

NOTES ON ACANTHODIAN SHARKS.

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WITH 36 FIGURES.

The following notes relating to Acanthodian material preserved in several European museums were brought together several years ago as an incident to another study, but they have now been transcribed for publication, since they deal with several unnoted, or little noted, features of these ancient sharks.

The Acanthodians are known to have constituted the earliest line of sharks which underwent a period of evolutionary prosperity. First known from the late Silurian, they gave rise to a series of highly modified forms in the Devonian (represented by at least three families and upward of twenty species), and became extinct by the close of the Permian. The earliest of the remaining groups of sharks, on the other hand, do not appear before the Devonian and were indeed sparingly represented during the maximum epoch of the Acanthodian; but by the coal times they had evolved characters which, as we have reason to believe, placed them under more favorable conditions for survival and thus enabled them to supersede their more specialized Acanthodian neighbors.

Dentition.—The dental structures of Acanthodians have received but little comment. It was known that while in many genera, *Acanthodes*, *Parexus*, *Diplacanthus*, *Climatius*, and *Cheiracanthus*, teeth are rudimentary (or even lacking), in other forms they are exceedingly conspicuous. Thus, in *Acanthodopsis*, according to A. S. Woodward, there are “a few large, laterally compressed, triangular teeth”; in *Ischnacanthus*, “a few large conical teeth, the interspaces between these teeth being occupied by a close series of minute cusps, all apparently in firm connection with a membrane bone in both jaws.” But no details of dentition have been given, in spite of the fact that they are of no little importance in comparing Acanthodians with other early sharks. Accordingly, we are led to give the accompanying figures, 1-11, with comments.

There are present in *Ischnacanthus gracilis*, cf. Fig. 1 (from specimen

in the Edinburgh Collection), teeth arranged in a graded series with stouter ones at the side and with longer and narrower ones in front (similar, accordingly, to the conditions in *Cladoseleache* and many modern sharks); the spaces between the teeth, however, appear somewhat irregular (artifact?). In Fig. 2, in a similar specimen, the heavier teeth show lateral cusps, distinctly cladodont in type. On each side of the jaw there can be counted about a dozen marginal teeth. There is also shown in this specimen (noted for the first time in Acanthodians) a second or successional row of teeth, *suc*; these are distinctly smaller than the functional teeth, and cannot be mistaken for the elements of the opposite half of the mandible. In Fig. 3 (British Museum, P. 6996) is shown a mandible of *Ischnacanthus* which illustrates strikingly the shape and prominence of the lateral teeth. In Fig. 4 (Edinburgh) there appear again the prominent lateral teeth, but with indications that their bases were somewhat as in other sharks,—not fused (as Smith Woodward and others believed) with the “membranous calcifications” of both jaws. The separateness of the teeth is also indicated in similar specimens (*I. gracilis*, in Edinburgh), shown in Figs. 5-8; in the first of these the bases of the separate teeth are particularly well shown, including the interlap of the bases, which here occurs very much after the fashion of certain modern sharks.¹ Interesting, also, is the arrangement of minor cusps on either side of the major one, which suggests clearly the teeth of Cladodonts. Strikingly Cladodont, moreover, are the various forms of teeth occurring in different regions of the mouth. Thus, the form of tooth shown in Fig. 9 occurs more nearly symphyseal than the form in Fig. 6, and this in turn precedes that of Fig. 7; in Fig. 8 is a detail of a favorably preserved series of lateral teeth. In the matter of the successional series of teeth no more definite result could be obtained than that shown in Fig. 2; *i. e.*, indicating a replacement of teeth, and showing in a more marked way than in Cladodonts or in modern sharks, a difference in size between the old and the new teeth.² The growth of the new teeth, we therefore infer, was conditioned quite differently than in the dental fold of later sharks. A single specimen (Edinburgh), Fig. 10, confirms the foregoing account of dental succession; it preserves, it is

¹ Cf. especially Figs. 6 and 8.

² There is accordingly a suggestion that in this order of sharks a dental trench and a successional series of teeth had not been perfectly attained; in the event of the loss of its large teeth, such an Acanthodian as *I. gracilis* would evidently have to depend upon the small teeth in the second row. That these teeth could then increase in size and finally equal the large teeth remains an open question; but it is clear that teeth could not be replaced as readily as in a modern shark.

true, only a fragment of the jaw, showing in visceral aspect the region of its articular margin. Here it presents a series of enlarged denticles which pass from the condition of shagreen tubercles into the marginal teeth; but it will be seen that as the submarginal denticles pass forward and outward toward the rim of the jaw, they become reduced to a single successional row, as already noted in Fig. 2.

In the genus *Acanthodopsis* a remarkably perfect dentition is shown in a specimen in the British Museum (Fig. 11). In each ramus there was present a row of a dozen (possibly there were several more) teeth which increase in size as they pass toward the region of the symphysis. They are certainly stouter in this form than in *Ischnacanthus*, and the symphyseal teeth were as conspicuous, or even more conspicuous, than the similarly situated teeth in a modern *Odontaspis* shark. Moreover, that they were here functionally important seems evident from the thickness of the anterior reach of the meckelian cartilage.

