



New data on the osteology and relationships of *Flagellipinna rhomboides*, a pycnodont fish (Pycnodontidae) from the Cenomanian (Upper Cretaceous) of Lebanon

Nouvelles données sur l'ostéologie et les relations de *Flagellipinna rhomboides*, un poisson pycnodonte (Pycnodontidae) du Cénomanien (Crétacé supérieur) du Liban

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Résumé: Le squelette du poisson fossile *Flagellipinna rhomboides*, un Pycnodontidae du Cénomanien marin (Crétacé supérieur) du Liban, est décrit et sa position systématique au sein de la famille discutée. Le frontal est court, courbé et large. Le processus en brosse du pariétal est raccourci. Les arcs neuraux et hémaux sont en contact hyper-complexe. Les dernières neurépine avant la queue sont vestigiales. La nageoire anale contient 50 à 53 ptérygophores. La nageoire caudale est verticale. Trois hypochordaux sont hypertrophiés. Il y a des écailles-barres non seulement dans la région abdominale mais aussi dans la région caudale du corps. Tous ces caractères indiquent clairement que *F. rhomboides* appartient aux Nursalliini, une tribu spécialisée de la sous-famille Pycnodontinae.

Mots-clés: Pycnodontiformes, Pycnodontidae, *Flagellipinna rhomboides*, ostéologie, relations, Cénomanien, Liban.

Abstract: The skeleton of the fossil fish *Flagellipinna rhomboides*, a Pycnodontidae from the marine Cenomanian (Late Cretaceous) of Lebanon, is described and its systematic position within the family discussed. The frontal is short, curved and broad. The brush-like process of the parietal is shortened. The neural and haemal arches are in hyper-complex contact. The last neural spines before the tail are vestigial. The anal fin contains 50 to 53 pterygiophores. The caudal fin is vertical. Three hypochordals are hypertrophied. There are bar-scales not only in the abdominal but also in the caudal region of the body. All these evolved characters clearly indicate that *F. rhomboides* belongs to the Nursalliini, a specialized tribe of the subfamily Pycnodontinae.

Key words: Pycnodontiformes, Pycnodontidae, *Flagellipinna rhomboides*, osteology, relationships, Cenomanian, Lebanon.

INTRODUCTION

Flagellipinna CAWLEY & KRIWET, 2019) is a recently erected genus of pycnodont fish from the marine Cenomanian (Upper Cretaceous) of Haql, Lebanon. The genus contains only one species, *Flagellipinna rhomboides* CAWLEY & KRIWET, 2019, and is referred to the family Pycnodontidae, a brush-like process being present on the parietal (named “postparietal” in CAWLEY & KRIWET, 2019). *F. rhomboides* is easily recognizable by its acute snout, its exceptionally elongate opercle, its extremely deep and rhomboid-shaped body and chiefly by its whip-like dorsal fin. Two specimens of the same species, from Haql, were already figured in GAYET *et al.* (2012: fig. p. 92, fig. p. 93, right) but left unnamed.

The original description is based on four specimens housed in the paleontological collection of the Muséum National d'Histoire Naturelle, Paris, France (CAWLEY & KRIWET, 2019: 2, Fig. 1A, B, C, D). Unfortunately, the preservation of these four samples is not perfect. Many anatomical features remain poorly known or even unknown. For this reason, the two authors were unable to precise the exact systematic position of *F. rhomboides* within the family Pycnodontidae.

The CAPASSO collection contains four specimens of *F. rhomboides* also from Haql. Their study allows to greatly complete the osteological description of this fossil fish and to discuss in a detailed way its precise relationships with the other members of the family. That is the aim of our present paper.

However, we will give only a short description, recalling the principal features of the skeleton. For more detailed information, we refer the readers to the original paper of CAWLEY & KRIWET (2019). We emphasize

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principally on some parts of the skull, of the vertebral axis, of the fins, of the caudal skeleton and of the squamation not described or not completely described by these two colleagues.

