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A new coelacanth from the Middle Triassic of Monte San Giorgio, Switzerland

By OLIVIER RIEPPEL[1])

ABSTRACT

A new coelacanth, *Ticinepomis peyeri* n. gen. n. sp., is described from the Grenzbitumen horizon of Monte San Giorgio. The new genus is characterized by peculiarities in the structure of the skull, of the pectoral girdle and of the dorsal fins. It can be interpreted as being structurally very close to *Undina picenus* as described by BASSANI (1896). The new form also shares some similarities with the genus *Coelacanthus*. If *Ticinepomis* is endemic in the Grenzbitumen horizon, it must be interpreted as a pelagic animal living in a shallow near-shore area.

ZUSAMMENFASSUNG

Ein neuer Coelacanthide, *Ticinepomis peyeri* n. gen. n. sp., aus der Grenzbitumenzone des Monte San Giorgio wird beschrieben. Die neue Gattung ist gekennzeichnet durch Merkmale des Schädels, des Schultergürtels und der Dorsalflossen. Die Form scheint strukturell der von BASSANI (1896) beschriebenen *Undina picenus* nahezustehen. Ähnlichkeiten bestehen auch zur Gattung *Coelacanthus*. Falls *Ticinepomis* in der Grenzbitumenzone endemisch auftritt, so ist er als pelagischer Fisch der Küstenzone zu interpretieren.

Introduction

The Actinistia are a group of fishes known from many fossil genera ranging from late Middle Devonian to Upper Cretaceous. The relationships of the Actinistia are still controversial (cf. ANDREWS 1973; BJERRING 1973). They have conventionally been included within the Crossopterygii and may be regarded as the sister group of the Rhipidistia. In a cladistic sense the Actinistia can be defined as osteichthyans possessing a rostral organ, a ventrally positioned kidney, no maxilla or branchiostegal rays, a double jaw joint in which the two points of articulation lie in tandem and a shoulder girdle which primitively has an extracleithrum (Forey, pers. comm.).

According to SCHAEFFER (1948), the Triassic may represent the peak of actinistian evolution. The presence of Actinistia in the Alpine Triassic of central and southern Europe has long been known, following the descriptions of the genera *Heptanema* (BELLOTTI 1857; cf. also ALESSANDRI 1910) and *Graphiurus* (KNER 1866), which is now known as *Graphiurichthys* (WHITE & MOY-THOMAS 1937). From the Upper Triassic of Lunz a large actinistian has been mentioned by TELLER (1891). This specimen is tentatively reffered to the genus *Coelacanthus* by REIS (1900).

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From the Triassic of Italy an actinistian specimen became known as early as 1862 through its description by COSTA. COSTA (1862) primarily used the name *Urocomus picenus* in reference to a fragment of fin rays of a caudal fin which was synonymized with *Colobodus ornatus* by WOODWARD (1895) but tentatively included within the Perleididae by ROMER (1966). The actinistian fish was referred with reservation to *Urocomus picenus* by COSTA. BASSANI (1896) transferred it to the genus *Undina* MÜNSTER when dealing with a second specimen. As pointed out by GARDINER (1960), the name *Undina* MÜNSTER is a *nomen nudum* and furthermore preoccupied by the generic name of a bird. Consequently, the name *Undina* MÜNSTER is to be replaced by the name *Holophagus* EGERTON. In 1916, ANDERSSON described some actinistian remains from the Cava Tre Fontane, which he referred to the genus *Holophagus*. Both STENSIÖ (1932) and MOY-THOMAS (1935) question the correct identification of these Alpine Triassic forms as *Holophagus*, the latter being a genus known from the Jurassic of Germany and southern England.

In the collections from Monte San Giorgio at the Paläontologisches Institut und Museum der Universität Zürich, there is a small and completely preserved actinistian of 17.5–18 cm total length. This fish appears to be similar to *Undina picenus* as described by BASSANI (1896). Since the fossil from Monte San Giorgio is more completely preserved than those described by COSTA (1862) and BASSANI (1896), it allows to determine differences from the genus *Holophagus*. The erection of a new genus thus seems to be justified. The probable generic synonymy of *Undina picenus* as described by COSTA (1862) and BASSANI (1896) with the actinistian from Monte San Giorgio might become established upon reexamination of the Italian fossils. The descriptions and figures given by COSTA (1862) and BASSANI (1896) are here considered to be insufficient to allow the formal proposition of such a synonymy.

Systematic Palaeontology

Class ***Osteichthyes***

Subclass ***Sarcopterygii***

Order ***Crossopterygii***

Suborder ***Actinistia***

Family ***Coelacanthidae***

Genus *Ticinepomis* n. gen.

Type species: Ticinepomis peyeri n. sp.

Known distribution. – Middle Triassic of southern Europe.

Diagnosis. – A coelacanth genus of up to 18 cm total length. Skull with large premaxillae, capping the snout, (?)two pairs of elongated frontal bones, parietal and supratemporal fused, postorbital and squamosal forming a narrow postorbital bar, opercular large and ornamented with a shagreen of tubercles, lacrimojugal with a concave lower border, pterygoid with a high anterior shank, dentary consisting of two horns, splenial single, angular large and ornamented externally, pectoral girdle massive, including a large scapulocoracoid and a clavicle with a distinct anterior

horizontal portion, basal plate of first dorsal fin triangular, first lepidotrichium of dorsal fin bearing 4 rows of spines on each side, first dorsal fin incorporating 8 lepidotrichia, vertebral column including approximately 51 neural spines, upper and lower lobe of caudal fin consisting each of 3 unsegmented and 15 distally segmented lepidotrichia, ornamentation of the scales consisting of elongate, blunt or pointed spines disposed in a rostrocaudal direction.

Ticinepomis peyeri n. sp.

Fig. 1-8

Etymology. - *Ticino*, Italian, Kanton Tessin (Switzerland), and *epomis*, Greek, shoulder, alluding to the massive pectoral girdle, *peyeri*, after the Late Prof. B. Peyer, who initiated research on the fossils from Monte San Giorgio.

Holotype. - T3925, a and b, almost complete fish on part and counterpart (Fig. 8).

Horizon and locality. - The specimen described in the present paper comes from point 902, upper part of Grenzbitumen horizon, Lower Ladinian, Triassic, Monte San Giorgio, Kanton Tessin, Switzerland.

Diagnosis. - Same as for genus. Differing from *Undina picenus* (COSTA 1862; BASSANI 1896) in having almost twice as many lepidotrichia in the second dorsal fin, in scale ornamentation and in attaining a smaller size of 18 cm only.

Description

Skull. - During fossilization the skull was strongly compressed laterally and at the same time sheared in an anteroventral direction. Upon recovery of the fossil, the slab was split into part and counterpart and this resulted in the splitting of the skull in a parasagittal plane. Some of the dermal bones covering the left cheek have been split off the skull, adhering to the counterpart. Consequently, the pterygoid is exposed in lateral view on the main slab. The left lower jaw was broken in a transverse plane both anteriorly and posteriorly. The tip of the jaw and its retroarticular process are fixed on the counterpart exposing the mesial surface, while the middle portion of the angular is found on the main slab exposed in lateral view.

The paired premaxillae (Fig. 2) are plate-like, elongated elements which capped the snout anterodorsally. This appears to be the primitive coelacanth condition (SCHAEFFER 1952). The premaxilla may become reduced to a small, marginal element in some Triassic genera (*Diplurus:* SCHAEFFER 1952). In *Latimeria* the premaxilla is composed of several small tooth plates. In *Ticinepomis peyeri*, the premaxilla bears small, conical and pointed teeth.

