (figure 11). Surrounding the anterior 3 or 4 cm of the notochord there is a synarcual of calcified cartilage (figure 8). In P 2979 and P 2276 there are traces of a median dorsal crest on the synarcual. Dean (1906, p. 142) described traces of segmentation in the synarcual of P 2276, but these are not present in any other specimen and appear to be due to post mortem damage.

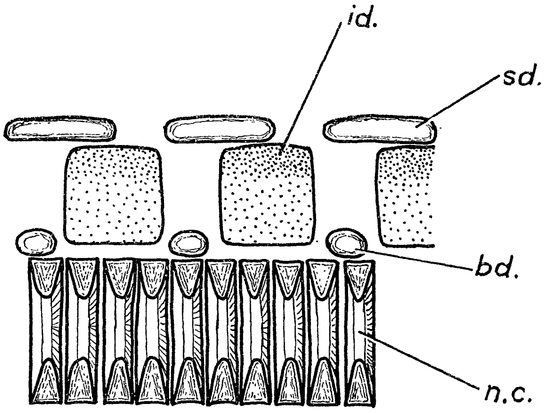

FIGURE 11. *Squaloraja polyspondyla* Agassiz. Restoration of a part of the vertebral column in the abdominal region, in sagittal section (× 3 approx.). From P 2080. *bd.*, Basidorsal; *id.*, interdorsal; *n.c.*, notochordal calcification; *sd.*, supradorsal.

Only a single specimen, P 2080, a fragment of vertebral column, shows any trace of the arcualia: figure 11 is based on this specimen. The pattern of the elements corresponds well with those in *Chimaera* (Goodrich 1909, text-fig. 136), but there is no sign of any calcification ventral to the notochord. There are between four and five notochordal calcifications in each segment, but there appears to be no constant relationship between the arcualia and the calcifications.

The pectoral girdle and fin are shown in dorsal view in figure 8. The details of the girdle are not well known: there is a fairly large scapular process and the coracoid is moderately broad. It is not known whether the two halves of the girdle were fused, as they are in living chimaeroids, but they were certainly in contact ventrally.

As Smith Woodward (1886, p. 535) saw, the pectoral fin is dibasal. Howes (1890, p. 687) noted the similarity of the two basals to the two basals of living chimaeroids, which he homologized with the propterygium and metapterygium of selachians. Articulating with the propterygium is a single, large, unsegmented cartilage. This evidently represents the fused anterior radials of the fin, and agrees exactly with *Chimaera* and *Rhinochimaera* (figure 1). In *Callorhynchus* the fusion of the radials is not so extensive (Garman 1904, pl. 10). Articulating with the metapterygium there are 22 radials. The first 15 radials are segmented once near the proximal end. The remainder were possibly segmented but their bases are not preserved in any specimen. In number and in their basal segmentation the pectoral radials of *Squaloraja* agree almost exactly with those of living chimaeroids but there is no sign of the separate distal cartilages or the multiple segmentation of the posterior radials which are characteristic of the living forms.

The pelvic girdle and fin are shown in figure 8. Once again, the agreement with living chimaeroids is very close. The two halves of the pelvic girdle were not fused (43307, P 2276). The tenacula consist of paired groups of enlarged scales borne on broad, flattened anterior processes of the girdle (figure 55, plate 24). There is only a single basipterygium: the partially separate 'propterygium' which Howes (1890, pl. 3, fig. 12) recognized in young *Chimaera* is not present. Articulating with the basipterygium there are 12 radials, all apparently unsegmented. The radials are approximately equal in number to those of living chimaeroids, but in the living forms the anterior radials are fused, there is a row of separate distal cartilages, and the posterior radials are segmented. The 'anterior radials' which Dean (1906, p. 141, fig. 138) described as articulating with the pelvic girdle in P 2276 are merely displaced scales. Between the basipterygium and the cartilage of the clasper there is a separate cartilage, as there is in *Chimaera* (Goodrich 1909, text-fig. 139). The clasper is similar in shape to that of *Callorhynchus* (Leigh-Sharpe 1922, fig. 10), but has a knob-like termination armed with about 6 recurved denticles, as in *Rhinochimaera* (Leigh-Sharpe 1922, fig. 13).

There is no trace of the median fins in any of the specimens of *Squaloraja* in the British Museum, but in RSM 1887.30.1 there is a long series of parallel radials lying above the notochord behind the pelvic fins (figure 8). These radials are in two groups; the first begins at the level of the hind edge of the clasper and contains 21 radials, the second group begins about 35 mm behind the end of the first and contains 47 radials. All the radials are simple, unsegmented cartilages, between 3 and 7 mm long. Of the two sets of radials, the first must represent the skeleton of the second dorsal fin of living chimaeroids, and the second the skeleton of the epichordal lobe of the caudal fin, as in *Ischyodus* (Heimberg 1949; figure 2). In no specimen of *Squaloraja* is there any sign of a dorsal fin spine, and this was certainly absent. Nor is there any trace of the skeleton of an anterior dorsal fin, but since *Squaloraja* still retains a synarcual with a dorsal crest it is possible that the loss of the dorsal fin spine and the loss or reduction of the first dorsal fin are specializations associated with flattening of the body and the adoption of a benthic habit, as in rhenanid and phyllolepid arthrodires (Stensiö 1963, p. 26).

As Dean (1906, p. 140) noted, the squamation of *Squaloraja* is much more extensive than that of living chimaeroids. The scales are placoid (synchronomorial) and are modified in various parts of the body. On the dorsal surface of the frontal clasper, near the mid-line on the dorsal surface of the trunk, and below the eye the scales are of the type shown in figure 12, varying only in size. On the edges of the rostrum, the underside of the frontal clasper, the flanks of the abdominal region, and in a single row along each side of the tail near the lateral line the crowns of the scales are produced into smooth, laterally compressed hooks, and are much enlarged except on the flanks of the abdominal region. The scales on the pre-pelvic tenacula are also of this type, but larger, and on the tip of the pelvic clasper they are similar in shape, but with the point directed forwards. The ventral surface of the fish was apparently naked, and the tail was naked except for the single row of scales along each side.

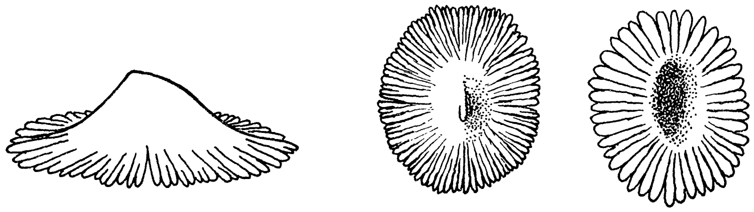

FIGURE 12. *Squaloraja polyspondyla* Agassiz. Scales from the dorsal surface of the trunk in lateral, dorsal and ventral view (× 10 approx.). After Agassiz (1836).

Smith Woodward (1887) first noticed that in *Squaloraja* the sensory canals were surrounded by 'calcified rings', as they are in living chimaeroids. The preservation of these structures allows the course of the sensory canals to be reconstructed (figure 9). Considered simply as a pattern of sensory lines, the system in *Squaloraja* is easily homologized with that of chimaeroids (*Callorhynchus*, *Rhinochimaera*, figure 6). The terminology of Holmgren & Pehrson (1949, p. 293) is used. The lateral line from the trunk passed on to the skull roof just lateral to the occipital condyle and there divided into two. The medial branch is the supratemporal commissure which probably anastomosed with the supraorbital canal (the posterior part of the latter and the medial part of the supratemporal commissure have not yet been seen), and the lateral branch is the otic innervated part of the main lateral line. This canal passed forwards below the eye and divided at the anterior edge of the orbit into a lateral branch, the mandibular line, and an anterior branch, the infraorbital line. The infraorbital line passed forwards over the lateral rostral process and there divided into the postnasal and prenasal ventral branches of the line, the postnasal branch passing antero-laterally and giving off the oral line and three short branches. This

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EXPLANATION OF PLATE 22

FIGURE 45. *Chimaera* sp. Transverse section of dorsal fin spine (× 22). P 45957. Recent. See figure 4*A* for interpretation.

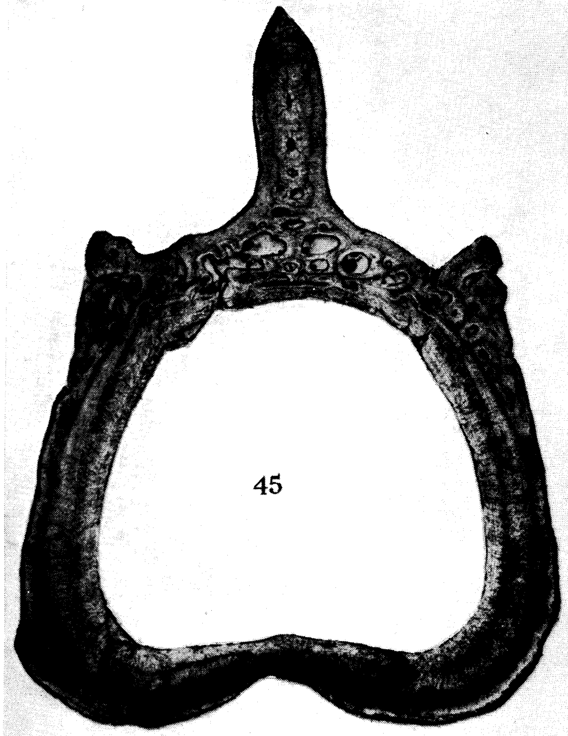
FIGURE 46. *Myriacanthus paradoxus* Agassiz. Transverse section of dorsal fin spine (× 4·75). P 1736.I. Lower Lias, Lyme Regis. See figure 17 for interpretation.

FIGURE 47. *Metopacanthus granulatus* (Agassiz). Incomplete transverse section of dorsal fin spine (× 14). 43065.I. Lower Lias, Lyme Regis. See figure 22 for interpretation.

FIGURE 48. *Helodus simplex* Agassiz. Transverse section of dorsal fin spine (× 7·5). P 2908.I. Coal Measures, Knowles Ironstone, Longton, Staffs. See figure 40 for interpretation.

FIGURE 49. *Oracanthus milleri* Agassiz. Transverse section cut near the base of the spine (× 11). P. 10981.I. Carboniferous Limestone, Forest of Dean. See figure 26 for interpretation.

FIGURE 50. ? *Oracanthus milleri* Agassiz. Transverse section of a median fin spine, possibly of this species (see p. 152) (× 8). P 45768.I. Lower Carboniferous Limestone, Armagh.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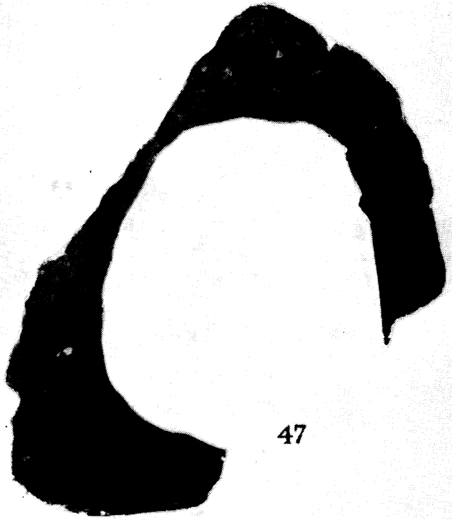
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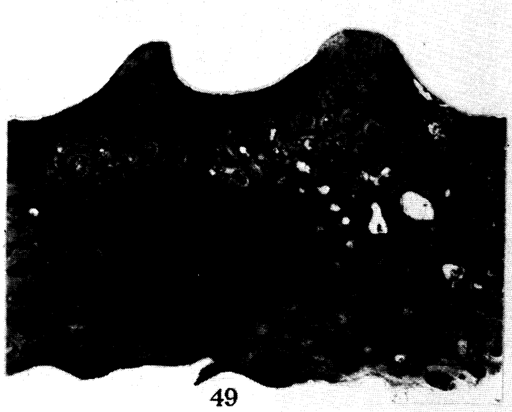
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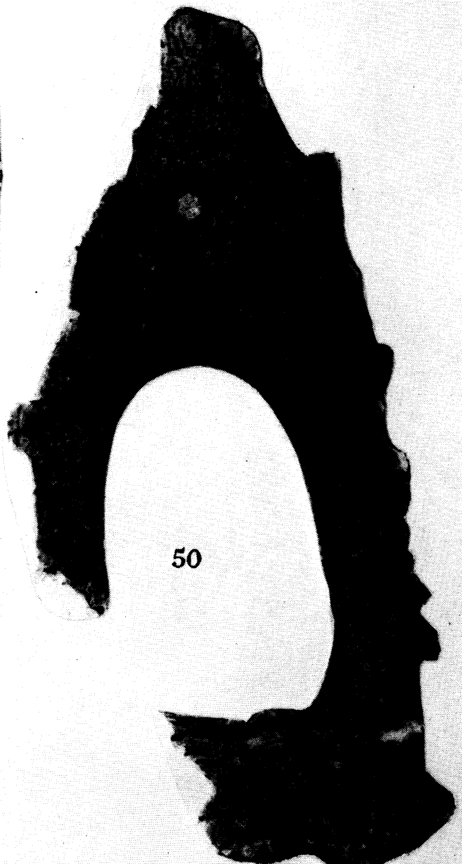
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(*Facing p.* 124)

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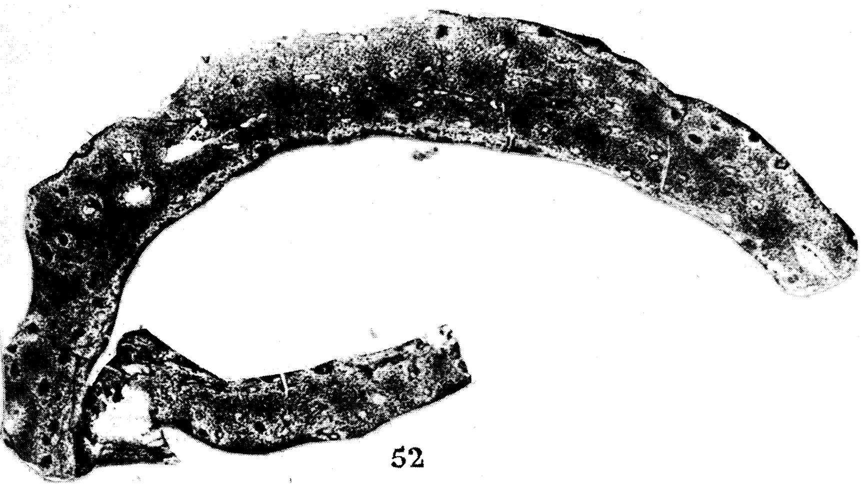

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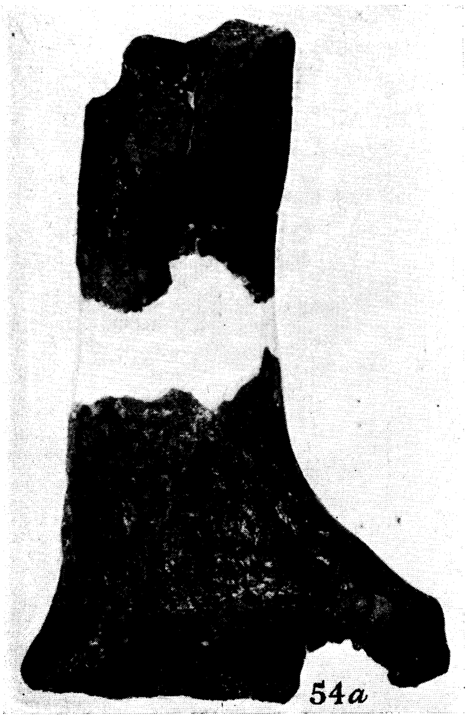

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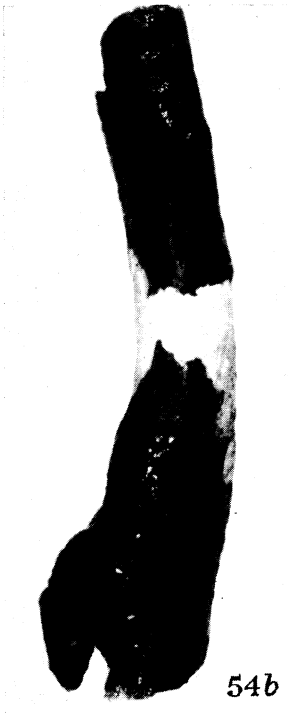

54*b*

54*c*

Plate 23

Figure 51. *Callorhynchus antarcticus* Lacépède. A fragment of the frontal clasper in section (× 55). P 45956. Recent.

Figure 52. *Squaloraja polyspondyla* Agassiz. Incomplete transverse section of the frontal clasper (× 26). P 4323*e*. Lower Lias, Lyme Regis.

Figure 53. *Menaspacanthus armaghensis* gen. and sp.nov. Transverse section of frontal spine (× 18). P 45766.I (holotype). Lower Carboniferous Limestone, Armagh.

Figure 54. *Menaspacanthus armaghensis* gen. and sp.nov. Proximal part of frontal spine in ventral (*a*), lateral (*b*) and dorsal (*c*) view (× 4). P 45766 (holotype). Lower Carboniferous Limestone, Armagh.

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PLATE 24

FIGURE 55. *Squaloraja polyspondyla* Agassiz. The pelvic region of P 2276, Lower Lias, Lyme Regis (× 3), showing the notochordal calcifications (*n.c.*), pelvic girdle (*p.g.*), the basipterygium (*bpt.*) and radials (*ra.*) of the pelvic fins, the skeleton of the pelvic claspers (*p.cl.*), the lateral line (*l.l.*), and the tenacula (*ten.*), which consist of groups of enlarged scales borne on anterior processes of the pelvic girdle.

FIGURE 56. *Squaloraja polyspondyla* Agassiz. Rostrum in dorsal view (× 1·75). 41354. Lower Lias, Lyme Regis. Cf. figure 9.

FIGURE 57. *Metopacanthus granulatus* (Agassiz). Part of the rostrum of P 4575, Lower Lias, Lyme Regis (× 30), showing normal scales and a sensory canal enclosed within modified scales.

FIGURE 58. *Metopacanthus granulatus* (Agassiz). Part of 43050, Lower Lias, Lyme Regis (× 1), showing notochordal calcifications (*n.c.*), the synarcual (*syn.*), the base of the spine (*sp.*) and the basal (*ba.*) of the first dorsal fin, and the occipital region of the neurocranium (*occ.*).

FIGURE 59. *Myriacanthus paradoxus* Agassiz. Part of P 10130, Lower Lias, Lyme Regis (× 1), showing the occipital condyle of the neurocranium, the synarcual, traces of notochordal calcifications, and the base of the spine and the basal of the first dorsal fin. Lettering as in figure 58.

Legend to plate 26 (*cont.*)

FIGURE 62. *Deltoptychius armigerus* (Traquair). Incomplete fish, RSM 1936.4, Calciferous Sandstone Series, Cementstones, Glencartholm, Eskdale, Dumfries (× 1). See figure 27. *e.sc.*, Enlarged scales of '*Listracanthus*' type; *m.sp.*, mandibular spines; *p.sp.*, posterior spines of head shield; *u.t.p.*, tooth plate of upper jaw.

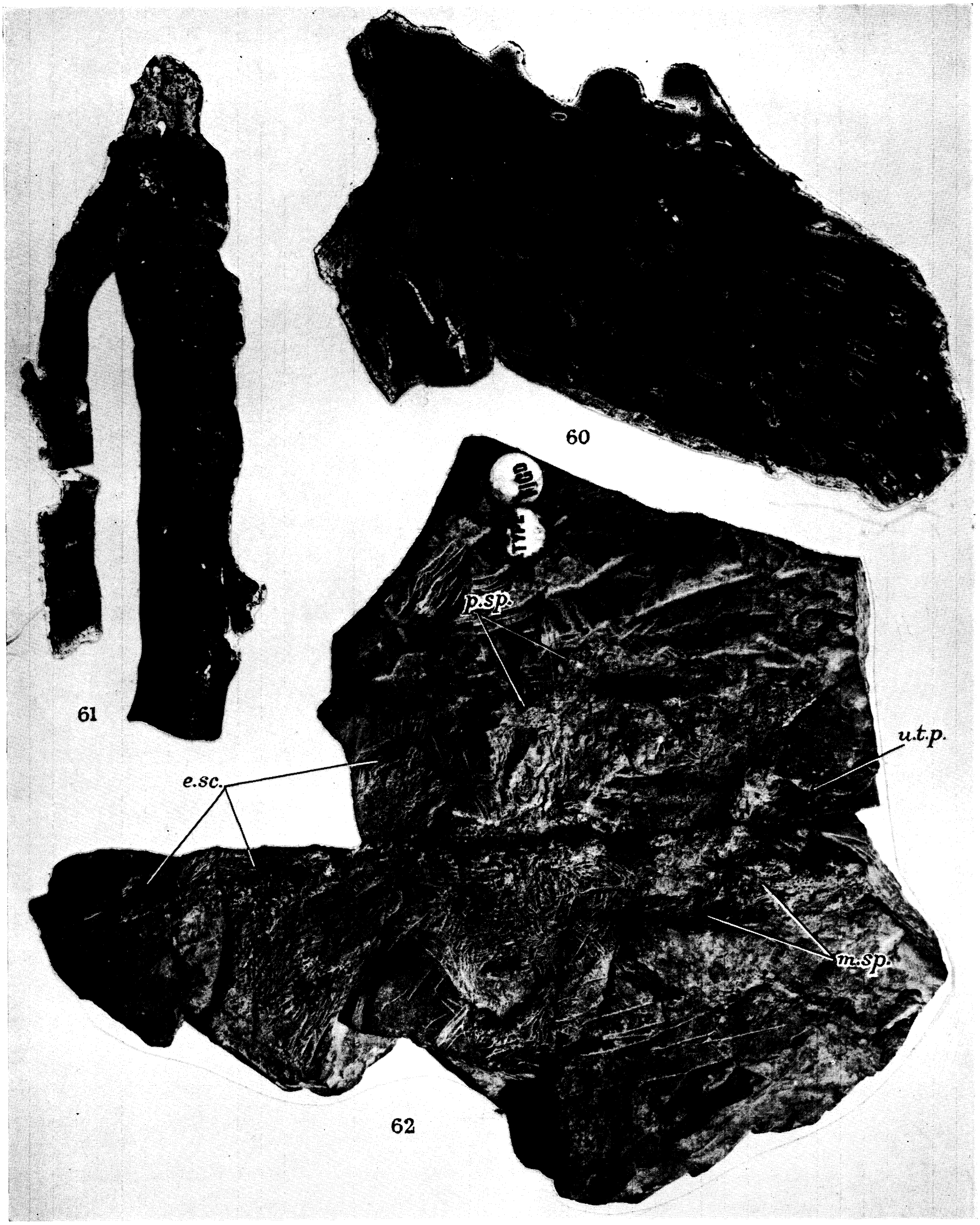

FIGURE 60. *Myriacanthus paradoxus* Agassiz. Transverse section of part of a dermal plate from the skull roof (× 23). P 151.I. Lower Lias, Lyme Regis. See figure 15 for interpretation.

FIGURE 61. *Deltoptychius armigerus* (Traquair). Incomplete transverse section of a mandibular spine (× 20). P 11358.I. Calciferous Sandstone Series, Abden Bone Bed, Kinghorn, Fife. See figure 29 for interpretation.


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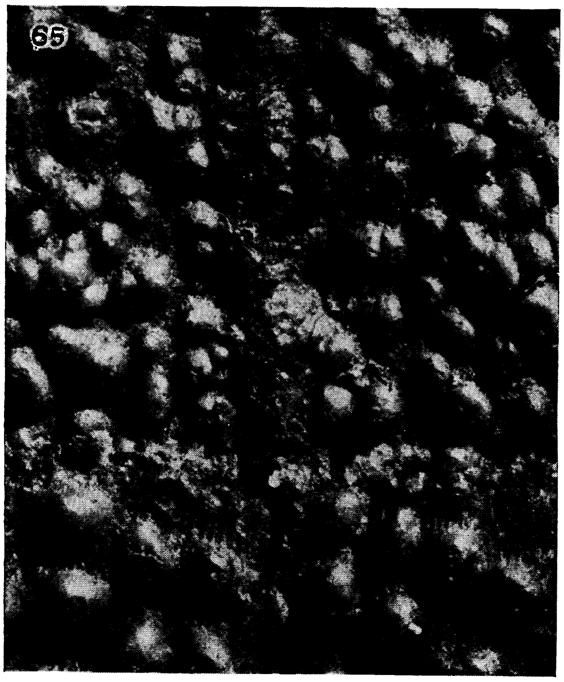
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PLATE 27

FIGURE 63. *Deltoptychius armigerus* (Traquair). Imperfect head shield in dorsal view (× 2). P 11372. ?Limestone Coal Group, Flex Coal, Loanhead, Edinburgh. See figure 30 for interpretation.

FIGURE 64. Part of the central region of the posterior part of the head shield shown in figure 63 (× 20), showing at the extreme left the course of the supraorbital sensory canal, and on the right, lines of fusion between tesserae.

FIGURE 65. *Deltoptychius moythomasi* sp.nov. Part of the posterior spine of a head shield to show the surface tubercles and the groove for the supraorbital sensory canal (× 10). P 2885. Lower Carboniferous Limestone, Armagh.

FIGURE 66. As figure 65, another specimen (× 10). P 2901. Lower Carboniferous Limestone, Armagh.

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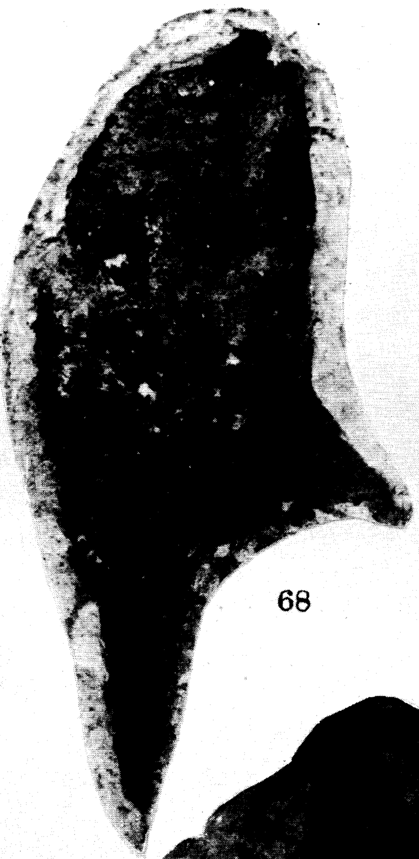

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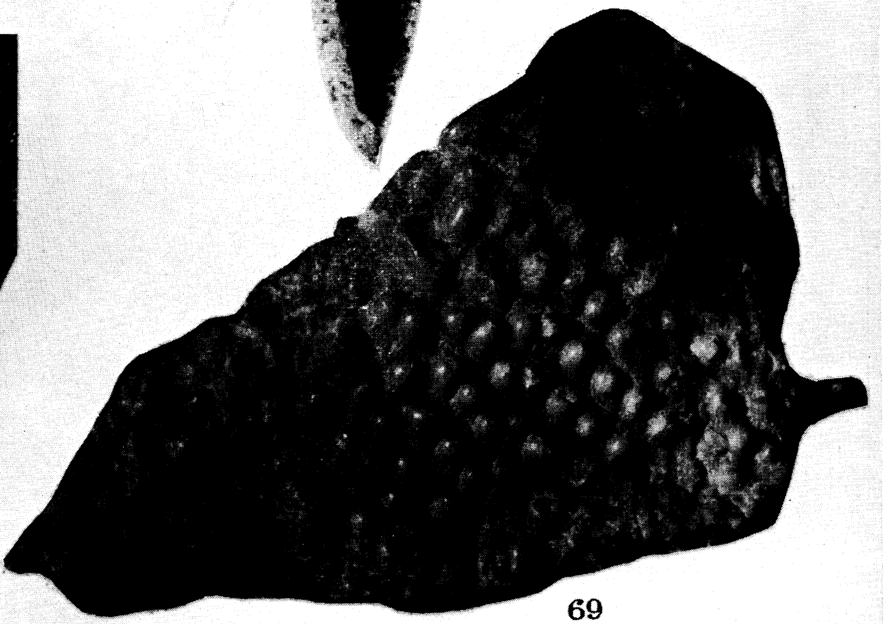

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interpretation agrees well with the pattern in *Rhinochimaera*, but leads to some topographical difficulties: it is necessary to assume that the oral line, after leaving the infraorbital line well in front of the mandibular symphysis, passed backwards on the ventro-lateral surface of the head until it reached the angle of the mouth, and that the mandibular line, after running forwards towards the labial cartilages, turned back again on the ventro-lateral surface of the head to reach the mandible. The only alternative interpretation seems to be to regard the 'mandibular' line as the oral and assume that the true mandibular line has not yet been seen. The 'oral' line would then correspond to the nasal line which branches from the postnasal ventral branch of the infraorbital line in living chimaeroids. In the absence of evidence as to the presence of a second canal at the level of the anterior edge of the orbit the first of these two interpretations is accepted. In either case it is clear that there are no great differences between the cephalic sensory canals of chimaeroids and *Squaloraja*.

The chimaeroids have three types of secondary sexual organs in males, the pelvic claspers, the tenacula or pre-pelvic claspers and the frontal clasper. All these are present in *Squaloraja*. In the British Museum there are four more or less complete skeletons of *Squaloraja*, a fifth is in the Royal Scottish Museum, and a sixth was figured by Agassiz (1836, pl. 42). Of these six skeletons, all except P 2079 and P 3184 in the British Museum show either or both the pelvic and frontal claspers, and are therefore males. P 2079 (Smith Woodward, 1886, pl. 55, figs. 3, 4 and 7) was described by Smith Woodward as a female, but the pelvic fins and girdle are not preserved, and since the specimen is lying ventral side uppermost the absence of a frontal clasper is only suggested by an excavation in the back of the block. P 2079 (Smith Woodward 1886, p. 529) is a large individual which Smith Woodward described as 'probably a female', but only a fragment of the pelvic fin is preserved and the anterior part of the head is much broken and inverted. There is thus no positive evidence of sexual dimorphism in *Squaloraja*. This point is discussed on p. 200. The pelvic claspers and tenacula are described above with the pelvic girdle and fin. The frontal clasper has been described by Reis (1895, p. 385, pl. 12, figs. 2, 4, 5), who showed

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Explanation of plate 28

Figure 67. *Myriacanthus paradoxus* Agassiz. Plate probably covering the ventro-lateral corner of the right side of the occipital region of the neurocranium, in ventral view (× 3·5). P 10130. Lower Lias, Lyme Regis.

Figure 68. *Deltoptychius moythomasi* sp.nov. Plate probably covering the ventro-lateral corner of the left side of the occipital region of the neurocranium, in ventro-lateral view (× 2·5). P 2884. Lower Carboniferous Limestone, Armagh.

Figure 69. *Deltoptychius moythomasi* sp.nov. Probable mandibular spine of the left side in ventral view, showing lines of fusion between tesserae at bottom left (× 4). P 2881. Lower Carboniferous Limestone, Armagh.

Figure 70. *Helodus simplex* Agassiz. Scale in longitudinal section (× 30). P 2908.I. Coal Measures, Knowles Ironstone, Longton, Staffs.

Figure 71. *Deltoptychius moythomasi* sp.nov. Transverse section of the head shield in the region of the groove for the supraorbital sensory canal (× 60). P 2901.I. Lower Carboniferous Limestone, Armagh. See figure 35 for interpretation.

that it consists of 'heavily calcified fibro-cartilage', not of dentine as earlier authors had supposed, and that it agrees in structure with the frontal claspers of living chimaeroids and the Jurassic *Ischyodus* (figures 51, 52, plate 23). Ørvig (1951, text-fig. 19) describes the substance of the clasper in *Squaloraja* as 'calcified cartilage of a special type'. Dean (1906, figs. 132 to 137) has shown how the frontal clasper of *Squaloraja* differs from those of living chimaeroids in its much greater size and more extensive squamation, with *Ischyodus* being intermediate between the two in both these features.

The affinities of Squaloraja

Squaloraja has previously been placed among the chimaeroids, as the only member of the family Squalorajidae Smith Woodward. Returning to the list of special characters of chimaeroids on p. 111, *Squaloraja* agrees with the chimaeroids in: (1) the holostylic suspension; (4) the number of tooth plates; (5) the structure of the tooth plates; (8) the position of the branchial arches; (11) the structure of the rostrum; (12) the large labial cartilages; (13) the structure of the notochord; (14) the presence of a synarcual; (15) the structure of the pectoral fin; (16) the separation of the halves of the pelvic girdle; (19) the structure of the second dorsal fin; (20) the structure of the scales; (22) the pattern of the cephalic sensory canals; (23) the specialized scales surrounding the sensory canals; (24, 25, 26) the presence of pelvic claspers, tenacula and a frontal clasper.

The structure of *Squaloraja* with regard to characters 3, 7, 9 and 10 (the interorbital septum, hyoid arch, spiracle and operculum) is not known.

Squaloraja differs from the chimaeroids in: (2) the absence of an ethmoid canal; (6) the absence of tritors on the tooth plates; (7) the absence of a fin spine and probably of an anterior dorsal fin; (21) the extensive squamation. Other differences between *Squaloraja* and the chimaeroids are the dorso-ventrally flattened body, the enlargement and fusion with the neurocranium of the rostral cartilages, the enlargement of the frontal clasper, the support of the tenacula by processes of the pelvic girdle rather than by independent cartilages and the thickening of the notochordal calcifications. The long list of important similarities between *Squaloraja* and the chimaeroids leaves no doubt that the two are closely related. But the differences, especially the absence of an ethmoid canal, justify a separate sub-order Squalorajoidei within the Chimaeriformes, defined on p. 116.

Of the characters of Squalorajoidei, the thick notochordal calcifications and the loss or reduction of the first dorsal fin and its spine are probably specializations, the absence of an ethmoid canal and tritors and the more complete squamation are certainly primitive, and the enlargement of the rostrum and frontal clasper and the dorso-ventral flattening may be either primitive or specialized, and are discussed below.

Since the Jurassic chimaeroid *Ischyodus* has a larger frontal clasper than do living chimaeroids, it is probable that the most primitive chimaeroids had an even larger clasper, and that the size of the structure in *Squaloraja* is a primitive feature: this is borne out by the comparison (p. 143) between myriacanthids and chimaeroids. And since there is no advantage in a long frontal clasper unless there is an equally long rostrum against which it may grip, it is also probable that the earliest chimaeroids had a large rostrum.

It seems likely that there is a correlation between the development of an ethmoid canal and the shape of the skull. De Beer & Moy-Thomas (1935, p. 299) and de Beer (1937,

p. 75) hold that the formation of the ethmoid canal is a mechanical consequence of the peculiar interorbital septum of the chimaeroids, which arises late in ontogeny by the coming together of the orbits above the brain: as Allis (1917, p. 121) says, the interorbital septum is produced by marked lateral compression of the head in post-embryonic stages. This would suggest that the ethmoid canal and interorbital septum of the chimaeroids are the results of lateral compression of an originally broad-headed form, and that the dorso-ventrally flattened shape of *Squaloraja* is a primitive feature. Against this hypothesis of the ethmoid canal being a consequence of the formation of the interorbital septum is the fact that in *Callorhynchus* the ethmoid canal arises in ontogeny while the orbits are still widely separated (Schauinsland 1903, pl. 23, figs. 165, 167; pl. 24, fig. 166), but that phyletic effect should precede cause during ontogeny is not impossible. Such evidence as there is indicates that the large frontal clasper, the large rostrum and the flattened form of *Squaloraja* are all primitive in comparison with the conditions in chimaeroids.

With regard to the origin of the chimaeroids, this comparison between Chimaeroidei and Squalorajoidei suggests that the earliest chimaeroids would have been broad-headed forms, with no ethmoid canal, a large rostrum and frontal clasper, little or no differentiation of the surface of the tooth plates into tritoral areas, and more or less complete squamation.

SUB-ORDER MYRIACANTHOIDEI nov.

Diagnosis: Chimaeriformes in which the head is not strongly dorso-ventrally flattened; two or three pairs of tooth plates in the upper jaw, a median symphysial tooth and one pair of tooth plates in the lower jaw, most of the tooth plates without tritors, tritors simple when present, tooth plates thin; rostrum and frontal clasper large, frontal clasper present in both sexes (?); one or more pairs of tuberculated dermal plates normally present on the head; synarcual present, calcified rings or crescents in the sheath of the notochord; first dorsal fin with a spine, lateral faces of spine usually tuberculated and outer zone of osteodentine thick; pelvic claspers not known, pre-pelvic tenacula represented by a group of enlarged scales without skeletal support; scales placoid (synchronomorial), squamation not reduced, sensory canals surrounded by specialized crescentic scales which are fused into short cylinders.

FAMILY MYRIACANTHIDAE Smith Woodward (1889*b*, p. 279)

Amended diagnosis: Myriacanthoidei in which there are three pairs of tooth plates in the upper jaw, the two anterior pairs small and with many small, simple tritors; rostrum and frontal clasper very large; a pair of tuberculated dermal plates or spines on the mandible, dermal plates on skull roof present or absent; fin spine tuberculated and with a series of denticles on the proximal part of the anterior edge.

As defined here, the Myriacanthidae contains only those species previously placed in the genus *Myriacanthus* Agassiz, which is here divided into two, *Myriacanthus* and *Metopacanthus* Zittel. The type species of both genera are known by incomplete skeletons from the Lower Lias of Lyme Regis, Dorset. *Myriacanthus paradoxus* also occurs in the Lower Lias of France (Terquem 1855, p. 241). A third species, *Myriacanthus bollensis* Fraas (1910, p. 61, pl. 3, fig. 7) from the Upper Lias of Holzmaden, Germany, should probably be retained in *Myriacanthus*. Casier (1959, p. 17, pl. 2, figs. 1, 3; pl. 3) has described as 'Myriacanthidae indet.' fragmentary tooth plates from the Lower Lias of Belgium, but these could well belong to the Chimaeropsidae (p. 143).

Genus **Myriacanthus** Agassiz (1837, p. 37)

Amended diagnosis: Myriacanthidae in which the head is not laterally compressed; mandibular dermal plates dorso-ventrally flattened and with three or four spines at the tip, three pairs of tuberculated dermal plates on the skull; tritors present only on the two anterior pairs of tooth plates in the upper jaw, lingual face of symphysial tooth flat; fin spine not compressed, heavily tuberculated, with an incomplete median and a complete paired series of denticles on the posterior face, most of these pointing upwards, lamellar tissue making up less than one-quarter of the thickness of the spine; scales polycuspid, at least on the head.

Type species: *Myriacanthus paradoxus* Agassiz.

Myriacanthus paradoxus Agassiz

Figure 46, plate 22; figure 59, plate 25; figure 60, plate 26; figure 67, plate 28; figures 13 to 19.

1836 *Myriacanthus paradoxus* Agassiz, **3**, pl. 6.
1837 *Myriacanthus paradoxus* Agassiz, **3**, p. 38.
1837 *Myriacanthus retrorsus* Agassiz, **3**, p. 39.
1838 *Myriacanthus retrorsus* Agassiz, **3**, pl. 8*a*, figs. 14, 15.
1855 *Chimaera* (*Ischyodon*) *johnsoni* Agassiz; Terquem, p. 241, pl. 14, fig. 1.
1891*a* *Myriacanthus paradoxus* Agassiz; Smith Woodward, p. 44, pl. 2, figs. 1 to 3. Lists other earlier synonyms.
1906*a* *Myriacanthus paradoxus* Agassiz; Smith Woodward, p. 2, pl. 1, figs. 1 to 5.
1906 *Myriacanthus paradoxus* Agassiz; Dean, p. 143, text-figs. 119, 119A, 142.

Diagnosis: *Myriacanthus* reaching well over 1 m in length, dorsal fin spine up to 60 cm in length.

Holotype: dorsal fin spine, BMNH P 6095 (Agassiz 1836, pl. 6, figs. 1, 2).

Material: specimens in the BMNH (including P 10130 in addition to those listed by Smith Woodward 1891*a*, p. 44); RSM 1963.8.

Horizon and locality: Lower Lias; Lyme Regis, Dorset; Hettange, Lorraine, France.

Description

The only moderately complete specimen of *M. paradoxus* is P 10130 (Smith Woodward 1906*a*, pl. 1, figs. 1 to 4); all other known specimens show only the dentition, the frontal clasper or the dorsal fin spine, sometimes with fragments of calcified cartilage and squamation.

P 10130 is the only specimen to show recognizable remains of the skull, and here no details of the neurocranium can be made out. But in all the specimens where the dentition is preserved it is crushed dorso-ventrally, suggesting that the skull was broad and flat. This is borne out by the breadth of the mandible (figure 13), and contrasts with the conditions in *Metopacanthus* (p. 138). The long, stout rostrum is preserved in P 10130, and appears to be similar in shape to that of *Metopacanthus* (figure 20), though the flap on the tip is not preserved. Apart from the median rostral cartilage in P 10130, there is no sign in any specimen of rostral or labial cartilages.

The mandible is well preserved in P 4664 (figure 13), and traces of it are preserved in P 151 and P 10130. The mandibular cartilages are fibrous and strongly calcified, and the two rami lay almost in the same transverse plane, with an angle of 30° or less between them. The two rami are fused at the symphysis, as they are in living chimaeroids, and in P 151 and P 4664 there is an independent cartilage (*s.c.*) at the anterior edge of the line of fusion which must represent the symphysial cartilage which occurs in embryos of *Callorhynchus* (Schauinsland 1903, pl. 17, fig. 124), but is fused with the mandible or lost in the adult. Holmgren (1942, p. 244) homologizes this cartilage with the postsymphysial plate of antiarchs: its persistence in the adult *Myriacanthus* may be a primitive feature, or may be because of the median symphysial tooth in the mandible. At the postero-lateral end of each ramus of the mandible there is one of the well-known dermal spines (Egerton 1872, pl. 8; Smith Woodward 1906*a*, pl. 1, figs. 4, 5; Dean 1906 text-fig. 142; figure 13). These spines are triangular, hollow, strongly compressed dorso-ventrally, and ornamented with bluntly pointed tubercles which when well preserved (P 10130) bear weak radial ridges. The tubercles are arranged in irregular rows in the plane of the mandibular ramus. The anterior edge of the spine bears a row of slightly enlarged, more pointed tubercles, and the posterior edge bears three or four much enlarged, recurved spines, of which the two at the tip are particularly large. The ventral face of the spine is triangular with a narrow unornamented strip at the base which was inserted in the dermis. The base of the dorsal surface of the spine is excavated, and the tubercles on this surface are smaller and more closely set than on the ventral face.

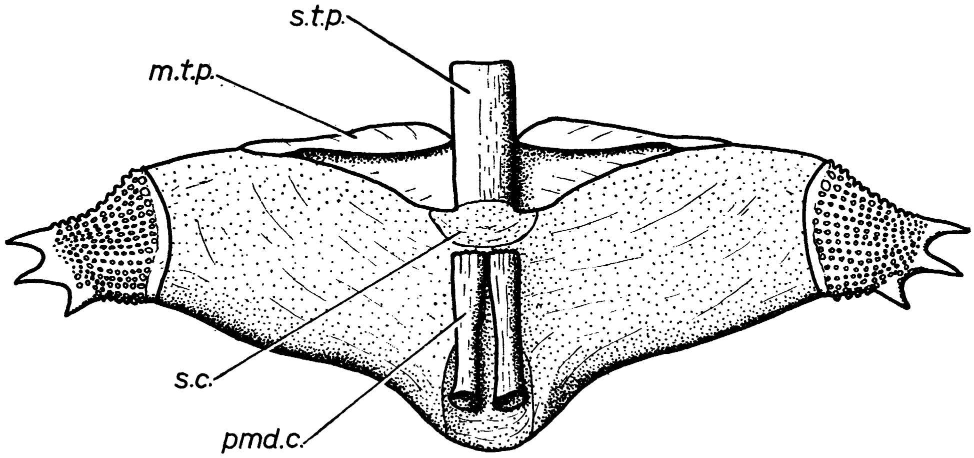

FIGURE 13. *Myriacanthus paradoxus* Agassiz. Restoration of mandible in antero-ventral view (× $\frac{2}{3}$ approx.). From P 4664. *m.t.p.*, Mandibular tooth plate; *pmd.c.*, premandibular cartilage; *s.c.*, symphysial cartilage; *s.t.p.*, symphysial tooth.

In P 4664 a pair of rod-shaped cartilages is preserved lying along the line of fusion between the rami of the mandible (*pmd.c.*, figure 13). These cartilages must be homologous with the premandibular cartilages of chimaeroids, which are especially large in *Callorhynchus* and *Rhinochimaera* (Holmgren 1942, text-figs. 52, 53).

As Smith Woodward (1889*b*, p. 280) noted, the skull of *M. paradoxus* bears tuberculated dermal plates in addition to those on the mandible. In P 10130, in addition to the mandibular spines, four of these plates are visible. Two lie near the right mandibular spine (Smith Woodward 1906*a*, pl. 1, fig. 1, 'II', 'III'), the third lies in front of the tooth plates and was identified by Smith Woodward (1906*a*, pl. 1, fig. 1, 'V') as a vomerine tooth plate, and the fourth lies behind the mandibular spine of the left side. All these plates are asymmetrical, and must have been paired. P 151 (Smith Woodward, 1891*a*, pl. 2, fig. 2)

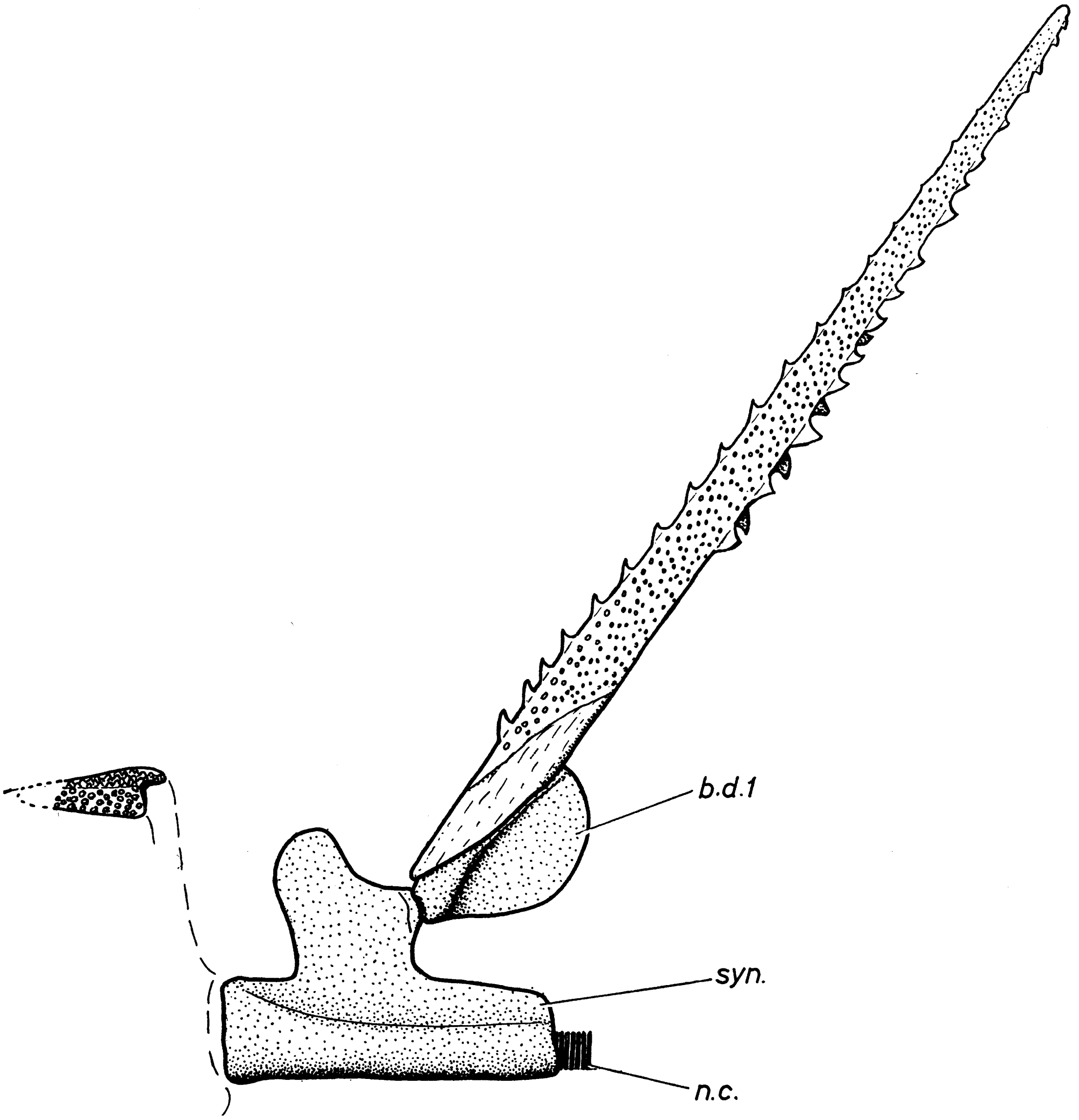

FIGURE 14. *Myriacanthus paradoxus* Agassiz. Restoration of anterior part of vertebral column and skeleton of first dorsal fin. The occipital region of the skull is indicated by a broken line, and one of the posterior pair of dermal plates on the skull roof is shown (× $\frac{1}{3}$ approx.). From P 10130 and RSM 1963.8. *b.d.* 1, Basal cartilage of first dorsal fin; *n.c.*, notochordal calcification; *syn.*, synarcual.

shows two plates lying near the right mandibular spine which correspond in shape with those in a similar position in P 10130. RSM 1963.8, a specimen in which only the fin spine and the occipital part of the neurocranium are preserved, shows a pair of plates lying on the dorso-lateral edges of the roof of the occipital region (figure 14). Where the outer surface of these plates is visible (especially in RSM 1963.8) it is ornamented with rounded tubercles which are like those on the mandibular spine but are more irregular in size. All the plates have a longitudinal ridge near their centre, and are roughly L-shaped in transverse section. The arrangement of the plates on the skull of *M. paradoxus* is not yet clear, but from the specimens described above some facts emerge. There were at least three pairs of plates on the skull in addition to the mandibular spines (P 10130). One pair of plates lay on the dorso-lateral corners of the occipital part of the neurocranium (RSM 1963.8). The occipital plates exposed in RSM 1963.8 seem to agree in shape with the posterior of the two plates which lie near the right mandibular spine in P 10130: this suggests that the anterior of these two plates is one of a pair which lay on the skull roof just behind the insertion of the frontal clasper. The two plates exposed in P 151 are probably members of these two pairs of roofing plates. The plate which lies in front of the tooth plates in P 10130 is thinner and less massive than the other plates, but it has a stout, tuberculated spine projecting obliquely from the end which is lying anteriorly (figure 67, plate 28). This plate is obviously displaced, and its position on the skull can only be guessed at, but in shape and in the projecting tuberculated spine it resembles P 2881 (figure 68, plate 28), a specimen from the Carboniferous Limestone of Armagh, Ireland, which is described on p. 168. It is there suggested that this plate covered the ventro-lateral corner of the occipital part of the neurocranium in *Deltoptychius moythomasi* sp.nov., with the spine projecting from its posterior end. There is a good evidence that the myriacanthids and the menaspoids, in which *Deltoptychius* is placed, are related (see p. 174). I would therefore suggest that the plate described above in P 10130 covered the ventro-lateral corner of the neurocranium in *M. paradoxus*. This interpretation is supported by the fact that a plate of somewhat similar shape has been restored by Reis in this position in the myriacanthoid *Chimaeropsis* (figure 23).

Transverse sections have been cut of plates from the skull roof in P 151 (figure 60, plate 26; figure 15) and RSM 1963.8. The basal three-quarters of the plate consist of tissue laid down in parallel lamellae which are perforated by vascular canals (*v.can.*). In the superficial part of the plate the vascular canals form a poorly marked layer of vascular tissue, more obvious in RSM 1963.8 than in the figured section. Passing out from the vascular canals there are sparse, branched tubules (*d.t.*) which are apparently identical with the dentine tubules in osteodentine. Not all the vascular canals are surrounded by osteons, and where these are present they are narrow (*d.ost.*). In the figured section the whole of the plate is penetrated by numerous straight, unbranched, sub-parallel canaliculi (*fib.*). These canaliculi contained uncalcified fibres ('Sharpey's fibres'). They have no connexion with the vascular canals and they often pass obliquely or almost horizontally through the lamellae of the tissue. Also penetrating the basal, lamellar part of the plate there are long, sinuous, much-branched tubules (*d.t.*) which pass vertically through the lamellae of the tissue, ending blindly below the superficial vascular layer. These tubules agree in every way with those given off from the vascular canals in both the lamellar and superficial parts of the plate. There are no cell spaces in the tissue. The tubercles on the surface of the plate (*tub.*) are built up by dentinal tubules radiating from vascular canals at the base of the tubercle, but in the adult both the tubules and the vascular canals have become occluded by hard tissue (*occ.v.can.*).