MATERIAL AND METHODS

The specimens described in our present paper belong to the CAPASSO registered collection (CLC) in Chieti.

The material was studied with a stereomicroscope Leica Wild M 8. The figures were drawn by the first author (L. T.) and the photos made by Mr. Luciano LULLO, from the University of Chieti-Pescara. Aspersions with ethanol and razing light were used to improve some observations.

The Capasso collection (CCL) in Chieti (Italy) is legally registered by a decree of the Ministero per I Beni e le Attività Culturali under the date of October 11th 1999, following the disposition of the Italian law 1089/39. The Soprintendenza per I Beni Archeologici dell'Abruzzo-Chieti has authorized the authors to study this collection by two letters bearing the dates of May 5th, 2011 (ref.: MBAC-SBA-ABR PROT 0004537 05/05/ 2011 Cl. 34.25.01/2.1) and July 30th, 2014 (ref.: MBAC-SBA-ABR PROT 0005618 31/07/2014 Cl. 34.25.01/2.1).

List of abbreviations used in text-figures

AN	=	angular
ART	=	articular
BRSTG	=	branchiostegal rays
CHY a., p.	=	ceratohyal (anterior, posterior)
CIRC	=	tubular bones of the circumorbital sensory canal
CLO	=	cloaca
CLT	=	cleithrum
DHYOM	=	dermohyomandibula
DN	=	dentary
DPTE	=	dermopterotic
DSOC	=	dermosupraoccipital
DSPH	=	dermosphenotic
ECPT	=	ectopterygoid
ENPT	=	entopterygoid (= endopterygoid)
EPCO 1-6	=	epichordals 1 to 6
FR	=	frontal
HCLT	=	hypercleithrum (= supracleithrum)
HHY	=	hypohyal
HP 16	=	haemal spine (sixteenth)
HYCO 1-	=	hypochordals 1 to
HYOM	=	hyomandibula
IHY	=	interhyal
IORB	=	infraorbital
LEP	=	lepidotrichium (= ray)
METH	=	mesethmoid
MPT	=	metapterygoid
MX	=	maxilla
NP 33	=	neural spine (thirty-third)
OP	=	opercle
PA	=	parietal
PCLT	=	postcleithrum
PCOEL	=	postcoelomic bone
PMX	=	premaxilla
POP	=	preopercle
PRART	=	prearticular
PRFR	=	prefrontal
PS	=	parasphenoid
PT	=	posttemporal
QU	=	quadrate
RAD	=	pterygiophores (= radials)
RI	=	ribs
SC	=	scales
SC clo.	=	cloacal scales
SCU d. 1	=	scutes of the dorsal ridge (first)
SCU v. 1-16	=	scutes of the ventral keel (first to sixteenth)
SY	=	symplectic
PT	=	posttemporal

VO	=	vomer
b. pr.	=	brush-like process (= branched peniculus) of the parietal
br.	=	broken
co. pr.	=	coronoid process of the prearticular
l.	=	left
sorb. c.	=	supraorbital sensory canal
r.	=	right
ro. reg.	=	rostral region
th.	=	teeth of the premaxilla
v. l. s. l.	=	ventral lateral sensory line

