Stuttgarter Beiträge zur Naturkunde

Serie B (Geologie und Paläontologie)

Herausgeber:

Staatliches Museum für Naturkunde, Schloss Rosenstein, 7000 Stuttgart 1

Stuttgarter Beitr. Naturk.	Ser. B	Nr. 97	41 S.	Stuttgart, 30. 12. 1983

Holocephalans in the Staatliches Museum für Naturkunde in Stuttgart

1. Myriacanthoids and squalorajoids

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With 5 Plates and 7 Figures

Abstract

Acanthorhina jaekeli Fraas is redescribed in detail from the unique specimen from the Toarcian of Holzmaden, and assigned to the Family Myriacanthidae. The neurocranium possesses an elongate rostrum with differentiated cartilage strips dorsally and ventrally. Tuberculated dermal plates are present in the angle of the lower jaw, anterodorsal to the orbit and possibly posterior to the orbit. The fin spine is recurved and tuberculated for the proximal two-thirds of its length. Posterior denticles are present along the distal third of the spine. The pectoral girdle bifurcates ventrally. The dentition comprises an arcuate lower symphyseal tooth plate, one pair of posterior lower tooth plates, and three tooth plate pairs in the upper jaw. Pronounced diagonal ridges on the posterior lower tooth plates and the tooth plates of the upper dentition allowed both shearing and crushing during occlusion. The frontal clasper is large. Gut contents and representations of the belly musculature are preserved. *Acanthorhina* probably fed on benthonic organisms, and was probably also capable of mid-water feeding, perhaps on belemnites and small fish.

The unique fin spine of *"Myriacanthus" bollensis* Fraas is redescribed and assigned to the genus *Metopacanthus*. A frontal clasper of *Squaloraja* is described.

Zusammenfassung

Anhand des bislang einzigen Exemplars wird *Acanthorhina jaekeli* Fraas aus dem Toarcium von Holzmaden eingehend neu beschrieben und der Familie Myriacanthidae zugeordnet. Das Neurocranium besitzt ein verlängertes Rostrum, das auf der Dorsal- und Ventralseite deutliche Knorpelstreifen aufweist. Granulierte Dermalplatten befinden sich im Bereich des Unterkiefers, anterodorsal vor der Orbita und möglicherweise auch hinter ihr. Der Rückenflossenstachel ist zurückgebogen und im proximalen Teil auf ⅔ seiner Länge gekörnelt. Auf der Rückseite ist der Stachel im oberen Drittel gezähnelt. Der Schultergürtel gabelt ventral auf. Die Bezahnung besteht aus einem eingekrümmten unteren Symphysealzahn, einem Paar hinterer Unterkieferzahnplatten und drei Zahnplattenpaaren des Oberkiefers. Ausgeprägte Diagonalkanten auf den hinteren Unterkiefer- und den Oberkieferzahnplatten wirken bei Okklusion scherend und brechend. Es ist ein großer Kopfstachel vorhanden. Darminhalt und Reste der Körpermuskulatur sind überliefert. *Acanthorhina* ernährte sich wahrscheinlich von benthonischen Organismen, jagte aber wahrscheinlich auch schwimmende Tiere, wie Belemniten und kleine Fische.

Der bislang einzige Fund eines Flossenstachels von „*Myriacanthus*" *bollensis* Fraas wird neu beschrieben und der Gattung *Metopacanthus* zugerechnet. Von *Squaloraja* wird ein Kopfstachel beschrieben.

Résumé

L'espèce *Acanthorhina jaekeli* Fraas est redécrite en détail à partir de l'unique specimen connu, provenant du Toarcien d'Holzmaden, et attribué à la Famille des Myriacanthidae. Le neurocrâne présente un rostre alongé dont ses zones ventrale et dorsale montrent un cartilage différencié. Trois paires de plaques dermiques tuberculées sont présentes: une à l'angle inférieur de la mandibule, une deuxième se localise en position antérodorsale par rapport à l'orbite, et la dernière se situait vraisembablement en arrière de l'orbite. L'épine dorsale est courbée et tuberculée sur les deux tiers proximaux de sa longueur. Des denticules sont présents sur le tiers distal des bords postérieurs de l'épine. La ceinture pectorale bifurque ventralement. La dentition comprends: à la mâchoire inférieure une plaque dentaire symphysaire arquée et un paire de plaques dentaires postérieures; a la mâchoire supérieure trois paires de plaques dentaires. Les crêtes diagonales très prononcées des plaques dentaires inférieures postérieures et des plaques dentaires supérieures traduisent la double faculté de trancher et de broyer les aliments. Le clasper frontal est proéminent. Le contenu intestinal et l'empreinte de la musculature du tronc sont préservés partiellement. *Acanthorhina* se nourrissait probablement d'organismes benthiques et semblait capable de se nourrir également en pleine eau, peut-être de belemnites et de menus poissons.

L'unique épine dorsale de „*Myriacanthus*" *bollensis* Fraas est redécrite et assignée au genre *Metopacanthus*. Un clasper frontal de *Squaloraja* est décrit.

Contents

1. Introduction

Remains of holocephalans are rare in the fossil record. They mostly comprise isolated mineralised parts of the skeleton, especially tooth plates and dorsal fin spines. Very few articulated entire or even fragmentary specimens are known; most of these are found in strata of quiet water deposition, such as the Lower Liassic (Hettangian to Sinemurian, Lower Jurassic) black shales of Lyme Regis, Dorset, England, the partly calcareous black shales of the Posidonienschiefer (Toarcian, Lower Jurassic) of Holzmaden in southern Germany, and the fine-grained lithographic limestones of the Plattenkalk (Tithonian, Upper Jurassic) in southern Germany.

Holocephalan remains from each of these and other areas are held in the Paläontologische Abteilung of the Staatliches Museum für Naturkunde in Stuttgart at Ludwigsburg. This is the first of a series of papers in which it is proposed to redescribe or newly describe these specimens. This first paper will consider the myriacanthoid and squalorajoid material. Others in the series are intended to deal with 1. whole-bodied *Ischyodus* and isolated fragments of chimaeroid holocephalans from the Tithonian deposits of Eichstätt, Solnhofen, and Nusplingen, 2. isolated skeletal fragments from other Jurassic and younger deposits, 3. a review of the taxonomy, origin and phylogeny of the Holocephali.

2. Systematic palaeontology

Class Chondrichthyes HUXLEY, 1880
Subclass Holocephali BONAPARTE, 1832
Order Myriacanthoidei PATTERSON, 1965

Family Myriacanthidae SMITH WOODWARD, 1889

Synonymy

1965 Acanthorhinidae PATTERSON, Phil. Trans. R. Soc. (B), **249:** 146.

Emended diagnosis: Myriacanthoidei in which there are three pairs of tooth plates in the upper jaw; the two anterior pairs are small and may or may not possess many small, simple tritors; diagonal ridges present on upper tooth plates and posterior lower tooth plates; rostrum large and elongate; 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 more or less tuberculated on the lateral face, anterior and posterolateral margins, and with a row of downturned denticles on the distal part of the posterolateral margins or a single median denticle row on the posterior wall.

The family Myriacanthidae contains *Myriacanthus paradoxus* AGASSIZ from the Lower Lias of Lyme Regis and France, *Metopacanthus granulatus* (AGASSIZ) from the Lower Lias of Lyme Regis, *Metopacanthus bollensis* (FRAAS) from the Toarcian (Lower Jurassic) of Germany, *Recurvacanthus uniserialis* DUFFIN from the Lower Lias of Lyme Regis, *Agkistracanthus mitgelensis* DUFFIN & FURRER from the Rhaetian (Upper Triassic) and Hettangian (Lower Jurassic) of Switzerland, and *Acanthorhina jaekeli* FRAAS from the Toarcian (Lower Jurassic) of Germany.

Genus *Acanthorhina* FRAAS, 1910

Type species by monotypy: *Acanthorhina jaekeli* FRAAS, 1910.

Diagnosis: A myriacanthid holocephalan possessing an elongate rostrum with differentiated dorsal and ventral cartilage strips. Tuberculated dermal plates are present at the angle of the lower jaw, antero-dorsal to the orbit, and possibly dorsal to the occiput. There is a strong, triangular posterodorsal sagittal crest and supraorbital ridge. The lower jaw articulation is prominent; the condyle appears to be double. The jaw suspension is holostylic. The dentition comprises three paired tooth plates on the upper jaw, one paired tooth plate and a single symphyseal tooth plate on the lower jaw. Pleromic hard tissue is present on all but the symphyseal tooth plate. Tritors are not present. The occlusal surfaces of the posterior and central upper, and posterior lower tooth plates comprise high, sharp, oblique ridges with triangular areas devoid of pleromic hard tissue anteriorly. The fin spine is long and slightly recurved, with denticulate posterolateral margins for the distal third, and tuberculate anterior margin for the proximal two-thirds of the total spine length. The lateral face of the spine is smooth. A large median ethmoid canal may be present in front of the large frontal clasper. The ethmoid region of the skull is moderately high. The pectoral girdle lies directly behind the neurocranium and is moderately angled, with a bifurcating anteroventral margin. The synarcual comprises a blade-like vertical component and a posteriorly-directed basal ramus.

Acanthorhina jaekeli Fraas, 1910

Figures 1, 2, 3 a, 5 a; Plates 1—4

1910 *Acanthorhina jaekeli* Fraas, Jh. Ver. vaterl. Naturk. Württ., **66**: 55—61, Plate 3, Figures 1,5.
1911 *Acanthorhina jaekeli* Fraas. — Zittel, Grundzüge der Paläontologie. Paläozoologie. II. Vertebrata: 70.
1932 *Acanthorhina jaekeli* Fraas. — Zittel, Textbook of Palaeontology, Palaeozoology. II. Vertebrata: 96.
1953 *Acanthorhina jaekeli* Fraas. — Hauff, Das Holzmadenbuch, 1st Edition: 22, Plate 37, Figure b.
1960 *Acanthorhina jaekeli* Fraas. — Hauff, Das Holzmadenbuch, 2nd Edition: 22, Plate 37, Figure a.
1965 *Acanthorhina jaekeli* Fraas. — Patterson, Phil. Trans. R. Soc. (B) **249**: 146—148, Figures 24, 25.
1979 *Acanthorhina jaaekeli* Fraas. — Urlichs, Wild & Ziegler, Stuttgarter Beitr. Naturk., Series C, Nr. **11**, Figure 23.

Holotype: SMNS (= Staatliches Museum für Naturkunde in Stuttgart), catalogue number 12579. An articulated skeleton preserving the skull, dorsal fin spine, certain postcranial elements and soft parts.

Type locality: Holzmaden, Baden-Württemberg, Southern Germany. No further details of the precise locality are available.

Type horizon: Posidonienschiefer or Schwarzjura $\epsilon\,\mathrm{II}_3$, Fleins (cf. Urlichs 1977: 12, Figure 8); *Dactylioceras tenuicostatum* zone, Lower Toarcian, Lower Jurassic.

Material: No other specimens besides the holotype known.

Description of the holotype

The specimen has been flattened by compaction and is preserved in right lateral view (Plate 1; Figure 1). The skull, lower jaw, dentition, dorsal fin spine, synarcual, possible labial cartilages, pectoral and pelvic fin bases are preserved. The specimen is 582 mm long from the tip of the rostrum to the apex of the dorsal fin spine.

