Myriacanthid holocephalan remains from the Rhaetian (Upper Triassic) and Hettangian (Lower Jurassic) of Graubünden (Switzerland)

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By Christopher J. Duffin[1]) and Heinz Furrer[2])

ABSTRACT

Dorsal fin spines and tooth plates of a new myriacanthoid holocephalan are described as *Agkistracanthus mitgelensis* n.g., n.sp. and *Agkistracanthus* sp. The material was collected from Rhaetian (Upper Triassic) and Hettangian (Lower Jurassic) strata in various tectonic units in the Upper Austroalpine nappes of Kanton Graubünden, eastern Switzerland, and Vorarlberg in western Austria. The fin spines are long, moderately recurved, with downturned denticles along the distal one third of the posterolateral spine margins, a shallow inserted portion, and a tuberculate lateral wall proximally. An open groove persists in the posterior wall of the spine. The spines grew in a similar way to those of hybodont selachians. The dentition comprises at least two upper tooth-plate pairs with elongate rhomboidal occlusal surfaces. There was at least one robust, trapezoid tooth-plate pair in the lower dentition, possessing a single diagonal occlusal ridge. The tooth plates lack tritors, and may show well developed wear facets. The material is most closely comparable to *Acanthorhina* (Toarcian, Lower Jurassic) amongst other myriacanthids. The material of *Agkistracanthus* was subject to post-mortem disarticulation before being finally incorporated into various microfacies of Kössen Beds limestones and Hettangian hardgrounds. This is the first record of a myriacanthid holocephalan in the Tethys realm, and extends the record of the group into the Upper Trias.

ZUSAMMENFASSUNG

Mehrere Rückenflossenstacheln und Zahnplatten eines neuen myriacanthoiden Holocephalen werden als *Agkistracanthus mitgelensis* n.g., n.sp. und *Agkistracanthus* sp. beschrieben. Das Material stammt aus obertriassischen und unterliassischen Schichten (Rhaetian und Hettangian) verschiedener tektonischer Einheiten der oberostalpinen Decken Graubündens (Schweiz) und Vorarlbergs (Österreich). Die Flossenstacheln sind lang und mässig gekrümmt. Auf dem distalen Drittel tragen sie längs ihrer seitlichen Hinterkanten hakenförmig nach unten gebogene Dentikeln. Der proximale Teil der Seitenflächen trägt Tuberkeln, während die kurze Wurzel glatt ist. Die Stacheln wuchsen in ähnlicher Weise wie diejenigen der hybodontiden Selachier. Die Bezahnung besteht aus mindestens zwei oberen Zahnplattenpaaren mit rhomboidförmigen Reibflächen und mindestens einem unteren Zahnplattenpaar, dessen kräftige trapezförmige Zahnplatten eine diagonale Reibkante besitzen. Den Zahnplatten fehlen Tritoralstrukturen; sie können aber gut ausgebildete Abnützungsfacetten aufweisen. Das Material lässt sich unter den Myriacanthiden am besten mit *Acanthorhina* (Toarcian, Unterjura) vergleichen. Die Überreste von *Agkistracanthus* wurden nach postmortalem Zerfall isoliert in mikrofaziell verschiedenartigen Kalken der Kössener Schichten (Rhaetian) oder Kondensationshorizonten des Hettangian eingebettet. Es handelt sich um den ersten Nachweis von myriacanthiden Holocephalen im Tethys-Raum und erweitert deren stratigraphische Verbreitung bis hinunter in die Obertrias.

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[1]) 126, Central Road, Morden, Surrey SM4 5RL (England).
[2]) Paläontologisches Institut der Universität, Künstlergasse 16, CH-8006 Zürich (Switzerland).

CONTENTS

Introduction

Vertebrate faunas of Upper Triassic and Lower Jurassic age in the Alps are rare. This is, in part, due to facies differences between the "Alpine type" facies of the Tethys realm and the "German type" facies in southern Germany, France and England. It is also due to difficulties in sampling and to the tectonic deformation of the relevant sequences in the Alps.

Vertebrate faunas and isolated records of vertebrate remains from the Rhaetian (uppermost Triassic) have been described from the Penninic belt, the Austroalpine nappes and the Southern Alps. These records comprise hybodont sharks, chondrosteans, holosteans and a placodont reptile from the "Rhétien" of the Swiss Prealps in the Penninic belt (JEANNET 1913); hybodont sharks, a neoselachian shark (*Raineria*, OSSWALD 1928), chondrosteans, holosteans, placodont, nothosaurid and ichthyosaur remains are known from the Kössen Beds of the Northern Calcareous Alps (Austroalpine nappes) in Austria and Southeast Germany (KÜHN 1942, ZAPFE 1976), while a nearly identical fauna including hybodont sharks, chondrosteans, holosteans and placodont reptiles is known from the Riva di Solto Shales and the Zu Limestone in the Lombardian Rhaetian of the Southern Alps (BONI 1937, PINNA 1978). In addition, TINTORI (1980) has recently recorded articulated tooth rows of the problematic selachian *Pseudodalatias* from the Riva di Solto Shales of the Lombardy Alps (see also TINTORI & ZAMBELLI 1980).

The bulk of these vertebrate fossils comprises isolated bones, teeth and scales, with occasional skull and dermal armour fragments in the case of the placodont reptiles. Articulated skeletons are extremely rare.

Several major groups, including dipnoans, amphibians, dinosaurs and mammals are not recorded in the Rhaetian of the Alpine area to date, presumably as a consequence of the fully marine character of these deposits. That the Alpine Rhaetian was deposited in marine conditions is demonstrated by presence of corals and echinoderms in these beds, and the lack of any demonstrably terrestrial or freshwater organisms.

To date, only isolated fish teeth and scales have been reported from the Austroalpine nappes in Switzerland. In recent years, larger vertebrate faunas have been collected from the Kössen Beds of different Upper Austroalpine nappes in Kanton Graubünden (Southeast Switzerland) during fieldwork undertaken for two diploma theses and one Ph.D. thesis (FURRER 1974 and in preparation, ROHRBACH 1976). This new material has been prepared chemically at the Paläontologisches Institut und Museum der Universität Zürich and includes the fin spines and tooth plates of the holocephalan fishes which form the subject of this paper.

The specimens described here are held to be a myriacanthid holocephalan. The myriacanthoids are the temporal, and to some extent morphological intermediates between the chimaeroid holocephalans and the bradyodonts of the Paleozoic. Previously, the myriacanthoids were believed to range from the Hettangian *(Myriacanthus)* to the Tithonian *(Chimaeropsis)* in Northwest Europe. The discovery of the Swiss material extends the record of the group into the Rhaetian. The myriacanthoids previously were known by four genera placed in three families: *Myriacanthus* (two species) and *Metopacanthus* (one species) comprise the family Myriacanthidae (DUFFIN, in press, describes a third, monotypic genus, *Recurvacanthus*, belonging to this family); family Chimaeropsidae comprising three species of *Chimaeropsis;* family Acanthorhinidae, comprising one species of *Acanthorhina*. Several of the species are known on the basis of unique holotypes. Only *Myriacanthus* and *Metopacanthus* are known from numerous specimens.

The Swiss material described below comprises a new genus of myriacanthid based upon several dorsal fin spines and numerous tooth plates. It forms the first record of the suborder Myriacanthoidei outside Britain, Belgium and Germany; it is the first record of an holocephalan from the Tethys realm.

Geology and stratigraphy

The Austroalpine nappes in Kanton Graubünden (Southeast Switzerland) can be subdivided into three units: the Lower Austroalpine nappes, the Central Austroalpine nappes and the Northern Calcareous Alps. The latter two units together form the Upper Austroalpine nappes (TRÜMPY 1980) (Fig. 1). The nappes comprise basement rocks and/or Mesozoic sediments overthrust upon the Penninic nappes.

The Austroalpine nappes originally formed part of the Triassic supercontinent Pangea and were situated, as were the Southern Alps, on the northwest margin of the late Triassic Tethyan ocean, the Paleotethys (BOSELLINI & HSU 1973, LAUBSCHER & BERNOULLI 1977).

All of the Austroalpine nappes in Kanton Graubünden contain evidence of wide intertidal to supratidal carbonate platforms during Upper Triassic times. These platform deposits form the Hauptdolomit Formation, up to 1 km thick, of Norian