The rostral complex of *Ticinepomis peyeri* is badly crushed. However, two distinct elements of similar, anteriorly tapering shape are identifiable rostrally (Fig. 1). The lower one of these is considered to be the left one. It is in contact with the left lateral side of the pterygoid and is consequently identified as the left autopalatine. The upper element represents the right autopalatine. The autopalatine is of a triangular shape, tapering anteriorly and bearing a thickened dorsal ridge.

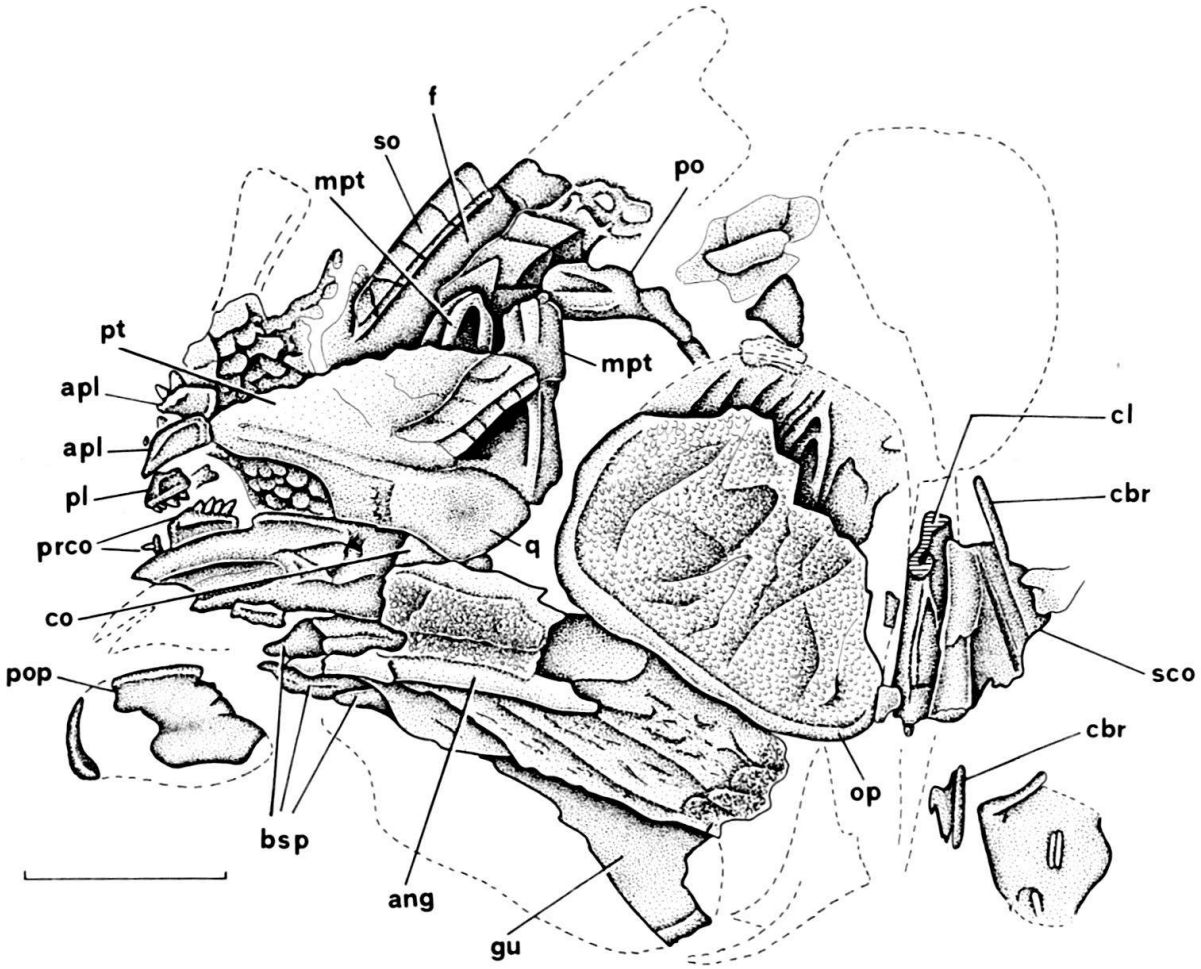

Fig. 1. The skull of *Ticinepomis peyeri* as preserved on the main slab. Scale equals 10 mm.

Abbreviations used in the figures

adf	= anterior dorsal fin	op	= operculum
af	= anterior frontal	p	= parietal
anfn	= anal fin	pdf	= posterior dorsal fin
ang	= angular	pf	= posterior frontal
apl	= autopalatinum	pfn	= pectoral fin
ar	= articular	pl	= palatinum
arbl	= airbladder	pm	= premaxilla
bpad	= basal plate of anterior dorsal fin	po	= postorbital
bppv	= basal plate of pelvic fin	pop	= preopercular
bs	= basisphenoid	pra	= prearticular
bsp	= basibranchial tooth plates	prco	= precoronoid
cbr	= ceratobranchial	ps	= parasphenoid
cl	= cleithrum	pt	= pterygoid
clv	= clavicula	pvfn	= pelvic fin
co	= coronoid	q	= quadrate
d	= dentary	scl	= supracleithrum
exsc	= extrascapular	sco	= scapulocoracoid
f	= frontal	so	= supraorbital
gu	= gular	sp	= splenial
laju	= lacrimojugal	splo	= supplementary lobe of caudal fin
lr	= lateral rostral	sq	= squamosal
mpt	= metapterygoid	st	= supratemporal

