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Research article

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On the "*Coccodus*" *lindstroemi* species complex (Pycnodontiformes, Gladiopycnodontidae) from the marine Late Cretaceous of Lebanon, with the description of two new genera

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Abstract. The osteology of "*Coccodus*" *lindstroemi* is studied in detail and it is demonstrated that this species does not belong to the genus *Coccodus*, but is a rather primitive member of the pycnodontiform family Gladiopycnodontidae. Indeed, the snout of "*Coccodus*" *lindstroemi* is elongated in a rostrum formed by the prefrontal and the premaxilla. This rostrum extends beyond the lower jaw level. The toothless premaxilla is sutured by its upper margin to the lower margin of the long and broad prefrontal. The pectoral fin is lost and replaced by a pectoral spine which articulates on the cleithrum. A long nuchal spine resting on the dermosupraoccipital is present. The body is entirely covered by scales that are flake-like in the abdominal region and scute-like in the caudal region. *Joinvillichthys* gen. nov. is thus erected with "*Coccodus*" *lindstroemi* as the type species. It is also shown that specimens with dumpier head and body, usually ranged in "*Coccodus*" *lindstroemi*, represent another species of the same genus for which the taxon *Joinvillichthys kriweti* gen. et sp. nov. is created. Specimens sometimes considered as possible juveniles of "*Coccodus*" *lindstroemi* form a distinctive new genus and species of gladiopycnodontid fish, *Pankowskichthys libanicus* gen. et sp. nov. *Pankowskichthys* differs from *Joinvillichthys* by many osteological structures.

Key words. Pycnodontiformes, osteology, relationships, marine Cenomanian, Lebanon

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Introduction

The recently erected family Gladiopycnodontidae is a highly specialized lineage of the fossil fish order Pycnodontiformes (Taverne & Capasso 2013). The family is endemic to the marine Late Cretaceous of Lebanon and contains about ten genera (pers. obs.) most of them still undescribed. They are small fishes with a large head and a rather fusiform body. Their snout ends in a rostrum that is formed by the

enlarged prefrontals and premaxillae that are sutured together. The pectoral fin is lost and replaced by a strong pectoral spine. Some genera bear frontal, occipital and/or nuchal horns. The pectoral girdle is hypertrophied and closely associated to the skull, forming a kind of cephalo-thorax. Three genera belonging to this family have previously been described: *Gladiopycnodus* Taverne & Capasso, 2013, *Monocerichthys* Taverne & Capasso, 2013 and *Rostropycnodus* Taverne & Capasso, 2013.

"*Coccodus*" *lindstroemi* Davis, 1890 is the first member of this family ever described. The original description was based on a single complete specimen from Haqel, Lebanon, which has an elongated head, a pointed snout and a long nuchal horn (Davis 1890: pl. 22). The fish was erroneously (Poyato-Ariza & Wenz 2002: 145) considered as a new species of the already known Lebanese genus *Coccodus* Pictet, 1850. Later, other specimens resembling the holotype but with a dumpier head and body were also referred to the species "*C.*" *lindstroemi* (Hay 1903: pl. 29, fig. 1; Gayet *et al*. 2012: 87, upper left photo). More recently, small samples with an extremely long nuchal horn were considered as possible juveniles of this species (Gayet *et al*. 2012: 87, upper right photo).

It should be noted that both the original description of "*C.*" *lindstroemi* by Davis (1890) and the redescription by Hay (1903) give practically no informative data on the skull and the caudal skeleton of the fish. Today, the osteology and the relationships of "*C.*" *lindstroemi* remain almost unknown. Poyato-Ariza & Wenz (2002: 145) considered this fossil fish as "in need of revision" and doubted its taxonomic assignment to the Pycnodontiformes.

The aims of the present paper are, firstly, to provide for the first time an adequate osteological description of the concerned fishes, secondly, to demonstrate that they are true Pycnodontiformes and members of the family Gladiopycnodontidae, and, thirdly, to show that three different species coexist within the "*C.*" *lindstroemi* complex as understood today by some authors, the true "*C.*" *linsdtroemi*, the dumpier species and the species comprising the so-called juveniles. The first two species are allocated to a first new genus, the third species is placed in a second new genus.

Material and methods

The material belongs to the collections of the Royal Belgian Institute for Natural Sciences (IRSNB), the Swedish Museum of Natural History (NRM), the American Museum of Natural History (AMNH) and the Capasso-registered collection (CLC) in Chieti.

