

Research article

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Osteology and relationships of *Acrorhinichthys poyatoi* gen. et sp. nov. (Pycnodontiformes) from the marine Late Cretaceous of Lebanon

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Abstract. The osteology of *Acrorhinichthys poyatoi* gen. et sp. nov., a pycnodontid fish from the marine Cenomanian (Late Cretaceous) of Lebanon, is studied in detail. The new fossil genus belongs to the order Pycnodontiformes, but is less evolved than the Pycnodontidae. It still exhibits a few bony plates (= *tesserae*) in the gular region, 3 teeth on the premaxilla and 5 teeth on the dentary, and its parietal is devoid of a brush-like process. It shares a few characters with *Akromystax*, the most primitive taxon within Pycnodontidae, characters lost in the other members of the family.

Key words. Pycnodontiformes, *Acrorhinichthys poyatoi* gen. et sp. nov., osteology, relationships, Cretaceous, Lebanon

Taverne L. & Capasso L. 2015. Osteology and relationships of *Acrorhinichthys poyatoi* gen. et sp. nov. (Pycnodontiformes) from the marine Late Cretaceous of Lebanon. *European Journal of Taxonomy* 116: 1–30. <http://dx.doi.org/10.5852/ejt.2015.116>

Introduction

The fossil beds from the Cenomanian of Haqel, Hgula and Ein Namoura and from the Santonian of Sahel Alma, in Lebanon, have provided the world's richest marine ichthyofauna known for the Late Cretaceous period.

Pycnodontomorpha are a major component of the fossil marine fauna from the Near East. These Lebanese fishes comprise not only a few classical deep-bodied pycnodont species, such as "*Nursallia*" *goedeli* Heckel, 1854, *Akromystax tilmachiton* Poyato-Ariza & Wenz, 2005, *Nursallia tethysensis* Capasso *et al.*, 2009 and *Rhinopycnodus gabriellae* Taverne & Capasso, 2013 (Heckel 1854; Poyato-Ariza & Wenz 2005; Capasso *et al.* 2009; Taverne & Capasso 2013b), but also three highly specialized and very strange families, the Coccodontidae (Gayet 1984; Nursall & Capasso 2008; Capasso *et al.* 2010; Taverne & Capasso 2014a), the Gebrayelichthyidae (Nursall & Capasso 2004; Taverne & Capasso 2014b) and the Gladiopycnodontidae (Taverne & Capasso 2013a, 2014c).

The aim of our paper is to describe and to clarify the systematic position of a new Lebanese genus and species of “standard”-bodied pycnodont fish from the Cenomanian of Haqel and Ein Namoura.

Material and methods

The material studied here belongs to Capasso’s registered collection (CLC) in Chieti (Italy). The specimens have been examined with a Leica Wild M 8 stereo microscope. The figures were drawn by the first author (L.T.) with a camera lucida and based on photos. Aspersions with ethanol were used to improve some observations.

List of abbreviations used in figures

AN	=	angular
APTE	=	autopterotic
ART	=	articular
ASPH	=	autosphenotic
BO	=	basioccipital
BRSTG	=	branchiostegal rays
CHY a., p.	=	ceratohyal (anterior, posterior)
CLO	=	cloaca
CLT	=	cleithrum
DHYOM	=	dermohyomandibula
DN	=	dentary
DPTE	=	dermopterotic
DSOC(1, 2)	=	dermosupraoccipital (anterior, posterior)
DSPH	=	dermosphenotic
ECPT	=	ectopterygoid
ENPT	=	entopterygoid (= endopterygoid)
EPCO 1-6	=	epichordals 1 to 6
EXO	=	exoccipital
FR	=	frontal
HAEM	=	haemal arch
HAEMEP	=	haemal spine
HCLT	=	hypercleithrum (= supracleithrum)
HP 3, 6	=	haemal spines 3 and 6
HYCO 1-11	=	hypochochordals 1 to 11
HYOM	=	hyomandibula
IORB 1, 2	=	infraorbital 1, 2
LEP	=	lepidotrichium (= ray)
LEP pelv.	=	ventral fin rays
METH	=	mesethmoid
MPT	=	metapterygoid
MX	=	maxilla
NEUR	=	neural arch
NEUREP	=	neural spine
NP 1-15	=	neural spines 1 to 15
OP	=	opercle
OSPH	=	orbitosphenoid
PA	=	parietal
PCOEL	=	postcoelomic bone
PELV	=	pelvic bone

PMX	=	premaxilla
POP	=	preopercle
PRART	=	prearticular
PRFR	=	prefrontal (= lateral dermethmoid ?)
PRO	=	prootic
PS	=	parasphenoid
PSPH	=	pleurosphenoid
PT	=	posttemporal
QU	=	quadrate
RAD	=	pterygiophores (= radials)
RI	=	ribs
SC	=	scales
SC b.	=	body scales
SC clo.	=	cloacal scales
SCL	=	sclerotic bone
SCU c.	=	caudal scutes
SCU d.1-8	=	scutes of the dorsal ridge (1 to 8)
SCU v.1-13	=	scutes of the ventral keel (1 to 13)
ST	=	supratemporal
SY	=	symplectic
SYN	=	synarcual
TES	=	gular bony plates (= <i>tesserae</i>)
UD 1, 2, 3	=	urodermal 1, 2 and 3
VO	=	vomer
b.c.	=	bar component of the scale
f.i.c.	=	foramen of the internal carotid
l.	=	left
poz.	=	postzygapophysis
r.	=	right
sorb. c.	=	supraorbital sensory canal
w.c.	=	wing component of the scale

Results

Systematic paleontology

Subclass Actinopterygii Klein, 1885
 Series Neopterygii Regan, 1923
 Division Halecostomi Regan, 1923 *sensu* Patterson 1973
 Superorder Pycnodontomorpha Nursall, 2010
 Order Pycnodontiformes Berg, 1937 *sensu* Nursall 2010

Genus *Acrorhinichthys* gen. nov.

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Type species

Acrorhinichthys poyatoi gen. et sp. nov. (by monotypy).

Diagnosis

As for the species (monospecific genus).

Etymology

From the Greek *akron*, *akrou*, point, *rhis*, *rhinos*, nose, and *ichthys*, fish. The name refers to the sharp end of the snout in this fish.

Acrorhinichthys poyatoi gen. et sp. nov.

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Figs 1–19

Diagnosis

Primitive pycnodontiform fish with a deep body, a rounded ventral margin and an angular dorsal profile. Head triangular in shape, with a rectilinear frontal profile and a long preorbital region. Pointed snout, with reduced jaws. Mouth gape obliquely oriented. Premaxilla bearing 3 incisiform teeth. Dentary bearing 5 incisiform teeth. Vomer covered by numerous small, rounded teeth arranged in regular rows. Prefrontal present. Few bony plates (= *tesserae*) present in the gular region. Parietal without brush-like process. No temporal fenestra. Dermohyomandibula fused to hyomandibula. Preopercle much larger than the exposed part of hyomandibula. A small ectopterygoid. Tubular infraorbitals. Cleithrum with a broad ventral branch. Pectoral fin with 16 or 17 rays. Ventral fin with 4 rays. Dorsal and anal fins strip-like. Dorsal fin origin located just behind dorsal apex. Dorsal fin with 51 to 55 pterygiophores. Anal fin with 36 to 41 pterygiophores. Neural and haemal arches not completely surrounding the notochord. 24 to 27 vertebral segments in front of epichordal series. 14 haemal spines in front of hypochordal series. Neural and haemal spines with anterior, wing-like expansion. One postzygapophysis on the neural and haemal arches in the caudal region. 9 to 10 pairs of broad ribs. Caudal peduncle very short. 4 or 5 epichordals. 10 or 11 hypochordals, of which 3 posterior ones slightly broadened. 2 urodermals. Caudal fin double emarginated, with 22 or 23 principal rays. Dorsal ridge containing 8 spiny scutes. The eighth dorsal scute larger and forming a small prominence at the dorsal apex. Ventral keel with 13 scutes, 2 of them postcloacal. Very large first ventral scute. A row of complete scales associated with the dorsal scutes. Scales only in the abdominal region, with scale bars in the dorsal part and complete scales in the ventral part. 2 imbricated scales above the cloaca, 1 small, triangle-shaped ventral one and 1 larger, dorsal one with a broad and concave ventral margin.

Etymology

The species name of the new Lebanese fossil fish is dedicated to the Spanish palaeontologist Francesco Poyato-Ariza, who has greatly improved our knowledge of pycnodontiform fishes.

Holotype

Sample CLC S-630a, b, part and counterpart of a complete specimen from Ein Namoura, Lebanon (Figs 1–2). Total length: 87 mm. Standard length: 72 mm.

Paratypes

Sample CLC S-461, a complete specimen from Ein Namoura, Lebanon (Fig. 3). Total length: 114 mm. Standard length: 98 mm.

Sample CLC S-1098, a nearly complete specimen from Haqel, Lebanon (Fig. 4). The caudal fin is crushed. Total length: 115 mm. Standard length: 102 mm.

Formation and locality

Marine Upper Cenomanian deposits of Haqel and Ein Namoura, Lebanon.

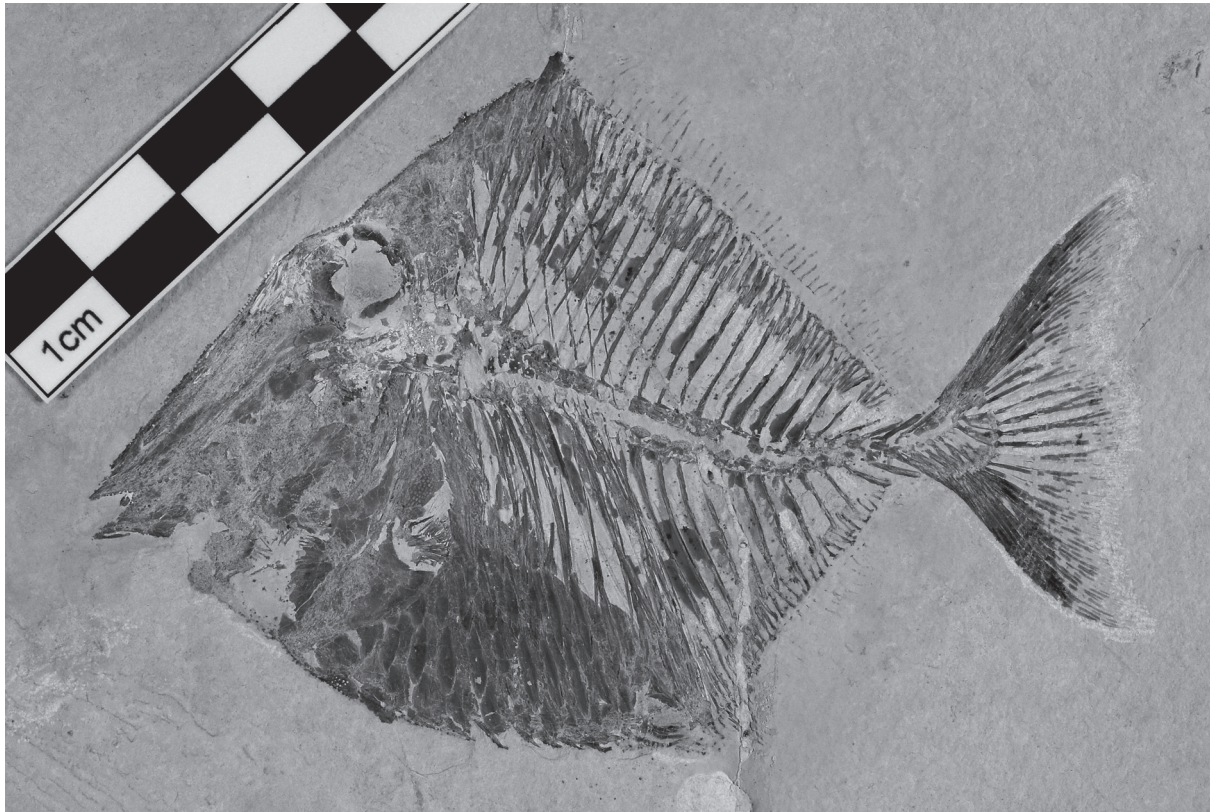


Fig. 1. *Acrorhinichthys poyatoi* gen. et sp. nov. Holotype CLC S-630a.

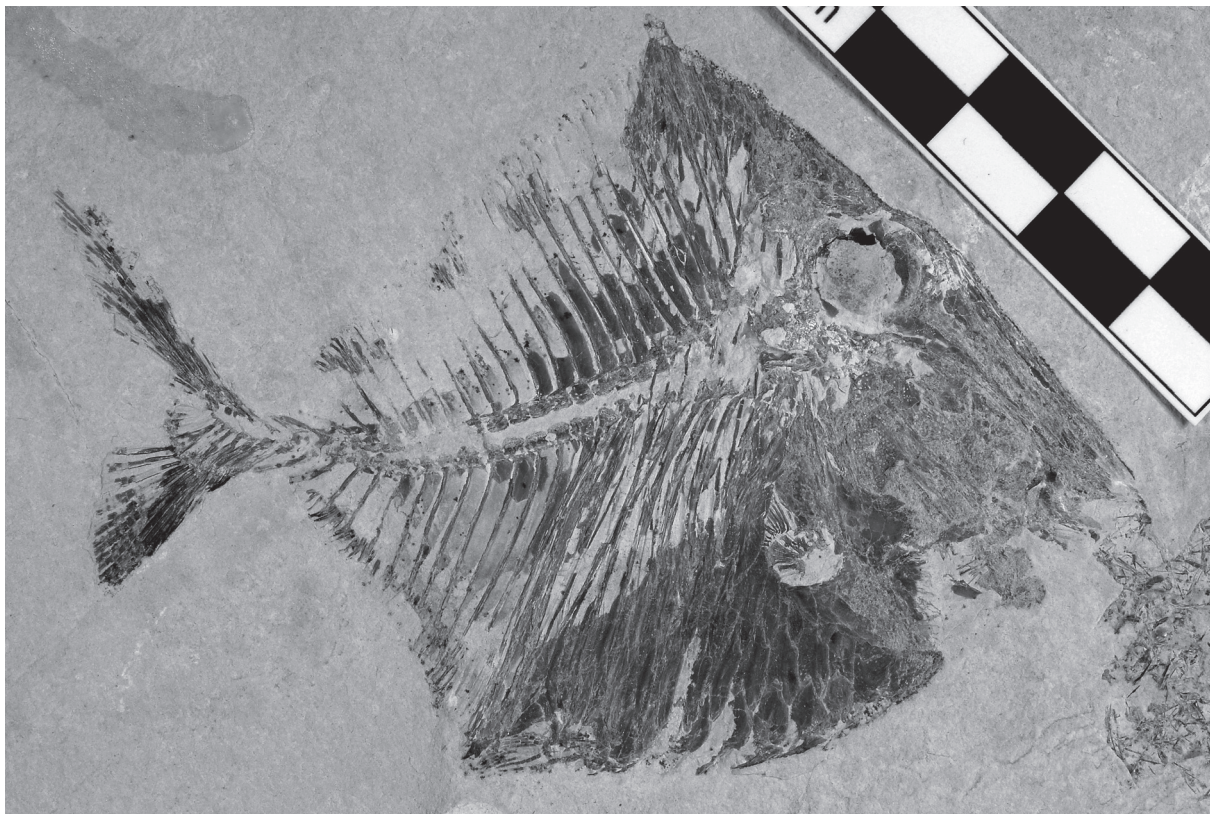


Fig. 2. *Acrorhinichthys poyatoi* gen. et sp. nov. Holotype CLC S-630b.