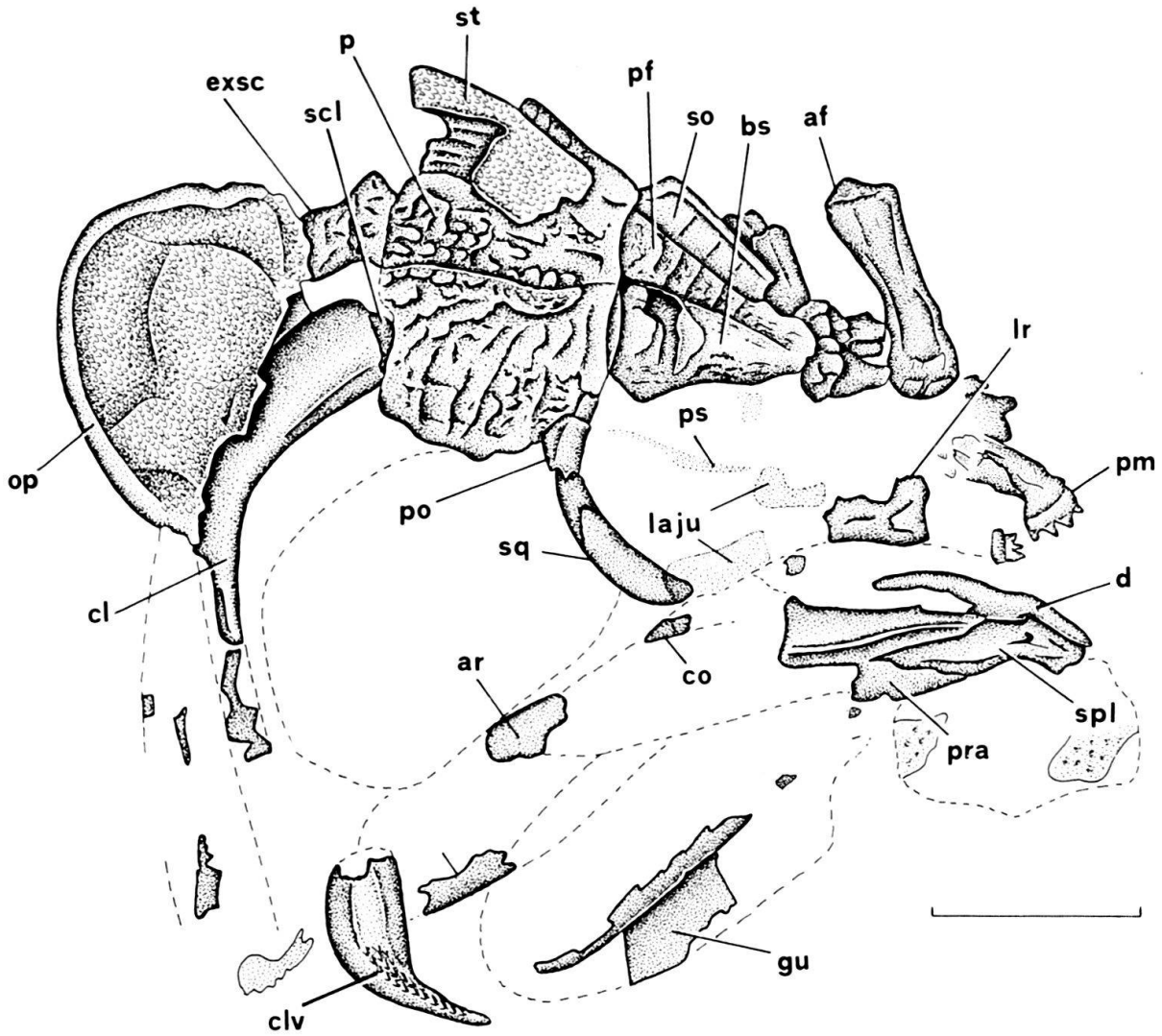

Fig. 2. The skull of *Ticinepomis peyeri* as preserved on the counterpart. Scale equals 10 mm.

Associated with the left autopalatine is the left palatine which bears two small anterior and two large posterior teeth. The right palatine is buried below the right autopalatine: only two large teeth project from below the latter.

Lateral to the autopalatine and behind the premaxilla was situated the lateral rostral. The bone is represented on the counterpart (Fig. 2) exposing its mesial surface. On its lateral surface it would bear a sensory canal. The lateral rostral shows an anteriorly ascending flange.

Caudal to the lateral rostral the elongated lacrimojugal formed the lower border of the orbit. It is preserved as an impression only on the counterpart (Fig. 2). It appears to have had a convex lower border. Again its lateral surface would carry a sensory canal.

The frontal complex is badly crushed. An elongate and narrow bony plate is found, lying alongside a series of supraorbitals on the main slab (Fig. 1). It is interpreted as the right posterior frontal, lying alongside a series of right supraorbitals.

A similar elongated element can be seen lying alongside the left supraorbital series on the counterpart (Fig. 2). It represents the left posterior frontal. The supraorbital series consists of at least 5 rectangular elements, but probably there were 6 or even 7, extending onto the snout region. A more anteriorly positioned elongated bone is interpreted as an anterior frontal. It might, however, as well represent a tectal bone as is observed in *Coelacanthus* (SCHAUMBERG 1978).

The posterior part of the skull roof is formed by the parietal shield. In coelacanths it usually consists of two bones on each side which are usually interpreted as parietals and supratemporals. In *Ticinepomis peyeri* the parietal and supratemporal on either side are fused, buth the presence of posterolaterally projecting lappets indicates the supratemporals (Fig. 2). Fusion of the supratemporal with the parietal may be an age related phenomenon (Forey, pers. comm.), occurring in the fully grown animal. The fusion of these bones thus indicates that *Ticinepomis peyeri* has reached adult size at a length of 17.5–18 cm.

Posterodorsal to the orbit lies a somewhat triangular-shaped postorbital bone (Fig. 2). On the counterpart, a narrow bony bar extends anteroventrally, much as a

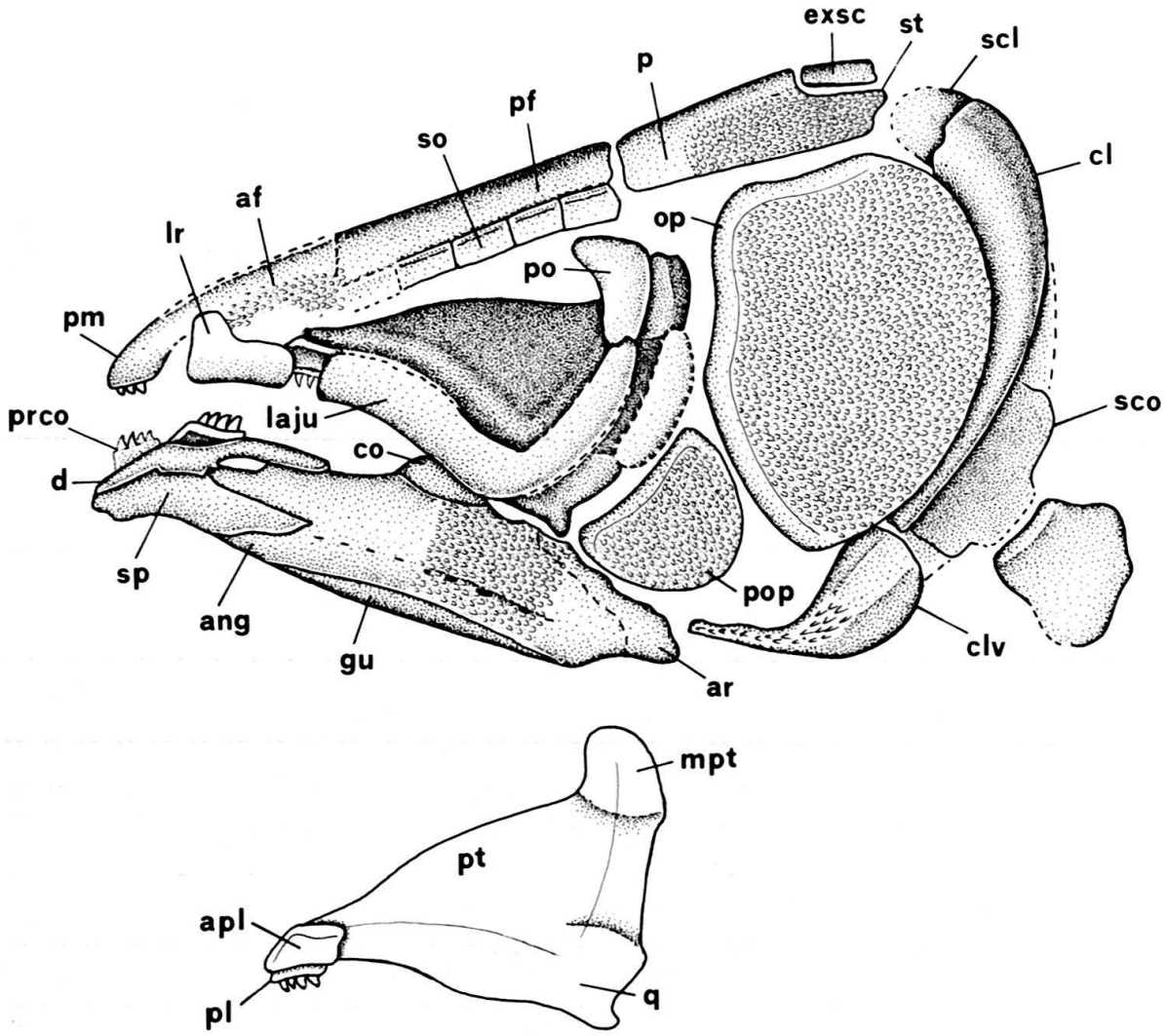

Fig. 3. A tentative reconstruction of the skull of *Ticinepomis peyeri*. Approx. ×2.5.

postorbital bar. Upon closer inspection it is observed, however, that what appears as a postorbital bar consists actually of two bones, superimposed one above the other. The superficial one does not contact the lower margin of the postorbital. Instead, its length and its curvature fit exactly the caudal edge of the pterygoid complex between the dorsal part of the metapterygoid and the quadrate on the main slab (Fig. 1). It is consequently interpreted as a squamosal, lying in front of the operculum, above the preocupercular and behind the postorbital bar. Below the squamosal and in contact with the lower tip of the postorbital lies a bone which is interpreted as dorsal continuation of the lacrimojugal, closing the orbit caudally much as in *Coelacanthus* (SCHAUMBERG 1978).