The specimens have been studied with Wild M 5 and Leica Wild M 8 stereo-microscopes. The figures were drawn by the first author (L.T.) with a *camera lucida*. Aspersions with ethanol were used to improve some observations.

List of abbreviations used in text-figures

AN = angular
ART = articular
ASPH = autosphenotic
BO = basioccipital
BRSTG = branchiostegal rays
BSPH = basisphenoid
CHY = ceratohyal
CLT = cleithrum
DHYOM = dermohyomandibula
DN = dentary
DPTE = dermopterotic

DSOC = dermosupraoccipital
DSPH = dermosphenotic
ENPT = entopterygoid (= endopterygoid)
EPCO 1-6 = epichordals 1 to 6
FR = frontal
HAEM = haemal arch
HAEMEP = haemal spine
HCLT = hypercleithrum (= supracleithrum)
HYCO 1-8 = hypochordals 1 to 8
HYOM = hyomandibula
HYP = hypural plate (= fused hypochordals)
IORB 1 = infraorbital 1
LEP = lepidotrichium (= ray)
METH = mesethmoid
MPT = metapterygoid
MX = maxilla
NEUR = neural arch
NEUREP = neural spine
NU = nuchal horn
OP = opercle
OSPH = orbitosphenoid
PA = parietal
PCLT = postcleithrum
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 b. = body scales
SCL = sclerotic bone
SCU d. = scutes of the dorsal ridge
SCU v. = scutes of the ventral keel
SPI = pectoral spine
ST = supratemporal
SY = symplectic
UD = urodermal
VO = vomer
f. V = foramen of the trigeminal nerve (V)
l. = left
r. = right

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
Superfamily Coccodontoidea Taverne & Capasso, 2013
Family Gladiopycnodontidae Taverne & Capasso, 2013

Joinvillichthys gen. nov.
urn:lsid:zoobank.org:act:6D820D8E-DF5C-41E9-B351-F46F7A9D4119

Type species: *Coccodus lindstroemi* Davis, 1890 (here designated).

Diagnosis

Gladiopycnodontid with an elongate prefrontal forming a short rostrum outpacing the lower jaw level. Anterior extremity of the prefrontal acuminate and spiny. Vomer bearing small rounded molariform teeth irregularly ranged. Orbitosphenoid, pleurosphenoid and basisphenoid present. Supratemporal sutured to the rear of the skull. Premaxilla long, broad, toothless and sutured by its upper margin to the prefrontal. Dentary bearing 2 incisiform teeth. Hypertrophied trapezoid preopercle covering the cheek. Large first infraorbital (only known in *Joinvillichthys kriweti* gen. et sp. nov.). Exposed part of the hyomandibula-dermohyomandibula much smaller than the preopercle. Long nuchal horn with a spiny posterior margin and articulated only on the dermosupraoccipital. Pectoral girdle closely associated to the skull, forming a cephalo-thorax. Cleithrum hypertrophied, with a gigantic posterior ventral process. Hypercleithrum hypertrophied. Well developed posttemporal, with an acuminate posterior extremity. 16 to 17 neural spines, all fused to the neural arches, before the epichordal series. 10 haemal spines before the hypochordal series (only known in *Joinvillichthys lindstroemi*). Short dorsal fin with 8 or 9 rays. Short anal fin with 7 to 9 rays. 7 to 9 spiny scutes in the dorsal ridge. 3 or 4 scutes in the ventral keel, the last scute or the two last ones associated to the postcoelomic bone. Body completely covered by small, flake-like scales in the abdominal region and by large, scute-like scales in the caudal region.

Etymology

The generic name is chosen in memory of Lord Jean de Joinville (1224–1317), seneschal of Champagne, who related in his biography of Louis IX the presentation of some Lebanese fossil fishes to this French king at Saïda during the seventh crusade (Gayet *et al*. 2012: 8). The Greek word *ichthys*, fish, is added.

Joinvillichthys lindstroemi (Davis, 1890)
Figs 1-11

Diagnosis

Joinvillichthys with a body depth comprising between 23.8 and 34.0 % of the standard length. No dorsal prominence on the frontal. Maxilla triangular in shape. Small parietal. Dermosupraoccipital sutured with the parietal and the dermopterotic. Dermopterotic deeper than long. Large dermosphenotic. Thin, rod-like opercle. Anterior ventral branch of the cleithrum present. Thin pectoral spine articulated on the rear of the cleithral posterior process. Caudal fin with a convex posterior margin.

