A NEW GENUS OF SHARK FROM THE MIDDLE TRIASSIC OF MONTE SAN GIORGIO, SWITZERLAND

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ABSTRACT. Associated material from the Middle Triassic of Monte San Giorgio, Kt. Tessin, Switzerland, demonstrates that the sharks *Nemacanthus tuberculatus* and *Acrodus bicarinatus* constitute a single taxon that must be included in a new genus, *Acronemus tuberculatus*. Finspine structure of *Acronemus* is distinctly different from that of *Nemacanthus monilifer*, but does correspond to the general ctenacanthiform pattern. Other features of *A. tuberculatus* such as tooth structure and placoid scales have previously been reported for Triassic hybodontiform sharks only. A discussion of the orders Ctenacanthiformes and Hybodontiformes concludes the study.

THE *Grenzbitumenzone* of Monte San Giorgio, Kt. Tessin, Switzerland, has so far yielded four hybodontiform shark genera, viz. *Hybodus*, *Acrodus*, *Asteracanthus*, and *Palaeobates*. A fifth selachian taxon, the most frequently found one in the deposits at Monte San Giorgio, will be described in the present contribution. This shark is important as it highlights some problems in the distinction of the Mesozoic orders Hybodontiformes and Ctenacanthiformes as defined by Maisey (1975).

Kuhn (1945) first described the genus *Acrodus* from the Middle Triassic of Monte San Giorgio. Kuhn's (1945) specimen *d* was not fully prepared at the time. The radiograph showed, however, that the proportions of the finspines of this shark were very different from those of *Acrodus*, and that the palatoquadrate was cleaver-shaped (Kuhn, 1945, fig. 4), a feature which is otherwise not known in the genus *Acrodus*. Peyer (1957) mentioned an *Acrodus* from Monte San Giorgio with a tuberculate finspine ornamentation. *Acrodus* finspines always show a costate ornament.

The misidentifications by Kuhn (1945) and Peyer (1957) are based on the fact that in the specimens mentioned by these authors typical *Acrodus* teeth are associated with stout and tuberculate finspines. The teeth and the finspines have been named and referred to different genera by earlier authors. Bellotti, in an unpublished manuscript on the fossil fishes at the Museo Civico di Milano (1873), had named the teeth *Acrodus bicarinatus* and the spines *Nemacanthus tuberculatus*. The first author to use these names in a formal publication was Bassani (1886). He used the names in connection with a valid diagnosis, referring to Bellotti's specimens and manuscript. According to the kind information provided by Professor G. Pinna, Museo Civico di Storia Naturale Milano, the entire old collection on which Bellotti's research was based has been destroyed during the Second World War. No type material has been preserved. Likewise, Bellotti's (1873) manuscript can no longer be located. The only material still available is unpublished drawings by Bellotti including those of *N. tuberculatus*.

The associated material from Monte San Giorgio demonstrates that *A. bicarinatus* and *N. tuberculatus* are a single taxon. Since Bassani (1886) is the formal author of both names, and since in his publication *N. tuberculatus* has page priority, the correct species name for this shark must be *tuberculatus*. The description of the Monte San Giorgio material will make it clear that this shark species cannot be included in the genus *Nemacanthus*, nor in the genus *Acrodus*. A new genus must consequently be erected. Since no original type material is preserved, it is appropriate to select a neotype for that species.

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SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES
Subclass ELASMOBRANCHII
Order CTENACANTHIFORMES incertae familiae
Genus ACRONEMUS n.gen.

Type and only known species. Acronemus tuberculatus (Bassani 1886).

Revised diagnosis. Small (30–35 cm long) ctenacanthiform shark; teeth *Acrodus*-like, with a single and blunt main cusp, crown ornamented with prominent longitudinal and transverse carinae, root without lingual torus; palatoquadrate cleaver-shaped; finspines short and stout, heavily tuberculated with a longitudinal ridge along the leading edge of the crown, not or only slightly recurved, posterior wall concave without denticulate ornamentation, central cavity displaced posteriorly; placoid scales with a lanceolate crown ornamented with three or five longitudinal striae.

Acronemus tuberculatus (Bassani 1886)

Selected synonymy

1886 *Nemacanthus tuberculatus*, Bassani, p. 30.
1886 *Acrodus bicarinatus*, Bassani, p. 31.
1891 *Nemacanthus tuberculatus*, Woodward, p. 117.
1910 *Acrodus bicarenatus*, Alessandri, p. 34, pl. 7, figs. 6–9.
1910 *Nemacanthus tubercolatus*, Alessandri, p. 36, pl. 7, fig. 10.

Neotype. Paläontologisches Institut und Museum der Universität Zürich T 1548, Monte San Giorgio, point 902, layer 118, collected 20.9.1957.

Diagnosis. Same as for genus.