The skull is robust and measures 249 mm from the tip of the rostrum to the back of the occiput. The palatoquadrate is indistinguishably fused to the neurocranium, giving a holostylic jaw suspension. The anterior extremity of the skull is produced to form a rostrum which is 100 mm long. The rostrum terminates in a sharp point and has a slight dorsal curvature. The dorsal and ventral surfaces of the rostrum possess strip-like areas

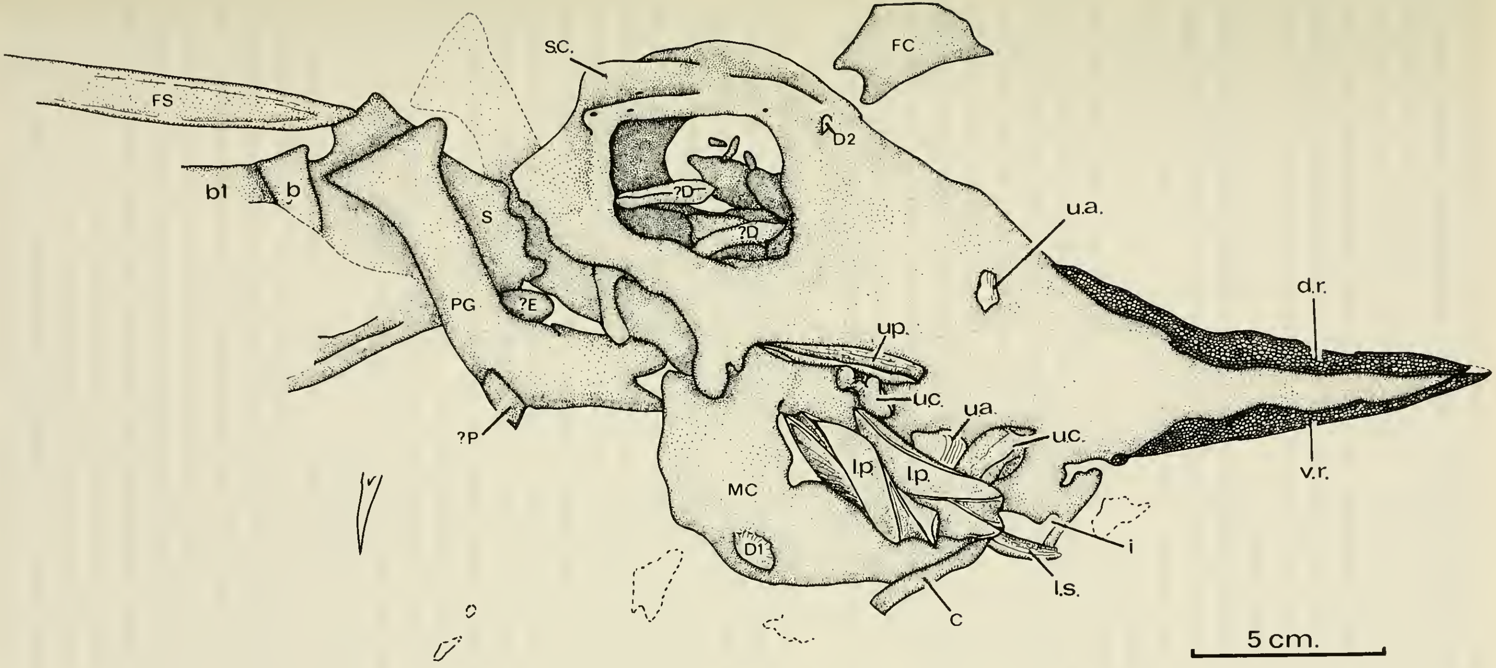

Fig. 1. Anterior part of the holotype (SMNS 12579) of *Acanthorhina jaekeli* Fraas (1910).
D1: dermal plate on the angle of the lower jaw; D2: dermal plate anterior to orbit; ?D: possible dermal plates derived from the posterodorsal part of the neurocranium; FC: frontal clasper; FS: dorsal fin spine; S: synarcual; SC: sagittal dorsal crest; PG: pectoral girdle; ?E: possible epibranchial; b: possible dorsal fin spine basal; bl: possible further basal cartilage to the dorsal fin; ?P: possible propterygium; MC: Meckelian cartilage; ls: lower symphyseal tooth plate; l.p.: lower posterior tooth plate; u.p.: upper posterior tooth plate; u.c.: upper central tooth plate; u.a.: upper anterior tooth plate; C: possible labial cartilage; d.r.: dorsal strip of differentiated rostral cartilage; v.r.; ventral strip of differentiated rostral cartilage; i: indentation for reception of anterior upper tooth plate. Non-stippled cartilage fragments appearing as outlines only ventral to the neurocranium are presently indeterminate.

of differentiated cartilage (d.r., v.r., Figure 1); these areas unite at the pointed apex of the rostrum (Plate 1; Figure 1). The maximum depth of each of these strip-like areas of rostral cartilage is 9 mm in each case. Each cartilage surface comprises a tesselated network of individual calcified prisms. These prisms are larger in the dorsal and ventral cartilage strips than are those which form the outer surface of the remainder of the rostrum, neurocranium, lower jaw, and preserved postcranial elements. The ventral rostral cartilage strip ends just above the most anterior upper tooth plate. The dorsal rostral cartilage strip is slightly longer.

The orbit is posteriorly placed and high on the neurocranium. There is no calcified interorbital septum. There is a well-developed circumorbital ridge. This ridge has a rectangular outline dorsally and posteroventrally, but there is a rounded and elongate orbital margin anteroventrally.

The skull has been flattened with a slight ventral inclination such that the supraorbital ridge of the left side is visible (Plate 1; Figure 1). Although the specimen is crushed, the interorbital area seems to have been fairly narrow. Anterior to the orbit and the base of the frontal clasper, a large marked indentation in the neurocranium appears in illustrations in previous works (Fraas 1910, Plate 3 Figure 1; Urlichs, Wild & Ziegler 1979; Figure 23); this has unfortunately been destroyed during subsequent preparation of this very fragile specimen. The pit may have represented the exit of the superior ophthalmic and profundus nerves (anterior opening of the ethmoid canal). Directly anterior to the orbit, the ethmoid region of the neurocranium is moderately high and elongate.

Medial to the posterodorsal margin of the orbit there is a high sagittal dorsal crest (S.C., Figure 1), which shallows anteriorly. The posterior margin of this sagittal crest is straight and upright; the crest has the shape of a right-angled triangle. Posterior to the sagittal crest, the posterodorsal skull margin descends sharply to the occipital region.

Up to four foramina are present in this dorsal region of the skull. There appear to be two foramina located midway along the base of the right lateral face of the sagittal crest. A single foramen is located on the supraorbital ridge above the posterolateral corner of the orbit. By comparison with the extant *Chimaera colliei* (Lay & Bennett) (Allis, 1917, Figure 3), this may represent the exit of the superficial ophthalmic nerve. A further tiny foramen may be present in a similar position above the anterolateral corner of the orbit. It remains possible, however, that these structures have resulted from the differential post-burial compaction of the specimen.

The notochordal pit is 10 mm deep, and is directed posteroventrally at an angle of approximately 50° to the upper jaw line. The pit is bounded by occipital condyles in dorsal, ventral and apparently lateral positions.

The occipital region of the neurocranium is very shallow in comparison to the deep anterior region. The ventral margin of the otico-occipital region of the neurocranium is convex and short. The suborbital part of the neurocranium is very shallow posteriorly but deepens anteriorly toward the lower jaw articulation. The point of articulation for the lower jaw is situated below and just anterior to the midpoint of the orbit (Plate 1; Figure 1). The articulation for the lower jaw comprises a prominent, rounded condyle. Just anterior to this is a smaller swelling which may also have been involved in the lower jaw articulation. This gives way anteriorly to the tooth-bearing margin of the upper jaw, which slopes ventrally to the origin of the rostrum.

Beneath the rostrum origin there is a prominent indentation (i., Figure 1) for the insertion of the anterior upper tooth plate (Plate 1; Figure 2). Anterior to this there is a downward projecting portion of the ventral margin of the neurocranium with an inflated, bilobate upper part containing a posteriorly-directed indentation (Plate 1, 3; Figure 1).

The lower jaw (Meckelian Cartilage, MC, Figure 1) is deep (in excess of 55 mm) posteriorly and has a rounded posterior margin. A posterior flange is developed one third of the way up the posterior margin. The ventral margin of the lower jaw is convex and curves upward to terminate and meet the tooth-bearing dorsal margin approximately 16 mm posterior to the anterior upper tooth plate insertion point. The tooth-bearing dorsal margin of the lower jaw is straight. At the posterior end of the tooth row there is a deep indentation for the reception of the posterior margin of the posterior lower tooth plate.

Beneath the lower dentition and the ventral margin of the lower jaw anteriorly, a curved strip of cartilage is exposed. The strip (C., Figure 1; Plate 1) measures 32 mm long; the anterior end is obscured by the displaced lower dentition, and the posterior end is lost due to the original preparation of the specimen. The dorsal margin of this cartilage is convex and follows the line of the ventral margin of the lower jaw. The ventral margin of the cartilage is convex and converges with the dorsal margin anteriorly. There is a hollow in the cartilage margin posteroventrally and the posterior part of the cartilage is directed posteroventrally. The cartilage is most probably a labial cartilage.

At least two dermal plates are present in this specimen; one (D1, Figure 1), the larger, is located below and anterior to the posterior flange on the lower jaw, in the angle of the jaw cartilage (Figure 1; Plate 1); the second (D2, Figure 1) is located between the anterodorsal corner of the orbit and the ethmoid margin of the neurocranium.

The dermal plate on the lower jaw is broken; only the anterior two-thirds are preserved, the remainder presumably having been lost during the original mechanical preparation of the specimen. The preserved length of the dermal plate is 11 mm anteroposteriorly. It comprises a central longitudinal tubercle, which is broken, and from which radiates a series of ridges. The plate narrows radially and has a complex stellate outline, due to the radiating ridges. Any external ornament that may have been present was removed during the original preparation of the specimen.

The dermal plate in front of the orbit (Plates 1, 3; Figure 1) measures 5 mm dorsoventrally and is broken. It comprises a central tubercle from which radiates a series of ridges, as in the previous example. In this case, however, the outer surface of the plate has not been destroyed by preparation; the ridges each have a series of small tuberculations running along their crests. The ridges appear to be more closely spaced in the neurocranial plate than are those on the lower jaw plate.

A cartilage (FC, Figure 1) is situated dorsal to the ethmoid region of the neurocranium, oriented at right angles to the dorsal neurocranial margin. This cartilage shows no detailed structure, but the position and orientation (Plate 1, 3 Figure 1; Figure 1) suggests that it is the frontal clasper. The cartilage is incomplete, being terminated by the edge of the block, and widens distally. The proximal margin comprises a larger medial indentation and a smaller ventral one. This outline shows some similarity to that of the dorsal neurocranial margin anterior to the anterodorsal margin of the orbit. It would appear that the frontal clasper has been displaced only a few millimetres from its original point of articulation.

The dentition of *Acanthorhina* appears to contain a single symphyseal tooth plate (l.s., Figure 1) and a pair of posterior tooth plates (l.t., Figure 1) in the lower jaw, and three tooth plate pairs in the upper jaw: a small anterior tooth plate pair (u. a., Figure 1), a medium central tooth plate pair (u.c., Figure 1) and a larger posterior tooth plate pair (u.p., Figure 1; Plate 1, 2; Figure 5 a).

The dentition is mildly disarticulated (Figure 1; Plates 1, 2). Both lower posterior tooth plates (l.p., Figure 1) are exposed in occlusal view; each is 48 mm long. The symphyseal margin of each lower posterior tooth plate is straight and raised. There is a short invagination on the anterior labial margin for the reception of the lateral extremity of the symphyseal tooth plate. The posterior extremity of this invagination is marked by a high ridge. Posterior to this ridge, the remainder of the labial border of the tooth plate is straight and itself raised to form a ridge. The lingual border of the lower posterior tooth plate has a sigmoidal outline. In occlusal view, the tooth plate is divisible into three areas (Figures 1, 5 a; Plates 1, 3); the triangular anterior region, bounded by the symphyseal margin, anterolingual margin and a ridge running obliquely from the anterolabial corner of the lignual border of the tooth; a leaf-shaped posterior area bounded anteriorly by the strong oblique ridge running from the anterolabial border to join a smaller ridge at the lingual border; and a small triangular area situated between the above, bounded by the two converging ridges lingually, and by the indented anterolabial border labially. Thus, the symphyseal and posterolabial borders of the tooth plate are elevated into ridges, and a further two ridges, the posterior of which is the more prominent, arise at two points on the anterolabial tooth margin, and converge to meet at the lingual margin of the occlusal surface of the tooth. Each of these ridges comprises pleromic hard tissue. Pleromic hard tissue is also present in the intervening anterior and posterior areas of the tooth plate, but not in the area between the converging ridges. This latter region is composed of lamellar osteodentine, and in each tooth plate from the lower jaw preserves a small but deep ante-mortem wear facet. In the lower posterior tooth plate from the right jaw, the wear facet is located midway along the anterior and weaker of the two transverse ridges, while in the left tooth plate it is found at the junction of the two converging ridges.

The lower symphyseal tooth plate (l.p., Figure 1) is preserved just anterior to the left lower tooth plate (Plates 1, 2). It is moderately strongly curved and does not appear to contain pleromic hard tissue. Instead, it comprises lamellar osteodentine. The lingual face of the tooth plate is more strongly curved dorsoventrally than is the labial face.

Two tooth plates are preserved dorsal to the left lower tooth plate. The anterior and larger of the two plates is an upper central (u.c., Figure 1; Plate 2), and has the occlusal surface and part of the lingual margin exposed. The symphyseal margin of the plate is flat and straight. The occlusal surface is flat mesially, but a strong longitudinal ridge is developed close to the lingual margin of the plate. This is flanked lingually by a fairly deep groove in which there is no pleromic hard tissue. A second, weaker longitudinal ridge marks the lingual border of the tooth plate, converging with the first, stronger ridge posteriorly. This second ridge comprises pleromic hard tissue, which is also developed at their junction.

The second, smaller and posteriorly situated tooth plate is an upper anterior (u. a., Figure 1). It has a small area of occlusal surface with pleromic hard tissue exposed, and a presumed anterior margin with lamellar osteodentine exposed. The tooth plate shows no further diagnostic characters.

One posterior upper tooth plate (u.p., Figure 1; Plate 3) is preserved in life position. It is situated on the ventral margin of the palatoquadrate and is preserved in right lateral view. It measures 37 mm in length and has a deep (4 mm) base of lamellar osteodentine.