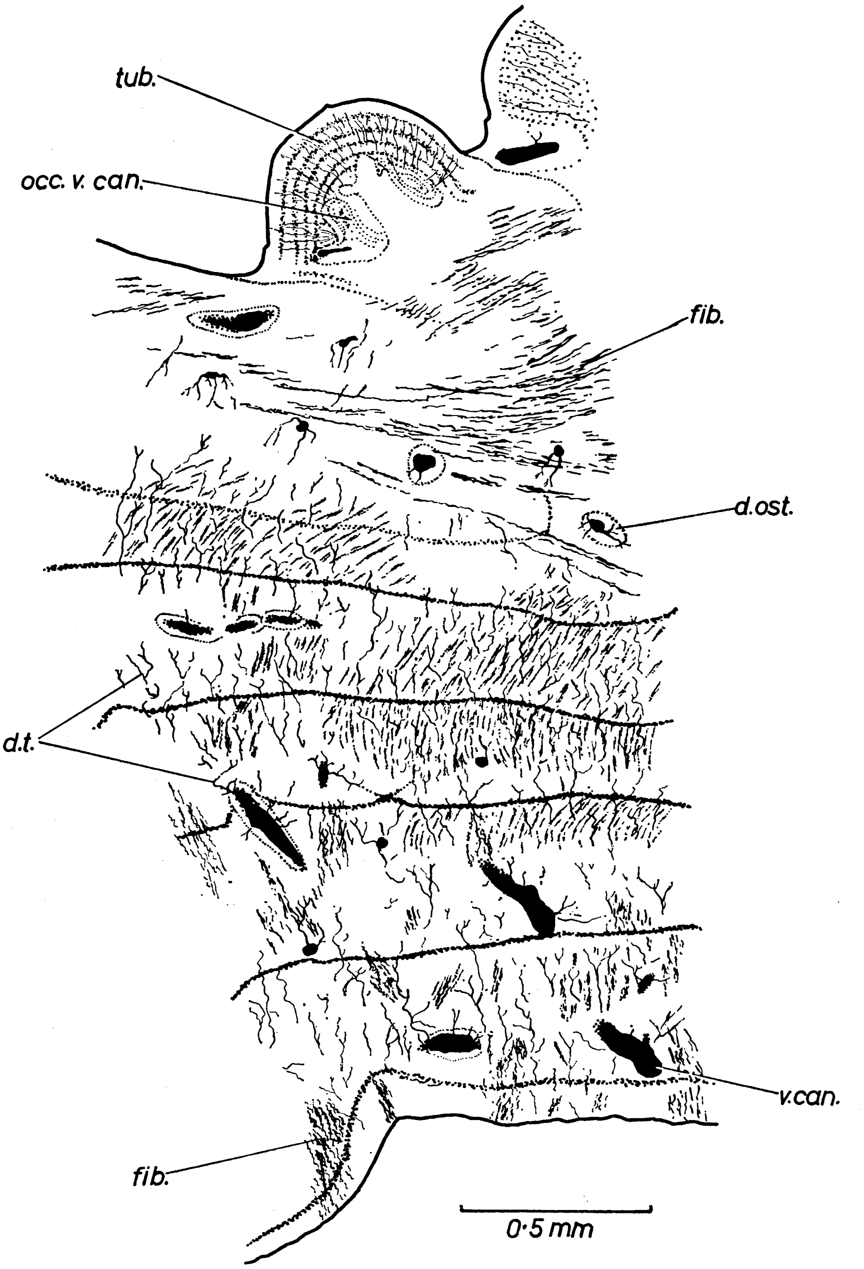

FIGURE 15. *Myriacanthus paradoxus* Agassiz. Transverse section of a dermal plate from the skull roof. P 151.I. *d.ost.*, Osteon; *d.t.*, tubules; *fib.*, Sharpey's fibres; *occ.v.can.*, occluded vascular canal; *tub.*, surface tubercle; *v.can.*, vascular canal.

Interpretation of this tissue presents difficulties. Ørvig (1951, pp. 356–377) has dealt at length with the role of dentine in the exoskeleton of lower vertebrates. He concludes (p. 376) that 'the substance in the basal parts of the scales and dermal bones of fishes . . . is true bone tissue, not dentine or any dentinous tissue resembling bone.' He shows that where dentine has been described in the basal layers of the exoskeleton it is because non-vascular canals of Williamson or the spaces occupied by uncalcified 'Sharpey's fibres' have been interpreted as dentine tubules. Ørvig's discussion of this point deals mainly with the scales in actinopterygians and acanthodians, but he also indicates (see also, Stensiö 1961) that the base or root of the cyclomorial scales of Palaeozoic elasmobranchs is bony. Ørvig does not deal with the fin spines of elasmobranchs but refers to the basal lamellar tissue in these as orthodentine (see p. 113). In the armour of *Myriacanthus* the tubules penetrating the basal lamellar tissue and those given off from the vascular canals do not seem to differ in any way from those in the lamellar tissue and the osteodentine of the fin spines of sharks and holocephalans. Pending an investigation of the true nature of this tissue, particularly whether or not the tubules are dentine tubules, the vascular and lamellar layers in the armour of myriacanthoids and menaspoids (see p. 166) will be referred to as osteodentine and lamellar tissue, as in the fin spines.

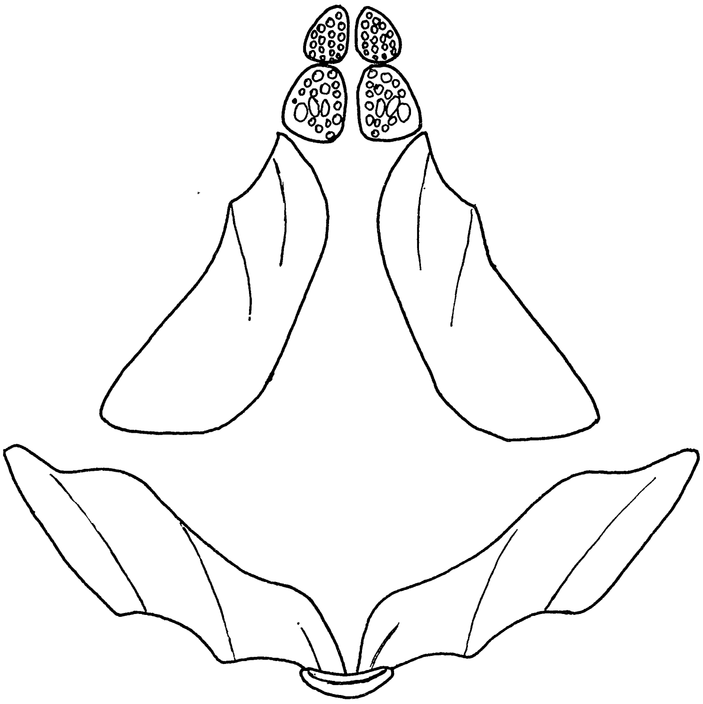

FIGURE 16. *Myriacanthus paradoxus* Agassiz. Dentition restored as if seen from in front with the mouth wide open (× $\frac{1}{2}$ approx.). Modified from Dean (1906).

There are no recognizable remains of the branchial arches in any specimen.

The dentition has been described by Smith Woodward (1889*b*) and Dean (1906, p. 143), and is restored in figure 16. The tooth plates are much thinner than the bulky tooth plates of chimaeroids. In the lower jaw there is a pair of large plates, each with two broad, oblique channels on the surface: as Smith Woodward (1891*a*, p. 44) noted, the whole surface is made up of tubular dentine, and there are no localized tritors. At the mandibular symphysis there is the median, chisel-like tooth which is characteristic of the suborder; again, the whole of the oral face of the tooth is made up of tubular dentine. In the upper jaw there are three pairs of tooth plates. The posterior pair ('palatine') is the largest. These posterior tooth plates are trapezoid, and are much more closely apposed than are the mandibular plates, lying with their medial edges almost in contact and with their long axes diverging only by about 30°. An oblique channel crosses each posterior tooth plate near the anterior end, but again the whole oral surface is made up of tubular dentine. The two anterior pairs of upper tooth plates ('vomerine 1 and 2') are alike in structure and differ only in size. Each is roughly triangular and has the oral surface raised in a series of transverse humps. The tubular dentine appears to be confined to these humps, and they are therefore equivalent to the tritors of chimaeroids.

The only specimens of *M. paradoxus* in which any part of the vertebral column is preserved are P 10130 and RSM 1963.8. In P 10130 a large synarcual of calcified cartilage is preserved (figure 59, plate 25; figure 14, *syn.*). The synarcual is long, with a high median dorsal crest which curves forwards a little. The crest of the synarcual is also preserved in RSM 1963.8. At the hind end of the synarcual in P 10130, where the cartilage of the exposed surface has been removed, there are traces of calcifications in the sheath of the notochord (figure 59, plate 25), but no more of the notochord is preserved. These calcifications appear to be similar to those in *Metopacanthus*, and are discussed on p. 139.

In P 10130 fragments of calcified cartilage are preserved in the region of the pectoral girdle and fin, but none are recognizable (the cartilage described by Smith Woodward (1906*a*, p. 2, pl. 1, fig. 1, 'pct.') as the ascending limb of the pectoral girdle is in fact the synarcual). Nothing is known of the pelvic girdle or fin.

The only parts of the median fins known are the spine of the first dorsal, known by many examples, and the basal of this fin which is preserved in P 10130 and RSM 1963.8. The spine (figure 14) has been described by Agassiz (1836–8, p. 38, pls. 6, 8*a*) and by Smith Woodward (1891*a*, p. 44). In structure the spine (figure 46, plate 22; figure 17) is quite different from the dermal plates on the head (figure 15). The spine is made up almost entirely of osteodentine (*osd.*), consisting of vascular canals (*v.can.*) which are surrounded by dentinal osteons (*d.ost.*) separated by abundant interosteonal tissue (*ist.*). The innermost layer of the wall of the spine consists of tissue (*cpd.*) which is laid down in parallel lamellae and contains few vascular canals. This lamellar tissue makes up between one-fifth and one-eighth of the thickness of the wall of the spine. The surface tubercles (*tub.*) contain bunches of elongated dentine tubules branching from vascular canals at the base of the tubercle. The terminal parts of these tubules form a poorly defined layer of pallial dentine, but there is no sign of any enamel. Near the surface of the spine there are traces of occlusion of the vascular canals by hard tissue just as in the dermal plates on the skull (figure 15).

In both P 10130 and RSM 1963.8 only a single basal is preserved in the dorsal fin (figure 14), and there is no sign of the distal cartilage which occurs in *Metopacanthus* (figure 20), but this is quite probably due to imperfect preservation.

Fragments of the squamation are preserved in P 10130 and P 151. P 10130 shows that the rostrum was thickly set with scales of the type shown in figure 18. In these scales the crown is divided into a number of independent, sharply pointed cusps, and the basal surface of the root is concave, with a single central pulp cavity. It has not proved possible to make satisfactory sections of these scales, but the simple pulp cavity and the available sections (P 151.II) show that the scales are placoid (synchronomorial, Stensiö 1961). P 10130 also shows that the dorsal surface of the base of the rostrum bore large scales with

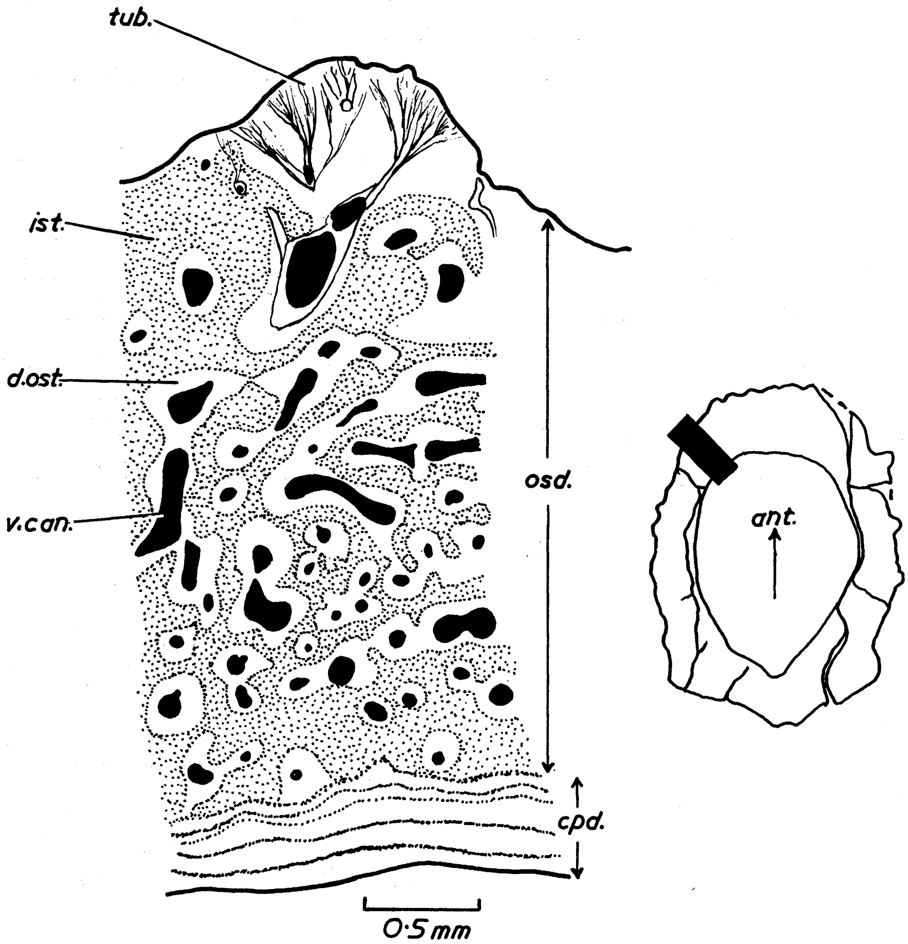

FIGURE 17. *Myriacanthus paradoxus* Agassiz. Transverse section cut near the middle of a dorsal fin spine. P 1736.I. Inset on the right is an outline of the complete section showing the orientation of the figured portion (*ant.*, anterior). *cpd.*, Lamellar tissue; *d.ost.*, dentinal osteon; *ist.*, interosteonal tissue; *osd.*, osteodentine; *tub.*, surface tubercle; *v.can.*, vascular canal.

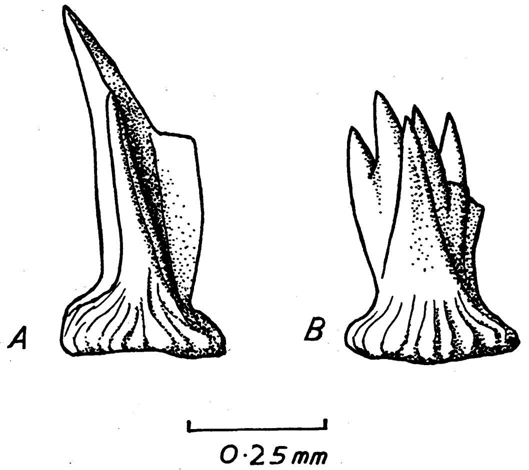

FIGURE 18. *Myriacanthus paradoxus* Agassiz. Scales from the dorsal surface of the head in lateral view. P 151.II. *A*, scale with three cusps in a transverse row and a single anterior cusp; *B*, polycuspid scale.

smooth, recurved, undivided crowns which were opposed by similar enlarged scales on the underside of the base of the frontal clasper. P 151 shows that scales like those shown in figure 18 covered the whole dorsal surface of the head. The squamation of the trunk is unknown.

The sensory canals of *M. paradoxus* are recognizable because they were enclosed within specialized scales, just as in *Squaloraja* and the chimaeroids, but the calcified rings are not separate as they are in chimaeroids, but are irregularly and more or less completely fused together (figure 19). P 10130 shows that two sensory canals ran the length of the rostrum, and P 151 shows traces of two canals on the dorsal surface of the head.

Of the secondary sexual characters of *M. paradoxus*, only the frontal clasper is known. The base of the clasper is preserved in P 10130, but the preservation in this specimen is only sufficient to show that the structure appears to be identical with that of *Metopacanthus* (p. 141). Whether *M. paradoxus* had pelvic claspers or pre-pelvic tenacula is unknown.

Genus **Metopacanthus** Zittel (1887, p. 111)

Amended diagnosis: Myriacanthidae in which the head is not much flattened; mandibular dermal plates conical and tuberculated, without large spines, no other dermal plates on the skull; tubular dentine confined to tritoral areas on all the tooth plates, lingual face of symphysial tooth plate concave; dorsal fin spine laterally compressed, the proximal part of the spine ornamented with small tubercles, no median row of denticles on the posterior face of the spine, the lateral denticles on this face pointing downwards; lamellar tissue making up about half the thickness of the spine; scales with simple, undivided crowns.

Type species: *Ischyodus orthorhinus* Egerton (= *Myriacanthus granulatus* Agassiz).

Metopacanthus granulatus (Agassiz)

Figure 47, plate 22; figure 57, plate 24; figure 58, plate 25; figures 20 to 22.

1837 *Myriacanthus granulatus* Agassiz, **3**, p. 40.
1837 *Leptacanthus tenuispinus* Agassiz, **3**, p. 27.
1838 *Myriacanthus granulatus* Agassiz, **3**, pl. 8*a*, fig. 16.
1843 *Leptacanthus tenuispinus* Agassiz, **3**, pl. 1, figs. 12, 13.
1871 *Ischyodus orthorhinus* Egerton, p. 275, pl. 13.
1887 *Metopacanthus orthorhinus* (Egerton) Zittel, p. 111.
1889*b* *Myriacanthus granulatus* Agassiz; Smith Woodward, p. 279.
1891*a* *Myriacanthus granulatus* Agassiz; Smith Woodward, p. 49, pl. 2, fig. 4; pl. 3, figs. 3, 4.
1906 *Myriacanthus granulatus* Agassiz; Dean, text-figs. 140, 141.

Diagnosis: As genus, only species; probably reaching about 1 m in length, dorsal fin spine up to about 20 cm long.

Holotype: dorsal fin spine, BMNH P 3070 (Agassiz, 1838, pl. 8*a*, fig. 16).

Horizon and locality: Lower Lias, Lyme Regis, Dorset.

Material: specimens in the BMNH (listed by Smith Woodward, 1891*a*, p. 49) and GSM TN 8005.

Description

Perhaps because of its smaller size, *M. granulatus* is known by more complete specimens than *Myriacanthus paradoxus*. 43050 (Egerton 1871, pl. 13; Dean 1906, text-fig. 140) is the most complete, but parts of the head are preserved in P 1158, P 4574 (Smith Woodward 1891*a*, pl. 2, fig. 4; pl. 3, figs. 3, 4) and GSM TN 8005 (Dean 1906, text-fig. 141).

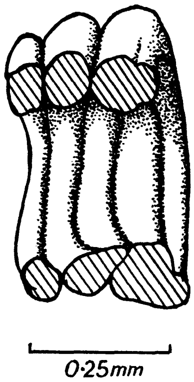

FIGURE 19. *Myriacanthus paradoxus* Agassiz. Modified scales from around a sensory canal on the head, drawn as if cut down the centre of the canal. P 151.III.

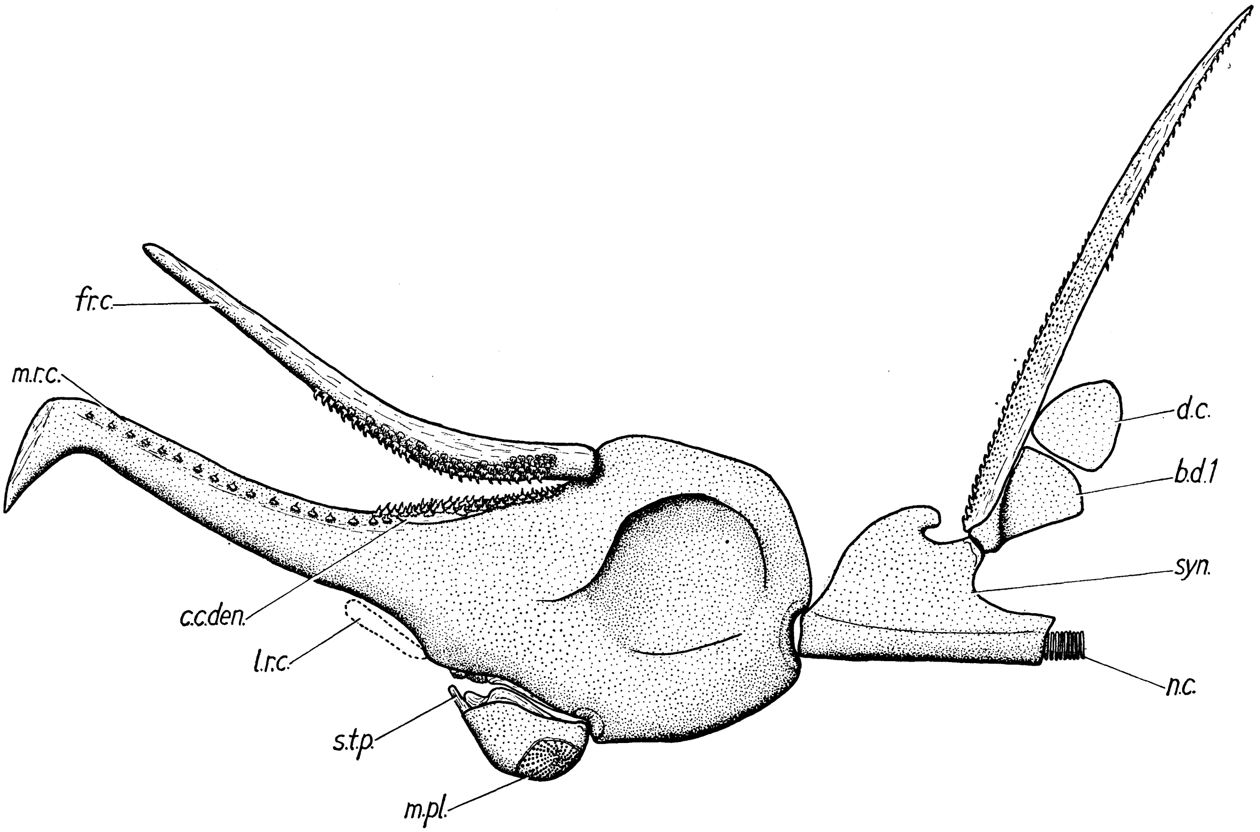

FIGURE 20. *Metopacanthus granulatus* (Agassiz). Restoration of the skeleton of the head and anterior part of the trunk (× $\frac{1}{2}$ approx.). Based on 43050., *b.d.* 1, Basal of first dorsal fin; *c.c.den.*, strip of calcified cartilage bearing denticles which oppose those on the frontal clasper; *d.c.*, distal cartilage in first dorsal fin; *fr.c.*, frontal clasper; *l.r.c.*, *m.r.c.*, lateral and median rostral cartilages; *m.pl.*, mandibular dermal plate; *n.c.*, notochordal calcification; *s.t.p.*, symphysial tooth; *syn.*, synarcual.

From 43050 and the other specimens mentioned above it is possible to make a very incomplete restoration of the skull (figure 20). None of the specimens are crushed dorsoventrally and 43050 is crushed laterally: this suggests that *M. granulatus* was a more laterally compressed fish than *M. paradoxus*. As in *M. paradoxus*, no details of the neurocranium can be made out in any specimen. The rostrum shows a 'hoe-shaped' tip in 43050 and P 4575, and the similarity of this to the rostrum of *Callorhynchus* was noted by Dean (1906, p. 143). But whereas in *Callorhynchus* the median rostral cartilage is slender and does not enter the flap at the tip of the rostrum, in *M. granulatus* the cartilage is very broad and forms the bulk of the terminal flap, where it is especially heavily calcified. Traces of one of the lateral rostral cartilages are visible at the base of the ventral part of the rostrum in P 4575, but there is no sign of the labial cartilages. The mandible is not so well known as in *Myriacanthus*, but from what is visible in 43050 and P 4575 and from the similarity of the mandibular teeth, it was like that of *Myriacanthus* in shape but narrower and deeper. Examples of the dermal plates which lay at the angle of the mandible can be seen in P 1158 (Smith Woodward 1891*a*, pl. 3, fig. 4) and P 4575. These plates differ markedly from those in *Myriacanthus* in being much less flattened dorso-ventrally (confirming that *M. granulatus* was a more compressed fish), so that they are in the form of shallow cones, and in lacking spines at the tip. The plates are ornamented with rounded tubercles which bear very weak radial striations, and are arranged in rows in the plane of the mandibular ramus. The anterior face of the plate bears a ridge on each side of which the tubercles are enlarged a little, but there is no trace of the large spines which occur in *Myriacanthus*. A rod-like cartilage projecting below the ventral edge of the mandible in 43050 (identified by Dean 1906, text-fig. 140, as the detached symphysial tooth) is probably one of the premandibular cartilages described in *Myriacanthus* (p. 129).

The only dermal plate which has been described in *M. granulatus* is the triangular plate in P 1158 mentioned by Smith Woodward (1889*b*, p. 277) and figured in the *Catalogue* (Smith Woodward 1891*a*, pl. 3, fig. 4). As described above, this is one of the mandibular plates. There is no evidence that there were any other dermal plates on the skull of *Metopacanthus*. Both 43050 and GSM TN 8005 show a large plate, evidently paired, lying on the skull roof below the proximal part of the frontal clasper, but a section of a fragment of this plate from GSM TN 8005 proves it to consist of heavily calcified cartilage of the same type as the substance of the frontal clasper. This pair of plates is evidently homologous with the paired strips of calcified cartilage which are present in this region in *Squaloraja*. P 1158 and P 4575 also show displaced fragments of thin, hard, smooth plates, but a section of one of these in P 1158 shows that again they consist of cartilage, not dentine. *Metopacanthus* evidently bore only a single pair of dermal plates, those on the angle of the mandible.

The dentition has been described by Smith Woodward (1889*b*, p. 277; 1891*a*, p. 49). As in *Myriacanthus*, there are three pairs of tooth plates in the upper jaw, and one pair and a median symphysial tooth in the lower jaw. The tooth plates differ from those of *Myriacanthus* in that the tubular dentine is restricted to tritoral areas on all of them. In *Myriacanthus* the two anterior pairs of tooth plates in the upper jaw have a number of small, raised tritoral areas, and the same is true of *Metopacanthus* (P 4575). In the mandibular tooth plates of *Myriacanthus* the whole oral surface is covered by tubular dentine, but in

Metopacanthus, as Smith Woodward (1889*b*, p. 277) noticed, the tubular dentine is confined to the surface of three oblique ridges on the tooth (P 3099, P 4575, 43050). The symphysial tooth in *Myriacanthus* has the whole oral face covered by tubular dentine, but in *Metopacanthus* the tubular dentine is confined to a band in the centre of the tooth (P 4575, Smith Woodward, 1891*a*, pl. 2, fig. 4*b*). The posterior tooth of the upper jaw, again without tritors in *Myriacanthus*, is exposed in *Metopacanthus* only in GSM TN 8005, where the tubular dentine appears to be confined to two oblique ridges on the surface. The tooth plates are thin in section, as in *Myriacanthus*, and are not thick and massive as they are in chimaeroids.

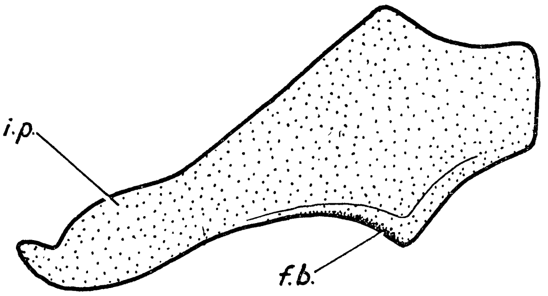

FIGURE 21. *Metopacanthus granulatus* (Agassiz). Restoration of right half of pelvic girdle in ventral view (× 1 approx.). From 43050. *f.b.*, Articular facet for basipterygium; *i.p.*, iliac process.

43050 is the only specimen in which any part of the vertebral column is preserved (figure 58, plate 25; figure 20). There is a large synarcual of calcified cartilage, articulating with a very broad occipital condyle on the neurocranium. In shape the synarcual agrees with those of living chimaeroids (figure 1) except that it appears to be longer, with a broader dorsal crest. I can find no trace of the 'segmentation' which Dean (1906, p. 144) described in the hind end of the synarcual of 43050. Beyond the synarcual in this specimen the notochord can be traced for about 55 mm by scattered remains of calcifications (figure 58, plate 25). These calcifications differ in colour and texture from the calcified cartilage of the skull and synarcual. They are obviously much more numerous than the segments of the trunk, but as no segmental structures are preserved, no estimate of the number per segment can be made. In shape the calcifications are apparently not ring-like as they are in *Squaloraja* and chimaeroids, but are rhomboid, arranged with their narrow faces towards the sagittal plane. The calcifications were evidently paired and crescentic, enclosing the notochord between them.

Again, 43050 is the only specimen in which any trace of the paired fins and girdles is preserved. The pectoral girdle and fin are missing, but at the edge of the block there are two elongated cartilages which are evidently the halves of the pelvic girdle (figure 21). The halves of the girdle were separate. In shape the girdle resembles those of the living chimaeroids rather than that of *Helodus* (Moy-Thomas 1936*b*, text-fig. 1), since it has a long iliac process, but there was apparently no cartilagenous anterior process supporting the tenacula as there is in *Squaloraja*. There is no trace of the pelvic fin.

As in *Myriacanthus*, the only parts of the median fins known are the spine and basals of the first dorsal fin. The spine has been described by Agassiz (1837–8, p. 40, pl. 8*a*, fig. 16) and Smith Woodward (1891*a*, p. 49). It is more laterally compressed than the spine of *Myriacanthus*, and the tubercles on its lateral faces are smaller than in the latter, and are absent on the distal quarter of its length (figure 20). As in *Myriacanthus*, there is a row of upturned denticles on the anterior edge of the spine, but there is no median row of denticles on the posterior face, and all the lateral denticles on the posterior face are downturned. In structure (figure 47, plate 22; figure 22) the spine consists of an inner zone of lamellar tissue (*cpd.*) and an outer zone of osteodentine (*osd.*). The lamellar tissue is much thicker than it is in *Myriacanthus* (figure 17), and makes up about half the thickness of the wall of the spine on the lateral and posterior surfaces (cf. *Ischyodus*, figure 4*B*). On the anterior wall of the spine the lamellar tissue is thinner (cf. *Chimaera*, figure 4*A*).

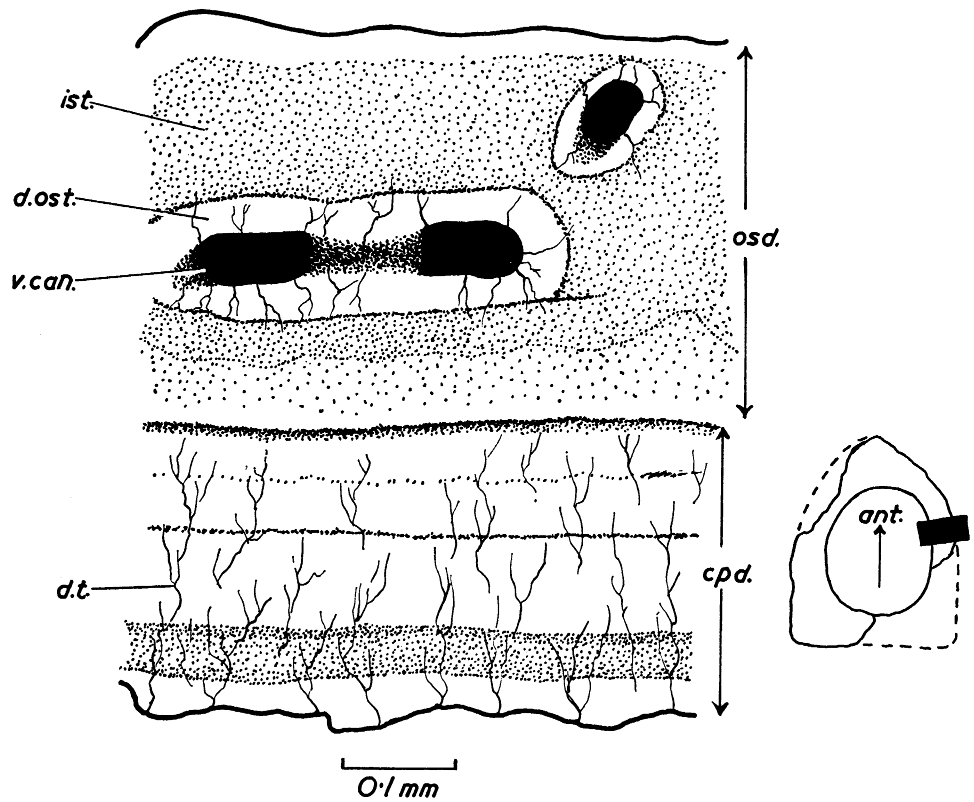

FIGURE 22. *Metopacanthus granulatus* (Agassiz). Transverse section cut near the middle of the dorsal fin spine. 43065.I. Inset on the right is an outline of the complete section showing the orientation of the figured region (*ant.*, anterior). *cpd.*, Lamellar tissue; *d.ost.*, dentinal osteon; *d.t.*, tubule; *ist.*, interosteonal tissue; *osd.*, osteodentine; *v.can.*, vascular canal.

The basals of the first dorsal fin are preserved in 43050 (figure 20). Dean (1906, text-fig. 143B, 146) interpreted this specimen as showing a separate cartilage between the triangular basal (*b.*) and the crest on the synarcual, but this is in fact the expanded facet by which the basal articulates with the synarcual. As Dean noted, there is a separate distal cartilage (*d.b.*), a structure which is absent in living chimaeroids, but is perhaps represented by the row of small cartilages which occurs in *Ischyodus* (figure 2).

The squamation of *Metopacanthus* is complete. On the trunk (43050), the head, the lateral surfaces of the rostrum and the dorsal surface of the frontal clasper the scales are very small (bases about 0·3 mm in diameter in 43050) with expanded, radially grooved roots and simple conical crowns which are recurved and bluntly pointed. The scales are enlarged towards the tip of the rostrum (GSM TN 8005). On the underside of the proximal part of the frontal clasper and on the dorsal surface of the base of the rostrum the scales are much enlarged (bases up to 3 mm in diameter and crowns up to 3 mm high in 43050), their roots are subdivided radially and their crowns are long and sharply pointed. There is evidence (GSM TN 8005) of a row of enlarged scales of this type along each side of the rostrum. There are no polycuspid scales of the type which occur in *Myriacanthus*.

Sensory canals are visible on the trunk and rostrum of 43050, on the head of P 1158, and in P 4575 (figure 57, plate 24), where a canal can be traced the whole length of the rostrum. As in *Myriacanthus* the sensory canals were surrounded by specialized scales which are irregularly fused together into short cylinders. In P 4575 it is clear that the rings are incomplete, as they are in living chimaeroids (figure 7).

The frontal clasper is preserved in 43050, P 4575, P 1158 and GSM TN 8005, that is, in all the specimens in which any part of the head is preserved. As in *Squaloraja*, this raises the question of whether the structure was present only in males or in both sexes (see p. 200). The clasper is very like that of *Squaloraja*, differing only in its greater upward curvature, its greater breadth and stoutness, and in the smaller scales on its dorsal surface.

43050 is the only specimen in which the pelvic girdle is preserved, and in this specimen there is no trace of pelvic claspers, but as the two halves of the girdle are dispersed and there is no trace of the pelvic fin the absence of claspers is quite possibly due to imperfect preservation. A cluster of about 15 enlarged scales in the region of the pelvic girdle of 43050 shows that pre-pelvic tenacula were present. These scales are about 2 mm in length, with a strongly recurved, pointed crown, a long, peg-like root, and a shoulder at the junction of root and crown. Since there is no anterior process on the pelvic girdle and since these enlarged scales are preserved some distance from the dissociated halves of the girdle, it is clear that in *Metopacanthus* the tenacula had no skeletal support.

Comparison between Myriacanthus *and* Metopacanthus

The preceding descriptions show that there are six main characters in which *Metopacanthus* differs from *Myriacanthus*.

(1) The head of *Metopacanthus* is more laterally compressed than that of *Myriacanthus*.

(2) The mandibular dermal plates of *Metopacanthus* are conical, not dorso-ventrally compressed as they are in *Myriacanthus*, and they bear no enlarged spines.

(3) In *Metopacanthus* the only dermal plates are the single pair on the mandible. In *Myriacanthus* there are also three pairs of tuberculated plates on the neurocranium.

(4) In *Metopacanthus* the tubular dentine is confined to a few large tritoral areas on the mandibular tooth plates and the posterior tooth plates of the upper jaw; in *Myriacanthus* tubular dentine covers the whole surface of these tooth plates.

(5) The dorsal fin spine of *Metopacanthus* is laterally compressed, only partially tuberculated, and bears two rows of denticles only on the distal part of its proximal face. In *Myriacanthus* the spine is not compressed, is tuberculated all over, has two rows of denticles along almost the whole of its posterior face and an incomplete third row in the mid-line.

The zone of lamellar tissue around the central cavity of the spine is also much wider in *Metopacanthus* than in *Myriacanthus*.

(6) The scales of *Metopacanthus* have simple, undivided crowns but those of *Myriacanthus* have the crown divided into a number of separate cusps.

These differences are of generic rank, and necessitate the resurrection of the genus *Metopacanthus* Zittel for *M. granulatus*. In all of these six characters, *Metopacanthus* is nearer to the chimaeroids than is *Myriacanthus*. The chimaeroids are laterally compressed, have tritoral areas on all the tooth plates, and have scales with simple, pointed crowns. The fin spines of chimaeroids are compressed, bear no tubercles, have two rows of denticles only on the distal part of the posterior face, and consist mainly of lamellar tissue. The absence of dermal plates on the neurocranium of *Metopacanthus* and the absence of spines on the mandibular dermal plates may be taken to be intermediate between the absence of dermal plates in the chimaeroids and the conditions in *Myriacanthus*.

These differences between *Myriacanthus*, *Metopacanthus* and chimaeroids may be read in two ways: it might be held that the dermal plates, the heavily ornamented spine and other features of *Myriacanthus* are specializations, with *Metopacanthus* being nearer to the generalized chimaeroid type (Smith Woodward 1891 *b*, p. xvi, inclined towards this view in holding that the dermal plates of Myriacanthidae are specializations) or that the conditions in *Myriacanthus* are primitive, with *Metopacanthus* showing advances towards the chimaeroid type. Comparison of *Squaloraja* with living chimaeroids (p. 126) has shown that the absence of localized tritors on the tooth plates and a dorso-ventrally flattened head are primitive features in the Chimaeriformes, and comparison with geologically older forms (*Deltoptychius*, *Menaspis*, p. 174) suggests that the presence of dermal plates on the skull roof, of spines on the mandibular plates and of scales with divided crowns are also primitive. Comparison of the fin spines of Chimaeriformes with those of selachians (p. 195) shows that heavy ornamentation and a narrow inner zone of lamellar tissue are primitive features. All these characters, therefore, show that the series can be read in one way only, with *Myriacanthus* as a primitive form and *Metopacanthus* showing advances towards the chimaeroids.

The affinities of the Myriacanthidae

The family Myriacanthidae (Smith Woodward 1889 *b*, p. 279) has previously always been placed among the chimaeroids. Referring to the list of special characters of Chimaeroidei on p. 111, the Myriacanthidae agree with chimaeroids in: (1) the holostylic suspension; (5) the structure of the tooth plates; (6) the presence of tritors on the anterior teeth of the upper jaw in *Myriacanthus* and on all the tooth plates of *Metopacanthus*; (11) the structure of the rostrum; (13) the presence of numerous calcifications in the sheath of the notochord, although in myriacanthids the calcifications are crescentic and paired rather than ring-like; (14) the presence of a synarcual; (16) the separation of the halves of the pelvic girdle; (17) the structure of the first dorsal fin, although in *Metopacanthus* there is an additional distal cartilage in the fin; (20) the structure of the scales (in *Metopacanthus*); (23) the presence of incomplete rings of hard tissue around the sensory canals, though in myriacanthids the rings are fused together; (25, 26) the presence of tenacula and a frontal clasper.

The structure of the Myriacanthidae is not known with regard to characters 2, 3, 7, 8, 9, 10, 12, 15, 19, 22 and 24 (ethmoid canal, interorbital septum, hyoid arch, branchial arches, spiracle, operculum, labial cartilages, pectoral fin, second dorsal fin, sensory canal pattern and pelvic claspers).

The Myriacanthidae differ from the chimaeroids in: (4) the presence of three pairs of tooth plates in the upper jaw and a median symphysial tooth in the lower jaw; (21) the unreduced squamation; and also in the presence of dermal plates on the skull. The Myriacanthidae differ from the chimaeroids and agree with *Squaloraja* in the very large median rostral cartilage and frontal clasper and also in the unreduced squamation. Other differences between the Myriacanthidae (especially *Myriacanthus*) and the chimaeroids are mentioned above (p. 141) in the comparison between *Myriacanthus* and *Metopacanthus*: the most important of these are the differences in the structure of the dorsal fin spine and the scales. Differences of less importance are the form of the notochordal calcifications and the absence of a cartilagenous skeleton in the tenacula of Myriacanthidae.

The large number of similarities between Myriacanthidae and Chimaeroidei compared with the few differences suggests that the relationship between the two groups is close: the similarities in the notochordal calcifications, the synarcual, the dorsal fin spine, the structure of the sensory canals, the tenacula and the frontal clasper are particularly striking evidence of affinity. Nevertheless, it is suggested that the Myriacanthidae should be made the type family of a new sub-order Myriacanthoidei (defined on p. 127) within the Chimaeriformes. This is because among the characters in which the Myriacanthidae, especially *Myriacanthus*, differ from the chimaeroids there are several in which they resemble the Carboniferous and Permian Menaspoidei (see p. 174). These characters include the three pairs of tooth plates in the upper jaw, the absence of tritors on the majority of the tooth plates, the dermal plates on the skull roof, the spines on the angle of the jaw and the form of the scales. The resemblances between the Myriacanthidae and the chimaeroids are much more numerous than those between the myriacanthids and the menaspoids, but the latter comparison is severely limited by very incomplete knowledge of the menaspoids, and the known similarities are no less striking than those between chimaeroids and myriacanthids. One is driven to the conclusion that the myriacanthids have close affinities with both the chimaeroids and the menaspoids: additional evidence of this is provided by the way in which almost all the differences between *Myriacanthus* and *Metopacanthus* involve the presence of menaspoid characters in the former and of chimaeroid characters in the latter. This relationship is best expressed by making the three groups sub-orders within a single order.

One character of the Myriacanthidae, the median symphysial tooth in the lower jaw, occurs nowhere else among Holocephali except in the other two families of Myriacanthoidei. We must assume that it is a specialized feature, but it does not necessarily exclude the myriacanthoids from the ancestry of the chimaeroids.

FAMILY CHIMAEROPSIDAE nov.

Diagnosis: Myriacanthoidei in which there are no dermal plates on the mandible; rostrum not elongated (?); upper jaw with two pairs of tooth plates, the anterior larger than the posterior, two tritors on the anterior tooth plate in the upper jaw, the other tooth plates without localized tritors; three pairs of tuberculated dermal plates on the skull; dorsal fin spine tuberculated, not much compressed, and with an anterior series of denticles; frontal clasper not known.

The only genus is:

Genus **Chimaeropsis** Zittel (1887, p. 113)

Diagnosis: as family, only genus.

Chimaeropsis contains three species. *C. paradoxa* Zittel (1887, p. 114, text-fig. 126), the type species, is known by an incomplete skeleton and an isolated dentition from the Lower Kimmeridgian lithographic stone of Eichstatt and Solenhofen respectively. *Chimaeropsis foussi* Casier (1959, p. 15, pl. 2, fig. 2, text-fig. 4) is known by a single tooth plate from the Lower Lias of Ethe, Belgium. *Chimaeropsis franconicus* (von Münster, 1840, p. 127, pl. 3, fig. 8) is known by a fin spine from the Upper Jurassic of Rabenstein, Bavaria.

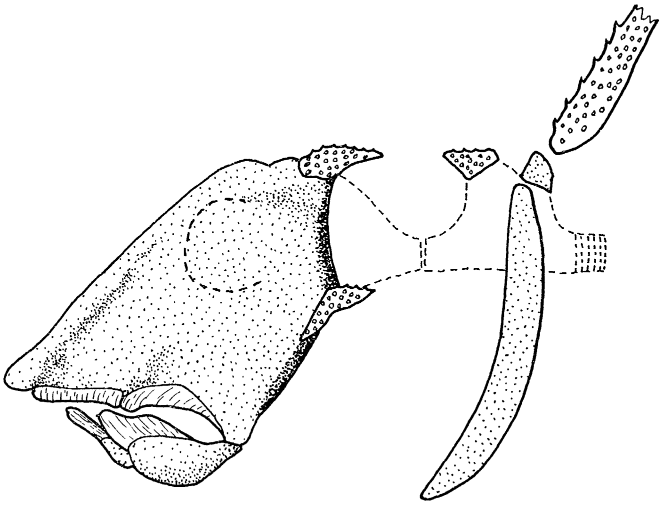

Figure 23. *Chimaeropsis paradoxa* Zittel. Skeleton of the head and anterior part of the trunk as restored by Reis (× $\frac{1}{4}$ approx.). After Reis (1895).

The most complete description of *C. paradoxa* was given by Riess (1887, p. 21, pl. 2, figs. 9 to 11; pl. 3, figs. 1 to 9), but the skeleton from Eichstatt, a fish about 1 m in length, has never been figured in entirety. Reis (1895, pl. 12, fig. 3) has given a restoration of the head (figure 23), but the accuracy with which the dermal plates are restored, particularly the placing of one on the crest of the synarcual, is doubtful. Apart from Reis's restoration, nothing is known of the cartilagenous skull in *Chimaeropsis*, but since no rostrum has been described it seems probable that the rostrum was not elongated as it is in Myriacanthidae. Both Zittel and Riess have described the dermal plates on the skull roof. Zittel mentions two pairs of plates lying behind the skull, and Riess says that there were at least three pairs of plates, that the plates are ornamented with tubercles like those on the dorsal fin spine, and that each plate bears a longitudinal ridge, presumably similar to the longitudinal angle in the dermal plates of *Myriacanthus*. Riess describes the plates as consisting of vasodentine in which the dentine tubules are much branched, and his figure (pl. 2, fig. 10) shows that the tissue is laid down in parallel lamellae perforated by vascular canals, as in *Myriacanthus* (figure 15), but that the plate is much thinner in relation to the size of the surface tubercles than in *Myriacanthus*. There is no clear evidence as to the position of the plates on the skull; Riess suggested that they lay on the side of the 'neck' region, and Reis's restoration shows one plate lying ventral to the other two. It is possible that this ventral plate lay on the angle of the mandible, as in Myriacanthidae, but no mandibular spines were found in association with the dentition from Solenhofen.

The dentition, described by Zittel and Riess, consists of a pair of large tooth plates and a median chisel-like tooth in the lower jaw, and two pairs of tooth plates in the upper jaw, of which the anterior is the larger (in contrast to the chimaeroids). The only tooth plate with localized tritors is the anterior tooth of the upper jaw, which has two raised tritors, one anterior and one posterior.

The vertebral column of *Chimaeropsis* has not been described, but Riess mentions that the column is preserved in impression in the Eichstatt specimen: this suggests that the notochord was surrounded by calcifications, since an uncalcified notochord would have left no trace in the rock. The trunk has been described very briefly by Zittel and Riess; all that is known is that the pectoral fins are large and lie below the first dorsal fin, that the pelvics are rather small, and that the tail tapers to a point. The dorsal fin spine is not much compressed, ornamented throughout its length with pointed tubercles, its posterior face bears two rows of denticles and its anterior face bears a single series of denticles which point upwards. The similarities of this spine to those of the Myriacanthidae are obvious, and in the lack of compression and the complete ornament it resembles *Myriacanthus* rather than *Metopacanthus*. The squamation of *Chimaeropsis* is complete, and the scales are small and conical, with radially grooved bases (Riess 1887, pl. 2, fig. 11), very like those of *Metopacanthus*.

Nothing is known of the sensory canals of *Chimaeropsis*, or of the secondary sexual characters.

The affinities of Chimaeropsis

Chimaeropsis was placed in the Myriacanthidae by Smith Woodward (1889*b*, p. 279), and has been retained in this family by later authors. Lack of knowledge of the skull, vertebral column and secondary sexual characters prevents an accurate assessment of the affinities of the genus, but it agrees with the Myriacanthidae in the mandibular symphysial tooth, the absence of tritors on all but the anterior teeth of the upper jaw, the tuberculated dermal plates on the head, the form of the dorsal fin spine and the scales. In the absence of tritors, in the tuberculation of the dermal plates and in the dorsal fin spine *Chimaeropsis* resembles *Myriacanthus*, in the simple scales it resembles *Metopacanthus*. These characters leave no doubt that the genus belongs in the Myriacanthoidei, and its range, from the Lower Lias (*C. foussi*) to the Kimmeridgian, shows that the myriacanthoids survived as contemporaries of the early chimaeroids in the Upper Jurassic. The upper dentition of *Chimaeropsis*, with only two pairs of tooth plates of which the anterior is the larger, differentiates the genus clearly from both the myriacanthids and the chimaeroids. It seems likely that the rostrum was not enlarged as it is in the myriacanthids, and there is no evidence of a pair of dermal plates on the mandible. For these reasons, especially the characters of the upper dentition, *Chimaeropsis* is here made the type of a new family *Chimaeropsidae*, defined as on p. 143.

FAMILY ACANTHORHINIDAE nov.

Diagnosis: Myriacanthoidei in which the dermal plates on the head are reduced or absent; the frontal clasper (?)enlarged; two pairs of tooth plates in the upper jaw of which the anterior is the larger; lamellate tritors on the posterior tooth plates of the upper jaw, the other tooth plates without tritors; dorsal fin spine laterally compressed, not tuberculated, without anterior denticles.

The only genus is:

Genus **Acanthorhina** Fraas (1910, p. 55)

Diagnosis: as family, only genus.

The type and only species is *A. jaekeli* Fraas (1910, p. 55, pl. 3, figs. 1 to 6). *A. jaekeli* is known by an incomplete fish and an isolated rostrum, both from the upper Lias of Holzmaden, Germany. Fraas's reconstruction of the species is shown in figure 24. According to Fraas, the skull is holostylic and chimaeroid-like, with a long, pointed rostrum bearing two rows of enlarged scales on its underside, with a very small, spine-like frontal clasper, and with three pairs of tooth plates in the upper jaw and one pair in the lower jaw, of which only the posterior pair in the upper jaw bears tritors in the form of transverse lamellae.

Some discussion of Fraas's interpretation of the head is necessary. In figure 25 the dentition and 'frontal clasper' of the holotype are shown as they are preserved. The 'frontal clasper' (*sp.*) lies just above the hind end of the mandibular tooth plates (*m.t.p.*): Fraas describes it as shiny and enamel covered, and compares it with the lateral head spines of *Hybodus* and *Acrodus*. But as Reis (1895, p. 386) has shown, the frontal clasper of holocephalans always consists of calcified fibro-cartilage, and cannot therefore be covered by enamel. The structure in *Acanthorhina* is possibly an enlarged scale, analogous with those which cover the underside of the frontal clasper and the base of the rostrum in Myriacanthidae, or it may be a modified dermal plate from the skull roof or the mandible: this can only be decided after a re-examination of the specimen. Fraas describes the rostrum as consisting of strongly calcified cartilage, with the dorsal side convex and the ventral concave, the ridge on each margin of the underside being set with a single row of 'flattened teeth', of which only the areas of attachment are known. This description suggests a frontal clasper rather than a rostrum, for the rostrum of holocephalans, even when much enlarged as it is in *Squaloraja* and Myriacanthidae, consists of cartilage calcified in polygonal tesserae, not in the very dense, fibrous form which Fraas's figures show, and when the rostrum is set with enlarged scales (*Myriacanthidae*, *Squaloraja*, *Callorhynchus*), the scales are always on the dorsal surface, not the ventral. The groove on the underside of the structure in *Acanthorhina* is confined to the proximal two-thirds of its length, and appears to be similar to the groove in which the depressor muscles were inserted on the claspers of Myriacanthidae and *Squaloraja*; the substance of the structure appears to agree exactly with the frontal claspers of *Squaloraja* and *Metopacanthus*, and the enlarged scales on the underside are also present in these two genera. It seems probable, therefore, that the 'rostrum' of *Acanthorhina* is in fact the frontal clasper, and that the true rostrum was either poorly calcified, or is obscured in the holotype by the crushed frontal clasper.