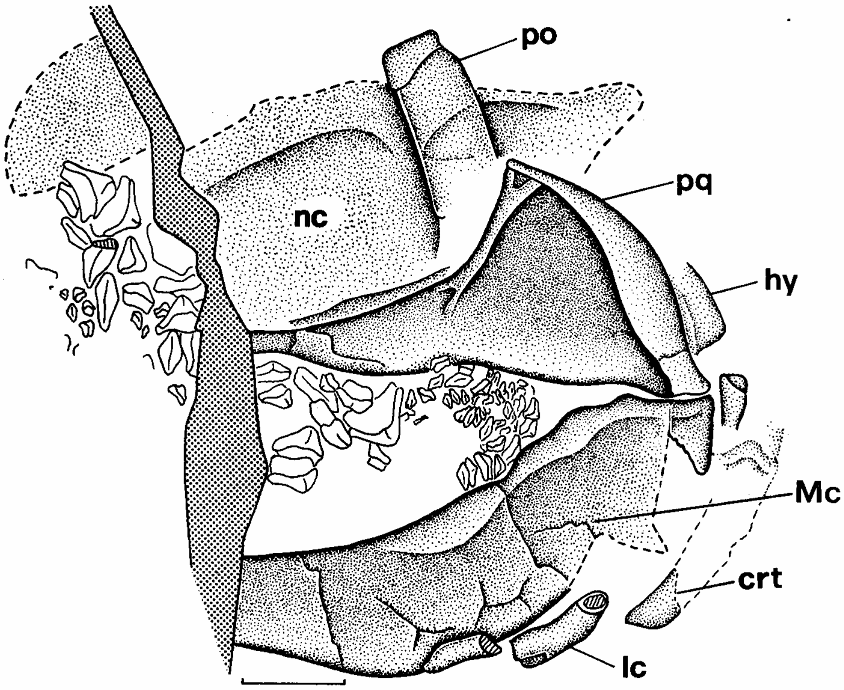
Referred material. All specimens with T-numbers belong to the Tessin collection, Paläontologisches Institut und Museum der Universität Zürich. T 1177, dentition and two finspines; T 1178, dentition, two finspines, skull fragments; T 1181, isolated tooth; T 1289, dentition, anterior finspine; T 1291, dentition, anterior finspine; T 1292, isolated tooth; T 1426, isolated tooth; T 1427, isolated tooth; T 1431, sectioned finspine; T 1434, isolated tooth; T 1448, dentition; T 1457, teeth, sectioned finspine; T 1487, dentition; T 1531, dentition and two finspines; T 1551, incomplete finspine; T 2465, dentition, upper and lower jaws, two finspines (see Kuhn 1945, fig. 4); T 3297, isolated tooth; T 3812, dentition; T 3818, two finspines; T 3819, dentition; T 3820, dentition; T 3821, dentition and jaw fragments; T 3822, dentition and anterior finspine; T 3827, dentition; T 3825, dentition and two finspines; T 3826, dentition; T 3828, posterior finspine; T 3829, dentition and anterior finspine; T 3831, dentition; T 3833, dentition; T 3834, dentition; T 3835, dentition and finspine; T 3836, dentition; T 3837, dentition; T 3840, sectioned finspine; T 3841, anterior finspine; T 3843, sectioned finspine; T 3844, finspine; T 3845, finspine; T 3846, sectioned finspine; T 3847, sectioned finspine; T 3849, fifty-two isolated teeth; British Museum (Natural History) P 19450, complete dentition.

Distribution. Middle Triassic of Southern Alps (Grenzbitumenzone of Monte San Giorgio, Kt. Tessin, Switzerland, and the same beds near Besano, Lombardy, Italy).

Description

Neurocranium and jaws. Virtually nothing is known of the neurocranium. Remains are observed in T 1548 (lateral view, text-fig. 1) and in T 2465 (dorsal view, text-fig. 2). There is a very prominent postorbital process which lies just in front of the otic process of the palatoquadrate. The rostrum appears to have been short and blunt, projecting little beyond the suborbital ramus of the palatoquadrate.

The palatoquadrate (text-figs. 1 and 2) shows a large postorbital ramus (slightly more than half the total length of the palatoquadrate) with a prominent otic process. The latter articulates with the postorbital process of the neurocranium. The anterior edge of the otic process is steeply inclined. The posterior edge is thickened and thus forms a rim which limits the area of origin of the m. adductor mandibulae externus. The lower end of the thickened posterior edge forms the articular condyle of the palatoquadrate which fits into a facet on the posterior end of Meckel's cartilage. The narrow, tapering suborbital ramus makes up slightly less than half of the total length of the palatoquadrate. A weak elevation of its dorsal edge in its anterior portion (text-fig. 2) forms the orbital process which articulates with the suborbital shelf of the neurocranium.



TEXT-FIG. 1. Skull remains in *Acronemus tuberculatus* T 1548. Abbreviations: crt, ceratohyal; hy, hyomandibula; lc, labial cartilages; Mc, Meckel's cartilage; nc, neurocranium; po, postorbital process; pq, palatoquadrate. Scale equals 10 mm.

Meckel's cartilages (text-figs. 1 and 2) are elongated and moderately deep. The ventral margin is convex and slightly thickened. The thickened ventral rim limits the site of insertion of the m. adductor mandibulae externus. The dorsal edge is concave except for the posterior portion where the dorsal edge is straight.

All the Monte San Giorgio material is strongly compressed, but from a thickening it appears that both the dorsal edge of Meckel's cartilage as well as the ventral edge of the palatoquadrate formed an outwardly turned shelf for the support of the teeth.

Labial cartilages. Only broken fragments are observed in T 1548 (text-fig. 1) along the ventral edge of Meckel's cartilage.

Hyoid arch. The articulation of the hyomandibula with the ceratohyal is preserved just posterior to the jaw articulation in T 1548 (text-fig. 1). The jaw suspension in a shark with a cleaver-shaped palatoquadrate may be assumed to have been amphistylic (Schaeffer 1967).

Cephalic spines. These are not recorded in any specimen.

Teeth. The teeth of *Acronemus tuberculatus* have long been known under the name of *Acrodus bicarinatus* (Bassani 1886; Alessandri 1910). The teeth are characterized by a single, blunt main cusp. No accessory lateral cusps are developed (Pl. 43, fig. 1). There is a marked longitudinal and a marked transverse ridge across the crown. The ridges meet at right angles on the apex of the main cusp (text-fig. 3 and Pl. 43, fig. 3). From the longitudinal and transverse ridges fine striae radiate towards the edges of the crown. The main cusp forms a bulbous lingual projection which overlaps the next inner tooth of the same tooth family. This results in a supporting mechanism for the outer functional tooth very similar to the one observed in *A. lateralis*.

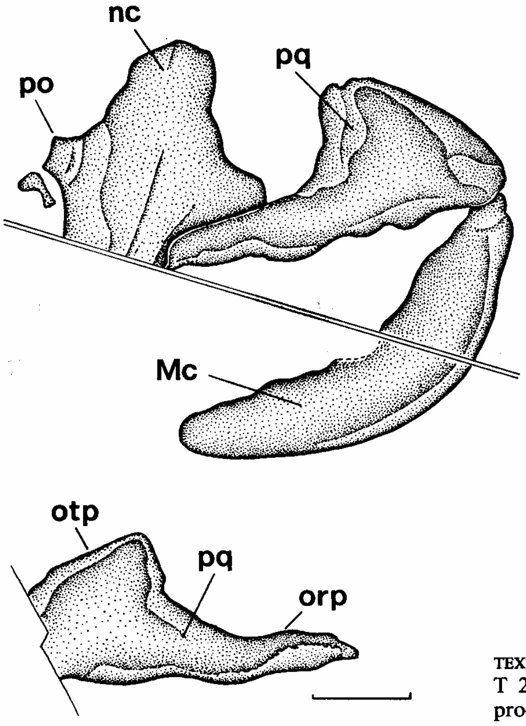
The enameloid layer covering the crown is of the single-crystallite type (Pl. 43, fig. 4) as defined by Reif (1973), without a superficial shiny layer. The root bears no expanded lingual torus. Root foramina were very difficult to observe because the bituminous matrix does not allow chemical preparation to expose these foramina.