The operculum is a large bone of rounded contours. Below the squamosal, between the lacrimojugal and the clavicle there was a preopercular which has been detached and displaced so that it now is found lying anteroventral to the anterior tip of the lower jaw (Fig. 1).

The left pterygoid complex is exposed in lateral view (Fig. 1). Due to crushing, however, the exact contours of the quadrate and of the metapterygoid cannot be determined. Nonetheless, the quadrate can be observed forming the articular condyle of the mandibular joint caudoventrally. The metapterygoid forms the processus ascendens which establishes the antotic articulation on the braincase. It can be seen that the quadrate lies roughly below the metapterygoid, which is typical of coelacanths (SCHAEFFER 1952; MILLOT & ANTHONY 1958).

The pterygoid lamella is applied to the mesial edge of the metapterygoid and quadrate in coelacanths, but due to crushing this relation is somewhat obscured in *Ticinepomis*. Laterally, the pterygoid lamella shows a smooth surface. Characteristic of *Ticinepomis* is the high anterior limb of the pterygoid lamella, which shows a weakly convex dorsal border. A high anterior shank of the pterygoid is unusual among fossil coelacanths. Among European Mesozoic genera the condition is somewhat approached by *Macropoma* (WATSON 1921). A high anterior limb with a straight dorsal border is observed in *Holophagus* (REIS 1888), *Mawsonia* (WENZ 1975) and in *Latimeria* (MILLOT & ANTHONY 1958).

Of the parasphenoid, only a weak impression can be observed on the counterpart (Fig. 2), running along the dorsal margin of the pterygoid lamella.

Lower jaw. - The dentary of *Ticinepomis* is of a very peculiar structure. It consists of an elongated anterior horn which is somewhat deflected in an anteroventral direction, and of an equally elongated posterior horn which lies alongside the upper edge of the angular. In other coelacanths, the dentary is an elongated but rather plate-like element, not forming the tapering anterior and posterior horn-like projections. The one genus approaching *Ticinepomis* with respect to this feature is *Diplurus* as described by SCHAEFFER (1952).

Above the impression of the left dentary, a tooth plate can be observed on the main slab (Fig. 1). It bears two small anterior and two larger posterior conical, pointed teeth. The orientation of this tooth plate and the concavity of its lateral surface suggest that it might have fitted on the dorsomesial edge of the left dentary. It is consequently interpreted as a precoronoid. In front of this (posterior) precoronoid and above the impression of the anterior horn of the left dentary there lies a

single tooth with a little bone attached to it. It may indicate that a second precoronoid was situated in front of the first one of the left dentary.

Below the dentary there is a single splenial with a blunt anterior and a tapering posterior end (Fig. 2).

The angular is an elongated element. Anteriorly it embraces the tapering posterior end of the splenial. Caudal to the mandibular joint, the articular forms a retroarticular process.

A coronoid bone is positioned at about the midpoint of the angular.

On the counterpart (Fig. 2), the mesial surface of the anterior part of the left lower jaw is exposed. A strong mesial ridge is observed, running longitudinally on

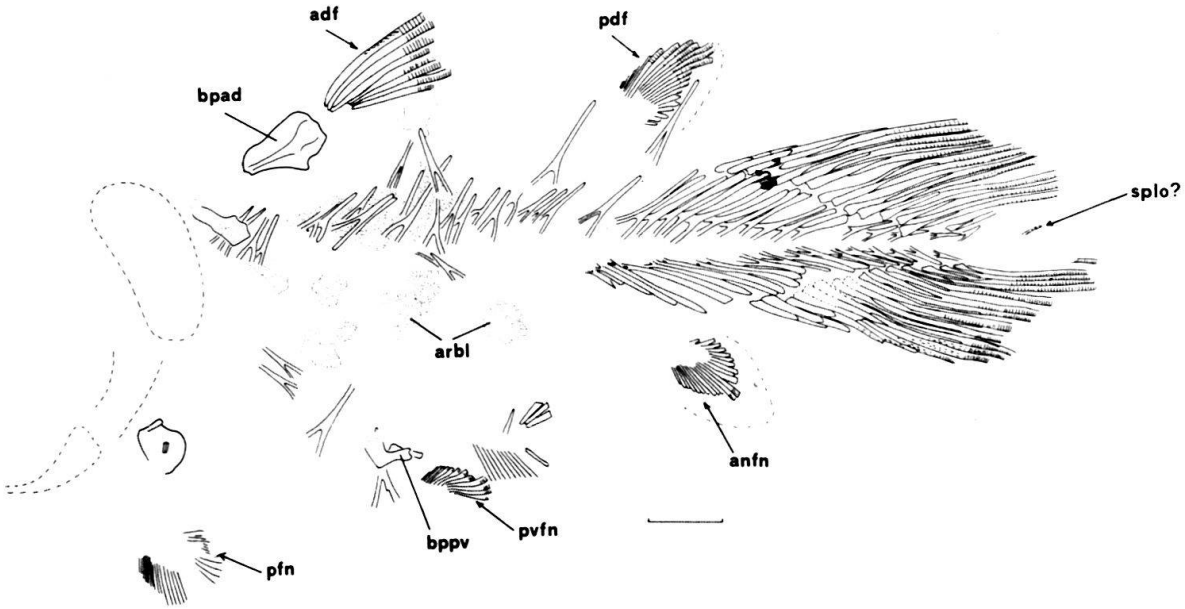

Fig. 4. The postcranial skeleton of *Ticinepomis peyeri* as preserved on part and counterpart (combined). Scale equals 10 mm.

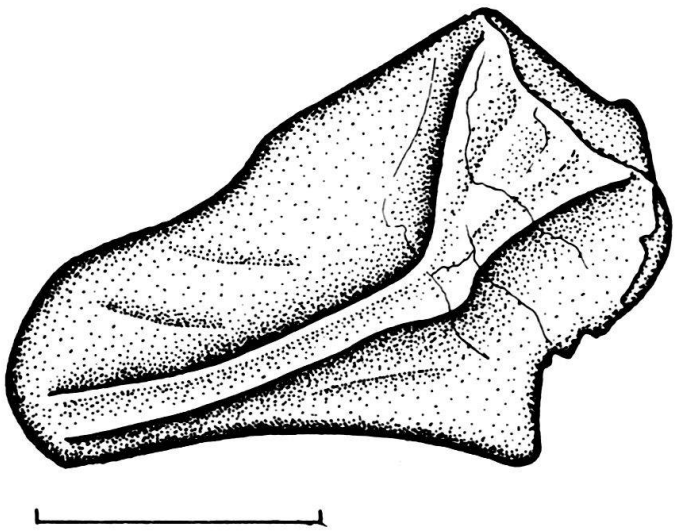

Fig. 5. The basal plate of the first dorsal fin of *Ticinepomis peyeri*. Scale equals 5 mm.

the mesial surface of the lower jaw as it is also observed in *Diplurus* (SCHAEFFER 1952). It indicates the suture between the angular dorsally and the prearticular ventrally, and at the same time it forms the lower margin of the adductor fossa.