This is surmounted by the shallow (1 mm) occlusal surface of pleromic hard tissue. The labial margin of the occlusal surface is curled under toward to tooth plate base along the labial margin. Anteriorly, the tooth plate base develops a small dorsoventral flange.

Ventral to this in situ tooth plate, an upper central tooth plate (u.c., Figure 1; Plate 2) is exposed in oblique occlusal view. The plate, measuring 15 mm long, has its labial margin placed in a dorsal position. The labial margin of the tooth plate is bilobate, reflecting the differential development of the pleromic hard tissue on the occlusal surface. The anterior and posterior margins of this tooth plate are both straight, but oblique to each other: each has a weak ridge developed along its length occlusally. The occlusal face of the tooth is quite strongly convex labiolingually and comprises two parts; triangular anterior and posterior tritoral areas are heavily worn at their labial apices, and combine to form a single occlusal covering lingually. Between the two lobes of the occlusal surface there is no pleromic hard tissue.

One further tooth plate, an upper anterior (u. a., Figure 1; Plate 2) is located above the mouth, on the ethmoidal region of the neurocranium. The plate comprises a thick base of lamellar osteodentine surmounted a small tritoral area of pleromic hard tissue. In occlusal view, the tooth plate has a trapezoid shape.

The dorsal fin spine (FS, Figure 1) is long (293 mm), slender, slightly curved, and exposed in lateral view (Plates 1, 3; Figure 2). The distal tip is broken. The proximal half of the spine has been crushed. The posterior face is 5 mm across, and has an open median canal running the exposed spine length. Lateral to the median canal, the posterior face is laterally convex. A row of slender, pointed, downturned denticles is present along the posterolateral border on each side of the posterior face, for a distance of 80 mm from the distal tip of the spine. Many of these denticles have been removed by the original preparation of the specimen. The average length of the denticles is 1 mm. A single row of occasional tubercles becomes associated with the posterolateral denticle row just below the distal tip of the spine. The tubercles are situated lateral to the denticle row, and become more numerous and larger proximally such that several tubercle rows are present at the base of the posterior denticle row on either side, for the distal two-thirds of the spine length. A few tubercles encroach upon the posterior margin of the lateral face of the spine proximally, where their distribution suggests growth lines. the bulk of the lateral face of the spine appears to be devoid of tubercles, although some may have been lost during the original mechanical preparation of the specimen. Scattered tuberculation is developed just under one third of the distance down the spine from the apex, but becoming more common proximally. At least five longitudinal rows of tubercles are developed just below the midpoint of the spine. The tubercles become progressively coarser and more numerous proximally, dying out approximately 20 mm from the spine base. The presence of unroofed mantle canals gives the lateral face of the spine the appearance of having longitudinal striations, especially proximally.

Two cartilages appear to be present for articulation with and support of the dorsal fin spine. The ?basal cartilage (b., Figure 1) is located ventral to the fin spine base (Plate 1; Figure 1), obscuring part of the posterior margin of the synarcual. The cartilage is rectangular and measures 15 mm dorsoventrally, and 9 mm anteroposteriorly. There appears to be a more elongate cartilage (b1, Figure 1) located posterior to the basal cartilage.

The synarcual (S., Figure 1; Plate 1) comprises a single blade-like triangular vertical component and a basal, posteriorly-directed ramus. The details of the posterior border of the synarcual are difficult to discern. The anterior margin ascends gradually posterodorsally to the apex of the vertical blade (Plate 1; Figure 1). From here, the posterior margin of the synarcual descends steeply basally, is obscured (by dorsal fin cartilages) and then swings anteriorly to form a deep notch for the reception of the notochord. A long (75 mm) basal posterior extension then projects backwards beneath the presumed position of the notochord. The anterior margin of the cartilage reflects the occiput in shape (Plate 1; Figure 1).

The pectoral girdles (PG., Figure 1) lie directly behind the neurocranium, the right one partially obscuring the synarcual dorsally. The scapulocoracoid measures 100 mm dorsoventrally and is moderately angled. The dorsal extremity is expanded and the straight dorsal margin is 35 mm in length (anteroposteriorly). The average length (anteroposterior) of the remainder of the girdle is 15 mm. The anterior extremity is divided into two prongs (Figure 1). The structure located on the ventral margin of the girdle at the base of the angle apears to be a separate cartilage (?P., Figure 1). It measures 10 mm in length and may be part of the propterygium (anterior basal) of the pectoral fin. Ventral to this structure, small, incomplete isolated cartilage fragments which have been exposed during early preparation may represent parts of the metapterygium (second basal) and possibly the proximal radials. Small fragments of what are probably distal radials are located along the ventral margin of the block. These cartilages appear as nonstippled items, occasionally with broken outlines, ventral to the remainder of the specimen, in Figure 1.

The position of the pectoral girdle suggests that the branchial skeleton lay beneath the neurocranium as in living chimaeroids. Three small isolated cartilage fragments (including ?E., Figure 1) are present in this position, but their partial obscuring by the pectoral girdle, synarcual and neurocranium makes precise identification difficult. Radiographs reveal the left scapulocoracoid completely enclosed in sediment (Figure 1). The left girdle has no small cartilage associated with it in a ventral position, strengthening the interpretation of a propterygium or similar structure present in the angle of the right pectoral girdle (i.e. the structure is not a part of the right scapulocoracoid itself).

There is no evidence of the branchial skeleton beneath the neurocranium. There are at least seven obscure structures present in the orbit, however. The most dorsal of these are three short (up to 6 mm long) elements (Figure 1). Whilst they may represent hypobranchials, their surface structure is unlike that of the remainder of the cartilages in the specimen, being fibrous in appearance. These structures remain obscure.

Two longer (up to 24 mm long) elements (?D., Figure 1) are present lower in the orbit. They are robust structures composed of lamellar tissue with flat, tuberculated faces dorsally. It is possible that these structures are displaced elongate dermal plates. They may have derived from position posterior to the orbit, on the posterodorsal corners of the neurocranium.

Two further, plate-like cartilages in the orbit (Figure 1) may represent opercular cartilages.

The pelvic girdle is located some 170 mm posterior to the pectoral girdle (Plate 1). Two cartilages are preserved in the pelvic region. the anterior cartilage measures at least 60 mm in length, is mildly sigmoid in shape and widens posteriorly. The anterior margin is straight. This cartilage is probably a pelvic girdle exposed in ?oblique ventral view. The posterior cartilage is also long (at least 80 mm) and curved, but narrows posteriorly. It may represent a long basipterygium, possibly a clasper cartilage, or more likely is the second pelvic girdle (?right). The shape of the cartilage is more suited to the latter interepretation, since clasper cartilages are usually straight, and basipterygia usually much smaller. The only possible evidence of clasper spines is an isolated structure of doubtful interpretation, posterior to the second cartilage. Six parallel radial fragments are present posterior to the second cartilage, toward the ventral margin of the block. A further cartilage fragment on the posteroventral corner of the block may well represent an additional part of the pelvic fin skeleton, and further ?radial fragments appear to be present toward the posterior margin of the block, in the area of the gut. Radiographic investigation of this part of the specimen failed to provide more conclusive evidence.

A small (4 mm long) isolated fragment is located anterior to the pelvic girdle, and bears at least three spikey projections. The fragment may represent the remains of the pelvic tenaculum.

A broad brown longitudinal mass extends posteriorly from the posterior margin of the synarcual to the posterior margin of the block (Plate 1). The debris in this region appears to include faecal material, muscle, dermal denticles and occasional calcifications. The calcifications are mostly of nondescript shape, but a few tiny (0.7 mm in diameter) circular examples can be seen (l.l.c., Figure 2). These are too small for notochordal sheath calcifications and must be from the lateral line. One small articulated section of the lateral line sensory canal is located 23 mm dorsal to the posterior tip of the more posterior pelvic girdle cartilage, and is exposed in lateral view.

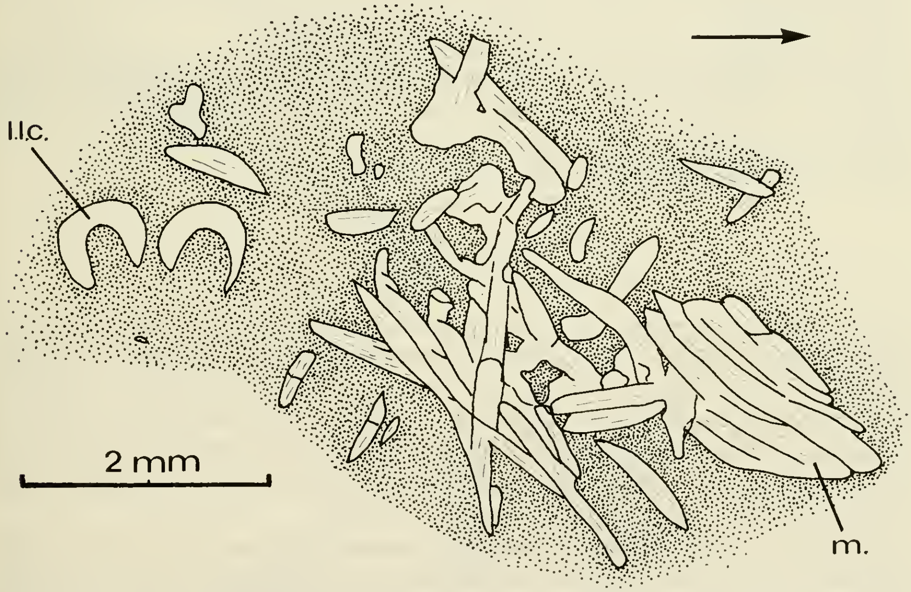

Fig. 2. Part of the representations of belly musculature and calcified lateral line canal rings in the holotype (SMNS 12579) of *Acanthorhina jaekeli* Fraas (1910).
l.l.c.: lateral line canal ring; m.: muscle tissue representation. The arrow is directed anteriorly.

The bulk of the material in this region appears to comprise muscle.Individual muscle fibre blocks can be discerned (m., Figure 2). The muscle mass is not arranged segmentally but in longitudinal and oblique muscle fibre groups. It is soft and very light in colour. Since the remainder of the specimen of *Acanthorhina* shows little disarticulation, it can be assumed that the representations of muscle described here are in close proximity to life position. The orientation of the bulk of the muscle and lack of segmental arrangement imply that it is either visceral or belly musculature. The muscle is mostly preserved in a ventral position and is not present throughout the presumed dorsoventral extent of the body cavity. No evidence of viscera is present; the muscle lies ventral to the presumed faecal material. This supports the interpretation that it is belly musculature. Unlike selachians, which have five muscles, extant chimaeroids have three muscles in the belly region (Nishi 1938). The obliquus dorsalis is dorsally placed; there is no evidence for this muscle in *Acanthorhina.* The obliquus rectus comprises muscle tissue obliquely oriented to the lateral midline, and the obliquus ventralis comprises parallel fibres in the midline. Whilst these two muscles are separate in sharks, they are surrounded by the same connective tissue sheath in extant chimaeroids. The individual muscle representations are cone-shaped and always taper posteriorly in *Acanthorhina* (Figure 2). Between these are connective tendons ("Inscriptiones tendinae" of Nishi 1938: 363). Whilst it is possible that the muscle tissue itself may have been preserved, it is far more likely that the intervening tendinous connective tissue has been preserved to give a representation of the muscle in *Acanthorhina.* The muscle represented in this specimen is most likely to be the common obliquus rectus and obliquus ventralis, by comparison with modern chimaeroids.

The faecal material in the gut region is light brown to black in colour, and disseminated. No individual faecal constituents can be recognized.

Several patches of skin containing dermal scales are present in this region of the specimen. The individual scales have virtually all been damaged during preparation of the specimen, so few details are available. Where visible, the dermal scales are evenly spaced, simple and apparently non-growing. There is a single internal cavity and the broken bases of the scales measure only 0.08 mm across.

Discussion of *Acanthorhina*

Fraas (1910) was the first to describe the holotype of *Acanthorhina.* Since then, Patterson (1965) has reviewed the myriacanthoids in relation to the phylogeny of the chimaeroids, and has reinterpreted parts of the anatomy of *Acanthorhina,* basing his considerations on the description by Fraas. *Acanthorhina* has also been figured in general works on the palaeontology of Holzmaden (Hauff 1953, 1960; Urlichs, Wild & Ziegler 1979), and as reconstructed by Fraas in textbooks of vertebrate palaeontology (Zittel 1911, 1932; Obruchev 1964; Romer 1966).

Acanthorhina is of special interest since it is represented by one of the most complete specimens of a fossil holocephalan known, and its stratigraphic occurrence coincides with one of the latest records of the myriacanthids (*M. bollensis* Fraas, described below), and pre-dates the oldest known true chimaerids (*Ischyodus* from the Bajocian of Germany, to be described in a later paper in this series, Duffin in preparation).