The large lateral teeth are symmetrical, with the main cusp in a fairly central position. The crown is high and the lower edge of the root is distinctly concave (text-fig. 3). Towards the symphysis the teeth become progressively smaller and the crown lower and asymmetrical in that the main cusp is shifted towards the distal side of the crown. The lower edge of the root becomes less concave or even straight (text-fig. 3). Distal to the large lateral teeth there is a series of very low but very elongated and distinctly asymmetrical teeth (text-fig. 3) with the main cusp displaced towards the mesial side of the tooth. The lower edge of the crown is almost straight. Again, the teeth diminish in size towards the distal end of the jaw.

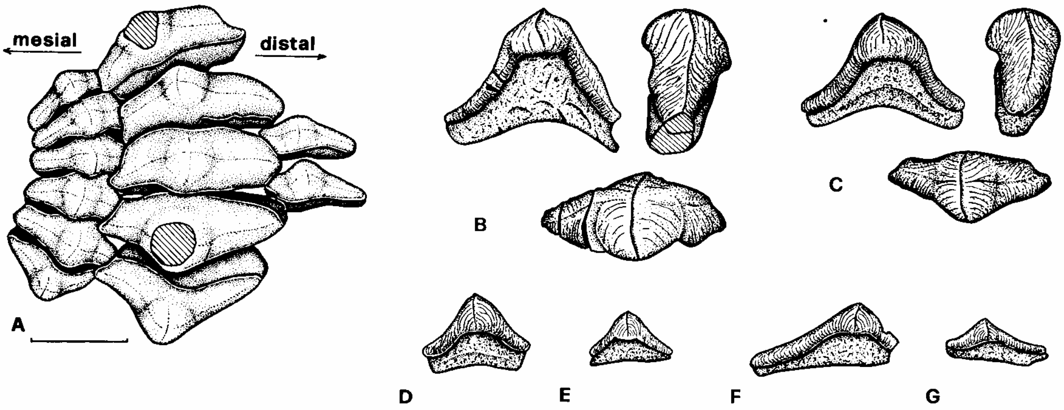
Pectoral girdle. The left pectoral girdle is preserved in T 1548 (text-fig. 4). Its structure clearly resembles that of *Acrodus* and *Hybodus* (Koken 1907). The suprascapular portion is an elongated, spinous structure curved in an anterior direction. The scapulocoracoid and the ventral coracoid bar are poorly preserved. Below the pectoral girdle, a single basal element of the pectoral fin is preserved (text-fig. 4). The incompleteness of the specimen does not allow the reconstruction of the basal skeleton of the pectoral fin.

Finspines. The finspines of *Acronemus* (syn. *Nemacanthus tuberculatus*) are relatively short and broad which results in characteristic stout proportions. The anterior finspines are relatively longer and relatively broader than the posterior finspines (text-fig. 5; Pl. 43, figs. 6, 7). The crown of the anterior finspine is frequently of a broad-based, upright triangular shape (text-fig. 6A). However, it may become somewhat elongated and recurved to a variable degree (text-fig. 5; Pl. 43, figs. 6, 8). The posterior finspines are relatively smaller and narrower with an upright crown that is never distinctly curved in a posterior direction.

The most characteristic feature of the spines is their conspicuous tuberculation. Large and rounded tubercles are arranged in a regular pattern on which it is possible to superimpose straight longitudinal lines. It is equally possible to superimpose on the pattern of tuberculation curved and obliquely oriented lines which run in a posterodorsal direction across the lateral surface of the crown (text-fig. 6A). There is in some spines the tendency of the tubercles to fuse into segments of ridges running in a curved posterodorsal direction across the lateral surface of the crown (text-fig. 6; Pl. 43, figs. 6, 7). The arrangement of the tubercles along curved, obliquely



TEXT-FIG. 2. Skull remains in *Acronemus tuberculatus* T 2465. Abbreviations: orp, orbital process; otp, otic process; others as in Text-fig. 1. Scale equals 20 mm.



TEXT-FIG. 3. The teeth of *Acronemus tuberculatus*. A: T 3821, articulated part of dentition (surface abraded). Scale equals 5 mm. B–G: T 3849, isolated teeth. B–C, large lateral teeth in lingual, lateral, and occlusal views; D–E, successive mesial teeth in lingual view; F–G, successive distal teeth in lingual view.

oriented lines reflects the growth pattern of the spine. The completely closed enameloid mantle of euselachian finspines frequently shows similarly oriented growth lines (Maisey 1977).