age. During Rhaetian times, probable early rifting in the oceanic Tethys led to a change in the environments. There was a strong influx of detrital material (clay and some silt) leading to the development of the characteristic black shales, dark
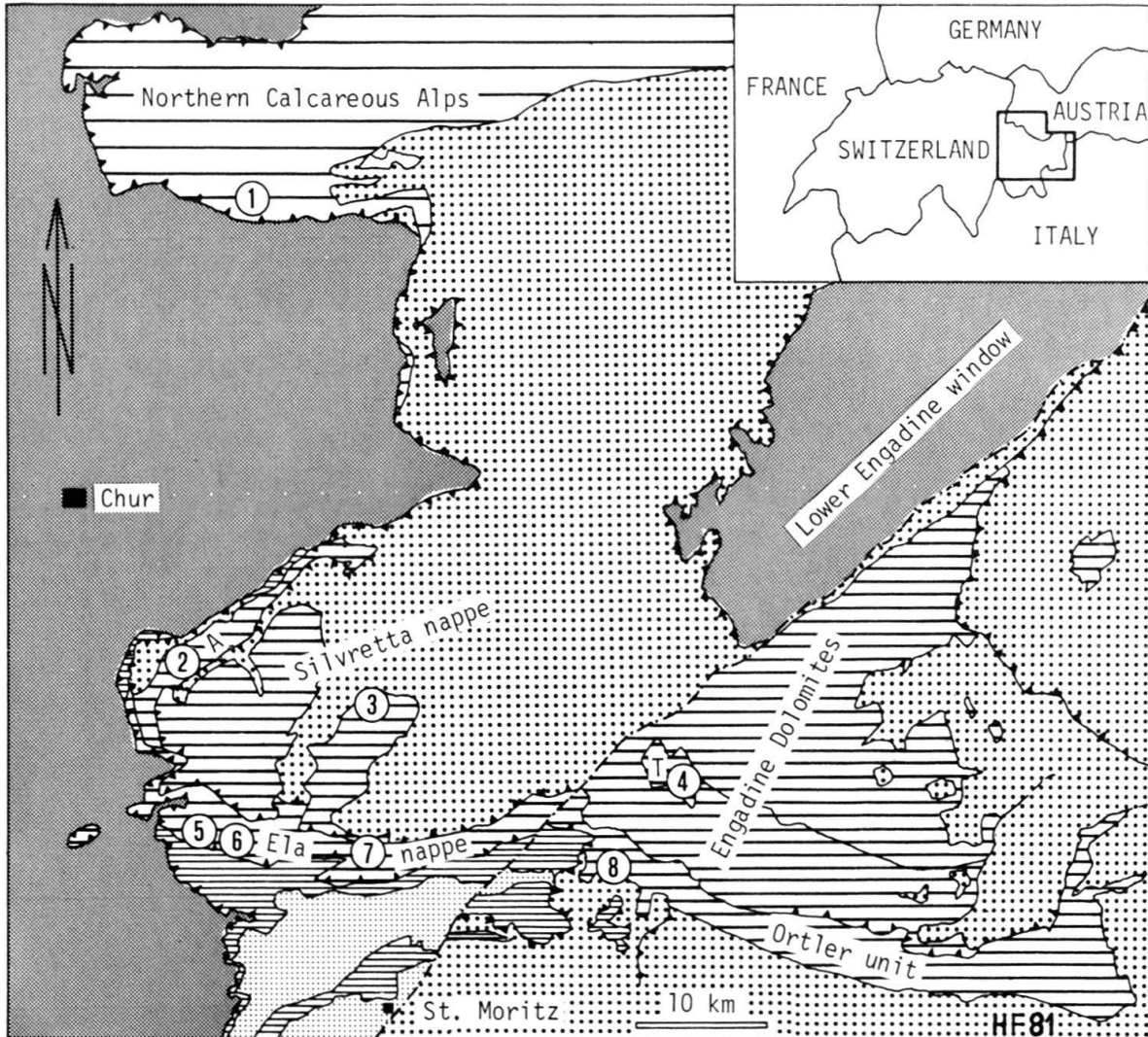
LEGEND

☐ Northern Calcareous Alps

☰ Mesozoic sediments ⎤ Central Austro-
▦ Basement   ⎦ alpine nappes

☰ Mesozoic sediments ⎤ Lower Austro-
░ Basement   ⎦ alpine nappes

▓ Penninic nappes

A   Arosa Dolomites

T   Terza unit

LOCALITIES YIELDING
MYRIACANTHID REMAINS

① Schesaplana
② Erzhorn
③ Alplihorn
④ Piz Murter
⑤ Piz Son Mitgel
⑥ Corn da Tinizong
⑦ Piz Zavretta
⑧ Piz Chaschauna

Fig. 1. Geological sketch map of Kanton Graubünden, Switzerland. Note the localities yielding myriacanthid holocephalan remains.

fossiliferous marls, marly limestones and yellow calcareous dolomites of the Kössen Beds. These deposits are visualized as representing wide, flat lagoons or shallow basins supporting a rich nektonic fauna and benthos. Later, a low-profile relief developed on the seafloor with muddy basins, carbonate mudbanks, coral banks, oolitic barriers, lagoons and intertidal flats. Closer to the Triassic–Jurassic boundary, carbonate sedimentation began to predominate once again, with grey reef and back-reef limestones and calcareous dolomites intercalating with a few minor shaley bands, forming the "Rhaeto-Lias Limestone".

The opening of Tethys and the Atlantic Ocean during the Lower Jurassic resulted in the breakup of the carbonate platforms along normal faults. This led to a higher-profile relief involving considerable changes in paleoslope, with small vestiges of the carbonate platforms remaining, together with submarine swells and deeper basins. Hardgrounds and red nodular limestones forming the Adnet Limestone developed on the swells whilst thick turbidite sequences built up in the basinal areas, forming the Allgäu Beds.

In the Austroalpine nappes of Graubünden, the biostratigraphic division of the Triassic sediments is problematic and uncertain because of the lack of useful index fossils (PEARSON 1970). In addition, there is current debate on the validity, chronological duration and stratigraphic distinction of the Norian and Rhaetian Stages (WIEDMANN et al. 1979). By analogy with the Northern Calcareous Alps we assume that the Hauptdolomit Formation is Norian, and that the Kössen Beds and "Rhaeto-Lias Limestone" are of Rhaetian and partly Hettangian age respectively (Fig. 2).

Distribution and preservation of the Swiss myriacanthoids

Myriacanthoid remains occur in all of the Upper Austroalpine nappes of Kanton Graubünden in either Rhaetian or Hettangian sediments (Fig. 1) but all four fin spines and most of the tooth plates described here were found on the mountains Piz Son Mitgel and Corn da Tinizong in the Central Austroalpine Ela nappe. Figure 2 shows the stratigraphic section at Piz Son Mitgel, the type locality.

The four fin spines and 22 tooth plates originate from the Rhaetian Kössen Beds and four tooth plates from the Hettangian hardgrounds at the base of the Adnet Limestone and the Allgäu Beds.

Rhaetian material

Eight tooth plates were found in situ in the middle and upper part of the Kössen Beds in measured sections (A/I 854, A/I 863, A/I 864, A/I 869, A/I 871, A/I 872, A/I 873, A/I 885). Three of these (A/I 863, A/I 864, A/I 885) were collected from the measured section at Corn da Tinizong, situated about 3.5 km east of the type locality at Piz Son Mitgel (Fig. 1) in beds that can be correlated with those of the type locality (Fig. 2).

In addition to the myriacanthoid remains described below, the Kössen Beds have yielded other, usually isolated vertebrate remains, including the teeth and fin spines of hybodont sharks *(Acrodus, Polyacrodus, Hybodus)*, chondrostean and holostean fish jaws, isolated teeth and scales *(Sargodon tomicus* PLIENINGER,

Gyrolepis, Saurichthys, Birgeria), teeth and dermal armour fragments of the placo-
dont reptile *Psephoderma alpinum* MEYER, the vertebrae, armour plates, ribs and
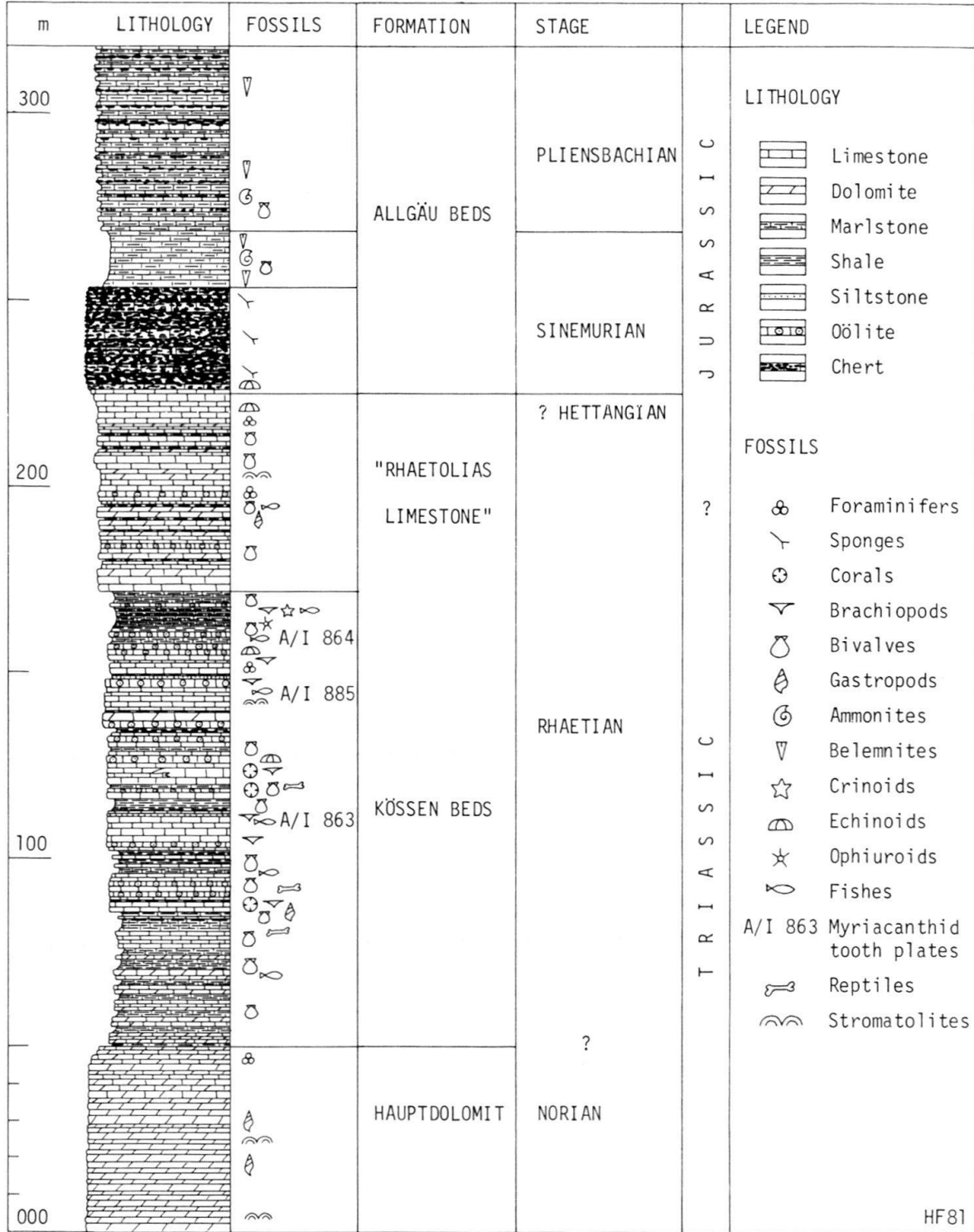teeth of a parasuchid reptile, and the vertebrae and ribs of a very large ichthyosaur.