From the evidence of dentition, accordingly, *Acanthodians*, in certain of the genera at least, resemble Devonian *Cladodonts*, and from this structural standpoint, there is suggested a closer kinship between the groups.³

³That the *Acanthodians* were in a general sense planktonophagous, as Dollo has recently suggested, '06, on the ground that in several genera teeth have not been described, is by no means evident. It is certainly possible, in view of the evidence that a widely diversified evolution took place within this group, that some of its members were specialized to secure plankton, just as were members of other optimum groups, euselachians, ganoids, teleosts. It is, however, clearly safer to conclude, as has hitherto been done, that the *Acanthodians* in which the dentition was reduced (or rudimentary) were forms whose diet was restricted to small or minute organisms. To specify that this food was plankton, and that the structures of the fish were typically planktonophilous, carries one beyond the limits of evidence. Nor does it seem safe to assume, as Dollo has done, that those *Acanthodians* which were not of this form were developed with an abyssal type of dentition, after the fashion of *Stomias*, *Aulops*, etc., seems equally wide of the mark. The present notes indicate a rather normal type of selachian dentition, primitive, we infer, in as much as the mouth-invading shagreen seems to have gone no farther than the mouth rim,—there being no evidence of a wide successional series of teeth as in euselachii. And we can assume, accordingly, that in the *Acanthodian*, as in other fishes, *Characinids* for example, large teeth predicate large prey and rapacious habits. But not necessarily bathybial. There is evidence on the other hand that *Acanthodians* could not have inhabited deep water, for the rule is fixed that bathybial forms, on account of the mechanical conditions of their habitat, are extremely defective in hard structures, scales, bones, and spines. The stout-walled spines and dense shagreen of *Acanthodians* should alone have precluded the assumption that they were deep-water forms.

Skull and Branchial Arches.—To discuss the complicated structure of the skull and branchial arches of Acanthodians is hardly the part of the present paper. I have had, however, thanks to the courtesy of Professor Jaekel, the privilege of examining the extraordinary and beautifully prepared series of the Permian species, *A. bronni*, in the Berlin Museum. And I am able to confirm the essential details given for this species, *i. e.*, the subdivision of the pterygo-quadrate and meckelian cartilages, as shown in Jaekel's Fig. 1, in Zeitschr. deutsch. geolog. Gesell., 99, or Reis's Fig. 1, Schwalbe's Morph. Arbeiten, Vol. VI.⁴ One certainly finds little reason to dissent from the interpretation of these elements in terms of the succeeding branchial arches, for, in view for example of the conditions in the young Chimaeroid, we have clearly the grounds for concluding that the mandibular arch of primitive elasmobranchs was probably a structure segmented like a branchial arch. Thus, in *Acanthodes bronni* (Fig. 12), the epibranchial element is represented in the mandibular arch by the element *q*, the pharyngo-branchial by *pt*, the cerato-branchial by *m*, the basi-branchial by *m'*, and the hypo-branchial by *c*. What the anterior element, *a*, represents is by no means as probable. I am not convinced that Jaekel's conclusion is a just one in regarding this as the "primary maxilla," nor indeed his transcendental views as to the homologies of such parts of the mandibular arch as an "infra dental," or an "articular," in his endeavor to demonstrate homologies between subdivisions of the Acanthodian mandible and the dermal bones of the jaw of higher forms.⁵ As regards the dermal sub-meckelian element, *m''*, one can also hardly subscribe unreservedly to the view that it represents the definite splenial of higher forms, for there is the obvious possibility, in view always of the fact that there are here no other dermal bones associated with the mandibular arch, that this element may be *sui generis*, without, however, going to the extreme view of Reis that it functioned as an extra-mandibular spine, which churned up the bottom and aided in securing the hidden food of the fish.

This view of Reis, it may be added parenthetically, is founded in part upon his assumption that this *dermal* sub-meckelian element bore a series of appendages somewhat as branchiostegal rays. I have, however, a suspicion—for a final judgment one should of course compare Reis's material—that the present appendages belonged in reality to the underlying hyoidean arch; they are beautifully shown, for example, in the

⁴ Cf. the present Fig. 12.

⁵ SB. Gesell. naturforsch. Fr. Berlin, 1905, p. 134 *et seq.*

Berlin specimen from which Fig. 12 was prepared. In any event they indicate that the ceratohyal region was more perfectly gill-bearing than in modern sharks.⁶

That the mandibular arch in *Acanthodes bronni* shows segmentation must, accordingly, be admitted; and that its elements indicate homologies with the branchial arches. On the other hand, unfortunately, these homologies cannot be accepted as final, for the following reason: The condition of the Permian species, *A. bronni* is not confirmed by the condition in several of the Lower Devonian forms. I refer particularly to such a specimen, for example, as that of *Ischnacanthus gracilis*⁷ (Fig. 13), in which no separate elements can be distinguished; and this is true, also, in a well-preserved jaw arch of *Cheiracanthus murchisoni* (Edinburgh). For it is obvious that if the earlier Acanthodians show no trace of these elements, the condition in the much later forms may, like Cope's "elements" in the crania of Xenacanth, be interpreted as artifact.