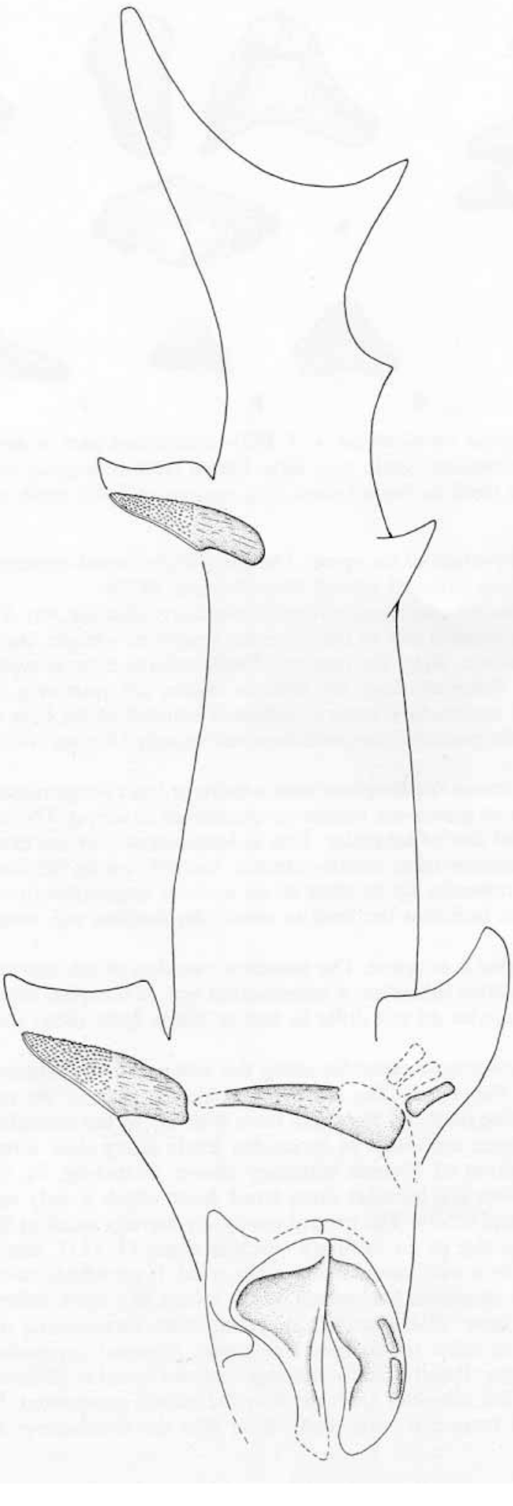
In some specimens the tubercles are small and scattered irregularly (text-fig. 6B). The scattered arrangement is probably due to wear, but the smaller size of the tubercles results in a larger number of longitudinal rows counted across the base of the crown. Also, the anterior finspines have a larger number of longitudinal rows of tubercles than the posterior finspines since the anterior spines are relatively broader. On the anterior finspines there are from 10 to 23 longitudinal rows of tubercles counted at the base of the crown, the average ranging from 13 to 15 rows. On the posterior finspines there are usually 13 rows of tubercles, variation ranging from 9 to 13 rows.

Along the leading edge of the crown the finspines bear a more or less conspicuously developed longitudinal ridge. In T 1289 this ridge, as far as preserved, retains an enameloid covering. The anterior ridge results from the fusion of a single anteromesial row of tubercles. This is demonstrated by the finspines of T 3825 in which this fusion is incomplete. The anterior ridge usually extends ventrally along the leading edge of the finspine beyond the lowermost anterior tubercles up to close to an anterior projection formed by the upper part of the root. This anterior projection indicates the level to which the finspine was inserted in the epaxial trunk musculature.

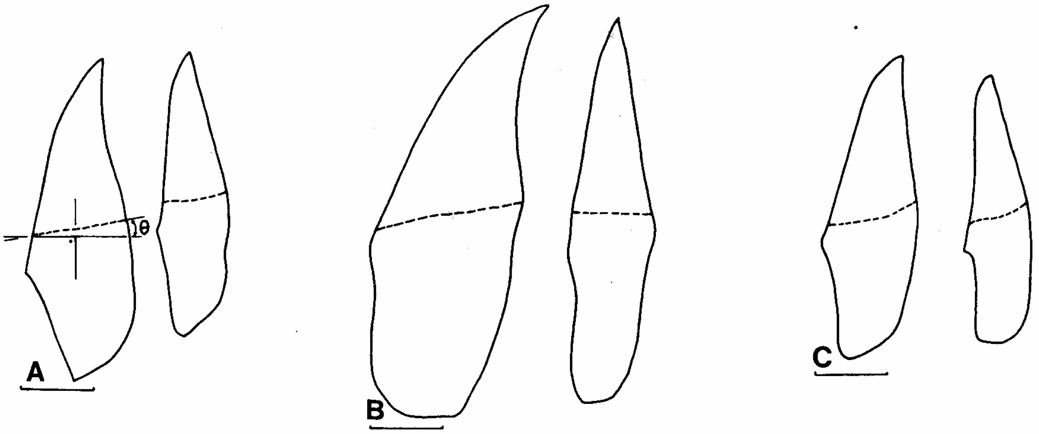
The posterior wall of the finspine is concave. The posterior opening of the central cavity extends upwards to the level of the lowermost posterior tubercles. A longitudinal row of tubercles runs along the posterolateral edge of the crown, but these tubercles do not differ in size or shape from those covering the lateral surface of the crown.

The line which connects the lowermost tubercles along the anterior and posterior edges of the finspine is chosen to represent the base of the crown. The angle θ between the base of the crown and the normal on the longitudinal axis of the finspine (text-fig. 5) ranges from 8 to 24° in the available spines.

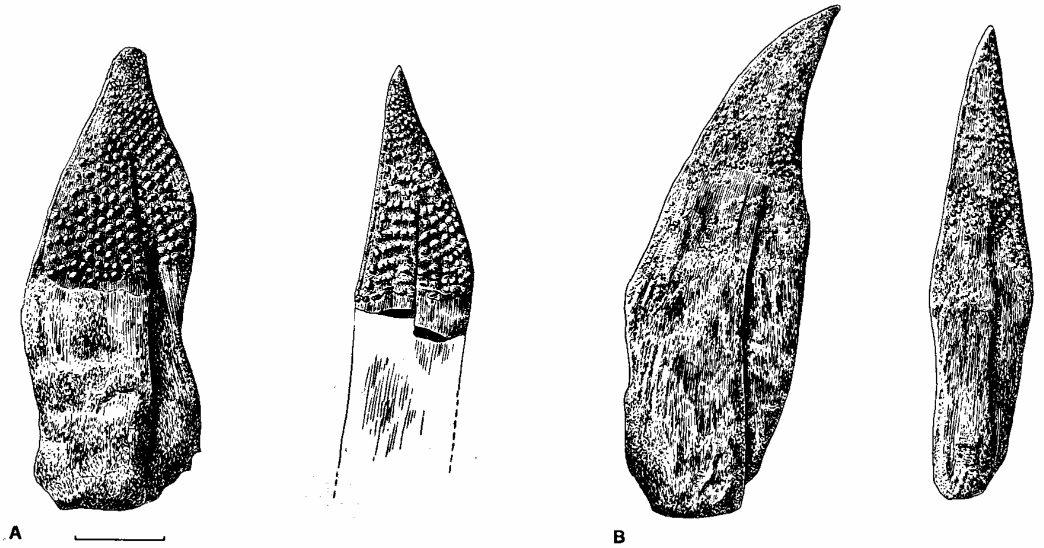
Five finspines of *Acronemus* were sectioned at successive levels along their long axis. A composite and slightly diagrammatic representation of finspine histology shown in text-fig. 7A may be compared to the section figured in text-fig. 7B. There is a lamellar inner trunk layer which is only apically distributed, above the posterior opening of the central cavity. The central cavity is generally small at this level, sometimes even (ontogenetically?) reduced to the size of an ordinary vascular canal (T 1431, section Nr. 8). The lamellar inner trunk layer is surrounded by a well vascularized outer trunk layer which also forms the entire root of the finspine. The central cavity is displaced backwards which results in a thick anterior wall largely made up by the vascularized outer trunk layer. The vascular canals and their surrounding denteons are rather small and widely spaced which gives the outer trunk layer a relatively compact appearance. Towards the leading edge of the spine a distinctly larger, longitudinally running vascular canal is observed lying straight in front of the central cavity (text-fig. 7). The tubercles are formed by the mantle component, but no clearcut boundary separates the mantle component from the outer trunk layer (for the terminology of finspine histology see Maisey 1979).