Synonymy

Coccodus Lindstroemi Davis, 1890: 567, pl. 22.

"*Coccodus*" *lindstroemi* – Poyato-Ariza & Wenz, 2002: 145.

Holotype

LEBANON: sample NRM PZ P. 2073, a complete specimen from Haqel (Fig. 1), total length: 76 mm.

Other specimens

LEBANON: sample IRSNB N° P 9276, a nearly complete specimen (the caudal fin is missing) from Hgula (Fig. 2), length: 93 mm; sample CLC S-138, a nearly complete specimen (a part of the caudal fin is missing) from Haqel (Fig. 3), length: 82 mm; sample CLC S-324, a complete specimen from Haqel, total length: 76 mm.

Formation and locality

Marine Upper Cenomanian, Haqel and Hgula, Lebanon.

Morphometric data (Fig. 4)

The morphometric data are given in % of the standard length for the holotype NRM PZ P. 2073 (64 mm) and for sample IRSNB N° P 9276 (93 mm). These two specimens represent the two extremes of the species morphometric variation, as measured on the four studied samples

	Holotype	P9276
Length of the head (dermosupraoccipital included)	55.8 %	56.3 %

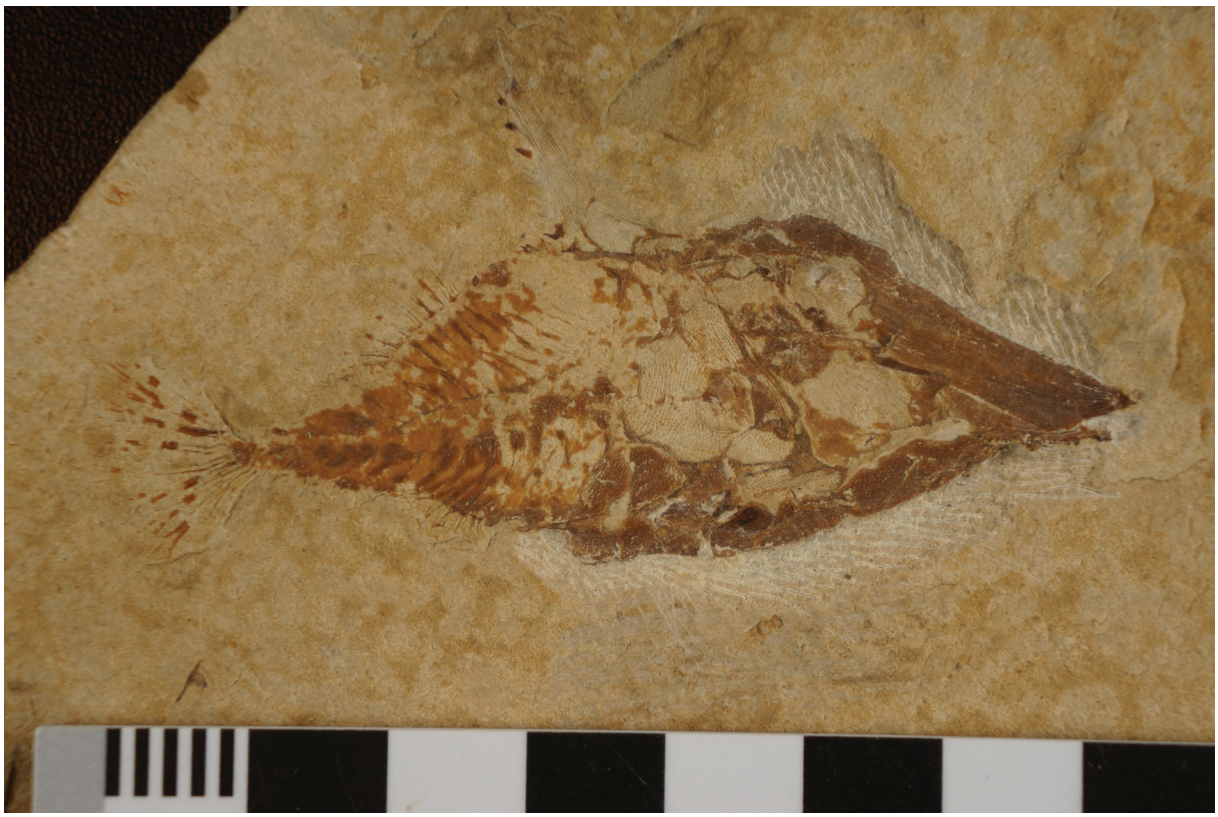

Fig. 1. *Joinvillichthys lindstroemi* (Davis, 1890). Holotype, NRM PZ P. 2073.