As far as the writer is aware the roofing of the Acanthodian skull with dermal elements has never been described in detail. Its interest, however, is patent, in as much as it represents an early, if not the earliest, form of strengthening the brain capsule in the gnathostome series. In certain genera it undoubtedly forms an effective shield for the brain, although, morphologically speaking, it must be regarded as but a parallelism of the dermal head shield of the higher fishes. For it consists not of a series of plates, each formed of fused shagreen elements, as one knows it in the ontogeny of recent fishes, but of a series of single, although greatly enlarged shagreen elements. Thus we see, for example, in *Climatius scutiger*⁸ (Fig. 14), that the broad head roof is protected with dermal plates, numerous (a score or more), arranged irregularly, not closely opposed to one another, and clearly not to be regarded as the homologues of parietals, frontals, pre- and postorbitals, etc. From their shape and radial ornamentation, they are obviously to be compared with the enlarged dermal denticles of many other elasmobranchs, *e. g.*, rays.⁹ It is evident, furthermore, from a comparison of the head-roofing

⁶ Dollo's recent suggestion, '06, that Acanthodians are plankton-eating forms, is recalled by these laminæ—if they be interpreted as branchiostegal, and not as traces of gill filaments.

⁷ Powrie Collection, No. 258, Edinburgh.

⁸ Brit. Mus. 35,908.

⁹ Cf. in this regard (Fig. 15) an enlarged dermal denticle from the head-roof of *Climatius reticulatus* in the Edinburgh Museum.

plates with the other dermal defenses in Acanthodians, that there exists an evolutionary range in the shape, size, and character of these structures; from the small denticles of the trunk of the fish we may trace transitional forms to the enlarged denticles which margin the structures of the lateral line, to those which constitute the dermal head-roof, and finally, to those which margin the eye; the last sometimes seven or eight in number, instead of the four usually described. That the dermal denticles of the trunk may in themselves be subject to an evolutionary range of forms is also evident; in certain species and genera these denticles may acquire the quadrate margins (Figs. 33 and 34), which suggest the bony plates of ganoids (fishes with which Agassiz and others associated them), others, on the contrary (Fig. 36), may imbricate their margins to such a degree as to suggest superficially the scales of teleosts. Moreover, prominent contour lines may be defended with rows of enlarged dermal denticles (already noted by Smith Woodward) to such a degree as to suggest the analogous scales of sturgeons or siluroids. Thus, in the specimen (*Climatius scutiger*), pictured in Fig. 14, enlarged denticles, shown at *r s*, form a ridge between the head and the dorsal fin. In such a ridge as many as ten successive elements may be counted.¹⁰

A final word regarding the head-roofing denticles. In some forms they may be small and tubercular, in others large and tubercular;¹¹ in still other forms they may be flattened and closely compacted.¹²

Vertebral Column.—The vertebral axis of Acanthodians is known to retain its notochordal condition and the arrangement of neural and hæmal spines has already been figured by several authors, Reis notably. Specimens, however, are rare in which these axial relations may be determined, and I might refer in this regard to a specimen of *Ischnacanthus gracilis*¹³ (Fig. 16). Here the neural and hæmal arches appear as distinct (metamerical?) elements; as in *Cladoselachus* there are no interneurals, and there is no evidence that the arches approached closely to the surface of the body (*i. e.*, are not connected with the bases of fins). A remarkable condition, on the other hand, is shown in a specimen of *Ischnacanthus gracilis* (Fig. 17), (counterpart of Powrie's type, No. 251, Edinburgh Collection), in which appears a series of superficial elements, *b*, in front

¹⁰ Specimens in Brit. Mus., P. 6955-56.

¹¹ Cf. specimens of *Parexus recurvus* and *falcatus*, in Edinburgh.

¹² Cf. *Euthacanthus macnicoli*, Edinburgh.

¹³ No. 334 in the Edinburgh collection.

of and in the neighborhood of the dorsal fins. They are distinctly separate from the neural arches and are apparently metameral; their interest is obvious from the standpoint of fin morphology, for they can be interpreted as the rudiments of the basalia of a more continuous type of unpaired fin.