Fraas (1910) suggested that the genus *Acanthorhina* was related to *Myriacanthus*, but noted how closely certain features resembled the anatomy of living chimaeroids. Smith Woodward (in Zittel 1932: 96) placed the genus in his Family Myriacanthidae, but Patterson (1965: 146) made it the type and only known member of the Family Acanthorhinidae Patterson 1965, pending reinvestigation of the holotype. The redescrip-

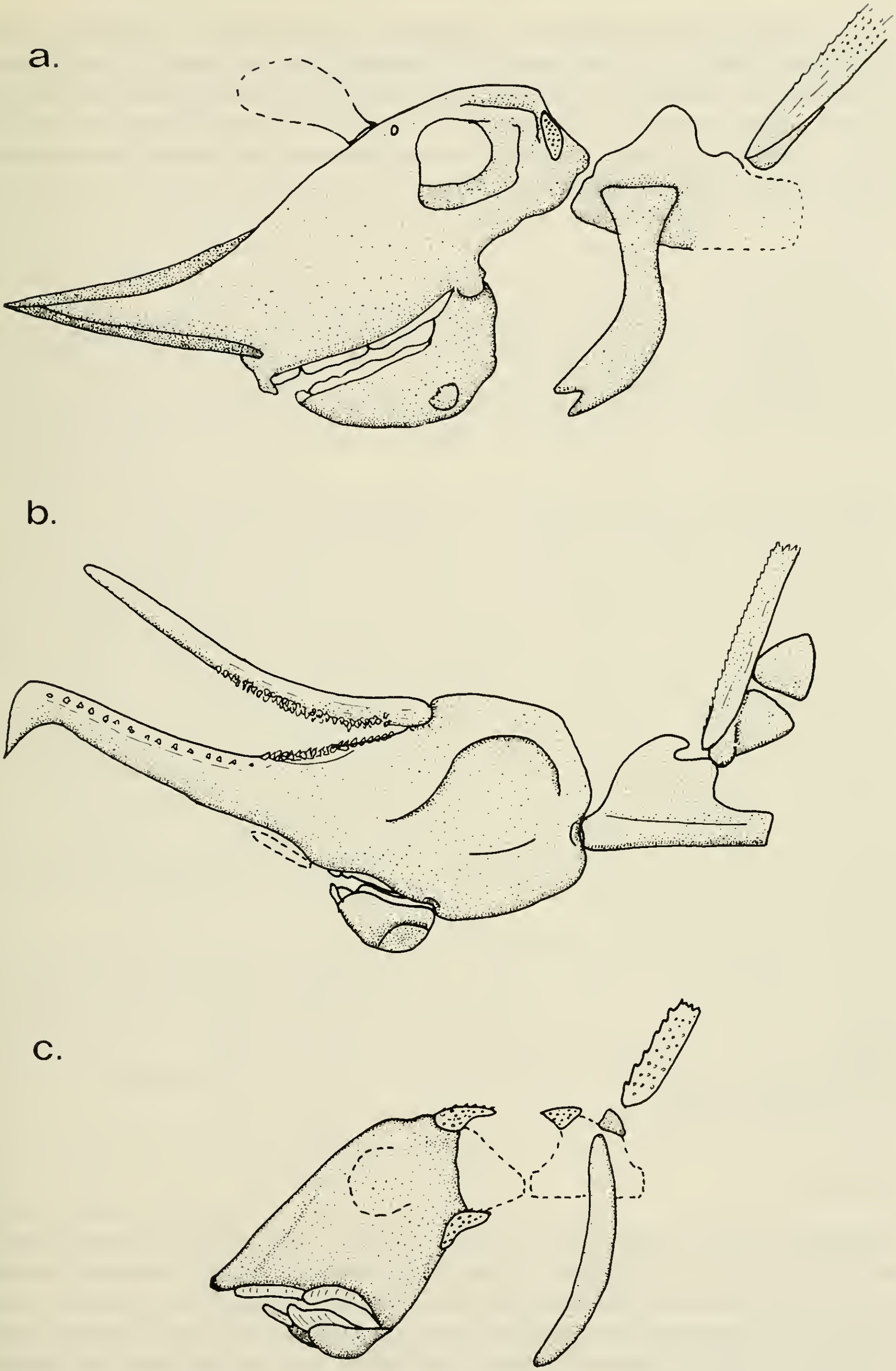

Fig. 3. Outline reconstructions of a: *Acanthorhina jaekeli* Fraas (1910); b: *Metopacanthus granulatus* Agassiz 1837), after Patterson (1965); c: *Chimaeropsis paradoxa* Zittel (1887), after Reis (1895).

tion of the holotype above allows a reconsideration of the affinities of the genus. Particularly important in this regard are the following characters: dorsal fin spine, frontal clasper, dentition, and the presence or absence of dermal skull plates. The details of these structures have been of importance in familial diagnoses (PATTERSON 1965); as might be expected, most have proved of such use since they are relatively common and well preserved parts of fossil holocephalans.

a. Dermal plates

FRAAS (1910) made no mention of dermal plates on the skull of *Acanthorhina*. At least two dermal plates are present and prominent on the specimen: one on the angle of the lower jaw, and the other high up on the anterior part of the neurocranium, just in front of the orbit (Figure 1; Plates 2, 3 Figure 1). Possibly a third, paired dermal plate, preserved in the orbit, may have been located in a dorsolateral position on the neurocranium, behind the orbit (Figure 3 a). At least one of these plates (the anterior one) possesses a tuberculate ornament, but this is also probably true for the other two plates.

The presence of dermal skull plates is characteristic of the holocephalan suborder Myriacanthoidei. Paired dermal plates are known from *Myriacanthus paradoxus* AGASSIZ (Lower Lias, Lower Jurassic, England), occurring in lateral positions on the lower jaw (PATTERSON 1965: 129, Figure 13), on the dorsolateral corners of the occiput (PATTERSON 1965: 131), possibly on the skull roof, just behind the insertion of the frontal clasper, and possibly (by comparison with *Deltoptychius* from the Lower Carboniferous of Scotland, PATTERSON 1965: 131, 156) at the ventrolateral corner of the neurocranium. *Metopacanthus granulatus* (AGASSIZ) (Lower Lias, Lower Jurassic, Dorset, England) possesses a single large paired plate in the angle of the mandible only (Figure 3 b) (see PATTERSON 1965, Figure 20). *Chimaeropsis paradoxa* ZITTEL (Lower Tithonian, Upper Jurassic of Eichstätt and Solnhofen, Southern Germany) is known to possess dermal plates, but their original positions are unknown (ZITTEL 1887; RIESS 1887; REIS 1895; PATTERSON 1965: 144) (Figure 3 c).

In *M. paradoxus* the dermal plates are known to comprise a basal lamellar tissue and vascular osteodentine (PATTERSON 1965: 131—133, Figure 15). Dermal plates are unknown in fossil and living holocephalans of the suborders Chimaeroidei and Squalorajoidei.

Thus, the presence of dermal plates on the skull serves to link *Acanthorhina* firmly with the Myriacanthidae.

b. Rostrum

FRAAS (1910: 56) considered that the posterior part of the skull of *Acanthorhina* had been crushed, and the anterior part including the rostrum had been rotated such that a ventral view was exposed. This is not the case. Certainly, the whole skull has been compacted, but it has come to rest in the sediment with a slight ventral inclination, as is the case in about 80% of all vertebrate fossils collected from the Holzmaden Posidonienschiefers (Dr. R. WILD, oral communication, and my personal examination). This is especially obvious in that the left supraorbital ridge is preserved above that of the right, the left pectoral girdle, discovered by radiography, (Figure 1) lies higher than the right, and that the presumed left pelvic girdle lies above the right. The anterior part of the neurocranium is not badly broken or strained at its junction with the posterior part, as it would be if it had rotated independently of the remainder of the skull. Furthermore, the presence of certain teeth in life position on the posterior upper jaw margin, and the form of the anterior upper jaw margin confirms that the anterior part of the neurocranium and rostrum are preserved in lateral view.

Because of his presumed orientation of the rostrum and the nature of a supposed second specimen of *Acanthorhina* (see below), FRAAS (1910: 56) considered that the robust strongly calcified cartilage had a dorsal convex side and a ventral concave side. It was supposedly flanked by two lateral cartilages which possessed "flattened teeth" on the underside.

FRAAS supposed that the second specimen of *Acanthorhina* would have come from an adult with ossified cartilage (FRAAS 1910: 56). The specimen (SMNS catalogue number 7789) is not cartilaginous but bony. It does not belong to *Acanthorhina*, but is almost certainly a large fulcral scale from the dorsal margin of the tail of *Chondrosteus hindenburgi* POMPECKJ. The structures interpreted by FRAAS as teeth are, in fact, small breakage surfaces.

Pending a re-examination of the specimens, PATTERSON (1965: 146) considered that, primarily on the basis of SMNS 7789, the feature restored by FRAAS as a rostrum was, in fact, a frontal clasper, and that this structure was crushed, obscuring the true rostrum in the holotype. The anterior groove in SMNS 7789 might thus represent depressor muscle insertions, and the "teeth" would be dorsally situated.

Since SMNS 7789 is not a specimen of *Acanthorhina*, the interpretation that it is a frontal clasper is incorrect. From the preservation of the holotype, the anterior cartilage extension of the neurocranium is continuous with the remainder of the neurocranium. There is no breakage zone or other junction. Thus, the structure should be considered a true rostrum. The two cartilage strips running the length of the rostrum are not laterally placed, as conceived by FRAAS, but dorsal and ventral, because of the resting position of the fossil in the sediment, as discussed above. Also, these longitudinal structures are true cartilages since they comprise calcified prisms. They are not enamelled, as suggested by FRAAS. The cartilage strips are merely areas of the rostrum which have differentiated: there is no evidence to suggest that they are distinct cartilages with articulation against the neurocranium. There is no sign of denticles on the upper surface of the dorsal cartilage strip.

Metopacanthus granulatus (Figure 3 b) possesses an elongate rostrum which is apparently calcified as a single unit. It has a gradual dorsal curvature for approximately 80 mm, over which distance the dorsal surface is denticulate, but there is a down-turned anterior extremity. A short strip of cartilage is located along the posterodorsal margin of the rostrum and the anterodorsal margin of the neurocranium. The upper surface of this cartilage is denticulate, the individual denticles opposing those on the frontal clasper (Figure 3 b; PATTERSON 1965: 138, Figure 20).

The rostrum in *Myriacanthus paradoxus* is preserved in BMNH (British Museum of Natural History) P. 10130, and appears to be similar in shape to that of *Metopacanthus*, although there is no sign of rostral or labial cartilages (PATTERSON 1965: 129).

REIS (1895, Plate 12 Figure 3) has restored the head of *Chimaeropsis paradoxa* (Figure 3 c), but the specimen, originally held by the Bayerische Staatssammlung für Paläontologie und Historische Geologie in München, must be presumed lost during the Second World War. PATTERSON (1965: 144) states that "it is probable that the rostrum was not elongated as it is in the Myriacanthidae", because the rostral calcification is quite short and blunt (REIS 1895, Plate 12, Figure 3).

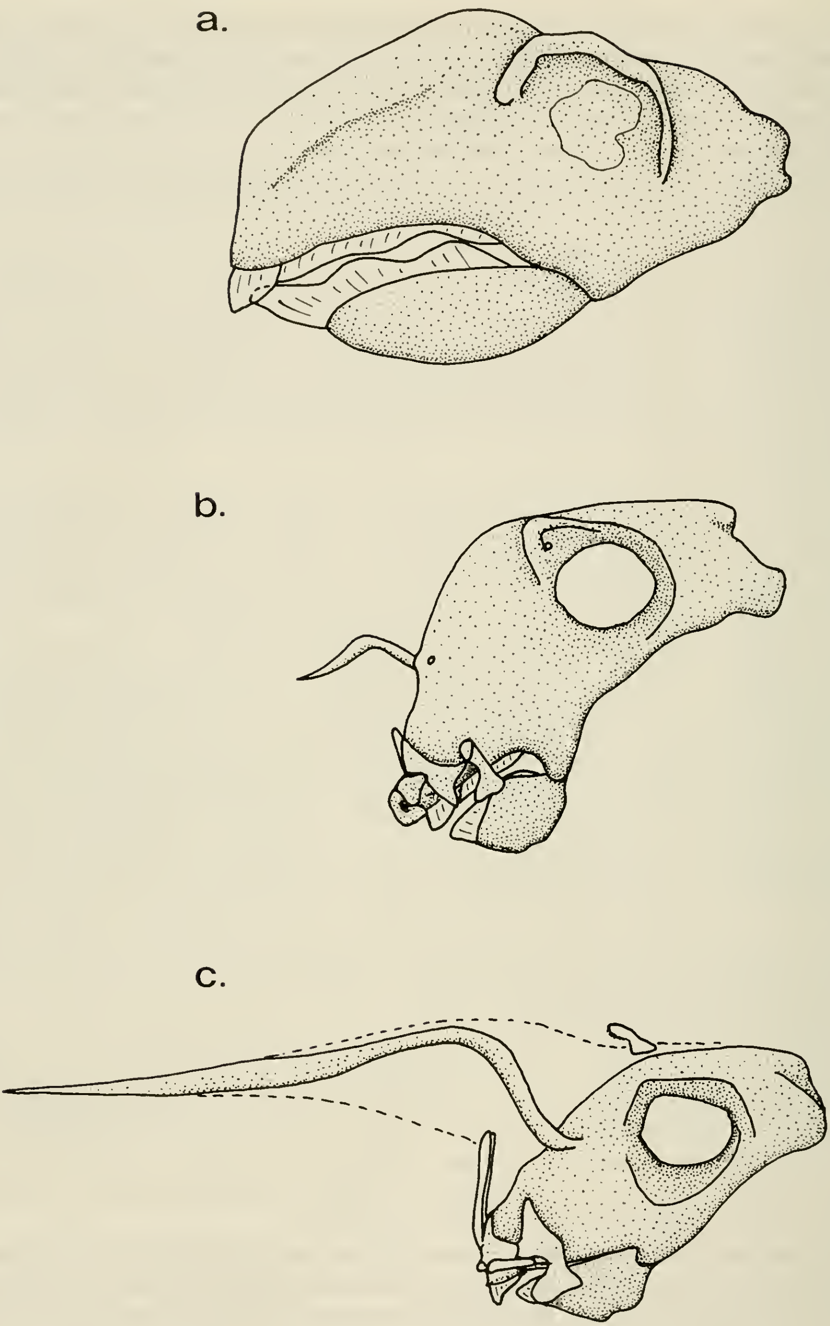

Fig. 4. Outline reconstructions of the skulls of a: *Ischyodus schuebleri* QUENSTEDT (after HEIMBERG 1949); b: *Chimaera colliei* (LAY & BENNETT) (after ALLIS 1917); *Rhinochimaera pacifica* (MITSUKURI 1901) (after GARMAN 1904).