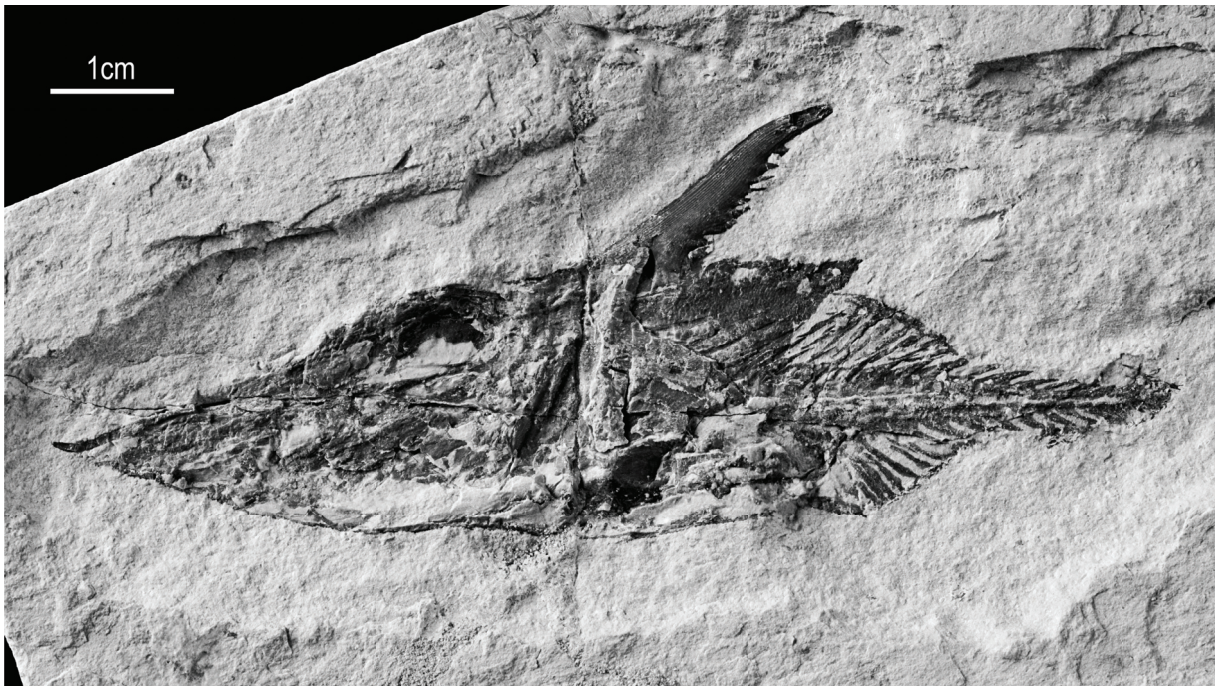

Fig. 2. *Joinvillichthys lindstroemi* (Davis, 1890). Sample IRSNB N° P 9276.