Two gular plates covered the throat ventrally between the lower jaw rami. They are elongate, with rounded posterior and tapering anterior ends.

Ornamentation of the dermal skull bones. - It can only be studied on bones with the lateral surface exposed. A shagreen of distinct rounded tubercles is observed on the lateral surface of the operculum and on the impression left by the lateral surface of the preopercular. The lateral surface of the angular bears the same type of ornamentation (Fig. 1). The parietal shield may have been ornamented, but a shagreen of tubercles is preserved on the supratemporal portion of this bone only (Fig. 2). Some splints of bone of the snout region also expose their lateral surface ornamented with rounded tubercles.

Lateral line canals. - Pores of the mandibular canal are observed on the lateral surface of the angular (Fig. 2). The pores of the sensory canals appear to be small and numerous.

Branchial arches. - Only fragments and impressions of two or three ceratobranchials can be observed on the main slab (Fig. 1). Below the left lower jaw but above the underlying gulars the two anterior tips of the paired anterior basibranchial tooth plates can be identified. The anterior tip of the second left basibranchial tooth plate which lies posterolateral to the first one is also exposed.

Caudal to the lower jaw and below the operculum a compacted mass of bone is observed. Due to crushing, no definite interpretation is possible. The bone of this area probably incorporates superimposed parts of the left and right gular plates, but it may also incorporate the urohyal.

Pectoral girdle. - The pectoral girdle consists of a massive cleithrum which is concave anteriorly, convex posteriorly, to fit the rounded posterior edge of the opercular. The cleithrum is broad dorsally but narrows ventrally (Fig. 2). At the top of the cleithrum, a remnant of the supracleithrum is observed.

The ventral part of the pectoral girdle is formed by a massive clavicle. This bone consists of a broad dorsal (vertically oriented) plate and of a tapering ventral (horizontally oriented) process. The latter bears a spiny ornamentation on its lateral surface. The presence of such a distinct horizontal portion of the clavicle can be considered as a primitive feature of *Ticinepomis* (cf. SCHAEFFER 1952).

Projecting posteriorly behind the cleithrum is a broad bony plate the upper and lower limits of which cannot be determined (Fig. 1). This plate most probably represents the scapulocoracoid. An alternative interpretation of this bone would be as an extracleithrum. This latter element is a neomorph, found only in actinistians among vertebrates, and as such it is a derived feature of the group (SCHAEFFER 1952). However, the extracleithrum is a scale-like element, lying smoothly along the lateroventral edge of the cleithrum rather than projecting posteriorly of it.

Posteroventral to the pectoral girdle a bony plate is observed on the main slab (Fig. 1). It is overlain by some fragments of lepidotrichia of the pectoral fin. This plate is interpreted as the first proximal element of the axial support of the pelvic

fin. If the interpretation of the scapulocoracoid is correct, the axial support of the pectoral fin articulated with it as shown in the reconstructions (Fig. 3, 6).

Axial skeleton. - As in all coelacanths, the notochord is persistent in *Ticinepomis.* The neural arches of the trunk region are scattered all over the specimen. It is possible, however, to count at least 33 neural arches which are not incorporated in the caudal fin (Fig. 4). Together with the 18 neural arches of the upper lobe of the caudal fin it results in some 51 neural arch elements incorporated in the vertebral column. The height of the neural arches increases from front to back up to those which support the anterior unsegmented lepidotrichia of the caudal fin (see below). Posteriorly, the height of the neural arches decreases again within the upper lobe of the caudal fin.

Haemal arches could be observed in the lower lobe of the caudal fin and in the region of the anal fin. They are symmetrical to the corresponding neural arches. No ossified ribs are observed.

Paired fins. - Both the pectoral and pelvic fins are poorly preserved in *Ticinepomis peyeri* (Fig. 4). In the area of the pectoral fin there are indications of 17 distally segmented lepidotrichia, the same number as indicated for *Undina picenus* by COSTA (1862) and BASSANI (1896). *Holophagus penicillata* shows 15 lepidotrichia in the pectoral fin (HEIMBERG 1949), *Diplurus* between 15 and 19 (SCHAEFFER 1952), and *Coelacanthus* 16 (MOY-THOMAS & WESTOLL 1935). The pectoral fin of *Ticinepomis* lies in front of the first dorsal.

The pelvic fin is situated between the first and the second dorsal fin. There are indications of 13 distally segmented lepidotrichia. This is almost certainly too low a number. *Holophagus penicillata* shows 27 rays in the pelvic fin (HEIMBERG 1949) and *Diplurus* between 15 and 21 (SCHAEFFER 1952). The basal plate of the pelvic fin is only incompletely preserved in *Ticinepomis peyeri* (Fig. 4). It most closely resembles the figure of the pelvic girdle of *Holophagus gulo* given by WOODWARD (1891), but this figure is said to be an incorrect representation by GARDINER (1960). At any rate, the pelvic girdle of *Ticinepomis* resembles the *Rhabdoderma* type with an anterior division (not preserved), a mesial process (partially preserved) and a posterior process, which corresponds to the primitive coelacanth pattern (SCHAEFFER 1941).

Unpaired fins. - The first dorsal fin is positioned anterior to the center of the body. It consists of eight distally segmented lepidotrichia, decreasing in length from front to back. All the lepidotrichia probably articulated directly on the caudodorsal border of the basal plate, as it is also observed in *Latimeria* (MILLOT & ANTHONY 1958). The basal plate of the first dorsal fin (Fig. 5) is well preserved. It is of a roughly triangular shape, with a rounded anterior edge and with a distinct postero-ventral spine. It most closely resembles the basal plate of *Coelacanthus* (SCHAEFFER 1941, Fig. 7c), *Diplurus* (SCHAEFFER 1952) and *Latimeria* (MILLOT & ANTHONY 1958). The basal plate of *Holophagus* is more pointed anteriorly (GARDINER 1960). The extent of the segmentation of the lepidotrichia is difficult to determine because of incomplete preservation of the latter and because of breakage of the unjointed parts. It appears that the lepidotrichia were segmented for about the distal third of their length. The first segmented lepidotrichium shows an ornamentation which

consists of four rows of spines distally. Proximally, the number of rows becomes reduced until the spines disappear. Spines can also be observed on the second lepidotrichium. Whether the other lepidotrichia showed a similar but less distinct ornamentation or not cannot be safely determined from their impressions alone. Only one lateral row of weakly pronounced spines is observed on the basal part of the sixth and seventh lepidotrichia.

A number of eight rays in the first dorsal fin appears to be characteristic of many Triassic coelacanths such as *Undina picenus* (COSTA 1862; BASSANI 1896), *Holophagus* (HEIMBERG 1949), *Heptanema* (ALESSANDRI 1910), *Whiteia* (LEHMAN 1952) and *Diplurus* (SCHAEFFER 1952).