Fig. 2. Stratigraphic section of the Central Austroalpine Ela nappe at Piz Son Mitgel, Kanton Graubün-
den, Switzerland. Note the three tooth plates of *Agkistracanthus mitgelensis* n.g., n.sp. in the middle and
upper part of the Kössen Beds (Rhaetian).

In the lower part of the Kössen Beds, these vertebrates are accompanied by the typical bivalve fauna of the "Swabian facies", with *Rhaetavicula contorta* PORTLOCK, *Gervillia inflata* (SCHAFHÄUTL), *Palaeocardita austriaca* (HAUER), *Atreta intusstriata* (EMMRICH), oysters, nuculids and others. These bivalves apparently lived mostly in monospecific populations with large numbers of individuals in shallow muddy lagoons and basins.

The middle and upper part of the Kössen Beds is dominated by brachiopods (*Rhaetina gregaria* [SUESS]) of the "Carpathian facies", together with coral banks (*Thecosmilia clathrata* [EMMRICH], *Astraeomorpha crassisepta* REUSS, *Thamnasteria rectilamellosa* WINKLER), echinoids, crinoids, megalodontid bivalves (*Conchodon infraliasicus* STOPPANI), foraminifers (*Triasina hantkeni* MAJZON) and stromatolites. The lithology and fossils indicate a depositional environment with a low-profile relief on the seafloor, with muddy basins, carbonate mudbanks, coral banks, oolitic barriers, lagoons and intertidal flats.

The myriacanthoid fin spines and tooth plates were always isolated and embedded in grey, mainly marly, sometimes dolomitic limestones. Various microfacies are present, including micrites, biomicrites, bio-oomicrites (Fig. 4b), biosparites and bio-oosparites, indicating different depositional environments.

The central cavities of the fin spines are filled with coarse-grained sediment with shell fragments (Fig. 4a, 4b). The disarticulation of fin spines and the infilling of central cavities by sediments probably indicate post-mortem disturbance. MAISEY (1978b) discussed possible ways of disarticulation of fin spines from the rest of the body. His discussion is useful in considering myriacanthoid fin spines from the Kössen Beds in Switzerland. He recognizes several possibilities:

1. Post-mortem biological disturbance by scavengers before fossilization. The high incidence of whole body and trace fossils in the Kössen Beds indicates the presence of a strong biological factor and hence the possibility of disarticulation by these means.

2. Post-mortem environmental disturbance due to winnowing action of bottom currents, prior to fossilization. This possibility is also true for the Kössen Beds fossils; bottom currents and turbulent water environments are indicated by ripple marks, oolites and not uncommon storm deposits.

3. Post-mortem, post-depositional reworking of sediments and enclosed organic remains after fossilization. Although neither the fin spines nor the tooth plates show evidence of prefossilization (REIF 1971), other fractured vertebrate remains and frequent coprolites which also occur in the coarse-grained sediments, indicate that reworking of prefossilized vertebrate remains and sediment may not have been uncommon in the Kössen basins (but see ANTIA 1979 for a critique on the characters of prefossilized vertebrate remains).

The sediments enclosing the Swiss myriacanthoid remains are usually very dark and contain disseminated small aggregates of pyrite. Invertebrate and vertebrate fossils are often marginally impregnated or encrusted by pyrite. The mineral has also grown in the usually calcite-filled vascular canals and fine dentine tubules of the fin spines (Fig. 5a–c). Weathering transforms the pyrite to limonite and the dark color of the sediments changes to lighter brown and yellow.

The thin sections of the fin spines and tooth plates show that at least part of the tissue is recrystallized. Figure 4b shows diagenetic apatite crystals in the inner part of the lamellar layer. Figures 5b and 5c show new, diagenetic apatite crystals having grown around the vascular canals in the osteodentine.

The fin spine thin sections also show a system of parallel cracks. These cracks resulted from tectonic deformation of the fossils during the Alpine orogeny. Larger-scale cracks and dislocations can be seen in fin spine and tooth plate whole specimens (Pl. 1, Fig. 1, Pl. 2, Fig. 4).

Hettangian material

All four of the liassic myriacanthoid tooth plates were found in Hettangian hardgrounds. Two of them were discovered in red biomicritic limestones in hardgrounds with ferromanganese crusts, rich in foraminifers, gastropods, bivalves, brachiopods, echinoderms and ammonites of Lower and Upper Hettangian age at the base of the Adnet Limestone as exposed at Schesaplana mountain. The remaining two tooth plates occured in hardgrounds of possible Hettangian age in the lowermost part of the Allgäu Beds. One tooth plate has been found in the Schesaplana mountain group in a grey micritic limestone, rich in bivalves, and with several thin brown ferruginous layers, just at the base of the Allgäu Beds. The latter plate has been collected from a hardground with bored pebbles, ferromanganese nodules, gastropods, bivalves and echinoderms. This hardground was located in a large redeposited block of a thick chaotic breccia at the base of the Allgäu Beds near Piz Chaschauna. This breccia is interpreted as a submarine landslide mass which originated on a submarine swell or seamount and slid into the deeper basin in response to normal faulting. The hardgrounds and the Adnet Limestone developed on the swells whilst the thick turbidite sequences of the Allgäu Beds built up in the basins.

Systematic palaeontology

Superclass *Chondrichthyes*

Class *Holocephali*

Order *Chimaeriformes*

Suborder *Myriacanthoidei* PATTERSON 1965

Family *Myriacanthidae* SMITH WOODWARD 1889

Agkistracanthus n. g.

Type species: Agkistracanthus mitgelensis n. sp.

Generic diagnosis. – A myriacanthid holocephalan known from dorsal fin spines and tooth plates. The fin spines are long (up to 280 mm) and recurved. The posterior wall of the spine is minimally concave and the posterolateral margins are ornamented by a series of hook-like, downturned denticles for the distal one-third of the spine

length. An open, narrow longitudinal canal runs the length of the posterior spine face in the midline. The lateral walls of the spine are vertically striated. Tubercular ornament is restricted to the proximal part of the lateral walls and anterior margin. Tubercles on the anterior margin of the spine may be coarser and upturned. The posterior spine wall lacks ornament. The tooth plates lack distinct tritoral areas. The basal lamellar layer contains diagonal vascular canals lingually. The lower tooth plate is trapezoid in occlusal view, with a single diagonal ridge. At least one smaller, narrower, more elongate tooth plate is present in the upper jaw. The upper jaw probably bears a second elongate tooth plate posteriorly.

Derivation of name. - Greek, agkistron ($\alpha\gamma\varkappa\iota\sigma\tau\rho\sigma\nu$), a fish hook, referring to the hook-like downturned denticles along the posterolateral spine margin; Greek, acantha ($\alpha\varkappa\alpha\nu\theta\alpha$), spine.

Agkistracanthus mitgelensis n.sp.
Pl. 1, Fig. 1-3; Pl. 2, Fig. 1-2; Fig. 3-6

Specific diagnosis. - As for genus.

Derivation of specific name. - From the mountain Piz Son Mitgel, Kanton Graubünden, Switzerland (type locality).

Holotype. - A/I 858, Paläontologisches Institut und Museum der Universität Zürich, Switzerland. A complete dorsal fin spine. Plate 1, Figure 1.

Type locality. - 1.1 km northwest of Piz Son Mitgel, Kanton Graubünden, Switzerland. Landeskarte der Schweiz 1:50,000, Blatt 258 Bergün (768.300/165.800/2590).

Horizon. - Kössen Beds (fallen block in a talus).

Age. - Rhaetian (Upper Triassic).

Tectonic unit. - Central Austroalpine Ela nappe.

Other material. - A/I 859, broken middle portion of spine (sectioned, Fig. 3-5); A/I 860, distal portion of juvenile spine (Pl. 1, Fig. 2); A/I 865, large spine with distal and proximal extremities missing (Pl. 1, Fig. 3).

Referred material. - 16 tooth plate fragments. A/I 862, right lower tooth plate (Pl. 2, Fig. 1); A/I 882, left lower tooth plate; A/I 857, ?anterolingual corner of lower tooth plate; A/I 861, left anterior upper tooth plate (Pl. 2, Fig. 2); A/I 884, left (?anterior) upper tooth plate fragment; A/I 854, ?posterior fragment of right (?posterior) upper tooth plate; A/I 856, right (?posterior) upper tooth plate; A/I 864, posterior fragment of ?left (?posterior) upper tooth plate; A/I 867, A/I 883, (?posterior) upper tooth plate fragments; A/I 855, indeterminate (?upper) tooth plate fragment; A/I 863, A/I 866, A/I 868, A/I 881, A/I 885, indeterminate tooth plate fragments.

Horizons and localities. - Specimens A/I 855, A/I 856, A/I 857, A/I 859, A/I 860, A/I 861, A/I 862, A/I 881, A/I 882, A/I 883, A/I 884: Information as for type locality.

Specimen A/I 854: Kössen Beds, Rhaetian (Upper Triassic), Central Austroalpine Ela nappe; 2.4 km NNW of Piz Son Mitgel, Kanton Graubünden, Switzerland.

Specimens A/I 863, A/I 864, A/I 865, A/I 866, A/I 867, A/I 885: Kössen Beds, Rhaetian (Upper Triassic), Central Austroalpine Ela nappe; 1.4 km northeast of Corn da Tinizong, Kanton Graubünden, Switzerland.

Specimen A/I 868: Kössen Beds, Rhaetian (Upper Triassic), Central Austroalpine Ela nappe; 1.5 km west of Piz Zavretta, Kanton Graubünden, Switzerland.