General morphology and morphometric data (Figs 1–5)

Acrorhinichthys poyatoi gen. et sp. nov. is a small pycnodontiform. The total length of the specimens does not exceed 12 cm. The fish is high-bodied but not discoid in shape. The dorsal profile is angular, with a well marked apex located midway between the snout and the caudal peduncle. This apex, built with the enlarged posterior dorsal scute, forms a small dorsal prominence. The ventral margin of the body is more or less rounded.

The morphometric data of the holotype (CLC S-630a, b) and of one of the paratypes (CLC S-461) are given in % of their standard length, 72 mm and 98 mm respectively:

	CLC S-630	CLC S-461
Length of the head (from the snout to the occipital region)	42.4 %	38.4 %
Depth of the head (including the pectoral girdle)	58.5 %	50.5 %
Maximum depth of the body (at the dorsal apex level)	80.5 %	70.3 %
Prepelvic length	61.0 %	55.2 %
Predorsal length	55.6 %	56.0 %
Basal length of the dorsal fin	53.7 %	47.4 %
Preanal length	2.7 %	66.8 %
Basal length of the anal fin	33.2 %	31.9 %
Depth of the caudal peduncle	7.3 %	7.3 %

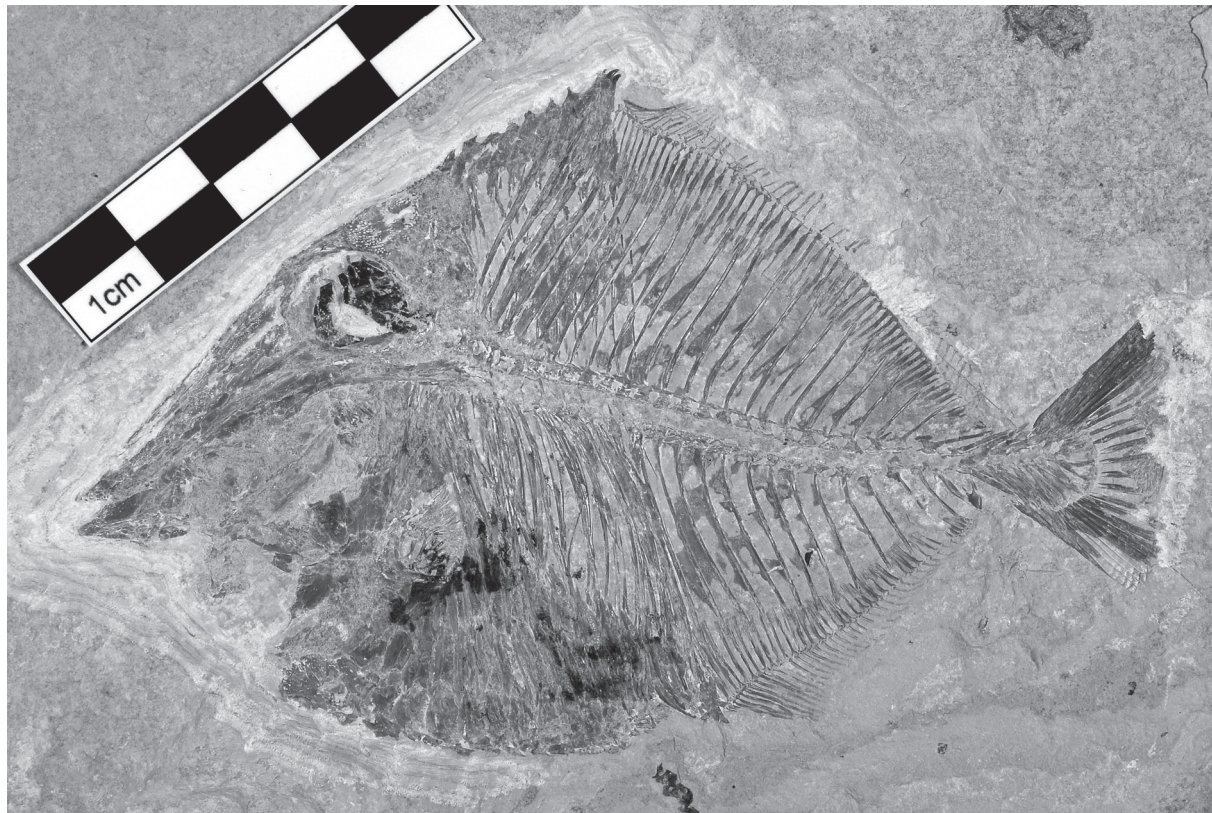


Fig. 3. *Acrorhinichthys poyatoi* gen. et sp. nov. Paratype CLC S-461.

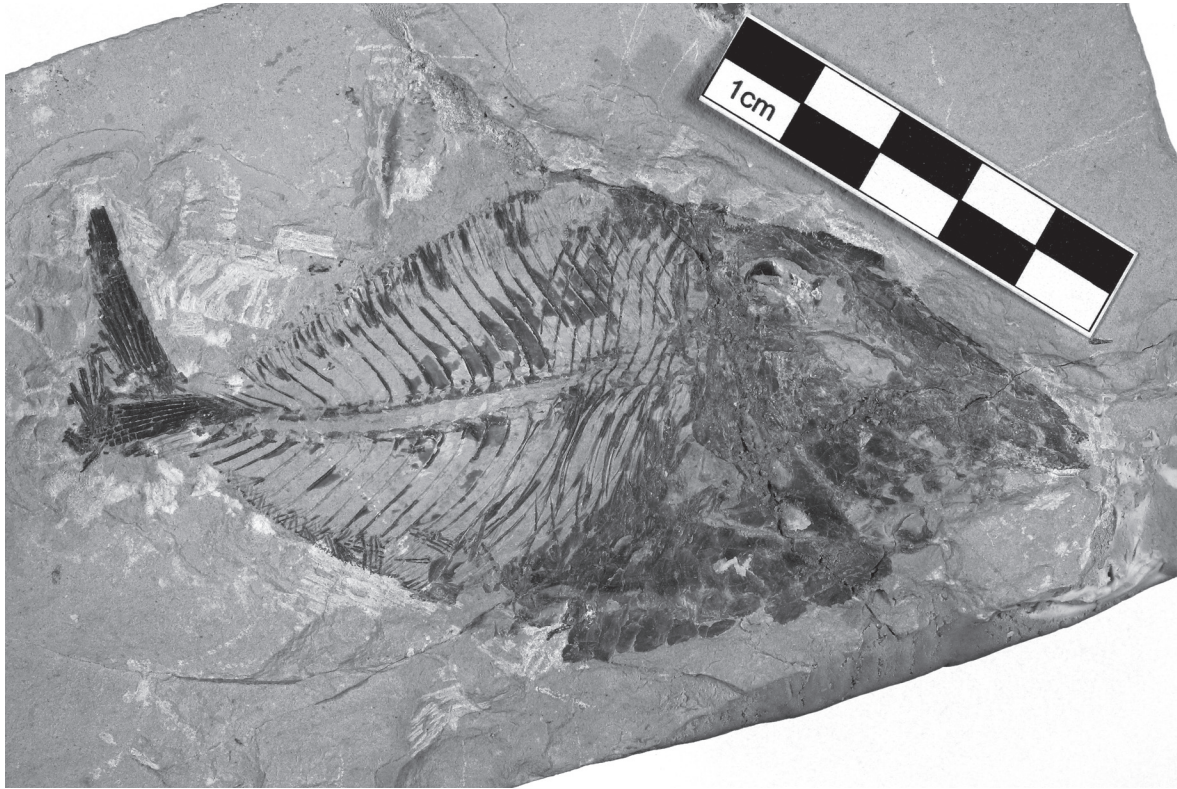


Fig. 4. *Acrorhinichthys poyatoi* gen. et sp. nov. Paratype CLC S-1098.

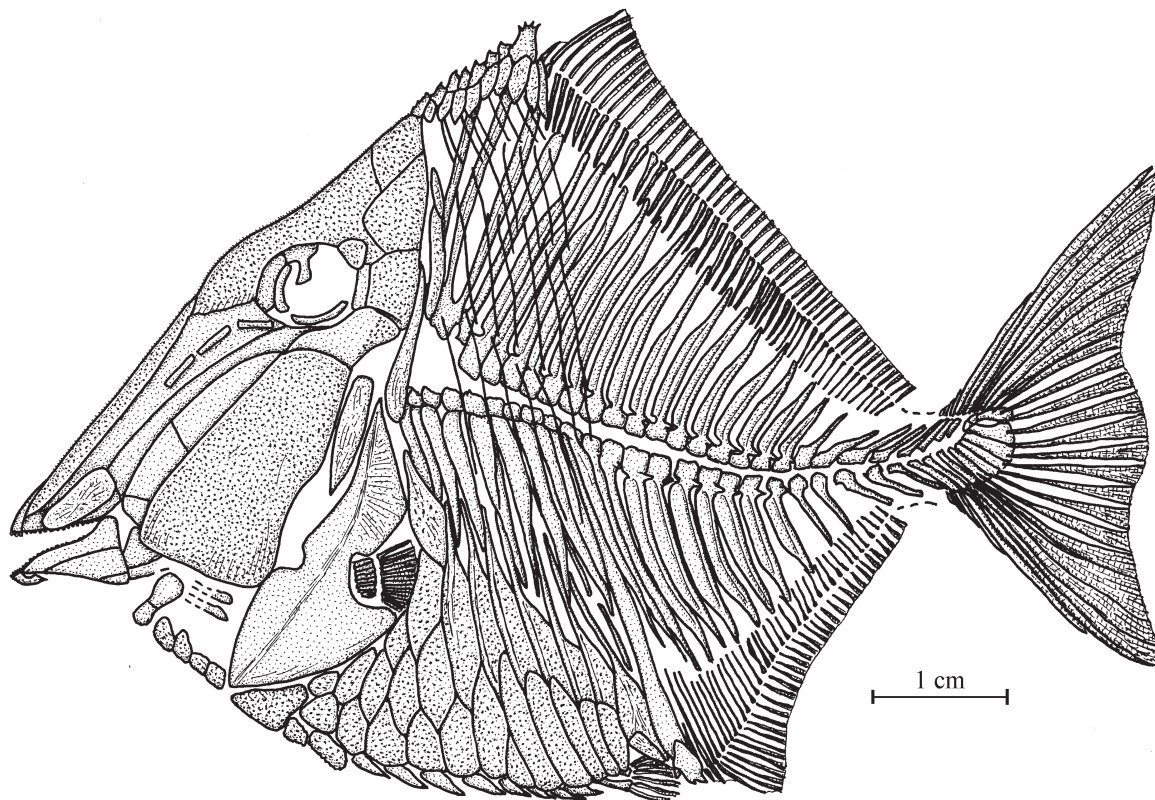


Fig. 5. *Acrorhinichthys poyatoi* gen. et sp. nov. Reconstruction based on the three specimens. The scale refers to the holotype CLC S-630a, b.

Osteology

1. The skull (Figs 6–11)

The overall shape of the head is triangular in lateral view, with a very long preorbital region, a large orbit, reduced jaws and a more or less pointed snout. The frontal profile between the occipital area and the snout is almost rectilinear. The dermal bones of the skull are ornamented with small tubercles and very thin ridges.

The mesethmoid is long and narrow. Its dorsal margin is covered by a pair of elongated and narrow prefrontals. The vomer is long and toothed, but it is not possible to determinate the number of tooth rows. Only one row is visible in the holotype. It contains 16 small, rounded teeth, the last ones being a little longer than the others.

The skull roof is formed by one dermosupraoccipital and paired frontals, parietals and dermopterotics. There is no temporal fenestra. The frontal is short and rather narrow, except in its posterior part. It covers the orbital area and exceeds this region only a little anteriorly and posteriorly. The dermosupraoccipital is small and the occipital region is conical in shape. The parietal is triangle-shaped, with a broad ventral margin and a pointed upper corner. The bone is devoid of a brush-like process. The dermopterotic is deeper than broad. A small supratemporal (= extrascapular) is located behind the parietal on the holotype CLC S-630a.

The posterior bones of the endocranium are not visible, except the autosphenotic that is partly covered by the dermosphenotic and the exoccipital that seems to be fused with a synarcual.

The very long edentulous parasphenoid is inflected downwards below the orbit. The anterior part of the bone is not enlarged. The orbitosphenoid and pleurosphenoid are preserved in the orbit of the holotype and in paratype CLC S-461. The orbitosphenoid is pressed against the mesethmoid. The pterosphenoid is a small bone. The presence of a basisphenoid is uncertain.