Fins and Girdles.—The fins of Acanthodians are beyond peradventure of a lateral fin-fold type, and as such they have been given a prominent place in the much-discussed problem of the origin of the vertebrate limbs. From this standpoint it is clear, either that the limb structure of Acanthodians and other primitive sharks must be reducible to a common plan, or that the curious spine supported Acanthodian webs must have arisen *sui generis*. The latter view is difficult to accept, since it is conceded unanimously that the paired limbs of all other vertebrates are homologous, and it seems, therefore, if only from purely *à priori* grounds, illogical to assume that Acanthodians, which are sharks in so many details of structure, could not have had fins based essentially upon shark-like structures. The view, moreover, of the homology of the fins of Acanthodians and sharks¹⁴ is supported by the evidence of Cladoselachian sharks whose fin structures are in important regards intermediate in type. In both forms the paired fins functioned as balancing organs, rather than as paddles, and in Cladoselachians there is a concentration of the supporting elements, radials, in the anterior rim of the fin which, I have maintained, served as the ancestral condition of the spine of the Acanthodian.¹⁵ This view is supported by the following facts: The caudal fin of Acanthodians shows the radials in the process of concentration in the anterior rim of the fin. There is no spine present, although the anterior fin margin is encrusted and stiffened by shagreen. Such a condition has already been noted by various writers; it is admirably seen in one of Professor Jaekel's beautifully prepared specimens of *Acanthodes bronni*, which I have figured herewith (Fig. 25). And similar conditions are known in other genera. In *Parexus falcatus*,¹⁶ for example, the hypural lobe of the caudal fin is strengthened by shagreen to such a degree as to

¹⁴ Cf. 1894, *Jour. Morph.*, Vol. IX, pp. 98-111; 1896, *Anat. Anz.*, Vol. XI, pp. 677-679; 1896, *Nat. Science*, Vol. VIII, pp. 245-253.

¹⁵ In this evolution the dermal elements played an important part, encrusting and strengthening the anterior rim of the fin, a process which caused or was accompanied by a reduction in the radials.

¹⁶ British Museum, P. 130.

suggest a spine-like fin support (Fig. 20). Indeed, in such a form as *Diplacanthus tenuistriatus*¹⁷ (Fig. 22) such a condition is actually attained. And the dermal elements arrange themselves in the series of rows characteristic of Acanthodian spines, while the hinder radials become obsolescent. If, accordingly, such a condition be compared with that shown in the second dorsal fin of *Euthacanthus macnicoli*¹⁸ (Fig. 23), we cannot fail to note the close correspondence; the fin spine is made up of radial components in which dermal tubercles are concentrated, and these even appear *behind* the fin spine strengthening a series of delicate rays which are evidently comparable with the obsolescent rays shown in the caudal fin of Fig. 22. A second dorsal spine of an Acanthodian is thus the homologue of the concentrated radials in a caudal fin. And it is easy to see how such a condition would readily become highly specialized in forms in which dermal structures present a wide range in their scheme of evolution. In such a broad spine, for example, as that shown in Fig. 26, *Climacodus reticulatus*,¹⁹ the broad striation in its dermal crust still testifies to the component radial elements,—the basal elements, or at least some of them, forming the region *b*. In Fig. 24, *Climacodus uncinatus*, a more highly modified type, there can still be seen traces of the component radials in a spine which has become curved. In other spines (Fig. 19) the dermal elements have completely obscured the core of radial elements over which primitively they have been laid down.

Admitting, then, that the fin spines of Acanthodians are founded upon the concentrated radials of a Cladoselachian fin, the puzzle of the paired fins of the Acanthodians becomes greatly simplified. And for a further study of the matter, I believe that an important hint is given us in the behavior of the dermal elements as contributing to the formation of fin spines. For if dermal elements play so important a part in strengthening the outer supports of fins, may they not also have pressed deeply into the integument and strengthened the basals? For it is these elements which have contributed no little confusion in the studies of the Acanthodian paired limbs. Without attempting to reconcile the differences which occur in the plan of the shoulder girdle and spines of various Acanthodians, I may point out that there is evidence not merely of a pair

¹⁷ Edinburgh Museum.

¹⁸ Brit. Mus., P. 35,907.

¹⁹ Brit. Mus., P. 1343.

of "inter-clavicular" or "claviculoid" membrane bones in certain genera, but that the basal region of a fin may be strengthened with *many* dermal elements. This is well shown in a specimen of *Parexus falcatus* in the British Museum, P. 130 (Fig. 21), of which an enlarged figure of the base of a pectoral fin is shown in the present Fig. 27; here as many as half a dozen dermal elements may be counted along the mesial margin of the basal plate, and it is even possible that the entire flat distal surface of this plate was strengthened by dermal elements. Accordingly, the shoulder girdle of Acanthodians, like the girdle of a teleost (siluroid, for example) is to be treated as including a dermal complex. Our present knowledge does not warrant us in attempting to homologize its elements with those in the higher forms (as, nevertheless, Jaekel has done in identifying "suprascapular," "scapular," "coracoid," and "cleithral" elements), since such structures can only be compared with the conditions in the higher vertebrates when it has been shown that the Acanthodians have closer phyletic relationships to the higher forms. Until this can be demonstrated the structural elements of the Acanthodians must evidently be interpreted in terms of their nearest kindred; *i. e.*, fossil and recent sharks. The safest conclusions in our present stage of knowledge are, I believe, these: That we are to regard the proximal portion of the shoulder girdle, the region of *sg* in Figs. 18, 19, 21 (elements *a, b, c*, of Jaekel) as equivalent to the proximal portion of the shoulder girdle in sharks; the distal portion becomes a region of concentrated fin-supporting elements, fused basals, a portion of the basal parts of the radials, with as an important if not a maximum component a dermal complex, *e. g.*, the region *d* in Fig. 19 or the more discrete elements in Fig. 27. With regard to the homology of the cartilaginous pieces which Jaekel and Reis describe in *A. bronni*, as fin-web-supporting elements placed immediately behind the pectoral spine, one may, I conclude, regard them as the remains of the series of baso-radial elements. The elements of this series had in general, as has been noted, fused at the base of the pectoral fin spine; but it is by no means improbable that in certain forms a number of the posterior elements remained discrete, retaining more or less accurately their primitive function. That there is the greatest range in the degree of concentration of fin-supporting structures in the Acanthodians all will, I think, agree who have examined these structures in many genera.