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

Family Pycnodontidae AGASSIZ, 1833 *sensu* NURSALL, 1996

Subfamily Pycnodontinae POYATO-ARIZA & WENZ, 2002

Tribe Nursalliini TAVERNE & CAPASSO, 2018

Genus *Flagellipinna* CAWLEY & KRIWET, 2019

Species *Flagellipinna rhomboides* CAWLEY & KRIWET, 2019

Emended diagnosis

Some characters must be added to the original diagnosis of CAWLEY & KRIWET (2019). Brush-like process of the parietal shortened. Small ventral “V”-shaped notch at the junction between the skull and the cleithrum. 31 to 33 neural spines before the epichordal series. 14 to 16 haemal spines before the hypochordal pieces. Neural and haemal arches in hyper-complex contact. Last neural spines before the tail vestigial. Dorsal fin with 50 to 53 rays and 48 to 51 pterygiophores. Anal fin with 51 to 54 rays and 50 to 53 pterygiophores. Caudal fin vertical, with 24 to 26 principal rays. Six epichordals. Eleven hypochordals. Three hypochordals hypertrophied. 17 to 21 spiny dorsal ridge scutes. 16 spiny ventral keel scutes, 12 pre- and 4 postcloacal. Complete scales in the cloacal region. Cloaca surrounded by 2 scales not in contact with the ventral scutes. Five postcloacal scales, four in contact with the ventral scutes, the last one on the postcoelomic bone.

Material

CLC S-305, a complete specimen (Fig. 1). Total length: 114 mm.

CLC S-487, a complete specimen (Fig. 6). Total length: 105 mm.

CLC S-1077a, b, a complete specimen, two faces (Figs 2, 3). Total length: 86 mm.

CLC S-1094a, b, a complete specimen, two faces (Figs 4, 5). Total length: 124 mm.



Figure 1: *Flagellipinna rhomboides*.
Specimen CLC S-305.



Figure 2: *Flagellipinna rhomboides*.
Specimen CLC S-1077 side a



Figure 3: *Flagellipinna rhomboides*.
CLC S-1077, side a



Figure 4: *Flagellipinna rhomboides*.
CLC S-1094, side ba



Figure 5: *Flagellipinna rhomboides*.
CLC S-1094, side b.



Figure 6: *Flagellipinna rhomboides*. Specimen CLC S-487

Formation and locality

Marine Late Cenomanian deposits (Sannine Formation) of Haqel, Lebanon.

Osteology

The skull (Figs 7-13)

The snout is elongate and acute, with an obliquely oriented mouth gape and a rather small lower jaw.

A small prefrontal is present on the mesethmoid. The frontal is short, curved and broad along its posterior margin. The parietal bears a very short brush-like process (= branched peniculus). There is no temporal (= dermocranial) fenestra.

The vomer is well visible on specimen CLC S-305 and is still better preserved on sample CLC S-1094a, b. Only one row of five teeth is visible. The first three teeth are small and supported by a short peduncle. The two last teeth are large, ovoid and molariform, with a concave surface. Their contour is devoid of crenulations.

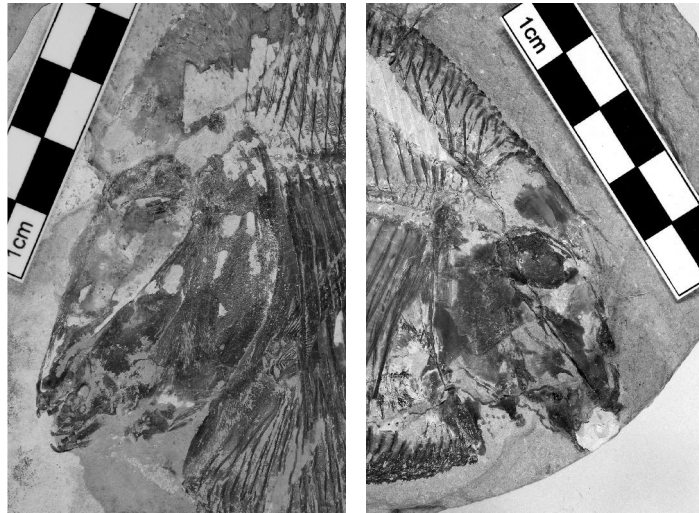


Figure 7: *Flagellipinna rhomboides*. **Figure 8:** *Flagellipinna rhomboides*.
Head region of specimen CLC S-305. Head region of specimen CLC S-487.

Both the premaxilla and the dentary bear two small incisiform teeth. The lower jaw is seen in internal view on the specimens CLC S-305 and CLC S-1094a, b. The coronoid process is high but with a narrow tip. The prearticular bears only two rows of molariform teeth, 6 in the upper row and 3 in the lower row. The most posterior teeth of each row are the largest. They have a concave surface and their contour is devoid of crenulations.