The jaws are very small when compared to the skull size. The mouth gape is obliquely oriented. As preserved in the holotype, the premaxilla bears 3 incisiform teeth and the dentary, reduced to its ventral branch, 5 teeth. The dentary is much shorter than the premaxilla. The maxilla, visible in paratype CLC S-1098, is longer than deep. The prearticular is triangle-shaped, with a well developed coronoid process. The bone bears small, rounded teeth, similar to those of the vomer, and they seem to be irregularly arranged. The angular partially covers the prearticular. The articular forms the posterior ventral corner of the mandible.

Both the quadrate and the symplectic articulate with the lower jaw. A small ectopterygoid and parts of the metapterygoid and entopterygoid are visible between the parasphenoid and the anterior border of the preopercle. The entopterygoid and ectopterygoid are toothless as is usual in Pycnodontiformes.

The dermosphenotic is a small, plate-like bone. Fragments of tubular infraorbitals are preserved on the holotype and paratype CLC S-461. A sclerotic ring is present and is composed of two elements.

The preopercle is by far the largest bone of the skull and covers practically the complete cheek. The small, deep, narrow, dorsally rounded and ventrally pointed opercle is wedged between the preopercle and the dorsal branch of the cleithrum. The posterior parts of two branchiostegal rays are preserved in paratype CLC S-461.

Fragments and impressions of a few ornamented bony tesserae are visible in the gular region of the holotype CLC S-630a.

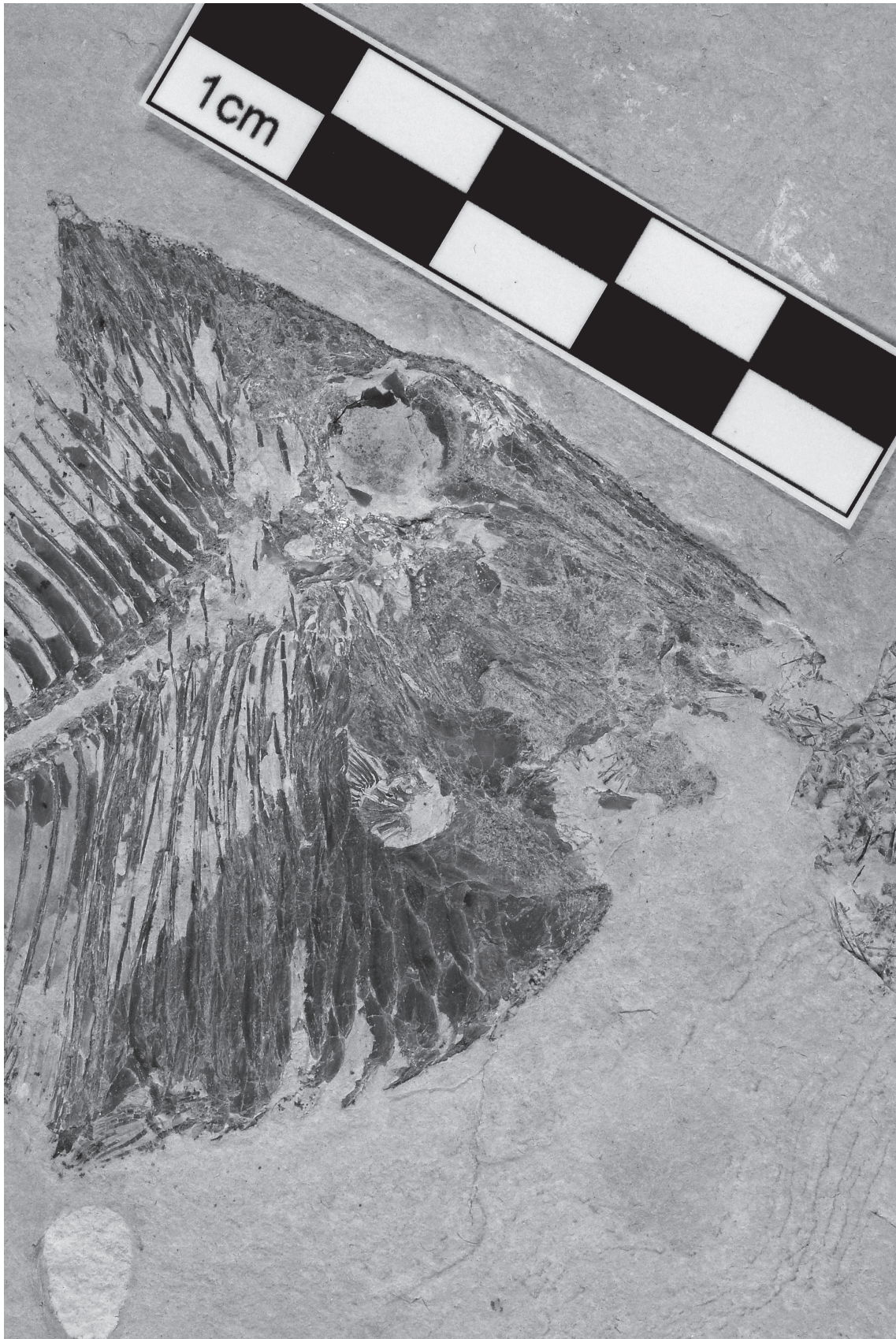


Fig. 6. *Acrorhinichthys poyatoi* gen. et sp. nov. Head and anterior region of the holotype CLC S-630a.

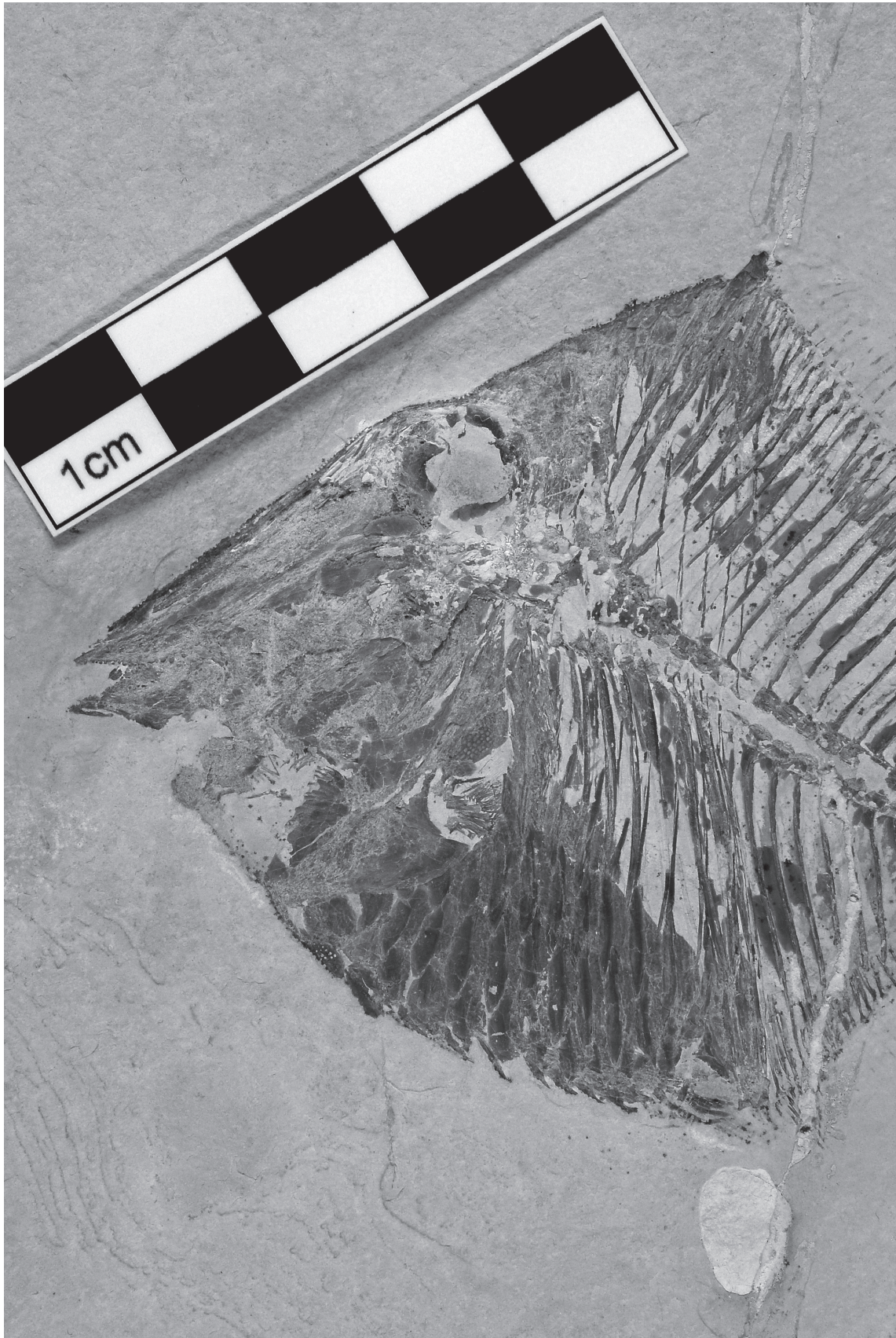


Fig. 7. *Acrorhinichthys poyatoi* gen. et sp. nov. Head and anterior region of the holotype CLC S-630b.

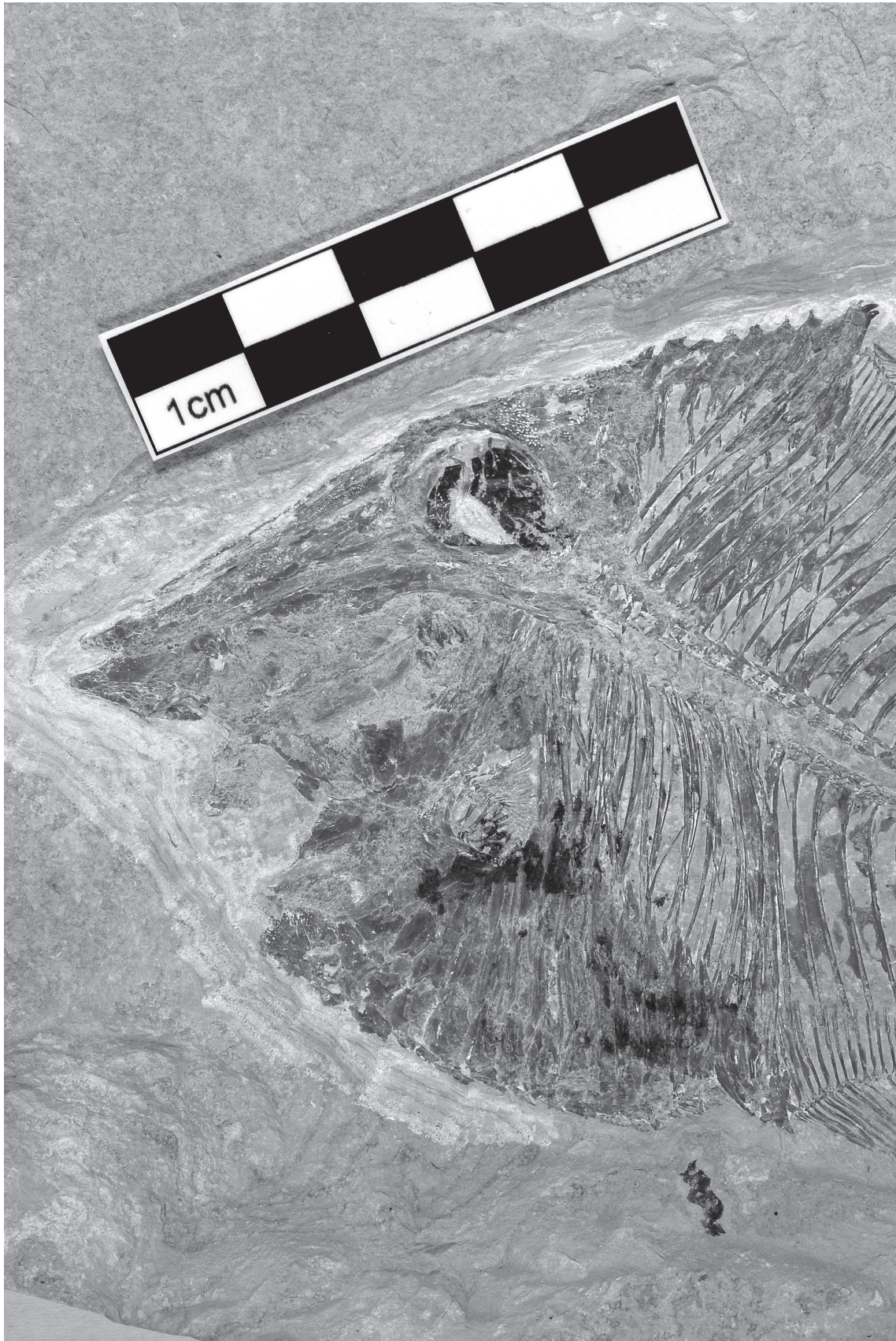


Fig. 8. *Acrorhinichthys poyatoi* gen. et sp. nov. Head and anterior region of paratype CLC S-461.