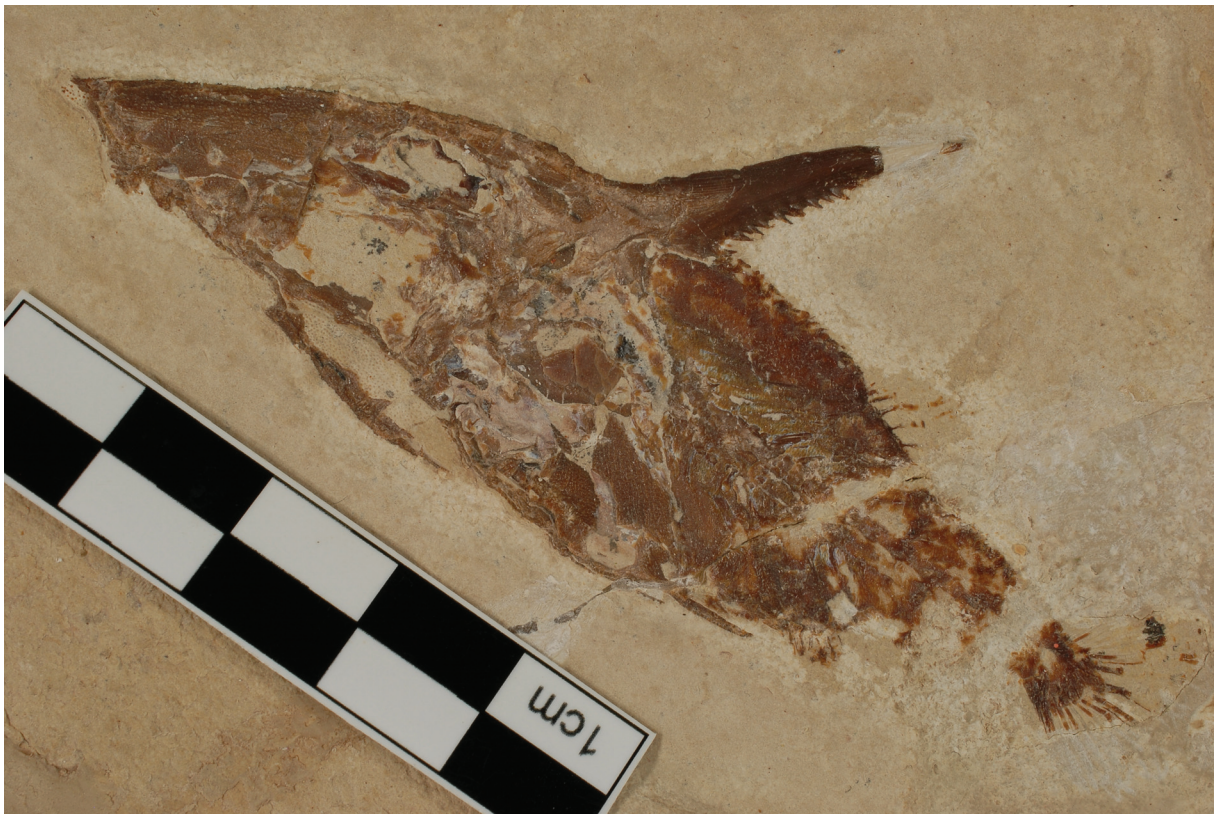

Fig. 3. *Joinvillichthys lindstroemi* (Davis, 1890). Sample CLC S-138.

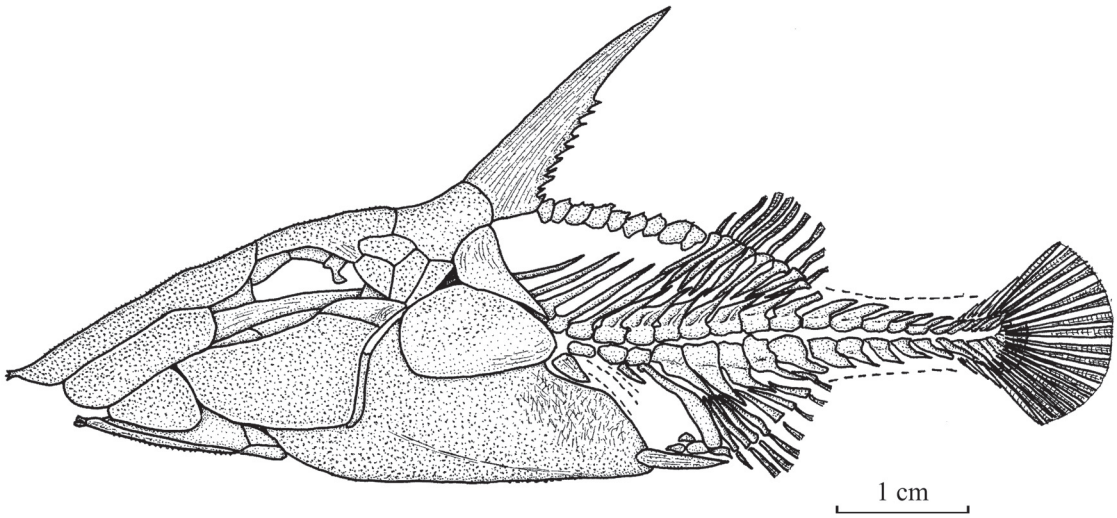

Fig. 4. *Joinvillichthys lindstroemi* (Davis, 1890). General reconstruction based on holotype, NRM PZ P. 2073 and samples IRSNB N° P 9276, CLC S-138 and CLC S-324. The scale refers to sample CLC S-138.