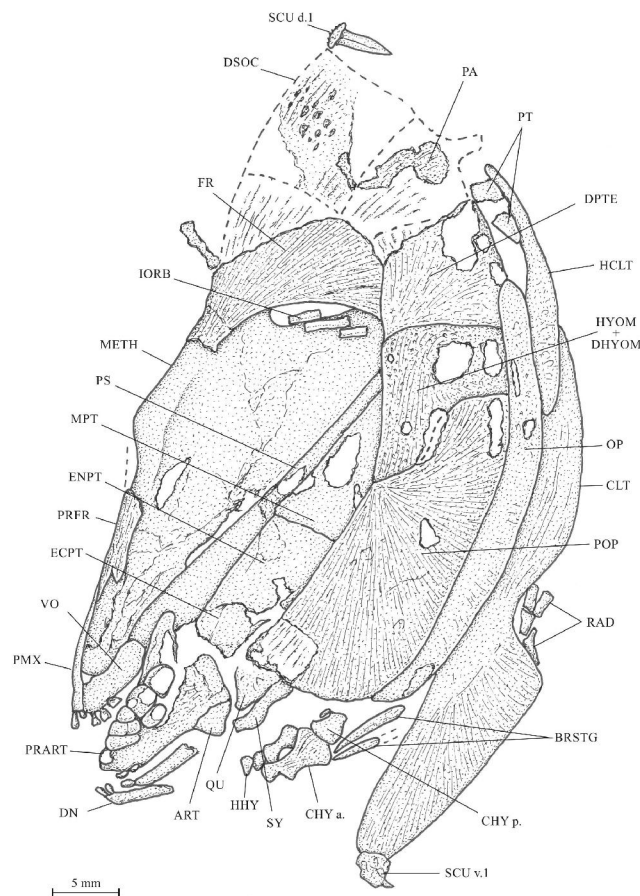


Figure 9: *Flagellipinna rhomboides*. Skull and pectoral girdle of specimen CLC S-305.

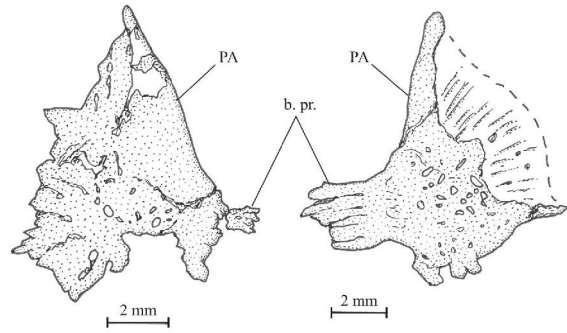


Figure 10: *Flagellipinna rhomboides*. Parietal of specimen CLC S-1077a (left) and of specimen CLC S-487 (right).

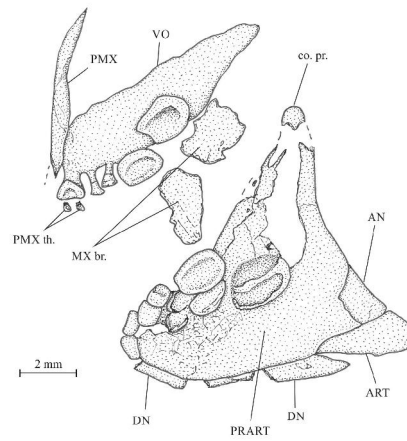


Figure 11: *Flagellipinna rhomboides*. Vomer and lower jaw of specimen CLC S-1094a.