The supports of the ventral fins, so important in the general discussion of the origin of the paired limbs, have, as far as I am aware, never been described. Interesting, accordingly, is the specimen of *Diplacanthus*

striatus in the British Museum, P. 36,582, cf. P. 1757, *a* (Fig. 19), which shows a distinct pelvic girdle, *p*. At the base of the fin spine the enlarged supporting mass, *r* + *b*, represents, we infer, the fused baso-radial elements. At *d* appears a pair of distinct plates, dermal apparently in origin. Whether they are related to the much discussed series of "fin spines passing between the pectoral and pelvic fins" is not clear.

Sense Organs.—Our knowledge of the end organs of Acanthodians appears to be confined to a few notes on the lateral line and on the large eyes protected by "four dermal plates." As to the former structure, Smith Woodward remarks²⁰ that "a single lateral line occurs high on each flank, marked not by any tubular or other excavation of the scales, but by the ridge-like displacement of two series, between which the organ originally extended. The supposed evidence of additional sensory canals appears to the present writer to be due to a misinterpretation of the displaced dorsal and ventral ridges, which exhibit no median series of scales." Reis, in this connection,²¹ has made the interesting observation that the lateral lines are joined by an occipital commissure very much as in recent elasmobranchs and teleostomes; and he refers also to the presence of a median canal in the forehead which he compares to (or parallels with?) the rostro-median canal of *Chimæra*; he figures, finally, a supraorbital canal and refers to the absence of a suborbital branch arising from the main canal in that region. Reis's figure representing these conditions²² is of especial importance. To the foregoing notes upon sensory structures I may add: The "additional sensory canals," in spite of the skeptical comment of Smith Woodward, are beautifully seen in several specimens in the British Museum and in the Edinburgh Collection. I refer particularly to *Climatius grandis* and *Ischnacanthus gracilis*²³ (Figs. 30, 31, Edinburgh, and 32, this after No. 241, Powrie Collection). In these particular forms the branching of the lateral line, *ll*, in the neighborhood of the dorsal spine is, indeed, so common an occurrence that one might even maintain that it was the normal condition. It has not, however, been observed to occur on both sides in the same individual; nor is it definite that it occurs always on the same side, although a close examination has convinced me that it occurs on the right side in most cases. The most remarkably preserved sensory structures in Acanthodians are probably shown in the specimens of *A. bronni* (from

²⁰ Cat. Foss. Fishes, Vol. II, p. 5.

²¹ Morph. Arb. Schwalbe, VI, pp. 195-196.

²² *Op. cit.*, p. 195.

²³ London, P. 6974.

Lebach) in the Berlin Museum, for the inspection of which I am greatly indebted to Professor Jaekel. For they show not only the lateral line but its many branches, the sensory canals of the head, and, most interesting of all, the auditory organs and the rim of the nasal capsule. Thus, in the specimen shown in Fig. 28, one readily distinguishes²⁴ the canals of right and left sides, *ll*, *ll*, from which a series of vertical branches arise very much as in recent selachians, cf. especially in the young specimens (20-30 cm.) of *Chlamydoselachus*; the lateral lines apparently draw together in the occiput and from this region pass forward, giving off various branches, a supraorbital canal, *supra o*; there, also, appear a suborbital canal, *sub o*, an auditory capsule, *au*, of extraordinary size, and traces of sensory canals, *br s*, in the branchial region, again a condition which suggests the modern shark (*Chlamydoselachus*). These conditions are shown to even better advantage in a specimen from the same collection shown in Fig. 29. Especially noteworthy are here: (I) The position of the suborbital canal, for it is seen to arise (contrast Reis's note given above) from the main canal passing to the trunk, *i. e.*, in the position usual in fishes. (II) The great size of the sensory branches passing to the region of the gills. (III) The structures of the auditory organ, the utricle, *utr*, and, prominently shown, a vertical semicircular canal, *vsc*. (IV) The upper margin of the nasal capsule, *nas*, which indicates accurately the position of this organ.

In the manner of the protection of the lateral line the Acanthodians show a range of evolutionary characters; in *Euthacanthus elegans* the canal is marked only by a ridge-like prominence of marginal scales (Figs. 34 and 34a); in *Acanthodes bronni* the marginal scales become enlarged and prosalient (Fig. 35); in *Euthacanthus gracilis* they may completely overlap and enclose the sensory canal (Fig. 33). It is finally observed that a great range in the manner of protecting the sensory structures is found at different regions in the same individual.