The development of a rostrum is also typical of the Chimaeroidei and Squalorajoidei (Figures 4, 6). In each case it is associated with labial and rostral cartilages, but only in *Squaloraja* is a cartilage known to be present along part of the dorsal rostral surface (Patterson 1965, Figure 9).

Thus, the possession of a rostrum in *Acanthorhina* is not remarkable: it is known in many other holocephalans. The presence of cartilage strips along the ventral and dorsal margins of the rostrum, and differentiated from it, meeting at the rostral tip, separates *Acanthorhina* from all other holocephalan genera. It may be that *Acanthorhina* is primitive in this regard.

The cartilage strip preserved ventral to the lower tooth plates in *Acanthorhina* may well be a labial cartilage. No further labial or rostral cartilages could be detected by radiography.

c. Frontal clasper

Fraas (1910, Plate 3 Figure 3) noted a hook-like object close to the central tooth-bearing margin of the upper jaw. He considered this to be a displaced small frontal clasper by comparison with the cephalic spines of male hybodont selachians. He restored it in a small pit on the anterior margin of the skull, just in front of the anterodorsal corner of the orbit (Fraas 1910, Plate 3, Figure 5; Patterson 1965, Figure 24 A; Romer 1966, Figure 65). Patterson was unhappy with Fraas' interpretation of the structure and considered that it "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", pending re-examination of the material (Patterson 1965: 146).

Fraas has misinterpreted the nature and shape of the specimen. He considered it to be shiny, covered with enamel and to comprise a single element. As described above, the objects in this position are slightly displaced tooth plates from the upper jaw (Figure 1; Plate 2). They comprise a basal lamellar portion with an external covering of pleromic hard tissue, not enamel. The structure figured by Fraas actually comprises parts of two tooth plates; the tritoral surface of the upper posterior tooth plate in lateral view and the central upper tooth plate in oblique occlusal view. The structure described by Fraas, therefore, is not a frontal clasper, or a modified dermal plate or enlarged scale, but parts of the upper dentition.

Fraas omitted to mention the presence of a fairly large cartilage fragment anterodorsal to the anterior neurocranial margin in front of the orbits, oriented at right angles to the skull margin itself (Fraas 1910, Plate 3, Figure 1; Figure 1; Plate 1, 3 Figure 1). This position and orientation suggests that it is the basal part of the frontal clasper. Assuming that its post-mortem disarticulation has been minimal, as in the remainder of the specimen, it would have been articulated with the anterodorsal surface of the neurocranium between the anterodorsal corners of the supraorbital ridges, just behind the marked pit in the dorsal neurocranial margin, in front of the orbits.

In members of the Chimaeroidei, frontal claspers are known only in males. The claspers are small, heavily calcified rods of fibro-cartilage armed with scales. Since four of the six known complete specimens of *Squaloraja*, and all four specimens of *Metopacanthus* in which the head is preserved possess a frontal clasper, it may be that the frontal clasper was present in all individuals (Dean 1909: 261; Patterson 1965: 200). It is possible, therefore, that it is not a sexually dimorphic feature in myriacanthoids, but one of unknown function possessed by all individuals.

d. Dorsal fin spine

Fraas (1910: 58) considered that the dorsal fin spine was smooth for its entire length, lacking tuberculate ornament completely. This is not the case. The lateral single rows of down-turned denticles on the posterior face give way basally to several rows of occasional tubercles. On occasions, these tubercles encroach onto the lateral face. The remainder of the lateral face of the spine is smooth. The anterior margin of the spine is tuberculate for the proximal two-thirds of the spine length. The tubercles become coarser and more persistent in several rows basally.

The tuberculate ornament of the anterior and posterolateral margins of the fin spine in *Acanthorhina* (Plate 3, Figure 2) serves to link the genus with the myriacanthoids. The fin spines of *Myriacanthus* Agassiz (1837), *Metopacanthus* Zittel (1887), *Chimaeropsis* Zittel (1887), *Recurvacanthus* Duffin (1981), and *Agkistracanthus* Duffin & Furrer (1981) all possess some tuberculation on the anterior margin, posterolateral margins and lateral faces of the dorsal fin spine. *Acanthorhina* is unique in having greatly reduced tuberculation on the lateral spine face.

The fin spine of *Acanthorhina* is slightly curved, as in *Agkistracanthus* and *Recurvacanthus*. The fin spines of *Metopacanthus*, *Myriacanthus*, and *Chimaeropsis* (cf. *C. franconicus* Münster 1840, Plate 3, Figure 8) are all straight.

Chimaeroid fin spines are all smooth with denticulate posterior borders. It has been remarked that they vary little and are "never diagnostic for species" (Case 1978: 24; see also Case & Herman 1973).

e. Dentition

Fraas (1910, Plate 3, Figure 4) reconstructed the dentition of *Acanthorhina* as having three tooth plates on each upper jaw and one mandibular tooth plate, in spite of his interpretation that some of the teeth represented a frontal clasper. He interpreted one blade-like tooth plate, lacking pleromic hard tissue, as a vomerine plate. He compared its structure with that of the lower symphyseal tooth plate of *Myriacanthus*, and concluded that there must have been a pair of such tooth plates in an anterior position in the upper dentition of *Acanthorhina*. Patterson (1965: 148) suggests that the tooth plate represents a single symphyseal element in the lower jaw on the basis of the shape and position of the specimen. This is the correct interpretation of the tooth plate. It is curved, single, and possesses a small strip of pleromic hard tissue. Its lateral extremities would have fitted into the notches on the anterolabial borders of the adjacent larger, paired tooth plates on each lower jaw (Figure 1, 5 a).

The dentition of *Acanthorhina* is reconstructed in Figure 5 a. The lower posterior, upper posterior and upper central tooth plates have distinctive occlusal surfaces. Very steep, high ridges of pleromic hard tissue transect the teeth so that there are variously three main tritoral areas. These are not distinct tritors since the pleromic hard tissue is present over the whole of the occlusal surface. Between the anterior labiolingual ridges in the lower and central upper tooth plates there is a small, elongate triangular area with its base formed by the labial tooth plate margin, lacking pleromic hard tissue. Instead,

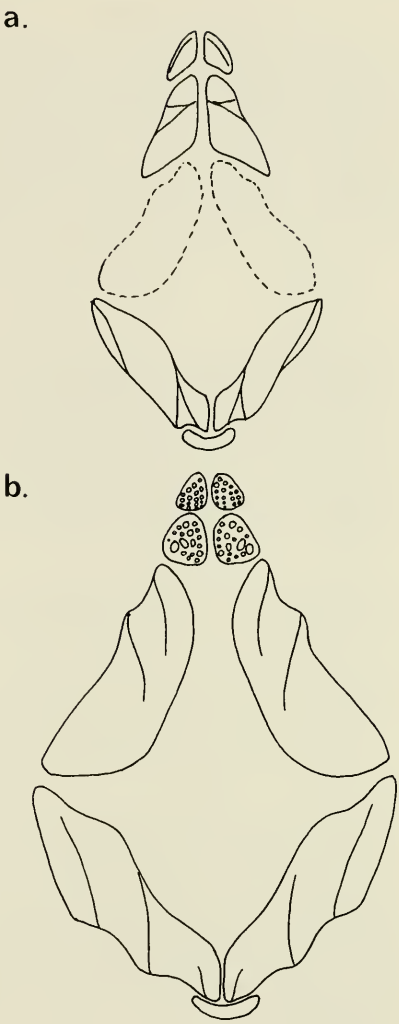

Fig. 5. The reconstructed dentitions, as if seen from the front, of a: *Acanthorhina jaekeli* Fraas (1910); b. *Myriacanthus paradoxus* Agassiz (after Patterson 1965).

the tissue here is lamellar, and in the two lower teeth, has marked wear facets. These were presumably produced by contact against the anterior part of the tritoral area of the central upper tooth plate during occlusion.

The lack of distinct tritoral areas is typical of myriacanthid teeth, although tritors are known on the central and anterior upper tooth plates of *Myriacanthus paradoxus* (Dean 1906; Patterson 1965, Figure 5 b), and in the upper tooth plate of *Chimaeropsis* (Patterson 1965: 143).

The arrangement of the dentition in *Acanthorhina* is most closely comparable with that of *Myriacanthus paradoxus*. The tooth arrangement is similar in that the posterior tooth plate is the largest in the upper jaw, followed by the central tooth plate and then the anterior upper tooth plate (although the anterior and central tooth plates do not possess tritors in *Acanthorhina*). The arrangement in the lower jaw is very similar in the two species; there is a single arcuate symphyseal tooth plate and a pair of posterior tooth plates. The arrangement of the transverse ridges is different in the two genera, however. In *Myriacanthus* the transverse ridges are sub-parallel and independent, trending labiolingually, while in *Acanthorhina* they either converge or diverge markedly in a lingual direction, depending on the position on the tooth plate. In *Myriacanthus,* the occlusal surface of the tooth plate is divided into three tritoral longitudinal areas of similar shape, whereas in *Acanthorhina* only two tritoral sections are developed, with an intervening area devoid of pleromic hard tissue. Also, the lower posterior tooth plates in *Acanthorhina* are more strongly convex labiolingually, smaller, and have a more regular labial margin (compare Figures 5 a and 5 b).

The transverse ridges found on myriacanthoid teeth produce variation in surface relief of the occlusal face which persists with wear and allows a long functional life of the tritoral areas. The very high and sharp ridges on the occlusal surface of the tooth plates of *Acanthorhina* are here interpreted as having a shearing function as well as being useful in grinding. Since *Acanthorhina* is extremely rare in the Holzmaden fauna, it may well be an exotic faunal component; perhaps it lived in deep water, as is the case with many extant chimaeroids. As such it may well have fed on nektonic invertebrates such as ammonites and belemnites, or even small vertebrates such as *Leptolepis,* all of which are more common in the Toarcian fauna (see discussion on p. 22—25 below).

Patterson (1965: 146) diagnosed the family Acanthorhinidae Patterson by the following characters: dermal plates on head reduced or absent; large frontal clasper; two tooth plate pairs in the upper jaw, of which the anterior is the larger; lamellate tritors on posterior tooth plates of upper jaw, other tooth plates without tritors; dorsal fin spine laterally compressed, not tuberculated, without anterior denticles.

These characters were based on the original interpretations of Fraas (1910). Re-examination of the specimen has revealed that dermal plates are present in positions on the skull which are usual in myriacanthids; the frontal clasper is only partially preserved; the disposition of the tooth plates in upper and lower jaws is normal for the myriacanthid condition; the fin spine is slightly laterally compressed, but is denticulate, possesses anterior tubercules, and even some tubercles on the lateral face, as in myriacanthids. Since these characters all correspond to the condition in the Family Myriacanthidae Smith Woodward, it must be concluded that *Acanthorhina* is a myriacanthid holocephalan, and that the Family Acanthorhinidae is a synonym of the Family Myriacanthidae.

Acanthorhina is distinct from all other myriacanthids in details of the dentition, fin spine, and neurocranium.

Genus *Metopacanthus* Zittel, 1887

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

Metopacanthus bollensis (Fraas 1910)

Plate 5, Figure 1

1910 *Myriacanthus bollensis* Fraas, Jh. Ver. vaterl. Naturk. Württ., **66:** 61—63, Plate 3, Figure 7.
1953 *Myriacanthus bollensis* Fraas. — Hauff, Das Holzmadenbuch, 1st Edition: 22, Plate 37, Figure a.
1960 *Myriacanthus bollensis* Fraas. — Hauff, Das Holzmadenbuch, 2nd Edition: 22, Plate 37, Figure b.