Description of the holotype

The fin spine is long (280 mm), slender and strongly recurved (Pl. 1, Fig. 1a). The specimen is preserved in right lateral view. Details of the posterior wall and anterior margin of the specimen are also available for study. The left lateral face of the specimen is obscured by matrix. The specimen is cracked in several places, and is slightly crushed at the proximal end. The anteroposterior length of the specimen is 19 mm. The transverse width of the spine is 6 mm across the posterior spine wall.

The posterior wall of the spine is minimally concave. A groove, the external expression of the incompletely closed posterior wall, runs the length of the posterior spine wall in the midline, and is flanked by a longitudinal convexity on either side. The proximal part of the posterior wall is open. This opening closes 65 mm from the preserved base of the spine. The posterior spine wall is faintly striated longitudinally. A row of moderate (up to 2 mm long) downturned, hook-like denticles is situated along each posterolateral margin. The denticle bases are oval in shape, and elongate longitudinally. The denticles are pointed. They are present for only the distal third of the total spine length.

The right lateral face of the spine is mildly convex anteroposteriorly. A series of longitudinal striations, representing unroofed longitudinal mantle canals in the trabecular outer layer of the fin spine, passes down the length of the spine (Pl. 1, Fig. 1b). These striations are very faint distally, but become coarser proximally. The base of the lateral face of the spine at the posterior margin is unornamented for a distance of 65 mm distally (i.e. ornamentation begins at the point of closure of the posterior wall). At the anterolateral margin, ornamentation begins 10 mm distal to the preserved spine base. Tuberculations are present on the crests of the longitudinal ridges intervening between the mantle canals. The distal tip of the lateral face of the spine is free of tubercles. The first lateral tubercles are encountered 42 mm down from the tip of the spine, in the middle of the lateral face and along the anterolateral border of the spine. The tubercles become more numerous proximally, but tend to be clustered in the middle section of the lateral face and around the anterolateral and posterolateral spine margins. The tuberculation is more indiscriminate toward the base of the ornamented part of the spine. The tubercles are occasionally closely packed in the middle of the lateral face, or they may be regularly spaced at 1.5 mm intervals proximally. The tubercles themselves are small (0.5 mm across the base, on average) and their spatial arrangement does not appear to reflect growth lines distally, although there is some concentric arrangement proximally (Pl. 1, Fig. 1b). Certain tubercles along the anterolateral border of the spine are slightly enlarged

and may be upturned. This is not a constant feature. Fin spine histology cannot be observed in the holotype.

Variation

1. A/I 865 (Pl. 1, Fig. 3) is a large fin spine (212 mm long) whose gross morphology closely parallels that of the holotype. It differs from the holotype only in that the posterior wall is strongly convex proximally, due to lateral compression and in the amount of ornament. The tubercles are much more numerous (Pl. 1, Fig. 3a) and closely spaced anteroproximally than in A/I 858. The anteroposterior length of the spine A/I 865 is 19 mm distally, and the transverse breadth 10 mm. When complete, the spine would have been bigger than A/I 858, and presumably came from a larger, possibly older individual. The increased tuberculation is in keeping with this suggestion. By comparison with growth in hybodont dorsal fin spines (MAISEY 1978a, p.664) the spine trunk outer layer (osteodentine, see below) grew by centrifugal dentine apposition. Successive osteodentine layers were laid down from the centre of the spine outwards. Tuberculation is thus a late ontogenetic feature which can be linked to growth of the fin spine.

2. A/I 859 (Fig. 3-5) is a fin spine approximately 125 mm long, which is badly crushed distally, and from which thin sections were made (see section on spine histology below). The gross morphology agrees with that of the holotype. The tuberculation at the base of the ornamented lateral face and anterior margin suggests that the tubercles developed on the longitudinal ridges in rough growth lines, as in the specimens described above. The canal running down the midline of the posterior spine face is well developed. The trunk inner layer (lamellar dentine, see below) can be seen on the internal faces of the spine from the broken base.

3. A/I 860 (Pl. 1, Fig. 2) is a small specimen measuring 22 mm long, 4.5 mm anteroposteriorly and 2.5 mm across the almost straight posterior wall. The base of the posterolateral denticle rows is preserved (up to five denticles on each side). From certain broken denticles it can be seen that they have an open central cavity. The posterior wall of the spine is open for its entire length (Pl. 1, Fig. 2a). There is no sign of the closure of this posterior wall. The internal faces of the spine show longitudinal vascular foramina entering the spine wall (osteodentine) from the spine lumen. There is no sign of an internal trunk lamellar layer. The lateral walls and anterior margin of the spine lack tubercular ornament entirely. The outer walls of the spine are smooth.

This specimen belongs to a juvenile. This is indicated by the lack of tubercular ornament and trunk internal lamellar layer (see discussion of A/I 865 above), the completely open posterior wall, and the open central cavities of the posterolateral tubercles. Closure of the posterior spine wall, development of tuberculation and dentinogenesis of the inner trunk lamellar layer and osteodentine denteons are all later ontogenetic occurrences.

Histology of the fin spines

Specimen A/I 859 was sectioned at two locations (Fig. 3). The spine histology is shown in Figures 4a-b, 5a-c. The spine becomes increasingly laterally compressed,

and the posterior wall becomes progressively thicker distally. The open posterior groove tends to narrow distally.

In general, the fin spine histology follows that described for myriacanthoids by PATTERSON (1965). In the proximal section (A/I 859A, Fig. 4a), the inner lamellar layer is best developed on the internal posterior and lateral walls of the spine, where it forms up to one-seventh of the thickness of the spine wall. The lamellar layer becomes progressively thinner anteriorly until it is only a very thin strip at the inner anterior margin (Fig. 4a). In the distal thin section (A/I 859B, Fig. 4b, 5a–c), the lamellar layer forms almost one-third of the thickness of the posterior wall of the spine (Fig. 5a), and up to half of the total thickness of the lateral wall of the spine. As in the proximal section, the lamellar layer narrows anteriorly such that at the anterior extremity it forms approximately one-tenth of the thickness of the spine wall. The lamellar tissue contains very few vascular canals (Fig. 5c).

Thus, the lamellar dentine layer is thicker toward the spine apex. This is because the apical part of the spine is the oldest. By comparison with growth in hybodont fin spines (MAISEY 1978a) the lamellar layer is centripetally deposited independent of spine growth (MAISEY 1978a, p. 664). This comparison with the hybodont condition is true if the thin sections and juvenile spine (A/I 860) described here are compared with the data of MAISEY (1978a).
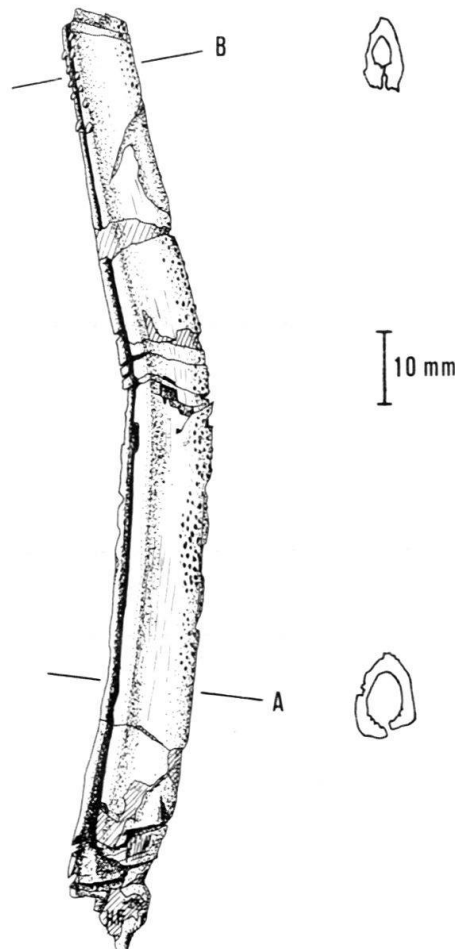