TEXT-FIG. 4. Tentative reconstruction of *Acronemus tuberculatus*, based on T 1548. Approx. ×0·4.



TEXT-FIG. 5. Variation in size and shape of the anterior (left) and posterior (right) finspines of *Acronemus tuberculatus*. A, T 1178; B, T 2465; C, T 1548. Scale equals 10 mm. For further explanations see text.

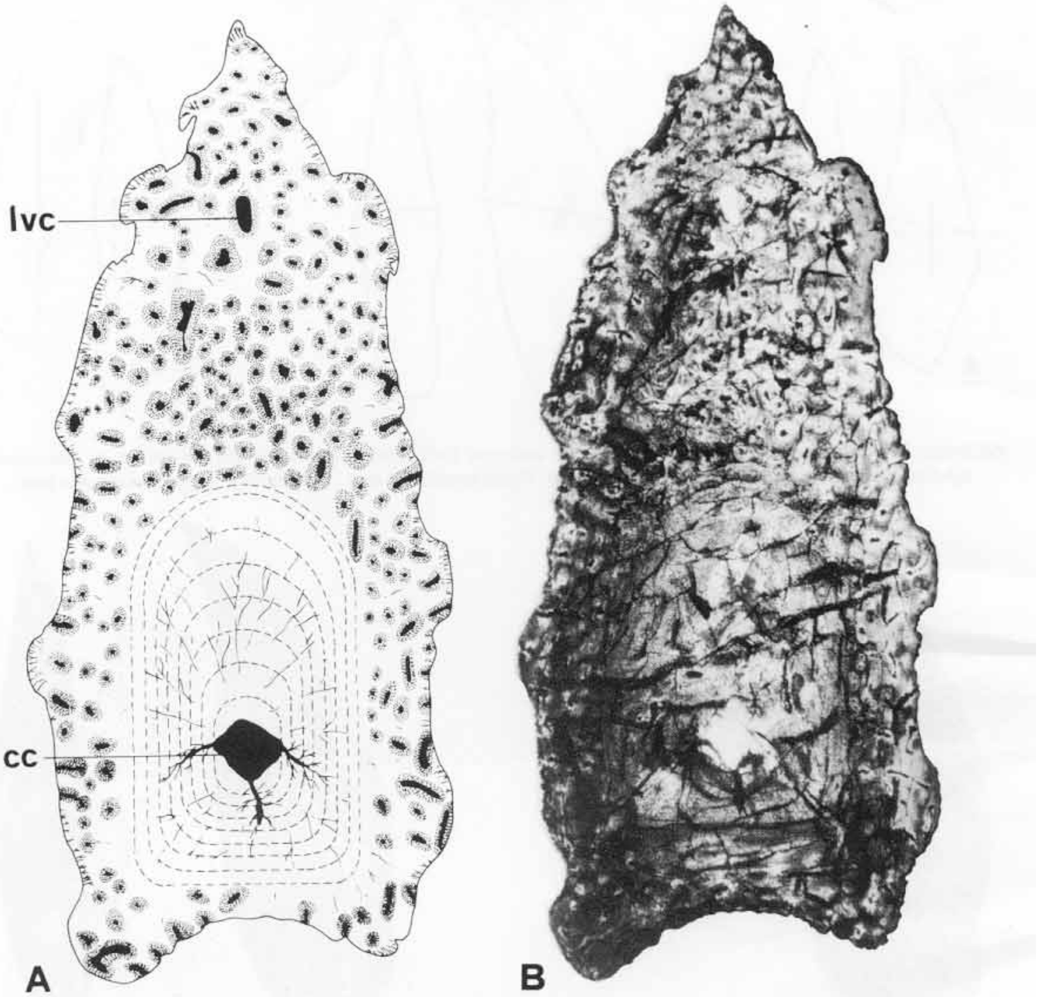


TEXT-FIG. 6. Ornamentation of the anterior (left) and posterior (right) finspines of *Acronemus tuberculatus*. A, T 3818; B, T 2465. Scale equals 10 mm.

Scales. Flank scales of the specimen T 1548 are shown on Pl. 43, fig. 5. They are of the non-growing, placoid type. They bear a recurved, lanceolate crown which is ornamented with three or five widely spaced longitudinal striae.