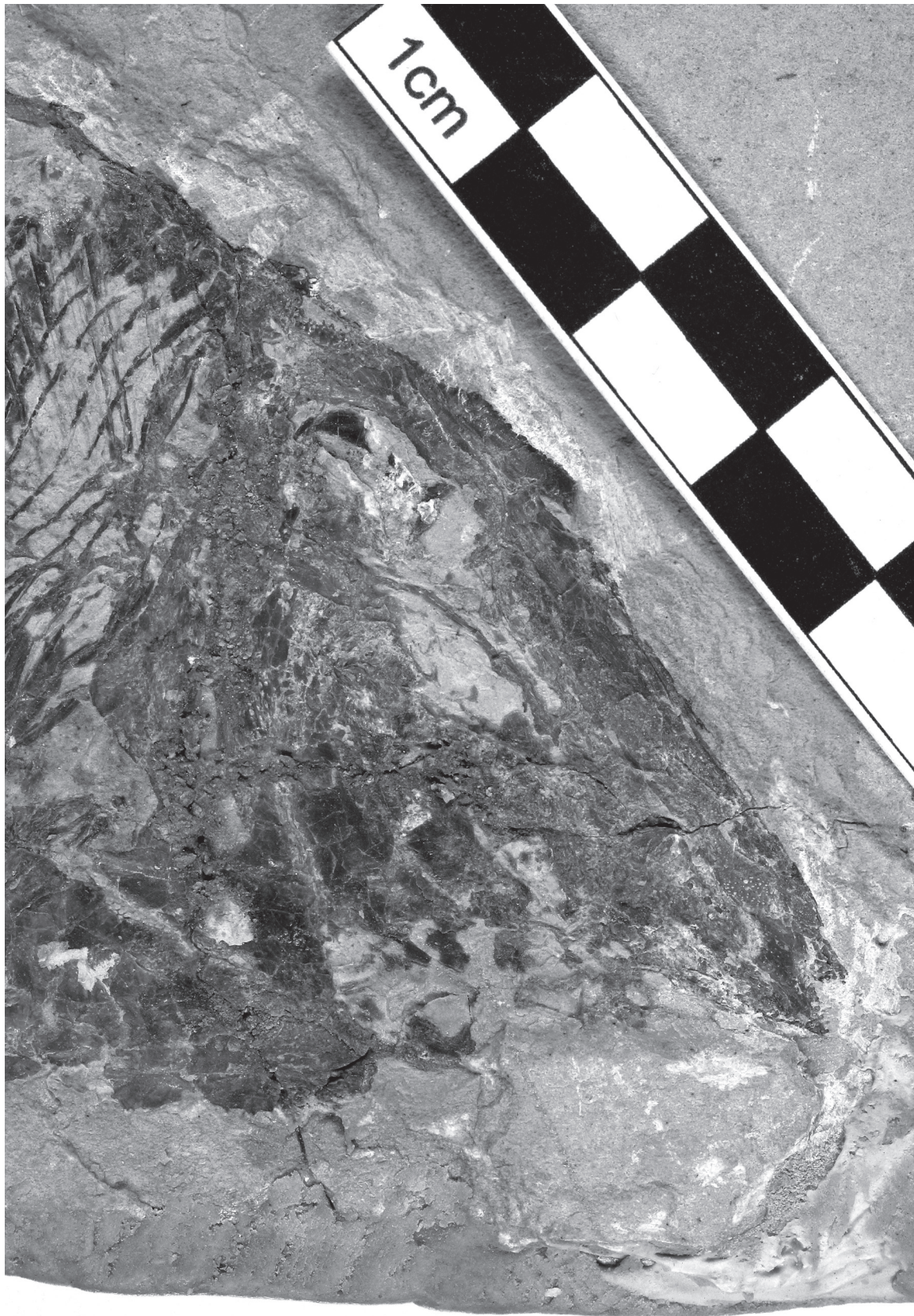


Fig. 9. *Acrorhinichthys poyatoi* gen. et sp. nov. Head and anterior region of paratype CLC S-1098.

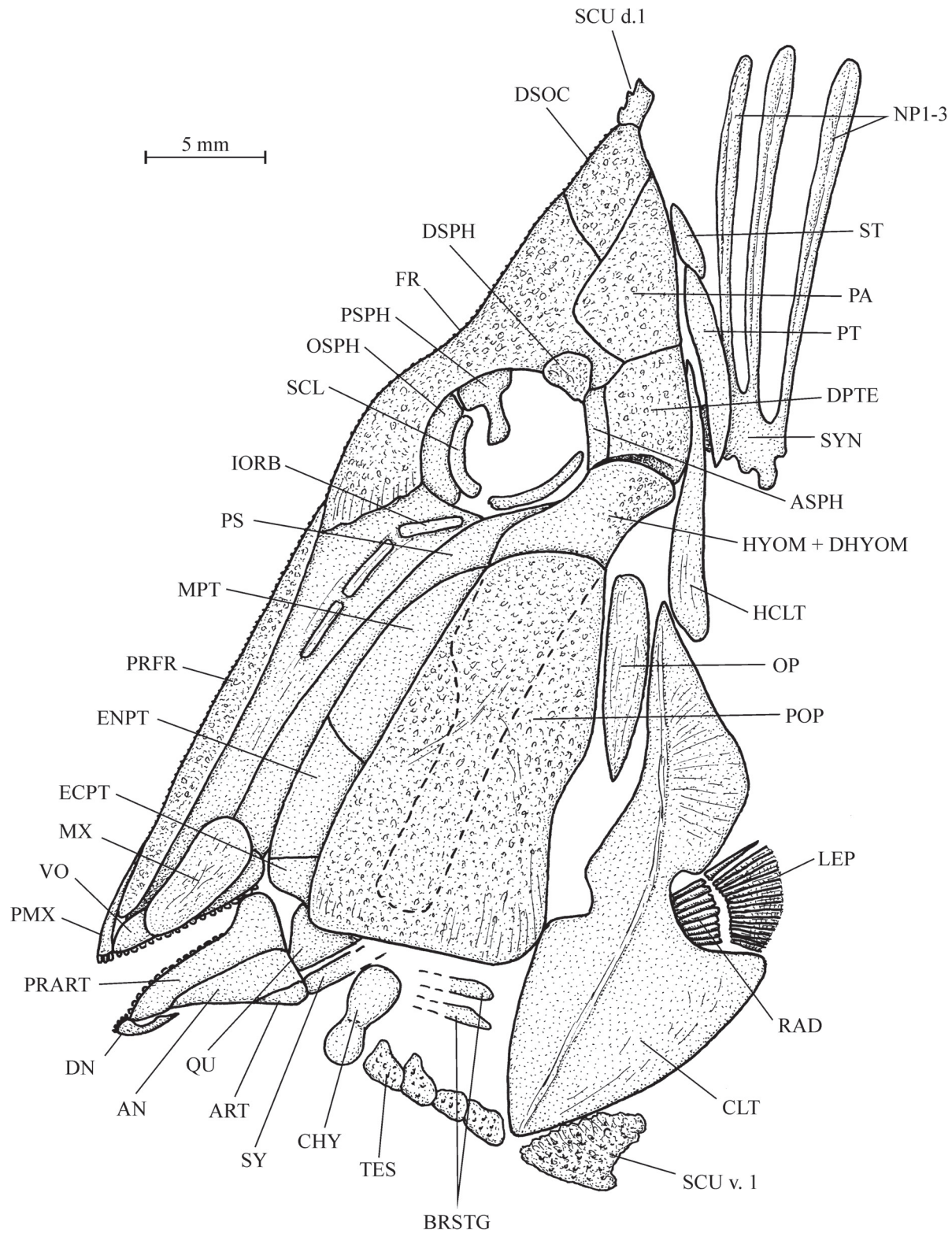


Fig. 10. *Acrorhinichthys poyatoi* gen. et sp. nov. Reconstruction of the skull and the shoulder girdle based on the three specimens. The scale refers to the holotype CLC S-630a, b.

The exposed part of the hyomandibula-dermohyomandibula is much smaller than the preopercle. The long and broad ventral branch of the hyomandibula is visible under the preopercle in paratype CLC S-461 and in the holotype. The hyomandibula is devoid of an opercular process. Traces of a rather large ceratohyal bar are visible in paratype CLC S-1098. The holotype shows a few long and thin branchiospines.

2. The girdles (Figs 6–10, 19)

The cleithrum is very similar to the one of *Proscinetes elegans* (Agassiz, 1833) as figured by Nursall (1996: fig. 11b). The two branches of the bone are separated by a large posterior concavity in which the pectoral fin is inserted. The anteroventral branch is more or less triangular, rather short but very broad and ornamented with a median crest. The dorsal branch is also triangle-shaped, but somewhat narrower than the ventral one and with an acuminate upper extremity. The posttemporal and the deep and narrow hypercleithrum (= supracleithrum) are visible in paratype CLC S-1098. The endochondral part of the girdle is not visible. The short pectoral fin is supported by 8 or 9 pterygiophores and starts with 1 dorsal spine followed by 16 or 17 short segmented rays.

The reduced pelvic girdle is well preserved on the holotype. Each pelvic bone bears 4 segmented rays.

3. The axial skeleton (Figs 1–10)

Samples CLC S-630 (a and b), S-461 and S-1098, respectively, possess 24, 25 and 27 neural spines in front of the epichordal series. All three specimens have 14 haemal spines in front of the hypochordal elements. There are 9 or 10 pairs of long ribs that are broadened in their upper part and so become

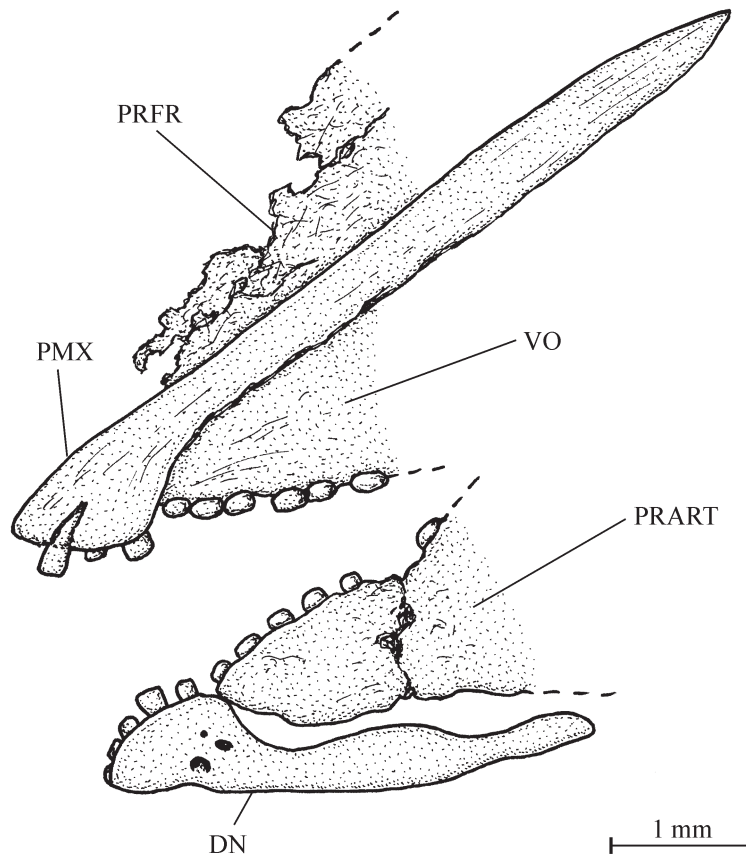


Fig. 11. *Acrorhinichthys poyatoi* gen. et sp. nov. Jaws of holotype CLC S-630a.

contiguous. There are no autogenous neural spines. The first three neural spines are fused to a synarcual that is articulated to the rear of the skull and also seems to include the exoccipital. The neural and haemal spines bear an anterior sagittal flange, except the few ones preceding the epichordal and hypochordal pieces. The neural and haemal arches are well developed, but they do not completely surround the notochord. At the level of the first vertebrae, the neural arches are simply in contact. At the end of the abdominal region and in the caudal region, most neural and haemal arches present a more complex contact by means of one single, small postzygapophysis.

4. The dorsal and anal fins (Figs 1–5)

The shape of the dorsal and anal fins is strip-like (type A2 of Poyato-Ariza & Wenz 2002: fig. 34). The holotype and paratype CLC S-461 have 51 and 55 pterygiophores in the dorsal fin and 36 and 41 pterygiophores in the anal fin, respectively. The dorsal and anal fins of paratype CLC S-1098 are incomplete. The dorsal fin begins just after the dorsal apex. Each dorsal pterygiophore bears a ray. The first ray is reduced to a short spine. The two following rays are long, segmented and pointed. The remaining dorsal rays are segmented and branched. The origin of the anal fin is located at a more posterior level than the dorsal one. The first anal pterygiophore is short and bears a small, spiny ray. The second and the third pterygiophores support longer, segmented and pointed rays. The other anal rays are segmented and branched.

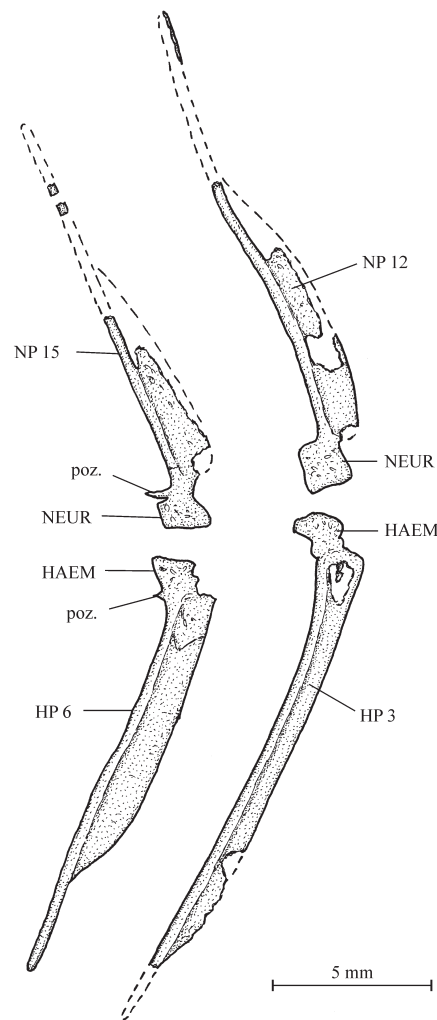


Fig. 12. *Acrorhinichthys poyatoi* gen. et sp. nov. Holotype CLC S-630b. Two vertebral segments, at the level of the twelfth and the fifteenth neural spines.

5. The caudal skeleton (Figs 12–16)

The caudal peduncle is very short because of the proximity of the dorsal and anal fins with the caudal fin. The caudal skeleton is composed of 4 or 5 epichordals, 10 or 11 hypochordals and 2 urodermals. Epichordals and hypochordals are rather long. The seventh, eighth and ninth hypochordals are slightly broadened, but there is no real hypertrophy.