The basal plates of both the second dorsal and anal fins are not preserved in *Ticinepomis peyeri*. The second dorsal fin consists of 22 or 23 rays. COSTA (1862) omitted the second dorsal fin from consideration. BASSANI (1896) counted only 12 rays in the second dorsal fin of *Undina picenus*. A similary low number (13) is observed in *Diplurus* (SCHAEFFER 1952). On the other hand, *Coelacanthus* shows 18–20 rays in the second dorsal fin, and *Holophagus penicillata* 21 (HEIMBERG 1949). The rays in the second dorsal fin of *Latimeria* (MILLOT & ANTHONY 1958) clearly outnumber those of *Ticinepomis* and *Holophagus*.

The anal fin of *Ticinepomis peyeri* consists of 22 rays, again segmented for the distal third of their length.

The upper and lower lobes of the caudal fin of *Ticinepomis* appear to be symmetrical in the specimen here described. As noted by STENSIÖ (1921), however, the ventral lobe of the coelacanth caudal fin usually incorporates a few more lepidotrichia than the dorsal lobe. In both the upper and lower lobe, the first three lepidotrichia progressively increase in length and are distally unsegmented (fulcral spines of REIS 1888). The following 15 lepidotrichia are segmented for about the distal half or third of their length. An accurate determination of the extent of the segmentation is again rendered impossible by the fine breakage of the unjointed parts of the lepidotrichia. Each lepidotrichium is supported by one radial which in turn articulates with one neural or haemal spine. The radials extend far upwards along the leading edge of the first five distally segmented lepidotrichia.

The last one of the unjointed and at least the following three distally segmented lepidotrichia are ornamented with a double row of spines on each side. On the fourth distally segmented lepidotrichium of the dorsal lobe only a single row of spines is observed. The other lepidotrichia appear to lack ornamentation, or the ornament consists of less conspicuous tubercles which may be obscured by the skin still covering the caudal fin.

The supplementary lobe of the caudal fin of *Ticinepomis* is not known. A trace of a fin ray is observed between the last lepidotrichia of the dorsal and ventral lobes, which might indicate that a supplementary caudal fin was present in the specimen (Fig. 4). It is consequently included in the reconstruction (Fig. 6).

Scales. – The surface of the scales of *Ticinepomis* is ornamented with closely packed, elongated, blunt or pointed spines disposed in a rostrocaudal direction. The spines project beyond the caudal edge of the scale and may converge towards the caudal tip of the scale. Very little variation could be found in the ornamentation of

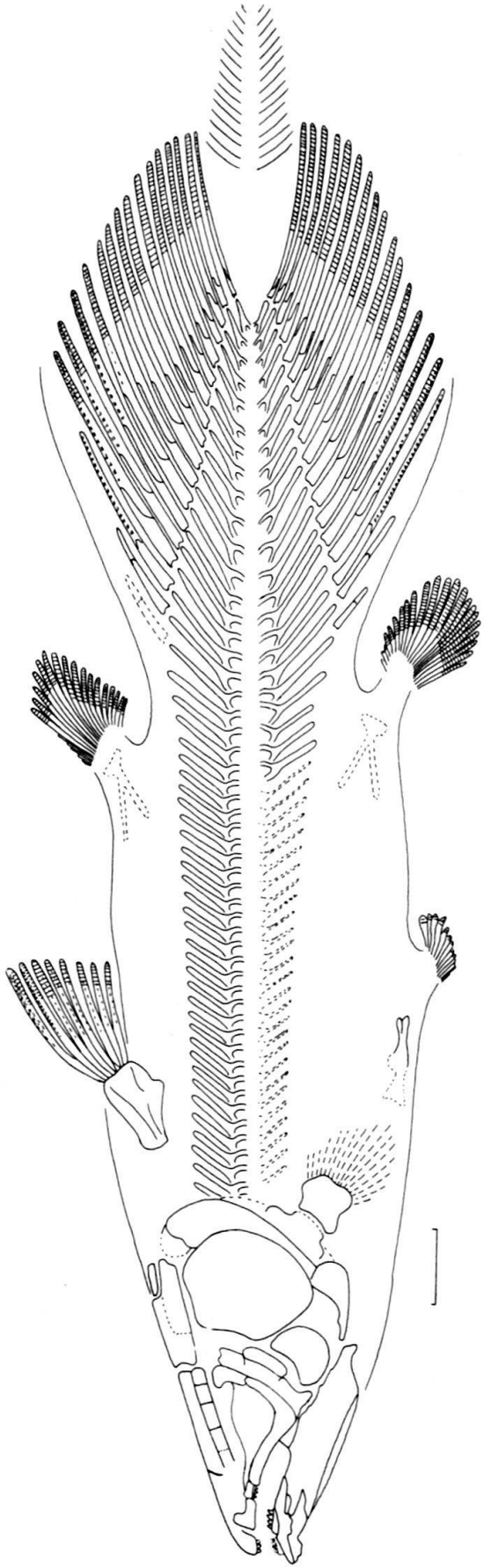

Fig. 6. A tentative reconstruction of *Ticinepomis peyeri*. Scale equals 10 mm.

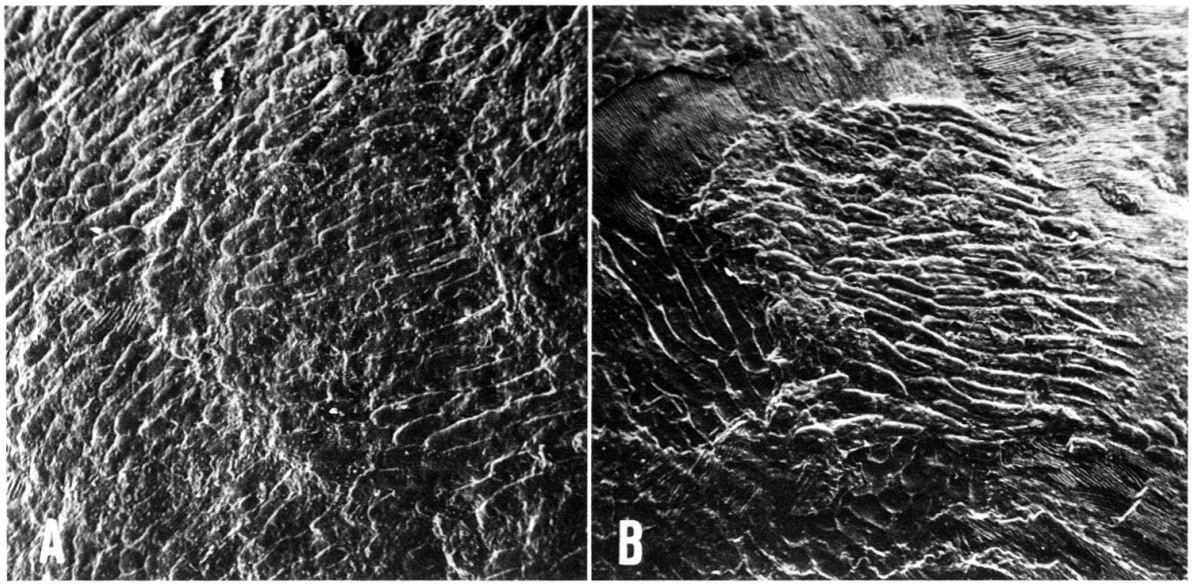

Fig. 7. SEM-micrographs of silicon casts of scales of *Ticinepomis peyeri*. A: Scales from above the pelvic fin; B: scales from below the second dorsal fin. Approx. × 15.

scales from different body regions. The extremes of variation are shown in Figure 7. The most commonly observed type of scale is shown in Figure 7A. Only in the region below the second dorsal fin was I able to find scales of the type shown in Figure 7B. The difference seems to relate to a wider spacing of the spines.