Fraas restores the dentition of *Acanthorhina* as consisting of three pairs of tooth plates in the upper jaw and one pair in the lower jaw. But his anterior tooth plate in the upper jaw is very different in shape from the other two, and in the holotype (figure 25, *s.*) only one tooth of this type is preserved, lying at the tip of the mandibular plates. Fraas describes this tooth as having a sharp cutting edge, and notes its resemblance to the mandibular

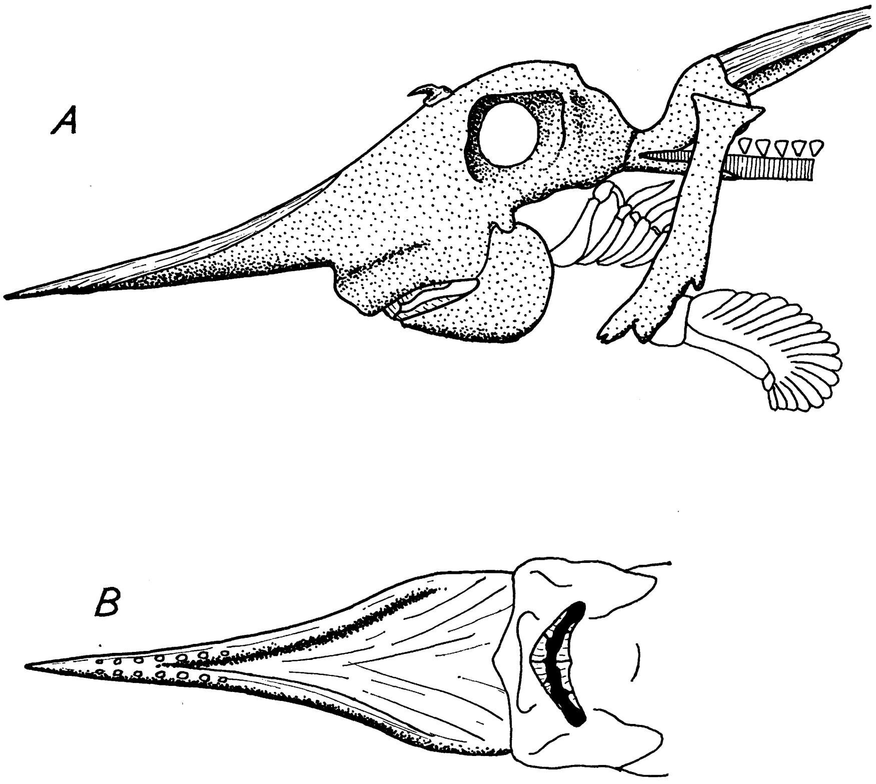

FIGURE 24. *Acanthorhina jaekeli* Fraas. *A*, Skeleton of the head and anterior part of the trunk as restored by Fraas (× $\frac{1}{4}$ approx.); *B*, the rostrum and jaws in ventral view as restored by Fraas (× $\frac{1}{3}$ approx.). Both after Fraas (1910).

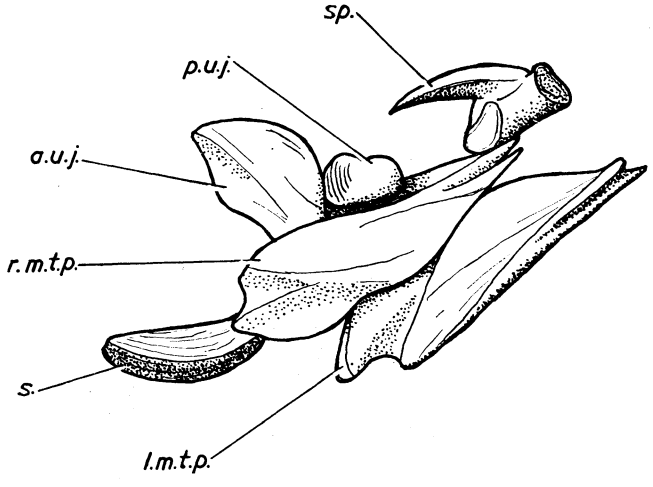

FIGURE 25. *Acanthorhina jaekeli* Fraas. The dentition and 'frontal clasper' as preserved in the holotype (× 1 approx.). After Fraas (1910). *a.u.j.*, Anterior tooth plate in the upper jaw; *l.m.t.p.*, *r.m.t.p.*, left and right mandibular tooth plates; *p.u.j.*, posterior tooth plate in the upper jaw; *s.*, symphysial tooth; *sp.*, 'frontal clasper'.

symphysial tooth of *Myriacanthus*. The shape and position of this tooth suggest that it was a symphysial tooth, and that *Acanthorhina* had two pairs of tooth plates in the upper jaw with the posterior the smaller, as in *Chimaeropsis*, and that the lower jaw contained one pair of tooth plates and a median symphysial tooth, as in other Myriacanthoidei.

Of the postcranial skeleton in *Acanthorhina* only the synarcual, the anterior part of the notochord, the pectoral girdle and the dorsal fin spine are known. The synarcual is like those of chimaeroids, and Fraas describes traces of numerous calcifications in the notochord, again as in chimaeroids. There is nothing notable in the known part of the pectoral girdle but its position close behind the neurocranium shows that the branchial arches lay below the neurocranium as they do in chimaeroids. The dorsal fin spine is exactly as in the chimaeroids: it is laterally compressed, slender and smooth, with no denticles on the anterior face and with downturned denticles on the distal one-fifth of the posterior face. Nothing is known of the squamation or the sensory canals.

The affinities of Acanthorhina

As in the case of *Chimaeropsis*, the precision with which the relationships of *Acanthorhina* may be worked out is reduced by lack of knowledge and doubt about the interpretation of structures in the holotype. Fraas suggested that the genus is related to *Myriacanthus*, and Smith Woodward (1932, p. 96) placed it in the Myriacanthidae, where later authors have retained it. *Acanthorhina* agrees with the Myriacanthoidei (Myriacanthidae and Chimaeropsidae) in the (presumed) presence of a median tooth in the mandible, in the absence of tritors on all but the posterior tooth plates in the upper jaw and the (presumed) enlarged frontal clasper. It agrees with the Chimaeropsidae rather than the Myriacanthidae in having two pairs of tooth plates in the upper jaw with the anterior the larger. The genus agrees with both the myriacanthoids and the chimaeroids in the shape of the skull and synarcual, and in the notochordal calcifications (although it is not known if the latter are paired, as in the myriacanthids, or ring-like, as in the chimaeroids). The characters of the dentition show that *Acanthorhina* belongs in the Myriacanthoidei, but the genus approaches the chimaeroids more closely than the other myriacanthoids in the loss or reduction of the dermal plates on the skull and in the structure of the dorsal fin spine, which agrees exactly with the chimaeroids. In view of these characters, and pending a re-investigation of the holotype, *Acanthorhina* should be made the type of a monotypic family Acanthorhinidae, defined as on p. 146.

SUB-ORDER MENASPOIDEI NOV.

Diagnosis: Chimaeriformes in which the head is not laterally compressed; a single pair of tooth plates in the lower jaw, one to three pairs in the upper jaw, tooth plates thin and without tritors; frontal clasper represented by paired structures or absent, rostrum not enlarged; a pair of dermal spines on the angle of the mandible, skull roof covered by a head shield consisting of a single plate or of a number of separate plates, with a pair of spines projecting posteriorly, a pair of dermal plates covering the ventro-lateral surface of the occipital part of the neurocranium; notochord uncalcified; no dorsal fin spine; scales cyclomorial where known, squamation not reduced, two rows of enlarged scales on the dorsal surface of the trunk, specialized scales surrounding the supraorbital sensory canal.

There are two families, Menaspidae and Deltoptychiidae, each with a single genus. The Deltoptychiidae will be dealt with before the type family since new information on the structure of *Deltoptychius* throws light on various features of *Menaspis*.

FAMILY DELTOPTYCHIIDAE nov.

Diagnosis: Menaspoidei in which the head shield is fused into a single plate and bears the supraorbital sensory canals; no frontal spines; three pairs of tooth plates in the upper jaw.

The only genus is:

Genus **Deltoptychius** Morris & Roberts (1862, p. 100)

Syn. *Platacanthus* M'Coy 1848*b*, p. 120, *non Platacanthus* Swainson 1839, p. 194.
Streblodus Morris & Roberts 1862, p. 101.
Listracanthus Newberry & Worthen 1870, p. 371.
Pnigeacanthus St John & Worthen 1875, p. 480.
Platyacanthus Woodward & Sherborn 1890, p. 151, *non Platyacanthus* Fritsch 1889, p. 113.

Diagnosis: as family, only genus.

Type species: *Deltoptychius acutus* M'Coy (1855, p. 621, pl. 31, fig. 24).

This genus is here used to contain the species previously described as *Oracanthus armigerus* Traquair, and it is necessary to review the genus *Oracanthus* to explain why this change has been made.

Review of the genus Oracanthus *Agassiz*

Oracanthus Agassiz (1837, p. 13), type species *O. milleri* Agassiz (1837, p. 13, pl. 3, figs. 1 to 4), was founded for spines from the Carboniferous Limestone. The main features of the holotype of *O. milleri* (from the Carboniferous Limestone of Bristol, and now in Bristol Museum) are its large size (*ca.* 35 cm in length, *ca.* 13 cm wide at the base), triangular shape, absence of bilateral symmetry, the presence of a wear facet asymmetrically placed on the leading edge of the tip, the ornament of stellate tubercles which tend to fuse into oblique or transverse ridges on the surface shown by the wear facet to be dorsal, and are arranged in a chevron pattern on the ventral surface, the large central cavity and the very narrow base of insertion. In the BMNH there are nineteen specimens which agree with the holotype in all these respects. They are 22665, 28857, P 11158–60, P 2241, P 2874–5, P 3125–6, P 3128–9, P 3131–2, P 10981 and P 45769–73.

Of these specimens, P 10981 is from the Carboniferous Limestone of the Forest of Dean, Gloucestershire, 22665, 28857, P 2241, P 3125–6 and P 45771–3 are from Bristol, and the remainder are from the Carboniferous Limestone of Armagh, Ireland. Those specimens in which the tip is complete suggest that the holotype of *Oracanthus minor* Agassiz (1837, p. 16, pl. 3, figs. 5 to 6) is merely the tip of an *O. milleri*, as Smith Woodward (1891*a*, p. 136) thought.

In histological structure (P 10981.I; figure 49, plate 22; figure 26) the spines of *O. milleri* consist of osteodentine containing many vascular canals (*v.can.*) which are especially large towards the central cavity. The vascular canals are surrounded by dentinal osteons (*d.ost.*)

which are separated by abundant interosteonal tissue (*ist.*). In the interosteonal tissue in the inner half of the section there are a few scattered osteocyte spaces (*osc.*). The surface tubercles consist of dentine permeated by long, stout, much-branched dentine tubules which are arranged in a poorly defined layer of pallial dentine. There is no enamel.

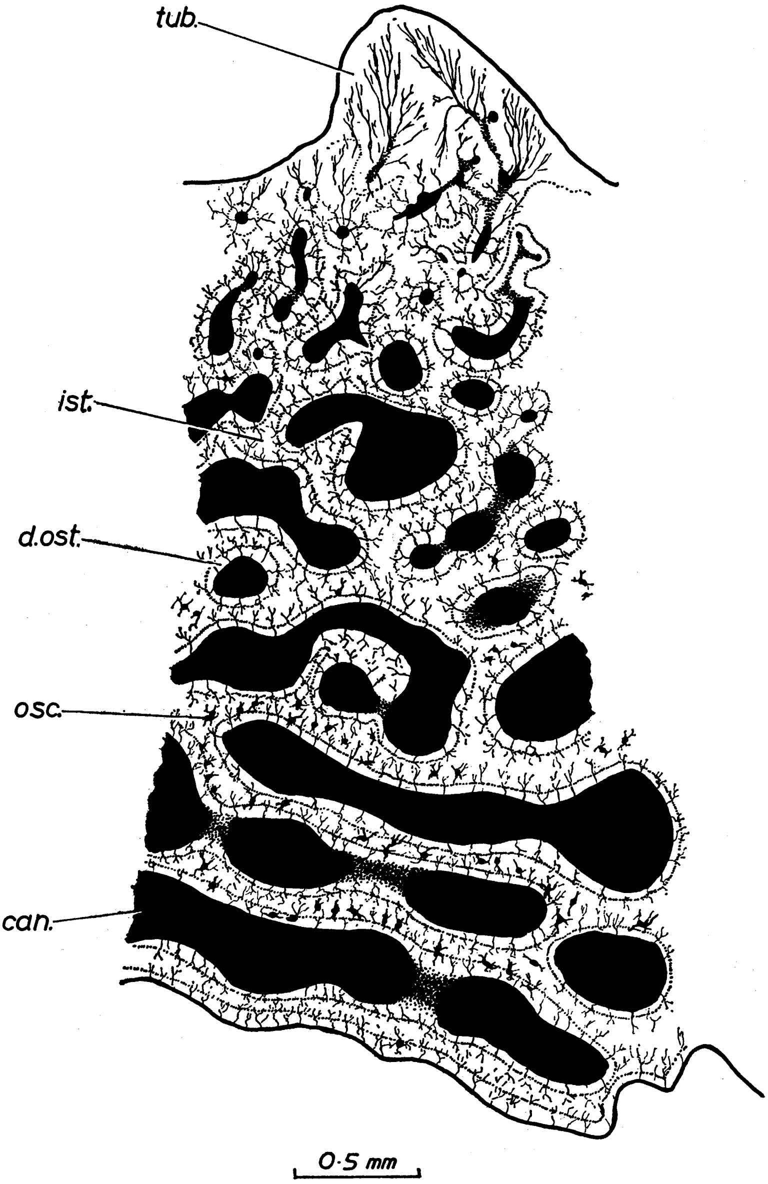

FIGURE 26. *Oracanthus milleri* Agassiz. Transverse section of spine cut near the base. P 10981.I. *d.ost.*, Dentinal osteon; *ist.*, interosteonal tissue; *osc.*, osteocyte cavity; *tub.*, surface tubercle; *v.can.*, vascular canal.

In addition to the type species, eleven other species of *Oracanthus* have been described, and other specimens have been placed in the type species (Davis 1883, p. 529; Smith Woodward 1891 *a*, p. 137). It is clear that all these species are not congeneric. The material may be divided into six groups.

(1) *Oracanthus* s.s.

Species which agree with *O. milleri* in most of their known characters, and which should be retained in the genus. These include:

O. pustulosus Agassiz (1837, p. 15, pl. 2, figs. 3, 4). This species is based on a specimen from the Carboniferous Limestone of Bristol whose main features include the large size (total length cannot be estimated, but must have exceeded 40 cm.), the more slender form than *O. milleri*, and the arrangement of the tubercles in longitudinal rows rather than in transverse or oblique ones, with no tendency for the tubercles to become confluent. Smith Woodward (1891*a*, p. 138) made *Phoderacanthus grandis* Davis (1883, p. 534, pl. 65, fig. 1) a synonym of *O. pustulosus*: *P. grandis* is known only by the holotype (P 4716), a specimen from Oreton, Shropshire, which agrees with Agassiz's holotype of *O. pustulosus* in its large size (total length *ca.* 65 cm) and its proportions, but in which the tubercles are arranged in transverse and oblique rows, and tend to become confluent, as in *O. milleri.* Four other specimens in the BMNH (42234*a*, 42235, P 4187, P 45775), all from Oreton, Shropshire, agree with the holotype of *O. pustulosus* in ornament and proportions, and are probably either small examples of the species or the terminal parts of large specimens, *Stichacanthus tortworthensis* Davis (1883, p. 532, pl. 65, fig. 2) is based on a specimen from the Carboniferous Limestone of Oreton which is very like the holotype of *Phoderacanthus grandis*, and possibly belongs in *O. pustulosus.*

Oracanthus vetustus Leidy (1856, p. 161, pl. 16, figs. 1 to 3; St John & Worthen 1883, p. 255, pl. 24, fig. 2; *non* Newberry 1897, p. 285, *nec* Eastman 1917, p. 267), from the St Louis Limestone of Illinois, Missouri and Iowa, is known by three specimens, two of which are almost complete spines showing asymmetry, ornament like that of *O. milleri*, and a wear facet at the tip.

O. ?obliquus St John & Worthen (1875, p. 477, pl. 22, fig. 16) and *O. rectus* St John & Worthen (1883, p. 257, pl. 25, fig. 3), both from the Lower Carboniferous of Illinois, are each known only by small fragments which appear to show the typical ornament and asymmetry of *O. milleri.*

Oracanthus bochumensis Jaekel (1891*a*, p. 755, pl. 37, figs. 1 to 5) is based on a single spine from the productive Coal Measures of Bochum, Westphalia. The spine agrees with *O. milleri* in its asymmetry and shape, but is ornamented with rounded tubercles which appear to be arranged in longitudinal rows. In histological structure (Jaekel 1891*a*, pl. 37, fig. 5) it consists of osteodentine, and although Jaekel remarks that osteocytes are absent, the small section figured seems to contain one or two cell spaces, and the structure probably agrees with *O. milleri.*

O. triangularis Eastman (1917, p. 268, pl. 5, figs. 5, 6) is known by two fragmentary spines from the St Louis Limestone of Missouri. The spine shown in fig. 5 is too imperfect for determination, but that in fig. 6 appears to agree with *O. milleri* in ornament.

None of the species of *Oracanthus* listed above has ever been found in association with any other skeletal remains, and the microstructure is known only in *O. milleri* and *O. bochumensis.* The systematic position of the genus is still unknown, but the presence of osteocyte spaces in the basal parts of the wall of the spine in *O. milleri* is an interesting feature which suggests that the genus may contain paired spines of acanthodians, for Krebs (1961, p. 187, pl. 1, fig. 2, text-fig. 6) has described bone cells in a similar position in a pectoral fin spine of the Upper Carboniferous acanthodian *Gyracanthus formosus*, and as Krebs and Ørvig (1957, p. 333) note, bone cells have not yet been described as a constant feature in any elasmobranch. Among acanthodians, the closest analogy with *Oracanthus* is found in the broad, hollow, triangular, tuberculated spines which were inserted on the underside of the pectoral region of the trunk in the Carboniferous *Gyracanthides murrayi* (Smith Woodward 1906*b*, p. 4, text-fig. 1).

(2) *Bilaterally symmetrical spines with the base of insertion elongated horizontally*

In this category are the specimens described as *O. vetustus* Leidy by Newberry (one spine from the Lower Carboniferous Kinderhook limestone of Iowa; 1897, p. 285, pl. 22, fig. 3) and Eastman (two specimens from the Kinderhook of Iowa; 1917, p. 267, pl. 8, fig. 2) and the spine described as *O. farringtoni* sp.nov. by Roy (also from the Kinderhook of Iowa; 1929, p. 218, pl. 46, figs. 1 to 4). These four spines are perfectly bilaterally symmetrical, and have a base of insertion which is about as long as the spine, and is produced horizontally (posteriorly according to Roy, anteriorly according to Newberry). These spines have not been found in association with any other fish remains, and their histological structure is unknown. There is no reason to think that there is any relationship between these specimens and *Oracanthus*, for the only similarity is in the ornament of stellate tubercles. Eastman noted the similarity of his specimens to *Xystracanthus* (= *Physonemus*) which is now thought to contain fin spines of edestids (Obruchev 1953, p. 57; Baird 1957, p. 1017), and they should probably be placed in a genus near to *Physonemus*.

(3) *Bilaterally symmetrical fin spines*

Smith Woodward (1891*a*, p. 137) listed four spines from the Carboniferous Limestone which he thought might belong in *O. milleri* (P 3134 (pl. 1, fig. 3), P 3134*a*, P 2238, P 3127). P 3138 and P 45767–8 are specimens of the same type. These spines are elongated, slender, apparently perfectly bilaterally symmetrical, and where complete (P 3134, P 45768) show a symmetrical wear facet on the leading edge of the tip. The spines are ornamented with irregular ridges running postero-dorsally; these ridges are very like those formed by fusion of the tubercles on the dorsal surface of *O. milleri*. The spines have all the features of fin spines; a narrow central cavity, a groove along the posterior face of the proximal half or two-thirds of their length, and a long base of insertion. P 3134*a*, P 3138 and P 45767–8 are all from the Carboniferous Limestone of Armagh, Ireland, and are of the same order of size (total length about 25 cm). The other specimen mentioned by Smith Woodward, P 3127, is from the Carboniferous Limestone of Castle Espie, Co. Down, Ireland: so far as it is preserved, it agrees with the other specimens except in its larger size (total length about 35 cm) and in being arched forwards a little. In this last character it agrees with the spines from the Russian Lower Carboniferous described by Inostranseff (1888, pl. 1) as *Dactylodus rossicus*. The Russian spines are identical in ornament with P 3127, but although they are bilaterally symmetrical in shape, the ornament is asymmetrical: they were said to have been found in association with petalodont teeth of *Polyrhizodus* type.

In structure (P 45768.I, figure 50, plate 22) these fin spines consist almost entirely of osteodentine, but around the posterior part of the central cavity there is a zone of lamellar tissue which makes up one-fifth of the thickness of the wall. There are no osteocyte spaces. The spines do not agree in structure with *O. milleri*, but this does not rule out a relationship, since there is no agreement in structure between the spines on the head and the dorsal fin spines in forms like *Myriacanthus* (figures 15, 17). It is possible that these spines armed the median fins of the animal on which the paired *O. milleri* spines were borne: the only evidence in favour of this is the similarity in ornament, in horizon and locality, and perhaps in number, since the BMNH contains six of the median spines from Armagh and eleven spines of *O. milleri* from the same locality. An alternative is that the spines are petalodont fin spines.

(4) *Asymmetrical dermal plates*

Davis (1883, p. 529, pl. 65, figs. 3, 4) described three specimens from the Carboniferous Limestone of Armagh (P 3135–7) which he referred to as part of the 'external covering' of *O. milleri*. To these Smith Woodward (1891*a*, p. 137) added a fourth specimen from Armagh (P 2887) and P 45774, a fragment also from Armagh, represents one end of a similar specimen. These structures, of which the largest, P 3135, is almost 30 cm in length, are elongated, narrow plates, slightly curved both in section and in length. On the outer face they bear stellate tubercles arranged in rows which form a chevron pattern, and in which the tubercles tend to fuse into irregular ridges. The ornament agrees exactly with that on the dorsal surface of the spines of *O. milleri* and on the symmetrical fin spines discussed above. At one end the plate broadens gradually, but the termination is not preserved in any specimen. At the other end the plate broadens suddenly into an oval spatulate expansion which bears a strong wear facet in its centre, where the ornament is completely abraded off. This plate was borne on the surface of the body of the fish, not as a projecting spine, since the entire inner face consists of trabecular tissue, obviously formed in contact with the dermis. In structure (P 3137.I), the plate agrees well with *O. milleri*: it consists of osteodentine, with no inner lamellar tissue, there are a few osteocyte spaces in the basal layers, and the structure of the surface tubercles is the same as in *O. milleri*. The only difference is that the vascular canals are not so large in the basal part of the section as they are in *O. milleri*. The ornament, the histological structure, the horizon and locality all suggest that the asymmetrical plates might well have formed part of the same animal as *O. milleri*, but against this must be set the rarity of the plates, for since they are paired structures, of large size and considerable thickness, one would expect them to be approximately as numerous as the spines of *O. milleri*, if they came from the same animal. The only record of similar structures is by Hussakof & Bryant (1918, p. 124) who mention examples 'exceedingly like' Davis's figures, from the Middle Devonian Onondaga Limestone of New York State. These plates were said to occur with the ptyctodont *Deinodus bennetti*. No definite conclusion can be reached on the nature of the Carboniferous plates, but their histological structure indicates that they probably belong at least to the same type of animal as *Oracanthus*.

(5) *Asymmetrical fin spines*

Newberry (1897, p. 288) transferred *Ctenacanthus pugiunculus* St John & Worthen (1875, p. 430, pl. 21, fig. 9), based on a spine from the Lower Carboniferous St Louis Limestone of Missouri and also known from the St Louis of Illinois, to *Oracanthus*, and added a new species, *O. lineatus* Newberry (1897, p. 289, pl. 22, figs. 4, 5), for a spine of unknown horizon and locality. The holotype of *Ctenacanthus pugiunculus* appears to be a normal *Ctenacanthus* except that it is very slender: I can see no grounds for removing it from *Ctenacanthus*. The *O. lineatus* spine is not bilaterally symmetrical, is ornamented with sparse, rounded tubercles, and has a groove reaching almost to the tip of the posterior face. The groove suggests that it is a fin spine, and the asymmetry indicates that it comes from a paired fin. The microstructure is unknown. There is no ground for thinking that this spine is in any way related to the typical spines of *Oracanthus*.

(6) *Mandibular spines*

Traquair (1888*a*, p. 86) made the new species *O. armigerus* for a spine from the Carboniferous Limestone series of Beith, Ayrshire, which is similar in shape and ornament to *O. milleri*, but is armed with three spines at the tip. A specimen mentioned by Traquair showed a spine of this type in association with cochliodont teeth. Smith Woodward (1915, p. lxviii, text-fig. 2) described another specimen showing a spine of *O. armigerus* in association with other dermal plates and cochliodont teeth which he identified as *Deltoptychius*. Moy-Thomas (1936*a*, p. 780, text-fig. 16) redescribed and figured Traquair's specimen and another specimen collected by himself. Moy-Thomas was able to describe the complete dentition of the fish, to show that the spine named *O. armigerus* was borne on the angle of the mandible, and that the skull bore other tuberculated dermal plates of which the most prominent was a pair of spines projecting from the postero-dorsal margin of the neurocranium. There is no evidence that the spine named *O. armigerus* bears any relationship to *O. milleri*. The histological structure of *O. armigerus* is shown in figure 29 and described on p. 156. It differs from *O. milleri* in having a broad internal zone of lamellar tissue which makes up about half of the thickness of the wall, and in having no bone cell spaces in the osteodentine. There is no reason for including the animal bearing spines with this structure in *Oracanthus*: the senior available generic name for the animal is *Deltoptychius* Morris & Roberts (see p. 149).

(7) *Bilaterally symmetrical dermal plates*

Davis (1883, p. 529, pl. 62, figs. 1 to 12, 14, 15) described as 'osseous plates' forming the 'cephalic covering' of *O. milleri* a number of specimens from the Carboniferous Limestone of Armagh. Smith Woodward (1891*a*, p. 137) included these specimens provisionally in *O. milleri*. Examination of the more complete of these specimens shows that the majority of them are parts of bilaterally symmetrical plates which bear a pair of projecting spines at one end and are traversed by a pair of longitudinal grooves, partially covered by parallel rows of tubercles, which contained sensory canals. A more complete example of this type of plate has been discovered from the Scottish Lower Carboniferous (P 11372, p. 159, figure 63, plate 27; figure 30), and comparison of this specimen with the most complete individual of '*O. armigerus*' shows that these plates formed the head shield or skull roof of the animal. The Scottish specimen is here included in *Deltoptychius armigerus* (below), and the Irish specimens are described as *D. moythomasi* sp.nov. (p. 164). The small, triangular spines or plates named *Pnigeacanthus pnigeus* (Newberry & Worthen 1866, p. 117, pl. 12, fig. 3; = *P. deltoides* St John & Worthen 1883, p. 259, pl. 24, fig. 4) from the Keokuk Limestone of Iowa and the St Louis Limestone of Illinois appear to be the terminal spines of similar head shields, although the characteristic sensory canal has not yet been seen on them.

To sum up this revision of the genus *Oracanthus*, *Oracanthus* s.s. is here limited to the seven species *O. milleri* Agassiz, *O. pustulosus* Agassiz, *O. vetustus* Leidy, *O. obliquus* St John & Worthen, *O. rectus* St John & Worthen, *O. bochumensis* Jaekel and *O. triangularis* Eastman, the last five species being very imperfectly known. *Oracanthus* possibly contains paired body spines of acanthodians. Some of the spines which have been included in *O. vetustus* Leidy do not belong to this species or to *Oracanthus*: these specimens and the spine described as *O. farringtoni* Roy are probably related to *Physonemus*, and are possibly edestid fin spines. Bilaterally symmetrical fin spines from the same horizon and locality as *O. milleri* may belong to that species, but differ from the typical forms in microstructure. Asymmetrical dermal plates from the same horizon and locality as *O. milleri* agree with the latter in ornament and microstructure, and may belong to the same animal, but similar structures are reported from the Middle Devonian of America, possibly in association with ptyctodont tooth plates. *Ctenacanthus pugiunculus* St John & Worthen is unrelated to *Oracanthus* and is probably a true *Ctenacanthus*. *O. lineatus* Newberry is a paired fin spine of unknown affinities. *O. armigerus* Traquair is a holocephalan unrelated to *Oracanthus*, and is referred to *Deltoptychius*. Symmetrical dermal plates previously placed in *O. milleri* are head shields of a holocephalan here named *Deltoptychius moythomasi* sp.nov.: *Pnigeacanthus* St John & Worthen probably contains similar structures.

The only species of *Deltoptychius* known by associated teeth and skeletal remains is:

Deltoptychius armigerus (Traquair)

Figures 61, 62, plate 26; figures 63, 64, plate 27; figures 27 to 33.

1887 *Oracanthus armigerus* Traquair *in* Anderson, p. 313 (*nom. nud.*).
1887 *Poecilodus elongatus* Traquair *in* Anderson, p. 314 (*nom. nud.*).
1887 *Deltoptychius* sp. Anderson, p. 314 (name only).
1888*a* *Oracanthus armigerus* Traquair, p. 86.
1888*b* *Oracanthus armigerus* Traquair; Traquair, p. 418.
1889*a* *Deltoptychius acutus* M'Coy; *partim*, Smith Woodward, p. 213 (46045).
1891*a* *Oracanthus armigerus* Traquair; Smith Woodward, p. 139.
1891*a* ?*Listracanthus* sp. Smith Woodward, p. 149.
1901 *Oracanthus armigerus* Traquair; Traquair, pp. 111, 112 (name only).
1903 *Oracanthus armigerus* Traquair; Traquair, pp. 694, 695 (name only).
1915 *Oracanthus armigerus* Traquair; Smith Woodward, p. lxviii, text-figs. 2A–D.
1936*a* *Oracanthus armigerus* Traquair; Moy-Thomas, p. 780, text-figs. 16–19.
1954 *Oracanthus armigerus* Traquair; Waterston, p. 37.

Amended diagnosis: *Deltoptychius* probably reaching about 30 cm in length, head shield up to 7 cm in length and 3 cm in breadth; mandibular teeth as *D. acutus* M'Coy, posterior teeth of upper jaw as *Streblodus colei* Davis; mandibular spine not much dorso-ventrally flattened, tuberculated, with three enlarged denticles at its postero-lateral corner, the proximal one often reduced; head shield longer than broad, the posterior spines broader than long, tubercles tending to lie in longitudinal rows, the sensory canal ending on the posterior edge of the shield medial to the posterior spine; scales with many cusps, two rows of enlarged scales of *Listracanthus* type along the back.

Holotype: a mandibular spine, RSM 1911.62.754.

Material: incomplete fish: RSM 1936.4 (Moy-Thomas 1936*a*, text-figs. 16, 18, 19); teeth with associated mandibular spines: RSM 1883.23.20 (Smith Woodward 1915, text-fig. 2A), BMNH P 22009–10, P 20146–9 (Moy-Thomas 1936*a*, text-fig. 17); isolated head shield: BMNH P 11372 (figure 30; figure 63, plate 27); fragments of head plates: RSM 1907.41.3; isolated mandibular spines: RSM 1911.62.754 (holotype, Smith Woodward 1915, text-fig. 2B), BMNH P 11336–8, P 11718 and specimens in RSM; isolated teeth: BMNH 46045, P 9123, P 11351, P 11346–8 and specimens in RSM.

Horizons and localities: Lower Carboniferous (Upper Tournaisian, Viséan and Lower Namurian), Scotland; Calciferous Sandstone Group, Cementstones (C 2), Glencartholm, Eskdale, Dumfries; Oil Shale Group (C 2–D 1), Abden bone-bed, Kinghorn, Fife, *Crangopsis* Bed, Ardross, Fife; Carboniferous Limestone Series, Beith, Ayrshire, ?Largo Ward, Fife; Limestone Coal Group (D 3), *Lingula* band above blackband ironstone in North Coal, Niddrie, Midlothian; Loanhead No. 1 Ironstone, Loanhead, Midlothian; South Coal, locality unknown; Flex Coal, Loanhead, Midlothian.

Description

The only specimen in which the skull is preserved is RSM 1936.4 (figure 62, plate 26; figure 27) a specimen already described by Moy-Thomas (1936*a*), and here very little can be made out. The skull consists of cartilage calcified in the usual polygonal tesserae. It is clear that the tooth plates of the upper jaw were attached directly to the skull, and that the suspension was holostylic. The 'step' in the roof of the skull above the posterior tooth plate of the upper jaw appears to be a genuine feature since the squamation follows the line of the edge of the cartilage. This 'step' is reminiscent of the similar feature at this point in the skulls of *Helodus* (figure 38), *Squaloraja* (figure 8) and *Callorhynchus* (figure 3); in *Squaloraja* and chimaeroids the 'step' marks the point of insertion of the frontal clasper. In RSM 1936.4 the tip of the snout is missing, and the condition of the rostrum is unknown.

The holotype and most of the isolated specimens of *D. armigerus* are spines which were shown by Moy-Thomas (1936*a*, p. 782) to have been borne on the angle of the mandible. There is a good deal of variation (figure 28) in these spines both in ornament and shape and it is quite possible that more than one species is represented. RSM 1936.4 shows that the anterior border of the spine, when complete, is much longer than it is in any of the isolated examples, and that the two spines must almost have met in the mid-line at the mandibular symphysis. In section (figure 29; figure 61, plate 26; P 11358.I) the mandibular spine consists of an inner layer of lamellar tissue (*cpd.*) making up about half the thickness of the wall, and an outer layer of osteodentine (*osd.*). The lamellar tissue is

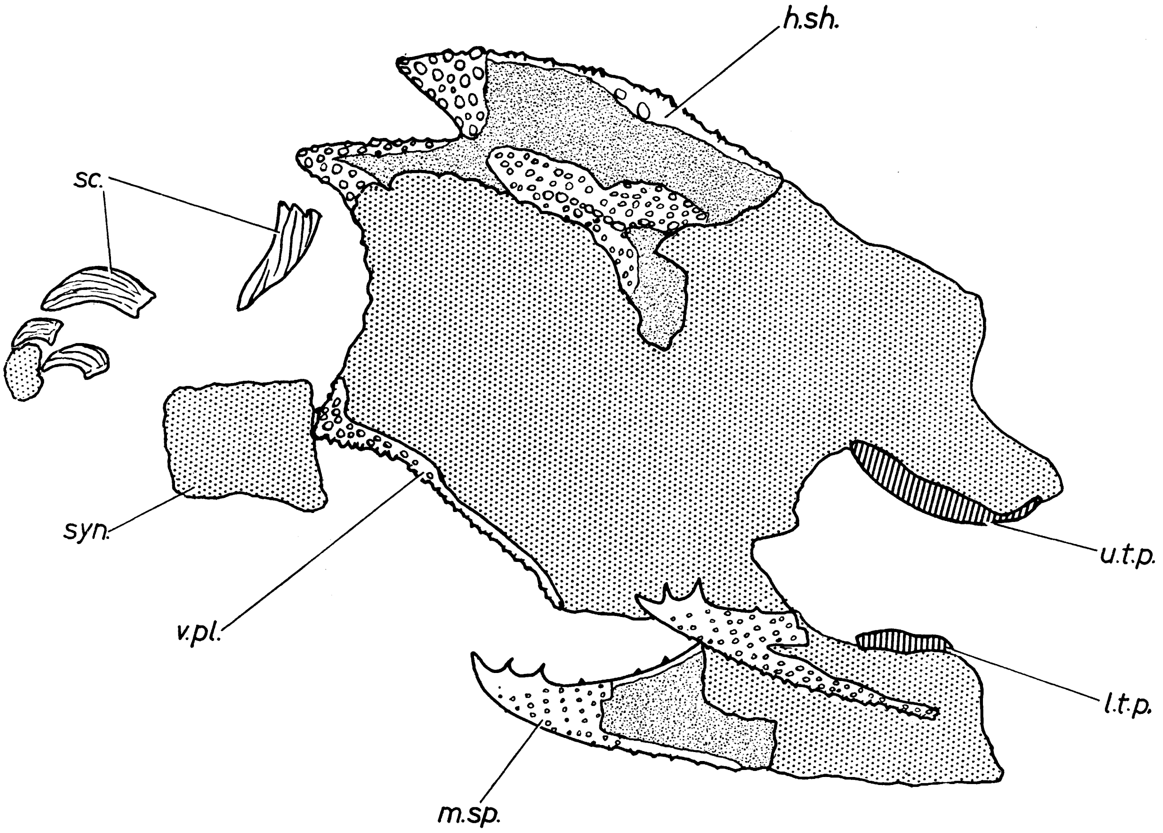

FIGURE 27. *Deltoptychius armigerus* (Traquair). The skull and anterior part of the trunk as preserved in RSM 1936.4 (see figure 62, plate 26) (× 1½). Regular stippling indicates calcified cartilage, irregular stippling indicates dentine in which the surface ornament is not preserved. ***h.sh.***, Head shield; ***l.t.p.***, tooth plate of lower jaw seen in section; ***m.sp.***, mandibular spine; ***sc.***, enlarged scales of '*Listracanthus*' type; ***syn.***, possible synarcual; ***u.t.p.***, posterior tooth plate of upper jaw seen in section; ***v.pl.***, ventral dermal plate on neurocranium.

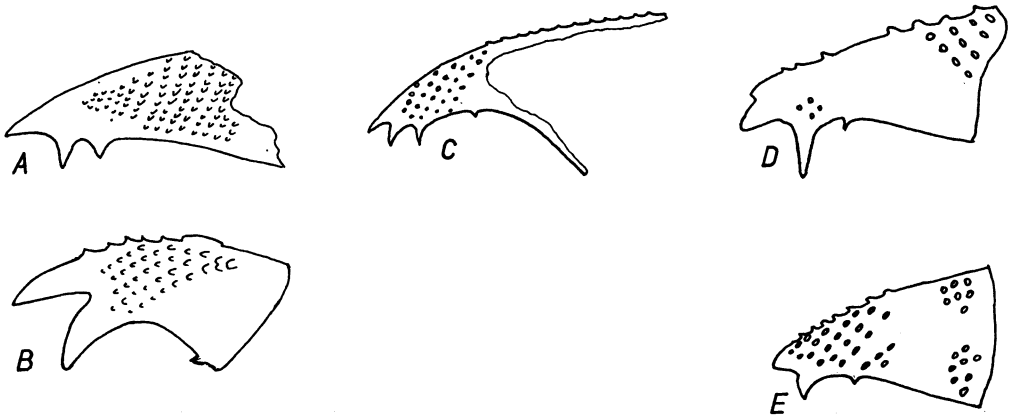

FIGURE 28. *Deltoptychius armigerus* (Traquair). Sketches of mandibular spines. *A*, RSM 1911.62.754 (holotype) (× 1½ approx.). After Smith Woodward (1915). *B*, RSM 1883.23.20 (× 2 approx.). *C*, RSM 1936.4 (× 1⅓ approx.). *D*, P 11356 (× 1⅔ approx.). *E*, P 11358 (1⅓ approx.). *A*, *B*, From Carboniferous Limestone series, Beith, Ayrshire; *C*, from Calciferous Sandstone series, Cementstones, Glencartholm, Eskdale, Dumfries; *D*, *E*, from Calciferous Sandstone series, Oil Shale group, Abden Bone Bed, Kinghorn, Fife.

perforated by a few narrow vascular canals (*v.can.*) and by many long, much branched tubules (*d.t.*). In the wall of the anterior part of the sectioned spine there is a layer of cell spaces enclosed in the outer part of the lamellar tissue; one of these cell spaces is present in the figured part of the section (*odb.*). This layer of cell spaces is present in only part of the section, and is probably an individual variation rather than a constant feature of the species. The osteodentine contains many moderately large vascular canals (*v.can.*), each surrounded by a dentinal osteon (*d.o.*) in which the dentine tubules are sparse. The osteons are separated by abundant interosteonal tissue. In parts of the section the interosteonal tissue is packed with dark, parallel fibres (*fib.*) which pass obliquely through the section. These structures possibly represent collagen fibres in the original tissue, and similar structures are commonly referred to as Sharpey's fibres, but as Tarlo (1963, p. 46) notes, in living vertebrates Sharpey's fibres normally occur only at the margins of hard tissues. In the present case the structures may be an artifact produced by shearing stresses in the rock. The surface tubercles (*b.tu.*) contain numerous vascular canals, each ending in a bunch

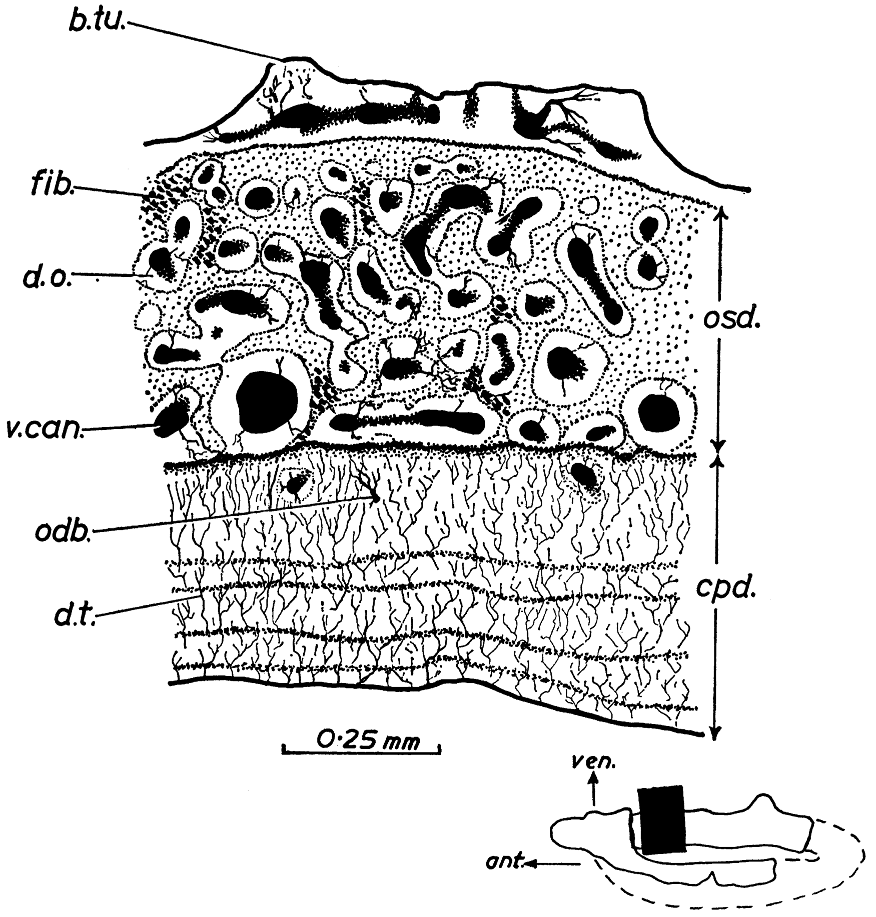

FIGURE 29. *Deltoptychius armigerus* (Traquair). Transverse section cut near the middle of a mandibular spine. P 11358.I. Inset at bottom right is an outline of the complete section showing the orientation of the figured part (*ant.*, anterior; *ven.*, ventral). *b.tu.*, Base of a surface tubercle; *cpd.*, lamellar tissue; *d.o.*, osteonal dentine; *d.t.*, tubule; *fib.*, fibrous structures in interosteonal tissue; *odb.*, cell cavity; *osd.*, osteodentine; *v.can.*, vascular canal.

of stout dentine tubules which do not form a recognizable layer of pallial dentine. There is no enamel.

Apart from the mandibular spines, fragments of other dermal plates have been mentioned in RSM 1883.23.20 by Smith Woodward (1915) and have been described and figured in RSM 1936.4 by Moy-Thomas. The first of these two specimens shows only much shattered fragments of plates bearing tubercles like those on the mandibular spines. In the second specimen (figure 27) there are the remains of two plates in addition to the mandibular spines. The larger plate (*h.sh.*) occupies the posterior two-thirds of the skull roof. The plate ends posteriorly in two blunt, triangular spines, ornamented with tubercles. The only other marked feature of the plate is a ridge on the exposed edge which divides at the level of the hind end of the mandibular spines into two ridges which diverge anteriorly. Although this plate is very imperfectly preserved, it is sufficient to show that P 11372 (figure 63, plate 27; figure 30) is a more complete example of the structure. P 11372 is a specimen from the Traquair collection of unknown horizon and locality, but the matrix indicates that it is very probably from the Flex Coal at Loanhead, Edinburgh, in which teeth of *Deltoptychius* occur. P 11372 is an elongated, bilaterally

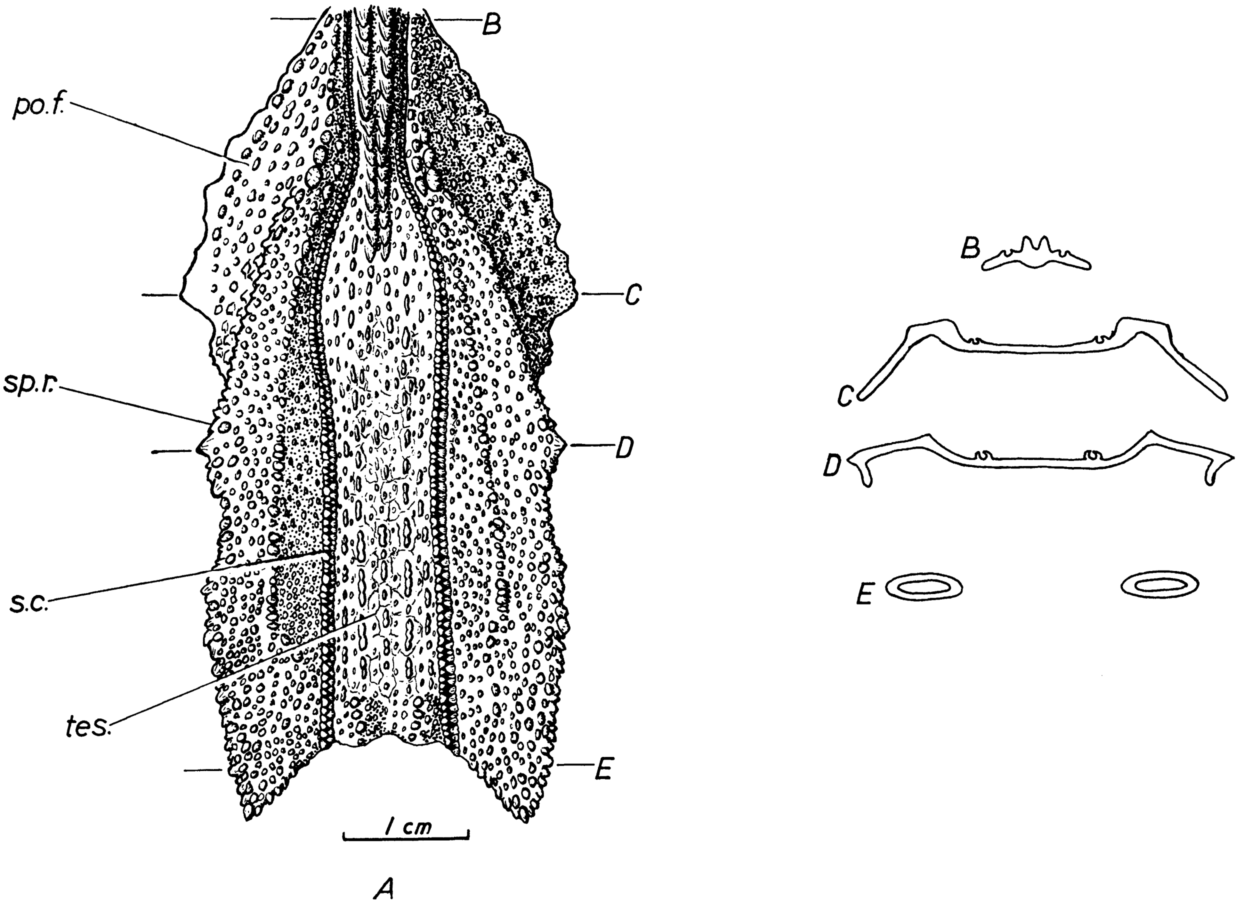

FIGURE 30. *Deltoptychius armigerus* (Traquair). *A*, Restoration of the head shield in dorsal view, based on P 11372; *B*, *C*, *D*, *E*, diagrammatic transverse sections of the shield at the levels indicated in *A*. *po.f.*, Preorbital flange; *s.c.*, course of supraorbital sensory canal; *sp.r.*, supraorbital ridge; *tes.*, incompletely fused tesserae in the central part of the shield.

symmetrical plate, incomplete anteriorly, which measures almost 7 cm in length and 3 cm in maximum breadth. Posteriorly the plate ends in a pair of dorso-ventrally flattened spines. The lateral edge of each of these spines extends forwards as a ridge which bends medially in the anterior half of the plate and runs parallel to its fellow again in the anterior fifth of its length. In the middle part of the plate (*D*, figure 30) a short flange extends ventrally from this ridge. In the anterior third of the plate (*C*, figure 30) a broad flange (*po.f.*) extends ventro-laterally. Medial to the main lateral ridge, there is a second longitudinal ridge, less pronounced, which marks off a broad median depression. The whole surface of the plate is ornamented with tubercles whose blunt points are directed postero-dorsally. Each tubercle bears about a dozen radial ridges which vary in strength from one tubercle to another. The tubercles are arranged in longitudinal rows on the anterior part of the plate and in the median depression on the posterior part of the plate, where they tend to become confluent, forming short ridges. On the posterior spines, where the tubercles are enlarged, and the region in front of these the tubercles are arranged irregularly. The tubercles are particularly large in a pair of longitudinal series near the mid-line in the narrow anterior part of the plate, and on the anterior part of the two pairs of longitudinal ridges described above. Near the mid-line on the posterior edge of the plate there is a pair of low knobs. Immediately lateral to each of these knobs there is the hind end of a double series of closely set tubercles (*s.c.*) which runs forwards near the edge of the median depression to the anterior edge of the plate. The tips of the tubercles in these series are bent towards their fellows in the adjacent row so that a partially covered groove is formed (figure 64, plate 27). This groove must have contained a sensory canal in life. The histological structure of this plate is discussed below under *D. moythomasi* (p. 166).

The plate described above roofed the posterior two-thirds of the neurocranium in *D. armigerus* and can properly be referred to as a head shield. The spines on the posterior end of the plate were probably complete distally (*E*, figure 30) as they are in *D. moythomasi* (p. 165), and they must have projected from the hind end of the head. The very prominent lateral ridge (*sp.r.*) in the middle part of the plate (*D*, figure 30) probably represents a supraorbital ridge, while the broad lateral flanges on the anterior part of the plate would have covered the dorso-lateral surfaces of the preorbital region, their posterior edges marking the border of the orbit. The sensory canal on the surface of the plate must be the supraorbital canal. There is no sign of any branching of the canal, and both the supratemporal commissure and the junction with the infraorbital canal, if present, must have lain behind the head shield. There are no sutures on the head shield, but there are clear indications that some of the tubercles and groups of confluent tubercles on the medial part of the shield (figure 64, plate 27; *tes.*, figure 30) were borne on independent polygonal tesserae which have become fused together during ontogeny. The homologies of this head shield are discussed on p. 201.

The second of the two plates present in RSM 1936.4 (*v.pl.*, figure 27) ends posteriorly in a marked angle below the posterior spines of the head shield, and extends forwards, exposed only in section, to the level of the tips of the mandibular spines. This plate appears to have covered the ventro-lateral corner and edge of the occipital part of the neurocranium. No other examples of it are known.

The dentition of *D. armigerus* was first noted by Smith Woodward (1915), who identified the tooth plates as *Deltoptychius*. Moy-Thomas (1936*a*), on the basis of RSM 1936.4 and another specimen which he had collected in Glencartholm (P 20146–9), was able to show that the pair of tooth plates which Smith Woodward had described as the upper was in fact the lower, and that the upper jaw contained one pair of large tooth plates with three pairs of small tooth plates of *Helodus* type in front of them. In the complete dentition described by Moy-Thomas (P 20146–9) I can find only two pairs of '*Helodus*' tooth plates in front of the large tooth plates in the upper jaw (figure 31). The dentition is preserved without any displacement of the tooth plates, and it seems that Moy-Thomas must have made an error in his interpretation of the specimen. The single pair of mandibular tooth plates is indistinguishable from the holotype of *Deltoptychius acutus* M'Coy (1855, p. 621, pl. 31, fig. 24): tooth plates of this type are known from the Carboniferous Limestone of Armagh, Yorkshire and Derbyshire (*D. armigerus* is not given the senior trivial name *acutus* because it seems very probable that teeth of this type from Armagh occurred in an animal with a different type of head shield, see p. 168). The posterior pair of tooth plates in the upper jaw appears to be identical with the paratypes of *Streblodus colei* Davis (1883, p. 426,

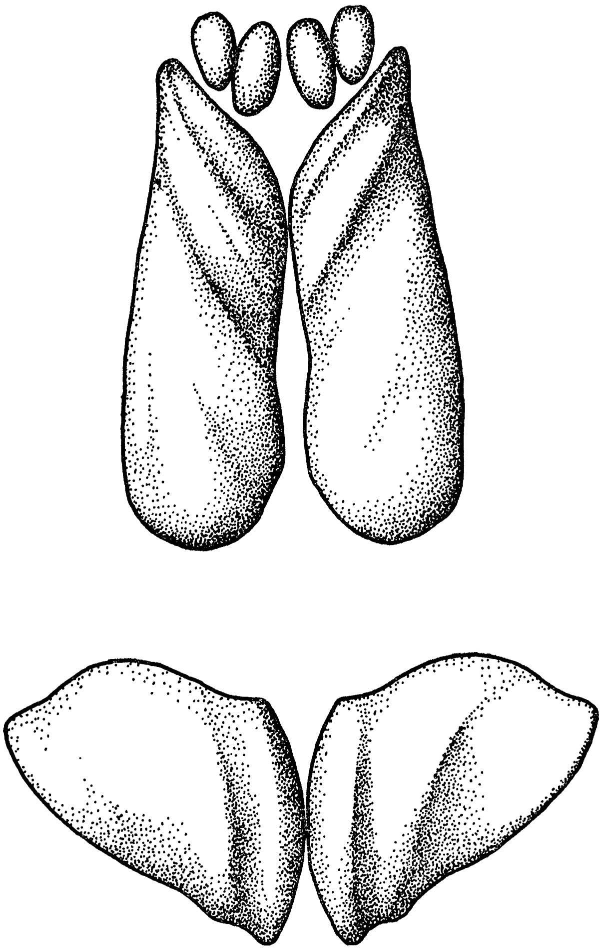

FIGURE 31. *Deltoptychius armigerus* (Traquair). Dentition restored as if seen from in front with the mouth wide open (× 2 approx.). Based on P 20146–9.

pl. 53, figs. 5, 6) from the Carboniferous Limestone of Armagh, confirming the opinion of St John & Worthen (1883, p. 92) that this species represents the upper tooth plates of *Deltoptychius acutus*.