Relationship of the Acanthodians.—It has been pointed out in the foregoing notes that the Acanthodians agree in a number of regards with the Cladoselachian sharks, and that from this evidence we conclude that they are more closely related to these forms than has hitherto been generally accepted. Dental characters, structures of fins caudal, unpaired and paired, vertebral axis, even the mode of protection of the eye, are

²⁴ In *A. bronni* the shagreen denticles are reduced in size; those only are large which protect the sensory canals, hence the clearness with which the arrangement of the canals may be followed.

distinctly cladoselachian in type. Taxonomically, therefore, Cladoselachians and Acanthodians should be more closely associated than should, for example, Cladoselachians and Xenacanth, or Acanthodians and Xenacanth. We are thus led to suggest again²⁵ that a group such as defined by Pleuropterygii (sharks with fins of fin-fold type); would justly include both Cladoselachians and Acanthodians. This group, however, might more accurately be regarded as of superordinal rather than of ordinal rank, and ordinal rank would thus remain in the groups Cladoselachia and Acanthodia.

The question as to which groups, Acanthodian or Cladoselachid has retained the more primitive character is indicated in the accompanying table (*v.* p. 221). In the great majority of structures one can only conclude that the Acanthodians have passed through a stage in evolution which is best represented by the Cladoselachian. In one regard only (apart from the matter of size) does the latter appear the more specialized, *i. e.*, in the unsegmented character of the mandibular arch (*v.* however, *supra*).

If these things be true, it may next be queried why is it that the more specialized group is known from an earlier horizon? For certainly the appearance of the Acanthodians in the upper Silurian (as against the Cladoselachian in the upper Devonian) is in general evidence of the greater primitiveness of their group. And this is in truth a question which can be answered only by the time-worn appeal to the defectiveness of the palæontological record, noting especially in this regard that the soft structures of the Cladoselachians would be less apt to be preserved than the hard structures of the Acanthodians. We may, however, safely predict that from the earliest Acanthodian horizon there will be discovered forms which will represent the ancestors of all of the early groups of sharks. And we may predict with almost the same degree of security that these forms will be found to picture the Cladoselachian in essential characters. For the Acanthodians, as we at present know them,²⁶ are obviously too specialized to have represented the ancestors of the line of Cladoselachians.

The causes of the extinction of the Acanthodians can, I believe, be suggested with a fair degree of probability. It is evident, of course, that the fin characters of this group premise great capability on the part of these fishes to dart forward, *i. e.*, in direct lines, a type of movement especially valuable when a definite kind of food is to be secured. On the

²⁵ Cf. J. Morph., Vol. IX, pp. 110-111.

²⁶ Cf. the accompanying table.

CONTRASTED CHARACTERS OF	CLADOSELACHIANS.	ACANTHODIANS.
<i>Dermal defenses.</i>	Smaller and more uniform in pattern throughout all regions. Practically unornamented. More gradual transition from shagreen denticles to sclerotic plates and to teeth. On anterior fin margins the denticles become large and concentrated, but do not produce spines. Denticles not specialized on the margins of lateral lines.	Large of size, varied in pattern, sometimes highly ornamented. In certain regions (head roof) individual scales become greatly enlarged and function as membrane bones. In general sharp contrast between shagreen denticles, teeth and sclerotic plates. High specialization of denticles margining sensory structures. Extraordinary development of spines, which may be regarded morphologically as collections of denticles enlarged and increased on anterior fin margins (as suggested in the condition in the caudals of Acanthodians and in the paired fins of Cladose-lache), or as huge single denticles.
<i>Head.</i>	Arches similar, apparently, to Notidanids.	Mandibular arch (Acanthodes) segmented like a branchial arch.
<i>Vertebral column.</i>	Notochordal. Neural and haemal elements heavy, not long and not connected with unpaired fins.	Notochordal. Neural and haemal elements shorter and more delicate than in Cladoselachian.
<i>Girdles.</i>	Both present; but small in size. The pelvic elements single, not conjoined (on the evidence of a new specimen of <i>C. kepleri</i>).	Both present, but their structure obscured by the invasion of dermal elements. Pelvic element on each side as in Cladose-lache, but longer and more varied in outline. In Acanthodes "segments" (artifact?) present in pectoral arch, but in other genera these are absent.
<i>Fins.</i>	Supporting basal and radial elements arranged similarly in paired and unpaired fins, concentrating anteriorward.	Spines supporting paired and unpaired fins. Caudal provided with radials as in Cladose-lache. Traces of radials in unpaired and paired fins.
<i>Sensory structures.</i>	Not well known. Eyes smaller (relatively) than in Acanthodians and less perfectly protected with dermal plates. Lateral line inconspicuous, open, apparently unbranched.	Eyes and auditory organs of large size. Marked branching of lateral line system. Usually but four (large) dermal plates protecting eye.

other hand, it is very probable that they could not have altered quickly their direction, speed, or plane of movement, and they would thus be placed at a serious disadvantage when competing with ganoids, dipnoans, even with other sharks, for the capture of varied forms of prey. So, also, the teeth of Acanthodians indicate a smaller range for functional adaptation than the dentition of other sharks. Finally, the elaborate specializations of the integumentary defenses of Acanthodians lead in the direction of enlarging individual dermal cusps, instead of that of fusing the bases of the cusps. And the result was an unfavorable one. For the limit of the size of the individual cusp could soon be reached, while that of the fused basal plate (a true membrane bone) was greater and more plastic. Even the most perfectly armored Acanthodian, therefore, could not compete in this regard with the contemporary ganoids.