COMPARISON WITH THE GENUS *NEMACANTHUS*

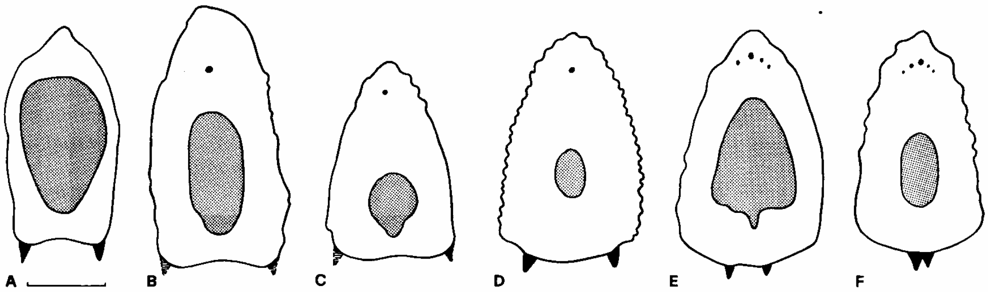
The finspines of *Acronemus tuberculatus* were originally referred to the genus *Nemacanthus* Ag. (Bellotti 1873, in Bassani 1886). Type species of the latter genus is *Nemacanthus monilifer* Ag., with which comparison thus must proceed. *N. monilifer* is represented by finspines from the Rhaetic of England which differ in several respects from those of *A. tuberculatus*. Assuming a relatively



TEXT-FIG. 7. Finspine histology of *Acronemus tuberculatus*. A. Semidiagrammatic representation of a transverse section through the crown of a finspine, based mainly on section T 3847/7. Abbreviations: cc, central cavity; lvc, longitudinal vascular canal. B. Ground section Nr. T 3847/7. Approx. × 30.

constant structure of the finspines within shark genera, this justifies the erection of a new genus to include the spines of *tuberculatus* (Maisey, pers. comm.).

The finspines of *N. monilifer* (comparative material used for this study is housed in the British Museum (Natural History) and is listed in the Appendix) are long and slender in comparison to *Acronemus*. They are regularly curved in a posterior direction. If the total height of the finspines is divided by their maximum width, the values obtained for two complete specimens of *N. monilifer* are 8·56 (BM(NH) P.8328) and 9·3 (BM(NH) P.46830). Nine anterior finspines of *A. tuberculatus* have a corresponding mean value of 3·15, while six posterior finspines have a mean value of 4·1. In both genera the finspines bear an anterior enamelled ridge as well as a tuberculate mantle ornament, but the tubercles are fewer in number in *N. monilifer*. In the latter genus one usually



TEXT-FIG. 8. Semidiagrammatic sections through the finspines of chimaeroids and selachians. A, *Leptacanthus longissimus*, BM(NH) Egerton coll.; B, *Ctenacanthus angustus*, BM(NH) P.9581; C, *Nemacanthus monilifer*, BM(NH) P.15497, section 10; D, *Palaeobates keuperinus*, BM(NH) P.7604; E, *Hybodus lawsoni*, BM(NH) P.2174a; F, *Hybodus acutus*, BM(NH) P.6157. Scale equals 5 mm.

counts less than ten rows of tubercles across the base of the crown, variation ranging from 7 rows in BM(NH) P.46830 to 11 rows in BM(NH) P.2852, whereas in *A. tuberculatus* one usually counts more than 10 rows (9–23) of tubercles across the base of the crown. The connection of the lowermost tubercles at the anterior and posterior margins of the finspine results in a line which slants much more steeply in a posterodorsal direction in *Nemacanthus* as compared to *Acronemus*. This line intersects the normal on the long axis of the spine at an angle θ (text-fig. 5) which in *N. monilifer* ranges from 60° (BM(NH) P.46830) to 78° (BM(NH) P.51433), but from 8–24° in *Acronemus*. A function of this angle is the fact that the tubercles approach the posterior edge of the spine only towards its apex in *N. monilifer*. The extent of tuberculation in *N. monilifer* may either be due to ontogenetic changes or to wear. In the specimen BM(NH) P.8328 isolated rudiments of a few worn or resorbed tubercles can be observed on the posteroventral part of the lateral surface of the crown, an area which lies well below the regularly tuberculated part of the crown but above the ventral end of the enamelled anterior ridge. The angle θ might be an indication of the degree of posterior inclination of the finspine insertion relative to the long axis of the body. Specimen BM(NH) P.8328 suggests that the degree of posterior inclination of finspine insertion increased during ontogeny in *N. monilifer*.

In both genera the posterior wall of the finspine is concave. In *Acronemus* longitudinal rows of unmodified tubercles run along the posterolateral edges of the crown. In some specimens of *N. monilifer* rows of small but pointed denticles are observed running along the posterolateral edges of the crown (Maisey 1977, Pl. 1. fig. D, and specimens BM(NH) P.1882, P.51433). Such posterolateral rows of denticles are also observed in some specimens of the genus *Ctenacanthus* (BM(NH) P.2525, P.2529).

The histology of the finspines is basically similar in *Acronemus* and *Nemacanthus*, except for the detailed histology of the thick anterior wall. In *N. monilifer* the vascular canals are large and closely juxtaposed, which results in the characteristic open spongy texture of the anterior wall (Maisey 1977, pl. 2, fig. C; Stromer 1927, text-fig. 12). This contrasts with the much more compact texture of the anterior finspine wall in *Acronemus*.

DISCUSSION: THE CLASSIFICATION OF *ACRONEMUS*

Maisey (1975) subdivided the phalacanthous sharks (*sensu* Zangerl 1973) into three groups of ordinal rank, the Hybodontiformes, the Ctenacanthiformes, and the Euselachiformes. The distinction of these three groups is based mainly on a detailed study of finspine structure. On the basis of finspine structure alone, *Acronemus* clearly has to be classified with the Ctenacanthiformes as defined by Maisey (1975). The structure of the palatoquadrate ties in well with such a conclusion.

It is cleaver-shaped in *Acronemus* as in some Palaeozoic ctenacanthiformes such as *Goodrichthys* (Moy-Thomas 1936), whereas *Hybodus* and its allies show a reduction of the otic process. The cleaver-shaped palatoquadrate probably is a primitive feature, however (Schaeffer 1967). Cephalic spines are not reported in ctenacanthiform sharks or in *Acronemus*.

However, other features do not support the classification of *Acronemus* with the Ctenacanthiformes. The teeth of *Acronemus* are very similar to those of *Acrodus*, and they lack an expanded lingual torus on the root. The teeth of Palaeozoic ctenacanthiforms are of the multicuspid cladodont type with a lingual torus on the root (Maisey 1975). Which type of tooth was possessed by the Lower Triassic (Stensiö 1921, 1932) or Rhaetic *Nemacanthus* is controversial (Maisey 1977). No associated *Nemacanthus* specimen has yet been found.

All Palaeozoic ctenacanthiform sharks have scales of a composite, growing type (Reif 1978). *Acronemus* has placoid scales which are typical of pre-Rhaetian hybodontids (Reif 1978, p. 126), as well as of euselachians.