It is very difficult to decide whether the scales from the Cava Tre Fontane described and figured by ANDERSSON (1916) and referred by him to the genus *Holophagus* represent the same type as those of *Ticinepomis*. A certain resemblance exists in that both scale types bear closely packed, elongated spines. But both the extent of the ornamented surface as well as the size are different in the two types.

A comparison of *Ticinepomis* with other Mesozoic coelacanths

From the Triassic of Spitzbergen, STENSIÖ (1921) described a number of coelacanth genera all of which are considered to be closely related to each other by SCHAEFFER (1941). Of these genera, *Mylacanthus*, *Sassenia* and *Wimania* are known from the skull only.

Axelia (STENSIÖ 1921) differs from *Ticinepomis* by the development of a crushing dentition. This genus also shows four supraorbitals only, and the anterior shank of the pterygoid is low but elongated.

Scleracanthus (STENSIÖ 1921) also shows the development of a crushing dentition. Moreover, it incorporates 15 lepidotrichia in its first dorsal fin, and the basal plate of the first dorsal fin has two ventral processes.

In 1932, STENSIÖ described *Laugia* from the Triassic of East Greenland. This genus is readily distinguished from *Ticinepomis* by the position of the pelvic fins which lie in front of the first dorsal fin in *Laugia*.

The Alpine Triassic of Europe yielded *Graphiurichthys* (KNER 1866). It is readily distinguished from *Ticinepomis* by the shape of the lepidotrichia and by the shape of the caudal fin.

Heptanema, a second genus from the Alpine Triassic of Europe is apparently difficult to separate from *Scleracanthus* (STENSIÖ 1932). However, the ornamentation of its scales is very characteristic (DEEKE 1889; ALESSANDRI 1910) and different from *Ticinepomis*.

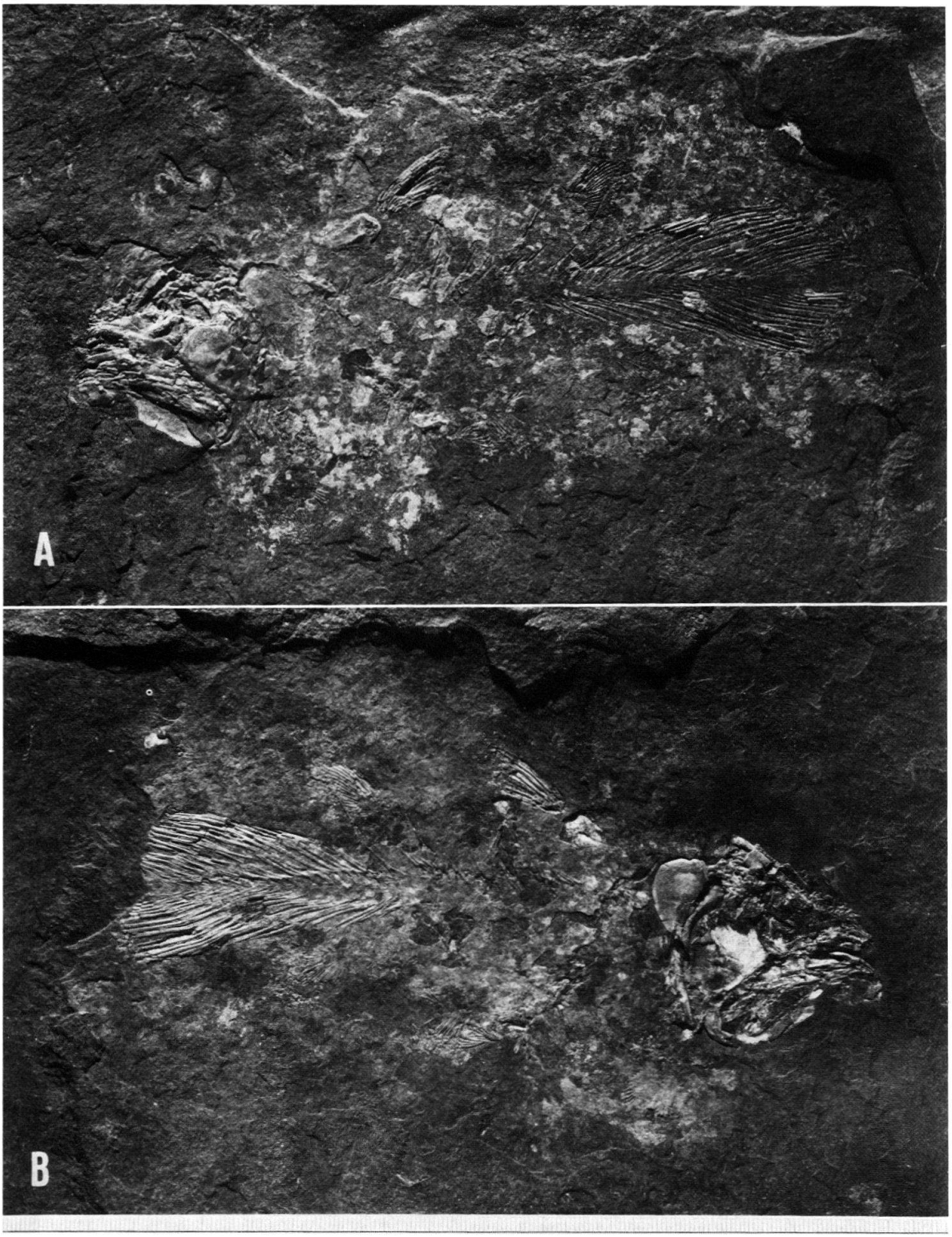

Fig. 8. *Ticinepomis peyeri* n. gen. n. sp. Holotype, part (A) and counterpart (B). Scale in mm.

Diplurus is the best known Mesozoic coelacanth from North America (SCHAEFFER 1941, 1948, 1952). The genus differs from *Ticinepomis* in the ornamentation of the scales and in the lack of an ornamentation of the external surface of the operculum. The postorbital reaches further ventrally in *Diplurus* than in *Ticinepomis*, and the premaxillae are reduced to small marginal tooth plates. On the other hand, the structure of the lower jaw of *Diplurus* approaches quite closely the conditions observed in *Ticinepomis*, including the shape of the dentary and the single splenial. Another similarity of *Ticinepomis* and *Diplurus* is the massive clavicle with a well-developed ventral horizontal portion - a primitive feature.

Another coelacanth from the Triassic of North America is *Moenkopia* (SCHAEFFER & GREGORY 1961), known only from the basisphenoid. In 1954 SCHAEFFER reinterpreted *Pariostegus* as a coelacanth from the Triassic of North America. The specimen is very incompletely preserved, however. Yet it lacks posterolateral lappets of the parietal shield, formed by the supratemporals, as are present in *Ticinepomis*.

Triassic coelacanth genera from Madagascar include *Whiteia* and *Piveteauia* (LEHMAN 1952). *Whiteia* differs from *Ticinepomis* in skull structure and in the small caudal fin. In *Piveteauia* the caudal fin is equally small as in *Whiteia*. Furthermore, the pelvic fins are positioned anteriorly to the first dorsal fin in *Piveteauia*, and the anterior shank of the pterygoid is low.

Hainbergia is a poorly preserved actinistian fish from the Lower Triassic of Germany (SCHWEIZER 1966). Due to its state of preservation, a comparison with *Ticinepomis* is impossible. Nevertheless, the ornamentation of the scales in *Hainbergia* is clearly different from *Ticinepomis*.

Unnamed actinistian remains from the Upper Triassic of Germany have been mentioned by DEHM (1956a, b). Their preservation is so poor that no meaningful comparison is possible.