DESCRIPTION OF FIGURES.

FIGS. 1-11. Teeth of Acanthodians. Figures of *Ischnacanthus*, excepting Fig. 11, which is of *Acanthodopsis wardi*.

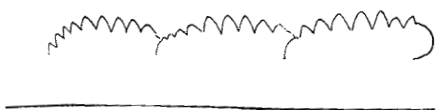
FIG. 12. Jaw and branchial arches of *Acanthodes bronni*. 13. Jaw arches of *Ischnacanthus gracilis*. 14. Head-roof of *Climatius scutiger*. 15. Detail of a shagreen denticle from the head-roof of *Climatius reticulatus*. 16. Neural and hæmal arches of *Ischnacanthus gracilis*. 17. Neural arches and dorsal fin, *ibid.* 18. Pectoral spines and girdle of *Climatius reticulatus*. 19. Pectoral and pelvic girdles and spines of *Diplacanthus striatus*.

FIGS. 20-27. Fins and related structures in Acanthodians. 20. *Parexus falcatus*. 21. *Ibid.* 22. Caudal of *Diplacanthus tenuistriatus*. 23. Second dorsal of *Euthacanthus macnicoli*. 24. Dorsal of *Climatius uncinatus*. 25. Caudal of *Acanthodes bronni*. 26. Detached spine of *Climatius reticulatus*. 27. Shoulder girdle (half) of *Climatius falcatus*, showing dermal elements.

FIGS. 28-36. Sensory structures in Acanthodians. 28, 29. *Acanthodes bronni*. 30. *Climatius grandis*. 31, 32. *Ischnacanthus gracilis*. 33. *Climatius*. Detail of lateral line at a point anterior to second dorsal fin. 34. *Euthacanthus elegans*. Lateral line. 34a. Detail of a shagreen denticle margining lateral line. 35. *Acanthodes bronni*. Detail of lateral line. 36. *Euthacanthus macnicoli*. Detail of enlarged scales of ventral body-wall.



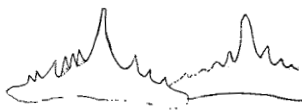
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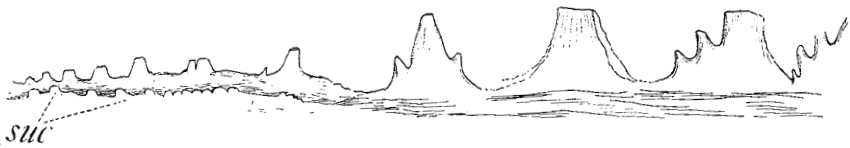
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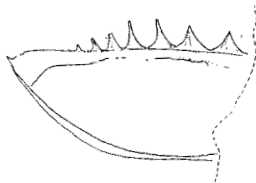
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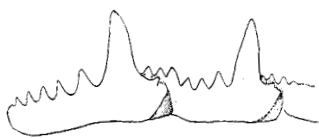
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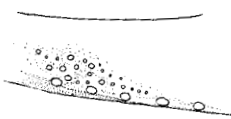
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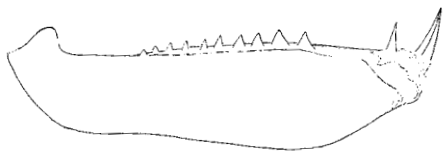
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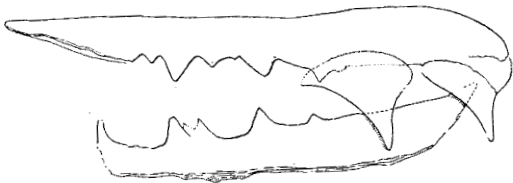
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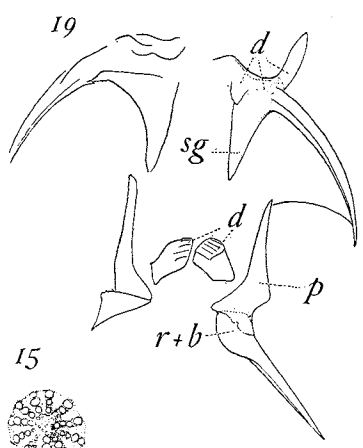
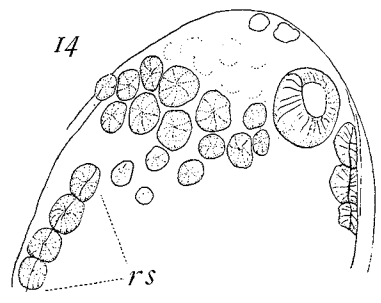
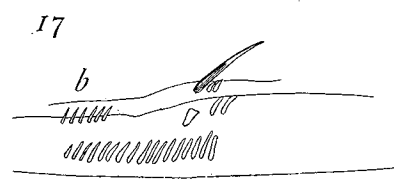
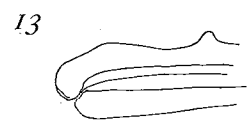
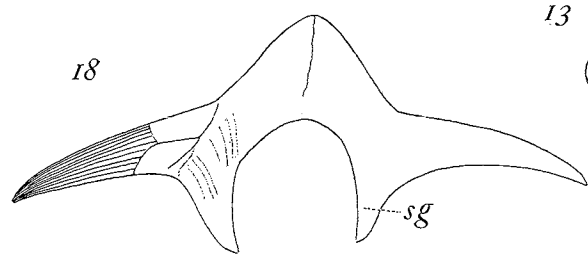
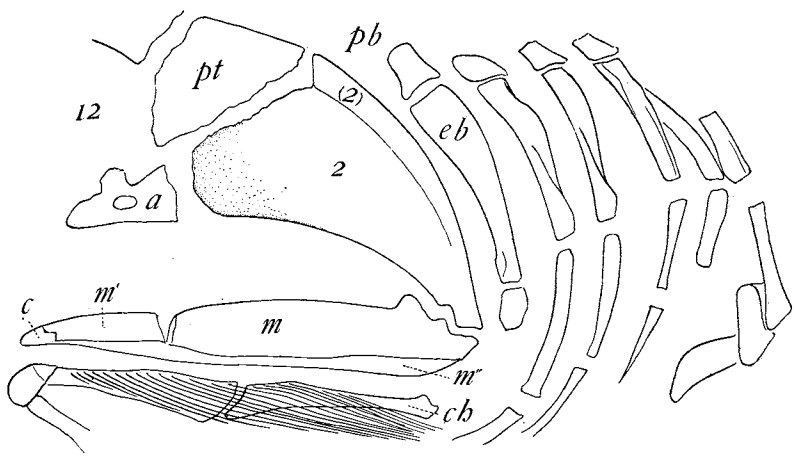