These latter features of *Acronemus* might indicate that the ctenacanthiform and hybodontiform sharks can only be recognized by their finspine structure. However, they might also indicate that the distinction between the two orders is not as clearcut as it would appear (Schaeffer and Williams 1977). In fact, some mixture of hybodontiform and ctenacanthiform features was noted by Dick (1978) in his description of *Tristychius*.

Among all those finspines examined by me (see Appendix) there is enough variability to substantiate this point. The only ctenacanthiform features which are really constant throughout the material examined are a flat or concave posterior wall and a posteriorly displaced central cavity which results in a relatively thick anterior wall. In hybodontiform finspines the posterior wall may be flat or convex to a variable degree, and the anterior wall of the finspine is never much thicker than the posterior wall. This latter feature is a function of the posteriorly displaced central cavity of ctenacanthiform spines, but the position of the central cavity may again be correlated at least to some extent with the degree of convexity of concavity of the posterior wall. If the central cavity is held at a constant distance from the leading edge of the spine it will appear in a central position if the posterior wall is strongly convex, but it will appear in a posteriorly displaced position if the posterior wall is strongly concave. The crown of the *Hybodus* finspine BM(NH) P.57794 is broken at successive levels. Examination of the four levels of breakage showed that the anterior wall gets relatively thicker towards the apex of the spine as the diameter of the central cavity diminishes. A finspine of *Nemacanthus monilifer* (BM(NH) P.15497) which was sectioned at successive levels from top to bottom shows that the relative thickness of the anterior wall remains constant throughout the length of the spine.

The anterior wall of the ctenacanthiform finspine is said frequently to be of an open spongy texture (Maisey 1975). This in fact is only true for *N. monilifer* (and for the euselachian genus *Breviacanthus* Maisey 1976). The anterior wall of the *Ctenacanthus* finspine has exactly the same

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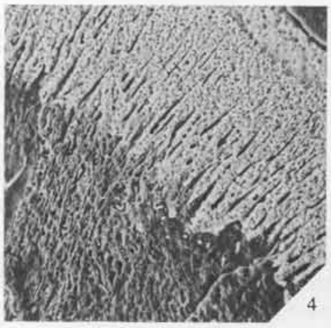
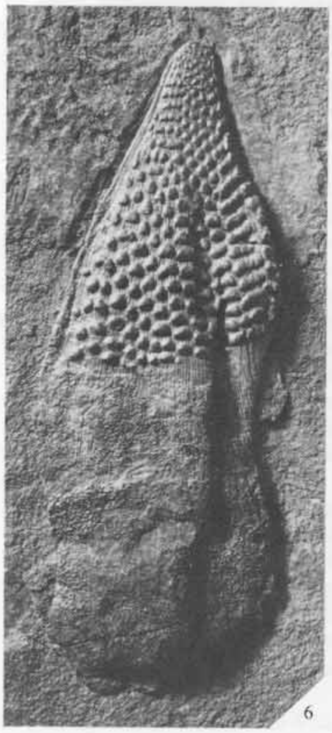
EXPLANATION OF PLATE 43

Acronemus tuberculatus

Fig. 1. Tooth T 3849 in lingual view, × 10.
Fig. 2. Tooth T 3849 in lateral view, × 10.
Fig. 3. Tooth T 3849 in occludal view, × 10.
Fig. 4. Tooth T 3849, cross-section etched with 2n-HCl for 5 sec. to show the single-cristallite enamel, approx. × 150.
Fig. 5. Placoid scale from specimen T 1548, approx. × 130.
Fig. 6. Anterior finspine from specimen T 3818, × 1·8.
Fig. 7. Posterior finspine from specimen T 3818, × 1·8.
Fig. 8. Anterior finspine T 1289, × 1·25.





RIEPPEL, Middle Triassic shark

vermiculate texture produced by relatively small vascular canals as is observed in typical hybodontiform finspines. *Acronemus* has an even more compact finspine histology.

Hybodontiform finspines are said to show a concentric ring of longitudinally running vascular canals around the central cavity (Maisey 1975, 1978). This is not always very clearly differentiated. In addition, a comparison with chimaeroid finspines (see Appendix) as well as with acanthodian finspines (Krebs 1960) indicates that concentrically arranged vascular canals are a primitive character-state in selachians. However, in all the hybodontiform and ctenacanthiform finspines examined by me there is a conspicuously larger longitudinal vascular canal which lies straight in front of the central cavity.

An important difference between hybodontiform and ctenacanthiform finspines is the ornamentation of the posterior wall in hybodontiforms, with one or two longitudinal rows of denticles, said to be absent in ctenacanthiforms (Maisey 1975). Hybodontiform finspines typically carry a double or a single row of rather large denticles close to, or on, the midline of the posterior wall. Such denticles indeed are absent in ctenacanthiforms. But in genera such as *Ctenacanthus* and *Nemacanthus* (Maisey 1977, Pl. 1, fig. D, and quotations above) rows of small denticles are arranged along the posterolateral edges of the crown which has a concave posterior wall. Maisey (1975) considers the denticles on the posterior wall of hybodontiform finspines as either highly modified mantle components or as specialized scales secondarily fused to the finspine. The posterolateral denticles of ctenacanthiform finspines are merely considered to represent 'posterolateral rows of pointed tubercles' (Maisey 1977, p. 265). This distinction appears meaningless since it is impossible to determine the morphogenetic status of the hybodontiform versus the ctenacanthiform denticles. If the denticles are considered homologous, it is possible to claim that posterolaterally placed denticles are a primitive character state while denticles which have shifted to a posteromesial position represent an advanced character state. Outgroup comparison with chimaeroid finspines (see Appendix) demonstrates that in this group there are usually two longitudinal rows of posterolaterally placed denticles, arranged along the edges of a concave posterior wall (text-fig. 8A). One undescribed chimaeroid finspine (BM(NH) P.2850) shows a single row of denticles along the midline of the concave posterior wall. This single row of denticles may well have originated from double rows of posterolaterally placed denticles that have shifted towards the midline of the posterior wall. A similar phenomenon has been noted for *Hybodus* finspines (Maisey 1978). A single row of posteromesially arranged denticles appears to originate from the superposition of two collateral rows of denticles on the midline of the posterior wall (text-fig. 8E–F). This point is further corroborated by a consideration of the finspines of *Palaeobates keuperinus* (text-fig. 8D). In fact, the structure of these finspines is perfectly intermediate between the ctenacanthiform and hybodontiform types and thus illustrates the potential difficulties in recognizing the two orders. In *P. keuperinus* the posterior wall of the finspine is weakly convex (as in some *Hybodus* finspines), but it carries two posterolaterally placed rows of denticles (as in ctenacanthiforms). The central cavity is small and somewhat displaced backwards as in ctenacanthiforms, but the posterior wall still retains a considerable thickness although it is thinner than the anterior wall.