Nothing is known of the labial cartilages or branchial arches of *D. armigerus*. Of the postcranial skeleton the only known trace is in RSM 1936.4, where a strip of calcified cartilage extends back from the skull at the level of the lower dermal plate (*syn.*, figure 27): this is the position in which one would expect to find a synarcual but the preservation is not sufficiently good for the identification to be certain. There is no trace of the vertebral column and the notochord was apparently uncalcified. Of the fins nothing is known, but there appears to have been no dorsal fin spine.

The squamation has been described by Moy-Thomas in RSM 1936.4, where it is fairly well preserved. Acid preparation of a fragment from the Glencartholm specimen collected by Moy-Thomas (P 20149*a*) has yielded a collection of beautifully preserved isolated scales. The squamation was complete, and scales covered the anterior part of the head, in front of the head shield. Moy-Thomas noted that the scales are of two types: the small scales covering the head and trunk resemble the Carboniferous scales known as *Petrodus*, and the spines which are present in two rows down the back resemble the spines known as *Listracanthus*. It is unfortunate that the name *Petrodus* has been used by Moy-Thomas (1935*a*) for a Carboniferous hybodont shark in which the only specimen shows a few scales of the same general shape as those of *Deltoptychius*. Examples of the scales are shown in figure 32. The crown of the scale is laterally compressed and is subdivided by vertical grooves into four or five cusps which may be almost completely separate in small scales (*B*, *C*) but in larger scales (*A*, *D*) are more or less fused. The anterior and posterior edges of the crown, particularly the latter, may bear several smaller cusps, and there are often small cusps on the lateral surfaces of the main cusps. In some large scales (*A*) small accessory groups of cusps (*a.c.*) develop near the lateral margin of the root. The crowns of the larger scales are almost always worn so that the tips of the cusps are lost and the pulp cavities (*p.c.*) exposed. The roots of the scales are expanded laterally and are subdivided by transverse grooves corresponding to the vertical grooves on the crown. The underside of the root is concave and perforated by many basal canals (*b.c.*). In some specimens (*A*) one basal canal is sunk in the centre of the concavity and appears more important than the others, but this is not a constant feature, and in scales where it occurs the position of the enlarged canal varies. At the junction of root and crown there are numerous neck canals (*n.c.*).

The *Listracanthus* spines are present in two rows along the back of the fish. The spines are shortest directly behind the head, and grow longer posteriorly. In RSM 1936.4 none of the spines shows the tip, as Moy-Thomas noticed, but in RSM 1883.23.20 one of the short spines behind the head is complete (figure 33). These spines cannot satisfactorily be differentiated from *Listracanthus*, which must become a synonym of *Deltoptychius*. It is clear that the spines do not differ from the scales of the trunk in any essential feature: they are simply scales in which the crown is enlarged and elongated. The spines have up to 8 separate cusps compared with 4 or 5 in the scales, but this is only a difference in degree. In the larger spines (up to 14 mm in length) preserved in RSM 1936.4, Moy-Thomas has described how the anterior edges of the vertical ridges on the spines bear 'a single row of elongated tubercles'. These tubercles are small cusps borne on the hind edge of the ridge immediately in front, and are homologous with the lateral cusps on the main cusps of the trunk scales. These lateral cusps are also present in other species of *Listracanthus* (*L. wardi* Smith Woodward; P 10004).

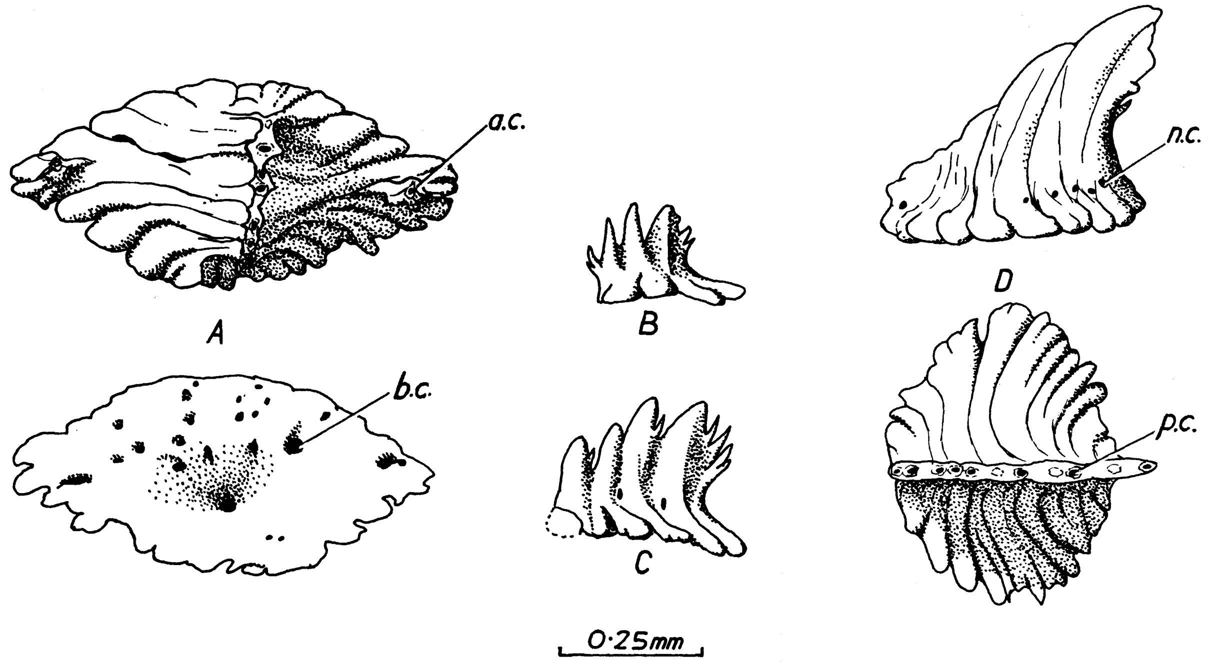

FIGURE 32. *Deltoptychius armigerus* (Traquair). Scales. *A*, Large scale in coronal (above) and basal views; *B*, *C*, small, unworn scales in lateral view; *D*, large scale in lateral (above) and coronal view. P 20144.I–IV. *a.c.*, Accessory cusp on lateral part of root of large scale; *b.c.*, basal canal; *n.c.*, neck canal; *p.c.*, pulp cavity of cusp exposed by wear.

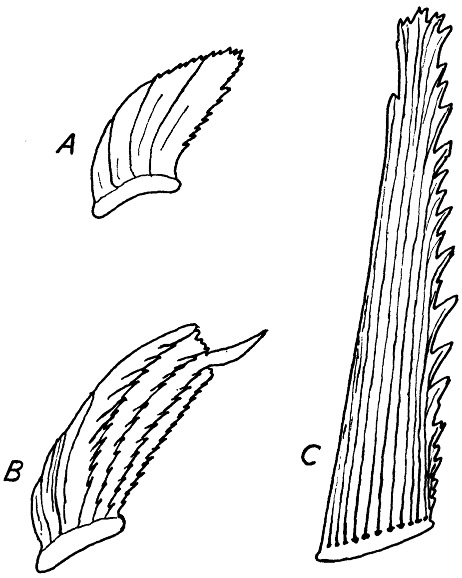

FIGURE 33. '*Listracanthus*' spines (enlarged scales). *A*, *B*, *Deltoptychius armigerus* (Traquair), in *B* the spine is incomplete distally. *A*, From RSM 1883.23.20 (× 5 approx.); *B*, from RSM 1936.4 (× 3 approx.). *C*, *Listracanthus wardi* Smith Woodward, Middle Coal Measures, Staffordshire (× 3 approx.), after Smith Woodward (1903).

The scales and spines of *D. armigerus* can be interpreted in the terms of the lepidomorial theory of Stensiö & Ørvig (Stensiö 1961). Each scale consists of a series of units (the central cusps) fused together. Since each main cusp may bear several lateral cusps and have more than one basal canal and neck canal, each unit is a group of lepidomoria developed synchronously and is therefore a synchronomorial unit. The complete scale is of the cyclomorial type, and the synchronomorial units were added only on the anterior and posterior faces of the primordium (cf. Stensiö 1961, pl. 2, figs. G, H). Shortage of material and the difficulty of grinding accurately orientated sections of small isolated scales have so far prevented the preparation of satisfactory sections, but from the structure of complete scales, from broken scales and from the sections available it is clear that the pulp cavities of the synchronomorial units are separate throughout their length, and that, at least in the distal part of the crown, each pulp cavity is surrounded by a complete wall of dentine. The scales are thus churtonal or semi-stiphronal (cf. Stensiö 1961, pl. 1, fig. T; pl. 2, fig. E) rather than stiphronal (in which only the primordium has a complete wall, the units added later being incomplete or thin-walled where they are in contact with pre-existing units).

Deltoptychius moythomasi sp.nov.

Figures 65, 66, plate 27; figures 68, 69, 71, plate 28; figures 34, 35.

1848*a* ?*Coccosteus* ?*carbonarius* M'Coy, p. 9.
1848*a* ?*Asterolepis verrucosa* M'Coy, p. 9.
1848*b* ?*Platyacanthus isosceles* M'Coy, p. 120.
1883 *Oracanthus milleri* Agassiz; *partim*, Davis, p. 525, pl. 62, figs. 1 to 4, 6, 8, 11, 12: *non* pl. 62, figs. 7, 13; pl. 63, figs. 1 to 4; pl. 64; pl. 65, figs. 3, 4; ?pl. 62, figs. 5, 9, 10, 14, 15.
1891*a* *Oracanthus milleri* Agassiz; *partim*, Smith Woodward, p. 135.

Note: although it is probable that each of M'Coy's three species listed above is synonymous with this species, in no case is the identity sufficiently certain for M'Coy's trivial name to be used.

Diagnosis: *Deltoptychius* known only by the posterior part of the head shield, which reaches about 5 cm in breadth; posterior spines longer than broad, tubercles arranged irregularly, supraorbital sensory canal running almost to the tip of the posterior spine.

Holotype: incomplete head shield, BMNH P 2876 (Davis 1883, pl. 62, fig. 1).

Material: 14 incomplete head shields or fragments of head shields in the BMNH: P 2876–9, P 2881, P 2883, P 2885–6 (Davis 1883, pl. 62, figs. 1 to 4, 6, 8, 11, 12), P 2901, P 47588–92.

Horizon and locality: Viséan, Lower Carboniferous Limestone (S 2–D 1), Armagh, Ireland.

Description

This species is known only by the posterior part of the head shield (figure 34*A*), which is similar to that of *D. armigerus*. Only in the holotype and P 2877 (Davis 1883, pl. 62, fig. 2) are both the posterior spines present; the remainder of the specimens show only one of the posterior spines accompanied by more or less of one side of the shield. Since the anterior part of the shield is unknown it is not possible to discover its proportions, but although the posterior spines are narrower than they are in *D. armigerus* the body of the shield seems to have been as broad as, or broader than, that of *D. armigerus*. In almost all the specimens the shield is badly distorted, and it is difficult to obtain any idea of its relief. It appears that the shield was flatter than that of *D. armigerus*, with the ridge lateral to the sensory canal less strongly marked but with a second longitudinal ridge medial to the canal, so that the latter lay in a depression. The ventral surface of the posterior spine is complete almost to its base. The spine is triangular in section, with the shortest side placed laterally (*D*). The holotype of *Coccosteus ?carbonarius* M'Coy (1848*a*, p. 9), now in the GSM collection, is possibly part of a posterior spine of the head shield of this species, but the specimen is too incomplete for certainty. Along the lateral border of the head shield there is a vertical flange (*C*) which is continuous with the lateral face of the posterior spine. Although the anterior part of the shield is not complete in any specimen, the holotype suggests that there was a narrow median ridge running forwards, as in *D. armigerus*, but that the tubercles on this ridge were not enlarged as they are in the latter.

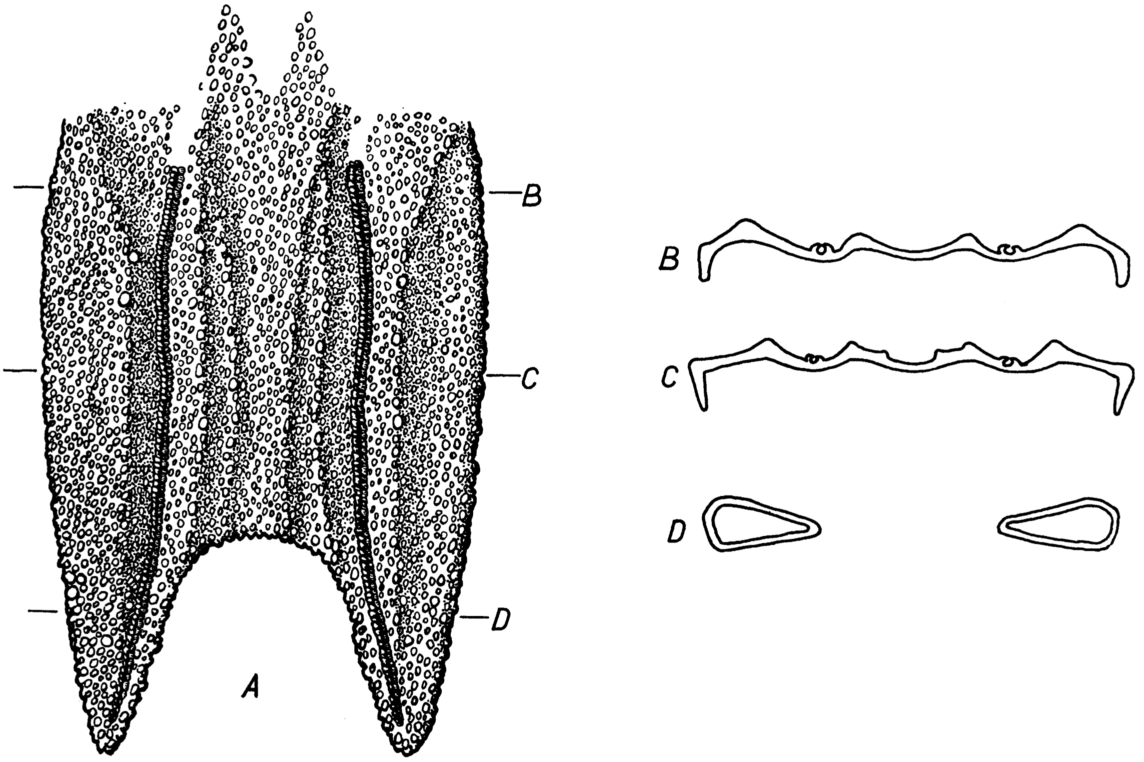

FIGURE 34. *Deltoptychius moythomasi* sp.nov. *A*, Restoration of the posterior part of the head shield in dorsal view, × 1; *B*, *C*, *D*, diagrammatic transverse sections through the shield at the levels indicated in *A*.

The ornament of the shield consists of tubercles which are usually smooth and rounded, but this is probably due to wear, for in a few examples (P 2885) there are unworn tubercles showing radial striations and a posteriorly directed point, just as in *D. armigerus*. On the dorsal surface of the shield the tubercles are irregularly distributed and there is no sign of the regular longitudinal series of tubercles which occur in *D. armigerus*, but on the underside of the posterior spine the tubercles are arranged in longitudinal rows. The tubercles are similar in size to those on the head shield of *D. armigerus* and, as in the latter, they are enlarged on the posterior spines and along the longitudinal ridges on the dorsal surface. In P 2886 (Davis 1883, pl. 62, fig. 12) the tubercles are much larger than in the other specimens and are strongly crimped around the base: it is possible that this specimen represents another species.

The course of the supraorbital sensory canal is marked, just as in *D. armigerus*, by a double row of tubercles which incline towards each other forming a partially closed groove (figure 34; figures 65, 66, plate 27). The sensory canal did not end on the posterior border of the shield as it did in *D. armigerus*, but ran back almost to the tip of the posterior spine.

In structure (figure 35; figure 71, plate 28; P 2901.I) the head shield consists of an inner layer of lamellar tissue (*cpd.*) and an outer layer of osteodentine (*osd.*), each making up about half the thickness. The lamellar tissue is penetrated by long, much branched tubules (*d.t.*) and sparse, slender vascular canals. The osteodentine contains fairly numerous vascular canals (*v.can.*), each surrounded by a dentinal osteon (*d.ost.*) in which there are few dentine tubules. The osteons in the osteodentine are separated by abundant interosteonal tissue (*ist.*). The surface tubercles contain many slender vascular canals, each ending in a bunch of coarse dentine tubules which together form a very poorly marked layer of pallial dentine. There is no recognizable enamel. In almost all these features of microstructure the head shield of *D. moythomasi* agrees with the mandibular spines of *D. armigerus* (p. 156, figure 29; figure 61, plate 26), the only differences between the two being the less numerous vascular canals in the osteodentine and the better developed pallial dentine in *D. moythomasi*. Since the agreement is so close, it seems certain that the head shield of *D. armigerus* will be found to have the same structure when specimens are available for sectioning. There are no cell spaces enclosed within the lamellar tissue of the head shield: this supports the suggestion (p. 158) that the cell spaces seen in part of the section of the mandibular spine of *D. armigerus* are an individual variation, not a constant feature.

Figure 35 also shows the groove for the supraorbital sensory canal and its enclosing tubercles in section. Below the groove there is a longitudinal canal (*c.n.*) which is larger than the vascular canals in the osteodentine, although like them it is surrounded by osteonal dentine; this canal must have carried the nerves and vessels supplying the organs of the sensory canal.

In none of the specimens of the head shield of *D. moythomasi* is there any sign of sutures or lines of fusion.

The head shield of *D. moythomasi* is so like that of *D. armigerus* that one would expect *D. moythomasi* to have had mandibular spines similar to those of *D. armigerus*. That such spines were present can only be confirmed by the discovery of an associated skeleton, but since the head shield of *D. moythomasi* agrees with the mandibular spines of *D. armigerus* in histological structure, the mandibular spines of *D. moythomasi* can be expected to have the same structure, and this will serve at least to eliminate spines which have a different structure. A search through the spines known from the Carboniferous Limestone of Armagh suggested that the only likely candidate is *Erismacanthus jonesi* M'Coy (= *Cladacanthus paradoxus* Agassiz), since this spine is not bilaterally symmetrical, is of the right order of size, is approximately as common as the fragmentary head shields of *D. moy-*

thomasi, is ornamented proximally with tubercles and bears enlarged spines at the tip. Jaekel (1890, p. 127) thought that *Erismacanthus* contained lateral head spines of an animal with cochliodont dentition, and included it in his group Trachyacanthidae. But a section of P 45794 shows that *E. jonesi* consists entirely of osteodentine, with no inner layer of lamellar tissue, and that the surface tubercles have a well developed layer of pallial dentine: association of *E. jonesi* with *D. moythomasi* is thus very unlikely.

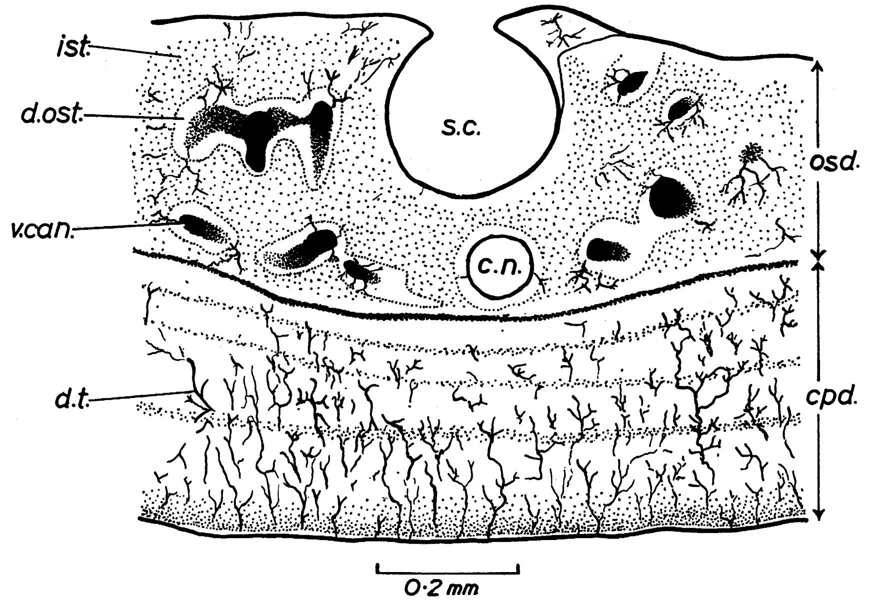

FIGURE 35. *Deltoptychius moythomasi* sp.nov. Transverse section of the head shield cut through the groove for the supraorbital sensory canal at the base of the posterior spine of the shield. P 2901.I. *c.n.*, Canal carrying nerves and vessels supplying the sensory canal; *cpd.*, lamellar tissue; *d.ost.*, dentinal osteon; *d.t.*, tubule; *ist.*, interosteonal tissue; *osd.*, osteodentine; *s.c.*, groove for supraorbital sensory canal; *v.can.*, vascular canal.

There is one other possible candidate for the mandibular spine of *D. moythomasi*. Among the material in the BMNH from the Carboniferous Limestone of Armagh there is a number of small spines labelled as '*Oracanthus*' which could well be the terminal parts of the posterior spines of the head shield of *D. moythomasi* or a similar form, but on which no groove for the sensory canal is visible. The majority of these spines are too incomplete to be of any value, but two examples, P 2880 (Davis 1883, pl. 62, fig. 5; figure 69, plate 28) and the holotype of *Platyacanthus isosceles* M'Coy (Davis 1883, pl. 62, fig. 9), now in the GSM, show enlarged, peg-like tubercles along one margin, seem to be ornamented more regularly than are the posterior spines of the head shield of *D. moythomasi*, have the tubercles arranged in oblique rows with the points of the tubercles directed obliquely rather than towards the tip of the spine, are broader in proportion to their length than are the posterior spines of the head shield in *D. moythomasi*, and show a wear facet on one margin of the tip. It seems likely that these are the mandibular spines of *D. moythomasi*, but some explanation is needed for the rarity of recognizable examples of the spine compared with examples of the head shield, for in *D. armigerus* specimens of the mandibular spine are fairly common but the head shield is extremely rare. If we assume an association between these spines and the head shield of *D. moythomasi*, then this species differed from *D. armigerus* in having no enlarged tubercles at the tip of the mandibular spine and also in being more dorso-ventrally flattened, for the spines described above are much more compressed than the mandibular spines of *D. armigerus*. These spines show one feature in common with the head shield of *D. armigerus*, the presence of lines of fusion around some of the tubercles near the base of the spine (figure 69, plate 28) which show that these tubercles were borne on independent polygonal tesserae which became fused during ontogeny.

In *D. armigerus* there is a dermal plate on the ventro-lateral face of the occipital part of the neurocranium. Examples of a similar plate in *D. moythomasi* are perhaps provided by P 2881 (Davis 1883, pl. 62, fig. 10; figure 68, plate 28), P 11162 and P 45793. These three specimens, the last two very incomplete, are from the Carboniferous Limestone of Armagh. This plate was about 4 cm in length and is bent almost at right angles along the long axis. Of the two flat surfaces so produced, one projects beyond the other in a slender, pointed spine, and the other projects, at the same end, in a triangular lateral flange. The plate is ornamented with tubercles like those on the head shield of *D. moythomasi*. The holotype of *Asterolepis verrucosa* M'Coy (1848 *a*, p. 9), now in the GSM, is possibly an incomplete example of this type of plate, but again the specimen is too imperfect for certainty. So little is known about the ventral dermal plate on the head of *D. armigerus* that direct comparison with the plate described above is not possible, but I would assign the plate provisionally to *D. moythomasi*.

Comparison with *D. armigerus* suggests that the dentition of *D. moythomasi* would have consisted of a pair of *Deltoptychius acutus* tooth plates in the lower jaw and in the upper jaw a pair of *Streblodus colei* and two pairs of '*Helodus*' teeth; all these teeth are well known from Armagh.

Comparison between Deltoptychius armigerus *and* D. moythomasi

The only structure in which direct comparison between *D. armigerus* and *D. moythomasi* is possible is the head shield. In *D. moythomasi* the mandibular spines and ventral head plates are associated with the head shield only by inference, and comparison with the same structures in *D. armigerus* is speculative.

The chief difference between the head shields of the two species is in the course of the groove for the supraorbital sensory canal. In *D. armigerus* the groove ends on the hind edge of the body of the shield, but in *D. moythomasi* it passes almost to the tip of the posterior spine. Since the ventral wall of the posterior spine in *D. moythomasi* is complete almost to the base the spine must have projected from the body, and it seems very unlikely that the sensory canal, running almost to the tip of this projecting spine, could have anastomosed with the main lateral line of the trunk or with a supratemporal commissure. In this the canal differs from the supraorbital canal of all other elasmobranchs, and can only be compared with forms such as the various arthrodires in which the supraorbital canal ends blindly, without meeting the lateral line or the supratemporal commissure, by assuming considerable distortion and reduction in the sensory canal system of *Deltoptychius*.

The lack of relief on the head shield of *D. moythomasi*, together with the compression of the presumed mandibular spines, suggests that the species may have been a more dorso-ventrally flattened fish than *D. armigerus*.

The affinities of Deltoptychius

Both *Deltoptychius* and '*Oracanthus armigerus*' were included in the Cochliodontidae until Moy-Thomas (1936*a*, p. 783) showed that there are similarities between *D. armigerus* and *Menaspis*. This led Berg (1940, p. 142) to include *Deltoptychius* in the family Menaspidae which he placed among the Chimaeriformes. The present study bears out the relationship between *Deltoptychius* and *Menaspis*, and the affinities of the two are discussed together on p. 172.

FAMILY MENASPIDAE *Smith Woodward* (1891*b*, p. 424)

Amended diagnosis: Menaspoidei in which the head shield is broken up into a number (unknown) of separate plates, supraorbital sensory canal running in the skin but surrounded by modified scales, three pairs of frontal spines of calcified fibro-cartilage present, only one pair of tooth plates in the upper jaw.

The only genus is:

Genus **Menaspis** Ewald (1848, p. 33)

Diagnosis: as family, only genus.

The type and only species is *M. armata* Ewald (1848, p. 33). *Menaspis* is known by six specimens, of which only two are moderately complete, from the Upper Permian Kupferschiefer of Germany. An excellent description of the most complete specimen is given by Jaekel (1891*b*) and the known specimens are reviewed by Weigelt (1930, p. 606, pl. 4; pl. 5, figs. 1 to 4; pl. 8, fig. 1). Most of the known features of the animal are clear from figure 36. The dorsal surface of the head is covered by a shield which projects posteriorly in a pair of spines (*p.sp.*). Jaekel referred to the shield as a complete armour, but described it as consisting of separate enlarged scales. The shield is ornamented with tubercles which are enlarged near the mid-line anteriorly and along a lateral ridge which is continuous with the lateral face of the posterior spine. The tubercles are arranged in longitudinal rows in the median part of the shield but are more irregular postero-laterally. From a point just medial to the base of the posterior spine of the shield a double line of small, closely set tubercles (*s.c.*) runs forwards to the anterior edge of the shield; Jaekel identified these tubercles as scales surrounding a sensory canal, and noticed a second canal (*so.*) on the right side of the specimen.

Articulating with the skull lateral to the narrow anterior part of the head shield there are three pairs of slender, sickle-shaped, smooth spines. The bases of these spines are expanded anteriorly. The second pair of spines is the largest, the third the smallest. The spines have a small pulp cavity, and were said by Jaekel to consist of vasodentine (= osteodentine).

Below the three pairs of spines there is a pair of shorter, broader spines, less strongly curved, ornamented with tubercles and with enlarged tubercles on the hind edge. These spines have a large pulp cavity, and as Moy-Thomas (1936*a*, p. 783) suggested, were almost certainly borne on the angle of the mandible.

The dentition of *Menaspis* consists of a single pair of tooth plates in each jaw. Jaekel compared the tooth plates with *Deltoptychius*.

Traces of the pectoral and pelvic fins are preserved. The pectoral lies close behind the head and has a broad anterior radial, probably formed by fusion, and nineteen slender radials. The pelvic fin has a single basal and about eleven radials.

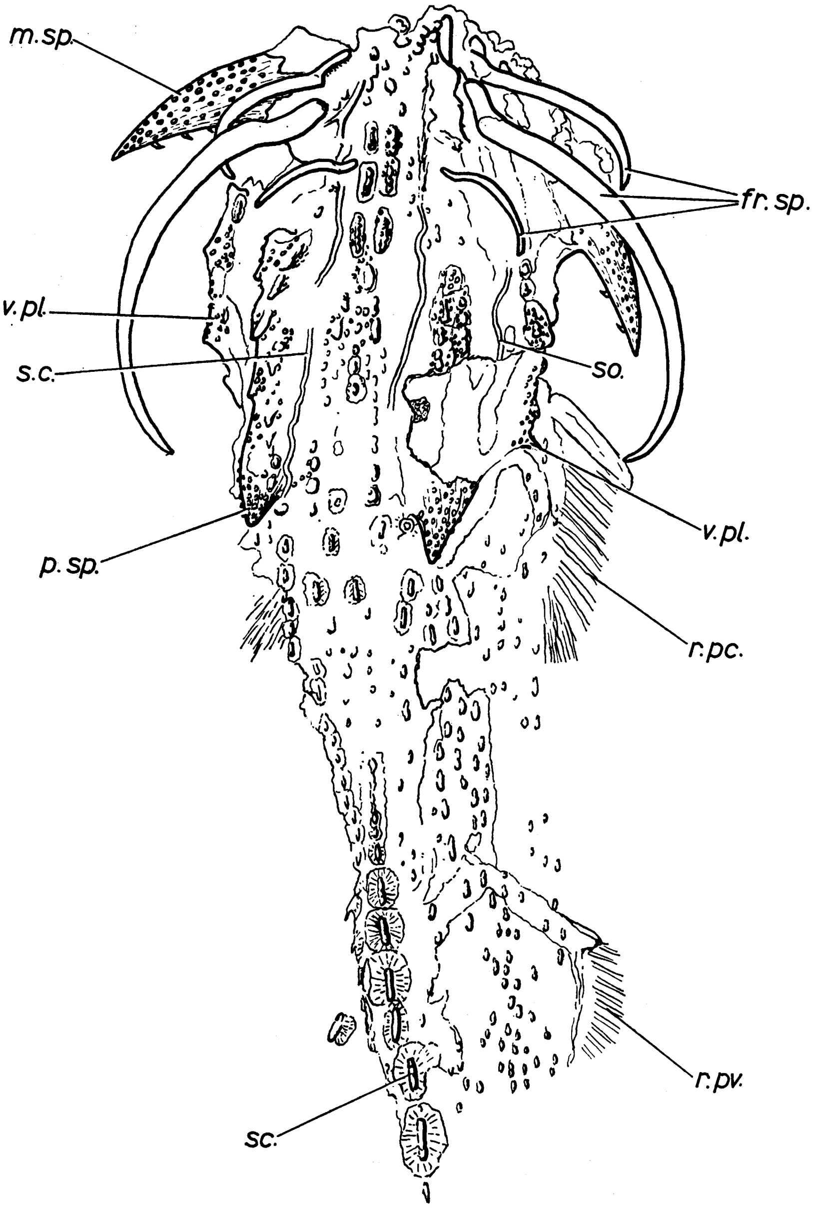

FIGURE 36. *Menaspis armata* Ewald. Incomplete fish in dorsal view, after Jaekel (1891 *b*) (× 1 approx.). *fr.sp.*, Frontal spines; *m.sp.*, mandibular spine; *p.sp.*, posterior spine of head shield; *r.pc.*, *r.pv.*, radials of pectoral and pelvic fins; *sc.*, enlarged scales on trunk; *s.c.*, course of supraorbital sensory canal; *so.*, course of infraorbital sensory canal; *v.pl.*, ventral dermal plate on neurocranium.

The trunk is covered by scales with simple, conical crowns (Weigelt 1930, pl. 4, fig. 4), of which one row along the back is much enlarged. Jaekel took this row of enlarged scales to be median, but examination of Jaekel's figure (figure 36) and of Weigelt's photograph of the specimen (1930, pl. 4, fig. 2) suggests that the row of enlarged scales is in fact a continuation of the paired row of enlarged tubercles, lying near the mid-line on the posterior part of the head shield, whose largest member lies on the posterior edge of the shield immediately medial to the sensory canal. There were thus two rows of enlarged scales along the back of the animal.

Comparison between Menaspis *and* Deltoptychius

Moy-Thomas (1936*a*, p. 784) found that *Menaspis* and *Deltoptychius armigerus* are very closely related. He based this conclusion on the presence of paired spines on the head, including one pair which lies on the angle of the mandible, on the presence of a series of enlarged scales along the back, and on the similarity of the tooth plates. Moy-Thomas's opinion is entirely confirmed by features of *Deltoptychius* described above. The resemblance between the head shields of *D. armigerus* (figure 30) and *Menaspis* (figure 36) is extraordinarily close: the outline of the shield, the posterior spines, the distribution of the ornament and the course and structure of the sensory canal, all leave no doubt of the relationship between the two. The major difference between the two head shields is that Jaekel considered the shield in *Menaspis* to be formed by separate enlarged scales, not by a completely fused plate as it is in *Deltoptychius*, and with the sensory canal running not on the surface of the shield, as it does in *Deltoptychius*, but between the groups of enlarged scales. Weigelt's (1930, pl. 4, fig. 2) photograph of the best specimen of *Menaspis* shows that the sensory canals follow a sinuous and irregular course, especially towards the front of the shield, and this confirms that the canals lay in the skin and that the scales enclosing them were not fused to the head shield as they are in *Deltoptychius*. From this it follows that the head shield, complete in *Deltoptychius*, is fragmented in *Menaspis* into a number of pieces. From published figures and descriptions of *Menaspis* it is impossible to discover the exact shape and number of the parts of the head shield, but the most important plates are obviously the posterior spines and the areas in front of them which in life would have covered the supraorbital ridge. Comparison between figures 30 and 36 suggests that the head shield of *Deltoptychius* is equivalent only to the middle part of the armour of *Menaspis*, not to the lateral parts (*v.pl.*). This lateral part of the armour in *Menaspis* is also shown in one other specimen, the holotype (Weigelt 1930, pl. 8, fig. 1; a cast in BMNH is numbered P 15346): this specimen is preserved ventral side uppermost and shows that the lateral parts of the armour consist of a single pair of elongated plates which are angulated near the posterior end and bear a spine projecting postero-laterally at the angle. From their position in figure 36 and their prominence in the specimen preserved ventral side uppermost, these lateral plates clearly lay ventral to the head shield. It seems certain that the plates are homologous with the pair of plates covering the ventro-lateral surface of the hind part of the neurocranium in *Deltoptychius* (*v.pl.*, figure 27), with which they agree both in shape and position. The second sensory canal described by Jaekel (*so.*) would thus lie on the side of the head, and is possibly the infraorbital canal. It is shown above that the row of enlarged scales along the back of *Menaspis* was paired, and this agrees with the two rows of '*Listracanthus*' spines on the back of *Deltoptychius*.

There are two main points in which *Menaspis* differs from *Deltoptychius*, the dentition and the three pairs of frontal spines. In *Deltoptychius* the upper jaw contains one pair of '*Streblodus*' tooth plates with two pairs of small '*Helodus*' teeth in front of them. In

Menaspis only a single pair of tooth plates is known in the upper jaw. Of the six specimens of *Menaspis* four show the dentition almost undisturbed: it seems unlikely that there can have been any small anterior upper teeth, although this is very surprising since in all other holocephalans in which the dentition is known there are at least two pairs of tooth plates in the upper jaw.

The three pairs of frontal spine in *Menaspis* appear to articulate with the area which in *Deltoptychius* is covered by the broad preorbital flange of the head shield. It must be assumed that in *Menaspis* this area of the head shield has been lost, since it is difficult to imagine how a spine, whether of dentine or fibro-cartilage, could develop outside and in articulation with an area covered by a sheet of dentine bearing dermal tubercles. The three pairs of spines are shown only in the two most complete specimens of *Menaspis*. Of the other four specimens only the one figured by Weigelt (1930, pl. 4, fig. 1) shows more than fragments of the head, and this specimen is very incomplete. Such as it is, the evidence indicates that the frontal spines were present in all individuals. In *Deltoptychius*, only RSM 1936.4 and 1883.23.20 are complete enough for one to expect any trace of similar spines had they been present: since neither specimen shows the spines one must assume that they were absent, and this is to be expected since the area on which the spines develop in *Menaspis* is still covered by the head shield in *Deltoptychius*. Jaekel described the frontal spines as consisting of vasodentine (= osteodentine). Reis (1895, p. 386) has proposed that it is more probable that the spines are of calcified fibro-cartilage, as are the frontal claspers of holocephalans, pointing out that Jaekel was not aware of the differences between the osteodentine of elasmobranch spines and the fibro-cartilage of holocephalan frontal claspers, and that the many vascular canals in the fibro-cartilage could well give the impression of osteodentine on a cursory examination. This question can be settled only by sectioning, but Reis's suggestion seems more likely to be true, for the lack of ornament, the form of the base of the spine, and the texture of the surface (seen in photographs and P 15346, a cast of the holotype) all suggest calcified fibro-cartilage rather than dentine.

In summary, the similarity of the armour in *Menaspis* and *Deltoptychius* leaves no doubt that the two genera are closely related. The main differences between the two are the absence of frontal spines in *Deltoptychius* and of small anterior tooth plates in the upper jaw of *Menaspis*, and the fragmentation and reduction of the head shield in *Menaspis*. A difference of less importance is in the form of the scales: in *Menaspis* the scales on the trunk have only a single cusp, while the enlarged scales on the back appear (Weigelt 1930, pl. 4, fig. 2) to have been similar in shape to the trunk scales of *Deltoptychius* but not elongated into '*Listracanthus*' spines. These differences, coupled with the great difference in age of the two forms, make a separate family necessary for *Deltoptychius*. The two families of Menaspoidei are defined on pp. 169 and 149.

The affinities of the Menaspoidei

Although both genera of Menaspoidei are poorly known, the group is of great interest because of the peculiar features shared by the two forms and the long period of time which separates them. Dean (1904) was the first to draw attention to the possibility of a relationship between *Menaspis* and the chimaeroids, noting the resemblance of the head spines to those of *Myriacanthus*, the resemblance of the sensory canals and dentition to those of the chimaeroids, and of the scales and paired fins to those of *Squaloraja*. Referring again to the list of chimaeroid character on p. 111, the menaspoids resemble the chimaeroids in: (1) the holostylic suspension; (5) the tubular dentine of the tooth plates; (8) the position of the pectoral fin in *Menaspis* shows that the branchial arches must have lain below the neurocranium; (15) although the basals are not known, the pectoral fin of *Menaspis* agrees with the chimaeroids in the structure of the radials; (23) the modified scales surrounding the sensory canals on the head of *Menaspis* are homologous with the crescentic calcifications in chimaeroids.

The structure of the menaspoids is unknown with regard to characters 2, 3, 7, 9, 10, 11, 12, 14, 16, 19, 22, 24 and 25 (ethmoid canal, interorbital septum, hyoid arch, spiracle, operculum, rostral and labial cartilages, synarcual (the evidence for a synarcual in *Deltoptychius* is poor), pelvic girdle, second dorsal fin, sensory canal pattern, pelvic claspers and tenacula).

The Menaspoidei differ from the chimaeroids in: (4) The number of tooth plates; *Deltoptychius* has three pairs of tooth plates in the upper jaw and in this agrees with *Myriacanthus* and *Metopacanthus*, but *Menaspis*, with only one pair of tooth plates in the upper jaw, disagrees with all known holocephalans. (6) The absence of tritors on the tooth plates: in this character the menaspoids agree with all Palaeozoic holocephalans. (13) The absence of calcifications in the notochord: this is typical of Palaeozoic elasmobranchs. (17) The absence of a dorsal fin spine. (20) In scale structure (well known only in *Deltoptychius*) the menaspoids differ from the chimaeroids, but they agree with *Myriacanthus* in the polycuspid scales, though in *Myriacanthus* the scales are placoid, as they are in all post-Palaeozoic elasmobranchs according to Stensiö and Ørvig. The simple scales of *Menaspis* agree in shape with those of *Metopacanthus* but the details of their structure are unknown. The two rows of enlarged scales along the back of menaspoids are a character which appears sporadically in the Mesozoic holocephalans (on the snout of *Metopacanthus*, on the back of *Squaloraja*), while in living chimaeroids the squamation of the trunk is reduced to two rows of scales along the back in Callorhynchidae and Rhinochimaeridae, and is completely lost in Chimaeridae. (21) The complete squamation: in this the menaspoids agree with the myriacanthoids. (26) The absence of a frontal clasper: the paired frontal spines of *Menaspis* are held by Reis (1895, p. 388) to be homologous with the frontal clasper of the chimaeroids and Mesozoic holocephalans; this possibility is discussed on p. 199 and is shown to be almost certainly true.

There are thus five characters in which the menaspoids agree with the chimaeroids (and also with the myriacanthoids and squalorajoids) and seven in which they differ from the chimaeroids. Of these seven characters, the menaspoids agree with the myriacanthoids in two (the number of tooth plates in the upper jaw and the complete squamation), three are typical of Palaeozoic holocephalans (the absence of tritors on the tooth plates and of calcifications in the notochord, and the cyclomorial scales), and one, the absence of a dorsal fin spine, occurs in several groups (squalorajoids, chondrenchelyids, petalodonts). Although menaspoids have no frontal clasper, the paired frontal spines of *Menaspis* are almost certainly homologous with the frontal clasper of chimaeroids and Mesozoic Chimaeriformes (see p. 199).

In addition to the characters discussed above, there is one feature in which there is a remarkable agreement between the menaspoids and the myriacanthoids, especially *Myriacanthus* and *Chimaeropsis*. This is the arrangement and structure of the dermal plates on the skull. The striking similarity between the mandibular spines of *Deltoptychius*, *Menaspis* and *Myriacanthus* has already been noted by Moy-Thomas (1936*a*, p. 785; figures 13, 28, 36). There is also a clear relationship between the complete head shield and the paired ventral plates on the neurocranium of *Deltoptychius*, the fragmented head shield and paired ventral plates of *Menaspis* and the three pairs of plates on the skull of *Myriacanthus* and *Chimaeropsis*: this sequence and the histological structure of the plates is discussed in detail on p. 201.

Although the menaspoids are still poorly known, we have enough information to make a fairly accurate estimate of their affinities. The known characters in which the menaspoids resemble the chimaeroids are typical of generalized holocephalans, only the specialized scales surrounding the sensory canals providing strong evidence of affinity with the more advanced forms. The menaspoids share one important character with the squalorajoids, the absence of a dorsal fin spine, but this is almost certainly due to convergence. With the myriacanthoids, as has been emphasized above, the menaspoids show much closer affinities, especially in the dermal plates on the head, the scale structure, and the dentition (as Moy-Thomas noted (1936*a*, p. 785), if *Myriacanthus* were known only by the dentition, it would probably have been placed in the Cochliodontidae, and the closest cochliodont genus is *Deltoptychius*). But the differences between *Deltoptychius* and *Menaspis* and the Myriacanthoidei, particularly the absence of a dorsal fin spine, of a symphysial tooth in the mandible, and of a median frontal clasper in the two Palaeozoic genera, justify a separate sub-order Menaspoidei, defined as on p. 148.

CHIMAERIFORMES incertae sedis: ?*sub-order Menaspoidei*

Menaspacanthus gen.nov.

Diagnosis: chimaeriform fishes known only by the proximal part of a paired frontal spine of calcified fibro-cartilage; spine dorso-ventrally compressed, base expanded, ventral surface with a muscle scar at the base and with weak tubercles representing the attachment of scales, dorsal surface smooth.

The type and only species is:

Menaspacanthus armaghensis sp.nov.

Figures 53, 54, plate 23; figure 37.

Diagnosis: as genus, only species; spine between 7 and 8 mm in breadth distal to the expanded base, base reaching 15 mm in breadth.

Holotype: BMNH P 45766, the proximal part of a frontal spine, P 45766.I, thin section of same specimen.

Material: the holotype only.

Horizon and locality: Middle Viséan, Lower Carboniferous Limestone (S 2–D 1), Armagh, Ireland.

Description

The holotype, shown in dorsal, ventral and lateral views in figure 54, plate 23, is the basal 22 mm of a spine. It has been cleared of matrix with acetic acid, and the middle part has been removed in the preparation of a thin section and restored in plaster. The distal two-thirds of the specimen is ellipsoid in section, 7 to 8 mm in breadth and 3·5 to 4 mm in maximum depth, with no appreciable tapering distally. The proximal one-third of the specimen is strongly expanded, reaching 14·5 mm in breadth, though the depth only just exceeds 4 mm. The two surfaces of the expanded base are differentiated by the presence of a broad, roughly triangular depression on one surface (figure 54*a*, plate 23). This depression is a muscle scar, and is ventral. The spine is not bilaterally symmetrical: the expansion of the base is confined mainly to one side, and is strongly asymmetrical. It is impossible with certainty to decide whether the spine is from the left or right side of the fish, but for the purposes of description it will be assumed to be from the right side, with the more strongly expanded side of the base anterior. There is a simple ellipsoid pulp cavity (figure 37*A*) which is open basally but is almost occluded at the distal end of the specimen. The dorsal edge of the base of the spine is straight, but the ventral edge is excavated a little, exposing the pulp cavity. The posterior edge of the shaft of the spine is rounded,

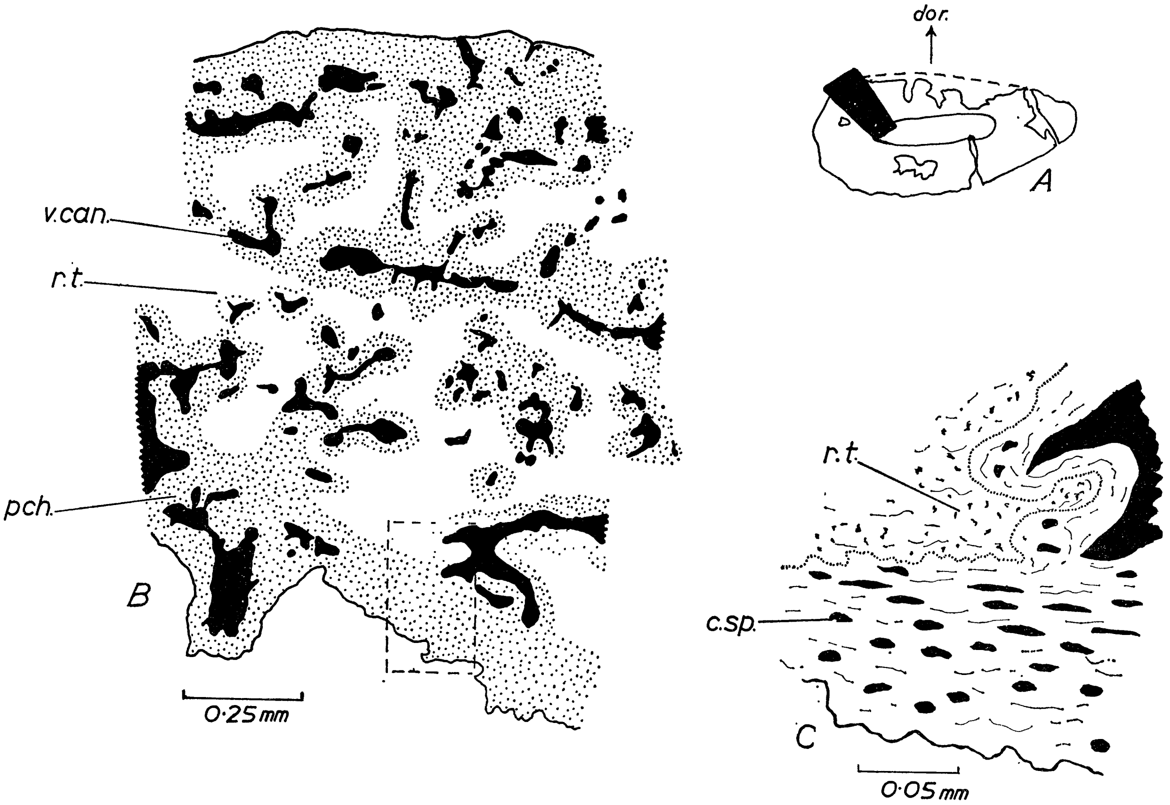

FIGURE 37. *Menaspacanthus armaghensis* gen. and sp.nov. Transverse section of frontal spine cut near the base. *A*, Outline of the complete section (*dor.*, dorsal); *B*, the area indicated in *A*; *C*, the area marked by a broken line in *B*. P 45766.I. *c.sp.*, Chondrocyte space; *pch.*, perichondrium; *r.t.*, tissue in which histological detail is not preserved; *v.can.*, vascular canal.

but the anterior edge is a blunt knife-edge. The spine has a marked curvature in the horizontal plane (figure 54*b*, plate 23), with the distal end curving ventrally. In the vertical plane there is no appreciable curvature, but a slight twisting, the posterior edge curving ventrally more sharply than the anterior. The dorsal surface of the spine is quite smooth except for irregularities in texture. The ventral surface, distal to the muscle scar at the base, bears low, smooth tubercles, apparently randomly distributed (figure 54*a*, plate 23). The muscle scar at the base is divided by a short ridge into a long, shallow anterior portion and a short, deep posterior portion.

The microstructure of the spine is shown in figure 37 and figure 53, plate 23. The spine does not consist of dentine or bone, as do all other known Palaeozoic ichthyodorulites, but of calcified fibro-cartilage. Irregularly distributed throughout the tissue are very numerous vascular canals (*v.can.*) which are smaller and more ramified than is normal in either bone or dentine. The perichondrium (*pch.*) lining the pulp cavity, the external surface of the spine and the vascular canals is still moderately well preserved, but in the remainder of the tissue there has been considerable replacement and deposition of haematite so that the structure is obscured. In the perichondrium (figure 37*C*) there are numerous cell spaces (*c.sp.*) varying in shape from spindles to irregular spheres. These cell spaces are apparently without processes of any kind, and agree in size and shape with normal chondrocytes.

The affinities of Menaspacanthus

The clue to the interpretation of *Menaspacanthus armaghensis* is given by the histological structure of the spine. As noted above, all other known Palaeozoic ichthyodorulites consist either of bone or dentine. The only known spines which consist of highly vascular calcified cartilage of the type seen in *Menaspacanthus* are the frontal claspers of the fossil and living Chimaeriformes (Ørvig 1951, p. 415 and references cited there, text-fig. 19; figures 51, 52, plate 23). In these frontal claspers the cell spaces in the body of the tissue are usually irregular in shape, with short processes, but in the perichondrium they are rounded or spindle-shaped just as in *Menaspacanthus*. *Menaspacanthus* agrees with these frontal claspers, especially with those of the Jurassic *Metopacanthus* and *Squaloraja*, not only in histological structure but also in the presence of a basal, triangular muscle scar which is divided by a ridge (Dean 1906, text-figs. 134A, 137A), and in the ornament of low, smooth tubercles, for exactly similar tubercles occur on the frontal claspers of these Jurassic forms, where they mark the attachment of the enlarged scales which armed the clasper. There can be little doubt that *Menaspacanthus armaghensis* is a structure homologous with the frontal clasper of Chimaeriformes. But it differs from the frontal clasper of these forms in being an asymmetrical, paired structure. The only member of the Chimaeriformes in which paired spines are known in the frontal region is the Permian *Menaspis* (figure 36). The histological structure of the frontal spines in *Menaspis* is not known, but there are good reasons (see p. 172) for thinking that they consist of calcified fibro-cartilage. The first two of the three pairs of spines in *Menaspis* resemble *Menaspacanthus* in that the expansion of the base is mainly confined to one side, the anterior, and it is by analogy with these spines that the holotype of *Menaspacanthus armaghensis* is orientated in the description above. It is not yet known whether the frontal spines of *Menaspis* had a muscle scar at the base or an armament of scales.