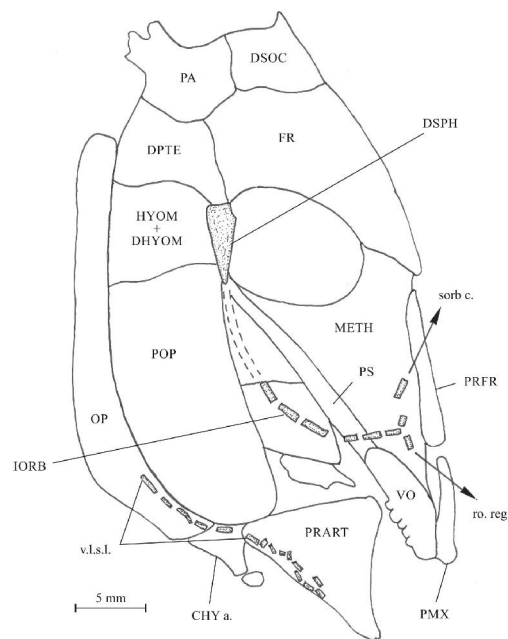


Figure 12: *Flagellipinna rhomboides*. The orbital bones and the ventral lateral sensory canal of specimen CLC S-487.

The orbital bones are completely preserved on specimen CLC S- 487. The series contains the dermosphenotic and nine small tubular infraorbitals that form an arched chain on the cheek. This chain is divided in two branches, one dorsal and one ventral, at its anterior extremity. Two elements are dorsally oriented towards the supraorbital sensory canal. A third piece is ventrally directed towards the rostral region. The dermosphenotic is arrow-head-shaped, with an acuminate ventral extremity.

The preopercle is much larger than the exposed part of the hyomandibula-dermohyomandibula. The opercle is narrow but much elongate than in any other known species of pycnodontiform fish. Its dorsal tip is located at the level of the dermopterotic, while its ventral extremity reaches the ventral margin of the preopercle.

The hyoid bar contains one hypohyal, the anterior and the posterior ceratohyals and a small interhyal. Two branchiostegal rays are attached to the anterior ceratohyal.

A series of small tubular bones extends from the level of the lower jaw to the most ventral region of the opercle in specimen CLC S-487. These small bones carry a short ventral lateral line canal.

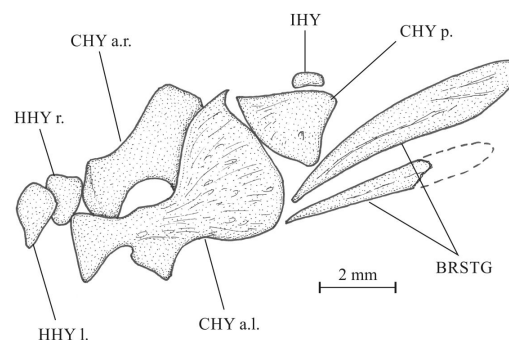


Figure 13: *Flagellipinna rhomboides*. Hyoid bar and branchiostegal rays of specimen CLC S-305.

The girdles (Figs 7-9)

The cleithrum has a long and narrow ventral branch. There is a ventral “V”-shaped notch at the junction between the skull and the cleithrum. This notch is however less pronounced than in *Nursallia* BLOT, 1987 and *Paranursallia* TAVERNE *et al.*, 2015.

The axial skeleton (Figs 1-6)

There are 31 to 33 neural spines before the epichordal series and 14 to 16 haemal spines before the hypochordal pieces. The first haemal spine is much shorter than the following ones. These neural and haemal spines bear an anterior bony sagittal wing. The first 6 to 8 neural spines are autogenous. The last neural spines before the caudal fin are vestigial. The neural and the haemal spines are in hyper-complex contact by a series of pre- and postzygapophyses. This highly specialized situation is not shown in the general reconstruction of the fish in CAWLEY & KRIWET (2019: fig. 2) but is however clearly visible on paratype MNHN.HAK1972b (*ibid.*, 2019: fig. 7). There are from 3 to 17 interdigitations depending on the specimens and on the location in the skeletal axis. There are 9 to 11 pairs of long ribs that are broadened in their upper part. The postcoelomic bone is long and narrow. It contacts the axial skeleton.