In summary it can be stated that hybodontiform and ctenacanthiform sharks together form a group of selachians with a finspine structure involving an apically distributed inner trunk layer surrounded by a trabecular outer trunk layer. The details of the histology of the outer trunk layer are quite variable and only characteristic at the generic level. There is no clearcut boundary between the outer trunk layer and the mantle component. The mantle ornamentation may be tuberculate or costate. As evidenced by the genus *Acronemus*, the orders Hybodontiformes and Ctenacanthiformes can at present be recognized on the basis of finspine structure alone. Ctenacanthiform finspines show a flat or concave posterior wall with two rows of posterolaterally placed denticles (primitive) and a posteriorly displaced central cavity. Hybodontiform finspines show a flat or convex posterior wall with one or two rows of denticles close to or on the midline of the posterior wall (derived). The central cavity is rather centrally positioned. However, intermediate forms such as *P. keuperinus* and *Tristychius* (Dick 1978) do occur.

On the basis of finspine structure, *Acronemus* can be classified as a ctenacanthiform shark. The posterior wall of the finspine is concave, and the central cavity displaced backwards. If such an arrangement is accepted it must be concluded that neither the 'hybodontiform' tooth structure nor the presence of placoid scales can be used to distinguish hybodontiform and ctenacanthiform sharks from the Triassic.

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REFERENCES

ALESSANDRI, D. DE. 1910. Studii sui pesci triasici della Lombardia. *Mem. Soc. ital. Sci. Nat., Milano*, **7**, 1-145.

BASSANI, FR. 1886. Sui fossili e sull'età degli schisti bituminosi triasici di Besano in Lombardia. *Atti Soc. ital. Sci. Nat., Milano*, **29**, 15-72.

DICK, J. R. F. 1978. On the Carboniferous shark *Tristychius arcuatus* Agassiz from Scotland. *Trans. R. Soc. Edinburgh*, **70**, 63-109.

KOKEN, E. 1907. Ueber *Hybodus*. *Geol. Palaeont. Abh.* (N.F.), **5**, 261-276.

KREBS, B. 1960. Ueber einen Flossenstachel von *Gyracanthus* (Acanthodii) aus dem Oberkarbon Englands. *Eclogae geol. Helv.* **53**, 811-827.

KUHN, E. 1945. Ueber *Acrodus*-Funde aus dem Grenzbitumenhorizont der anisischen Stufe der Trias des Monte San Giorgio (Kt. Tessin). *Eclogae geol. Helv.* **38**, 662-673.

MAISEY, J. G. 1975. The interrelationships of phalacanthous selachians. *N. Jb. Geol. Palaeont. Mh.* **1975** (9), 553-567.

—— 1976. The Middle Jurassic selachian fish *Breviacanthus* n.g. *N. Jb. Geol. Palaeont. Mh.* **1976** (7), 432-438.

—— 1977. The fossil selachian fishes *Palaeospinax* Egerton, 1872 and *Nemacanthus* Agassiz, 1837. *Zool. J. Linn. Soc.* **60**, 259-273.

—— 1978. Growth and form of finspines in hybodont sharks. *Palaeontology*, **21**, 657-666.

—— 1979. Finspine morphogenesis in squalid and heterodontid sharks. *Zool. J. Linn. Soc.* **66**, 161-183.

MOY-THOMAS, J. A. 1936. The structure and affinities of the fossil elasmobranch fishes from the Lower Carboniferous rocks of Glencartholm Eskdale. *Proc. zool. Soc., Lond.* **1936**, 761-788.

PEYER, B. 1957. Ueber die morphologische Deutung der Flossenstacheln einiger Haifische. *Mitt. naturf. Ges. Bern* (N.F.), **14**, 159-176.

REIF, W.-E. 1973. Morphologie und Ultrastruktur des Hai-'Schmelzes'. *Zoologica Scripta*, **2**, 231-250.

—— 1978. Types of morphogenesis of the dermal skeleton in fossil sharks. *Palaeont. Z.* **52**, 110-128.

SCHAEFFER, B. 1967. Comments on elasmobranch evolution. *In* GILBERT, P. W., MATHEWSON, R. F. and RALL, D. P. (eds.). *Sharks, Skates and Rays*. John Hopkins Press, Baltimore. Pp. 3-35.

—— and WILLIAMS, M. 1977. Relationships of fossil and living elasmobranchs. *Amer. Zool.* **17**, 293-302.

STENSIÖ, E. 1921. *Triassic fishes from Spitzbergen, Pt. 1.* Adolf Holzhausen, Vienna. i-xxviii, 1-307, pls. 1-35.

—— 1932. Triassic fishes from East Greenland, collected by the Danish expeditions in 1929-1931. *Medd. om Grønl.* **83**, 1-305.

STROMER, E. 1927. Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Aegyptens. 2. Wirbeltier-Reste der Baharîje-Stufe (unterstes Cenoman). 9. Die Plagiostomen, mit einem Anhang über käno- und mesozoische Rückenflossenstacheln von Elasmobranchiern. *Abh. Bayr. Akad. Wiss., math.-natw. Abt.* **31**, 1-64.

WOODWARD, A. S. 1891. *Catalogue of the fossil fishes in the British Museum (Natural History), Vol. 3.* British Museum (Natural History), London. Pp. i-xliv, 1-567, pls. 1-16.

ZANGERL, R. 1973. Interrelationships of early chondrichthyans. *In* GREENWOOD, P. H., MILES, R. S. and PATTERSON, C. (eds.). Interrelationships of fishes. *Zool. J. Linn. Soc.* **53**, Suppl. 1, 1-14.

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