Holotype: SMNS catalogue number 12578. An isolated, almost complete fin spine.

Locality: Holzmaden, Baden-Württemberg, southern Germany. No further details of the precise locality are available.

Horizon: Posidonienschiefer or Schwarzjura εII3, Fleins; *Dactylioceras tenuicostatum* zone, Lower Toarcian, Lower Jurassic.

Diagnosis: A myriacanthid holocephalan known on the basis of a unique dorsal fin spine. The spine is long and straight. The lateral face is lightly striated and tuberculate for the proximal nine-tenths of its length. The posterolateral spine margins are ornamented by a single row of downturned for the distal half of the spine length. Upturned denticles are present for an indeterminate extent on the anterior spine margin.

Description

The fin spine is preserved in right lateral view and is 330 mm in length. It is straight, pointed distally, and widens basally (Plate 5, Figure 1). The anteroposterior width at the preserved spine base is 20 mm. The proximal two thirds of the spine is crushed laterally.

The posterior face of the spine is convex and is ornamented by a row, assumed to be paired, of fifteen downturned, sharply pointed denticles. The visible denticles are large and elongate proximodistally. The average length of the denticle base is 3 mm. A series of light to medium vertical striations ascend the lateral and distal faces of the denticles, but are very short, terminating well before the denticle apex. The denticle row extends from 13 mm below the distal tip of the spine for a distance of 77 mm along the posterolateral margin. This gives way to an area 28 mm long which is free of denticles. The denticle row then begins again, giving way to several rows of occasional tubercles basally. These tubercles are initially closely spaced, becoming more isolated basally. The tuberculate ornament of the posterolateral margin is presumably an encroachment of the lateral face tuberculation onto the posterior spine wall, and terminates 120 mm from the preserved base of the spine.

The lateral face of the spine is ornamented by closely packed tubercles measuring 1 mm long on average basally. The tubercles have little organisation, although rough growth lines appear to be reflected in their distribution in certain places along the anteroproximal spine border. While the tubercles are closely spaced for the lower third of the lateral face of the spine, they tend to become more widely spaced proximally, and to be more organised into longitudinal rows. Distally, the tuberculation tends to die out on the anterolateral and posterolateral spine margins, leaving a central set of tubercles which terminates 30 mm below the spine apex. Certain enlarged, upturned denticles are visible on the anterior margin of the spine, but these have been badly damaged during the original mechanical preparation of the spine. These anterior denticles are just over 1 mm long, and the extent of their development is difficult to judge.

The histology of the spine is not available for study.

Discussion of affinities

The tuberculate superficial ornament of this spine attests to its myriacanthid affinity, as previously concluded by Fraas (1910) and Hauff (1953, 1960). Of the myriacanthid genera known, only two are closely comparable with this specimen; *Metopacanthus* and *Myriacanthus*. The fin spines of *Agkistracanthus* (Duffin & Furrer 1981, Plate 1) and *Recurvacanthus* (Duffin 1981, Plate 1) are strongly curved, whereas the spine of *M. bollensis* is straight. The fin spine of *Acanthorhina* is slightly curved and has reduced tubercular ornament; *M. bollensis* is strongly tuberculated. The fin spines of *Chimae-*

ropsis are poorly known, but appear to be tuberculate, and characterised by the presence of upturned denticles along the anterior spine margin as in *M. bollensis* (Münster 1840, Plate 4 Figure 8; Reis 1895, Plate 12 Figure 3; Patterson 1965: 145). *Myriacanthus paradoxus*, however, typically possesses upturned denticles along the posterior face of the spine, and downturned denticles along the anterior spine margin (Patterson 1965: 129, 141, Figure 14). Fin spines of *Metopacanthus,* on the other hand, have upturned denticles on the lower part of the anterior margin, and downturned denticles on the upper part of the posterolateral margins, as in *M. bollensis.* Thus, the unique fin spine described above is concluded to belong to *Metopacanthus* since it possesses upturned denticles on the lower part of the anterior margin, and downturned denticles on the upper part of the posterolateral margins.

Palaeoecology of the toarcian myriacanthids

Associated fauna

The specimens of *Acanthorhina jaekeli* and *Metopacanthus bollensis* were recovered from sequences of black shales and occasional intercalated limestones generally preserving a diverse vertebrate and invertebrate fauna (Hauff 1953, 1960; Urlichs, Wild & Ziegler 1979). The marine reptiles in the fauna include ichthyosaurs (*Stenopterygius, Leptopterygius* and *Eurhinosaurus*; Mc Gowan 1979), mesosuchian crocodiles (*Steneosaurus, Pelagosaurus, Platysuchus*; Westphal 1962) and plesiosaurs (*Plesiosaurus, Thaumatosaurus*). Pterosaurs (*Dorygnathus, Campylognathoides*) and dinosaurs (*Ohmdenosaurus*) are exotic elements of the vertebrate fauna. Toarcian fishes found in the Holzmaden successions include sharks (*Hybodus, Bdellodus, Paleospinax*), other holocephalans (*Metopacanthus* sp., Reif 1974), coelacanths (*Trachymetopon*), holosteans (*Lepidotes, Dapedium, Pachycormus, Euthynotus, Hypsocormus, Sauropsis, Caturus, Tetragonolepis, Leptolepis* and *Pholidophorus*), and palaeonisciforms (*Ptycholepis, Saurorhynchus, Chondrosteus* and *Ohmdenia*). Further, there is a diverse ammonite (*Dactylioceras, Harpoceras, Hildaites, Hildoceras, Lobolytoceras, Pseudolioceras* and *Zetoceras*) and belemnite and teuthoid fauna (*Phragmoteuthis, Loligosepia, Teudopsis, Salpingoteuthis* and *Passaloteuthis*; Riegraf 1981). These are accompanied by the actively swimming bivalve, *Posidonia,* the burrowing *Goniomya* and *Solenomya,* the bysally attached *Oxytoma, Chlamys, Gervillia, Meleagrinella* and *Inoceramus,* and the cemented *Ostrea. Orbiculoidea* is a common brachiopod, accompanied by crinoids (*Pentacrinus* and *Seirocrinus*), echinoids (*Diademopsis*) and decapod crustaceans (*Proeryon* and *Uncina*). Gastropods are *Loelodiscus* and an unnamed specimen (Keller 1979).

Not all of these genera are recorded from the precise horizon which yielded *Acanthorhina* and *Metopacanthus bollensis,* but the list serves to illustrate the general faunal setting of the specimens.

Feeding in *Acanthorhina*

The form of the dentition in *Acanthorhina* suggests a shearing and crushing action during occlusion. The strong, arcuate, narrow surface of the lower symphyseal tooth plate, and the diagonal ridges on the upper and lower posterior tooth plates would have been effective shearing agents. The anterior upper tooth plates, and broad areas of pleromic hard tissue on all posterior tooth plates are adapted for crushing. This crushing mechanism is further aided by the holostylic jaw suspension and presumed (on the basis of preorbital surface area) moderate development of the levator mandibulae musculature.

Extant chimaeroids inhabit a wide geographical range and variety of depth of marine conditions. Chimaeroids are known from the deep sea (around 2000 metres, DEAN 1906: 13) and from shallow shelf seas (less than 20 metres, DEAN 1906: 14). *Chimaera colliei* (LAY & BENNETT) has been found in both situations. Thus, by comparison with the distribution of extant chimaeroids, it is not possible to state whether the single occurrences of *Acanthorhina* and *M. bollensis* in the Holzmaden Posidonienschiefer might be representative of an indigenous fauna or exotic deep water chimaeriform element.

There are little data available on the diet of modern chimaeroids. DEAN (1906: 20) records broken mollusc shells and crustaceans in the gut of *Chimaera colliei* together with less frequent annelids, fish, nudibranchs and squid remains. JOHNSON & HORTON (1972: 424) record similar contents in the gut of *Chimaera colliei,* with shrimps, molluscs and echinoderms being most numerous in 283 specimens. OLSSEN (1896) and LEGENDRE (1944) report that *Chimaera monstrosa* LINNAEUS feeds on molluscs, annelids, amphipods, echinoderms, and coelenterates. GRAHAM (1939) found that the diet of *Callorhynchus milii* BORY comprised bivalve and gastropod molluscs, crustaceans and fish. RIBBINK (1971: 66) records a wide variety of crustaceans together with some bivalves, gastropods and annelids in the gut of *Callorhynchus capensis* DUMERIL. These data suggest that extant chimaeroids are opportunistic feeders, taking advantage of a wide variety of available prey species at or near the sea floor. It can be seen from the faunal list of the Holzmaden Toarcian above (p. 22) that a similar variety of prey was available, in general terms, to the Jurassic myri-acanthids.

Acanthorhina possessed a pronounced rostrum that may have been useful in disturbing subsurface benthos during feeding, as well as opposing the frontal clasper. The rostra of extant chimaeroids vary in size, and are softer than would have been that of *Acanthorhina,* being supported by rostral cartilages (Figures 4 b, c) rather than being completely calcified. RIBBINK (1971) suggests that certain associated labial cartilages may aid feeding in extant chimaeroids. In *Callorhynchus,* premandibular labial cartilages may operate to form a shovel-like lower lip for driving into the bottom sand in order to dislodge prey. The upper labial cartilages may be used to manipulate the food into the mouth. Labial cartilages may well have been present in *Acanthorhina* (see p. 7 above), although more complete and better preserved specimens are needed to verify this. PATTERSON (1965, Figure 20) restores a premandibular cartilage in *Metopacanthus granulatus* and suggests that similar cartilages may well have been present in *Myriacanthus paradoxus* (PATTERSON 1965: 130, Figure 13). The cartilages in these myriacanthid genera, so far as can be told, are more robust than thoses of extant chimaeroids (Figure 3 b). *Acanthorhina* and the myriacanthids may have used their labial cartilages in a similar way to those of *Callorhynchus.*

The benthonic feeding of *Callorhynchus* (GORMAN 1963, RIBBINK 1971) is aided by a ventrally-oriented mouth (ALEXANDER 1967). The mouth of *Acanthorhina* shows moderate ventral orientation (Figure 3 a), whereas in *Metopacanthus granulatus* it was subhorizontal (Figure 3 b).

Callorhynchus is capable of feeding on small free living crustaceans above the sediment/water interface. RIBBINK (1971: 67) suggests that members of this genus may capture crustaceans and small fish by one or all of the methods outlined by ALEXANDER (1967) in his consideration of teleost feeding mechanisms, i.e. by swimming up to and engulfing the prey, by sucking the prey into the mouth, or a combination of both. It is suggested (Ribbink 1971: 67) that this mode of feeding might be permitted in both teleosts and holocephalans as a result of the operculum.

Thus, *Acanthorhina,* on the basis of comparison with extant *Callorhynchus,* may well have been capable of efficient benthonic feeding. The rostrum, and possibly the labial cartilage may have served to dislodge buried or surface-living invertebrates (e.g. *Orbiculoidea, Goniomya, Solenomya, Inoceramus, Chlamys,* annelids, crustaceans and echinoids) and manoeuvre them into the ventrally inclined mouth with its battery of shearing and crushing tooth plates. Active surface-dwelling invertebrates may have been taken, and possibly carcasses of larger organisms scavenged by this means.

The extant *Chimaera colliei* also possesses a ventrally oriented mouth (Figure 4 b), and, as noted above, is equally at home in shallow and deep water. It presumably is efficient as both a benthonic and midwater feeder. *Acanthorhina* may also have fed higher in the water column, possibly on small fish (e.g. *Leptolepis*), and perhaps ammonites and belemnites, by either engulfing or sucking means. If *Acanthorhina* possessed a similar body form to that of modern chimaeroids, though, it is unlikely that it was a rapid swimmer.

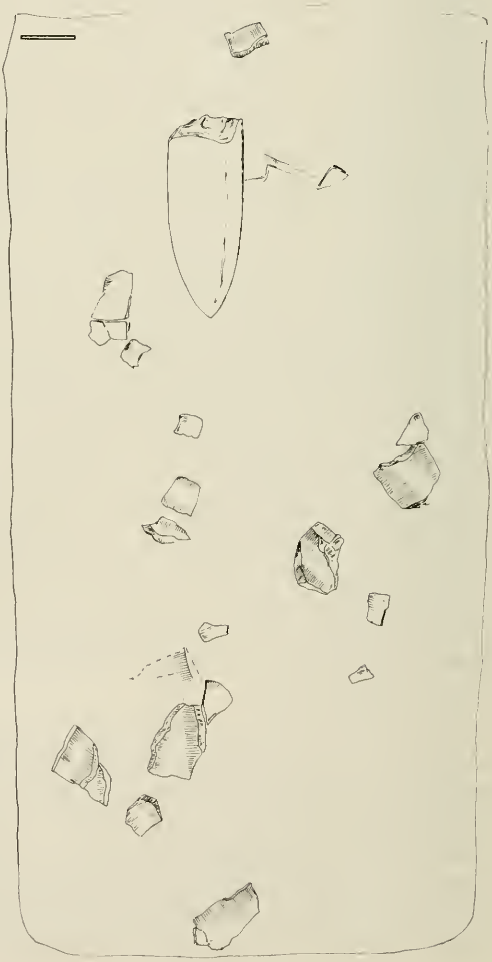

Fig. 6. The rostrum of *Dactyloteuthis incurvata* (Zieten), GPIT 1532/163. The specimen shows what may be the fragmented prey remains left by a myriacanthid holocephalan. Note the fairly close association of phragmocone fragments from the single organism, and the intact nature of the rostrum solidum. Bar scale = 1 cm. Drawing by T. Keller.