The holotype of *Menaspacanthus armaghensis* shows that as early as the Lower Carboniferous there were fishes which bore paired spines which are identical in microstructure with the median frontal claspers of myriacanthoids, squalorajoids and chimaeroids, and which were armed with scales in the same way. The muscle scar at the base of *M. armaghensis* shows that these spines were mobile. This information is of some importance in the problem of the origin of the frontal clasper, and is discussed further on p. 199.

With regard to the systematic position of *Menaspacanthus*, the only structures with which the genus is directly comparable are the frontal spines of the Permian *Menaspis*. This suggests that the genus should be placed in the sub-order Menaspoidei of the Chimaeriformes, but since the only well-known Carboniferous menaspoid, *Deltoptychius*, apparently had no frontal spines (see p. 172) one cannot be certain of this. It is quite possible that the spine named *Menaspacanthus* was borne on the head of one of the many Lower Carboniferous cochliodonts whose teeth resemble those of the menaspoids but whose anatomy is otherwise unknown. In the absence of information on their structure, these forms (*Cochliodus*, *Deltodus*, etc.) are here (p. 106) considered to be Chimaeriformes *incertae sedis*. *Menaspacanthus* should be placed in a similar position, though tentatively it can be referred to the Menaspoidei.

ORDER HELODONTIFORMES nov.

Diagnosis: Holocephali in which the teeth are numerous, with about ten series of teeth in each ramus of the jaws, each series containing several teeth, a few series in each jaw usually more or less completely fused into tooth plates, crowns of teeth flattened or weakly cuspidate, without tritors, no enlarged symphysial teeth, roots shallow and simple; no dermal plates on the head; no frontal clasper, no ethmoid canal; synarcual present, notochord uncalcified, first dorsal set rather far back, with a smooth, laterally compressed spine of osteodentine; paired fins as in Chimaeriformes but halves of pectoral girdle separate; no pelvic claspers or tenacula known; squamation complete, scales placoid (synchronomorial), no specialized scales surrounding the sensory canals.

This order is made to contain those holocephalans in which the teeth are flattened and simple, with little fusion into tooth plates and without the deep roots and acuminate crowns which occur in the petalodonts or the enlarged symphysial teeth which occur in edestids. *Helodus simplex* is the only species known by complete skeletons, but *Psephodus magnus*, known by an almost complete dentition (Traquair 1884), is another form of the same type, and many of the isolated teeth or tooth plates under the names *Helodus*, *Psephodus*, *Pleurodus*, *Lophodus*, etc., also belong to the group. All these forms can be placed in a single family Helodontidae.

FAMILY HELODONTIDAE nov.

Diagnosis: as Helodontiformes, only family.

Type genus: *Helodus* Agassiz (1838, p. 104).

As noted above, the Upper Carboniferous *Helodus simplex* Agassiz is the only helodont known by the complete skeleton. *Helodus simplex* has been described by Moy-Thomas (1936*b*) on the basis of material from the Knowles Ironstone (upper part of Middle Coal

Measures) at Fenton, Staffordshire. *H. simplex* (figure 38) was a moderately elongated fish with a broad, dorso-ventrally flattened head and a tapering trunk. It is the only Palaeozoic holocephalan in which the skull is well known. The skull (figure 39) is broad, flat, and similar in its main features to those of chimaeroids. The suspension is holostylic. There is no ethmoid canal, but the preorbital part of the skull roof bears a pair of parallel, vertical laminae. Moy-Thomas interpreted these laminae as upgrowths of the lamina orbitonasalis, and since they enclose the efferent foramina of the superficial ophthalmic nerves between them he thought that they represent a stage in the development of an ethmoid canal. This interpretation is discussed on p. 187, and is found to be unlikely, but the function of these laminae remains unknown.

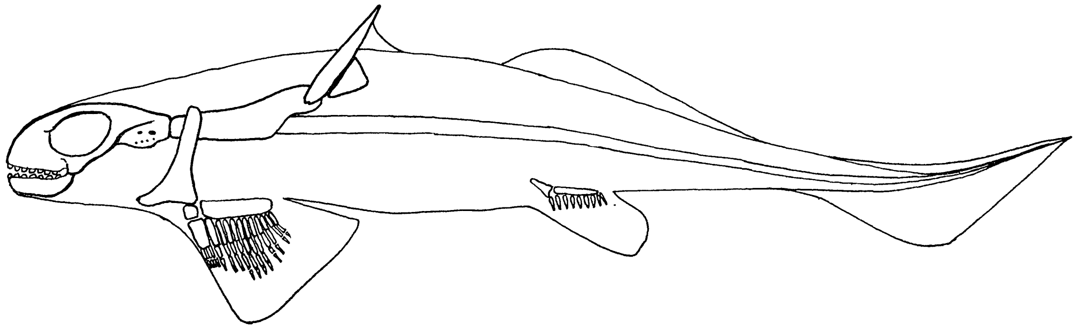

FIGURE 38. *Helodus simplex* Agassiz. Restoration of fish in lateral view (× $\frac{1}{3}$ approx.). Modified from Moy-Thomas (1936*b*).

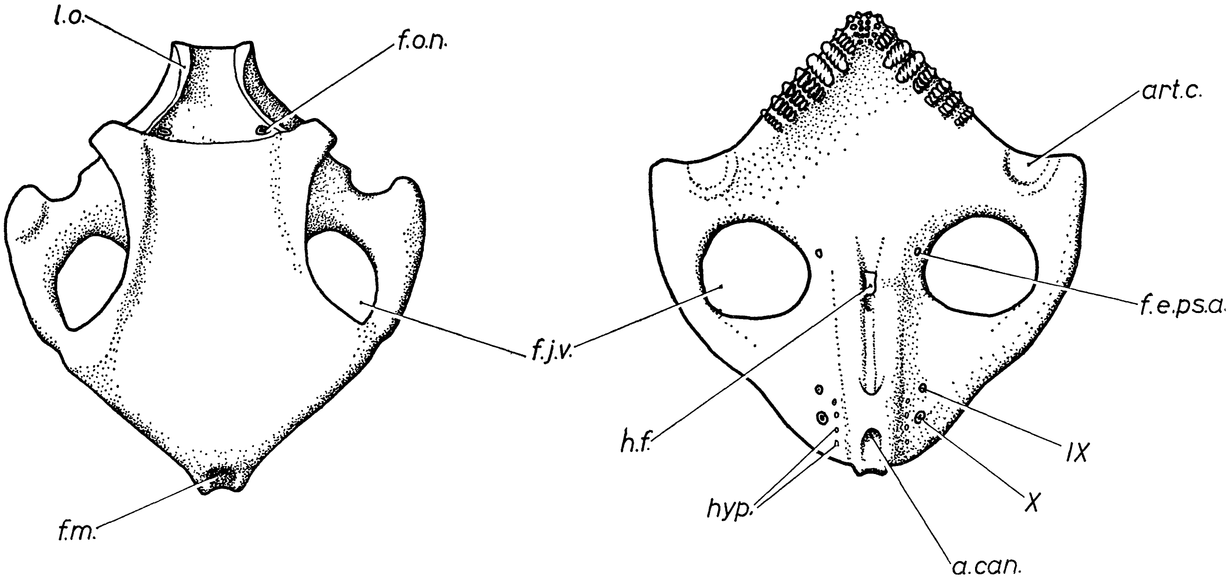

FIGURE 39. *Helodus simplex* Agassiz. Restoration of the neurocranium in dorsal (left) and ventral view (× 1 approx.). Redrawn from Moy-Thomas (1936*b*). *a.can.*, Aortal canal; *art.c.*, articular facet for mandible; *f.e.ps.a.*, foramen of efferent pseudobranchial artery; *f.j.v.*, foramen transmitting the jugular vein, orbital artery and hyomandibular and palatine nerves; *f.o.n.*, efferent foramen of superficial ophthalmic nerves; *f.m.*, foramen magnum; *h.f.*, hypophysial fenestra; *hyp.*, foramina of hypoglossal nerves; *l.o.*, lamina orbitonasalis; IX, X, foramina of glossopharyngeal and vagus nerves.

In *H. simplex* Moy-Thomas described an interorbital septum containing a large fenestra though which the orbits were in contact, but I can find no trace of this in the material, and P 8212, the best preserved neurocranium, seems to show a rather wide cranial cavity between the eyes. There are no dermal plates or spines on the skull. The dentition consists of eight or nine series of teeth in each ramus of the jaws, each series containing about five successional teeth. In most of the series the crowns of the teeth are simple ovoids ('*Helodus*'), but about the middle of each ramus of the jaws, where the teeth are largest, one or two series of teeth are more or less completely fused into a tooth plate ('*Pleurodus*') which is divided by constrictions into cusps corresponding with the separate teeth of the neighbouring series. At the symphysis of the lower jaw a bicuspid tooth ('*Diclitodus*') is sometimes present, evidently equivalent to members of the most medial paired series of teeth. The crowns of the teeth consist of typical tubular dentine and are without tritors.

No trace of rostral or labial cartilages is visible in any specimen. Several specimens show the snout well, and there was certainly no rostrum of any size. The detailed structure of the branchial arches is not known, but the branchial skeleton lay below the neurocranium as it does in chimaeroids.

In P 8212 and P 6707 there is an elongated mass of calcified cartilage behind the skull, between the scapular processes of the pectoral girdle, which is almost certainly a synarcual (figure 38). There is a series of neural arches of calcified cartilage but no other trace of the vertebral column, and the notochord must have been uncalcified. The two halves of the pectoral girdle are separate. The pectoral fin is dibasal, with four partially fused radials articulating with the small propterygium and about 13 radials articulating with the metapterygium. Each radial is segmented three or four times. The halves of the pelvic girdle are also separate, and the pelvic fin has a single basipterygium and about 10 radials. In neither of the two specimens which show the pelvic fins (P 8209, P 8212) is there any trace of pelvic claspers. The first dorsal fin lies behind the level of the pectoral fins, further back than it does in chimaeroids and myriacanthoids, and the synarcual is much extended. The first dorsal contains a short, strongly compressed and unornamented spine and a single triangular basal cartilage. The spine (figure 40; figure 48, plate 22) consists entirely of osteodentine, with no inner lamellar layer or outer layer of pallial dentine. There are no osteocyte spaces. The vascular canals (*v.can.*) are more extensive towards the pulp cavity, and the interosteonal tissue (*ist.*) is more extensive towards the surface. The surface of the spine is quite smooth, and has a layer of dentine in which the dentine tubules pass inwards from the surface, as in chimaeroids (figure 4).

A long, low second dorsal fin was present but its skeleton is unknown. The tail was heterocercal.

Moy-Thomas described the scales as being simple, with a broad root and a radially grooved, conical crown, but although scales of this type appear to be present on the web of the fins, the scales on the head and trunk are more variable. The great majority of the more complete specimens of *H. simplex* are preserved in ironstone, and no satisfactory method of preparing the scales in these specimens has yet been found. But a few specimens occur in the shale above the Knowles Ironstone, and a collection of well-preserved scales has been obtained from one of these, a fragment of P 8215 taken from just behind the dorsal fin spine, by treatment with 20% hydrofluoric acid and ultrasonic cleaning. The squamation of P 8215 is disturbed and the sample probably contains scales from more than one part of the body. Examples of scales of various types are shown in figure 41. The majority of the scales can be assigned to one of two main types, the first type shown in figure 41 *A* to *E*, the second in figure 41 *F* to *H*, the first being roughly one-and-a-half times as abundant as the second. Scales of the first type again fall into two categories, those of the type shown in figure 41 *A* to *C* and those in figure 41 *D*, *E*. In the first of these the scales have a broad crown which is subdivided by vertical grooves into a number of lobes. The number of lobes varies from 4 to 7, but is usually 5. These lobes are arranged without any obvious bilateral symmetry, but the highest point of the crown normally lies near one margin, and in larger scales, where the surface of the crown is worn, the wear surface is oblique, not horizontal (figure 41 *B*): the highest point of the crown in unworn scales and the highest point of the wear surface in worn scales is probably posterior. In unworn scales the surface of the crown is perfectly smooth. At the junction of crown and root lie the foramina of a number of neck canals. The roots of these scales are expanded and more or less subdivided by radial grooves. The basal surface of the root is flat or slightly convex,

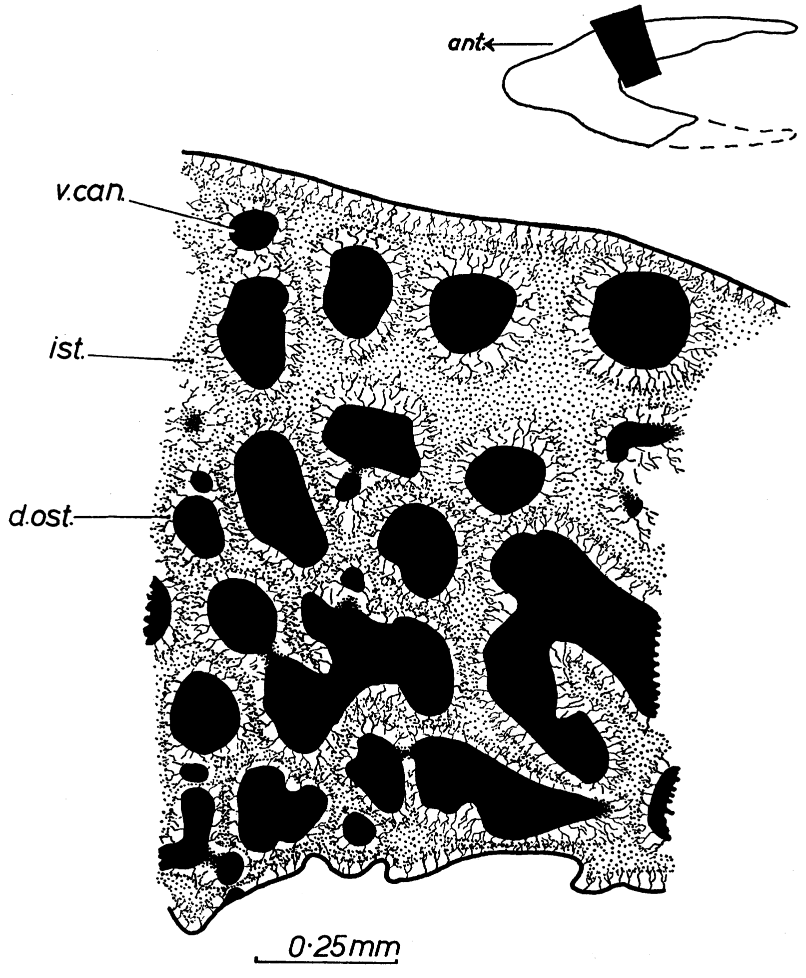

FIGURE 40. *Helodus simplex* Agassiz. Transverse section of the dorsal fin spine cut near the base of the exserted portion. P 2908.I. Inset at top right is an outline of the complete section showing the orientation of the figured region (*ant.*, anterior). *d.ost.*, Dentinal osteon; *ist.*, interosteonal tissue; *v.can.*, vascular canal.

and is perforated near the centre by the foramina of a number of basal canals. No satisfactory sections of these scales have yet been cut, but the internal structure can be seen in a large number of broken scales. In the smaller scales of this type the crown is thin-walled, and has a single, large pulp cavity. In larger scales this pulp cavity is occluded and subdivided by trabeculae and fenestrated sheets of dentine laid down within it. The basal plate of the root is not proportionately thicker in large scales than in small scales except in so far as dentine trabeculae are apposed on its distal face, in the pulp cavity.

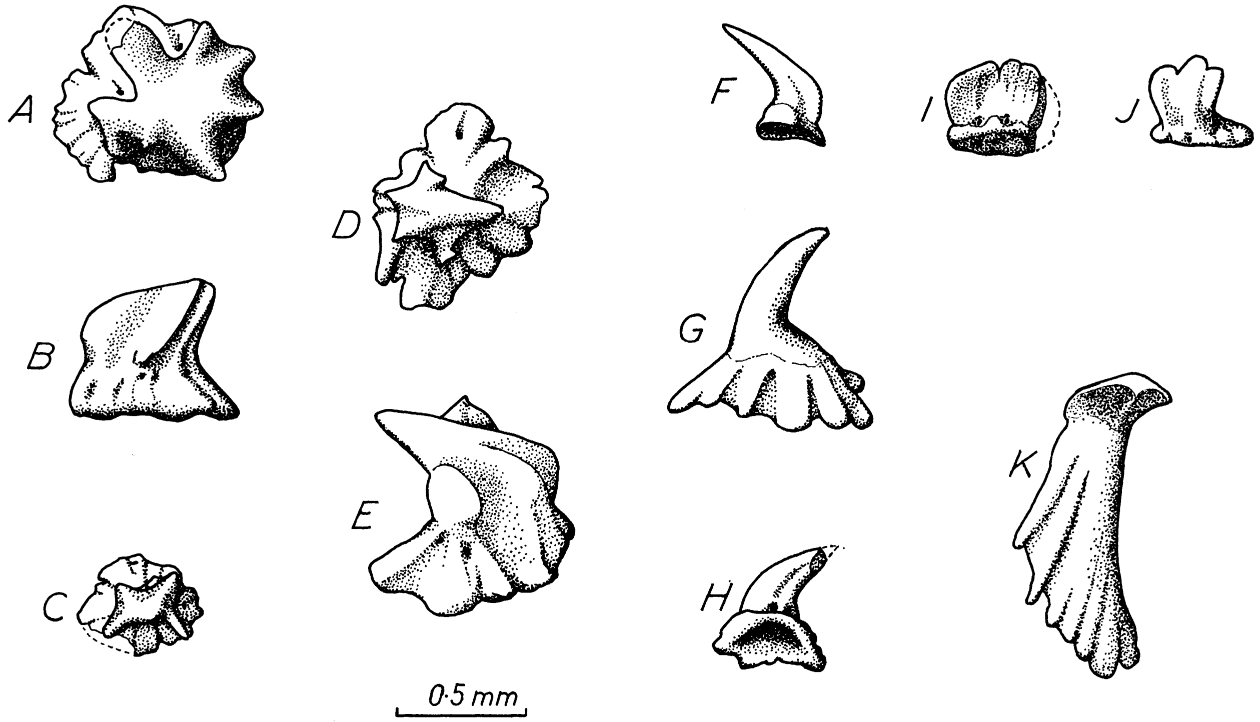

FIGURE 41. *Helodus simplex* Agassiz. Scales from the trunk. P 8215.I–XI. *A*, *C*, *D*, In coronal view; *B*, *F*, *G*, *I*, *J*, *K*, in lateral view; *E*, *H*, in oblique lateral view, *E* from above, *H* from below. See text for explanation.

Scales of the type shown in figure 41*D*, *E* seem to agree exactly with those in figure 41*A* to *C* described above, except that in these the crown is bilaterally symmetrical, with a main cusp directed postero-dorsally, the anterior face of the base of this cusp being normally divided by a vertical groove, and with a pair of smaller lateral cusps. There are also scales which are intermediate in shape between those with asymmetrical, flattened crowns (*A* to *C*) and those with symmetrical, tricuspid crowns (*D*, *E*).

Examples of the second common type of scale are shown in figure 41*F* to *H*. In these scales the crown is a simple, curved cone, sometimes quite smooth (*G*), sometimes with weak grooves (*F*, *H*) which relate these scales to the tricuspid type (*D*, *E*). These monocuspid scales exhibit neck canal foramina (*n.c.*) at the junction of root and crown, and have essentially the same expanded, radially subdivided root as the first type of scale, but in some examples (*H*) the pulp cavity remains open basally, even in large scales, and the pulp cavity in the crown normally remains open, and is not subdivided and occluded as it is in the first type of scale. The simple structure of these monocuspid scales is also shown by sections (figure 70, plate 28).

Interpretation of these scales in the light of Stensiö & Ørvig's lepidomorial theory (Stensiö 1961) shows that both types of scale are synchronomorial (placoid), not cyclomorial (zonally growing). This is clearly so in the case of the monocuspid scales (*F* to *H*), which are apparently identical in structure with the scales of such Mesozoic holocephalans as *Metopacanthus* and *Squaloraja*. The polycuspid scales (*A* to *E*) are shown to be synchronomorial by the simple undivided pulp cavity of the smaller scales and by the thin, flat, basal plate of the root. In shape they agree well with the synchronomorial scales of Permian edestids which Stensiö has figured (1961, fig. 2, K to N).

Two other less common types of scale in *H. simplex* should be mentioned. Figures 41 *I*, *J* show two scales in which the root is broad and compressed and the crown is thin, leaf-like and arched, with traces of two or three poorly marked cusps. Scales of this type are rare, forming 5 % or less of the sample. In shape they are reminiscent of the tubercles which enclose the grooves for the sensory canals on the head shield of *Deltoptychius* (figures 30, 34; figures 64 to 66, plate 27). It is possible that in *Helodus* these scales may have lain along the sensory canals in the same way, although there is no sign in any of the complete specimens of *Helodus* of alignment of scales along the possible course of sensory canals.

The fourth type of scale (figure 41 *K*) has a simple, smooth, leaf-like crown which must have lain almost horizontally, and a very stout, long root. Scales of this type are about as common as those (*I*, *J*) described above. Their function and position on the body are unknown.

The scales are particularly large on the underside of the trunk between the pectoral and pelvic fins, but they are not concentrated into pre-pelvic tenacula. There is no frontal clasper.

The affinities of Helodus

Moy-Thomas (1936*b*) placed *Helodus* among the Cochliodontidae, later (1939) raising this family to sub-ordinal rank, but not differentiating *Helodus* from any other form within the group. *Helodus* has been retained among the cochliodonts by later authors (see p. 105), the group being treated variously as a family, a sub-order and an order.

Referring again to the list of chimaeroid characters on p. 111, *Helodus simplex* agrees with the chimaeroids in: (1) the holostylic suspension; (5) the tubular dentine of the teeth; (8) the position of the branchial arches; (14) the presence of a synarcual; (15) the structure of the pectoral fin; (16) the separation of the halves of the pelvic girdle; (17) the structure of the first dorsal fin (although the fin lies farther back than it does in chimaeroids and the histological structure of the spine is quite different); (20) the placoid (synchronomorial) scales.

The structure of *Helodus* is unknown with regard to characters 7, 9, 10, 11, 12, 19 and 22 (hyoid arch, spiracle, operculum, rostral and labial cartilages, second dorsal fin and sensory canal pattern).

Helodus differs from the chimaeroids in: (2) the absence of an ethmoid canal; (3) the absence of an interorbital septum above the brain; (4) the numerous teeth; (6) the absence of tritors on the teeth; (13) the absence of notochordal calcifications; (18) the structure of the fin spine; (21) the complete squamation; (23) the absence of modified crescentic scales surrounding the sensory canals; (24), (25) and (26) the absence of pelvic claspers, tenacula and a frontal clasper.

Helodus also differs from the chimaeroids in its dorso-ventrally flattened shape and in the separation of the halves of the pectoral girdle.

Comparison of *Helodus* with the other sub-orders of the Chimaeriformes shows that most of the characters in which it differs from the Chimaeroidei are primitive. With the Squalorajoidei it shares the absence of an ethmoid canal and the dorso-ventrally flattened form, with the Myriacanthoidei it also shares the complete squamation, and with the Menaspoidei it shares the absence of tritors and notochordal calcifications. *Helodus* differs from both the myriacanthoids and menaspoids in having no dermal plates or spines on the head.

In spite of its resemblances to the chimaeroids and the other sub-orders of the Chimaeriformes, *Helodus* presents something of a puzzle. Passing back from the chimaeroids through the myriacanthoids in the Jurassic and the menaspoids in the Permian and Carboniferous a clear line can be traced in which a more and more complete armour is present on the head, tritors disappear from the tooth plates, the number of tooth plates increases slightly and becomes more variable, the dorsal fin spine becomes more complex in structure and then disappears, and the scales become cyclomorial. The evidence for this sequence presented earlier in this paper is so strong that I do not think it can be doubted. *Helodus* does not fit into this sequence because of its selachian type of dentition, with several series of teeth and several teeth in each series, because it has no armour on the head, and because it has a fin spine of peculiar type. There are two main alternatives which can be offered to explain this:

(1) *Helodus* is more primitive than the menaspoids. Then in menaspoids the armour on the head and the absence of a dorsal fin spine are advanced features, and the loss of armour and the appearance of a fin spine in the myriacanthoids and chimaeroids are secondary. An alternative to this is that the myriacanthoids are not directly descended from the menaspoids but from a stock with many similar features but with a fin spine.

(2) *Deltoptychius* is more primitive than *Helodus*. Then the numerous teeth and the fin spine of *Helodus* are advanced features, and the spine has developed in parallel with the spine in myriacanthoids and chimaeroids.

The decision as to which of these two statements lies nearer the truth is of the greatest importance, for if *Helodus* is the more primitive form the ancestry of the holocephalans is to be sought among unarmoured forms with a selachian type of dentition, and we must look in the direction of the earliest sharks, but if *Deltoptychius* is the more primitive form we must look for the origin of the holocephalans among armoured forms with a chimaeroid type of dentition such as the arthrodires. There are three questions to be answered in choosing between the two alternatives: what type of dentition was present in the earliest holocephalans; is the armour of menaspoids a primitive feature; and how do fin spines arise? These questions are discussed in the comparative part of this paper on pp. 189, 197 and 201.

One further point may be taken up here, the structure of the scales. It is shown above that all the scales of *Helodus simplex* are synchronomorial (placoid), whereas in *Deltoptychius* all the scales are cyclomorial. In this, at least, *Deltoptychius* is clearly more primitive than *Helodus*. Stensiö (1961, p. 237) has not yet discovered placoid scales in any form earlier than the Permian, and in the Permian edestids which he and Ørvig have studied the scales are about 50% placoid and 50% cyclomorial. According to Stensiö all Carboniferous elasmobranchs have cyclomorial scales only. That *Helodus*, in the Upper Carboniferous, should have only placoid scales is very surprising, and must be taken to be a very advanced feature, for squamation of this type is not yet known in any other Palaeozoic elasmobranch.

To return to the matter of the systematic position of *Helodus*, although *Helodus* shares a number of characters with the Chimaeriformes, it does not, particularly in its dentition, form part of the main evolutionary trend within that order, and there seems to be no good reason for including it in the Chimaeriformes. The dentition of *Helodus* shows strong similarities with two other holocephalan groups, the Petalodontiformes and Edestiformes, in both of which the teeth are arranged in the same way as they are in *Helodus*. For these reasons I believe that *Helodus* should be made the type genus of a new order Helodontiformes, defined as on p. 177.

ORDER CHONDRENCHELYIFORMES

Amended diagnosis: Holocephali in which the upper jaw contains four pairs of tooth plates, the two posterior pairs elongated and lying side by side, the two anterior pairs small and lying in longitudinal series; the lower jaw contains three pairs of tooth plates, a small anterior pair and two elongated posterior pairs lying side by side; no dermal plates or spines on the skull; no frontal clasper; no synarcual, a single ring-like notochordal calcification in each segment; the halves of the pectoral girdle separate; pectoral fin with a segmented axis and pre- and post-axial radials; pelvic fin with a long segmented axis; dorsal fin continuous along the back with several radials to each segment, no dorsal fin spine; pelvic claspers present; no tenacula; scales simple, monocuspid, no specialized scales around the sensory canals.

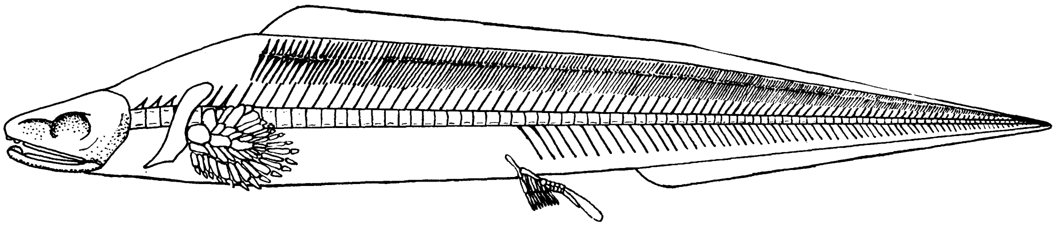

FIGURE 42. *Chondrenchelys problematica* Traquair. Restoration of fish in lateral view (× ⅝ approx.). After Moy-Thomas (1935*b*).

This order contains two species, *Chondrenchelys problematica* Traquair and *Eucentrurus paradoxus* Traquair, both from the Lower Carboniferous Calciferous Sandstone series of Scotland. Both species have been redescribed by Moy-Thomas, *C. problematica* in 1935*b* and *E. paradoxus* (known only by the holotype) in 1937. Moy-Thomas (1937, p. 184) considered it probable that *Eucentrurus* is related to *Chondrenchelys*, but that it represented a separate family; the order thus contains two families, the Chondrenchelyidae and Eucentruridae. So little is known of *Eucentrurus* that nothing is to be gained from discussing it; the ordinal diagnosis above must be considered provisional since we do not know if many of the points mentioned apply to *Eucentrurus*. *Chondrenchelys* is much more completely known thanks to Moy-Thomas's excellent account. *C. problematica* (figure 42) was a small elongated fish with a flattened head (since it is always crushed dorso-ventrally). There are no dermal plates or spines on the head. The suspension is almost certainly holostylic, and the teeth consist of tubular dentine (Moy-Thomas 1936*a*, p. 779). The arrangement of the tooth plates as described by Moy-Thomas is given in the ordinal diagnosis above. In the small anterior tooth plates, of which there are two pairs in the upper jaw and one in the lower, Moy-Thomas (1935*b*, p. 393) describes 'seven or eight small, rounded, grinding surfaces along one edge'. On one of the large tooth plates of the lower jaw he describes 'small tubercles and ridges running in lines' over the oral surface, and on the surface of one of the large upper tooth plates 'transverse rows of tiny tubercles'. These grinding surfaces, ridges and tubercles suggest that tritors were present, but examination of Moy-Thomas's specimens in the BMNH, particularly P 18055 and P 18057, shows that the tubercles are the tips of the dentinal osteons of the tubular dentine, and that the osteons are rather sparse and are arranged in rows across the surface of the plates, as they are in many ptyctodonts (Ørvig 1960, p. 311).

The axial skeleton of *Chondrenchelys* is well known. There is no synarcual (P 18055) but about one hundred ring-like 'centra', each with a neural arch, and in the caudal region a haemal arch, of calcified cartilage. The 'centra' show 'a fibrous structure in section, but no bone-cells'. Since these structures are complete rings, it seems likely that they are not true centra but calcifications in the sheath of the notochord like those in *Squaloraja* and the chimaeroids, with which they appear to agree in structure, but are segmental rather than being more numerous than the segments as they are in the chimaeroids.

The halves of the pectoral girdle are separate, and the fin is archipterygial, with both pre- and post-axial radials. The halves of the pelvic girdle are also separate, and the pelvic fin has a segmented axis but only pre-axial radials. Long pelvic claspers are present in all the three specimens in which the pelvic fin is preserved.

There is a continuous dorsal fin extending from a point just behind the level of the insertion of the pectoral fin to the tip of the tail. The fin is supported by a double series of radials, with three or four radials to each segment of the trunk. There is no dorsal fin spine.

The squamation of *Chondrenchelys* is very incomplete. There are a few small, conical scales scattered over the anterior part of the trunk and on the pre-axial border of the pectoral fin. There are no tenacula and no frontal clasper.

The affinities of Chondrenchelys

Moy-Thomas first held (1935*b*, p. 402) that *Chondrenchelys* was a representative of a 'very primitive group of sharks, possibly descended from the common ancestor of both the Holocephali and the Pleuracanths'. Later (1936*a*, p. 780), after examining the microstructure of the tooth plates, he thought 'that it is a Bradyodont which has in many ways come to resemble the Pleuracanths', and in 1939 (p. 15) he made *Chondrenchelys* the type of an order Chondrenchelyidi equal in rank to the Eubradyodonti, in which all the other holocephalan groups were placed. Berg (1940, p. 139; 1955, p. 74) and Obruchev (1953, p. 57) follow Moy-Thomas in making the chondrenchelyids equal in rank to all the other holocephalans combined, Berg as a sub-class and Obruchev as a super-order. Arambourg & Bertin (1958, p. 2057) make the chondrenchelyids a family equal in rank to each of the other Palaeozoic groups of holocephalans, in a super-order in opposition to a super-order

Holocephali containing the post-Palaeozoic forms. I believe that a course between these two is more satisfactory: since nothing is known of the anatomy of the psammodonts and the copodonts, and since the petalodonts are known by little more than the dentition, it is quite possible that the peculiar structure of the fins and vertebral column in *Chondrenchelys* will be repeated in one or more of these groups. Among the edestids Bendix-Almgreen (1962) has given a preliminary description of the fins in the Permian *Fadenia* which suggests that in this form the fins resemble those of *Cladoselache*, and diverge from the typical chimaeriform type as much as those of *Chondrenchelys*. At present, therefore, there is no good reason for placing the chondrenchelyids in opposition to all the other holocephalans. I would suggest that the chondrenchelyids should be made an order Chondrenchelyiformes, defined as on p. 184, equal in rank to each of the other major groups of holocephalans.

Holocephalan characters of *Chondrenchelys* are the holostylic suspension, the tubular dentine of the tooth plates, and perhaps the segmental notochordal calcifications. *Chondrenchelys* differs from all known holocephalans in the structure of the paired and median fins. The pelvic claspers are shared with the Chimaeriformes, the selachians, and some arthrodires (see p. 198).

V. COMPARATIVE ANATOMY

In this section the history and origin of various characters of Chimaeriformes will be discussed in the light of the information obtained in the systematic part.

(*a*) *The holostylic suspension and the complete hyoid arch*

These two features are linked functionally and may be discussed together. The holostylic suspension is present in the Upper Carboniferous *Helodus simplex* apparently in exactly the same form as in living chimaeroids; it is obviously a very ancient feature of holocephalans. How the condition appears in ontogeny is not yet known since the palatoquadrate is completely fused to the neurocranium in the youngest embryo yet studied (Schauinsland 1903, pl. 18). De Beer (1937, p. 76) and Holmgren (1942, p. 188) disagree over whether the floor of the orbit in the adult chimaeroid is formed by the otic process of the palatoquadrate or by the subocular shelf of the neurocranium. Both de Beer's and Holmgren's hypotheses are based on the same embryological material, interpreted by comparison with selachians. Of the two interpretations Holmgren's is more recent and is based on a more detailed comparison with selachians: this suggests that the earliest holocephalans would have had a short, deep palatoquadrate of arthrodiran type. The fossil holocephalans neither confirm nor deny this.

The function of the holostylic suspension is clearly to give added support to a crushing dentition, but Moy-Thomas (1936*b*, p. 500) suggested that the origin of the fusion need not have been adaptive since it was fully developed in *Helodus* where the dentition is not highly adapted for crushing. It is suggested here (p. 192) that the shark-like dentition of *Helodus* may be derived from a more chimaeroid-like set of tooth plates, and if this is so the origin of the holostyly would certainly be adaptive.

The only fossil holocephalan in which the hyoid arch is known is the Permian edestid *Fadenia*, where Bendix-Almgreen (1962) has given a brief preliminary description of new material in which an unspecialized hyoid is preserved. If the hyoid arch is complete and unmodified in living chimaeroids (note Watson's objection to this, footnote on p. 103) it is probable that it must have been so throughout the history of the group. If the holocephalans arose from arthrodires then the ancestral arthrodires must have had the palatoquadrate suspended simply by articulation with the neurocranium (autodiastylic, de Beer & Moy-Thomas 1935, p. 307). A suspension of this type is figured in the ptyctodonts *Ctenurella* (Ørvig 1962, text-fig. 2*B*) and *Rhynchodus* (Stensiö 1963, text-fig. 124). Stensiö (1963, p. 377) has recently amplified his earlier statement (1950, p. 38) that the arthrodires were originally hyostylic. He finds that the rhenanids *Gemuendina* and *Jagorina* had a hyostylic suspension with a long, powerful hyomandibular. Gross (1962, p. 56) has also described a suspensory hyomandibular in *Stensioella*, which he now (1963, p. 68) tentatively associates with the rhenanids, and he confirms the presence of a hyomandibular in *Gemuendina* (1963, p. 54). Stensiö interprets the non-suspensory hyomandibular of ptyctodonts as a modification of the rhenanid condition, but it is difficult to see how this interpretation can account for the pharyngohyal which Stensiö (1963, p. 129) admits to be present in chimaeroids.

(*b*) *The ethmoid canal*

The ethmoid canal has been discussed at some length in the description of *Squaloraja* (p. 119). The absence of an ethmoid canal in *Squaloraja* suggests that the canal is a structure which arose late in the history of the holocephalans and is confined to the Chimaeroidei. The possibility that *Squaloraja* is a specialized form in which the ethmoid canal has been lost cannot be ignored, but there is no evidence to support this, and the very massive frontal clasper tends to oppose it for reasons given below. This question can only be settled when well-preserved myriacanthoids are discovered: if there should be an ethmoid canal in this group then its absence in *Squaloraja* would probably be a specialization. The form of the ethmoid canal in the laterally compressed chimaeroids and the absence of the structure in the dorso-ventrally flattened *Squaloraja* suggest (p. 127) that the canal arose as a consequence of the formation of the interorbital septum, by the compression of an originally broad-headed form. The appearance of the ethmoid canal late in holocephalan history leads to certain difficulties in connexion with the frontal clasper. In chimaeroids the frontal clasper articulates with the roof of the ethmoid canal, but in *Squaloraja* it articulates with the roof of the skull between and in front of the efferent foramina of the superficial ophthalmic nerves, this area being apparently homologous with the floor of the ethmoid canal in chimaeroids. If the development of the ethmoid canal entailed the shifting of the insertion of the frontal clasper on to the roof of the canal, it is particularly difficult to see how the canal could have arisen in the way suggested by Moy-Thomas (1936*b*, p. 501), with a stage in which only the lateral walls of the canal were present, as in *Helodus*, for in this stage the frontal clasper would either have had to be sunk between these walls or would have had no firm base of attachment. This tends to support Holmgren's (1942, p. 196) hypothesis of the origin of the ethmoid canal as a part of the cranial cavity secondarily segmented off in connexion with the formation of the interorbital septum, since in this case shifting of the insertion of the clasper would not be necessary. In whatever way the canal arose, it is unlikely that it should have appeared while the frontal clasper was as massive as it is in *Squaloraja* and the myriacanthoids. The very small frontal clasper of living chimaeroids appears late in ontogeny, long after the completion of the ethmoid canal. The reduction in size of the clasper in chimaeroids is perhaps due to postponement of the development of the structure, this postponement having appeared in order to accommodate the changes below the insertion of the clasper which the ethmoid canal entails.

(*c*) *The interorbital septum*

There is no evidence in any fossil holocephalan of an interorbital septum of the type seen in living chimaeroids. As suggested above (p. 127), I believe the interorbital septum to be a recent acquisition in the group, like the ethmoid canal, both structures having developed as a result of lateral compression of a broad-headed form.

(*d*) *The dentition*

There are three characters in which the dentition of the chimaeroids is peculiar, the tubular dentine of which the tritors are composed, the tritoral areas, and the number of tooth plates, two pairs in the upper jaw and one in the lower.

Tubular dentine (discussed on p. 107) is present in the teeth of all holocephalans and also in the dipnoans. A similar tissue occurs in the tooth plates of the ptyctodonts and in the teeth of rays and some durophagous sharks. As noted on p. 107, this type of tissue is obviously an adaptive feature in a crushing or grinding dentition, and it has developed independently in the holocephalans, the dipnoans and the sharks. The significance of the tissue in ptyctodonts is discussed below on p. 210.

It is clear from the history of the Chimaeriformes that the tritoral areas in the tooth plates of the chimaeroids are a specialized feature which appeared in the early Mesozoic. All the Palaeozoic holocephalans have the whole tooth crown formed of tubular dentine (though in *Chitonodus tribulis* St John & Worthen 1883, p. 119, pl. 7, figs. 18 to 21, a cochliodont from the Lower Carboniferous of Iowa and Illinois, on the anterior part of the tooth plate there is a number of irregularly distributed humps which may represent simple tritors). In the myriacanthoids tritors are present only on some of the tooth plates and are very simple, usually few in number, and are regularly distributed over the surface of the plate. In *Squaloraja* the whole surface of the tooth plate is made up of alternate bands of osteonal dentine and interosteonal tissue (a type of tubular dentine which also occurs in chimaeroids such as *Elasmodus*) and there are no localized tritors. The function of the tritors in the chimaeroids is clearly to produce variation in the relief of the tooth surface which will persist as the crown is abraded away because of the difference in hardness between tubular dentine and osteodentine. With the exception of the edestids and petalodonts, in which the teeth tend to become acuminate, the Palaeozoic holocephalans had smooth, flat tooth plates and were evidently bottom feeders, probably eating shelled invertebrates. *Squaloraja* was obviously another bottom feeder. The myriacanthoids, with their tendency towards the development of tritors in the upper jaw and the chisel-like tooth in the lower jaw, were also apparently less dorso-ventrally flattened than the Palaeozoic forms and *Squaloraja*, but their dentition seems still to be mainly adapted to bottom feeding. The chimaeroids are strongly compressed fishes and often have the tritors arranged so that blade-like cutting edges are formed; they are almost omnivorous (Dean 1906, p. 20; Bigelow & Schroeder 1953, p. 521), feeding on shelled invertebrates, teleosts, polychaetes, squid, etc., and feed both on the bottom and in open water. The development of tritors in chimaeroids is an adaptation to an omnivorous habit and is correlated with compression of the body. These changes took place in the Jurassic and coincided with the appearance of the rays and of sharks specialized for bottom feeding which have filled the niches previously occupied by the holocephalans. The chimaeroids have survived because they are adapted to life in open water as well as on the bottom.

In all chimaeroids there is a single pair of tooth plates in the lower jaw and two pairs in the upper jaw. This arrangement is also present in *Squaloraja*, but in the myriacanthoids and the Palaeozoic Chimaeriformes the number of tooth plates becomes more varied. It has been generally assumed (Smith Woodward 1921, p. 34; Moy-Thomas 1936*b*, p. 488) that the type of dentition seen in *Helodus simplex* is the most primitive in the cochliodont-chimaeroid assemblage. This assumption has been made because the teeth are arranged in *Helodus* as they are in typical selachians. The possibility that the numerous teeth of *Helodus* are the result of fragmentation of a more typical bradyodont dentition seems to have been considered only by Jaekel (1899, p. 296; 1926, p. 231; etc.). We know that a selachian type of tooth arrangement occurs in the holocephalans since it is present in the helodonts, the petalodonts, and particularly in the edestids. The question is whether this arrangement, with several or many tooth series and several or many teeth in each series, is more or less primitive than the few large tooth plates of the Chimaeriformes. The evidence on this point may be considered under the three headings stratigraphical, comparative anatomical and embryological.

(i) *Stratigraphical evidence*

In the Lower Carboniferous all the various groups of holocephalans are already present —cochliodonts, helodonts, psammodonts, copodonts, petalodonts, edestids and chondrenchelyids. In the Devonian the known holocephalan fauna is much more limited, and all but one of the species occur only in North America. The following Devonian forms have been recorded:

?Eifelian. Psammodus antiquus Newberry (1857), from the Middle Devonian 'Corniferous Limestone' (?Delaware Limestone) of Ohio. The specimen has never been figured or redescribed. It is the only record of a holocephalan before the Upper Devonian and as both the anatomy of the specimen and the horizon are imperfectly known, much weight cannot be given to it.

Lower Frasnian. Acmoniodus clarkei Hussakof & Bryant (1918, p. 151, pl. 55, fig. 3), from the Conodont Bed, Lower Genesee, Erie Co., New York. This is a large, bilaterally symmetrical plate bearing two raised cusps in the mid-line. It is not clear from the original description whether the body of the plate consists of osteodentine and is a broad root, or whether it consists of tubular dentine, but Smith Woodward (1932, p. 93) took it to be an extended root. The bilateral symmetry suggests that *Acmoniodus* is a copodont, and it has been placed in the Copodontidae by most authors.

Lower Frasnian. Orodus devonicus Hussakof & Bryant (1918, p. 153, pl. 44, fig. 4), from the Conodont Bed, L. Genesee, Erie Co., New York. This tooth is a very doubtful *Orodus*. It has three rounded cusps, the middle one enlarged, which are striated near the base on the posterior and lateral faces. It is described as having no punctae on the surface, and this raises doubts as to whether it is holocephalan: it could well be a worn tooth of cladodont type.

Lower Frasnian. Synthetodus calvini Eastman (1908, p. 33, pl. 2, fig. 19; pls. 10, 11, 12), from the State Quarry Limestone, Johnson Co., Iowa, and the Conodont Bed, Erie Co., New York. Eastman described this species as a dipnoan tooth plate, but Hussakof & Bryant (1918, p. 150) suggested that it is more probably holocephalan. The tooth has a single cusp, is bilaterally symmetrical, and appears to be a typical copodont. Hussakof & Bryant also suggested that *Synthetodus trisulcatus* Eastman (1908, p. 231, pls. 9, 11) and *Conchodus variabilis* Eastman (1908, p. 230, pl. 8), both from the State Quarry Limestone of Iowa, are holocephalans, not dipnoans. *Synthetodus trisulcatus* contains bilaterally symmetrical teeth which are possibly copodont. *Conchodus variabilis* contains asymmetrical plates whose nearest relatives among the holocephalans seem to be the lateral teeth of the Lower Carboniferous (?copodont) *Mazodus.*

Upper Frasnian or Lower Fammenian. Helodus gibberulus Agassiz was reported by Newberry (1889, p. 102) from the Chemung at Warren, Pennsylvania. No specimen has been figured, but Newberry described the teeth as having a subconical central cusp and a low subsidiary cusp on each side, and as being indistinguishable from Mississipian *H. gibberulus.*

Middle Fammennian. Thoralodus cabrieri Lehman (1953, p. 64, pl. 1, fig. 3), from the M. Famennian of Cabrières, France, is the only holocephalan known from the European Devonian. The only specimen is a large, asymmetrical tooth plate with a smooth, slightly convex surface. It appears to be closest to the cochliodont *Sandalodus* but is more irregular in shape.

Upper Famennian. Sandalodus minor Bryant & Johnson (1936, p. 657, text-fig. 1), from the Lower Chaffee Formation, Tennant Co., Colorado. This species is known by a single small tooth plate of typical *Sandalodus* form.

Upper Famennian. Xenodus hertzeri (Newberry 1889, p. 67, pl. 27, figs. 11–15), from the Huron Shale of Delaware, contains several small, asymmetrical ridged plates of various shapes. They do not resemble any known holocephalan, and are possibly dipnoan or arthrodiran.

Uppermost Devonian or Lowest Mississipian. Five species of Holocephali are known from the Grassy Creek Shales of Missouri. This formation is placed at the junction of the Devonian and Mississipian, with a recent tendency towards inclusion in the Mississipian (Weller *et al.* 1948, p. 102). The species are:

Eoorodus typus Branson (1914, p. 68, pl. 4, figs. 22–24). Branson interpreted the holotype of this species as an incomplete tooth of orodont type, but it seems more likely to be a complete copodont tooth since it is symmetrical about the long axis and has a single low, rounded cusp.

Helodus clivulus Branson (1914, p. 67, pl. 4, figs. 1, 2, 5, 6); *H. devonicus* Branson (1914, p. 66, pl. 4, figs. 19, 20); *H. incipiens* Branson (1914, p. 67, pl. 4, figs. 11 to 16) and *H. rowleyi* Branson (1914, p. 66, pl. 4, figs. 25, 26). These four species contain typical isolated helodont teeth, and all except the last range up into the overlying Bushberg Sandstone, which is undoubtedly Mississipian.

?*Upper Devonian. Helodus subtuberatus* Lambe (1913, p. 20, pl. 2), from Roche Miette, Alberta, is based on two typical helodont teeth with a central cusp and incipient lateral cusps. The specimens are 'from the limestone bed at the summit of Roche Miette', and from a nearby locality on the eastern face of Bullrush Mountain. Roche Miette consists mainly of Upper Devonian Palliser formation, but there are patches of Mississipian rocks on the mountain as well (Baird 1963, p. 128), and the record must be considered doubtful.

From this survey of Devonian holocephalans three points are clear. First, the copodonts, a group in which the dentition is completely unlike the selachian type, are certainly present in the Devonian (*Acmoniodus*, *Synthetodus*, possibly *Eoorodus*). Secondly, the only cochliodonts known in the Devonian are *Sandalodus* and the related *Thoralodus*, and these are certainly tooth plates, not isolated teeth from a selachian type of dentition, and show no sign of separation into cusps as in the '*Pleurodus*' plates of *Helodus*. Thirdly, helodont teeth do not appear until the base of the Mississipian except for Newberry's unfigured specimens of *Helodus gibberulus*, otherwise a Mississipian species, and Lambe's record of unconfirmed age.

Although there is no conclusive evidence here as to the type of dentition present in the earliest holocephalans, the presence in the Devonian of copodonts, *Sandalodus* and *Thoralodus*, the absence of '*Pleurodus*', and the doubtful nature of the records of *Helodus* do not oppose the idea that the earliest holocephalans had a few large tooth plates rather than the selachian type of dentition seen in *Helodus*.

(ii) *Evidence from comparative anatomy*

The 'selachian' type of tooth arrangement and succession is normally taken as being primitive for gnathostomes. It occurs in acanthodians, selachians, the porolepid-osteolepid-tetrapod assemblage, the coelacanths and the actinopterygians. In the earliest dipnoans the dentition consists of tooth plates very like those of living forms, but the arrangement of the cusps on these tooth plates suggests the arrangement of the teeth in a selachian type of dentition, and Lison (1941, p. 298) has shown that the tooth plates of living dipnoans arise in ontogeny by the fusion of many individual primordia. These facts suggest that dipnoans have a modified 'selachian' type of dentition. We do not know a common ancestor for all of these groups, or for any two of them, and there is no evidence that all these groups have inherited the mode of tooth succession. But although it is possible that it has developed independently in each of them, it is natural to assume that it represents a common heritage. The only gnathostome group in which the teeth are not arranged and replaced in the selachian way is the arthrodires, and it is within or near the arthrodires that the origin of the holocephalans is commonly thought to lie. Though Watson (1934, p. 462) has said that the arthrodires originally had a selachian type of dentition, presumably basing this on the description of this type of tooth arrangement in coccosteids and *Jagorina* by Stensiö (1925, pp. 177, 185), recent opinion (Gross 1962, p. 66) is against this, and Ørvig (1957, p. 344) has said that Stensiö's description of coccosteid dentition is in fact based on acanthodian material.

Smith Woodward (1889*a*, p. 169) held that the inrolled outer border of the tooth plates of cochliodonts showed that the tooth plates are the result of the fusion of a selachian type of tooth series. But although the shape of the plate in section is evidence that it grew by addition to the inner border in the same way as a selachian tooth series, it is not evidence that the plate is formed by fusion of independent teeth, or that the series of teeth were once numerous. It is also important to notice that the inrolling of the outer border of the tooth plate is least marked in forms like *Sandalodus* which are the first to appear in time.

(iii) *Embryological evidence*

As in most questions involving the embryology of living holocephalans, the evidence here is scanty. Schauinsland (1903, p. 13) has given an account of the development of the tooth plates in *Callorhynchus*. The conclusions to which his observations lead are best summed up in the words of Dean (1906, p. 120): 'The...observations of Schauinsland... are disappointing to those who on *a priori* grounds anticipated that the dental plates of chimaeroids would in the ontogeny of recent species be found to be formed of the coalesced bases of separate tooth elements'. Dean goes on to find similarities between the development of the tritors in chimaeroids and selachian tooth arrangement, but since tritors are quite certainly a recent acquisition in holocephalans this argument has no force.

To sum up this discussion, neither the stratigraphical evidence nor the embryological gives any support to the hypothesis that the earliest holocephalans had a selachian type of dentition, and the evidence from comparative anatomy can be read in either way. I can find no firm ground on which one can oppose the proposition that the earliest holocephalans had a dentition consisting of a few large tooth plates retained throughout life, and that the appearance of a selachian type of tooth arrangement and succession in the helodonts, edestids and petalodonts is secondary.

(*e*) *The position of the branchial arches*

In chimaeroids and in all fossil holocephalans the branchial arches lie crowded below the neurocranium. This feature is shared with the arthrodires and in this the arthrodires and holocephalans are sharply contrasted with the acanthodians and selachians, in which the branchial arches lie behind the neurocranium. Correlated with the forward position of the branchial arches is the position of the pectoral fin close behind the skull, and very probably the presence of an operculum. In arthrodires the branchial arches lie below the neurocranium because the body armour, which contains the pericardium, articulates with the hind end of the neurocranium. Watson (1934, p. 460) suggests that the operculum of arthrodires is present because of the need for increasing the area of the gill filaments by deepening the gill slits and allowing the filaments to proliferate within an enclosed chamber. In no fossil holocephalan is there direct evidence of the presence of an operculum, but in view of the similarity in position of the branchial arches to the operculate chimaeroids and arthrodires it seems reasonable to assume that one was present. In holocephalans it is difficult to find any other explanation of the structure of the branchial region than that it is inherited from ancestors of arthrodiran type. This is discussed further on p. 209.