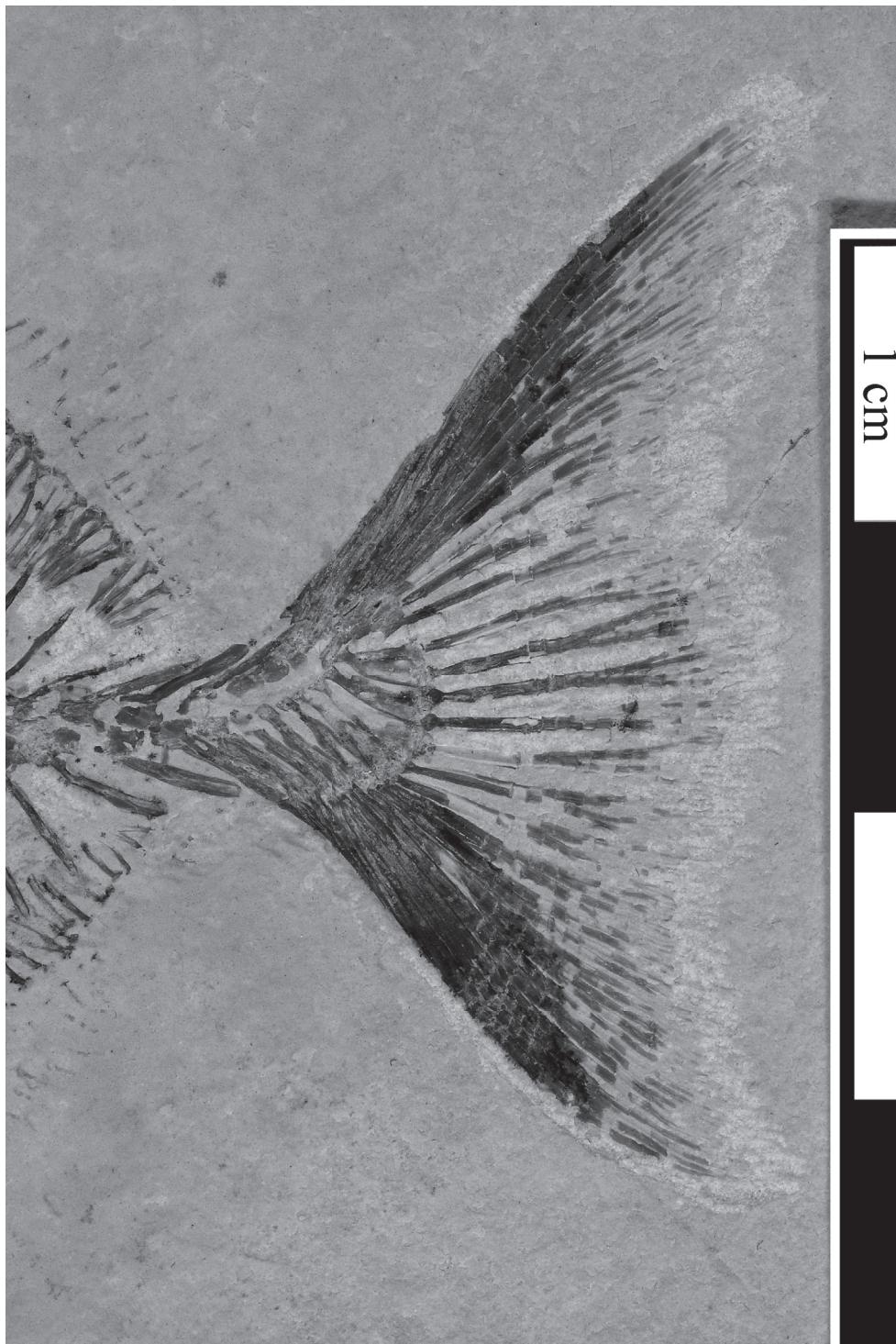


Fig. 13. *Acrorhinichthys poyatoi* gen. et sp. nov. Caudal region of the holotype CLC S-630a.

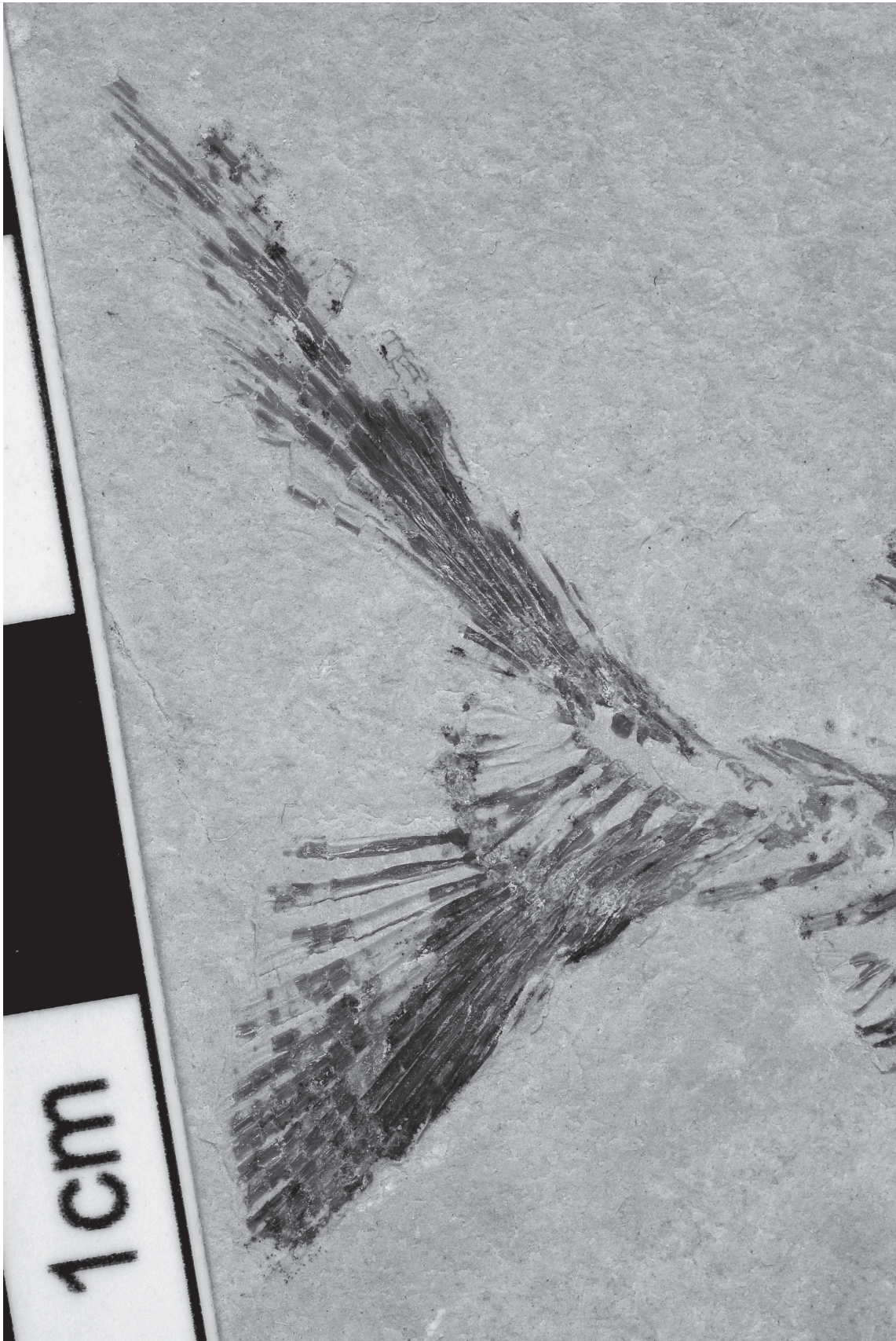


Fig. 14. *Acrorhinichthys poyatoi* gen. et sp. nov. Caudal region of the holotype CLC S-630b.

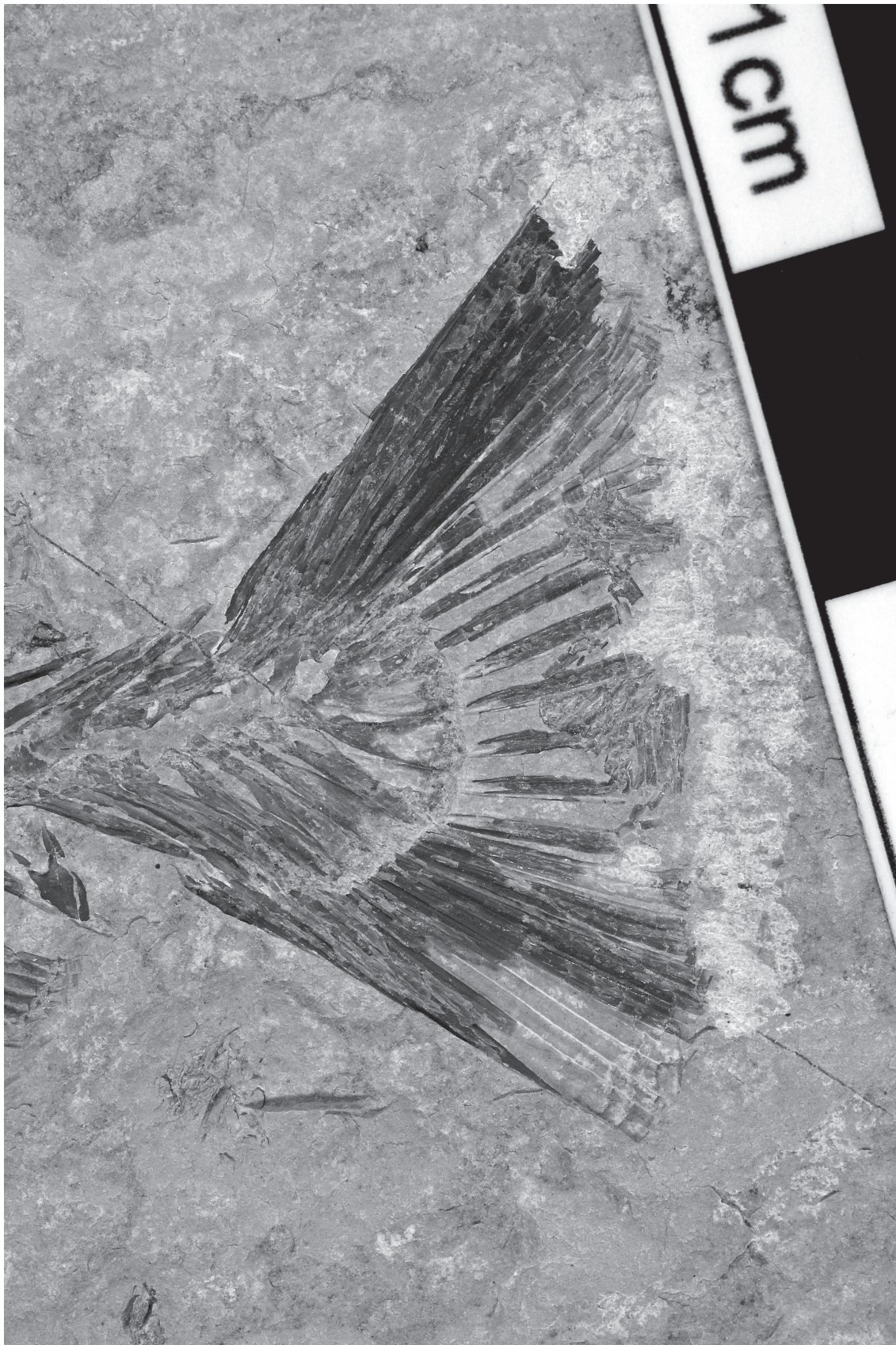


Fig. 15. *Acrorhinichthys poyatoi* gen. et sp. nov. Caudal region of paratype CLC S-461.

The caudal fin is large and its contour is double emarginated (Poyato-Ariza & Wenz 2002: fig. 36E). There are 22 or 23 principal caudal rays, 4 to 6 dorsal and 5 to 6 ventral procurent rays. The most external dorsal and ventral principal rays are segmented and pointed. The other principal rays are segmented and branched.

In paratype CLC S-461, there are a small dorsal and a larger ventral scute preceding the caudal fin.

6. Squamation (Figs 5, 17–18)

The dorsal ridge is perfectly preserved in paratype CLC S-461. It is composed of 8 spiny scutes. The first one bears three small spines and rests on the dermosupraoccipital. The last one bears four spines and is much larger than the preceding scutes. This large eighth scute forms a small prominence at the dorsal apex level.