The dorsal and anal fins (Figs 1-6)

The dorsal fin origin is located at the dorsal apex. The fin contains 50 to 53 rays and is supported by 48 to 51 pterygiophores. The first rays are extremely elongated, giving a whip-like shape to the fin.

The anal fin is falcate (POYATO-ARIZA & WENZ, 2002: fig. 34, outline B). Its origin is positioned at the ventral apex. There are 51 to 54 rays and 50 to 53 pterygiophores.

The caudal skeleton (Figs 14-16)

Neither the holotype nor the three paratypes allow a good description of the caudal endoskeleton. Only a small part of this skeleton, reduced to the first five hypochordals, is figured by CAWLEY & KRIWET (2019: fig. 7). The caudal skeleton is complete and well preserved in our material. There are 6 epichordals and 11 hypochordals. The first four epichordals bear a short neural spine while the last two ones are devoid of neural spine. Three posterior hypochordals are strongly hypertrophied. No urodermal is visible.

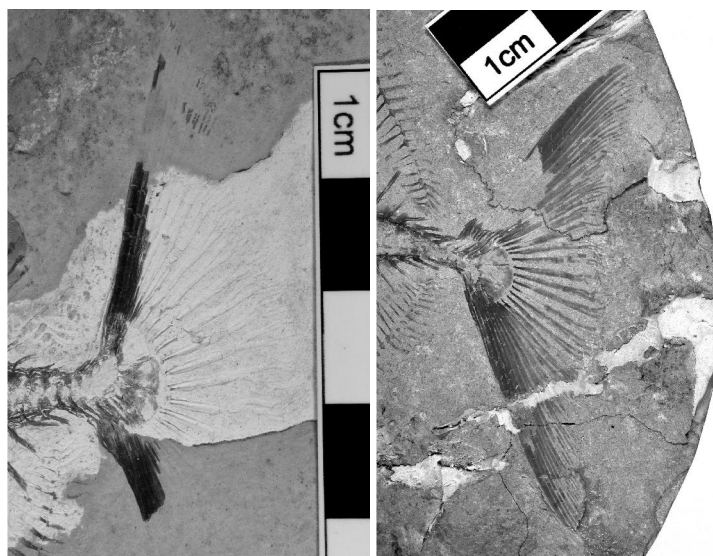


Figure 14: *Flagellipinna rhomboides*. **Figure 15:** *Flagellipinna rhomboides*.
Tail region of specimen CLC S-305 Tail region of specimen CLC S-487.

The caudal fin is incomplete and badly preserved on the holotype and the paratypes (CAWLEY & KRIWET, 2019: fig. 1A, B, C, D). Their general reconstruction of the fish (ibid., 2019: fig. 2) shows a small triangular fin, with a straight posterior margin. That is erroneous. The fin is complete and well visible on our material. Its outline is vertical (cf. POYATO-ARIZA & WENZ, 2002: fig. 36F). This vertical shape is also visible on the holotype and on paratype MNHN.F.HAK1972a (CAWLEY & KRIWET, 2019: fig. 1A, C). The caudal fin contains 24 to 26 principal rays, 2 or 3 dorsal and 4 or 5 ventral procurent rays (= basal fulcra).

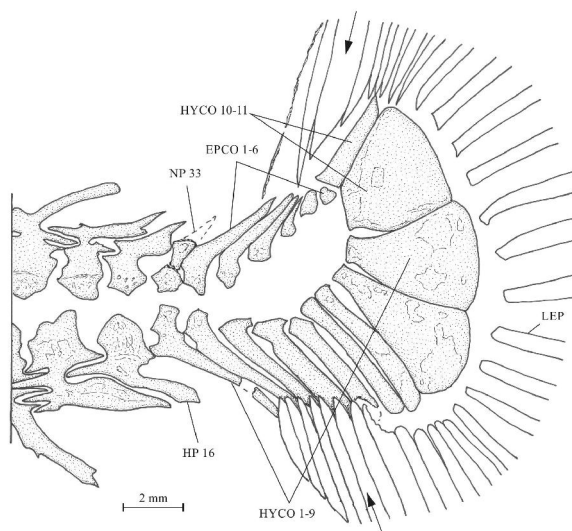


Figure 16: *Flagellipinna rhomboides*. Caudal skeleton of specimen CLC S-305.