Fig. 3. *Agkistracanthus mitgelensis* n. g., n. sp. Diagram to show the location of thin sections A and B cut from the dorsal fin spine A/I 859.
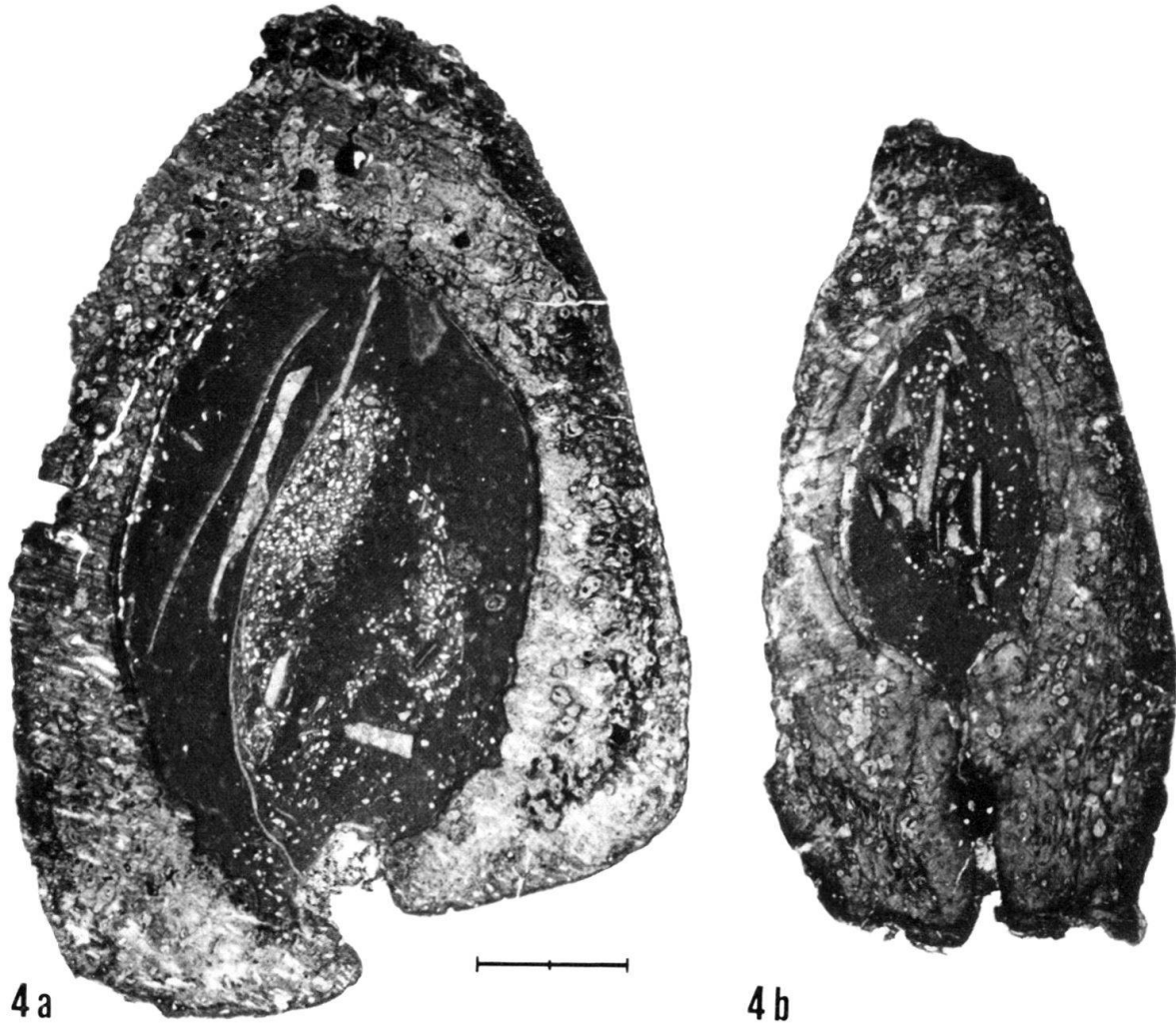
Fig. 4. *Agkistracanthus mitgelensis* n. g., n. sp. Thin sections taken from proximal (4a) and distal regions (4b) of the dorsal fin spine A/I 859; photographed using transmitted light. Bar scale 2 mm. Note the increased narrowing of the open canal on the posterior face, the increased lateral compression and the increasing thickness of the lateral and posterior spine walls distally. The inner layer, comprising lamellar dentine, contains few vascular canals, is centripetally deposited and shows some growth rings. The outer, osteodentine layer is highly vascular, the bulk of the vascular canals being longitudinal. The central cavity of the spine contains coarse-grained bio-oomicrite. Pyrite marginally encrusts the spine and is present in the dentine tubules. Cracks in the specimen are due to tectonic deformation.

The outer trunk layer comprises osteodentine. It is consistently thickest at the anterior margin of the spine, and contains numerous vascular canals. The bulk of these vascular canals is longitudinal, but occasional radial and irregularly branched transverse canals are present. The lumina of the vascular canals are surrounded by varying thicknesses of concentrically arranged dentine lamellae (Fig. 5b). These are denteons (ØRVIG 1976) ("dentinal osteons" of PATTERSON 1965, and earlier papers by ØRVIG). The interstices between the denteons are filled with interosteonal tissue.

The tubercles which ornament the external lateral and anterior faces of the spine contain bunches of dentine tubules arising from basal vascular canals fed by radial canals within the osteodentine. No surface enameloid was noticed by light microscopy in any of the thin sections.
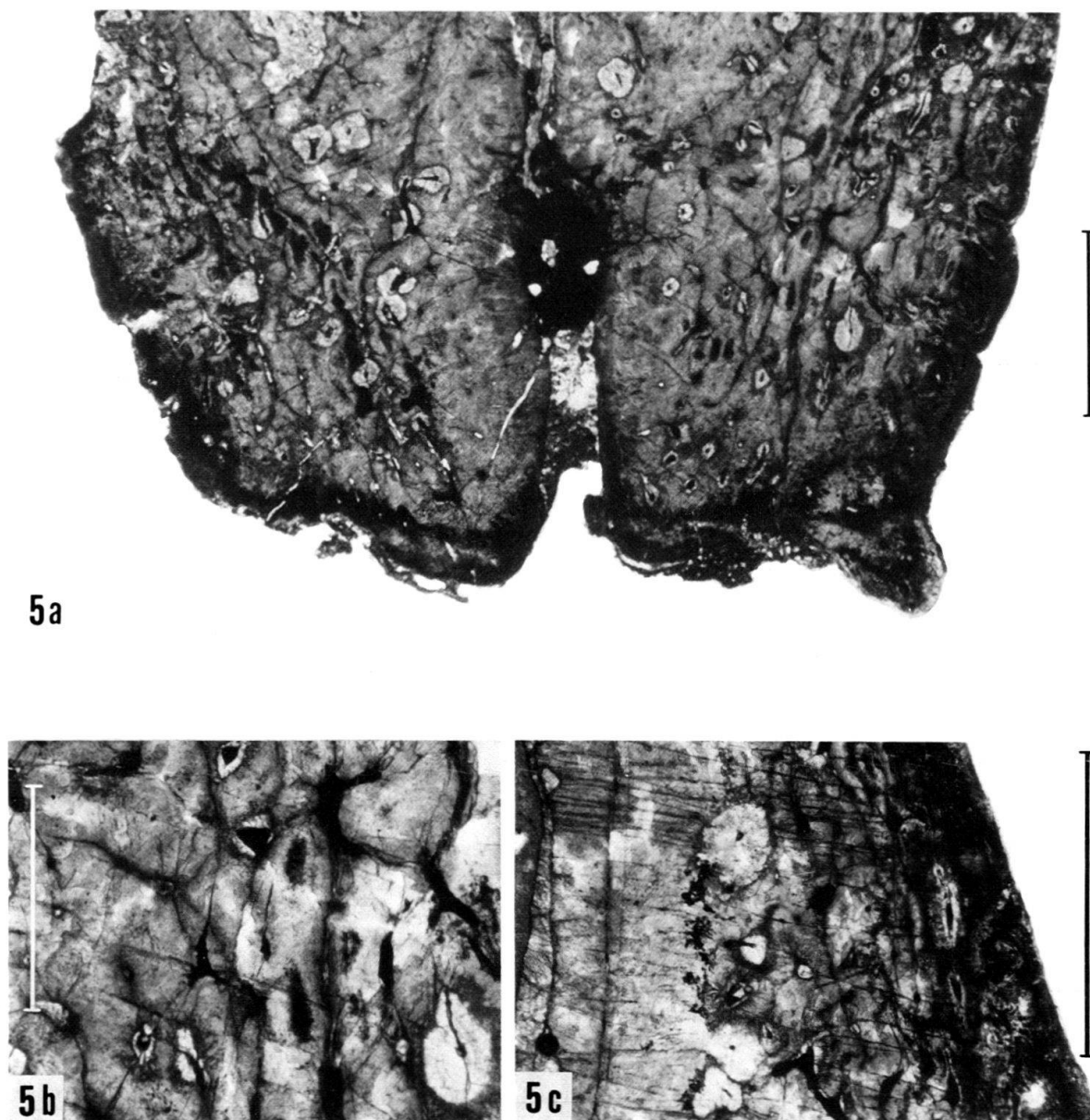
Fig. 5. *Agkistracanthus mitgelensis* n.g., n.sp. The distal part of fin spine A/I 859 in thin section B, photographed using transmitted light.

5a = Posterior spine wall showing the open posterior groove with growth of diagenetic pyrite. Note the denticle in the right posterolateral position and the thick osteodentine layer. Bar scale 1 mm. 5b = Detail of osteodentine. Note the denteon development with interosteonal tissue, and pyrite-filled dentine tubules. Bar scale 0.5 mm. 5c = Detail of the lateral wall showing the poorly vascularized inner lamellar dentine and relatively thin osteodentine with longitudinal and oblique vascular canals. Bar scale 0.5 mm.

In both thin sections there is a prominent anterior longitudinal vascular canal (more prominent in A/I 859A, proximal region) flanked by up to two large longitudinal subsidiary vascular canals (Fig. 4a–b). This is similar to the arrangement in hybodont fin spines (MAISEY 1978a, p. 644, Pl. 2, Fig. 7), although in the hybodonts, the lateral canals are not so distinct. The osteodentine in *Agkistracanthus* is also similar to that of hybodonts in that there may be several distinct osteodentine layers present (compare Fig. 4, 5a with MAISEY 1978a, Pl. 7, Fig. 8, and cf. p. 664).

Description of the tooth plates

The tooth plate fragments described here are assigned to *Agkistracanthus mitgelensis* on the basis of their association with the fin spines of the genus in rocks of similar age at identical and other localities (see horizons and localities above). No articulated material is known.

The tooth plates are mostly small fragments. Several tooth plate morphotypes can be discerned in the better preserved material. Each tooth morphotype will be described from the best specimen and referred material listed at the end of each descriptive section. This is followed by discussion on the relative positions of the tooth plate morphotypes in the dentition.

Right lower tooth plate (A/I 862) (Pl. 2, Fig. 1)

The tooth plate is trapezoid in occlusal view (Pl. 2, Fig. 1a). The longest edge of the specimen (labial) is 57 mm long. The lingual margin is shorter and measures 33 mm. The anterior and posterior margins are 29 mm and 27 mm respectively. The ventral surface of the plate is smooth and labiolingually concave (Pl. 2, Fig. 1b). The ventral anterolabial, posterior and lingual margins are marked by strong downwardly projecting root walls providing marginal anchorage on the lower jaw (Meckels cartilage). The labial margin of the tooth plate is the best preserved (Pl. 2, Fig. 1c). In lateral view it is deep (12 mm at the deepest point) and concave. The longitudinal groove running its length is deeper anteriorly.