Jurassic coelacanths from Europe are represented by the genera *Holophagus*, *Coccoderma* and *Lybis*. The diagnoses of these three genera have been revised by REIS (1888). *Coccoderma* differs from *Ticinepomis* in having very weakly ornamented scales and by a smooth outer surface of the operculum. The anterior shank of the pterygoid is low and has a concave dorsal border. *Lybis* differs from *Ticinepomis* by the smooth surface of the dermal bones of the skull and by the large pores of the lateral line canal.

Macropoma is an Upper Cretaceous genus from Europe. It has also been discussed by REIS (1888). It differs from *Ticinepomis* not only by its size but also by skull structure.

The Mesozoic coelacanth genera not yet compared with *Ticinepomis* are *Holophagus* and *Coelacanthus*. The latter is primarily an Upper Permian genus, but it extends into the Triassic.

A comparison of *Ticinepomis* with *Holophagus* is important because of ANDERSSON'S (1916) mention of the latter genus from the Cava Tre Fontane. *Ticinepomis* and *Holophagus* share a number of features such as a high number of rays in the second dorsal fin, the fusion of the supratemporal with the parietal and, perhaps most significantly, a high anterior shank of the pterygoid. On the other hand, distinct differences separate the two genera. *Holophagus* shows plate-like postorbital bones, and the pectoral girdle of *Holophagus* consists of rather delicate, narrow

elements and bears a much smaller scapulocoracoid in comparison to *Ticinepomis*. REIS (1888) observed two splenials in *Holophagus penicillata* whereas the splenial is single in *Ticinepomis*. The dentary of *Holophagus gulo* as described by GARDINER (1960) is much different from the one of *Ticinepomis*. *Holophagus penicillata* as described by REIS (1888) shows a dentary vaguely similar to the one of *Ticinepomis*, however. Finally, the ornamentation of the scales is different in *Holophagus* and *Ticinepomis*.

Coelacanthus is a genus from the Upper Permian and Lower Triassic of Europe and Madagascar. It has recently been redescribed by SCHAUMBERG (1978). There exist a number of similarities which *Coelacanthus* shares with *Ticinepomis*. The postorbital is reduced to a small, narrow element lying posterodorsal to the orbit in both genera. The lateral rostral looks exactly similar in both genera, bearing the characteristic anterior flange. The autopalatine is of a similar triangular shape in both genera. The frontal bone is elongated in *Coelacanthus* as is the posterior frontal bone in *Ticinepomis*. In front of the frontal bone the snout is covered by a series of nasal bones laterodorsally and by an elongated tectal plate laterally in *Coelacanthus*. It might be possible that what I called anterior frontal bone in *Ticinepomis* actually represents a similar tectal plate. The dorsal surface of the snout of *Ticinepomis* might have been covered by a number of small bones which are completely crushed in the specimen.

The dentary of *Coelacanthus* is elongate, tapering both anteriorly and posteriorly, resembling the dentary of *Ticinepomis*. Below the dentary there is a single splenial bone in *Coelacanthus*, tapering caudally and embraced by two anterior projections of the angular, again as in *Ticinepomis*.

On the other hand *Coelacanthus* differs in many details from *Ticinepomis*. The premaxilla of *Coelacanthus* is reduced to a number of small marginal tooth plates. The anterior pterygoid shank is low, with a concave dorsal border. The pectoral girdle is delicate and narrow and bears no caudally projecting scapulocoracoid (MOY-THOMAS & WESTOLL 1935; SCHAUMBERG 1978). The lepidotrichia of the first dorsal and caudal fins lack any ornamentation. There are 11–13 rays in the first dorsal fin (MOY-THOMAS & WESTOLL 1935).

Discussion

Relationships

The new coelacanth from the Middle Triassic of Monte San Giorgio appears to be similar to *Undina picenus* as described by COSTA (1862) and BASSANI (1896). A synonymy of this latter form with *Ticinepomis* at the generic level appears probable but has to be based on a reinvestigation of these Italian fossils.

BASSANI (1896) indicates 12 rays in the second dorsal fin of *Undina picenus*, whereas *Ticinepomis peyeri* shows at least 22 rays in the second dorsal fin. A distinct difference between the two species is adult body size. Both specimens of *Undina picenus* described by COSTA (1862) and BASSANI (1896) measure between 30 and 35 cm, whereas *Ticinepomis peyeri* is only about 18 cm long. This is taken as adult body size since the supratemporal has fused with the parietal. Scale structure appears to be different in *Undina picenus* and in *Ticinepomis peyeri*. Both COSTA

(1862) and BASSANI (1896) figure diagramatically the scale ornamentation in *Undina picenus*. Of the two figures, the one given by BASSANI seems more reliable. The scales of *Undina picenus* consist of a broad, not ornamented, overlapping part showing concentric growth rings. The non-overlapping part of the scale is ornamented by several rows of rather short spines. In *Ticinepomis peyeri*, the exposed portion of the scales is proportionally larger and covered by elongated spines.

Compared with other Mesozoic coelacanths, it is difficult to define the genus *Ticinepomis* as presently known by specializations of its own. Some characteristics of *Ticinepomis* such as the large premaxillae capping the snout or the massive shoulder girdle are primitive features. Other characteristics such as the high anterior shank of the pterygoid, the elongated frontal bone and fin structure are also found in other coelacanths. A distinct specialization of *Ticinepomis* appears to be the structure of its dentary.

Among other coelacanths, the genus *Ticinepomis* appears most closely related to the genus *Coelacanthus*. A specialized feature of the two genera is the reduced size of the postorbital bone, with the lacrimojugal forming most of the posterior border of the orbit. Further similarities of the two genera include the structure of the lateral rostral, of the autopalatines, of the supraorbitals and the general structure of the lower jaw.

Paleoecology

Actinistians appear to have radiated from a basic marine stock (SCHAEFFER 1948). The Upper Devonian forms are known from marine sediments in Germany. Carboniferous and Permian forms occur mainly in freshwater deposits, although the Carboniferous genus *Rhabdoderma* also occurs in marine deposits (Forey, pers. comm.). During the Triassic, the worldwide distributed coelacanths were predominantly marine, except for the genus endemic in the Newark group of freshwater deposits in North America. During the Jurassic and Cretaceous coelacanths are found in marine sediments (SCHAEFFER 1948, 1952).

The sedimentation of the Grenzbitumen horizon occurred at a very slow rate in a fairly small marine basin of a diameter of approximately 9 km. With a depth of 30–100 m, the basin was rather shallow; it was surrounded by a complex of reefs and lagunes (ZORN 1971). Benthic organisms are virtually lacking in the Grenzbitumen horizon, which may indicate a deficiency or even a lack of oxygen in the benthic zone (RIEBER 1973). The bottom layer of water may even have been poisoned by the presence of H_2S (RIEBER 1973). These conditions can be explained by the assumption that the marine basin contained a stagnant deep layer of water (ZORN 1971; RIEBER 1973). Such environmental conditions could only be maintained for all the time during which the slow sedimentation took place, if it is assumed that the coastal basin was fairly well closed off from the open sea.

If *Ticinepomis peyeri* was naturally occurring in the environment in which it has become fossilized, it is to be interpreted as a pelagic animal living in shallow, near-shore areas. The presence of *Birgeria* in the sediments of the Grenzbitumen horizon (SCHWARZ 1970) indicates, however, that pelagic fishes of the open sea occasionally approached near-shore areas, and possibly even got trapped in basins such as the

one characteristic of the Monte San Giorgio locality. The same explanation might account for the presence of *Ticinepomis peyeri* in the Grenzbitumen horizon of Monte San Giorgio.

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