Squamation (Figs 17, 18)

There are bar-scales not only in the abdominal but also in the caudal region of the body, before the tail. The scales are complete in the ventral part of the abdominal region. In this region and before the cloacal level, the bar-like component represents the posterior margin of the scale, the wing-like component forming the anterior part of the scale.

Traces and fragments of 15 dorsal ridge scutes are present on sample CLC S-305 and 21 dorsal scutes are preserved on specimen CLC S-487. Each scute is associated to an underlying deep scale that have a central bar-

like component and anterior and posterior wing-like components, as in *Nusallia veronae* BLOT, 1987 from the Eocene of Italy (BLOT, 1987: fig. 61). The scutes have a spiny dorsal margin. The spines are very small in the first scutes but become progressively larger on the last scutes. The last scute is the largest of the series. It bears an acuminate upper tip that rises up just before the first ray of the dorsal fin.

The ventral keel of specimen CLC S-305 is completely preserved. It contains 16 scutes, 12 before and 4 behind the cloaca. All these scutes are spiny. The first scute is attached to the cleithrum. The twelfth scute, located just at the cloacal level, is reduced. The sixteenth and last scute is enlarged and divided in two branches that surround the ventral extremity of the postcoelomic bone.

The scales of the cloacal region are perfectly preserved in specimen CLC S-305. All these scales are complete but most of them are devoid of bar-like component. The cloaca is surrounded by two scales that are not in contact with the ventral scutes. There are five postcloacal scales. The first four ones are in contact with the ventral scutes. The fifth scale lies on the postcoelomic bone.

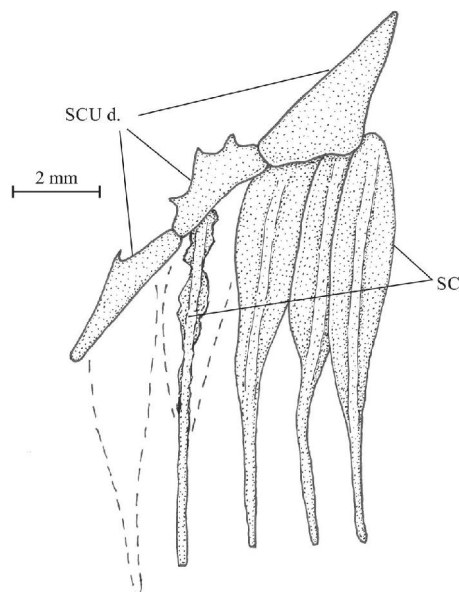


Figure 17: *Flagellipinna rhomboides*.
The three last dorsal ridge scutes of specimen CLC S-305

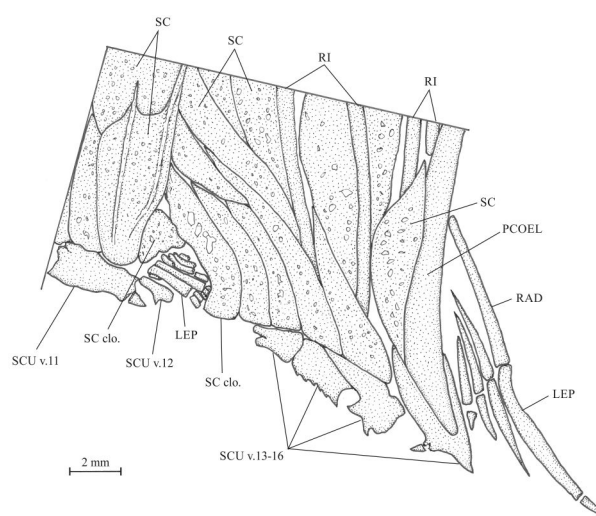


Figure 18: *Flagellipinna rhomboides*.
Scales of the cloacal region of specimen CLC S-305.