Most of the occlusal surface is intact in this specimen. Only the anterolabial corner is missing. No tritoral areas are developed. The margins of the occlusal surface are all curved in occlusal view (Pl. 2, Fig. 1a). A convex ridge crosses the occlusal surface diagonally from the posterolingual corner to a point just behind the anterolabial corner (Pl. 2, Fig. 1a). The ridge divides the occlusal surface of the tooth into mildly concave elongate rectangular anterior, and larger triangular posterior portions. The occlusal surface comprises a thin (up to 2 mm thick) layer of pleromic hard tissue ("tubular dentine"); individual dentine columns are visible. The base of the tooth plate comprises up to 3 mm of lamellar tissue. The posterior wall of the tooth plate base is inclined posteriorly from the occlusal surface (Pl. 2, Fig. 1c, d). Individual vascular formina are visible on the ventral surface. Their shape and orientation indicate that blood vessels entered the tooth plate base from the posterior margin.

Referred material: The bulk of the material listed here may be only tentatively assigned to lower tooth plates. They might equally well belong to upper posterior tooth plates, but because of the lack of well preserved comparative material, are placed here for convenience: A/I 862 (right), A/I 882 (left), A/I 855, A/I 883, A/I 867, A/I 885, A/I 864, A/I 869.

Anterior upper tooth plate (A/I 861) (Pl. 2, Fig. 2)

The tooth plate comes from the left jaw and is of elongate oval shape in occlusal view (Pl. 2, Fig. 2b). At its longest point it measures 45 mm, at its widest (labiolingually) 13 mm.

The ventral surface is very strongly concave labiolingually, especially toward the labial margin. The labial margin comprises a strong, 3 mm thick root wall which is deep and strongly curved under anteriorly. The external face of the labial root wall is concave as in A/I 862, but this is only visible for the posterior part of its length since a thin (less than 1 mm thick) upcurl from the anterolabial margin obscures it anteriorly (Pl. 2, Fig. 2a). The lingual root wall is thin (1.5 mm thick), composed of lamellar tissue, and projects lingually.

The preserved occlusal surface is roughly rhomboidal (Pl. 2, Fig. 2b). It is strongly convex labiolingually and possesses curved anterior and posterior, and straight labial and lingual margins. The occlusal surface comprises a 1 mm thick layer of pleromic hard tissue surmounting a 1.5 mm thick lamellar base. A strongly developed deep, longitudinally concave, oval wear facet is developed on the occlusal surface anteriorly (Pl. 2, Fig. 2a, b, d). At the anterior extremity of the tooth plate there is a flat end wall with spiral development of the labial root wall (Pl. 2, Fig. 2c). The anterior labial root wall (symphyseal) is anchored to the lamellar base of the lingual root wall by growth of an interconnecting trabecular tissue.

Referred material: A/I 884 (left).

Posterior upper tooth plate

A/I 856 may represent a fragment of a right posterior upper tooth plate. The occlusal surface is not so labiolingually convex as in A/I 861 and far less massive than A/I 862 from the lower jaw.

Tooth histology

A thin section was made of A/I 881. The base of the tooth plate comprises lamellar tissue. In the thinner part of the section (i.e. the lingual side, Fig. 6a, c), the lamellar dentine is largely devoid of vascular canals. Vascular canals become progressively more common labially (Fig. 6b). The canals feed the pleromic hard tissue forming the occlusal surface of the tooth plate diagonally from a ventroligual direction (Fig. 6a, b). This feature is reflected in the appearance and attitude of the entrant vascular foramina on the ventral face of all of the tooth plates studied (Pl. 2, Fig. 1b, 2c, 3b, 4b). A thin, nonvascular zone marks the top of the lamellar dentine layer, forming one-fifth to nine-tenths of the total thickness of the lamellar layer. The lamellar layer is overlain by the pleromic hard tissue. Common vascular canals mark the junction of these two layers (Fig. 6c).

Agkistracanthus sp.

Pl. 2, Fig. 3-4

Certain tooth plates collected from different tectonic units to the material described above, and in some cases from sediments belonging to a different stratigraphic stage, are here referred to as *Agkistracanthus* sp. With the exception of one specimen the material is very fragmentary.

Material. – 10 tooth plate fragments. A/I 870, a complete ?posterior upper tooth plate (Pl. 2, Fig. 3); A/I 874, a fragment of a similar tooth plate; A/I 875, a ?pos-
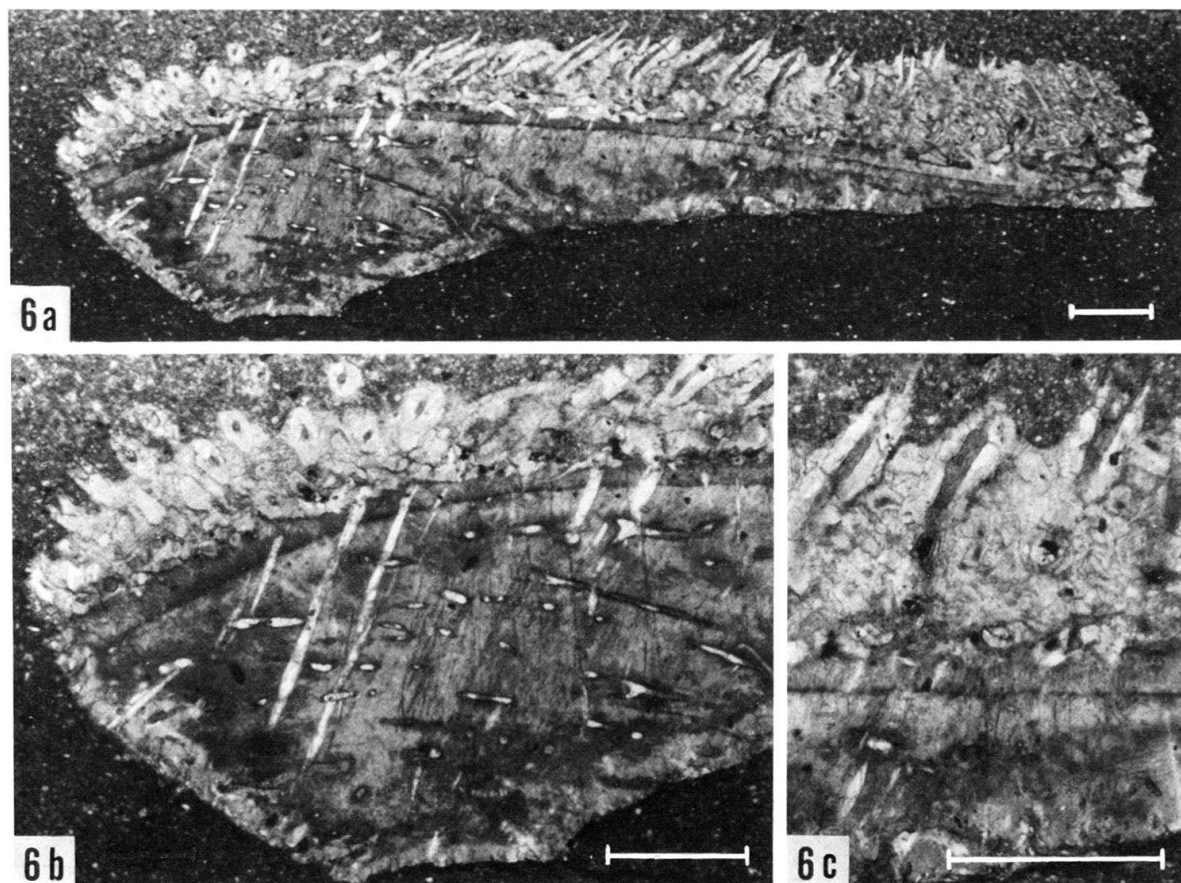
Fig. 6. Thin section of the tooth plate A/I 881, assigned to *Agkistracanthus mitgelensis* n. g., n. sp., photographed using transmitted light.
6a = Whole mount. 6b = Labial part. Note the oblique vascular canals in the basal lamellar layer.
6c = Central part, showing the junction of the lamellar and occlusal pleromic hard tissue layers with dentinal pillars. Bar scale 1 mm in all photographs.

terior upper tooth plate fragment (Pl. 2, Fig. 4); A/I 876, A/I 877, two fragments of ?lower tooth plates; A/I 869, A/I 871, A/I 872, A/I 873, A/I 878, indeterminate tooth plate fragments.

Horizons and localities. – A/I 869: Kössen Beds, Rhaetian (Upper Triassic), Central Austroalpine Arosa Dolomites; 0.75 km southeast of Erzhorn, Kanton Graubünden, Switzerland.

A/I 870: Kössen Beds, Rhaetian (Upper Triassic), Central Austroalpine Silvretta nappe; 0.3 km southeast of Alplihorn, Kanton Graubünden, Switzerland.

A/I 871, A/I 872, A/I 873: Kössen Beds, Rhaetian (Upper Triassic), Terza unit of the Central Austroalpine Engadine Dolomites; 0.6 km (A/I 871) and 1.3 km (A/I 872, A/I 873) NNW of Piz Murter, Swiss National Park, Kanton Graubünden, Switzerland.

A/I 874: Kössen Beds, Rhaetian (Upper Triassic), Northern Calcareous Alps; 0.9 km northeast of Schesaplana, Vorarlberg, Austria.

A/I 875, A/I 876: Adnet Limestone (basal hardground), Hettangian (Lower Jurassic), Northern Calcareous Alps; Schafköpfe, 1.7 km WNW of Schesaplana, Vorarlberg, Austria.

A/I 877: Allgäu Beds (basal), ?Hettangian (Lower Jurassic), Northern Cal-
careous Alps; Kleiner Zirmenkopf, 1.0 km northeast of Schesaplana, Vorarlberg,
Austria.

A/I 878: Allgäu Beds (resedimented block in a basal breccia), ?Hettangian
(Lower Jurassic), Ortler unit of the Central Austroalpine Engadine Dolomites;
2.8 km northwest of Piz Chaschauna, Swiss National Park, Kanton Graubünden,
Switzerland.