The holotype (CLC S-630a, b) exhibits the best preserved ventral keel. There are 13 scutes, of which 11 are located between the pectoral girdle and the cloaca, and 2 posterior to the cloaca. They are ornamented with small tubercles. The first one is triangularly shaped, located just below the cleithrum, and is by far the largest of the series. The second and third ones are smaller and rectangular in shape. The eight other

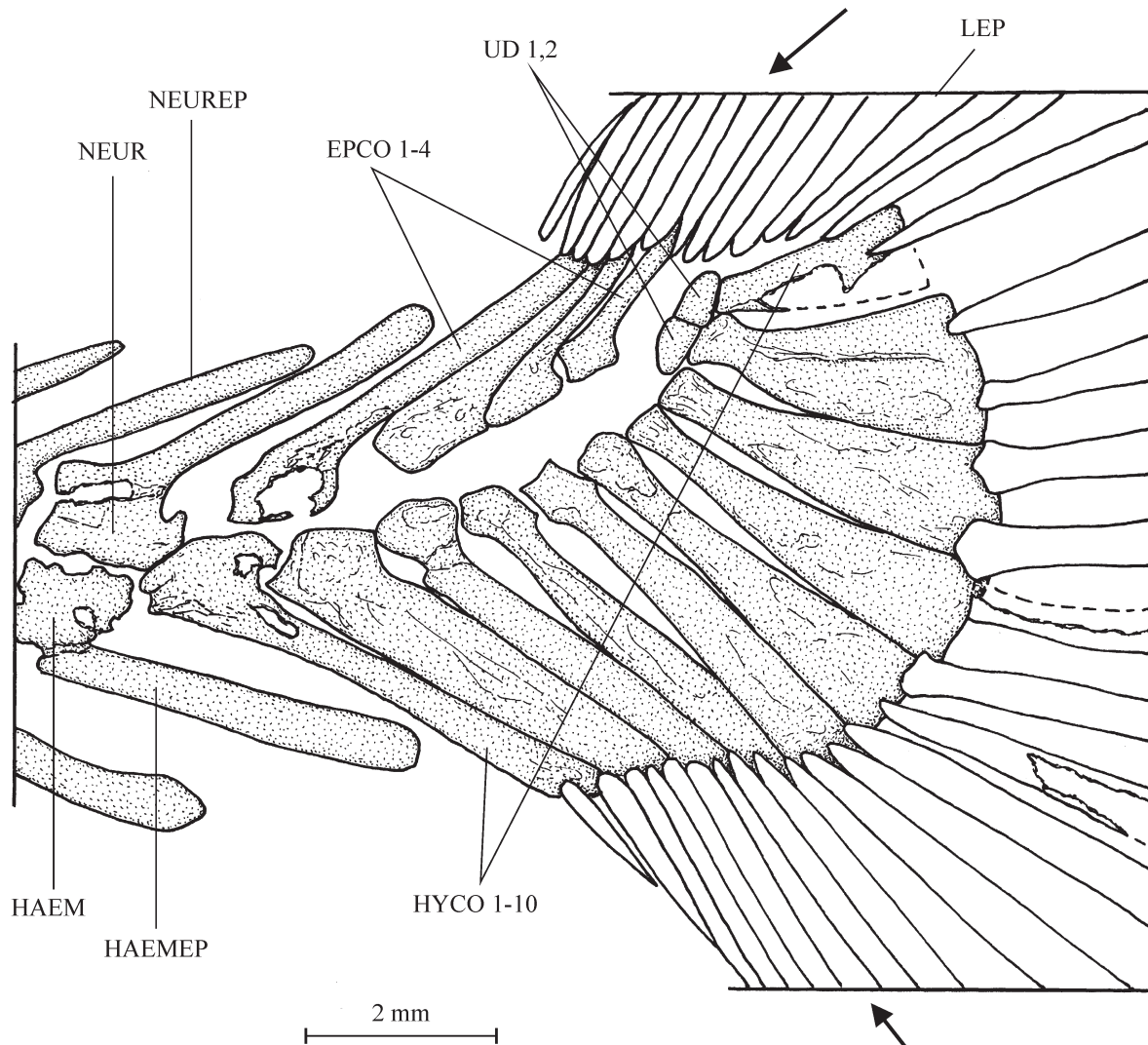


Fig. 16. *Acrorhinichthys poyatoi* gen. et sp. nov. Caudal skeleton of the holotype CLC S-630a, completed with face b. The arrows point to the most external principal caudal rays.

precloacal scutes are smaller still, with a pointed posterior extremity. The two postcloacal scutes are associated with the ventral extremity of the postcoelomic bone. The first one is very small. The second one is much larger and bears two small spines.

The flank scales are restricted to the abdominal region of the fish. A row of complete dorsal scales is associated with the dorsal ridge scutes. The two or three last scales of this series overlap the first dorsal pterygiophores. The scales are also complete in the ventral part of the abdominal region. The other flank scales are reduced to their bar-like component.

Two complete scales are located just above the cloaca. They are imbricated, one overlapping the other. The ventral one is small and triangular. The dorsal one is much deeper, with a lateral wing and a well developed bar-like component. Its ventral margin is broad and concave.

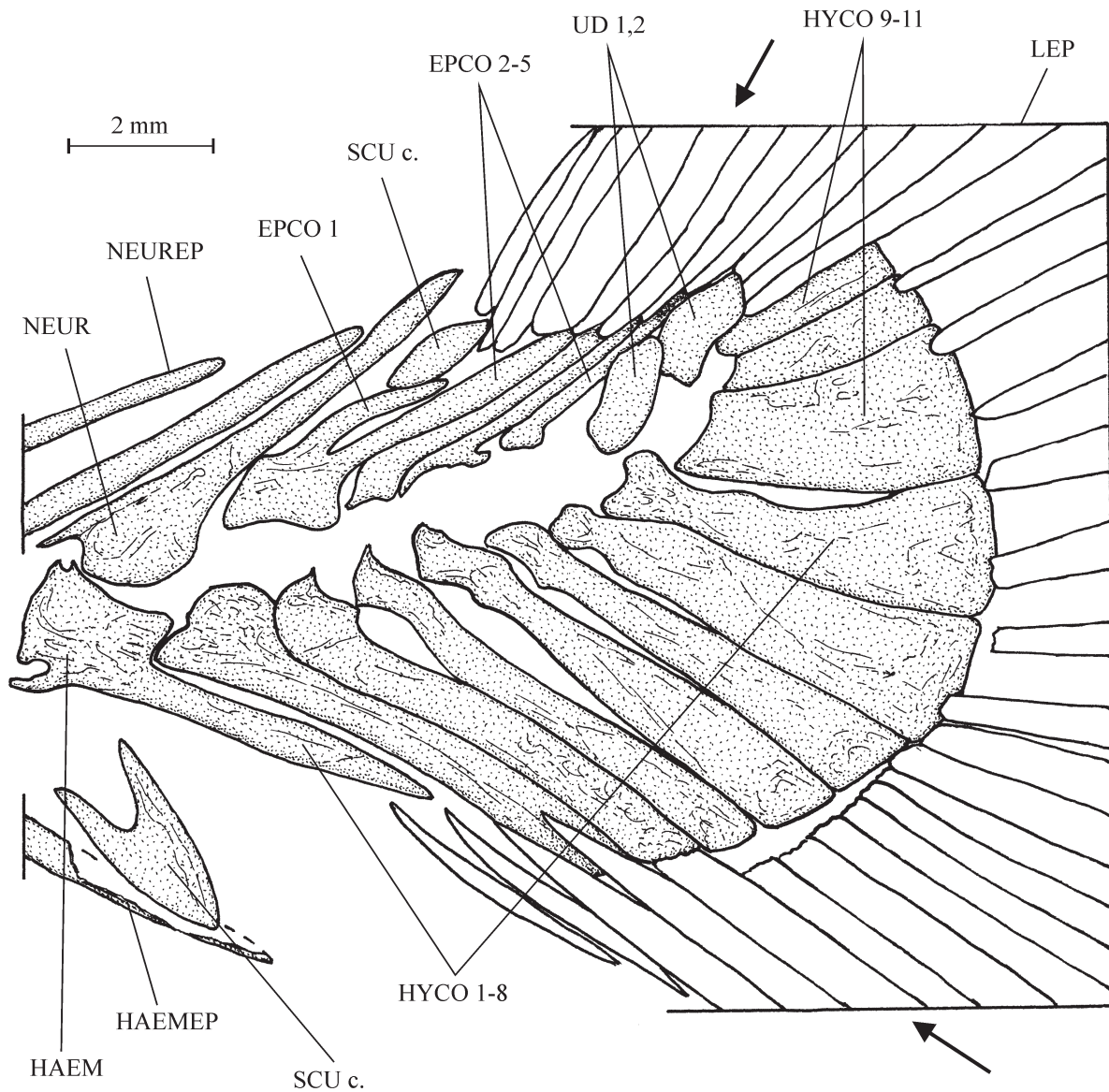


Fig. 17. *Acrorhinichthys poyatoi* gen. et sp. nov. Caudal skeleton of paratype CLC S-461. The arrows point to the most external principal caudal rays.

Discussion

1. *Acrorhinichthys* gen. nov. within Pycnodontomorpha

Nursall (2010) placed the pycnodont fishes in a super-order, Pycnodontomorpha [new usage for the former Pycnodontiformes], divided in two orders, the Gyrodontiformes and the Pycnodontiformes [new usage for the former Pycnodontoidei]. Gyrodontiformes possess a dentary with dorsal and ventral branches, a short, more or less rectilinear parasphenoid, two dermosupraoccipitals, styliform teeth on the premaxilla and dentary, and small bony tesserae covering the cheek and the gular region. In Pycnodontiformes, the dentary preserves only its ventral branch, the parasphenoid is elongated, the teeth on the premaxilla and dentary are incisiform, the bony tesserae of the cheek are lost and there is only one dermosupraoccipital, except in Brembodidae where two dermosupraoccipitals are preserved.

The osteological characters of *Acrorhinichthys* gen. nov. clearly place this fossil fish in the Pycnodontiformes and not in the Gyrodontiformes.

2. *Acrorhinichthys* gen. nov. within Pycnodontiformes

We hereafter use the phylogeny of Pycnodontiformes proposed by Poyato-Ariza & Wenz (2002, 2005) and based on cranial and postcranial characters.

Brembodidae represents the most basal family and the most ancient lineage in the order (Figs 20–23; Tintori 1980; Nursall 1996, 1999; Poyato-Ariza & Wenz 2002). They date from the Upper Norian (Late Triassic) of North Italy. Two genera are known, *Brembodus* Tintori, 1980 and *Gibbodon* Tintori, 1980. They are deep-bodied fishes, with an important dorsal gibbosity or an elongate, spiny dorsal process. *Brembodus* still possesses two well developed dermosupraoccipitals, the posterior one being especially

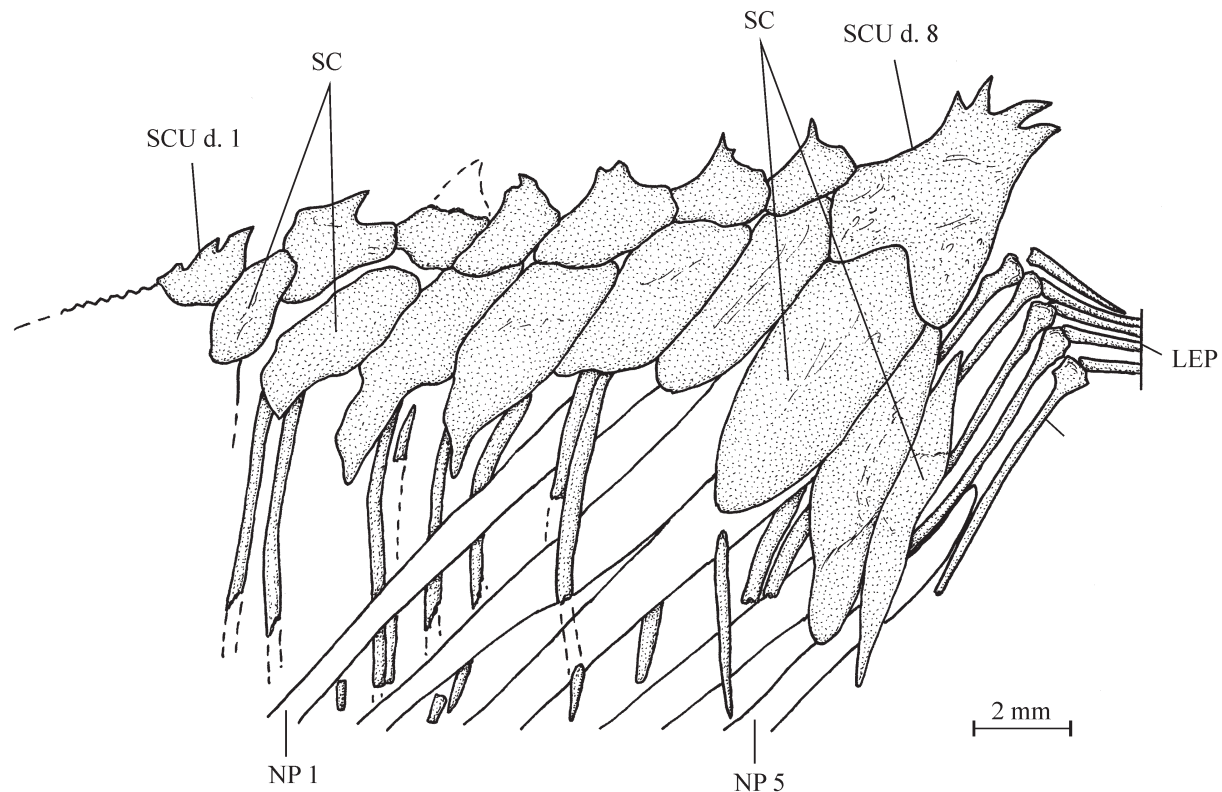


Fig. 18. *Acrorhinichthys poyatoi* gen. et sp. nov. Dorsal ridge scutes of paratype CLC S-461.

elongated. It is to be noted that Tintori (1980: fig. 1) considers the posterior dermosupraoccipital of *Brembodus* as the first scale of the dorsal ridge, and Nursall (1996: 145, character 94) and Poyato-Ariza & Wenz (2002: 195, character 84[1]) as a dorsal spine. However, this large bone not only articulates with, but is also sutured to the anterior dermosupraoccipital and the parietal, exactly as the posterior dermosupraoccipital in the five gyrodontiform genera. So, if this bone is considered as a posterior dermosupraoccipital in Gyrodontiformes, there is no valid reason to give it another name in *B. ridens*. The case of *Gibbodon* is more problematic. Tintori (1980: fig. 2) shows two dermosupraoccipitals in this genus but Poyato-Ariza & Wenz (2002, fig. 6 B) figure only one occipital bone preceding the first small dorsal scute. Both brembodid genera possess tubular posterior infraorbitals and a gigantic first infraorbital completely covering the cheek. They preserve small bony tesserae in the gular region. They have 3 teeth in the upper jaw and 4 or 5 teeth on the dentary. The margins of their unpaired fins bear fringing fulcra. There is a series of urodermals in the caudal skeleton. The scales cover their body totally as in Gyrodontiformes. However, these scales are much deeper than broad, with an important development of the bar component, while the flank scales of *Gyrodus* are less deep and the bar component is less marked (Hennig 1906: pl. 11; Lambers 1991: fig. 3a). There is a mosaic of small scales in the cloacal region of Brembodontidae as in *Gyrodus* (Poyato-Ariza & Wenz 2002: fig. 40A).