DISCUSSION

As already written, CAWLEY & KRIWET (2019) refer *Flagellipinna rhomboides* to the family Pycnodontidae. Indeed, a short brush-like process is attached on the posterior margin of the parietal and this osteological feature is the main character defining the family (POYATO-ARIZA & WENZ, 2002, node 13, character 14[1]).

A more detailed analysis of the systematic position of *F. rhomboides* within the lineage is not given by the two authors. However, a few anatomical characters visible in our material allow a more precise understanding of the relationships of *F. rhomboides*.

The new Lebanese genus has a short, curved and broad frontal. The neural and haemal arches are in hyper-complex contact. The last neural spines before the tail are vestigial. There are 50 to 53 pterygiophores in the anal fin. The caudal fin is vertical. There are scales not only in the abdominal but also in the caudal region of the body. All these features are characteristic of the Nursalliini, a tribe of the subfamily Pycnodontinae (cf. POYATO-ARIZA & WENZ, 2002, node 25, characters 9[3], 54[3], 57[3], 70[4], 73[6] and 76[2]). The brush-like process of the parietal is shortened. Such a reduction is the rule in Nursalliini (BLOT, 1987: pl. 27; TAVERNE *et al.*, 2015: fig. 10) and the process could even completely disappear in some members of the lineage (*ibid.*, 2015: figs 4, 9, 11). *F. rhomboides* also exhibits three hypertrophied elements in the hypochordal series. Within Pycnodontidae, this evolved feature is known in the Nursalliini and in a few other Pycnodontinae (POYATO-ARIZA & WENZ, 2002, node 22, character 59[2]).

The conclusion is clear. *Flagellipinna rhomboides* undoubtedly belongs to the subfamily Pycnodontinae and the tribe Nursalliini.

Today, the Nursalliini contains four genera, *Palaeobalistum* DE BLAINVILLE, 1818, *Nursallia* BLOT, 1987, *Abdobalistum* POYATO-ARIZA & WENZ, 2002 and *Paranursallia* TAVERNE *et al.*, 2015, and one

species, presently named “*Nursallia*” *goedeli* (HECKEL, 1854) but originally referred to *Palaeobalistum*. To establish the phylogeny within the tribe is not easy. Indeed, *Palaeobalistum* and *Abdobalistum* have crushed and badly preserved skulls. “*Nursallia*” *goedeli* belongs neither to *Nursallia* nor to *Palaeobalistum* and is in need of revision. This species probably represents a new genus. Unfortunately, the type is an incomplete specimen reduced to the tail and the caudal region of the body (HECKEL, 1856: pl. 2, fig. 3).

Nursallia and *Paranursallia* seem the most specialized members of the tribe. They share a few evolved characters. They have an enlarged head, a strongly curved frontal profile, a large “V”-shaped notch at the ventral junction between the skull and the elongate cleithrum and a shortened and rounded body (TAVERNE *et al.*, 2015: figs 3, 4, 9-11). The head is proportionally smaller, the frontal profile less curved, the ventral notch less pronounced and the body longer in *Flagellipinna*, *Palaeobalistum* and *Abdobalistum*.

Flagellipinna, *Nursallia* and *Paranursallia* have a reduced number of prearticular teeth that are ranged in two or three rows (the number of rows is unknown in *Nursallia veronae*). *Palaeobalistum* and *Abdobalistum* possess numerous prearticular teeth that are ranged in three or four rows (BLOT, 1987: figs 42, 49), a less specialized state.

We can thus conclude that, within the phylogeny of the tribe Nursalliini, *Flagellipinna* occupies and intermediate position between the plesiomorphic *Palaeobalistum* and *Abdobalistum*, on the one hand, and the apomorphic *Nursallia* and *Paranursallia*, on the other hand.

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