Description of A/I 870 (Pl. 2, Fig. 3)

This tooth plate is most closely similar to A/I 861. The length of A/I 870 is
61 mm, and its width (labiolingually) is 19 mm at the widest point. The specimen
has a tear-drop shape in occlusal view (Pl. 2, Fig. 3 a). The posterior part of the root
wall is broken (Pl. 2, Fig. 3 b), but would have been 3 mm thick. Anteriorly, the
downcurled portion of the labial root wall is preserved (4 mm deep), but is not so
strongly developed as in A/I 861. The anterior part of the labial root wall is an-
chored to the central surface of the tooth plate by a growth of interconnecting
trabecular tissue. The occlusal surface is pear-shaped with curved margins, and is
mildly convex labiolingually. It comprises a thin layer of pleromic hard tissue. An
elongate oval wear facet is developed on the labial side of the occlusal face anterior-
ly (Pl. 2, Fig. 3 a, c). Random scratch marks due to the functional wear of food on the
tooth plate are present over the wear facet.

There is a fairly long ?symphyseal extension to the tooth plate base. The
lingually projecting root wall is 1.5 mm thick. The ventral surface of the plate is
moderately concave labiolingually.

Referred material: A/I 874.

A/I 861 has a much more slender outline than A/I 862. The robust labial
downcurl of the labial root wall, and overall slender shape of A/I 862 suggests a
tooth plate from the upper jaw. The presence of the trabecular tissue at the antero-
ventral extremity of the tooth plate suggests that it is the most anterior tooth plate
on the jaw. It is likely that the palatine terminated at this trabecular bridge. The
shape of the deep wear facet anteriorly reflects occlusion against an anterior tooth
plate in the lower jaw. The wear facet could well have been produced by occlusion
against a diagonal ridge such as is present on the occlusal surface of A/I 862.

The diagonal ridge on A/I 862 diverges from the anterior margin of the tooth
plate posteriorly. This is reasonable since the anterior part of the tooth plate is the
oldest, and the tooth plate grew in a posterolingual direction.

A/I 870 has a more slender shape than A/I 862, and differs from A/I 861 in the
shape of the occlusal surface (compare Pl. 2, Fig. 2 b, with Pl. 2, Fig. 3 a), the anterior
prolongation of the convex lingual root border, and the presence of a longer anterior
wear facet. The overall shape of the tooth plate suggests that it belongs to the upper
jaw. The presence of trabecular bridge tissue anteroventrally suggests an extreme
anterior location, but the overall shape of the plate suggests that it is not from the
same position as A/I 861. Because of the difficulty in placing this tooth plate in the
dentition of *Agkistracanthus mitgelensis*, it is assigned to *Agkistracanthus* sp.
together with other tooth plates which derive from different tectonic units and

stratigraphic levels to the type material. It may be that A/I 870 belongs to a different species of myriacanthid to A/I 861, although further material is necessary before this can be discussed further.

Discussion of the dentition of *Agkistracanthus*

Articulated dentitions of fossil holocephalans are rare in the geological record. Of those known in museum collections, few are completely prepared or exposed in useful views. In spite of this, complete dentitions of certain bradyodonts (PATTERSON 1968), myriacanthoids (DEAN 1906, PATTERSON 1965) and chimaeroids (WARD & McNAMARA 1977) are available for comparison. Several well preserved specimens amongst the Swiss material can be assigned to definite locations in the mouth as a result of these comparisons.

The labial margin of myriacanthid teeth is indicated by the presence of a downcurled root wall (Pl.2, Fig.1d, 2a). This is the oldest part of the tooth and deepest anteriorly. The presence of this structure closely resembles the condition in bradyodont tooth plates from the Palaeozoic (cf. *Cochliodus contortus* AGASSIZ, BMNH P.2424, PATTERSON 1968, p.195, Fig.12D; compare with *Myriacanthus paradoxus* AGASSIZ, BMNH P.4464, restored in PATTERSON 1965, Fig.13). The lingual margin of myriacanthid tooth plates comprises a thinner, lingually-projecting root wall.

A/I 862 is assigned to the right lower jaw on the basis of comparison with *Myriacanthus paradoxus* (P.151, BMNH, cf. WOODWARD 1891, p.48, Pl.2, Fig.2). In the English material and A/I 862 the tooth plate is robust and trapezoid in occlusal view. A/I 862 has a straight anterior margin which would abut against a similar edge on the corresponding tooth plate on the left lower jaw.

Discussion of affinities

Myriacanthoid and chimaeroid holocephalans differ in a number of anatomical features (PATTERSON 1965, LUND 1977). Myriacanthoids possess dorsal fin spines in which the outer osteodentine trunk layer is thick, and the lateral spine walls are tuberculated; the fin spines of chimaeroids are smooth, with a narrow layer of osteodentine forming the trunk outer layer. The fin spines of *Agkistracanthus mitgelensis* show the myriacanthoid condition. The tooth plates assigned here to *Agkistracanthus* lack tritors on the occlusal surface. This is a myriacanthoid feature; chimaeroid tooth plates possess distinct tritoral areas.

In addition to *Agkistracanthus*, five genera of myriacanthoid are known at the present time: *Myriacanthus* AGASSIZ (1837) (two species, *M. paradoxus* from the Lower Lias [Lower Jurassic] of Lyme Regis, Dorset, England, and the Hettangian of Lorraine, France [PATTERSON 1965, p.128]; *M. bollensis* FRAAS from the Toarcian of Holzmaden, southern Germany); *Metopacanthus* ZITTEL (1887), based on *M. granulatus* (AGASSIZ) from the Lower Lias of Lyme Regis, England; *Recurvacanthus* DUFFIN (in press), known from a single specimen of *R. uniserialis* DUFFIN from the Lower Lias of Lyme Regis; *Acanthorhina jaekeli* FRAAS (1910) comes from the Toarcian of Holzmaden; *Chimaeropsis* ZITTEL (1887) is represented by three species

- *C.paradoxa* ZITTEL from the Kimmeridgian of southern Germany, *C.foussi* CASIER from the Lower Lias of Ethe, Belgium (CASIER 1959), and *C.franconicus* (MÜNSTER) from the Upper Jurassic of Bavaria. PATTERSON (1965) discusses the affinities and interrelations of these genera in detail.

The fin spines of *Agkistracanthus* differ from those of the other myriacanthoids listed on several counts. As in all myriacanthoids except *Recurvacanthus, Agkistracanthus* possesses a row of small, hook-like, downturned denticles along each posterolateral margin of the spine. In *Agkistracanthus* this double denticle row is restricted to the distal third of the spine; in *Metopacanthus* the denticle rows are present for the distal half of the spine (PATTERSON 1965. Fig.20); in *Myriacanthus* almost the entire length of the posterior margins of the spine is denticulate, and an impersistent denticle row may be developed in the midline of the posterior face (PATTERSON 1965, p.141); *Chimaeropsis* appears to possess denticulate posterolateral margins for the greater part of the length of the posterior spine face (MÜNSTER 1840, Pl.3, Fig.8). According to FRAAS (1910, p.58) the fin spine of *Acanthorhina* is denticulate for the distal fifth of its length.

As in *Metopacanthus* (PATTERSON 1965, Fig.20) and *Recurvacanthus* (DUFFIN, in press, Pl.1), the lateral walls of the fin spine of *Agkistracanthus* are tuberculate for the proximal part only. In *Agkistracanthus* the lateral tubercules tend to be restricted to the anterolateral and posterolateral margins, and the midline of the lateral face, unlike all other myriacanthoids, in which the tuberculation is indiscriminate across the lateral walls. Fin spines of *Myriacanthus* (PATTERSON 1965, Fig.14) and *Chimaeropsis* (MÜNSTER 1840, Pl.3, Fig.8) are tuberculate for the entire length of the lateral walls. FRAAS (1910) states that the lateral walls of the fin spines of *Acanthorhina* are smooth.

Certain denticles along the proximal anterior margin of the fin spine become enlarged and form upturned denticles in *Metopacanthus, Myriacanthus* and *Chimaeropsis.* This is a poorly developed and impersistent feature in *Agkistracanthus* and *Recurvacanthus.*

The fin spines of *Myriacanthus* and *Chimaeropsis* are straight, while those of *Metopacanthus* are slightly recurved. The fin spines of *Recurvacanthus, Agkistracanthus* and *Acanthorhina* are moderately recurved distally.

The dentition is known in *Myriacanthus, Metopacanthus, Chimaeropsis* and *Acanthorhina.* Myriacanthoid dentitions typically comprise a robust, arcuate symphyseal tooth plate in the lower jaw, flanked by one large tooth plate on each side. The lower posterior tooth plate possesses two ridges in *Myriacanthus* (DEAN 1906, PATTERSON 1965, Fig.16) and *Acanthorhina* (FRAAS 1910, Pl.3, Fig.4). The only genus to possess tritoral areas on the lower tooth plates is *Metopacanthus.* Tooth plates from assumed lower and posterior positions in *Agkistracanthus* are unique in possessing only one diagonal ridge on the occlusal surface. Like most other myriacanthoid genera, however, the pleromic hard tissue is not organized into tritors in the lower dentition.

The upper dentition of myriacanthid holocephalans may comprise two tooth plate pairs of which the anterior is the larger (*Chimaeropsis* and possibly *Acanthorhina,* see PATTERSON 1965, p.148), or three pairs of tooth plates, in which the anteriors are considerably reduced and the posterior plates are by far the largest *(Myriacan-*

thus, Metopacanthus). Tritoral areas may be found on just the first anterior tooth plate pair *(Chimaeropsis),* both anterior tooth plate pairs *(Myriacanthus),* or even all three upper tooth plate pairs *(Metopacanthus)* (the dentition of *Acanthorhina* should be reexamined).

Conclusions

The dorsal fin spines of *Agkistracanthus mitgelensis* from the Kössen Beds of the Upper Austroalpine nappes of eastern Switzerland should be classified with the myriacanthid holocephalans. This is demonstrated by the presence of a thick outer osteodentine trunk layer and narrow inner layer of lamellar dentine in the fin spine histology, together with a shallow insertion and tuberculate lateral walls. Features unique to the fin spines of *Agkistracanthus,* distinguishing it from other genera, are the presence of denticle rows along the distal third of the posterolateral margins of the spine, a tendency for restricted tuberculation on the lateral faces of the spine, and the presence of an open groove in the posterior wall of the spine.