Riegraf (1981: 123, Figure 254; see also Hölder 1955, 1973; Mehl 1978, and Riegraf in Keller 1977) suggests that belemnite rostra (*Passaloteuthis paxillosa*, *Acrocoelites oxyconus*, *Youngibelus tubularis* and *Dactyloteuthis incurvata*), all from the Lower Toarcian of southern Germany, may have been bitten and broken during predation by chimaeriforms such as *Acanthorina* and *Meteop-acanthus*. A detailed survey and discussion of Fraßreste from the Posidonienschiefer is beyond the scope of this work, but some comments are necessary. Those made here contain some information kindly provided as written communications by W. Riegraf and T. Keller, and are reproduced with permission.

Belemnite rostra with associated fragments form a high percentage of the total finds of dibranchiates in finely laminated clays, marls, bituminous shales and lithographic limestones of the southwest German Jurassic. It is known that certain ichthyosaurs contain dibranchiate arm hooklets in the gastric mass (Coles 1853; Moore 1856; Pollard 1968; Keller 1976, and others). Belemnite rostra have not been discovered in the gastric contents of ichthyosaurs, but are known from a single specimen of *Hybodus hauffianus* (SMNS 10062; Brown 1900; Shimanskiy 1949, Rietschel 1977). No gastric contents have been described from fossil holocephalans.

The belemnite Fraßreste of the Posidonienschiefer and Oberjura-Plattenkalke comprise closely associated, mildly disarticulated rostral fragments on single bedding surfaces (Figure 6). The posterior part of the rostrum is usually intact. Biting appears to have taken place around and just posterior to the base of the phragmocone (cf. Riegraf 1981, Figures 254 a, b); the soft parts, ink sac and proostracum are missing from the specimens. It is interesting to note that specimens of belemnite soft parts, although very rare, are often isolated; no known specimen contains the soft parts, ink sac and the rostrum. The anterior part of the belemnite animal to just below the base of the phragmocone is the most rewarding part of the organism for a predator to attack. Maximum nutrient returns are obtained with minimal resistance from the endoskeleton of the prey; the alveolus of the phragmocone is that part of the endoskeleton offering the least resistance to crushing. Myriacanthid holocephalans certainly possess a dentition capable of feeding on belemnites.

There are several possible explanations for the belemnites debris described by Riegraf and others:

1. The belemnite was bitten while alive and swimming in the water column. The anterior part of the body was swallowed by the predator, and the posterior part allowed to settle to the sea floor. If so, considerable variation in degree of association of the rostral fragments might be expected. Broken fragments of rostrum might fall from the water column to cover a small area of sediment in the absence of significant currents. Alternatively, fragmented rostral components might remain anchored to the flesh and survive in minimally disarticulated positions, depending upon the strength of later bottom currents and effects of the decay process. Certain specimens (GPIT [= Geologisch-Paläontologisches Institut der Universität Tübingen] 1534/160; Riegraf 1981, Figure 254 a) show very little disarticulation of the rostral fragments and tend to support this hypothesis.

2. The belemnite was attacked in mid-water, and the hard parts expelled from the mouth as oral ejecta. This might account for specimens showing greater disaggregation of the rostral fragments. The consistent preservation of the posterior tip of the rostrum is rather unusual if this method of feeding was employed. Also, the dentition of holocephalans might also be expected to be capable of dealing with the entire belemnite and

thus eliminating the need for removing rostral fragments from the mouth. Oral ejecta might also be occasionally expected to comprise the remnants of several individual belemnites attacked close together, and to include shards from the proostracum as well as the phragmocone and rostrum. RIEGRAF (written communication) has fully reconstructed the pieces of one belemnite Fraßrest and finds that the remains of only one individual are present. To my knowledge, no parts of the proostracum or anterior part of the phragmocone are known in the specimens from the Posidonienschiefer. ZANGERL & RICHARDSON (1969) describe specimens which they interpret as oral ejecta from the Carboniferous of the U.S.A. These specimens usually contain traces of faecal material; no faecal material is associated with the specimens from the Posidonienschiefer. Also, no evidence of further prey species, e.g. fish scales etc., is associated with the belemnite rostra.

3. The belemnites were dead and lying on the sea floor. Chimaeroids scavenged these carcasses during normal benthonic feeding, in a similar manner to suggestion (1) above. This would certainly allow close association of the rostral fragments.

Of the three suggestions above, numbers 1 and 3 are the most likely; indeed, both may have taken place, since *Acanthorhina* is suggested as being capable of benthonic and mid-water feeding. Unfortunately, no individual faecal constituents can be identified in the light brown contents of the belly region in *Acanthorhina*.

Certain belemnite rostra do appear to have been bitten by some predator; scratches interpreted as bite marks have been reported on some specimens (HÖLDER 1973; RIEGRAF 1973, 1981). These scratch marks appear to have been made by piercing, rather than shearing and crushing dentitions, as in the myriacanthids.

KELLER (1977: 122, Figure 1) further suggests that some ammonite Fraßreste may have been caused by predators armed with tooth plates. Note also that MEHL (1978) considers that fish were not predators upon ammonites, but that large dibranchiates were.

It remains possible that *Acanthorhina* fed upon belemnites, and perhaps also ammonites. Unfortunately, feeding in extant chimaeroids has not been directly observed.

Acanthorhina is restored in Plate 4.

Sub-Order Squalorajoidei PATTERSON, 1965

Family Squalorajidae SMITH WOODWARD, 1886

Genus *Squaloraja* RILEY, 1833

Type species: *Squaloraja polyspondyla* (AGASSIZ)

Squaloraja polyspondyla (AGASSIZ, 1836)

Plate 5 Figure 2; Figure 7

1833 *Squaloraja dolichognathos* RILEY, Proc. geol. Soc. London, **1**: 484. — [Nomen nudum]
1836 *Spinacorhinus polyspondylus* AGASSIZ, Recherches sur les Poissons Fossiles, **3**: Plates 42, 43; Feuill. 94.
1837 *Squaloraia dolichognathus* RILEY. — RILEY, Trans. Geol. Soc. (2) **5**: 83, Plate 4.
1843 *Squaloraja polyspondyla* AGASSIZ. — AGASSIZ, Recherches sur les Poissons Fossiles, **3**: 381.
1872 *Squaloraja polyspondyla* AGASSIZ. — DAVIES, Geol. mag., **9**: 145, Plate 4.
1885 *Squaloraja polyspondyla* AGASSIZ. — HASSE, Palaeontogr. **31**: 4, Plate 1, Figures 2, 3.
1886 *Squaloraja polyspondyla* AGASSIZ. — SMITH WOODWARD, Proc. Zool. Soc. London, 1886: 527, Plate 55, Figures 1—5, 7, 8.
1887 *Squaloraja polyspondyla* AGASSIZ. — SMITH WOODWARD, Proc. Zool. Soc. London, 1887: 481.

1890 *Squaloraja polyspondyla* Agassiz. — Howes, Proc. Zool. Soc. London, 1890: 687.
1891 *Squaloraja polyspondyla* Agassiz. — Smith Woodward, Catalogue of the fossil fishes in the British Museum (Natural History). II: 41, Plate 3, Figure 2.
1895 *Squaloraja polyspondyla* Agassiz. — Reis, Geol. Mag., **32**: 385, Plate 12, Figures 1, 2, 4, 5, 6.
1906 *Squaloraja polyspondyla* Agassiz. — Dean, Publ. Carneg. Instn., **32**: 141, text-figures 120, 133, 137, 137A, 138, 139.
1922 *Squaloraja polyspondyla* Agassiz. — Leigh-Sharpe, J. Morph., **36**: 193, text-figure 3.
1935 *Squaloraja polyspondyla* Agassiz. — De Beer & Moy-Thomas, Phil. Trans. R. Soc. B, **224**: 304, text-figure 19.
1951 *Squaloraja polyspondyla* Agassiz. — Ørvig, Arkiv Zool. (2) **2**: 416, textfigure 19.
1965 *Squaloraja polyspondyla* Agassiz. — Patterson, Phil. Trans. R. Soc. B, **249**: 116, text-figures 8—12, Plate 23 Figure 52, Plate 24, Figures 55, 56.

Note on the holotype: After description by Agassiz (1836), the type specimen of *Squaloraja polyspondyla*, a virtually complete fish, was purchased from Mary Anning (1799—1847), the famous collector of Lower Jurassic fossils who lived at Lyme Regis, Dorset (Lang 1935), by Mr. J. Naish Sanders. Sanders deposited the specimen in what was then the Museum of the Bristol Institution. The specimen was registered as number Ca 7106. The specimen has not been traced. It must be presumed to be destroyed during the bombing of what is now the Bristol City Museum and Art Gallery (Queens Road, Bristol BS8 1RL) during 1940. However, "a portion of the tail, subsequently found" was acquired from Lyme Regis independently by the Philpot sisters (Edmonds 1978: 46). This specimen is now housed in the Philpot collection of Oxford University Museum, Parks Road, Oxford OX1 3PW, Catalogue number J 3097 (Powell & Edmonds 1978: 52). I am grateful to Dr. M. D. Crane of Bristol City Museum for his advice concerning the holotype.

Note on taxonomy: Riley (1833: 484) first referred to the species as *Squaloraja dolichognathos* Riley, without giving a description or figuring the specimen. This name is therefore a nomen nudum. Riley (1837) redescribed and figured the holotype. He withdrew the specific name as inappropriate and changed the spelling of the generic name to *Squaloraia* (ex errore). Meanwhile Agassiz (1836) had named the same specimen *Spinacorhinus polyspondylus* Agassiz. As Patterson (1965: 117) remarks, the name *dolichognathus* has not been used as a senior synonym in primary literature for over fifty years. Thus it would appear that it is a nomen oblitum. Patterson (1965) states otherwise that the inappropriate nature of the specific name does not render it unavailable, and awaited possible emendation of the International Code of Zoological Nomenclature, expecting that the species should become *Squaloraja dolichognathus*. Under the 1964 edition of the Code it would appear that the status of the specific name is unchanged since Patterson's comments. The generic name, *Spinacorhinus*, proposed by Agassiz (1836) was later synonymised with Riley's *Squaloraja* (Agassiz 1834; Smith Woodward 1891 etc.), and has remained unused as a senior synonym since, apart from being listed as *Spinacorhinus polyspondylus* Agassiz by Powell & Edmonds (1978: 52). Thus, current usage for the species is *Squaloraja polyspondyla*, although this may need to be reviewed under the next edition of the Code of Zoological Nomenclature.

Material: A complete frontal clasper, purchased from R. F. Damon of Weymouth, Dorset, England, SMNS 9443.

Locality: Lyme Regis, Dorset, England. No further locality details are available.

Age: Lower Lias, Lower Jurassic. No further stratigraphical details are available.

Description

The specimen (Plate 5 Figure 2) measures 132 mm in length and is exposed in ventral view. Posteriorly there is an expanded triangular area 25 mm wide. This area is divided into two by a thin medial ridge of tissue. This central ridge is flanked on either side by smooth depressions for muscle attachment. Anteriorly, the central ridge expands to the clasper proper, which comprises densely calcified fibrocartilage. The ventral surface of the specimen bears numerous corrugations proximally, and narrows distally.

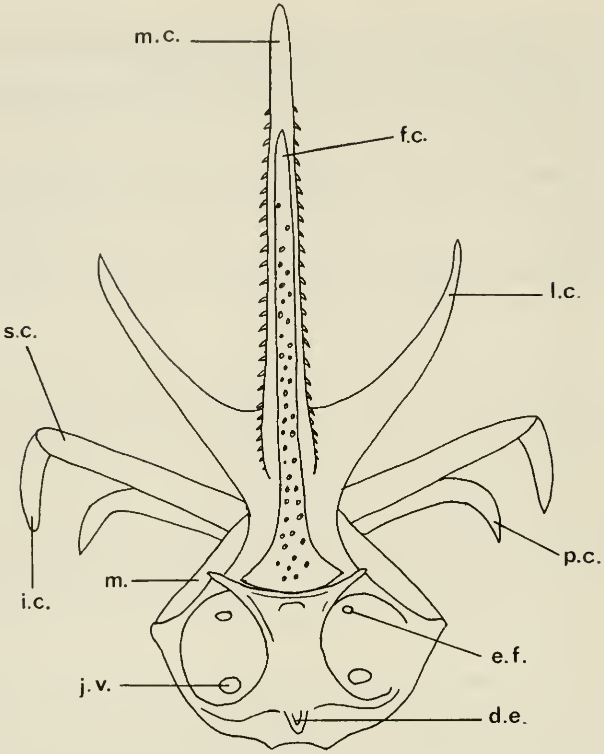

Fig. 7. The skull of *Squaloraja polyspondyla* (AGASSIZ) in dorsal view, showing the position of the frontal clasper (after DE BEER & MOY-THOMAS 1935).
mc: median rostral cartilage; f.c.: frontal clasper; l.c.: lateral rostral cartilage; p.c.: premaxillary labial cartilage; s.c.: supramaxillary labial cartilage; i.c.: inframaxillary labial cartilage; m.: mandible; j.v.: foramen transmitting the jugular vein, orbital artery and hyomandibular and palatine nerves; e.f.: foramen probably transmitting efferent pseudobranchial artery; d.e.: ductus endolymphaticus.