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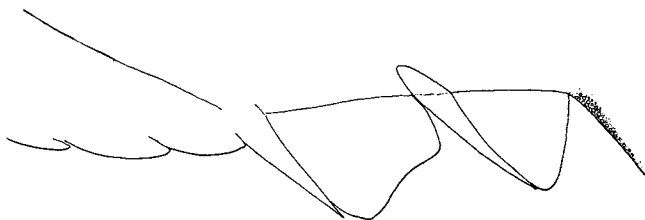
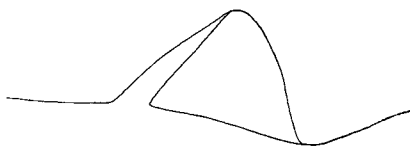


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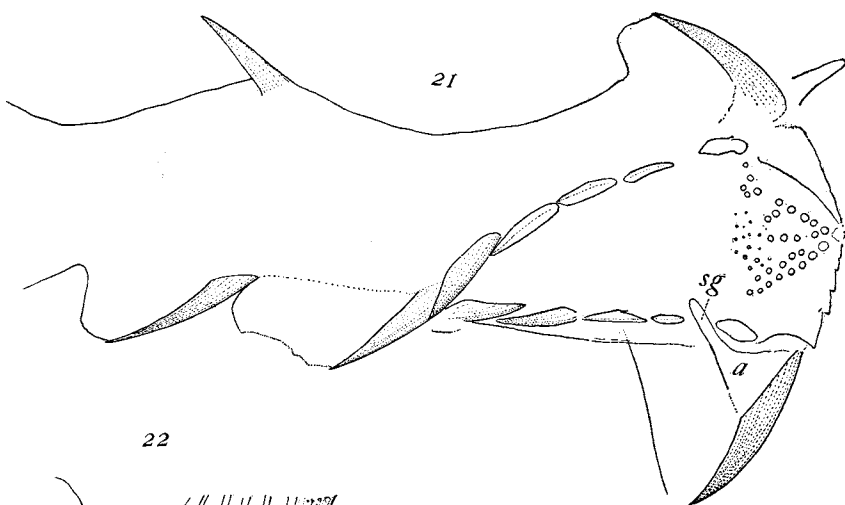




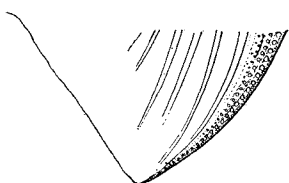
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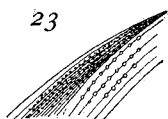
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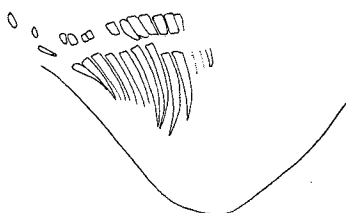
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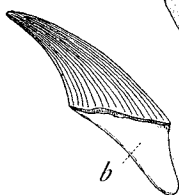
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