Isolated tooth plates from the Kössen Beds are assigned to *Agkistracanthus mitgelensis* on the basis of a similar stratigraphic distribution. The tooth plates are myriacanthid, since they lack distinct tritoral areas. Instead, the occlusal surface comprises pleromic hard tissue throughout, broken only by the presence of occasional wear facets (located anteriorly). The anterior upper tooth plate pair has an elongate rhomboidal occlusal surface. Alone amongst the myriacanthids, the single pair of lower tooth plates is trapezoid in occlusal view, possessing a single diagonal ridge. Complete tooth plates are unfortunately rare, and it has not been possible to reconstruct the complete dentition.

The histology of the fin spines and the tooth plates is examined. It seems that myriacanthid fin spines grow in a similar fashion to those of the hybodont sharks. The distal tip of the spine is the oldest part. The inner lamellar layer is thicker toward the spine apex and is centripetally deposited, with preference given to the posterior wall. The outer osteodentine layer is thicker anteriorly and highly vascular. The open groove in the posterior wall of the fin spine persists in a partially closed condition in mature specimens.

In the tooth plates, the pleromic hard tissue of the occlusal surface is fed by vascular canals arising from the underlying lamellar dentine. Vascularization is limited to a few canals only in the lamellar dentine, several of which trend lingually. The tooth plates grow in a lingual direction by addition from the downcurled labial root wall, as in the tooth plates of bradyodonts from the Paleozoic.

Further tooth plates from Hettangian hardground deposits (Lower Jurassic) are assigned to *Agkistracanthus* sp., together with other tooth plates found in the Kössen Beds of tectonic units different to those yielding confidently determined *A. mitgelensis* remains.

The myriacanthid remains from the Swiss Rhaetian and Hettangian were subject to post-mortem disarticulation, before being incorporated into calcareous sediments. The enclosing sediments mostly belong to the "Carpathian facies" of the Kössen Beds, and yield a further rich fauna of brachiopods, corals, echinoids and bivalves. Whilst recent holocephalans are normally deep water fish, it may be that *Agkistra-*

canthus inhabited the straits between coral banks, oolitic barriers and carbonate mudbanks, feeding on the rich benthos.

A comparison of the fin spines and tooth plates of *Agkistracanthus* with those of other myriacanthids, shows that the Swiss material resembles *Acanthorhina* from the Toarcian of Holzmaden most closely.

Acknowledgments

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Plate 1

Dorsal fin spine of *Agkistracanthus mitgelensis* n.g., n.sp., a myriacanthoid holocephalan from the Kössen Beds (Rhaetian) of the Central Austroalpine Ela nappe of Kanton Graubünden (Switzerland).

Fig. 1.   A/I 858, the holotype. Kössen Beds at Piz Son Mitgel.

1a = Right lateral view. Note the crushing due to tectonic deformation, moderate distal spine recurvature, the proximal distribution of tubercles on the lateral wall and the row of downturned denticles on the distal part of the posterolateral margin. Bar scale 100 mm.

1b = Detail of the proximal part of the right lateral face. Note the shallow insertion, unroofed mantle canals and intervening lateral tubercles arranged into very rough growth lines. Bar scale 10 mm. See p. 812.

Fig. 2   A/I 860, distal part of the dorsal fin spine of a juvenile. Kössen Beds at Piz Son Mitgel.

2a = Posterior view. Note the double row of distally situated, downturned posterolateral denticles and the open posterior wall.

2b = Right lateral view. Note the more subdued posterior curvature and lack of tubercular ornament on the lateral face. Bar scale 10 mm. See p. 813.

Fig. 3   A/I 865, dorsal fin spine from a mature individual. Kössen Beds at Corn da Tinizong.

3a = Right lateral view.

3b = Posterior view. Note the incomplete closure of the posterior wall. Bar scale 100 mm. See p. 813.

All material in the Paläontologisches Institut und Museum der Universität Zürich, Switzerland.
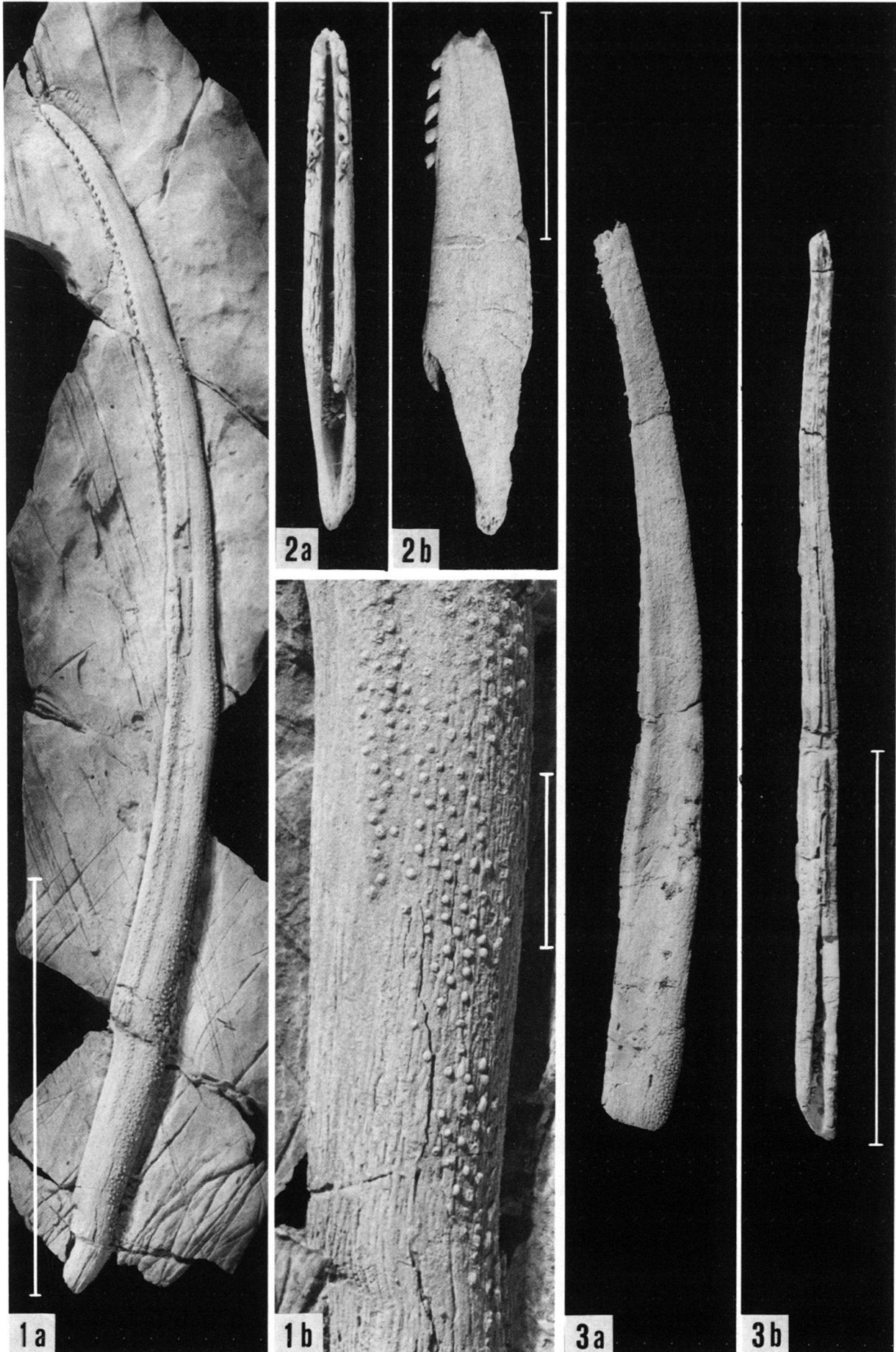
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Plate 1

Plate 2

Tooth plates assigned to *Agkistracanthus mitgelensis* n.g., n.sp., and *Agkistracanthus* sp.

Fig. 1   *Agkistracanthus mitgelensis* n.g., n.sp., A/I 862, a right lower tooth plate from the Kössen Beds (Rhaetian), Central Austroalpine Ela nappe at Piz Son Mitgel, Kanton Graubünden, Switzerland.
1a = Occlusal view. 1b = Ventral view. 1c = Labial view. 1d = Lingual view. Note the diagonal ridge on the trapezoid occlusal surface and the downcurled labial root wall. Bar scale 10 mm. See p. 817.

Fig. 2.   *Agkistracanthus mitgelensis* n.g., n.sp. A/I 861, an anterior upper tooth plate from the Kössen Beds (Rhaetian), Central Austroalpine Ela nappe at Piz Son Mitgel, Kanton Graubünden, Switzerland.
2a = Labial view. 2b = Occlusal view. 2c = Ventral view. 2d = Lingual view. Note the roughly rhomboidal occlusal surface with a deep anterior wear facet and the strongly downcurled root wall. Bar scale 10 mm. See p. 817.

Fig. 3.   *Agkistracanthus* sp. A/I 870, a left ?posterior upper tooth plate from the Kössen Beds (Rhaetian), Central Austroalpine Sivretta nappe at Alplihorn, Kanton Graubünden, Switzerland.
3a = Occlusal view. 3b = Ventral view. 3c = Labial view. Note the tear-drop shape of the occlusal surface, elongate oval anterior wear facet and shallow profile. Bar scale 10 mm. See p. 820.

Fig. 4   *Agkistracanthus* sp. A/I 875, a specimen of uncertain location from the Adnet Limestone (Hettangian), Northern Calcareous Alps at Schesaplana, Vorarlberg, Austria. Note dislocation due to tectonic deformation. Bar scale 10 mm. See p. 819.

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