Discussion

The specimen is clearly a frontal clasper of *Squaloraja* by comparison with material held in the British Museum (Natural History), but shows less obvious squamation than in most other specimens (compare with REIS 1895, Figure 6; DEAN 1906, Figure 133). The two depressions on the posteroventral surface would have been for the insertion of depressor musculature. It is presently unclear as to whether the frontal clasper was present in all individuals of *Squaloraja,* or was restricted to males (see PATTERSON 1965: 200, and p. 17 above for further discussion).

The frontal clasper is shown restored in life position on the skull of *Squaloraja* in Figure 7.

Acknowledgments

I am very grateful to the following for allowing access to comparative material during the course of my work on holocephalans: Drs. COLIN PATTERSON (London), HEINZ FÜRRER (Zürich), H. RIEBER (Zürich), P. WELLNHOFER (München), G. VIOHL (Eichstätt) and F. WESTPHAL

(Tübingen). Dr. M. Crane (Bristol) kindly gave information on the holotype of *Squaloraja*, and W. Riegraf (Tübingen) and T. Keller (Frankfurt) discussed various aspects of Posidonienschiefer palaeoecology. I am grateful to Mr. H. Lumpe (Ludwigsburg) for help with some of the photography, Miss. A. Longbottom for assistance with the radiography, and particularly Mr. Stafford Howse (London) for painting the palaeoecological reconstruction of *Acanthorhina*. Dr. Jacques Herman (Brussels) kindly helped with the French summary. The manuscript was critically read by Dr. Colin Patterson and Mr. David Ward (Orpington). Very special thanks go to Dr. Rupert Wild (Ludwigsburg) for his hospitality, discussion, encouragement and help in many other ways connected with this project.

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Plate 1

The holotype of *Acanthorhina jaekeli* Fraas (1910), SMNS 12579.

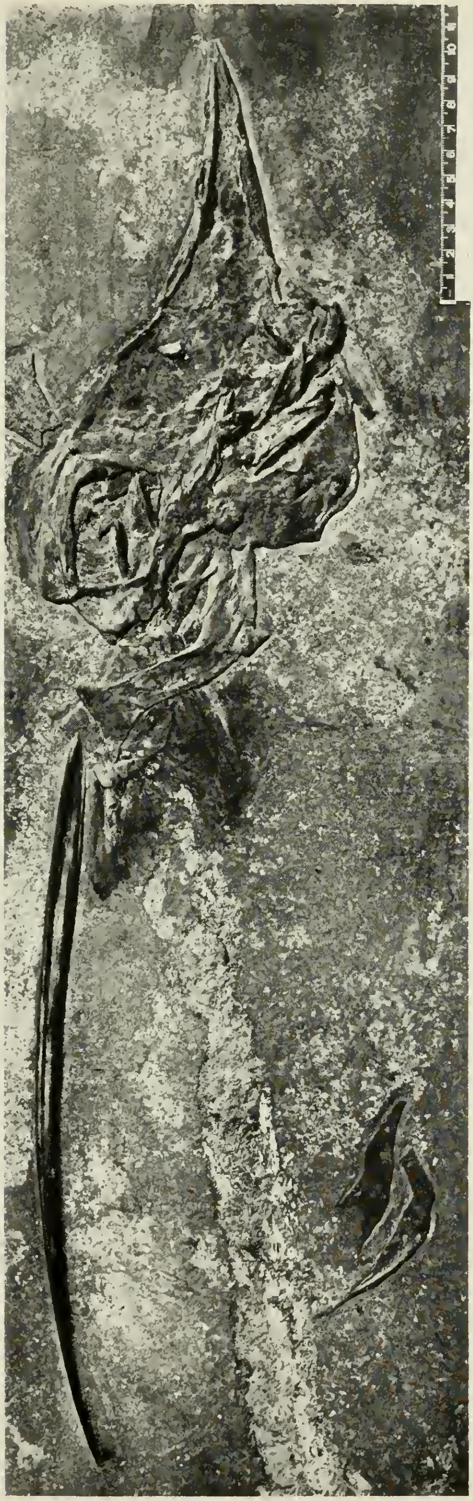

Plate 2

The dentition of *Acanthorhina jaekeli* FRAAS.


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Plate 3

Fig. 1. The frontal clasper and preorbital dermal plate of *Acanthorhina jaekeli* Fraas.

Fig. 2. The fin spine of *Acanthorhina jaekeli* Fraas.

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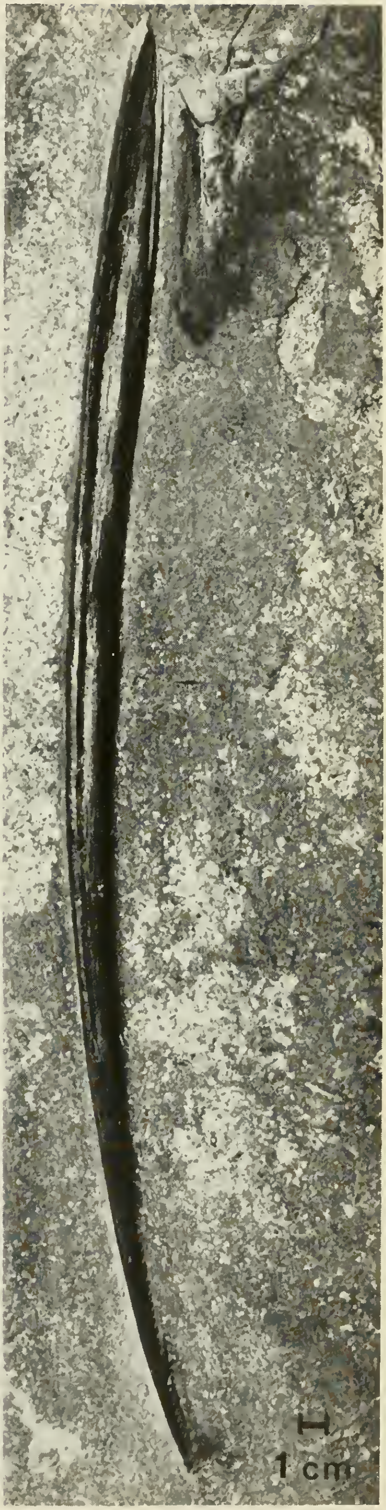

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Plate 4

A pictorial palaeoecological reconstruction of *Acanthorhina jaekeli* FRAAS in the Toarcian sea, painted in watercolour by STAFFORD HOWSE. *Acanthorhina* (midpicture) swims amongst *Dactylioceras* above a sea floor with surface dwelling Orbiculoidea. A crinoid-encrusted log floats above *Acanthorhina,* higher in the water column.

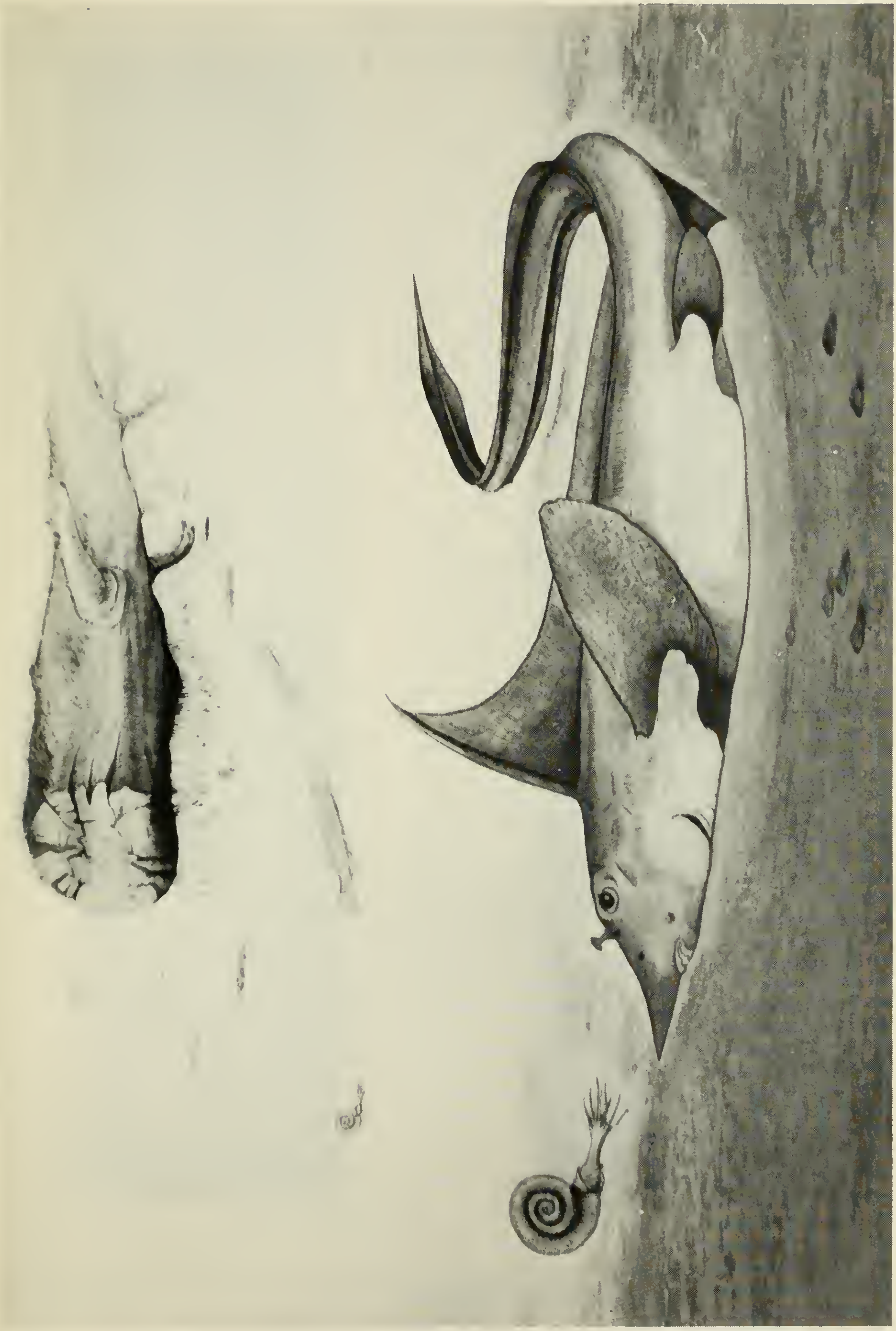
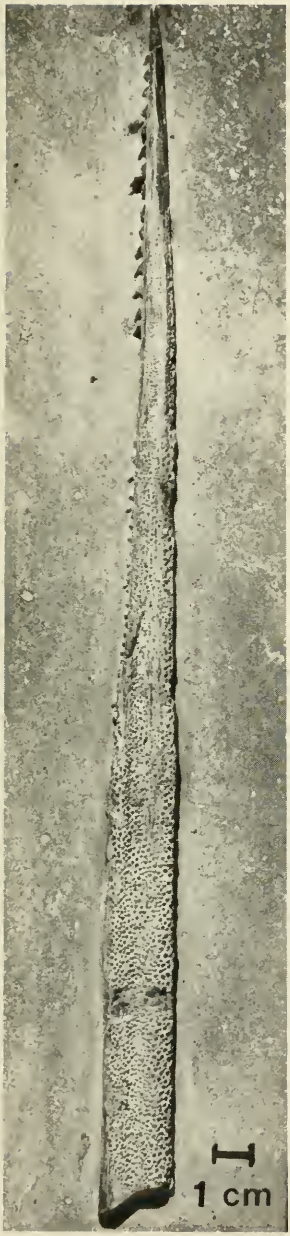


Plate 5

Fig. 1. The fin spine of *Metopacanthus bollensis* (Fraas, 1910). SMNS 12578.

Fig. 2. The frontal clasper of *Squaloraja polyspondyla* Agassiz. SMNS 9443.



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Zeitschrift/Journal: Stuttgarter Beiträge Naturkunde Serie B [Paläontologie]

Jahr/Year: 1983

Band/Volume: 97_B

Autor(en)/Author(s): Duffin Christopher J.

Artikel/Article: Holocephalans in the Staatliches Museum für Naturkunde in Stuttgart 1. Myriacanthoids and squalorajoids 1-41