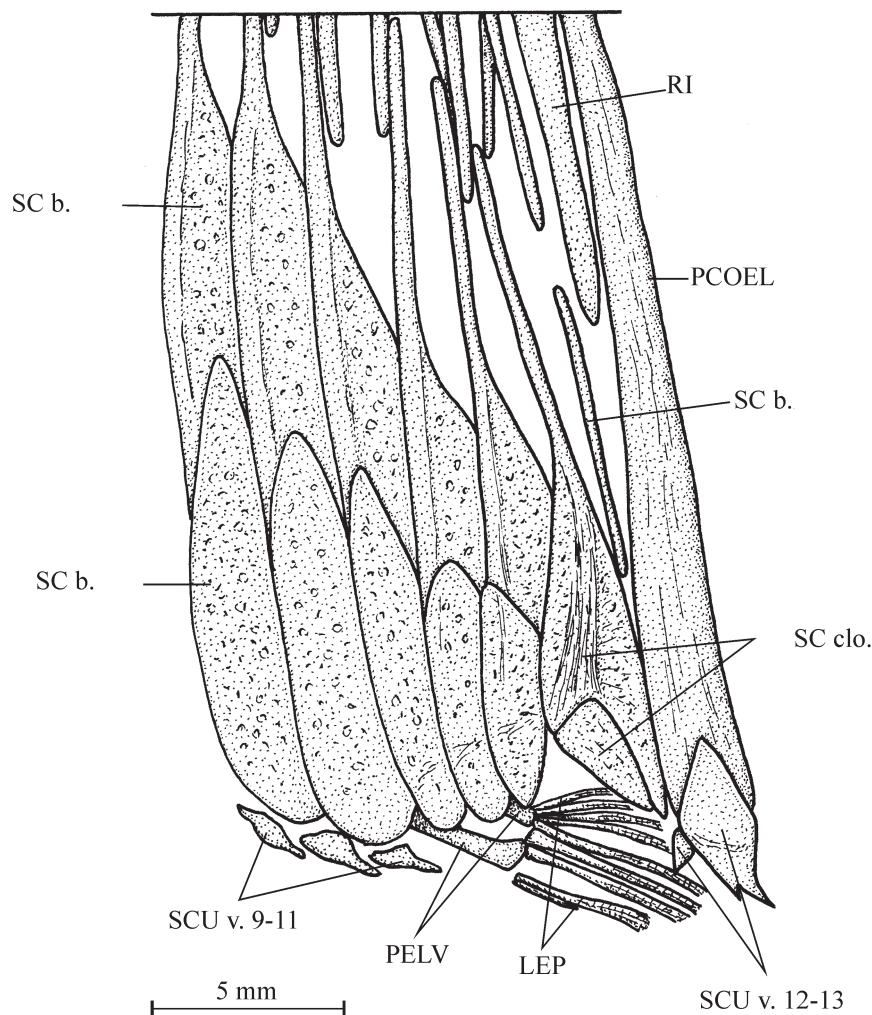


Fig. 19. *Acrorhinichthys poyatoi* gen. et sp. nov. Reconstruction of the pelvic girdle and the scales of the cloacal region based on the holotype CLC S-630a, b.

The new Lebanese fossil fish and the other Pycnodontiformes share at least two apomorphic characters not present in Brembodidae, i.e., the loss of the fringing fulcra and the presence of scales only in the abdominal region of the body.

Macromesodon Blake, 1905 (= *Eomesodon* Woodward, 1918 *pro parte*) seems to be the most basal member of this remaining group (Woodward 1918; Poyato-Ariza & Wenz 2002, 2004). There is a large dorsal prominence as in Brembodidae. Tubular infraorbitals are present, but some bony tesserae are still covering part of the cheek. There is a series of 5 or 6 urodermals in the caudal skeleton. The cloacal region is still covered by a mosaic of small scales as in the most plesiomorphic Pycnodontomorpha. All body scales are completely ossified. *Macromesodon* is generally devoid of fringing fulcra on the impaired fins. However some rare samples still exhibit a few fringing fulcra (Lambers 1991: fig. 25c; Poyato-Ariza & Wenz 2002: 192).

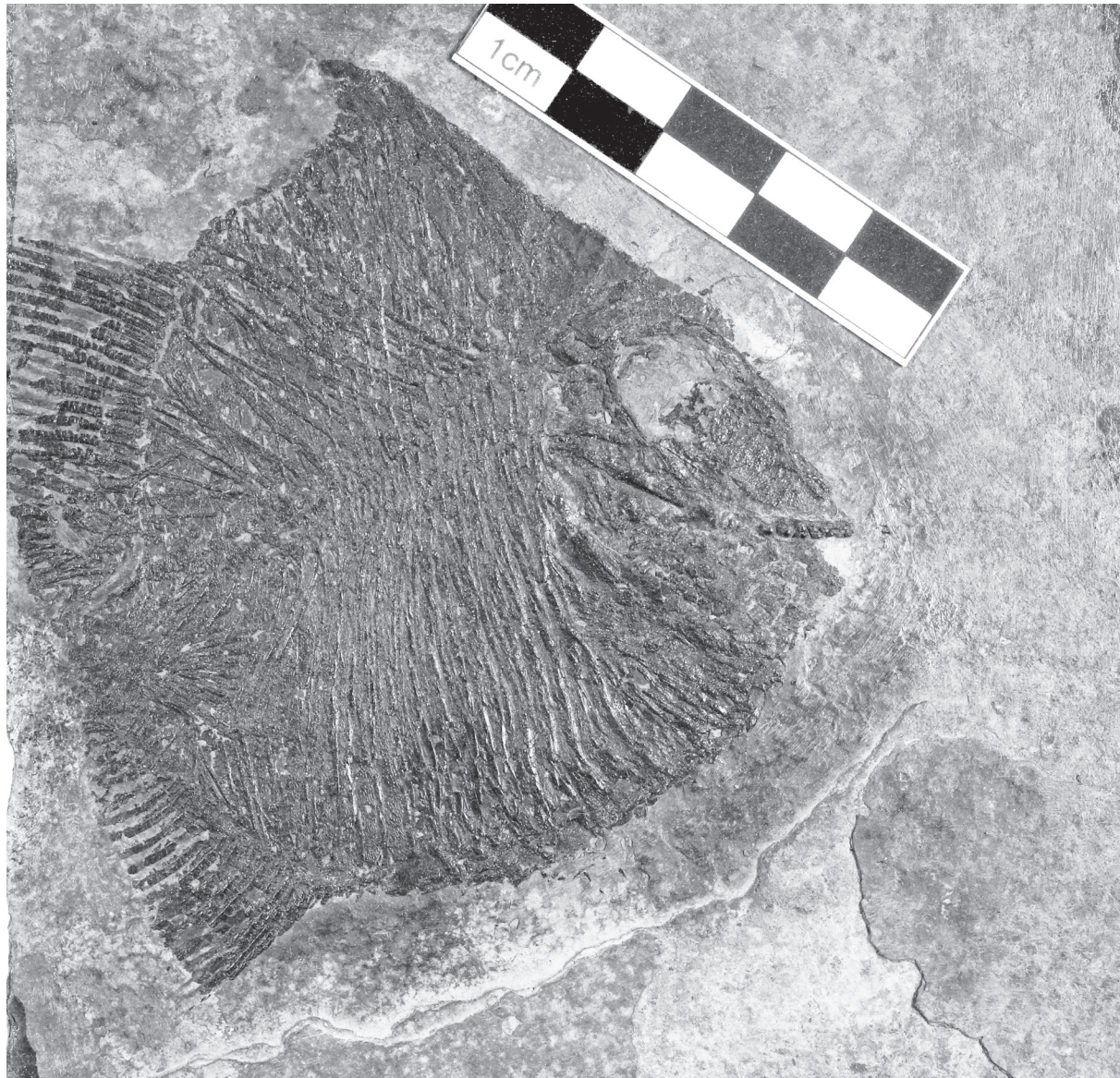


Fig. 20. *Brembodus ridens* Tintori, 1980. Sample CLC J-420 from Zogno, Zorzino Formation, Upper Norian (Late Triassic), Lombardy, Italy.

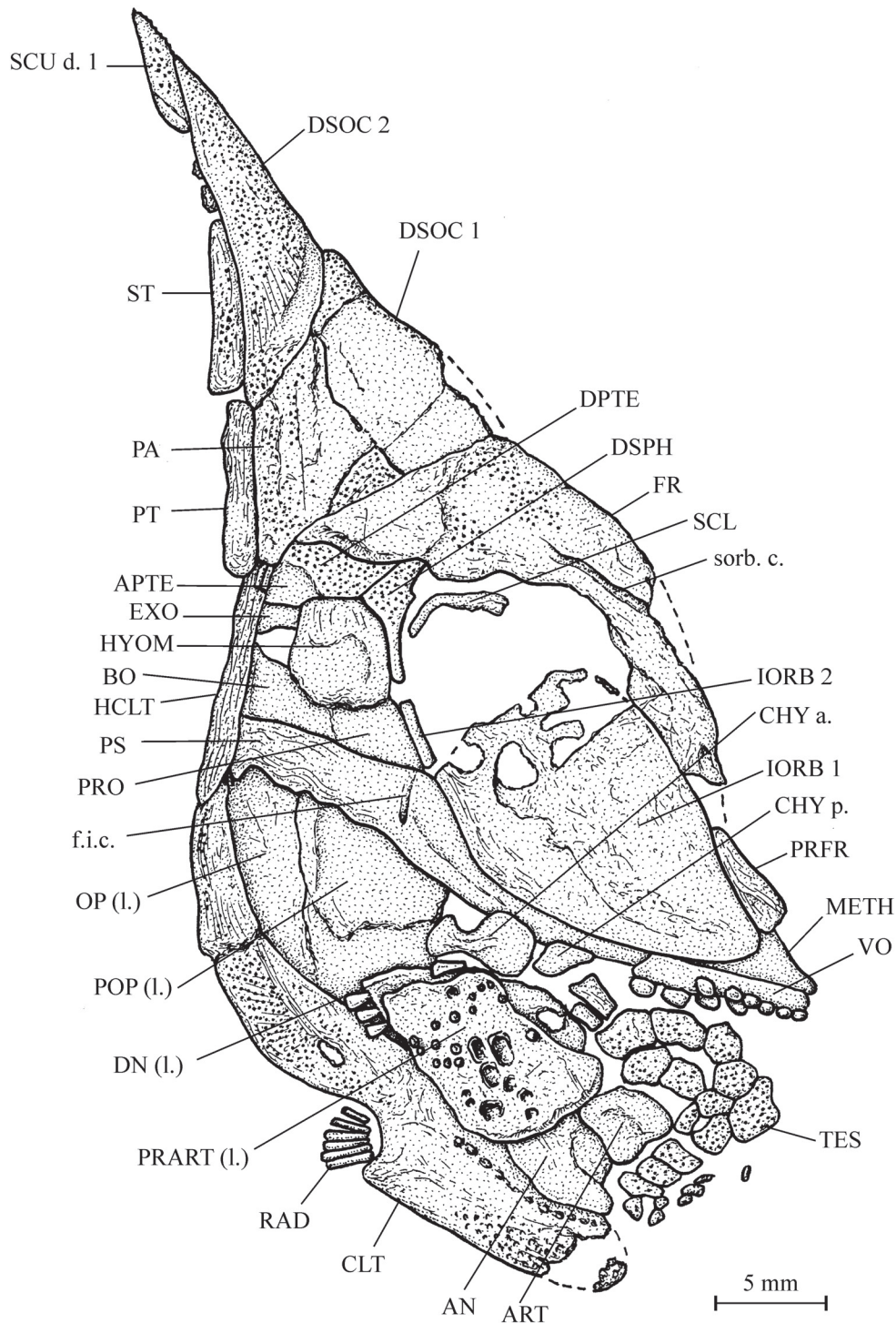


Fig. 21. *Brembodus ridens* Tintori, 1980. Skull and pectoral girdle of sample CLC J-420. The right opercle and preopercle, the ventral part of the hyomandibula, the maxillae, the premaxillae and the right mandible are lost. The left mandible and the hyoid bar are displaced due to the fossilization. The left mandible is seen from its inner face. The first tooth of the dentary is displaced under the anterior ceratohyal. A small part of the inner face of the left opercle and preopercle is visible.

Acrorhinichthys gen. nov. and the more advanced Pycnodontiformes exhibit some new apomorphic characters. A dermohyomandibula is fused with the hyomandibula. There are anterior sagittal flanges on the neural and haemal spines. At least some neural and haemal arches are connected to each other by means of one or more postzygapophyses. The ventral keel contains less than 18 scutes. The urodermal series is reduced to 2, 1 or 0 elements. A part of the body squamation is composed of scale bars. The number of scales in the cloacal region is greatly reduced.

Acrorhinichthys gen. nov. is the most plesiomorphic genus within those remaining Pycnodontiformes. It still possesses a small dorsal prominence and a few gular bony tesserae, two plesiomorphic characters already disappeared in Coccodontidae, Gladiopycnodontidae, Gebrayelichthyidae and Pycnodontidae.

Coccodontidae, Gladiopycnodontidae and Gebrayelichthyidae are three highly specialized families of Pycnodontiformes (Gayet 1984; Nursall & Capasso 2008; Capasso *et al.* 2010; Taverne & Capasso 2013a, 2014a, b, c). Their morphology and osteology are completely different from those of *Acrorhinichthys* gen. nov.