(*f*) *The rostral and labial cartilages*

There is no evidence of rostral cartilages in any holocephalan before the Jurassic. Although this is very possibly due to the enormous gaps in the record, it seems clear that there was no prominent rostrum in either *Helodus* or *Menaspis*. In *Deltoptychius* the snout has not yet been seen, but the similarity to *Menaspis* in other features suggests that no large rostrum was present.

The rostral cartilages are very large in the Myriacanthidae and in *Squaloraja*. In *Callorhynchus* and the Rhinochimaeridae the rostrum is large but the rostral cartilages are smaller than in the Jurassic forms. The enlarged scales on the rostrum of the Jurassic holocephalans show that one of the main functions of the rostrum was to oppose the very large frontal clasper. In the chimaeroids, where the frontal clasper is much reduced, the large rostrum has taken on a sensory function in the Rhinochimaeridae and in *Callorhynchus*, but it is reduced in the Chimaeridae.

The arrangement of the rostral cartilages in holocephalans is the reverse of that in the selachians, where the median cartilage is ventral to the paired ones. Holmgren (1942, p. 206) considered the lateral rostral cartilages of holocephalans to be homologous with the rostral appendices of rays. Nothing in the palaeontological record of holocephalans confirms or denies this suggestion.

The only evidence of labial cartilages in any holocephalan earlier in time than, or more primitive than, *Squaloraja* is the single pair of large labials which Jaekel (1899, p. 269, pl. 15, fig. 1) described in the Permian petalodont *Janassa*. In *Squaloraja* the labial cartilages appear to agree with those of living forms but are much enlarged. Holmgren (1942, p. 244) has given a detailed discussion of the labial cartilages of chimaeroids. As they are normally provided with a well-developed musculature, he thinks that they represent a more primitive condition than is seen in any other living gnathostome, and he proposes homologies between them and the buccal skeleton of *Petromyzon*.

(*g*) *The notochordal calcifications*

The notochordal calcifications of the Chimaeriformes, several to each segment, are a character which occurs in no other vertebrate group. Their occurrence in any fossil form is very strong evidence of relationship with the chimaeroids, but since they are absent in *Callorhynchus* their absence in any fossil is not evidence against such a relationship. The calcifications occur in Chimaeridae, Rhinochimaeridae, *Squaloraja* (where they reach their maximum development) and in Myriacanthoidei. In the Myriacanthidae they are represented by paired elements. There is no evidence that they occurred before the Jurassic. The function of the calcifications is presumably mechanical, but if this is so it is strange that they should be most massive in *Squaloraja*, which one would expect to be a less active swimmer than the laterally compressed chimaeroids. In the Lower Carboniferous *Chondrenchelys* the vertebral column contains segmental 'centra'. Moy-Thomas (1935*b*, p. 400) describes these as thin-walled rings showing a fibrous structure in section, and this suggests that they may well be calcifications in the sheath of the notochord.

(*h*) *The synarcual*

The only other vertebrate groups in which a structure similar to the synarcual of holocephalans occurs are the arthrodires and the rays. In the rays the structure has appeared in relation to the enormous increase in size of the pectoral fin. In arthrodires the synarcual lies within the body armour and served for the insertion of muscles which anchored the axial skeleton to the body armour: the dorsal crest on the synarcual articulates with the median dorsal plate. In chimaeroids and myriacanthoids the synarcual serves to support the anterior dorsal fin and the large fin spine. If the synarcual were present in early holocephalans in which there was no dorsal fin spine, this would be strong evidence of relationship with the arthrodires. Although a synarcual is present in the spineless *Squaloraja* there is only inconclusive evidence of its presence in *Deltoptychius* and no evidence of the axial skeleton in *Menaspis*. But there is evidence that a synarcual was present in *Helodus*, and since the fin spine of this form appears to have originated independently (see p. 201) this suggests that the earliest holocephalans also had a synarcual.

(*i*) *The paired fins and girdles*

Among fossil Chimaeriformes the pectoral fin is known in *Ischyodus*, *Squaloraja* and *Menaspis*. In these the fin agrees closely with living chimaeroids: the number of radials is similar, the anterior radials are fused, and the fin is dibasal where the basals are known (*Ischyodus*, *Squaloraja*). In *Helodus simplex* the pectoral is of exactly the same type, dibasal and with fused anterior radials. Among the other holocephalan groups, the pectoral is known only in *Chondrenchelys* and in the edestid *Fadenia*, where Bendix-Almgreen (1962) has given a preliminary description of new material from the Permian of East Greenland. In *Chondrenchelys* the fin is 'archipterygial', like that of the xenacanth sharks. In *Fadenia* the fin is of plesodic type, and appears to be similar to the pectorals of cladoselachid sharks. This suggests that the pectoral fins of holocephalans will eventually be found to be as varied as those of selachians, but there is not yet enough information to relate these various types of fin to each other, nor to decide what type was present in the earliest holocephalans. The archipterygial fin of *Chondrenchelys* is no longer considered to be primitive: this type of fin appeared independently in dipnoans, xenacanth sharks and *Chondrenchelys*. The plesodic fin of *Fadenia* is a remarkable structure which is to be described in detail by Bendix-Almgreen. At present one need only note that Harris (1951, p. 693) has suggested that the plesodic pectorals of *Cladoselache* may not represent the ancestral condition in selachians: it is not impossible that a similar type of fin should have evolved in a fast-swimming holocephalan like *Fadenia*, possibly by paedomorphosis.

The pelvic fin is known in *Ischyodus*, *Squaloraja*, *Menaspis* and *Helodus*, and in these it agrees with living forms. The pelvic girdle, known in *Ischyodus*, *Squaloraja*, *Helodus* and *Metopacanthus*, has the halves separate in all, and in *Helodus* and *Metopacanthus* the small anterior cartilage which supports the tenaculum in male chimaeroids is absent. In *Squaloraja* this cartilage is fused to the girdle, not separate as it is in chimaeroids. In *Chondrenchelys* the pelvic fins are 'archipterygial', with a segmented axis but without postaxial radials.

(*j*) *The dorsal fins*

The first dorsal fin is very similar to those of living chimaeroids in *Ischyodus*, Myriacanthidae and *Helodus*. In *Squaloraja* and menaspoids the first dorsal fin is apparently absent, but it may well have been present without a spine. In the Permian edestid *Fadenia*, where there is no fin spine, Bendix-Almgreen (1962) has described the first dorsal as containing a triangular basal and a row of distal radials. Primitively, the first dorsal fin may have had a series of simple parallel radials, like those in the second dorsal fin, but if such a fin were discovered in a fossil holocephalan it would not necessarily be a primitive feature since Holmgren (1941, p. 93) has shown that in sharks reduction or loss of the dorsal fin spine is accompanied by fragmentation of the triangular basal which lies behind the spine.

The second dorsal fin is known only in *Squaloraja* and *Ischyodus*, in both of which it agrees with living chimaeroids. The long dorsal fin of *Chondrenchelys* with its double series of radials is not easily related to the dorsals of other holocephalans: like the paired fins, it may well be a specialized feature.

(*k*) *The dorsal fin spine*

In living chimaeroids the dorsal fin spine is laterally compressed and triangular in section, its sides and anterior edge are smooth, and there are a few denticles in two rows on the distal part of the posterior face. The spine consists of lamellar tissue surrounded by a narrow and incomplete zone of osteodentine (figure 4*A*; figure 45, plate 22). In early chimaeroids such as the Jurassic *Ischyodus* and *Ganodus* the spine differs from those of living chimaeroids only in having a wider outer zone of osteodentine (figure 4*B*) and a longer series of denticles on the posterior face. Passing back to the myriacanthoids, this trend continues through *Acanthorhina*, where the spine is as in chimaeroids, to *Chimaeropsis* and *Metopacanthus* (figures 20, 22) in which the lateral faces of the spine are partially tuberculated, the posterior series of denticles is more complete, there is a series of denticles at the base of the anterior edge of the spine, and a wider zone of osteodentine, and finally to *Myriacanthus* (figures 14, 17), in which the whole of the lateral surface is tuberculated, there is a complete series of paired denticles on the posterior face and incomplete median series as well, a long series of anterior denticles, and the zone of lamellar tissue has decreased until it makes up less than one-fifth of the thickness of the wall.

It is remarkable that a similar series of changes take place as the fin spines of sharks are traced back (Stromer 1927; Peyer 1957). In the few living sharks which retain dorsal fin spines (*Heterodontus*, *Squalus*, *Oxynotus*, etc.) the spine is enamelled but unornamented, without posterior denticles, and consists almost entirely of lamellar tissue, with a very thin and incomplete outer zone of osteodentine. In fossil heterodontids like the Liassic *Palaeospinax* the spine is exactly similar except that the enamel is often broken up into a few tubercles at the base of the spine. In the Mesozoic hybodonts (*Hybodus*, *Acrodus*, *Asteracanthus*, etc.) the lateral surfaces of the spine are tuberculated or ribbed more or less completely, there is a double series of denticles near the mid-line on the posterior face, and the zone of lamellar tissue makes up only about half (*Hybodus aschersoni*, Middle Cretaceous, Stromer 1927, text-fig. 13) or one-third (*Nemacanthus monilifer*, Upper Trias, Stromer 1927, text-fig. 12) of the thickness of the wall. Finally, in the Carboniferous and Upper Devonian spines (*Ctenacanthus*, *Sphenacanthus*, etc.) the denticles on the posterior face become laterally placed and the lamellar tissue disappears so that the spine consists entirely of osteodentine.

From the similarity of the changes which have taken place during their history, especially the way in which osteodentine is gradually replaced by lamellar tissue, it seems obvious that the spines of sharks and Chimaeriformes are similar structures which have arisen and evolved in the same way. Thus although little is known of the embryology of the spine in chimaeroids, the similarity of its structure to those of sharks suggests that the type of development seen in sharks, where the zones of osteodentine and lamellar tissue arise independently and only fuse in the fully developed spine (Markert 1896), will also apply to chimaeroids, and that the origin of the spines will have been similar in the two groups. It should also be noted that an analogous series of changes has been shown to take place in the fin spines of acanthodians (Krebs 1961; Gross 1947, 1957). Among the earliest acanthodians in the Upper Silurian, some fin spines consist almost entirely of bone (*Nostolepis*), others almost entirely of dentine (*Gomphodus*). In these Silurian forms there is a layer of circumpulpar tissue of variable extent, which may be bone (*Nostolepis*) or dentine (*Gomphodus*). In the Devonian *Onchus* the spine consists entirely of osteodentine. In the Upper Carboniferous *Gyracanthus* a layer of circumpulpar tissue appears in the distal part of the spine, the rest of the spine consisting of osteodentine with a few bone cells in its inner layers.

Three interpretations of the fin spines of sharks have been made. Markert (1896) saw the spine as a single modified scale, and this hypothesis has received some acceptance (Goodrich 1909, p. 168; Bertin 1958, p. 509). Other authors (Dean 1895, p. 28; Smith Woodward 1915, p. lxix; 1935, p. 393; Krebs 1961, p. 824) regard the spine as the result of fusion of many scales, of which the tubercles in forms like *Asteracanthus* are the individual crowns. A third opinion is that of Peyer (1957) who regards the spine as a compound structure, the outer layer of osteodentine and the tubercles which are present in Palaeozoic and Mesozoic forms being produced by fusion of scales, and the inner layer of lamellar tissue being a single enlarged scale. Peyer's theory falls because lamellar tissue is absent in the earliest shark spines. Peyer figured (1957, pl. 2) a section of a Carboniferous *Ctenacanthus* and noted the absence of 'orthodentine', but surmised that this was because the section was cut near the base of the spine, but P 31735 and several polished specimens in the BMNH show that this is not so. The inner layer of lamellar tissue is a later addition to the spine, and it is very difficult to see how it can be an enlarged scale which has developed *de novo* within a pre-existing spine. It seems more likely that the lamellar tissue is an adaptive feature which gives greater rigidity than the more loosely organized osteodentine.

Of the other two hypotheses, that the spine is either a single enlarged scale or a mass of fused scales, the second is certainly preferable, for in the oldest spines the tubercles are most marked, and the features which led Markert to interpret the spine as a single scale are mainly recent adaptations and are not present in Palaeozoic spines. Yet the hypothesis that the spine is formed by fusion of scales suffers from the fact that we now know something of the structure of the scales in the earliest elasmobranchs (Stensiö 1961, pl. 1, fig. X: the scales have the same structure in *Cladoselache*, P 9570, *Cladodus*, P 40149, and *Sphenacanthus*, P 12363). In these forms, as in the acanthodians, the root of the scale consists of dense osteoid tissue, laid down in lamellae, without dentine tubules, and is quite unlike the osteodentine of the spine which is held to have been formed by fusion of units of this type. Further, the tubercles on Palaeozoic spines do not resemble the crowns of the scales of Palaeozoic elasmobranchs, which Stensiö (1961) has shown to be complex, zonally growing structures, but rather they are like the crowns of the placoid scales of Mesozoic and Recent forms. However, the structure of the supposed units of the spines, with a placoid type of crown and a root of osteodentine, appears to be directly comparable with the teeth of Palaeozoic elasmobranchs, and everything suggests that the teeth are modified scales. To sum up, it is most probable that the spines of elasmobranchs are the result of fusion of scales, but there is no direct evidence of how this fusion took place.

In sharks, there is good evidence that fin spines are a primitive feature: spines of *Ctenacanthus* appear in the Middle Devonian with the earliest selachian teeth, and although there are no fin spines in *Cladoselache* and *Diademodus* (Harris 1951) they occur in the majority of Palaeozoic sharks. In holocephalans the history of the dorsal fin spine is clear as far back as theLiassic myriacanthoids, but before this a fin spine is known only in *Helodus*, in petalodonts, where *Polyrhizodus* is thought to have borne fin spines of *Physonemus* type (Jaekel 1899, p. 281), although the Permian *Janassa* was certainly without spines, and, more doubtfully, in edestids, which Obruchev (1953, p. 57) and Baird (1957, p. 1017) suggest had spines of *Physonemus* type, though again the Permian forms were without spines. We can extrapolate back in time in the series of changes which have taken place in the structure of the spine in Chimaeriformes (p. 195). The predecessor of *Myriacanthus* would be expected to have a heavily tuberculated spine consisting entirely of osteodentine, analogous in structure with the spine of *Ctenacanthus*. The spine of *Helodus* does not fit this prediction. Smith Woodward noted long ago (1889*a*, p. xxi) that the fin spine of *Helodus* was the only smooth and unornamented fin spine known in Palaeozoic rocks. This still seems to be true of elasmobranch fin spines. The question is whether unornamented spines represent a primitive stage in the sequence of changes which takes place in chimaeriform spines, or whether they are part of a different series. Although superficially similar to the spines of advanced Chimaeriformes, the spine of *Helodus* differs in consisting entirely of osteodentine. The only way in which the *Helodus* spine can be considered as ancestral to the spines of Chimaeriformes is by proposing that in holocephalans the spine did not arise by fusion of scales but by the development of a spine of osteodentine to which scales later became fused as tubercles. This is very unlikely since it would be a prerequisite of the process that the spine should be covered by scales, and a number of moderately well-preserved specimens of *Helodus simplex* show that this was not so. I can find no grounds for regarding the spine of *Helodus* as a primitive stage in the chimaeriform sequence. The only alternative seems to be that the spine of *Helodus* is part of a different series of changes. This leaves the chimaeriform series of spines with no beginning. There is good evidence for a relationship between the myriacanthoids and the menaspoids, in which there is no spine. The structure of the spine in *Myriacanthus*, with its very narrow zone of lamellar tissue and its heavy ornament, is primitive and suggests that the spine had not been in existence for very long. Although I know of no other examples of an elasmobranch fin spine appearing during the comparatively recent history of a group, it seems reasonable to suggest that the fin spine of the Chimaeriformes arose during the late Palaeozoic or early Mesozoic on a previously unarmed fin.

(*l*) *The squamation*

The very incomplete squamation of the chimaeroids is a recent adaptation. In *Squaloraja* only the belly and tail are without scales, and in all the more primitive forms the squamation seems to have been complete. The scales of chimaeroids are very like those of living selachians in structure. Although Moy-Thomas in his discussions of holocephalan history (1935*b*, p. 401; 1936*b*, p. 499) referred to the scales of chimaeroids as hollow cones with wide pulp cavities, the pulp cavity is very small (figure 5*B*).

This study shows that during the history of the Chimaeriformes the scales have undergone a change in structure which has occurred independently and roughly contemporaneously in at least two other groups of elasmobranchs, the selachians and the edestids (Stensiö 1961): the change from a cyclomorial, zonally growing scale (in *Deltoptychius*, figure 32) to a placoid (synchronomorial) scale in which growth does not take place (in Jurassic and later forms). The scales of the Upper Carboniferous *Helodus simplex* (figure 41) are apparently all placoid. *Helodus simplex* is the only known Palaeozoic elasmobranch in which this condition is reached.

(*m*) *The sensory canals*

The details of the distribution of the sensory canals are known only in *Ischyodus* and *Squaloraja* among fossil holocephalans. In neither of these forms does the pattern differ significantly from that in living chimaeroids, and the fossils provide no evidence in relating the various canals of chimaeroids to those of other groups.

The sensory canals on the head and trunk are enclosed in incomplete rings of hard tissue in chimaeroids, in *Squaloraja* and in the myriacanthoids (figures 7, 19). In *Menaspis* similar structures surround the canals on the head but the canals on the trunk are not known. There can be no doubt that the structures enclosing the supraorbital canals in *Menaspis* (figure 36) are homologous with the tubercles which enclose the grooves for these canals on the head shield of *Deltoptychius* (figure 30). The tubercles on the head shield of *Deltoptychius* are modified scales (p. 203). From this it is clear that the structures in myriacanthoids and chimaeroids are modified scales; they probably include elements of both the crown and the base of the scales (see Schauinsland 1903, p. 13) and must consist of modified dentine and osteoid tissue, though no dentine tubules or other structures are visible in them.

There is no evidence of modified scales surrounding the sensory canals on the trunk in any form more primitive than *Metopacanthus*, and in menaspoids and helodonts the lateral line may well have been naked.

In *Helodus* there are scales (figure 41*I*, *J*) whose crowns are similar in shape to the tubercles enclosing the grooves for the sensory canals on the head shield of *Deltoptychius*. It is possible that these scales lay along the sensory canals on the head and trunk, but no such alignment of scales is visible in any specimen.

(*n*) *The pelvic claspers*

Pelvic claspers are known to occur among holocephalans only in chimaeroids, in *Squaloraja*, and in *Chondrenchelys*. The pelvic fin is unknown in both the myriacanthoids and the menaspoids. In *Helodus simplex* two specimens show the pelvic fin and in neither is there any trace of pelvic claspers. Moy-Thomas (1936*b*, p. 500; 1939, p. 3) found that the chief objection to a separate origin for the holocephalans and selachians was the question of the pelvic claspers, as these were then thought to have been absent in the earliest sharks, and their presence in both holocephalans and recent sharks was strong evidence that the two groups had diverged from a post-Devonian shark-like ancestor. With the discovery of pelvic claspers in an Upper Devonian shark (*Diademodus*, Harris 1951) and in an arthrodire (*Ctenurella*, Ørvig 1962) this objection has been removed, and the apparent absence of claspers in *Helodus simplex* must be attributed either to specialization (as it has recently been in *Cladoselache* by Harris (1951)) or to defective preservation.

(*o*) *The tenacula*

In living male chimaeroids the tenacula are rather complex structures (Parker 1886; Bigelow & Schroeder 1953, p. 520) containing a gland, an armament of scales and a skeleton of from one to three separate cartilages articulating with the antero-ventral border of the pelvic girdle, the whole structure being retractable into a pocket in the skin. In *Squaloraja* (figure 8; figure 55, plate 24) the tenaculum consists of a group of enlarged scales borne on an anterior process of the pelvic girdle, not on a separate cartilage, and the tenaculum was therefore probably not retractable. In *Metopacanthus* (p. 141) there is simply a group of enlarged scales, and apparently no supporting cartilage. There is no evidence of tenacula in any other myriacanthoid or in any Palaeozoic holocephalan. It appears that the tenacula originated simply as a group of enlarged scales, and that the independent skeleton and the pocket into which the apparatus retracts are comparatively recent specializations, present only in chimaeroids. The fusion of the supporting cartilage with the pelvic girdle in *Squaloraja* shows the repeated assertion that the skeleton of the tenaculum represents anterior pelvic radials (Dean 1906, p. 13) to be untrue.

Although there is no record of tenacula in any holocephalan before the Jurassic, tenacula could well have been present in menaspoids, where the pre-pelvic region is unknown. They appear to have been absent in *Helodus* and *Chondrenchelys*. Ørvig (1960, p. 327) has described a pair of 'small dermal spines, ornamented with pointed tubercles' in front of the pelvic fins of the Middle Devonian ptyctodont *Ctenurella*, and suggests that these are homologous with the tenacula of chimaeroids. Gross (1962, p. 63) has found a pair of oval tuberculated plates lying below the pelvic girdle in the Lower Devonian stensioellid *Stensioella*; these plates possibly represent similar structures to the spines in *Ctenurella*.

(*p*) *The frontal clasper*

In living chimaeroids the frontal clasper is a small rod of heavily calcified fibro-cartilage, armed with scales. In the Jurassic chimaeroid *Ischyodus* the clasper is a little larger. In *Squaloraja* and in Myriacanthidae the clasper is very large and is armed on its underside with much enlarged scales. Nothing is known of the frontal clasper in *Chimaeropsis*. In *Acanthorhina* there is doubt as to which of the structures on the head is the frontal clasper, but it seems likely that the clasper was large and broad (p. 146). A median frontal clasper is not known to occur in any Palaeozoic holocephalan, but Reis (1895) has argued that the three pairs of frontal spines in *Menaspis* (figure 36) are the 'paired serial homologues' of the frontal clasper of chimaeroids and that the frontal clasper originated as a paired structure. The composition of the frontal spines of *Menaspis* is discussed on p. 172, and it is concluded that it is more likely that they consist of calcified fibro-cartilage, as Reis suggested, than of dentine. The frontal spines in *Menaspis* appear to be inserted on the neurocranium at the same level as the frontal clasper of chimaeroids. Reis (1895, p. 387) gives two reasons for thinking that the frontal clasper in chimaeroids was originally a paired structure; the bilateral symmetry of the blood vessels in the claspers of *Chimaera* and *Squaloraja*, and his identification of BMNH 47018 (Reis 1895, pl. 12, fig. 1 *a*) as the rostrum of a female *Squaloraja* in which the rudiments of the clasper are represented by a pair of splints of calcified fibro-cartilage. The first of these arguments carries little weight, and I am unable to agree with

Reis in his interpretation of 47018: the fragments of lateral rostral cartilage in this specimen show that it is exposed in ventral view, not in dorsal view, and paired strips of calcified fibro-cartilage occur on the dorsal side of the rostrum in individuals where the frontal clasper is present (figure 9). Nothing is known of the ontogeny of the frontal clasper in chimaeroids, and there is no evidence as to whether it arises from median or paired rudiments. In *Metopacanthus* some examples of the frontal clasper show a paired central cavity throughout the greater part of their length (P 3188), but in others (P 1158, P 4575) the cavity is median. The strongest piece of evidence for a paired origin of the frontal clasper is the specimen described on p. 174 as *Menaspacanthus armaghensis* gen. and sp.nov. This specimen provides clear evidence that in the Lower Carboniferous there were fishes with paired structures identical in histological structure with the frontal claspers of myriacanthoids and chimaeroids, and there is a strong similarity in shape between *Menaspacanthus* and the frontal spines of *Menaspis*. On balance, I believe that there is good evidence that the frontal clasper was originally a paired structure, and *Menaspis* shows that in some forms there was more than one pair.

There is one other question to be raised in connexion with the frontal clasper. It has been noted above (pp. 125, 141, 172) that in *Squaloraja*, *Metopacanthus* and *Menaspis* (the only genera of primitive Chimaeriformes in which the frontal clasper has been seen in more than one specimen) there is no positive evidence of sexual dimorphism in the frontal clasper. In *Squaloraja* six complete specimens are known; four of these show either or both pelvic and frontal claspers and the other two are preserved in ventral view so that the absence of a frontal clasper cannot be confirmed. In *Metopacanthus* a frontal clasper is present in all four specimens in which the head is preserved, and in *Menaspis* the three pairs of frontal spines are present in both the specimens in which anything more than fragments of the head are preserved. Out of twelve specimens of these three genera only two do not show a frontal clasper, and in both of these the head is preserved in ventral view. Although it could be argued that the large frontal claspers of these forms would have made the heads of males more conspicuous to collectors than females, there is a strong possibility that in the squalorajoids, myriacanthoids and menaspoids the frontal clasper was present in all individuals.

In living chimaeroids the only evidence for the use of the frontal clasper in copulation seems to be that of Dean (1906, p. 23) who described scars presumably made by the frontal clasper on the dorsal fins of female *Hydrolagus colliei*. In living chimaeroids the frontal clasper, like the tenacula, can be retracted into a pouch in the skin. In *Squaloraja* and the myriacanthids the very large frontal clasper could not have been retractable, but the distribution of the scales, with much enlarged scales on the underside of the clasper opposed by similar scales on the dorsal surface of the rostrum, shows that the organ must have been used for grasping, though not necessarily in copulation. The strong curvature of the paired frontal spines in *Menaspis* makes it unlikely that they could have been used in this way, although the muscle scars at the base of *Menaspacanthus* show that these paired spines must have been mobile, and *Menaspacanthus* was armed with scales on the underside. In *Menaspis*, at least, it seems more likely that the frontal spines were defensive rather than copulatory.

Although much of this discussion is based on scanty evidence, the following history of the frontal clasper is suggested. The frontal clasper is confined to the Chimaeriformes. In the earliest Chimaeriformes (*Deltoptychius*) there was no frontal clasper since the preorbital part of the skull roof was covered by the head shield. The frontal claspers arose as paired organs on the lateral parts of the preorbital skull roof after the head shield had become reduced. The claspers were originally present in both sexes, and were defensive, not copulatory in function. In *Menaspis* there were three pairs of claspers. In the early Jurassic Chimaeriformes the claspers became fused into a single median organ of large size which was still present in both sexes, and may not have been copulatory in function. Only in Chimaeroidei, first appearing in the Middle Jurassic, is the frontal clasper present only in the male, and here it is reduced in size, and can be retracted into a pocket in the skin.

(*q*) *The dermal armour*

During the evolution of the Chimaeriformes there is a remarkably clear sequence of reduction of armour on the head. The Lower Carboniferous *Deltoptychius* has a large and complete head shield, a pair of ventral plates on the skull and a pair of mandibular spines. The Upper Permian *Menaspis* has the same armour except that the head shield is reduced in area and fragmented into a number of plates. In Myriacanthoidei this process goes further, with the mandibular spines, present in Myriacanthidae, being lost in *Chimaeropsis*, the much reduced head shield and the ventral plates being retained in *Myriacanthus* and *Chimaeropsis* but lost in *Metopacanthus*, and all armour being lost in *Acanthorhina*. In *Squaloraja* and Chimaeroidei there is no armour, but in *Callorhynchus* Holmgren (1942, p. 218) has described irregular calcifications, which stain with alizarin, in the corium lateral to the subotic and subocular shelves of the neurocranium, and in the mid-line above the eyes. Holmgren saw these calcifications as rudiments of dermal bones. He also interpreted the crescents surrounding the sensory canals in chimaeroids as the remains of the sensory canal bones of arthrodires, but as there is no difference between the crescents around the sensory canals on the head and those around the lateral line on the trunk, it is not obvious why this should be so. Holmgren's calcifications in the corium correspond in position to the head shield and the ventral plates of menaspoids and myriacanthoids, and may be relics of these.

The gradual reduction in dermal armour during the history of the Chimaeriformes, and the occurrence of *Deltoptychius*, the most heavily armoured form, in the Lower Carboniferous are convincing evidence that armour is a primitive feature in the Chimaeriformes. But since there is no armour in *Helodus* and *Chondrenchelys* and no armour is known to occur in any other holocephalan group the question arises as to whether armour is a primitive feature among holocephalans, or whether it was absent in the earliest holocephalans and is a specialized feature confined to the Chimaeriformes. Opinions on the nature of the armour in Chimaeriformes have been varied. Smith Woodward (1891*a*, p. xvi; 1921, p. 37), Dean (1906, p. 144) and Goodrich (1909, p. 168) held that the armour was a specialized feature produced by fusion of scales. Holmgren (1942, p. 217, footnote) seems to think that this is true of the armour in *Myriacanthus*. Stensiö (1925, p. 188), de Beer & Moy-Thomas (1935, p. 309) and Ørvig (1962, p. 56) have all suggested that the armour of myriacanthoids may be a primitive feature, a remnant of more complete armour in arthrodiran ancestors. It is a tempting hypothesis to see the armour of *Deltoptychius* as arthrodire armour, but there seem to be no grounds on which such a comparison can be made. There is no body armour in *Deltoptychius* nor in any other holocephalan. The head shield of *Deloptychius* (figure 30), consisting as it does of a single piece with a single pair of longitudinal sensory canals, is not directly comparable with the head shield of any arthrodire, and none of the usual features of the arthrodire skull roof (pineal opening or plate, middle and posterior pit-lines, etc.) are present on it. Nor is it possible to homologize the ventral plate of *Deltoptychius* with any arthrodire element, since although the plate corresponds approximately in position to the suborbital of arthrodires, it appears to have had no connexion with any sensory canal. The mandibular spine is an element which occurs in no known arthrodire: although superficially similar to the spinal plate of arthrodires, the specimen of *Myriacanthus* shown in figure 14 leaves no doubt that it was attached to the mandible and had no connexion with the pectoral girdle.

On the other hand, there is no evidence of unarmoured holocephalans which are either older than or demonstrably more primitive than *Deltoptychius*. *Helodus simplex* is an Upper Carboniferous form, and cannot be shown to be more primitive than *Deltoptychius* in any character (the dentition and fin spine are discussed on pp. 192, 197), while it is certainly more advanced in the structure of its scales. *Chondrenchelys* is a contemporary of *Deltoptychius*, but is not obviously more primitive, and is specialized in the vertebral column, the fins and the reduced squamation.

The only evidence of pre-Carboniferous forms with armour of the type seen in *Deltoptychius* is in the Lower Middle Devonian Onondaga Limestone of New York State, where Hussakof & Bryant (1918, p. 124) have described plates which 'both in shape and ornamentation, are very suggestive of certain Carboniferous plates and spines...figured by J. W. Davis' (1883, pl. 62, figs. 3, 4, 7, 13; pl. 65, figs. 3, 4) as *Oracanthus milleri*. Hussakof & Bryant say that spines of the 'so-called *Oracanthus*' occur in the same rock. The specimens figured by Davis to which Hussakof & Bryant refer are of two types: the first four figures mentioned show imperfect head shields of *Deltoptychius moythomasi* (figure 34), the last three figures show paired plates of the type discussed on p. 153, and suggested to be acanthodian. Hussakof & Bryant suggested that their specimens belonged to the ptyctodont *Deinodus bennetti*. Also in North American Middle and Upper Devonian rocks there are various plates (*Eczematolepis*; Ørvig 1957, p. 328) which show some resemblance to armour of the type present in *Deltoptychius* and which have been provisionally associated with the ptyctodonts (see p. 204).

There is an increasing body of evidence showing that dermal armour arises by fusion of scales. The most complete discussion of this process is that by Stensiö (1958, pp. 187–9, 244–336) on the Osteostraci and Heterostraci. In these groups the exoskeleton arose, according to Stensiö, by fusion of cyclomorial scales which had lost their overlap and become polygonal. These tesserae became fused to each other, and in the Osteostraci to the underlying endoskeleton. In arthrodires a similar process appears to have taken place, as is shown by *Radotina* (Gross 1958), *Stensioella* (Gross 1962) and *Gemuendina* (Gross 1963), but in these forms the fusion of tesserae may account only for the outer layer of the exoskeleton, since separate and larger dermal bones are present at a lower level in the exoskeleton of *Radotina*. Buistrov (1957) formed a similar idea of the origin of arthrodire armour on histological grounds. There is also clear evidence that in some of the geologically younger members of the Agnatha the exoskeleton has undergone regressive changes which result in separation of the tesserae: similar regressive changes may account for the tesserae in the exoskeleton of the Upper Devonian arthrodire *Jagorina.*

It is clear that the armour of *Deltoptychius* has been formed by a similar process of fusion of scales. This is shown by the tesserae which occur near the mid-line on the head shield of *D. armigerus* (figure 64, plate 27), and by those which occur at the base of the (presumed) mandibular spine in *D. moythomasi* (figure 69, plate 28). The question to be answered here is whether these tesserae represent a primitive stage in the development of armour, where the tesserae are not yet completely fused (as in *Radotina*), or whether they are the first signs of the breaking up of a previously complete armour. There is no completely satisfactory method of distinguishing between these two situations. In the heterostracan *Turinia* Stensiö (1958, p. 334) was able to show that the fragmentation of the exoskeleton is secondary because the scales are synchronomorial, not cyclomorial as they are in primitive forms, because the heterostracans have a long history before the Lower Devonian in which *Turinia* occurs, and because the endoskeleton of *Turinia* shows advanced characters. The application of criteria of this kind to *Deltoptychius* does not give such positive results. In *Deltoptychius* the tesserae are very similar in structure to the trunk scales: they were cyclomorial and zonally growing, as is shown by their radial structure (figure 64, plate 27), and the elongated tubercles which they bear are apparently identical with the crowns of the larger trunk scales (figure 32). These similarities to trunk scales are most marked in the tesserae near the mid-line of the head shield; towards the margins of the shield the tubercles become less and less like the crowns of trunk scales, and there is no sign of separate tesserae. There is only very equivocal evidence (p. 202) of the existence of armoured forms like *Deltoptychius* before the Carboniferous. These points tend to show that the tesserae in the middle part of the head shield are primary, not secondary, and that the armour of *Deltoptychius* is in a primitive condition. One piece of evidence supports the opposing view, the fact that in *Menaspis* the head shield is broken up into tesserae to a greater extent than it is in *Deltoptychius*, but I do not believe that much importance can be attached to this because of the very long period of time which separates the two forms.

This problem can also be approached from the point of view of the histological structure of the armour in *Deltoptychius* (figures 29, 35; figure 61, plate 26; figure 71, plate 28). The dermal bones of typical arthrodires such as dolichothoracids and brachythoracids consist of three layers which are in a general way comparable to the three layers seen in *Deltoptychius*. There is an outer layer of tubercles, normally formed of semi-dentine (Ørvig 1951, p. 348), a middle layer of cancellar bone and a basal layer of lamellar bone: these last two layers contain osteocyte spaces. Although in *Deltoptychius* the armour consists of three roughly similar layers, the two inner layers (lamellar tissue and osteodentine) contain no cell spaces, and the surface tubercles are formed of true dentine. It is possible that phylogenetic changes might transform the bone and semi-dentine of arthrodire armour into the dentine-like tissue of *Deltoptychius* armour, in the same way as dentine seems to have replaced bone in the fin spines of acanthodians (p. 196), but there is no evidence that this has taken place, and the complete dissimilarity between the morphology of the armour of *Deltoptychius* and that of typical arthrodires is against it. A more fruitful comparison seems to be between the armour of holocephalans and the fin spines.

In histological structure, the armour of Chimaeriformes (known only in *Deltoptychius*, *Myriacanthus* (figure 15) and *Chimaeropsis* (p. 144)) is very like the fin spines, with one remarkable difference, that the structure of the armour in one species is not like that of the fin spine in the same species, but like that of much later forms. Thus the armour of *Deltoptychius* (figures 29, 35), with about half the thickness of osteodentine and half of lamellar tissue, is similar to the fin spine of the Liassic *Metopacanthus* (figure 22) or the Upper Jurassic *Ischyodus* (figure 4*B*). In the same way, the armour of *Myriacanthus* (figure 15), which consists almost entirely of lamellar tissue, is quite unlike the fin spine (figure 17), which is almost all osteodentine, but like the fin spine of living chimaeroids (figure 4*A*). These facts suggest that the armour of Chimaeriformes has gone through the same changes in histological structure as the dorsal fin spine, with the gradual replacement of osteodentine by lamellar tissue, but that these changes took place in the armour much earlier than they did in the spine: speaking in the most general terms, in the Lower Carboniferous the armour has reached the stage shown by the fin spines in the Jurassic, and in the Lower Jurassic the armour has reached the stage seen in the fin spines of Tertiary and Recent forms. From this general similarity to the dorsal fin spine, we can draw several tentative conclusions about the armour. First, both the armour and the fin spine are likely to have originated in the same way: this is to be expected as both are thought to have originated by fusion of scales (pp. 196, 203). Secondly, the time-lag between the histological changes in the armour and those in the fin spine suggests that the armour originated long before the fin spine (this conclusion had also been reached by different means, p. 197). Thirdly, we can extrapolate back in time in the series of histological changes and predict that when the armour first appeared it consisted, as did the fin spine, entirely of osteodentine, and it is likely that this appearance was in the Devonian.

The only known Devonian armour which fits this prediction—plates consisting of osteodentine with tubercles of dentine on the surface—is *Eczematolepis fragilis* (Newberry). This is one of the species from the Onondaga of New York mentioned above (p. 202) as showing some similarity to the armour of *Deltoptychius* in morphology, and it is the only one of these in which the histological structure is known (Ørvig 1957, p. 329). Ørvig describes these plates as consisting of 'trabecular bony tissue without cell-spaces which is not essentially different from that in the exoskeleton of various Elasmobranchiomorph fishes, e.g. in the basal part of the teeth and spines of some selachians'. This definition appears to mean osteodentine in the sense in which the term is used here. The surface tubercles are made up of dentine penetrated by long dentine tubules arising from vascular canals below the tubercles. There is no enamel. Ørvig believes that these plates belong to ptyctodonts. He gives two reasons for this, first, they occur in the same beds as ptyctodont tooth plates, and secondly, among arthrodires 'as far as is now known, exoskeletal elements consisting of much the same dentine and acellular bone tissue as in *Eczematolepis* are only met with in some, at least, of the Ptyctodontida'. Ørvig gives no reference to published descriptions of ptyctodont armour with this type of structure. Wells (1944, pl. 7, figs. 2–4, 6–8) has figured without description thin sections of the armour of the ptyctodont *Rhynchodus* from the Lower Middle Devonian Columbus and Delaware formations of Ohio, the horizons from which Ørvig's *Eczematolepis* came. Of these sections, that in figure 6 seems to have a basal lamellar layer, but that in figure 2 is apparently trabecular throughout its depth: figures 4 and 8, however, show that these tissues contain abundant osteocyte spaces, and are not comparable either with *Eczematolepis* or with the armour of holocephalans.

To sum up this discussion, the armour of *Deltoptychius* cannot be homologized with that of any arthrodire. The structure of the tesserae in parts of the armour of *Deltoptychius* suggests that the armour is in a primitive condition and is not undergoing secondary reduction. Comparison of the histology of the armour with that of holocephalan fin spines suggests that the armour originated in the Devonian and that it consisted originally of osteodentine. The only known armour of this type is the Middle Devonian *Eczematolepis*. *Eczematolepis* and similar forms are similar in shape to the mandibular spines and the posterior spines of the head shield in primitive Chimaeriformes. There is no evidence of armour in any holocephalan group except the Chimaeriformes, nor is there evidence that any unarmoured holocephalan is more primitive than the armoured forms.

VI. THE ORIGIN OF THE HOLOCEPHALI

The results of the discussion (§ V) of the comparative anatomy of various characters of Chimaeriformes can be summarized as follows. Of the characters of chimaeroids listed on p. 111, the ethmoid canal, interorbital septum, three pairs of tooth plates, tritors, notochordal calcifications, dorsal fin spine, reduced squamation, placoid scales, specialized scales surrounding the sensory canals, tenacula and frontal clasper have all been acquired as specialized characters during the evolution of the chimaeroids from primitive Chimaeriformes like the menaspoids. There is no evidence of conditions in the early holocephalans with regard to the hyoid arch, rostral and labial cartilages, pectoral fin, second dorsal fin and pattern of sensory canals. The remaining characters, the holostylic suspension, tubular dentine of the tooth plates, position of the branchial arches, synarcual, separation of the halves of the pelvic (and also of the pectoral) girdle and the pelvic claspers appear to be primitive, and are to be expected in the ancestor of the holocephalans. In addition, this ancestor will have a complete covering of cyclomorial scales.

In the discussion of the affinities of *Helodus* (p. 183) it was proposed that a question of great importance in holocephalan phylogeny is whether *Helodus* is more primitive than menaspoids like *Deltoptychius*. The answer to this question was found to rest on three points, the nature of the dentition in the earliest holocephalans, the mode of origin of fin spines, and the significance of armour in menaspoids. These three points have been discussed at some length in § V. In no case is the evidence sufficiently complete for an unequivocal answer. There is some evidence that the earliest holocephalans did not have a shark-like dentition of the type seen in *Helodus*. The fin spines of *Helodus* and the Chimaeriformes appear to have originated independently. The armour of menaspoids is probably not a primitive feature of the holocephalans as a whole. These three tentative conclusions suggest that neither *Helodus* nor *Deltoptychius* can be regarded as a primitive and generalized holocephalan: *Helodus* is specialized in its dentition and fin spine, *Deltoptychius* is specialized in its armour. These two forms appear to represent two independent lines of holocephalan evolution, *Helodus* belonging to a line including the Helodontiformes, Petalodontiformes and Edestiformes, and *Deltoptychius* to a line containing the

Chimaeriformes. The Copodontiformes are already present in the Upper Devonian (p. 191), and their dentition is not easily related to either of these lines: they probably represent a third group. The position of the Psammodontiformes is not yet clear, but their few large tooth plates place them near the Chimaeriformes. The Chondrenchelyiformes are probably another independent group. If a common origin for these groups is to be found, it must have been in the Middle Devonian or earlier.

In considering the origins of the holocephalans there are only two groups which need be considered as possible relatives. Although many authors had suggested that the chimaeroids are the most primitive living gnathostomes (the grounds on which this claim was made are summarized by Dean 1906, pp. 4, 5) until 1925 it seems to have been generally accepted that the holocephalans were related to the selachians and derived ultimately from a shark-like ancestor. Stensiö (1925, p. 189) proposed that the holocephalans might be more closely related to the arthrodires than to the selachians: this view has since gained considerable support and is now commonly held.

(*a*) *Evidence for relationship between Holocephali and Selachii*

The evidence in favour of a relationship between the holocephalans and the selachians has been summarized by Dean (1906), Goodrich (1909, p. 168) and Holmgren (1942, pp. 187–220). As Watson (1937, p. 141) noted, it has never been doubted that the holocephalans are close to the selachians. The chief exponent of the hypothesis of a selachian origin of the holocephalans was Dean (1906). Having reviewed all the literature and material then known he concluded that the chimaeroids 'are a highly modified group descended from selachian ancestors'. He found that the palaeontological evidence showed that the holocephalans originated much later than the sharks, and that the early holocephalans retained shark-like characters in the squamation, the frontal clasper (which he interpreted as a displaced fin spine), the retention of traces of segmentation in the anterior part of the vertebral column, and in the distribution of the tritors on the anterior teeth of *Myriacanthus*. None of these points now carries any weight: the earliest sharks appear in the Middle Devonian, the earliest undoubted holocephalans in the Upper Devonian, this difference is not of great importance; the squamation of holocephalans has evolved in parallel with but independent of that in sharks so far as its history is known (p. 197); the frontal clasper is not a modified fin spine; the arrangement of the tritors is not significant (p. 192).

There is little point in discussing the similarities of the soft parts in holocephalans and selachians since no direct comparison with arthrodires is possible. Similarly, the point made by de Beer & Moy-Thomas (1935, p. 307) that there is a great similarity between chimaeroids and sharks in the 'histological picture presented by sections' is not admissible since no comparison with arthrodires is possible.

Only two of the resemblances between selachians and holocephalans seem worth reiterating:

(1) In both groups the endoskeleton is cartilagenous and without bone, and no bone-cells have yet been discovered as a normal feature in any member of either group.

(2) In both groups cartilage calcifies in polygonal prisms. This type of calcification is not known to occur in any arthrodire (Ørvig 1951, p. 345), and although Ørvig (1951,

p. 426) has shown that forms with prismatic calcifications are descended from forms with globular calcification of arthrodire type, this remains a striking similarity between the two groups.

Other resemblances which once appeared very striking such as the presence of pelvic claspers, similar egg-cases and ceratotrichia in both selachians and holocephalans have lost much of their force with increased knowledge of arthrodires. Pelvic claspers are known in the ptyctodont *Ctenurella* (Ørvig 1962, p. 56) and it follows that egg-cases are likely to have been formed. Ceratotrichia have been described in *Bothriolepis* (Stensiö 1948, p. 166; Jarvik 1959, p. 17).

The present study has not produced any new evidence of affinity between holocephalans and selachians, but has suggested that the dentition of holocephalans is perhaps less closely related to that of selachians than it was previously thought to be. In the structure of the fin spines and the dentition, the holocephalans and selachians have evolved in parallel throughout a large part of their history. I think that these points are strong evidence of genetic affinity between the two groups, but I do not believe that any direct relationship between the two groups is at present demonstrable.

(*b*) *Evidence for relationship between Holocephali and Arthrodira*

Stensiö (1925, p. 189) first proposed the possibility of a relationship between the holocephalans and the arthrodires. He noted six resemblances between the two groups:

(1) The nature of the joint between the head and the vertebral column.

(2) The presence of an operculum.

(3) The resemblance between the dentition of specialized arthrodires and chimaeroids.

(4) The dorsal extension of the pelvic girdle.

(5) The general shape of the body.

(6) Certain characters of the arterial system.

In 1934 (pp. 29, 66–68) Stensiö added:

(7) The position of the branchial arches below the neurocranium.

(8) The superognathals of arthrodires have the same relations with the endoskeleton as the upper tooth plates in chimaeroids.

(9) The presence of a well-developed rostral face in the neurocranium.

Holmgren (1942, pp. 215–220) pursued Stensiö's ideas further and compared the chimaeroids with the ptyctodonts, then well known only by *Rhamphodopsis* Watson (1938), in which the tooth plates are most chimaerid-like. Holmgren found the following additional resemblances between *Rhamphodopsis* and the chimaeroids:

(10) The short and deep palatoquadrate (based on his interpretation of the floor of the orbit in chimaeroids as a subocular shelf, not an otic process).

(11) The structure of the first dorsal fin, with a spine and a triangular basal cartilage.

(12) The structure of the second dorsal fin.

(13) The resemblance between the two rows of scales near the mid-line of the back in *Callorhynchus* and the median ridge-scales of *Rhamphodopsis*.

(14) The structure of the labial cartilages (based on his reinterpretation of the structure described by Watson as the hyoid arch in *Rhamphodopsis*).

(15) The presumed homology between the sensory canal bones of arthrodires and the crescents around the sensory canals in chimaeroids, and between the non-sensory canal bones of arthrodires and the calcifications in the corium of *Callorhynchus* (see p. 201).

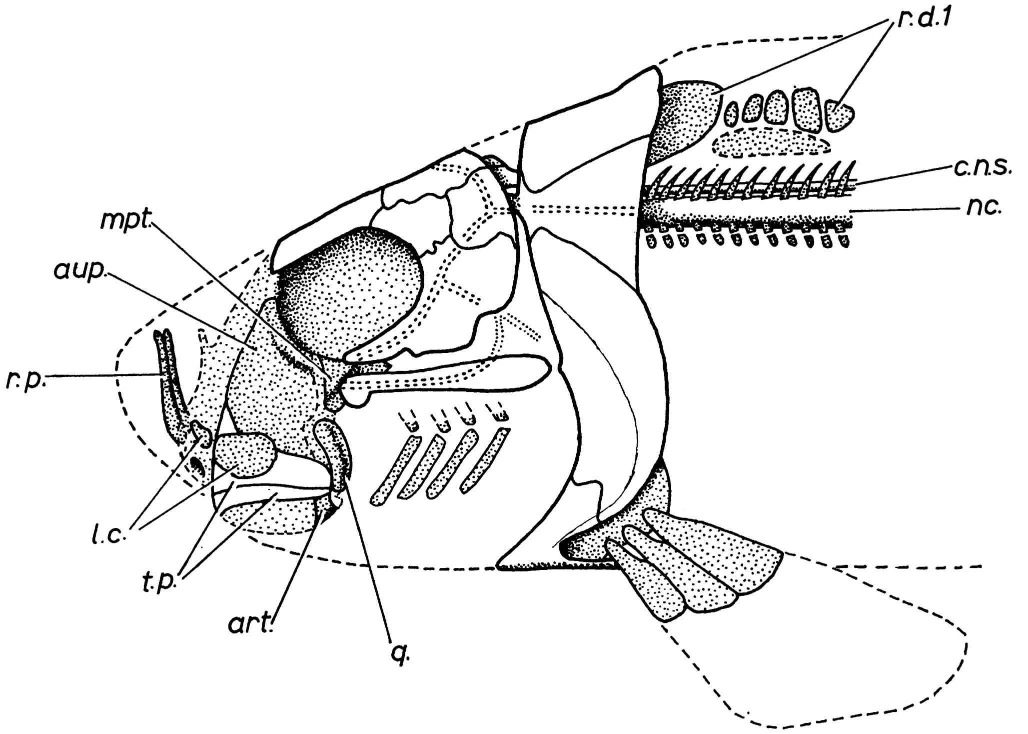

FIGURE 43. *Ctenurella gladbachensis* Ørvig. Restoration of skeleton of the head and anterior part of the trunk in lateral view (× 3 approx.). After Ørvig (1962). *art.*, Articular ossification; *aup.*, autopalatine ossification; *c.n.s.*, nerve cord; *l.c.*, labial cartilages; *mpt.*, metapterygoid ossification; *nc.*, notochord; *q.*, quadrate ossification; *r.d.*1, radials of first dorsal fin; *r.p.*, rostral processes; *t.p.*, tooth plates.

Ørvig (1960) described a new and excellently preserved ptyctodont, *Ctenurella* (figures 43, 44), in which the following chimaeroid features are present:

(16) Paired upwardly directed rostral processes (*r.p.*).

(17) A crested synarcual.

(18) A pair of tuberculated, pre-pelvic spines, held by Ørvig to be homologous with the tenacula of chimaeroids (*ten.*).

(19) The (presumed) presence of a small pair of anterior tooth plates in the upper jaw.

(20) The shape of the neurocranium—short, high, with an elongated, antero-ventrally directed ethmoid region, a fairly narrow interorbital septum, and short otic and occipital regions.

In 1962 Ørvig added four more resemblances to chimaeroids in *Ctenurella*:

(21) The short palatoquadrate, with a metapterygoid process passing back below the eye (*mpt.*).

(22) The position of the mandibular articulation and the shape of the mandible.

(23) The presence of a strip of labial cartilage alongside the upper jaw (*l.c.*).

(24) The presence of pelvic claspers.

Finally, Stensiö (1963, pp. 377, 381, 405, 407–9) has given further attention and emphasis to a number of these points, in particular the nature of the operculum and the suspension of the jaws, and has added two more resemblances:

(25) In several arthrodire orders the infrapharyngo-premandibular (palatoquadrate commissure) is fused into the neurocranium, as in chimaeroids, not into the palatoquadrate as it is in selachians.

(26) In ptyctodonts the fenestra endonarhina communis opened ventrally, as it does in chimaeroids.