Pycnodontidae are principally characterized by the brush-like process of the parietal, a structure absent in *Acrorhinichthys* gen. nov. However, *Akromystax* Poyato-Ariza & Wenz, 2005 from the Cenomanian of Lebanon (Fig. 24), the most plesiomorphic genus within Pycnodontidae, has preserved some archaic characters absent in the more evolved Pycnodontidae but present in *Acrorhinichthys* gen. nov., such as

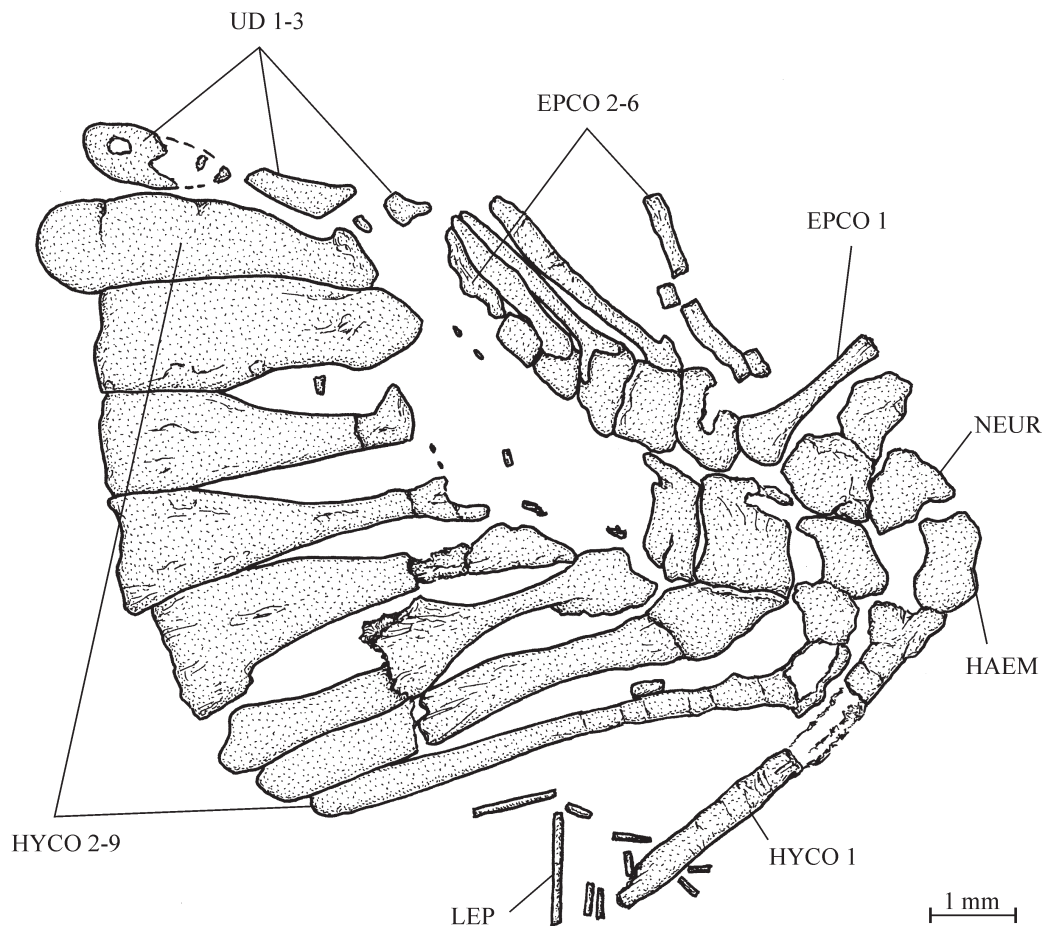


Fig. 22. *Brembodus ridens* Tintori, 1980. Caudal skeleton of sample CLC J-420.

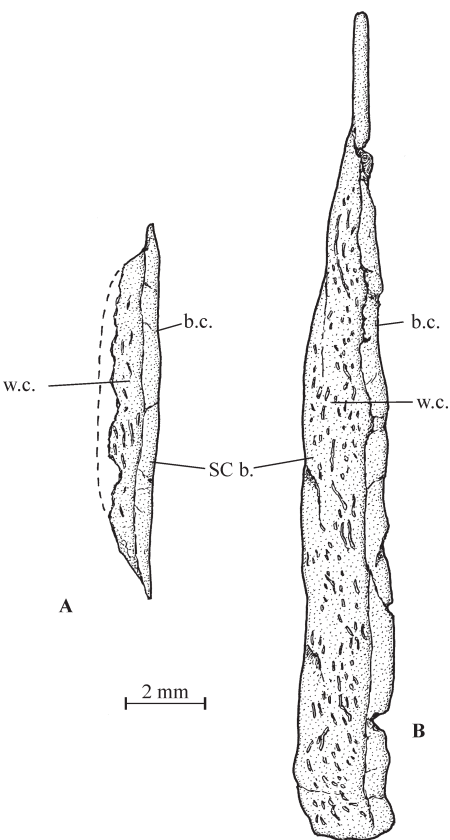


Fig. 23. *Brembodus ridens* Tintori, 1980. Sample CLC J-420. **A.** Scale of the dorsal region. **B.** Scale of the ventral region.

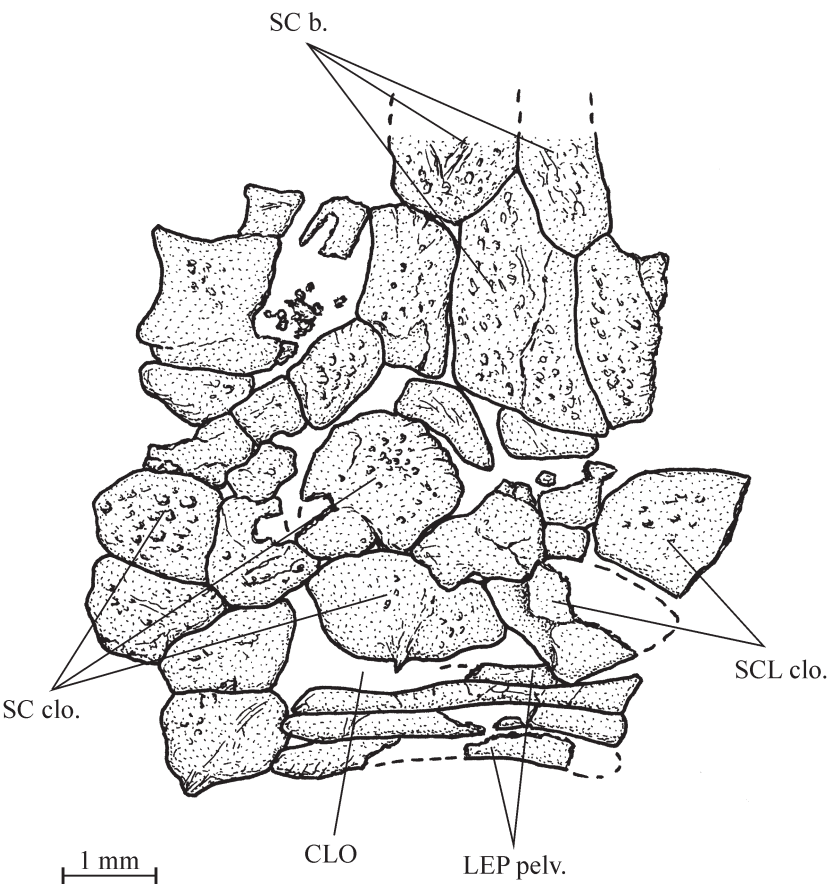


Fig. 24. *Brembodus ridens* Tintori, 1980. Sample CLC J-420. Small scales forming a mosaic surrounding the cloaca.

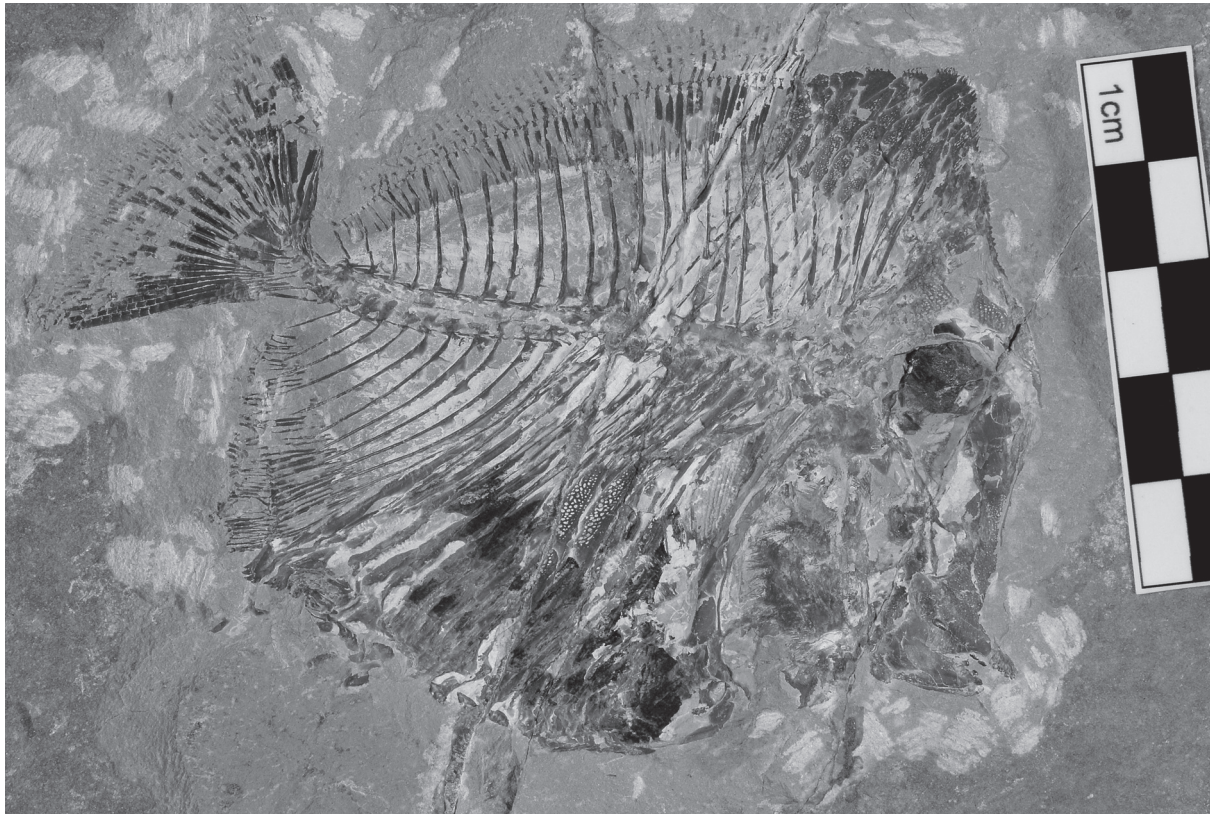


Fig. 25. *Akromystax tilmachiton* Poyato-Ariza & Wenz, 2005. Sample CLC S-712 from the marine Cenomanian of Haqel, Lebanon.

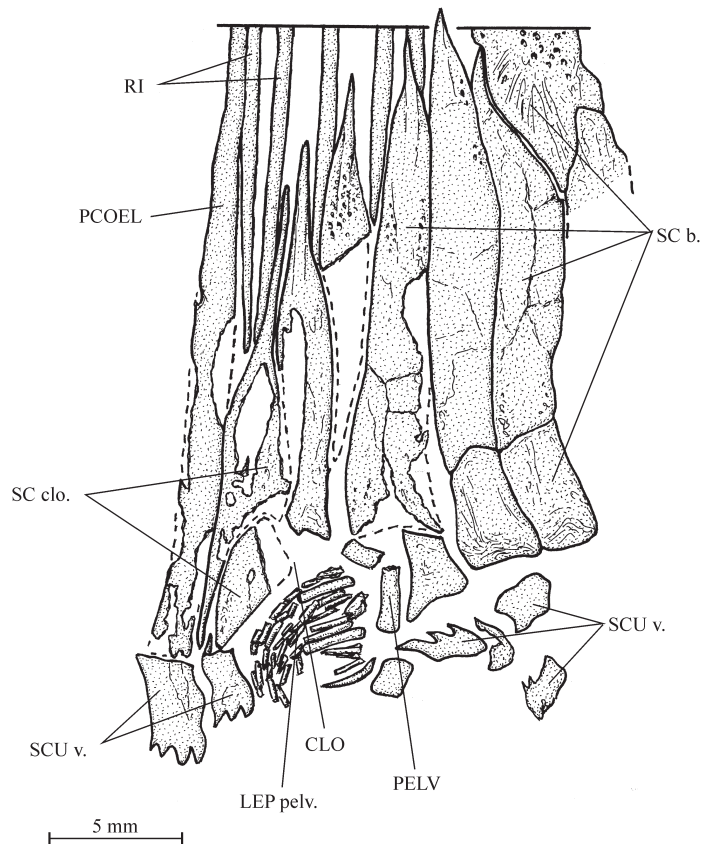


Fig. 26. *Akromystax tilmachiton* Poyato-Ariza & Wenz, 2005. Pelvic girdle and scales from the cloacal region of sample CLC S-712.

a series of complete scales associated with the dorsal ridge scutes (Poyato-Ariza & Wenz 2005: fig. 2), two imbricated complete cloacal scales, a small ventral triangular one and a deeper dorsal, one with a well developed bar component and a broad concave lower margin (Fig. 25), and more than two teeth on the premaxilla and the dentary (Poyato-Ariza & Wenz 2005: fig. 7).

Conclusion

Acrorhinichthys poyatoi gen. et sp. nov. belongs to the order Pycnodontiformes but is less evolved than the Pycnodontidae. It still possesses a few bony plates (= *tesserae*) in the gular region, 3 teeth on the premaxilla and 5 teeth on the dentary. Its parietal is devoid of brush-like process. It shares a few characters with *Akromystax*, the most plesiomorphic genus within Pycnodontidae, characters that have been lost in the other members of the family.

Acknowledgements

We are particularly grateful to Dr. Andrea Pessina, Superintendent of the Soprintendenza per i Beni Archeologici dell'Abruzzo – Chieti, for allowing us to study the fossil fishes of the Luigi Capasso's collection. We thank M. Adriano Vandersypen and M. Wilfried Miseur of the Royal Belgian Institute of Natural Sciences, and M. Luciano Lullo from the University of Chieti for their technical help. We are also indebted to Dr. Jürgen Kriwet (University of Vienna) and to an anonymous reviewer who read and commented on our text.

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Manuscript received: 17 July 2014

Manuscript accepted: 6 January 2015

Published on: 13 March 2015

Topic editor: Christian de Muizon

Desk editor: Kristiaan Hoedemakers

Printed versions of all papers are also deposited in the libraries of the institutes that are members of the *EJT* consortium: Muséum National d'Histoire Naturelle, Paris, France; Botanic Garden Meise, Belgium; Royal Museum for Central Africa, Tervuren, Belgium; Natural History Museum, London, United Kingdom; Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Natural History Museum of Denmark, Copenhagen, Denmark.

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Zeitschrift/Journal: [European Journal of Taxonomy](#)

Jahr/Year: 2015

Band/Volume: [0116](#)

Autor(en)/Author(s): Taverne Luis, Capasso Luigi

Artikel/Article: [Osteology and relationships of *Acrorhinichthys poyatoi* gen. et sp. nov. \(Pycnodontiformes\) from the marine Late Cretaceous of Lebanon 1-30](#)