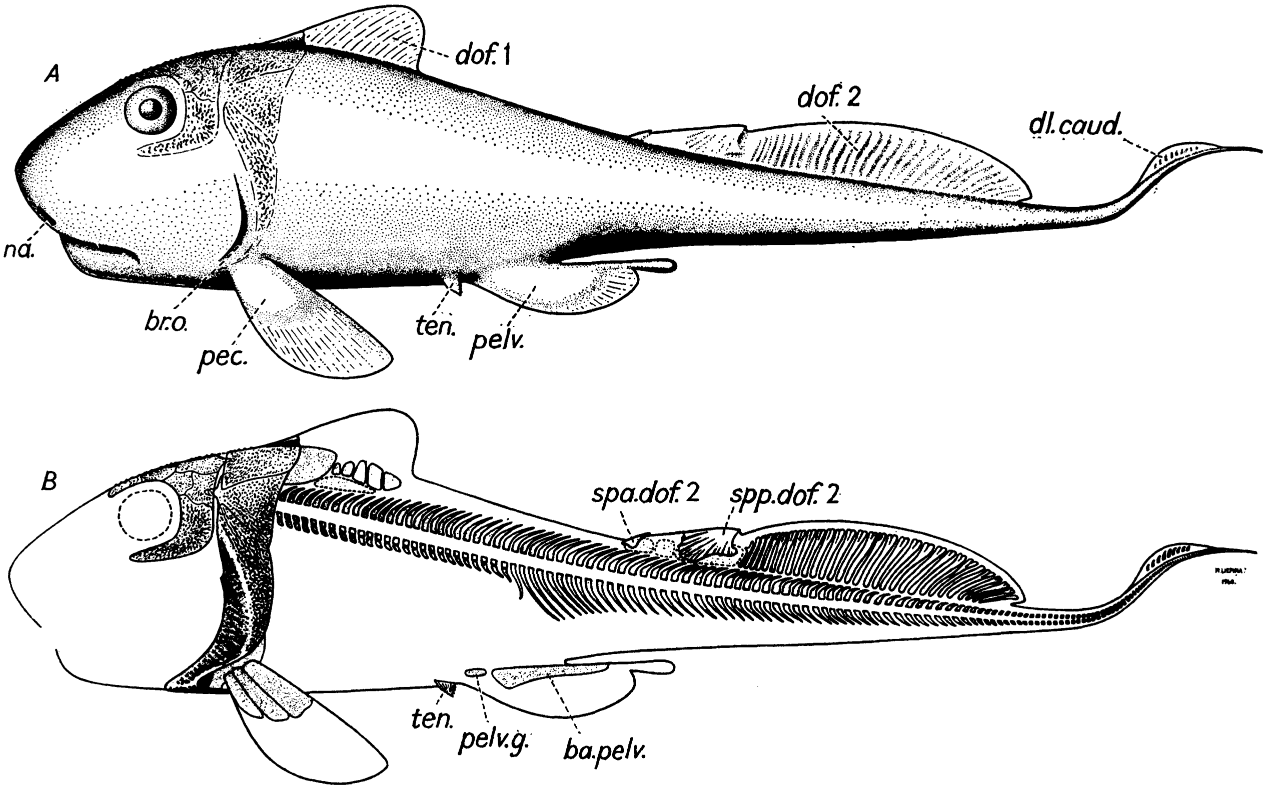

Figure 44. *Ctenurella gladbachensis* Ørvig. Restorations of fish in lateral view (× 1 approx.). From Ørvig (1960). *ba.pelv.*, Basal of pelvic fin; *br.o.*, branchial opening; *dl.caud.*, *dof.*1, *dof.*2, dorsal lobe of caudal fin, first and second dorsal fins respectively; *na.*, nostrils; *pec.*, *pelv.*, pectoral and pelvic fins; *pelv.g.*, ossification in pelvic girdle; *spa.dof.*2, *spp.dof.*2, anterior and posterior spines of second dorsal fin; *ten.*, tenaculum-like structure in front of pelvic fin.

These twenty-six points of similarity between arthrodires and holocephalans are of very unequal value. The most striking resemblances seem to be those of the branchial region: the structure of the joint between skull and vertebral column, the crested synarcual, the operculum, and the position of the branchial arches (1, 2, 7, 17). Among holocephalans these characters are not confined to the chimaeroids, but appear to be primitive for the group as a whole (p. 205). It is possible that the cranial joint and the synarcual might have developed independently in holocephalans in connexion with the first dorsal fin, and there is little direct evidence (p. 193) that this is not so. At first sight, this group of characters appears to provide strong evidence for the descent of holocephalans from forms in which body armour was present, since all these characters in arthrodires seem to be connected with the body armour. But White (1952, p. 290) has argued convincingly that the endoskeletal cranial joint of arthrodires developed before the exoskeletal armour, that a cervical joint was present in the armour when it first appeared, and that the function of this joint was primarily respiratory. If this is true, it follows that the occipital joint, the operculum, the anteriorly placed branchial arches and possibly the synarcual must have been present in the primitive arthrodires in which the scales had not yet fused into armour. The occurrence of these characters in holocephalans is therefore not necessarily evidence of relationship only with armoured arthrodires, but also with primitive unarmoured forms.

The four characters of the branchial region discussed above not only ally the holocephalans and arthrodires, but set the holocephalans sharply apart from the selachians. The same is true of the structure of the second dorsal fin (12), which seems to have borne a spine and resembled the first dorsal in the earliest selachians, of the fusion of the palatoquadrate commissure with the neurocranium (in pachyosteomorphs, dolichothoracids and coccosteomorphs) (25), and of the paired rostral processes and the 'tenacula' in *Ctenurella* (16, 18). As noted on p. 199, 'tenaculum'-like structures are also present in the stensioellid *Stensioella*, which in other ways is very unlike the ptyctodonts, and these structures may be of wide distribution in the arthrodires. Their resemblance to the tenacula of chimaeroids is probably fortuitous, since it is shown on p. 199 that chimaeroid tenacula are represented in primitive Chimaeriformes simply by groups of enlarged scales. Paired rostral processes and a second dorsal fin of chimaeroid type are known among arthrodires only in the ptyctodonts, but the very simple second dorsal of holocephalans seems to be simply an almost unmodified part of the median fin fold, and is therefore not necessarily evidence of relationship with the ptyctodonts in particular.

Less weight can be attached to the presence of pelvic claspers in *Ctenurella* (24) and the structure of the first dorsal fin in ptyctodonts (11) since pelvic claspers are also present in Devonian sharks (*Diademodus*), and a first dorsal fin of this type not only occurs in early sharks (*Ctenacanthus*) but is of sporadic distribution among arthrodires and was probably not present in early holocephalans (p. 197).

The similarity between the dentition of arthrodires and chimaeroids (3, 8, 19) has long been known, but the variability in the number of tooth plates in myriacanthoids and menaspoids shows that it is not possible to make direct comparisons between the two pairs of superognathals and one pair of inferognathals in most arthrodires and the three pairs of tooth plates in chimaeroids, nor is it necessary, as Ørvig (1960, p. 317) has done, to postulate an anterior superognathal in ptyctodonts. Further, Ørvig (1957, p. 321) has found that the histology of ptyctodont tooth plates shows that a direct relationship between ptyctodonts and holocephalans is unlikely. The dentition of holocephalans seems to show a general resemblance (8) to that of arthrodires (p. 191) but not to ptyctodonts in particular.

If the resemblance between the dentitions of ptyctodonts and holocephalans is not due to direct relationship but to convergence, then the similarities of the jaws (10, 21, 22) are equally likely to be convergent, and cannot be taken as independent evidence of relationship.

The holocephalans resemble the arthrodires in general in the shape of the body (5) and the rostral face of the neurocranium (9). The resemblances in the shape of the neurocranium (20, 26) and the labial cartilages (14, 23) are with ptyctodonts in particular, but these comparisons are known to apply only to advanced Chimaeriformes and, like the shape of the jaw, may well be convergent because of the similar dentition and feeding habits.

Stensiö's comparison between the dorsal extension of the pelvic girdle in arthrodires and chimaeroids (4) was based on the girdle in *Coccosteus*. In *Ctenurella* there is no dorsal extension (Ørvig 1960, text-fig. 5), nor is one present in *Helodus* (figure 38): the resemblance between *Coccosteus* and Chimaeriformes is doubtful evidence of relationship.

In ptyctodonts there are one or two small spines (enlarged scales?) in the mid-line in front of the second dorsal fin, and in *Rhamphodopsis* there is a row of median ridge-scales between the second dorsal and the caudal fins. Holmgren and Ørvig compare these with the paired row of scales along the back in living chimaeroids (13). Paired rows of enlarged scales also occur along the back in menaspoids and *Squaloraja*, but there does not seem to be any good reason for comparing the median structures in ptyctodonts with the paired ones in holocephalans.

Holmgren's comparison (15) of the bones of the armour in arthrodires with the dermal calcifications which he found in *Callorhynchus* and the crescents surrounding the sensory canals in chimaeroids cannot be sustained. The crescents around the sensory canals are modified scales (p. 198) and the dermal calcifications, if in fact they are vestigial structures, are much more probably relics of the armour of myriacanthoids and menaspoids (p. 201), and there are no good grounds for relating this with arthrodiran armour.

Stensiö's comparison between the arterial systems of *Macropetalichthys* and chimaeroids (6) is based on the arrangement of the efferent branchials, the dorsal aorta and its main branches. These resemblances are almost certainly due to the similar position of the branchial arches in the two groups and cannot be taken as independent evidence of relationship.

There is one other possible resemblance between holocephalans and ptyctodonts which has arisen during this work, the similarity between the armour of the Carboniferous menaspoids and various fragments of Devonian armour such as *Eczematolepis* (p. 204) and the specimens described by Hussakof & Bryant (1918) (p. 202). These Devonian fragments occur in the same beds as ptyctodont tooth plates, and are thought by those who have described them to be ptyctodont armour. I believe that the apparent resemblance of these structures both to ptyctodonts and to armoured holocephalans is due simply to inadequate knowledge of the structures. Hussakof & Bryant's material has never been figured, and its microstructure is unknown. *Eczematolepis* agrees with the armour of holocephalans in being dentine-like, whereas ptyctodont armour, so far as is known at present (p. 204), is cellular bone.

This review of the resemblances between arthrodires and holocephalans shows that many of the presumed similarities between ptyctodonts and holocephalans do not stand up to critical examination, and of those which do the majority are generalized arthrodire characters rather than characters of ptyctodonts in particular.

The greatest obstacle to a relationship between the ptyctodont arthrodires and the holocephalans, and the one which has forced me to examine the supposed similarities between the two groups in the most critical light, is the structure of the armour and squamation in *Deltoptychius*. In ptyctodonts the trunk is naked, and in arthrodires generally the squamation is under reduction (Stensiö 1959, p. 13). *Deltoptychius*, like the early selachians, retains a complete covering of cyclomorial scales which agree in structure with Stensiö's type 'B' in arthrodires (1959, p. 13), such as occurs in *Gemuendina*, *Stensioella* and *Radotina*. The armour on the head of *Deltoptychius* is formed by fusion of scales of this type, and is not homologous with the armour of any known arthrodire. If the holocephalans have evolved from ptyctodonts or ptyctodont-like forms, as Holmgren and Ørvig believe, then it is necessary to assume that the armour of ptyctodonts, which is itself derived from that of less specialized arthrodires (petalichthyids according to Ørvig, arctolepids according to Westoll 1962, p. 952), must have been completely lost, that it must have broken up into cyclomorial scales, and that by the Lower Carboniferous these scales must have fused again into an entirely different type of armour which was again reduced and lost during the evolution of the Chimaeriformes. That this sequence of events has taken place seems extremely unlikely.

(*c*) *Conclusions*

To sum up the preceding discussion, there is evidence of genetic affinity between the holocephalans and the selachians, but no evidence of any direct relationship between the two groups. The holocephalans have a number of features which ally them with the arthrodires. The most important of these are the various features of the branchial region and the anterior part of the vertebral column, but it is likely that these were present in the unarmoured ancestors of the arthrodires. In the dentition, the shape of the skull and trunk, and perhaps in the pelvic girdle, the holocephalans also show resemblances to the arthrodires. In the paired rostral cartilages, the labial cartilages and the second dorsal fin the holocephalans resemble the ptyctodonts in particular. But the squamation and armour of *Deltoptychius* seem definitely to exclude the holocephalans from direct relationship with any known arthrodire group. Only in the rhenanid arthrodires (*Stensioella*, *Radotina*, *Gemuendina*, etc.) does the exoskeleton approach the generalized condition from which that of forms like *Deltoptychius* can be derived. Apart from the similarities in the exoskeleton there are one or two points in which there is some resemblance between the rhenanids and the holocephalans: in *Stensioella* there is a pair of tuberculated plates in front of the pelvic fins which is reminiscent of the tenacula of advanced Chimaeriformes (and the pelvic spines in the ptyctodont *Ctenurella*); in *Pseudopetalichthys* the pectoral fin is dibasal (Gross 1962, p. 75), as it is in all known Chimaeriformes and in *Helodus*, though this is probably of little significance when the structure of the pectorals in *Chondrenchelys* and *Fadenia* is taken into account (p. 194); Gross (1962, p. 73) compares the peculiar jaws of *Pseudopetalichthys* with those of holocephalans rather than arthrodires, although the 'teeth' in this form seem to be unlike those of any other fish; in *Gemuendina* Gross (1963) finds that there was no spiracle (p. 50), that the sensory canals on the head and trunk (except the supraorbital) were enclosed between peculiar double tubercles (p. 50) which seem very like those enclosing the supraorbital canal on the head shield of *Deltoptychius*, and that the pelvic girdle was very like that of *Chimaera* (p. 63); in *Farnellia*, known only by the holotype of *F. tuberculata* Traquair (1898, p. 69, pl. 1, fig. 4), from the Lower Old Red Sandstone of Farnell, Angus, Scotland, the vertebral column contains segmental ring-like 'centra' which seem very similar to those in *Chondrenchelys*, and White (personal communication) is of the opinion that *Farnellia* is related to the rhenanids. But against any relationship between the rhenanids and the holocephalans must be set the facts that body armour is present in all rhenanids, that the head shields of rhenanids are in general comparable with those of more normal arthrodires, and that in *Stensioella*, *Gemuendina* and *Jagorina* there is a suspensory hyomandibular.

It appears that the resemblances between the rhenanids and the holocephalans, particularly in the exoskeleton, are due simply to the primitive condition of the rhenanids*, not to any direct relationship. At present, one is led to the conclusion that the arthrodires are the group most closely related to the holocephalans, but that this relationship is not direct, and that the two groups must have diverged from a common ancestor. This hypothesis leaves much unexplained, especially the long period between the first appearance of the arthrodires in the Upper Silurian and that of the holocephalans in the Upper Devonian. On this hypothesis we are forced to assume that the resemblances between the ptyctodont *Ctenurella* and the chimaeroids are due to convergent evolution, perhaps acting on the similar gene pool which results from common ancestry at pre-arthrodire level. Ørvig, (1960, p. 333), realizing that the holocephalan characters of the ptyctodonts are largely those of the chimaeroids, postulated that the descendants of the ptyctodonts 'survived in a secluded niche of their own' until they appeared in the fossil record as chimaeroids in the Jurassic. But the gradual acquisition of such peculiar chimaeroid characters as the frontal clasper, the tenacula, the specialized scales around the sensory canals, etc., which can be demonstrated in the succession from the 'cochliodont' *Deltoptychius* through *Menaspis* and the myriacanthoids leaves little doubt of the true origin of the chimaeroids.

Many of the problems raised and left unsolved in this work can be expected to be settled in the future by work on the embryology of living chimaeroids and by search for well preserved holocephalans in marine deposits of Devonian and Carboniferous age. Zangerl & Richardson (1963, p. 125) have recently recorded the discovery of abundant 'placoderms' in marine shales of Pennsylvanian age: systematic studies of these fishes have not yet been made, but the description of 'animals of overall tadpole habitus, with a calcified cartilage skeleton and a set of presumably dermal bones and elements consisting of dentine' suggests immediately that these are menaspoids or related to the menaspoids. Detailed description of this new material should solve many problems.

It is a pleasure to acknowledge the help I have received during this work. Dr E. I. White, F.R.S., in whose department the work was done, has given me every encouragement, and has been kind enough to read the manuscript. I am particularly grateful to Mr S. E. Bendix-Almgreen of Copenhagen for allowing me to see his unpublished work

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* There is disagreement on the nature of the exoskeleton in rhenanids and stensioellids. Stensiö (1963, p. 403) interprets the tesserae in the exoskeleton of acanthothoracids, rhenanids and stensioellids as secondary products of the reduction from below of normal arthrodire dermal bones. He bases this opinion on the condition of the tesserae in *Jagorina* and on his interpretation of *Radotina* and acanthothoracids, the earliest arthrodires known, as highly specialized forms. Gross (1958, 1962, 1963), on the other hand, finds the tesserae in *Radotina*, rhenanids and stensioellids to be primary structures, preceding the formation of dermal bones, and concludes (1963, p. 72) that *Radotina*, the rhenanids and possibly the stensioellids should be made a third group of placoderms, equal in rank to the antiarchs and arthrodires.

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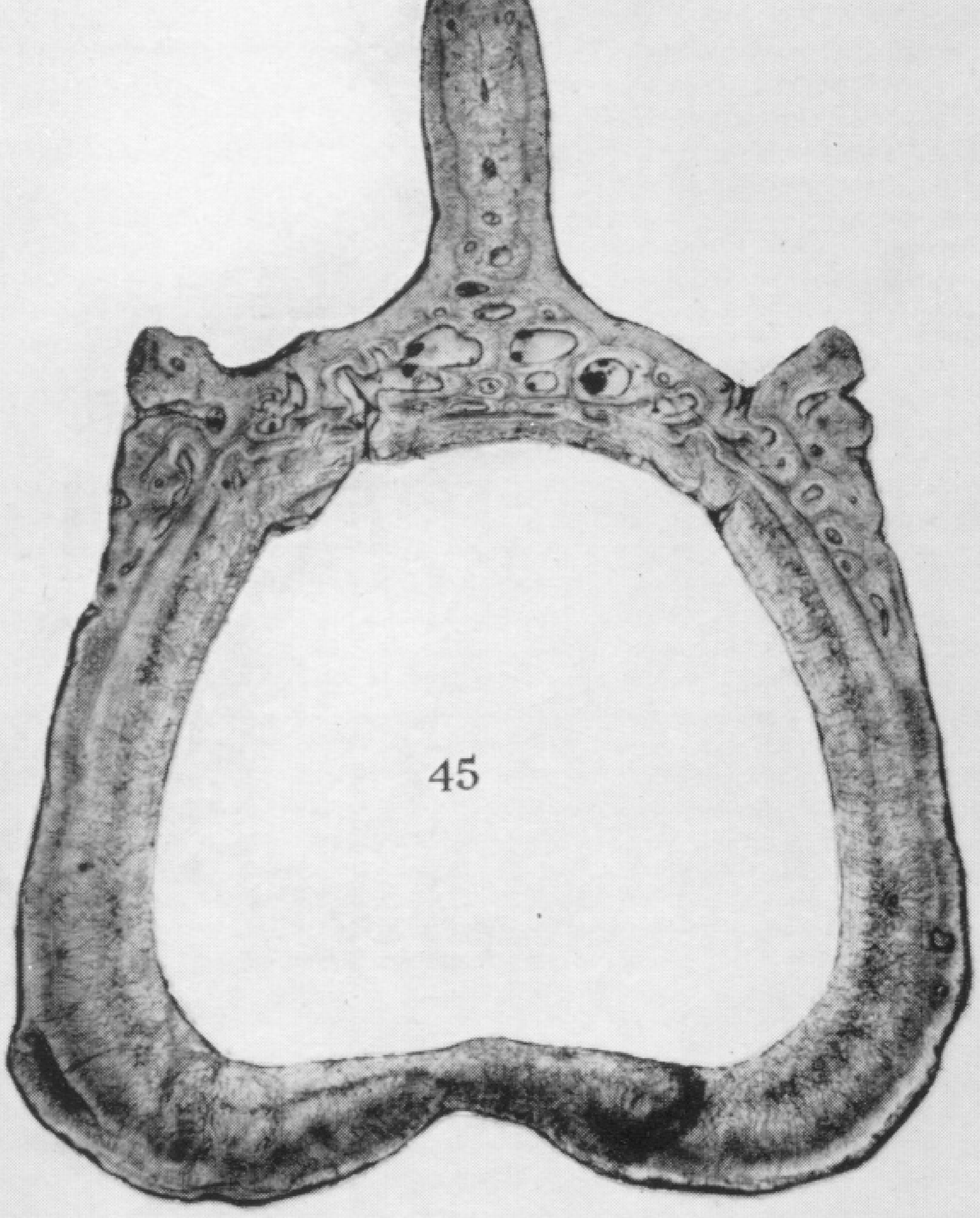
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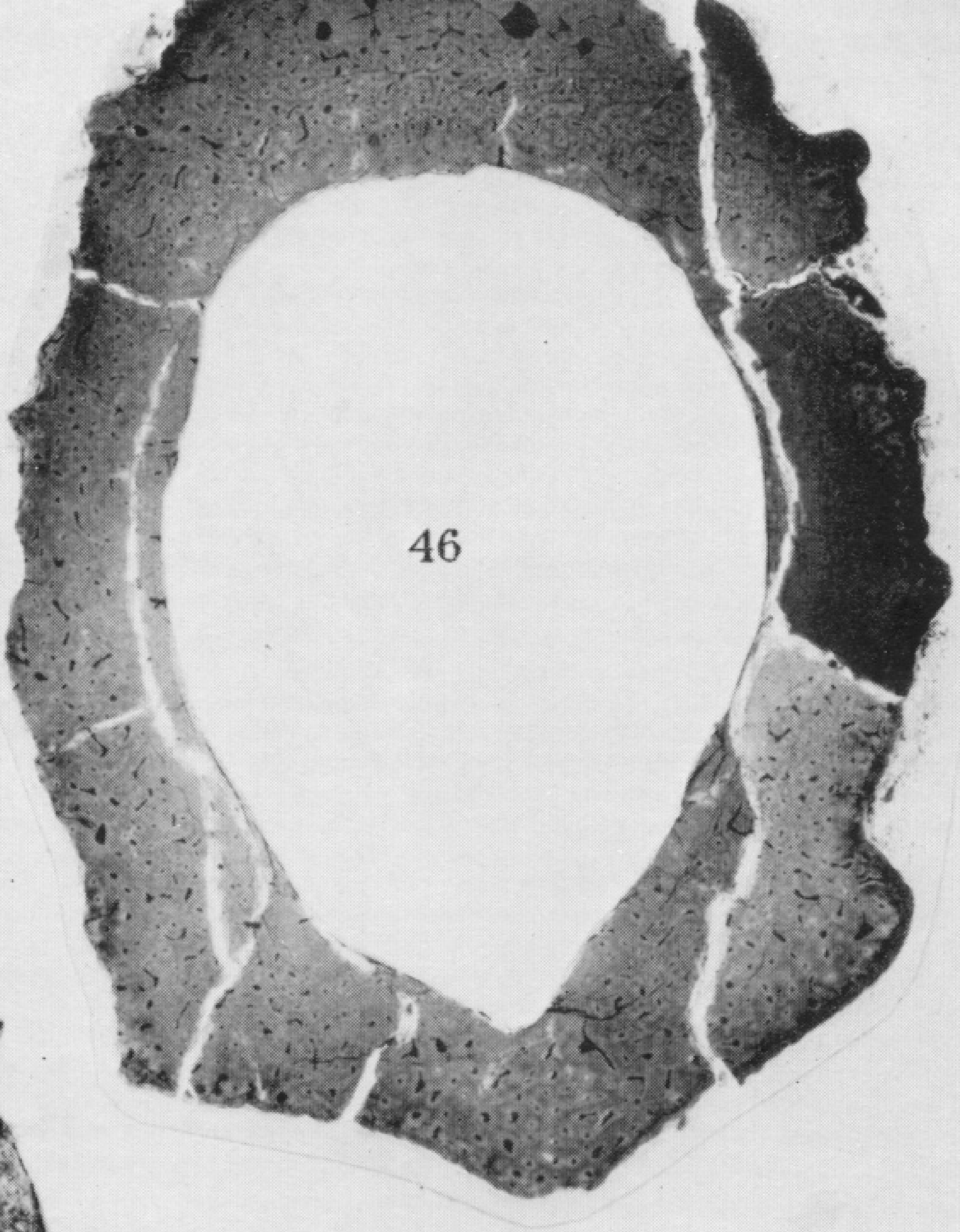
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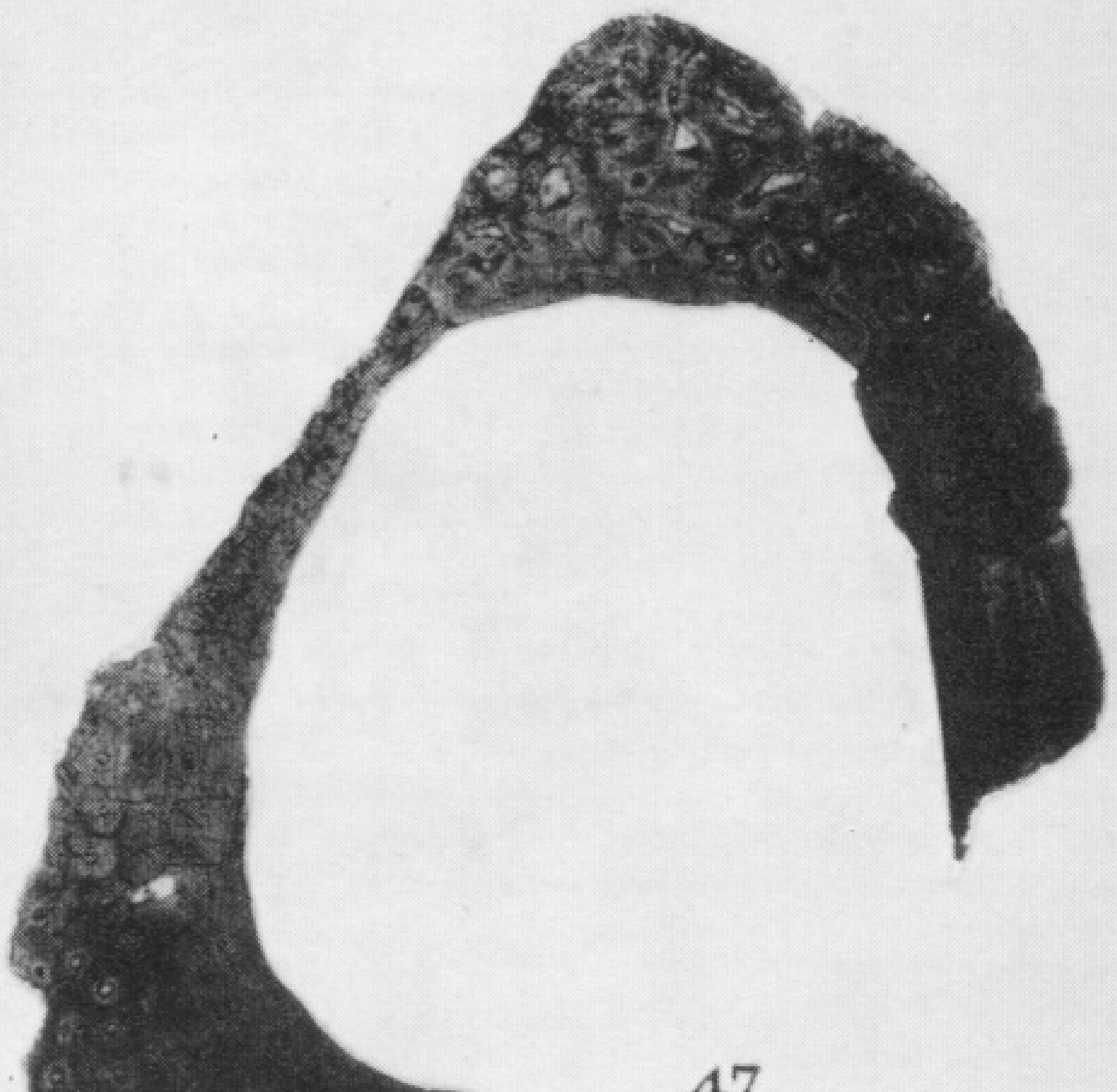
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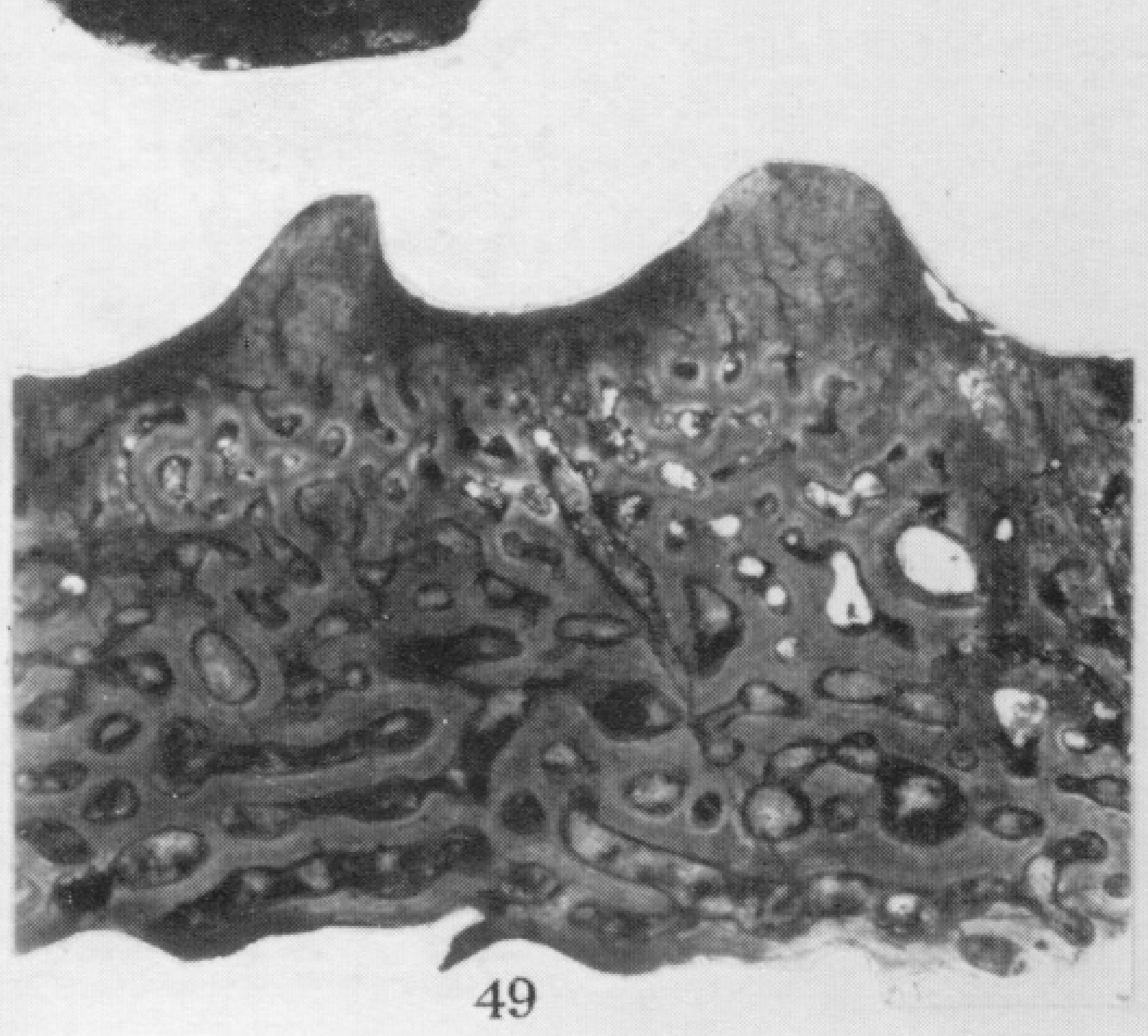
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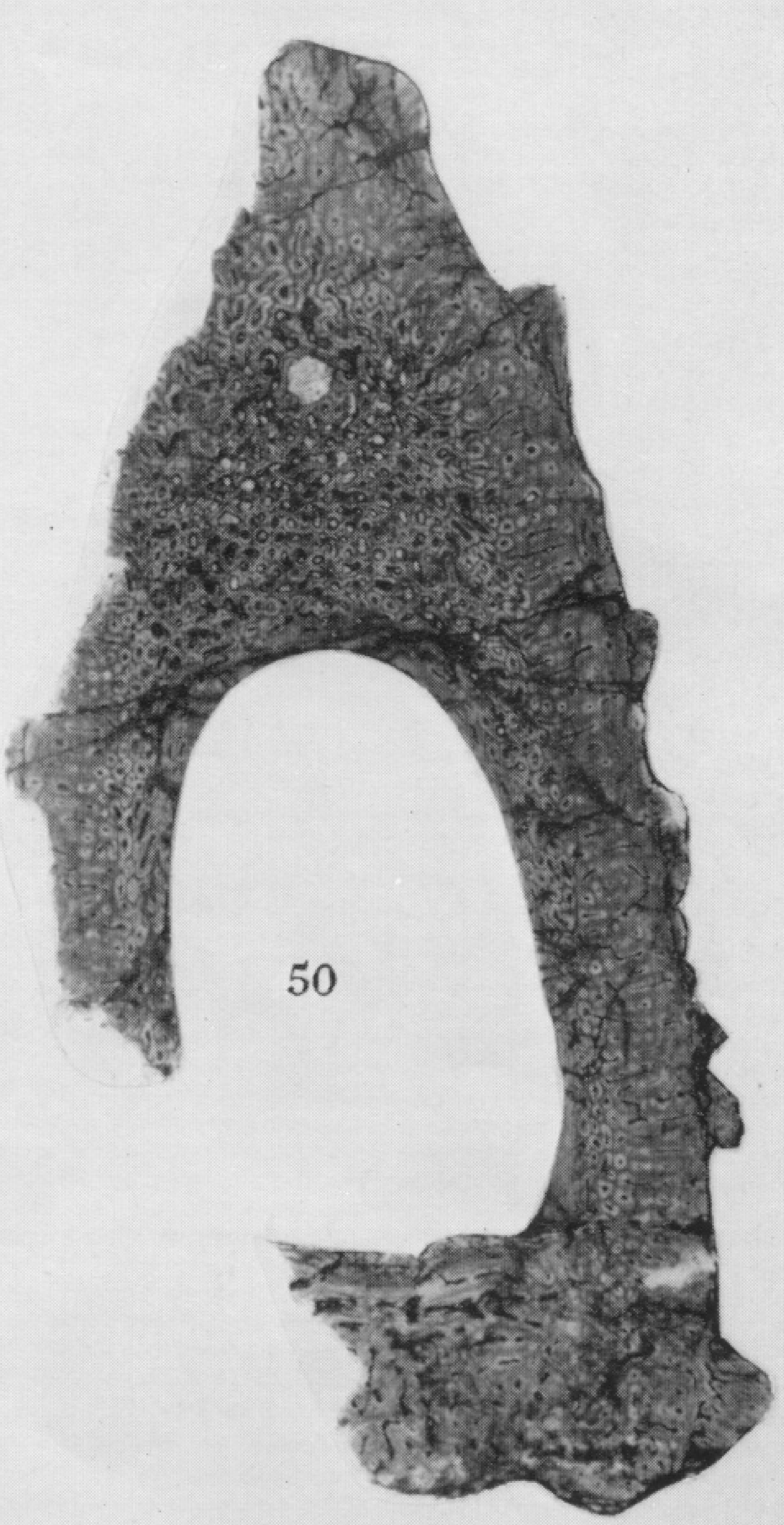
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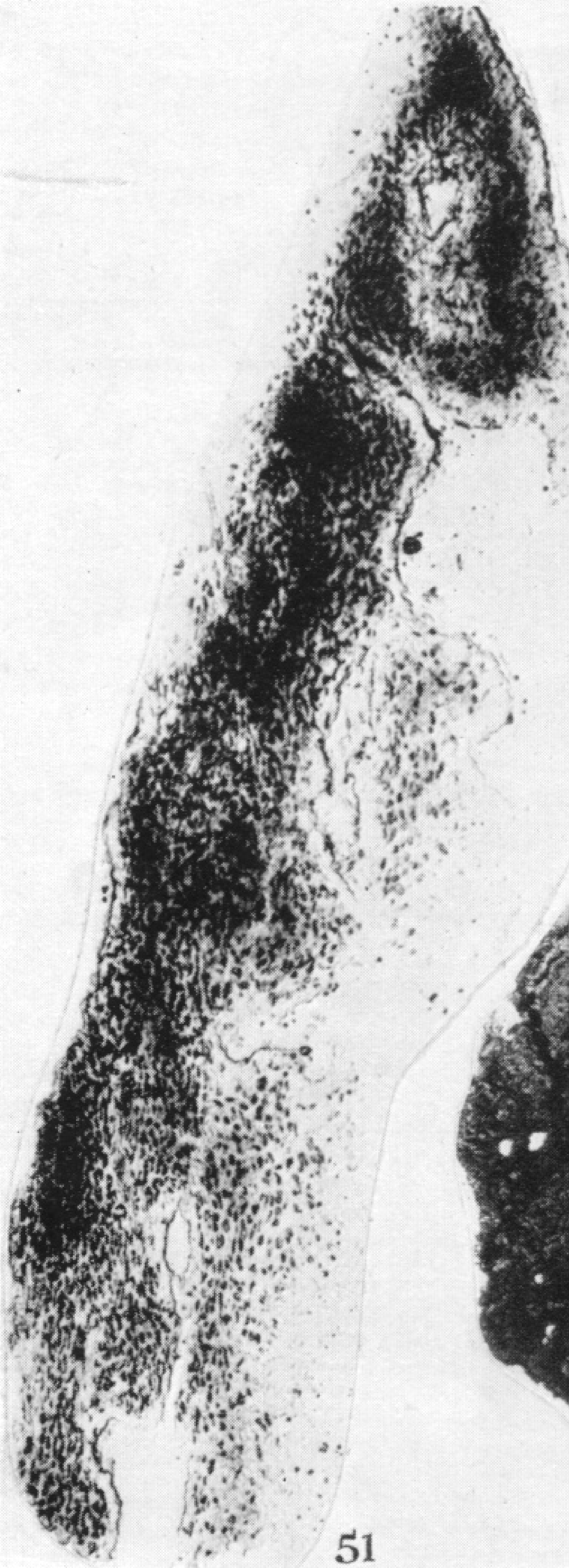

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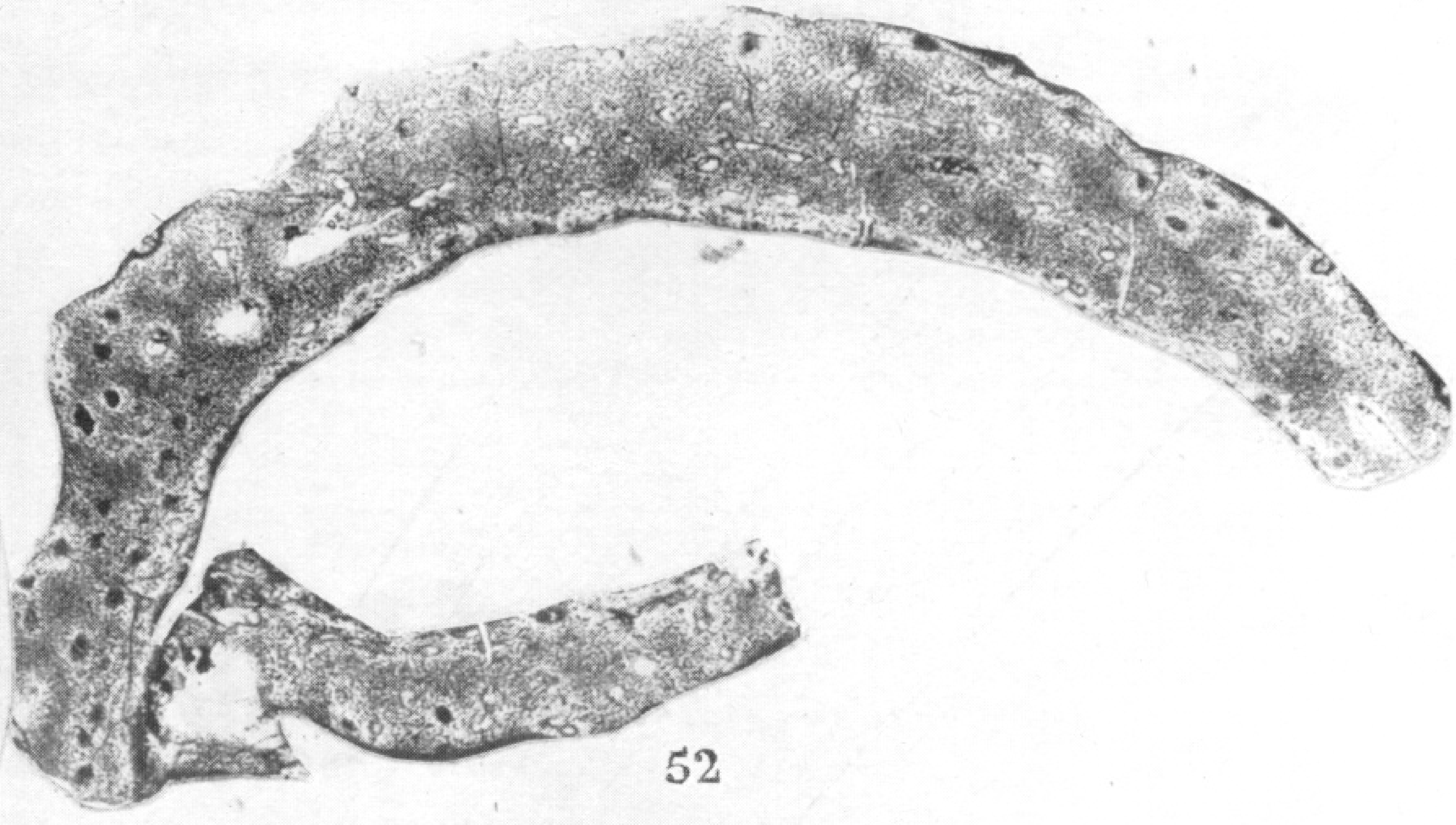

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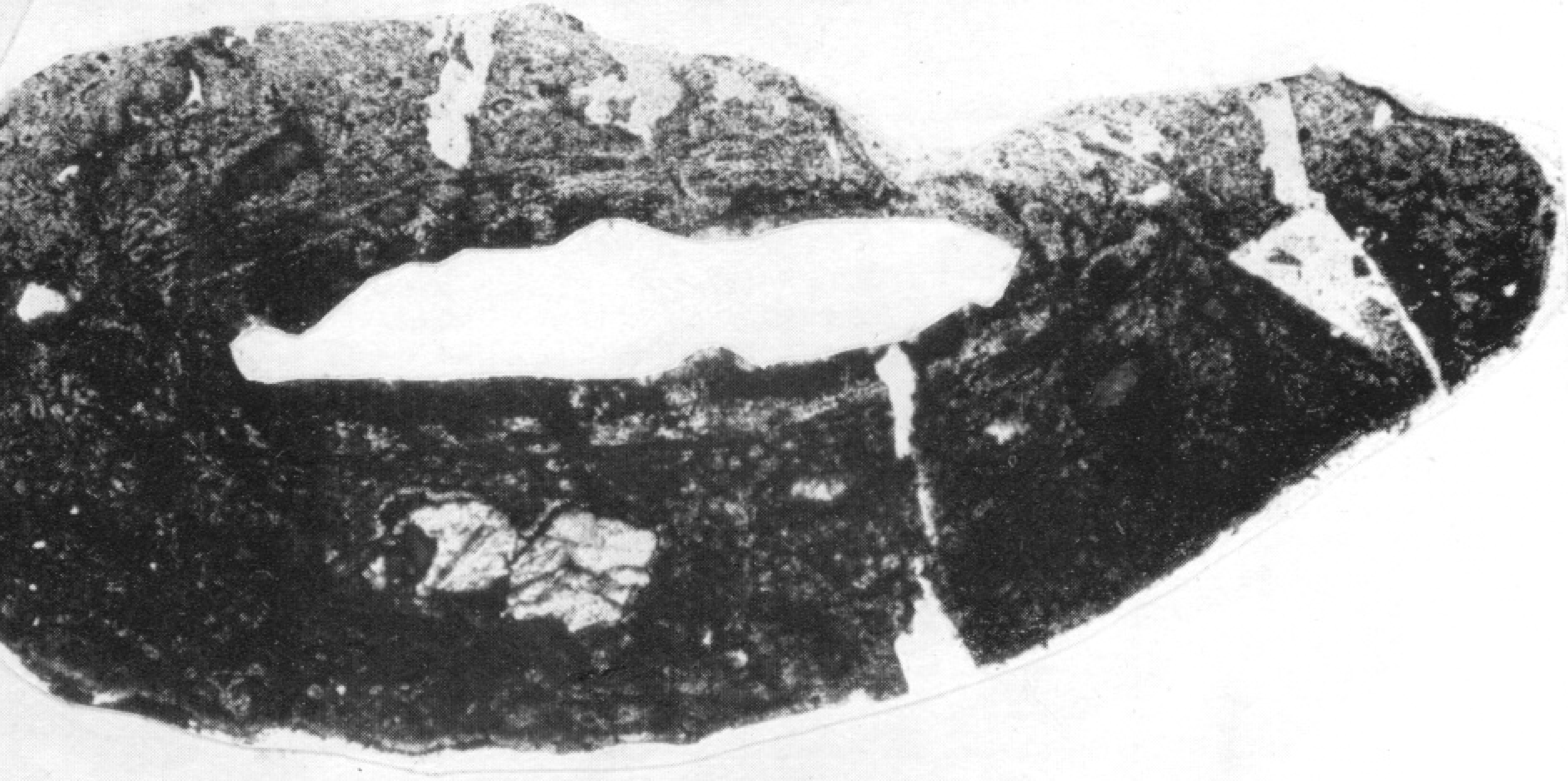

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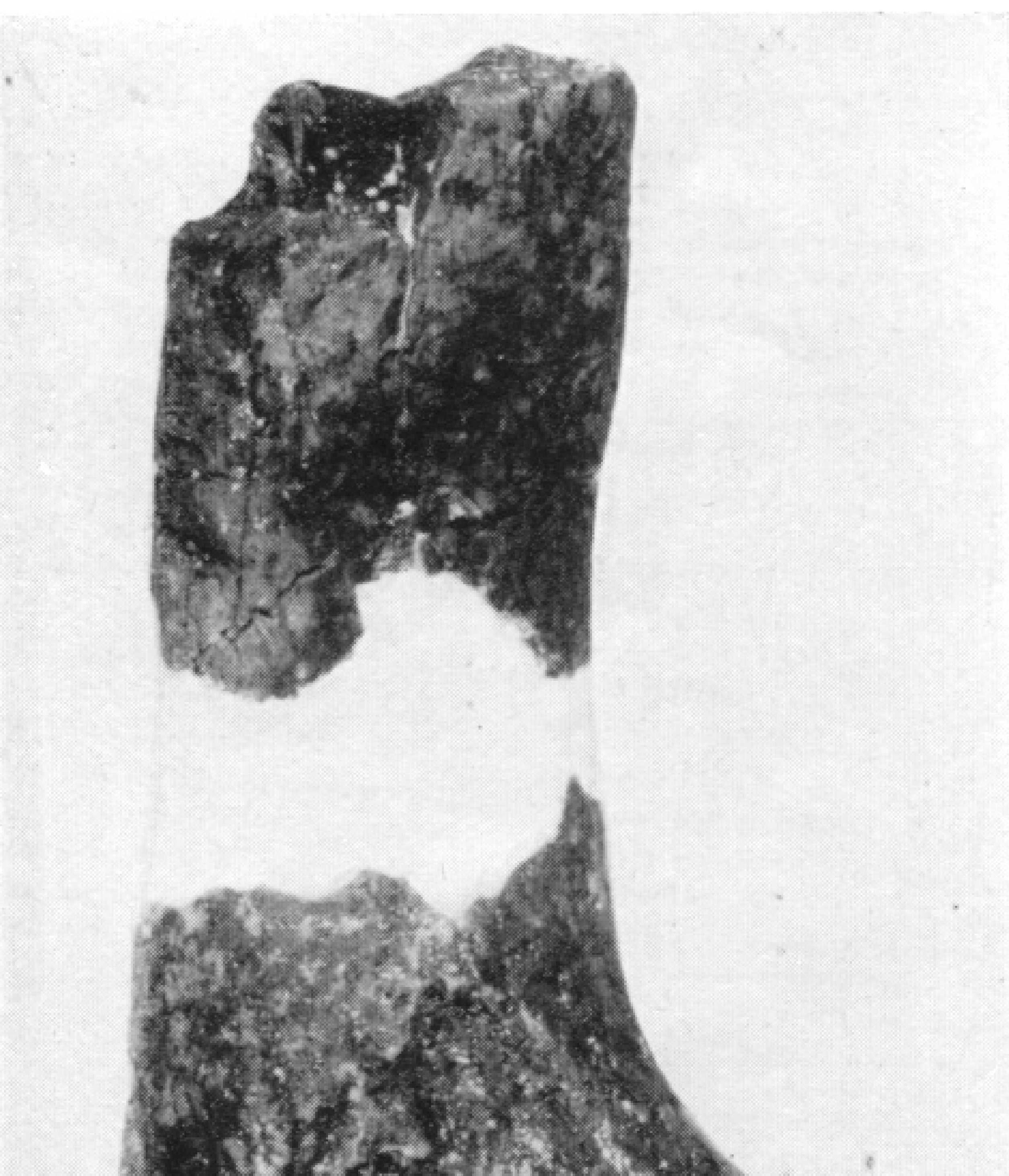

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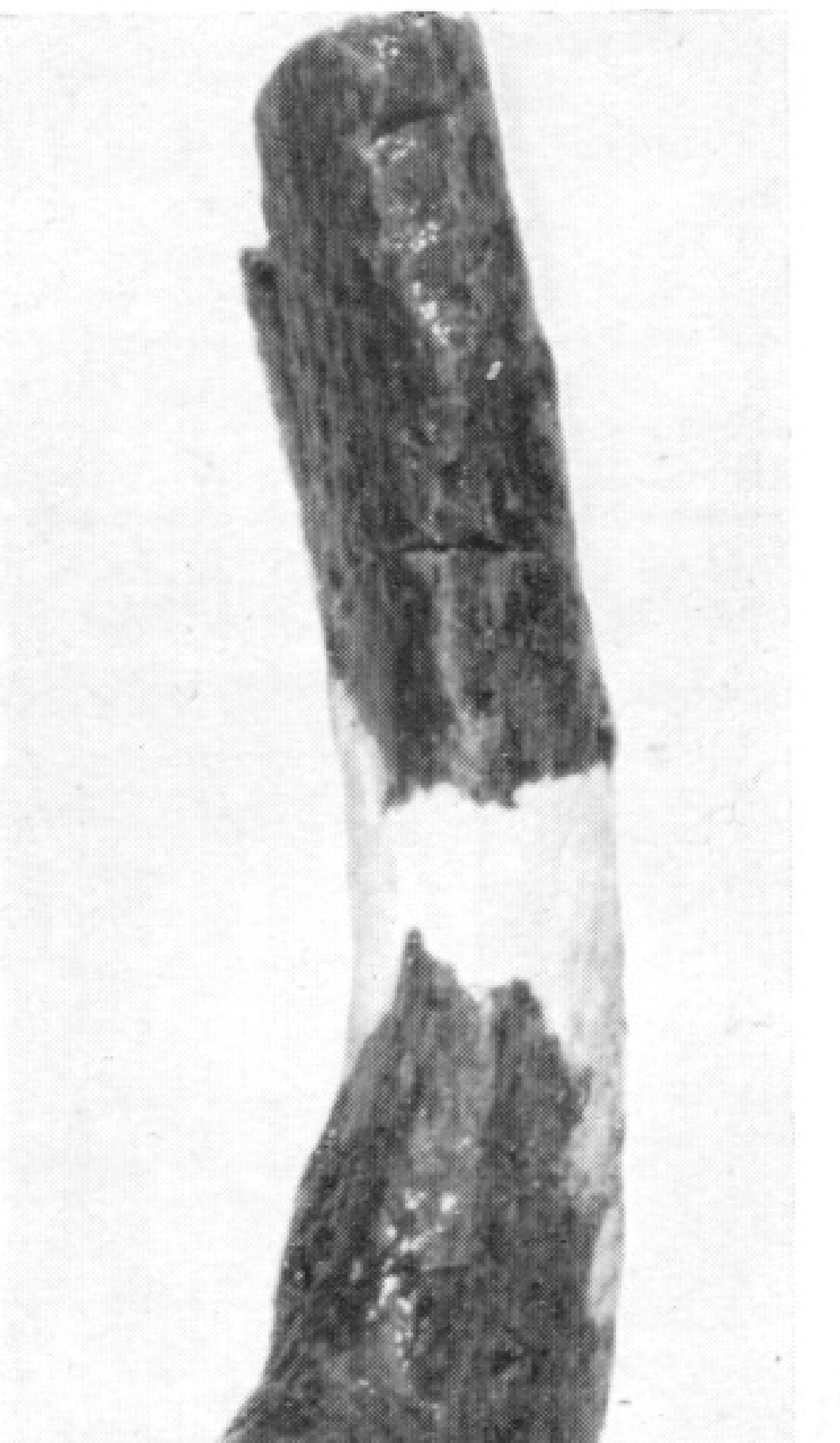

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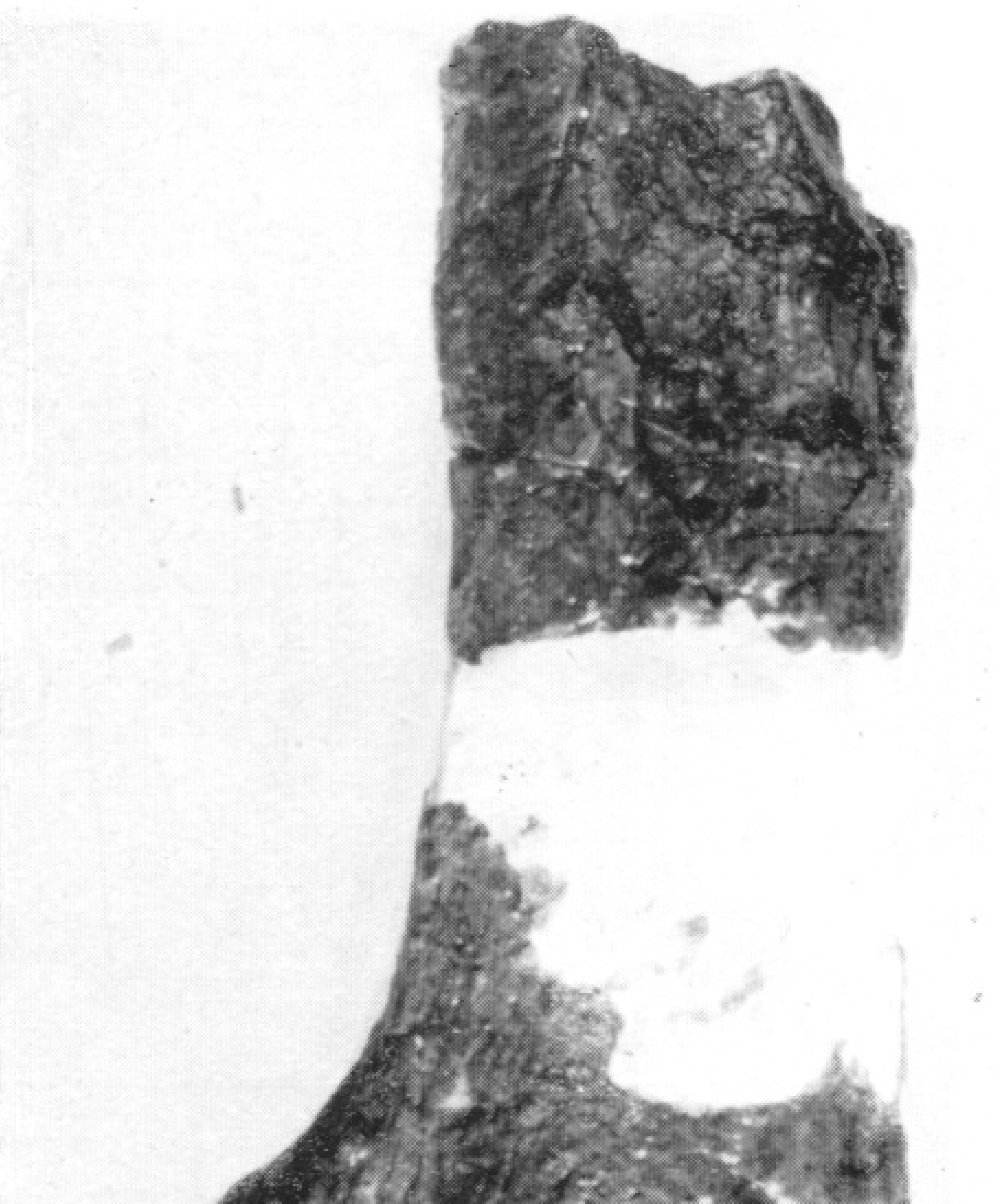

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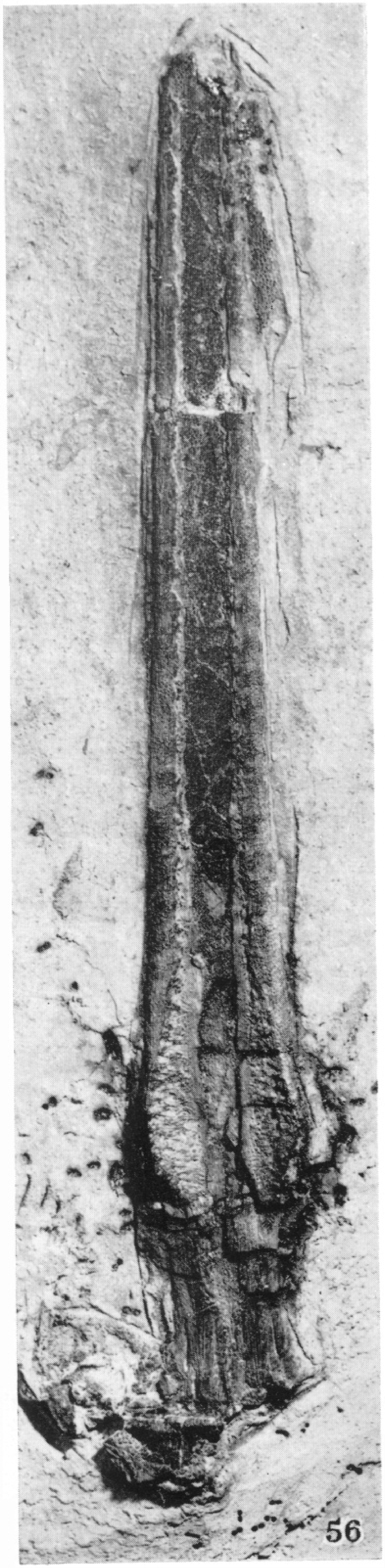

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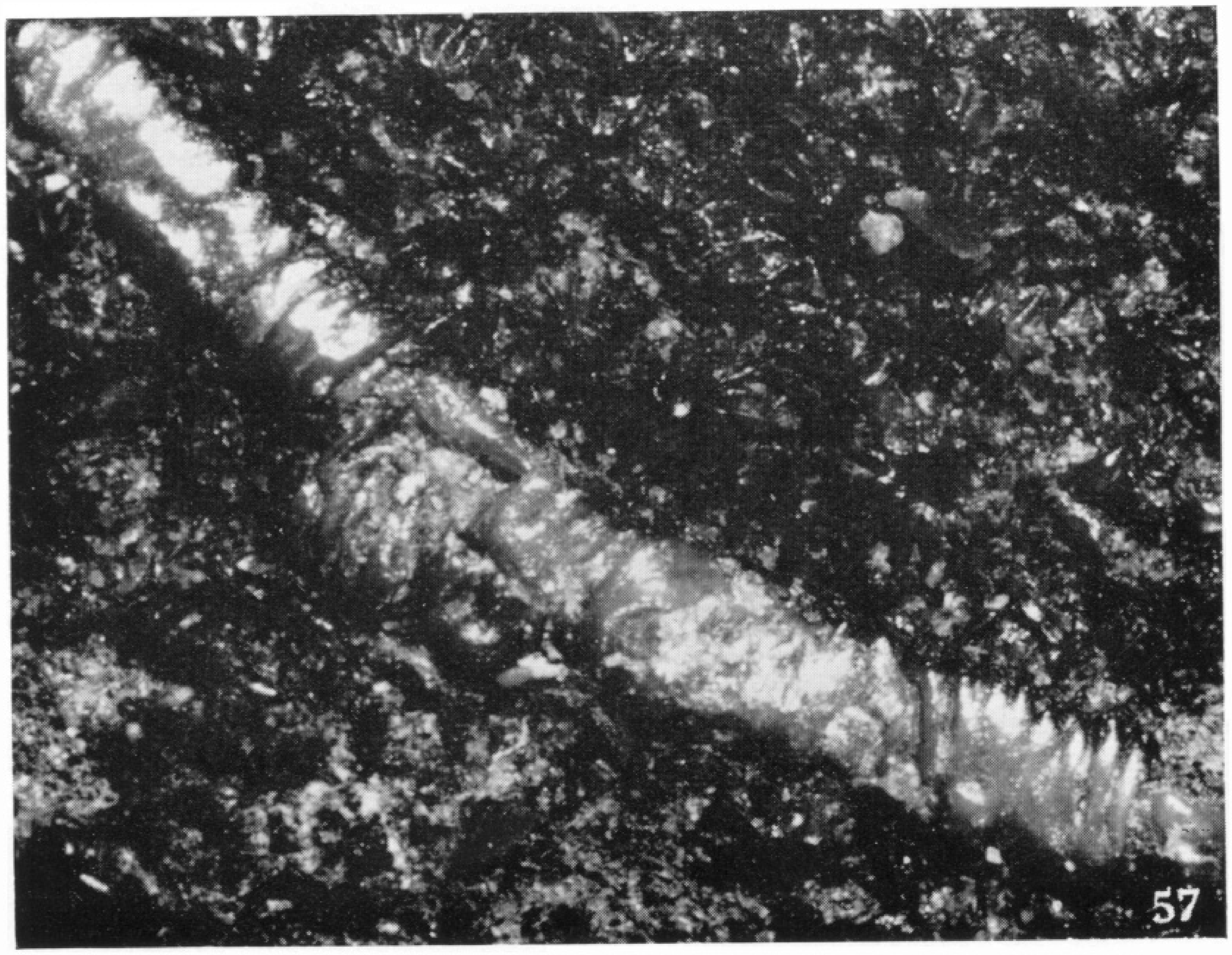

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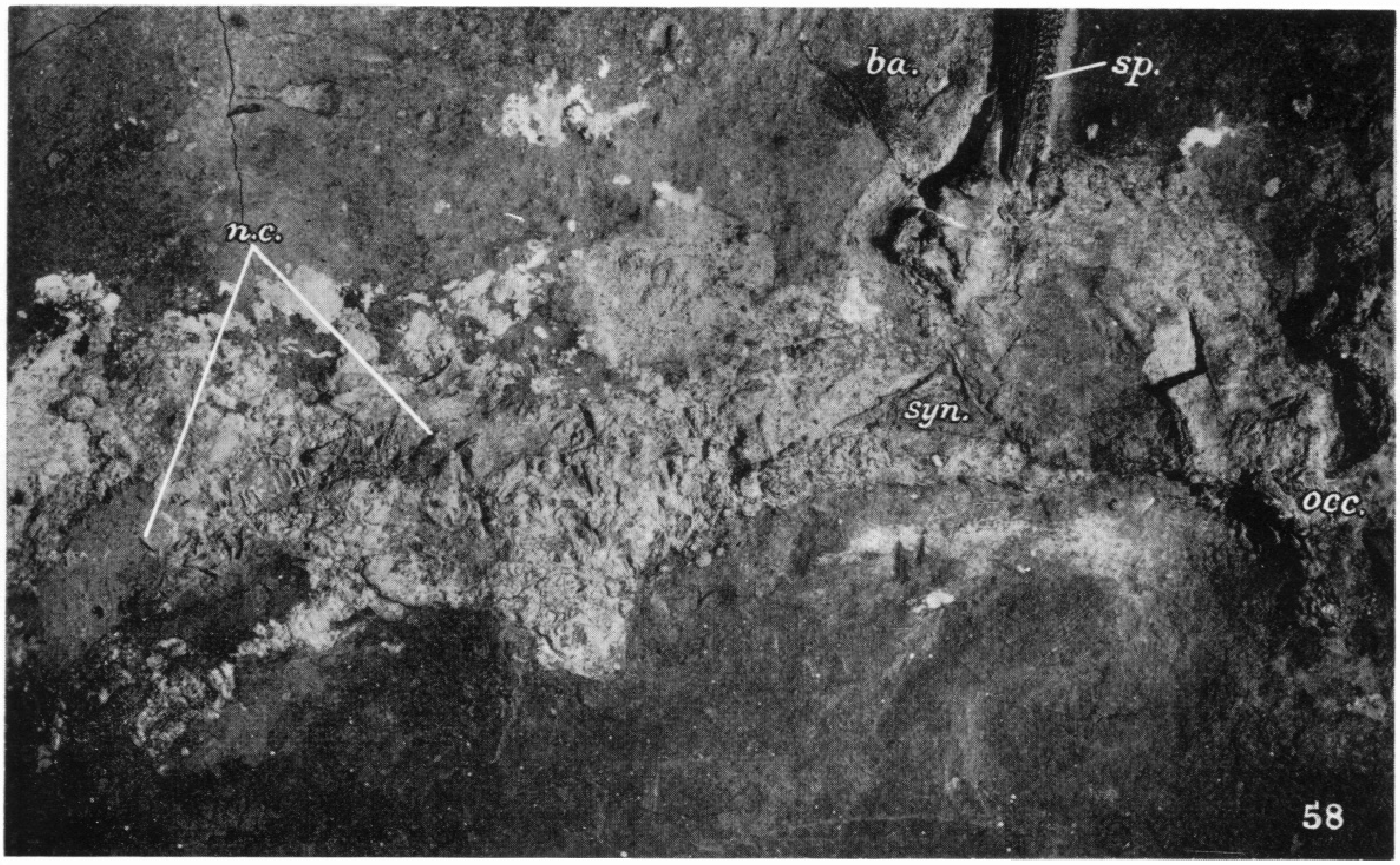


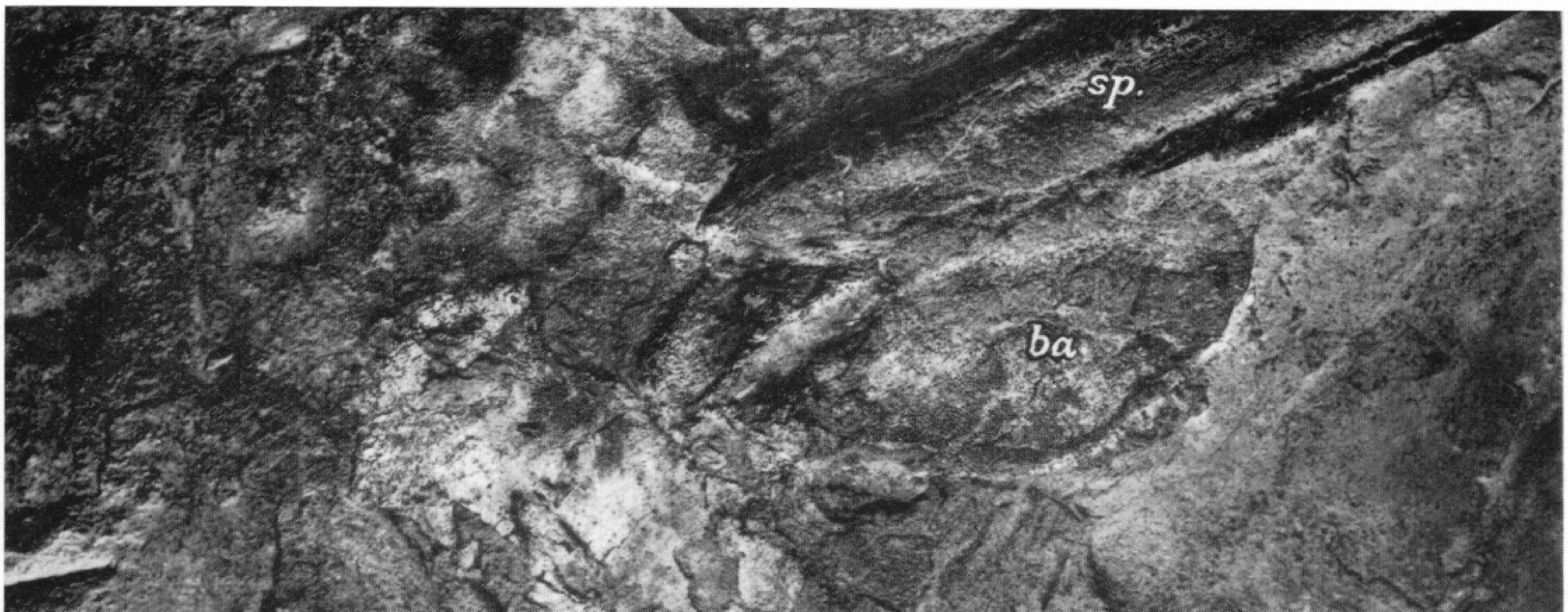
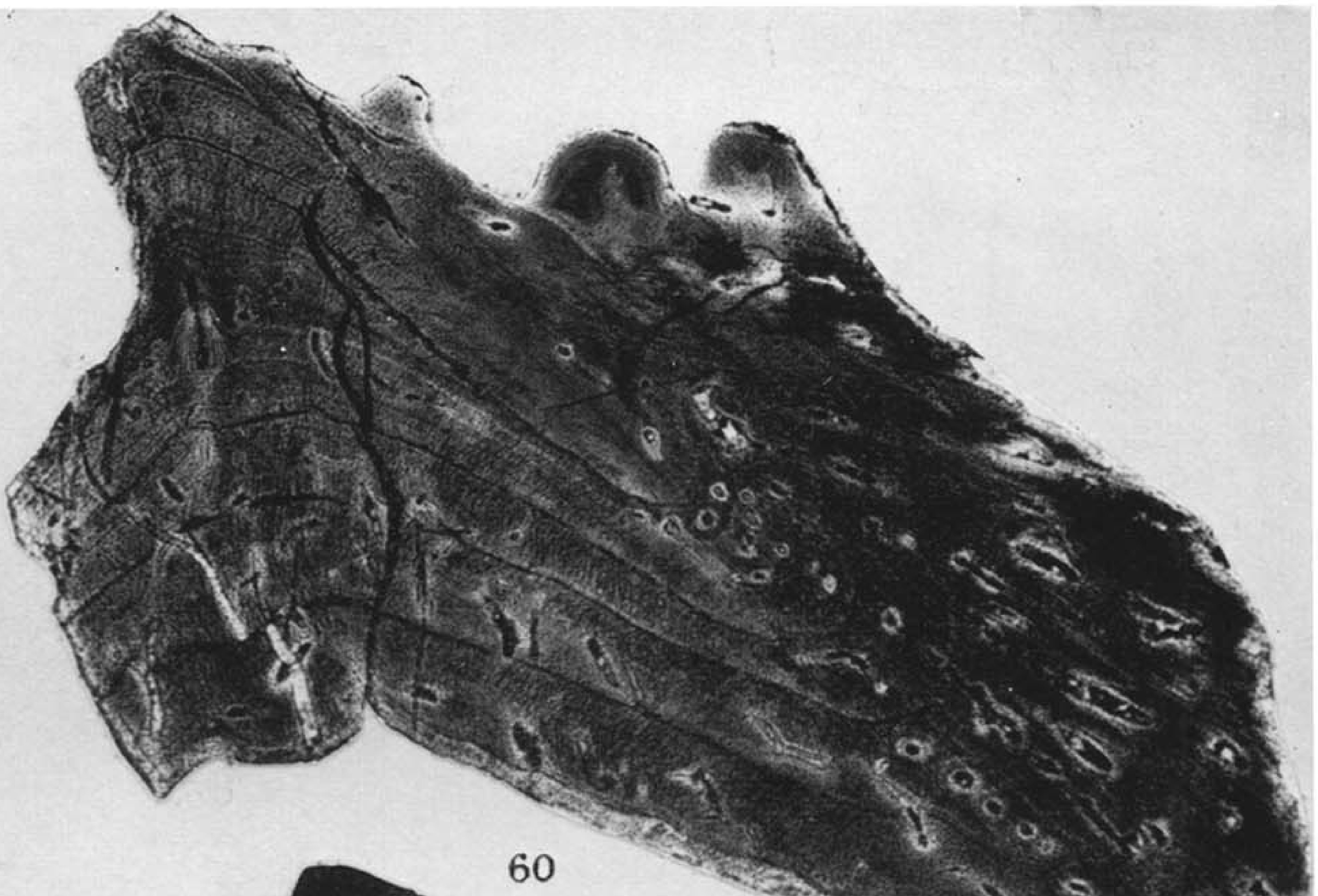


FIGURE 58. *Metopacanthus granulatus* (Agassiz). Part of 43050, Lower Lias, Lyme Regis (× 1), showing notochordal calcifications (*n.c.*), the synarcual (*syn.*), the base of the spine (*sp.*) and the basal (*ba.*) of the first dorsal fin, and the occipital region of the neurocranium (*occ.*).

FIGURE 59. *Myriacanthus paradoxus* Agassiz. Part of P 10130, Lower Lias, Lyme Regis (× 1), showing the occipital condyle of the neurocranium, the synarcual, traces of notochordal calcifications, and the base of the spine and the basal of the first dorsal fin. Lettering as in figure 58.



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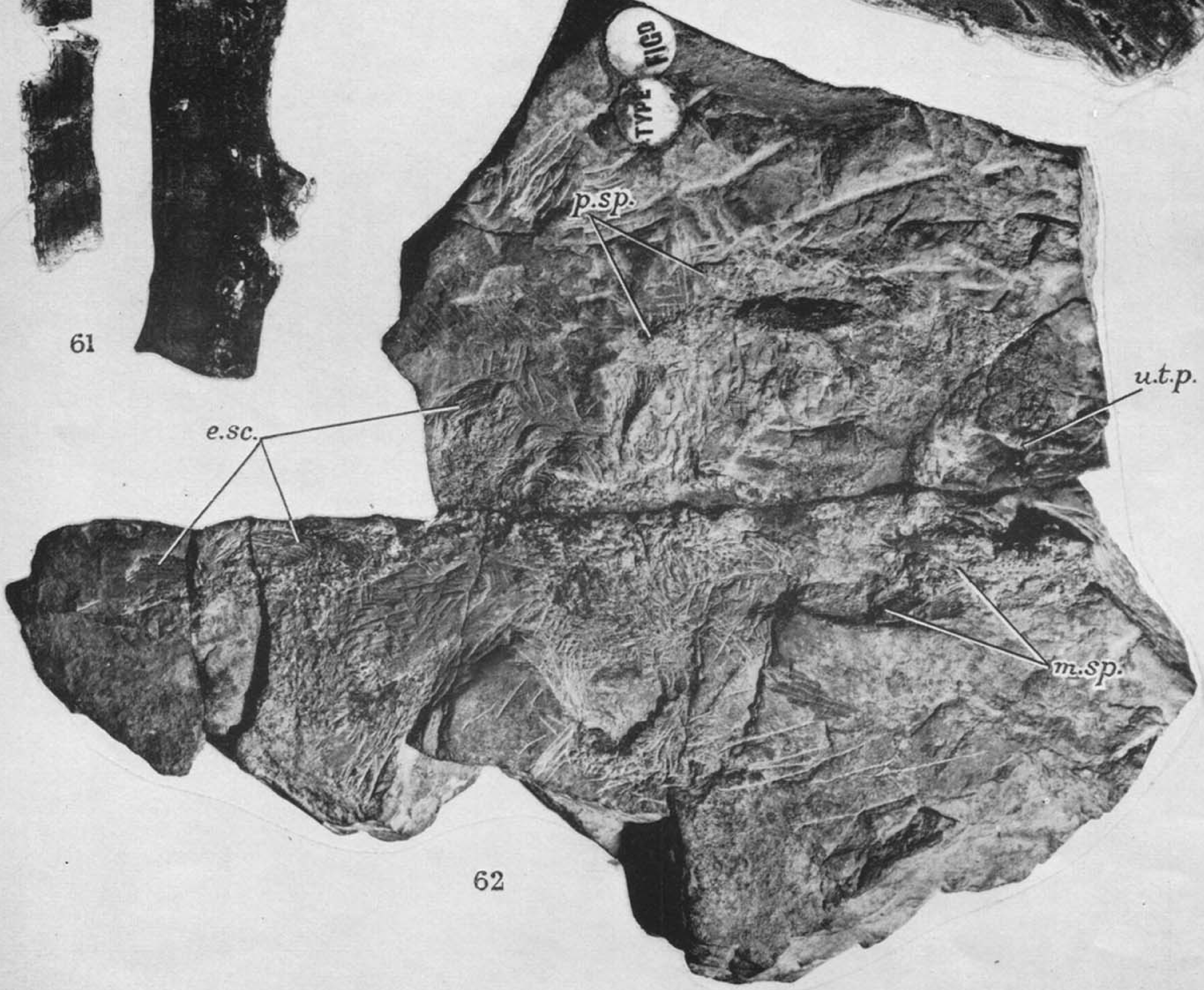

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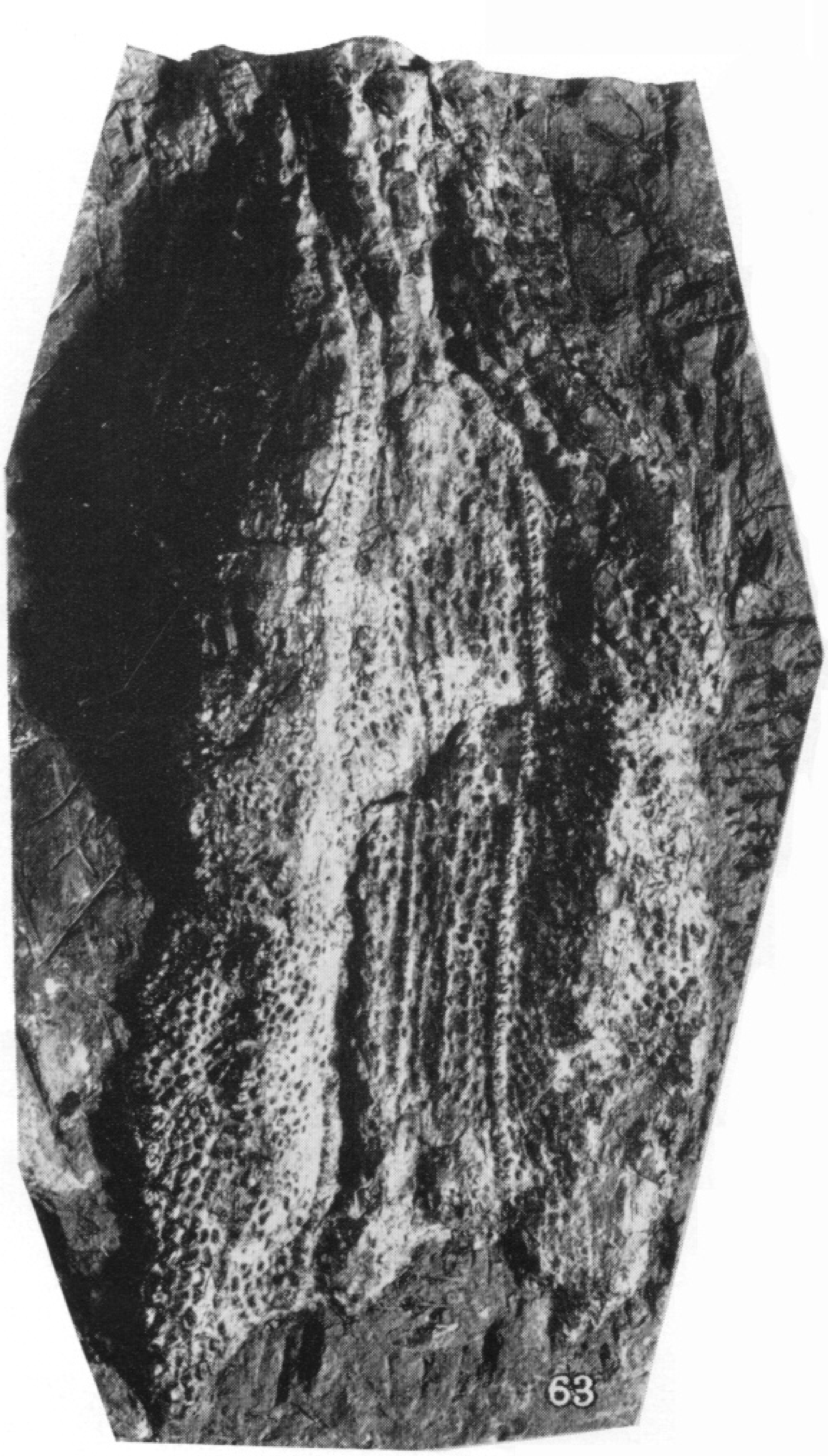
Figure 60. *Myriacanthus paradoxus* Agassiz. Transverse section of part of a dermal plate from the skull roof (× 23). P 151.I. Lower Lias, Lyme Regis. See figure 15 for interpretation.

Figure 61. *Deltoptychius armigerus* (Traquair). Incomplete transverse section of a mandibular spine (× 20). P 11358.I. Calciferous Sandstone Series, Abden Bone Bed, Kinghorn, Fife. See figure 29 for interpretation.

Figure 62. *Deltoptychius armigerus* (Traquair). Incomplete fish, RSM 1936.4, Calciferous Sandstone Series, Cementstones, Glencartholm, Eskdale, Dumfries (× 1). See figure 27. *e.sc.*, Enlarged scales of '*Listracanthus*' type; *m.sp.*, mandibular spines; *p.sp.*, posterior spines of head shield; *u.t.p.*, tooth plate of upper jaw.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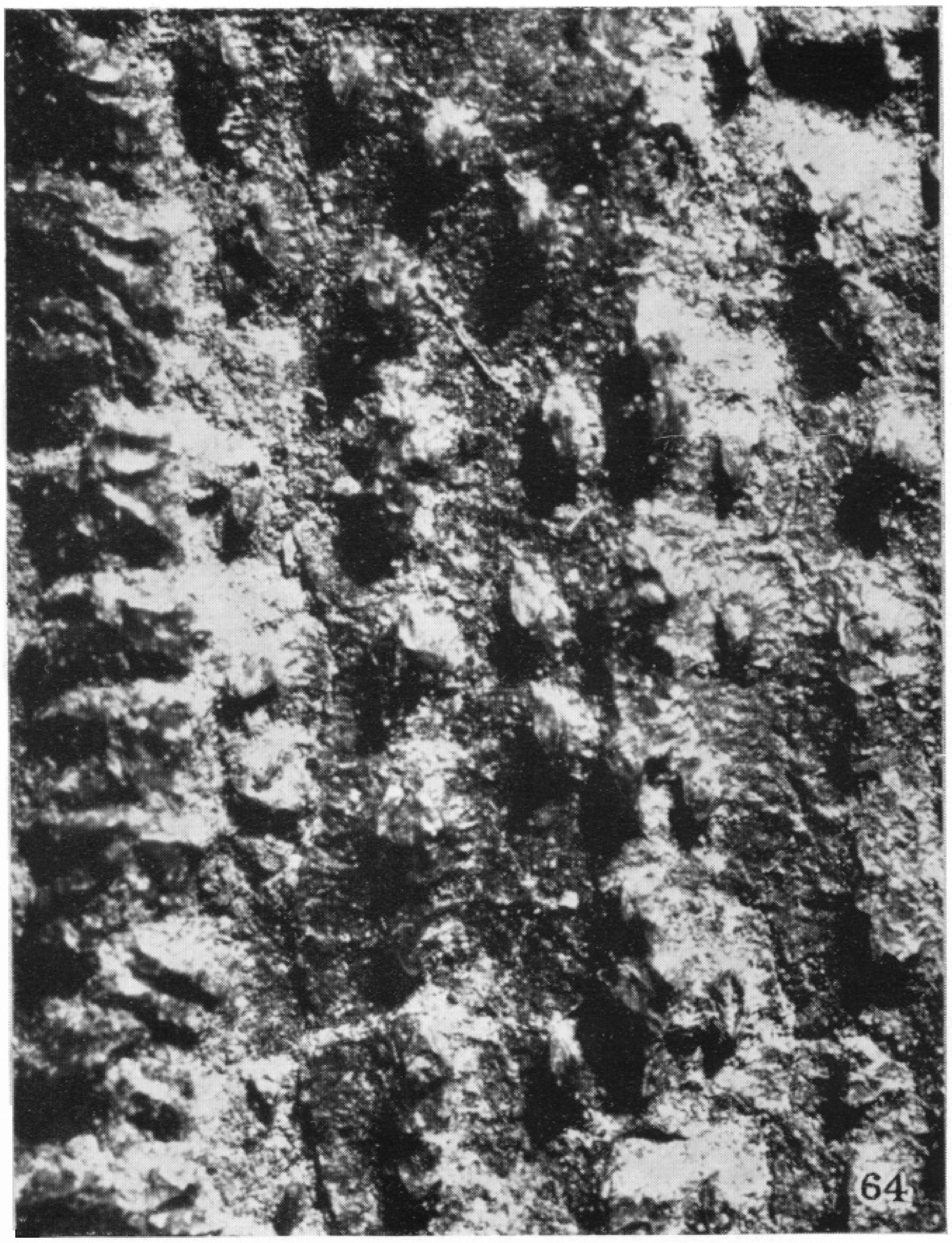
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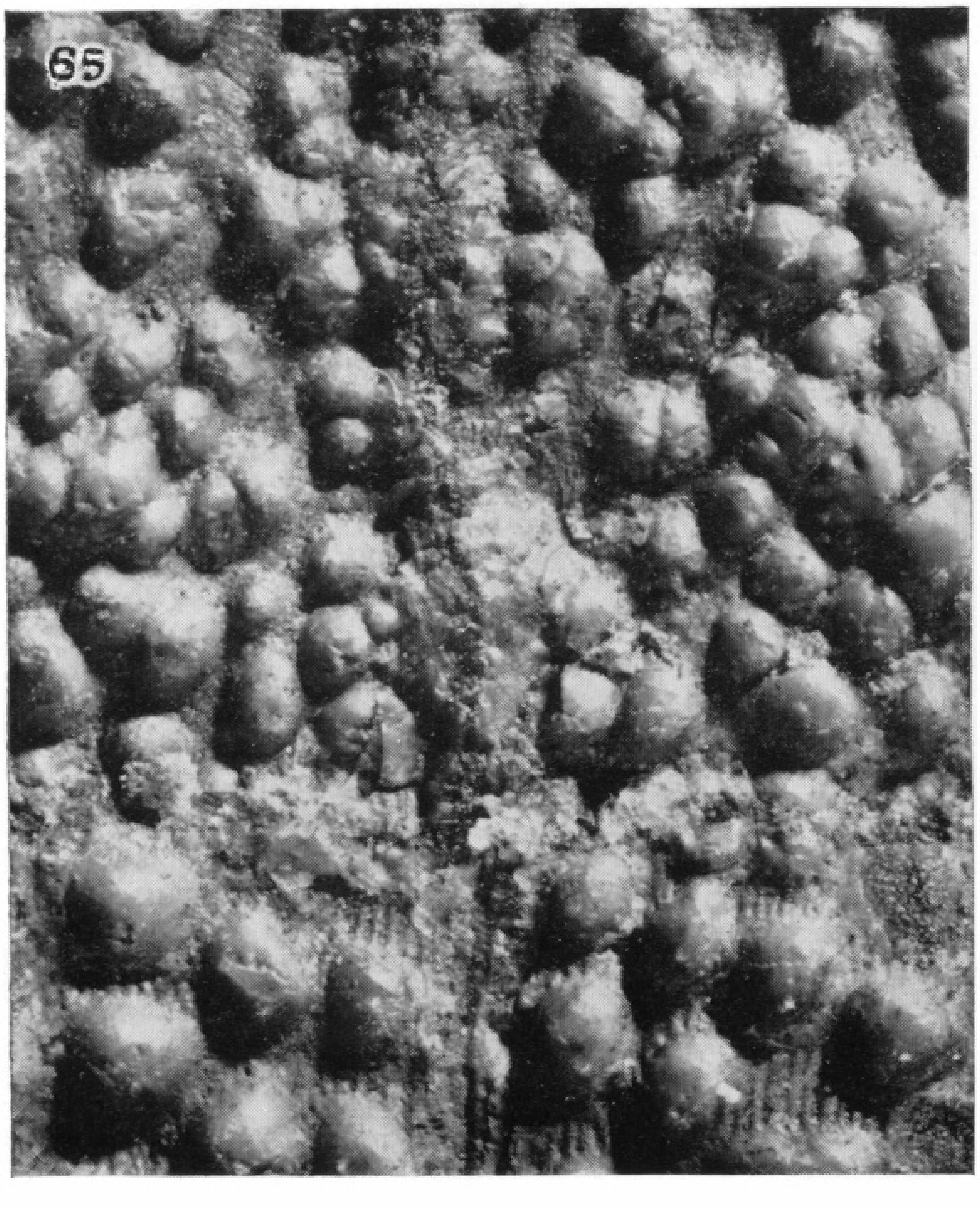
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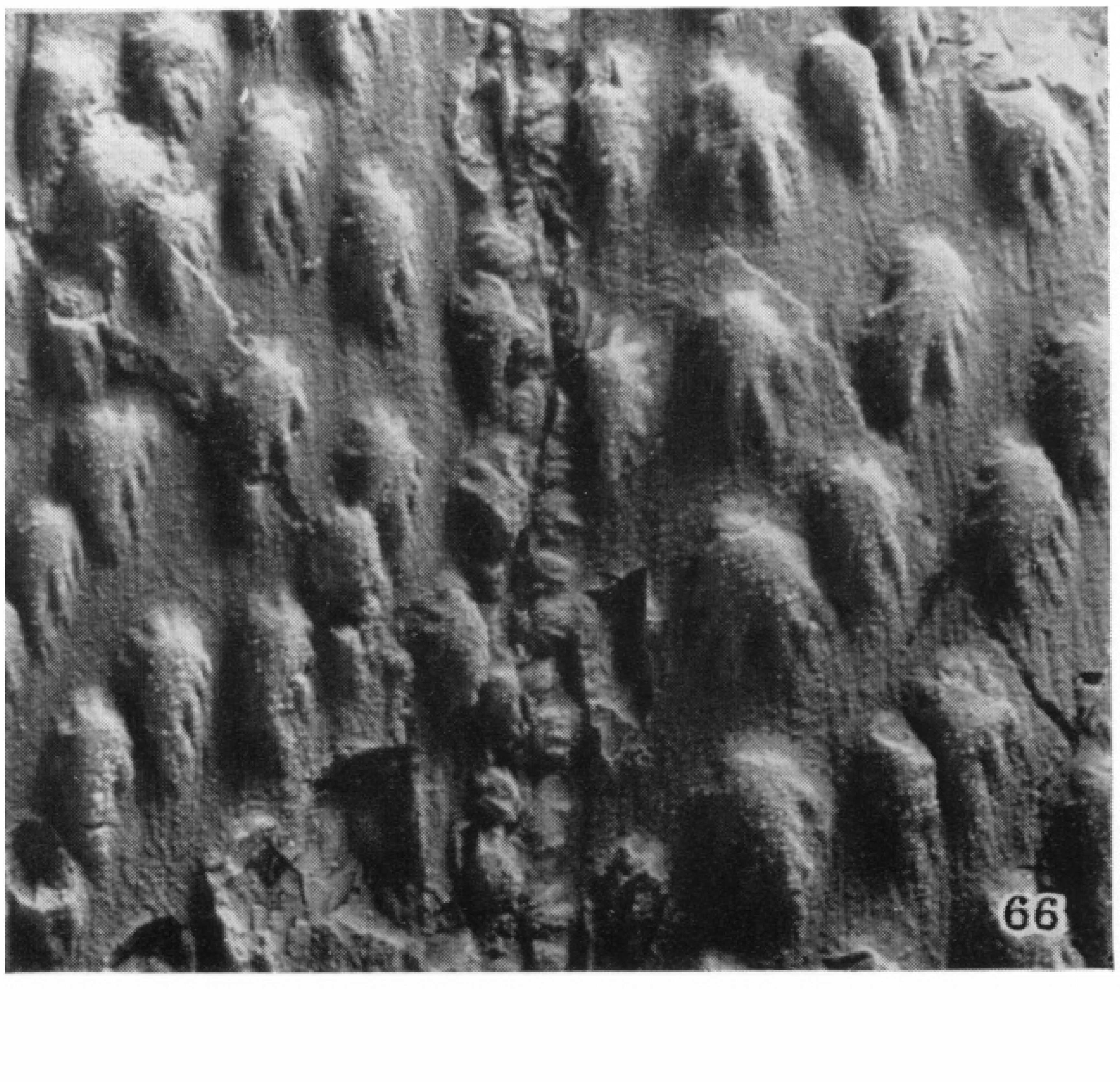
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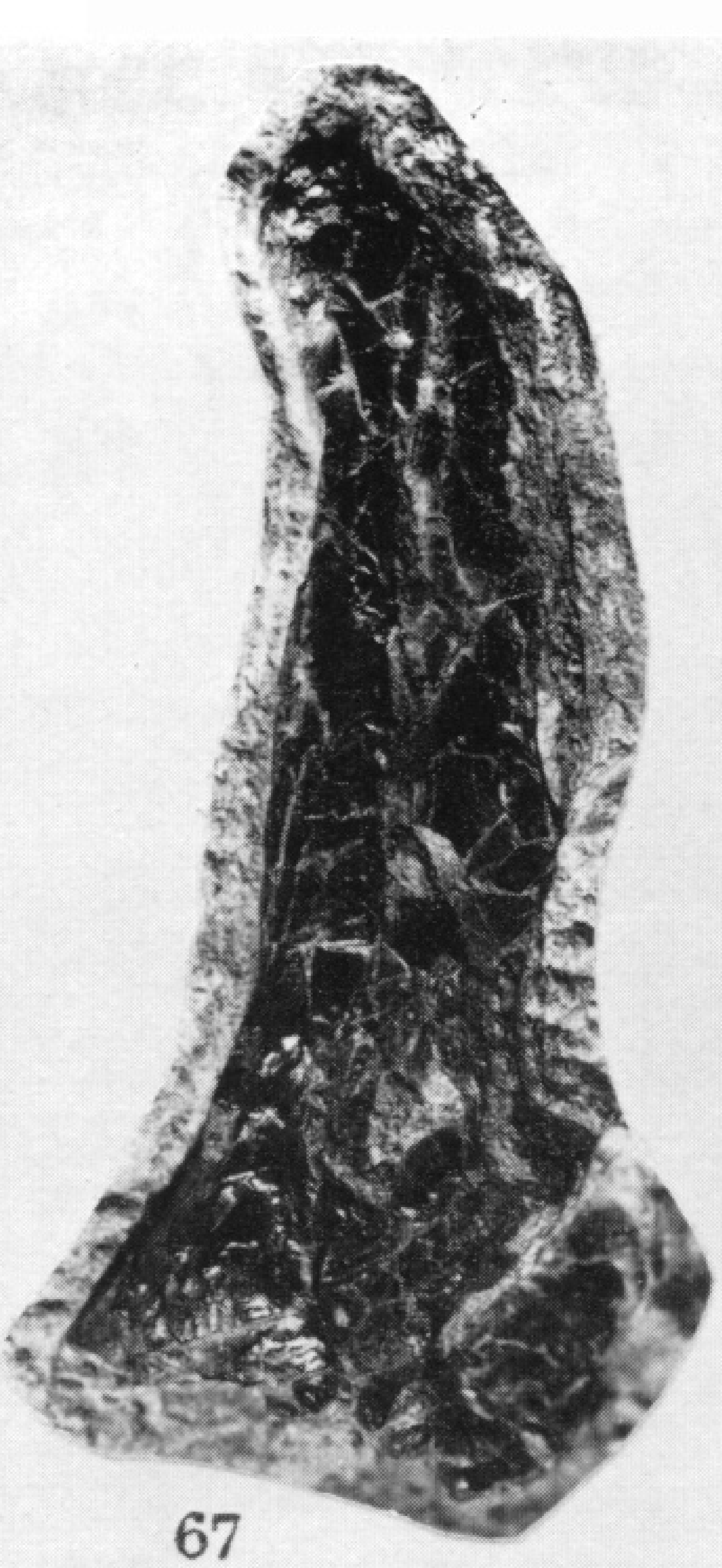

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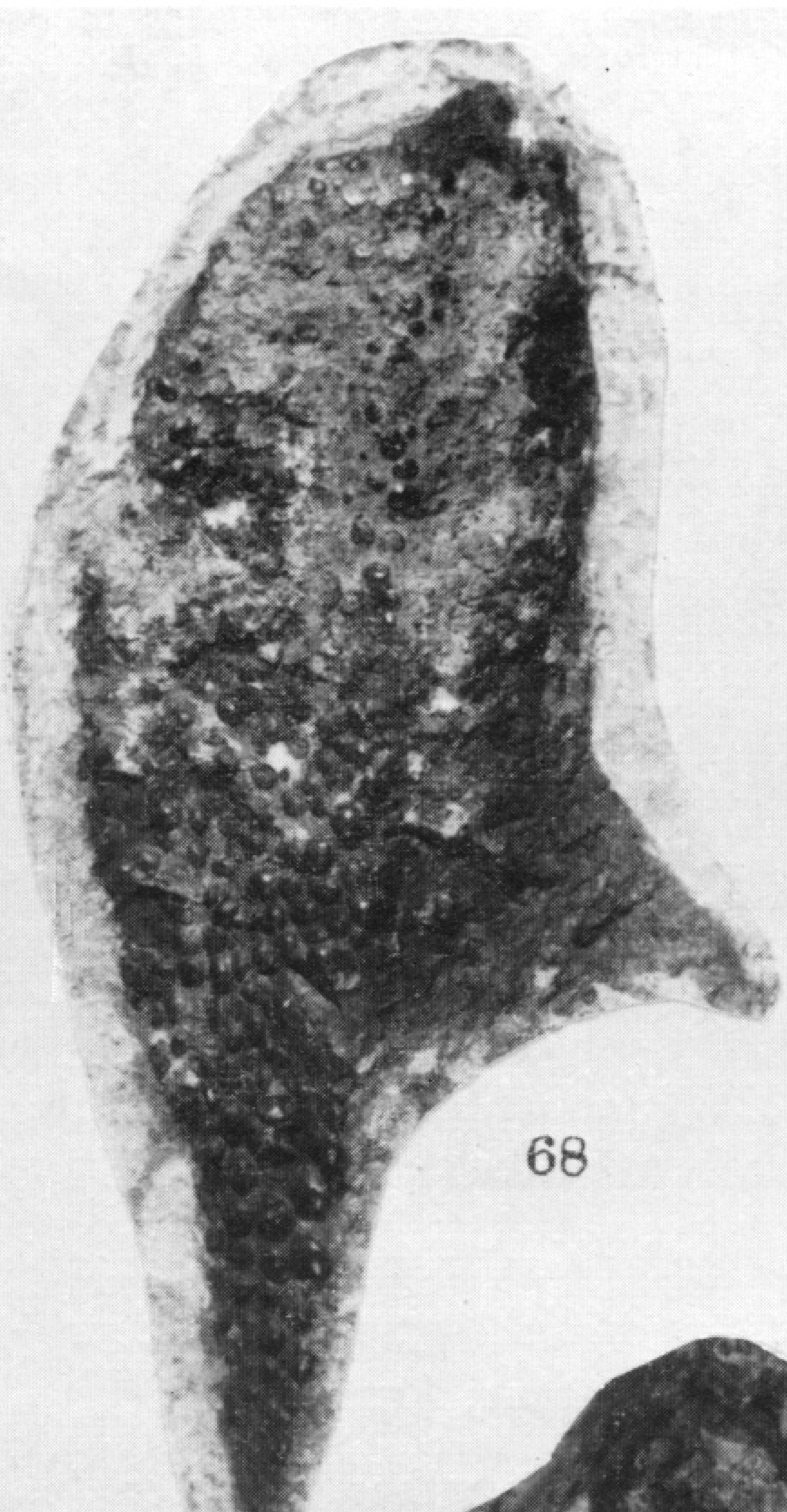

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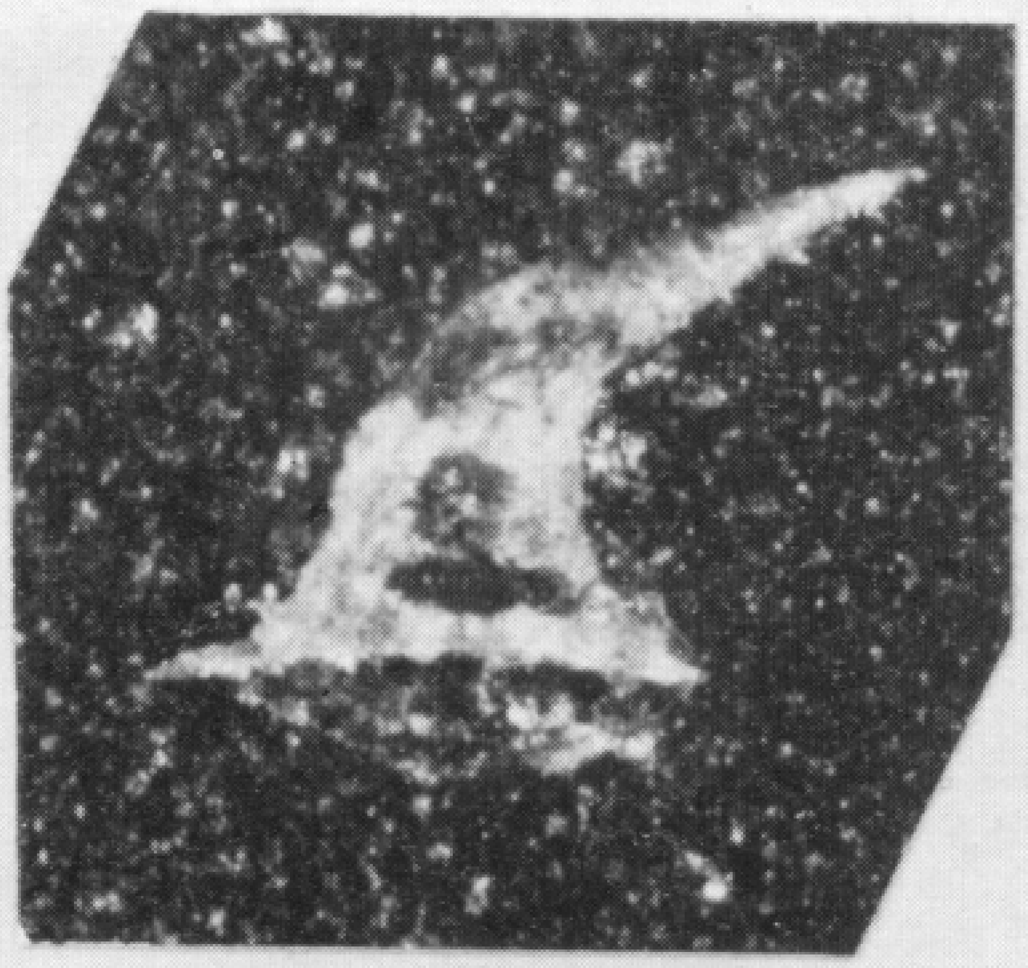

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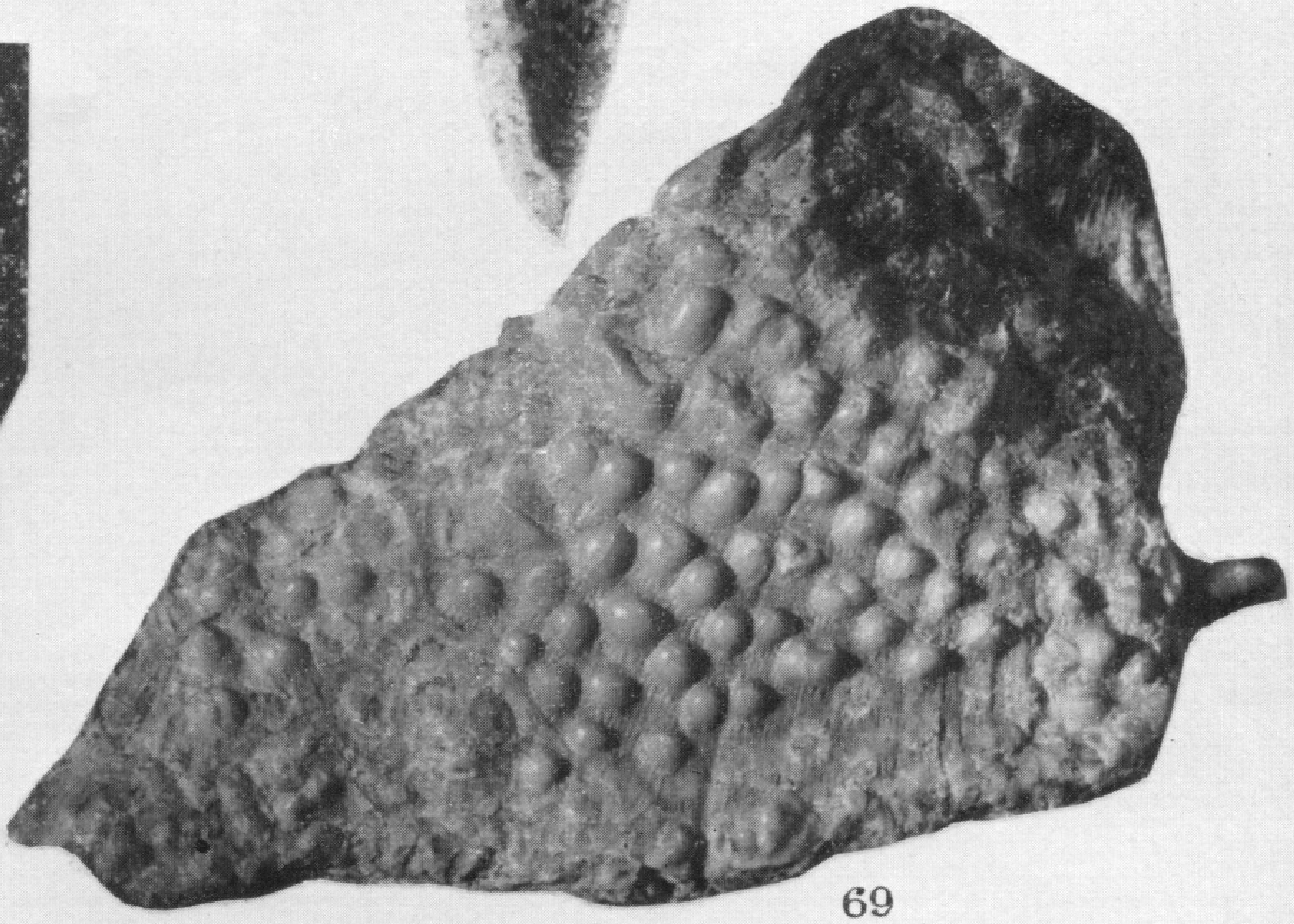

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