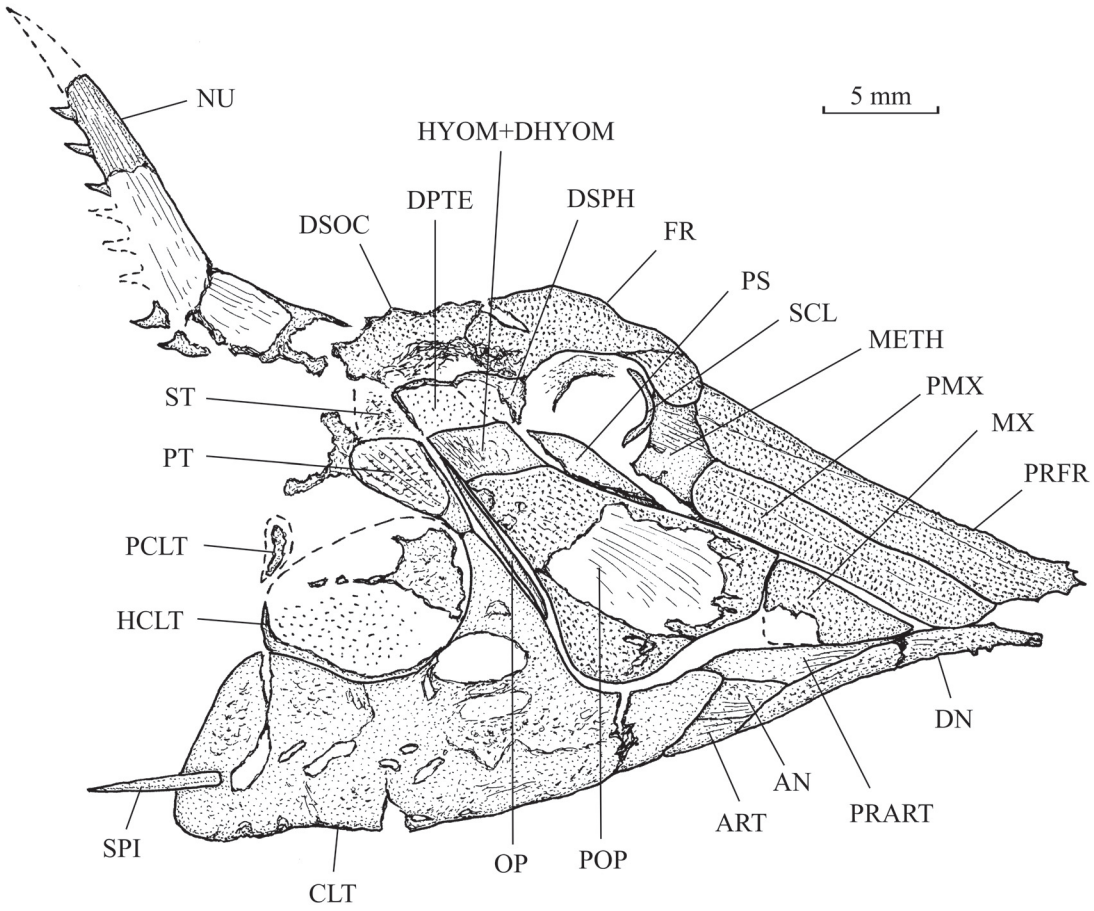

Fig. 5. *Joinvillichthys lindstroemi* (Davis, 1890). Skull and pectoral girdle of holotype, NRM PZ P. 2073.

Length of the cephalo-thorax (cleithrum included)	63.9 %	68.1 %
Depth of the head (without the nuchal horn)	35.4 %	25.0 %
Length of the nuchal horn	25.2 %	25.6 %
Maximum depth of the body (just behind the nuchal horn)	34.0 %	23.8 %
Predorsal length	74.8 %	73.1 %
Basal length of the dorsal fin	9.5 %	10.6 %
Preanal length	72.1 %	73.7 %
Basal length of the anal fin	8.2 %	9.4 %
Depth of the caudal peduncle	5.4 %	5.3 %

The important individual differences in the values of the head and body depths are probably due to sexual or seasonal variations.

Osteology

1. The skull (Figs 5–8)

The head is very large. Its length, from the tip of the snout to the basis of the nuchal horn, is equal to the body length. According to the specimens, its depth, from the upper margin of the dermosupraoccipital to the lower margin of the cleithrum, represents from 48 to 67 % of its length. The dermal bones of the skull are ornamented with small tubercles.

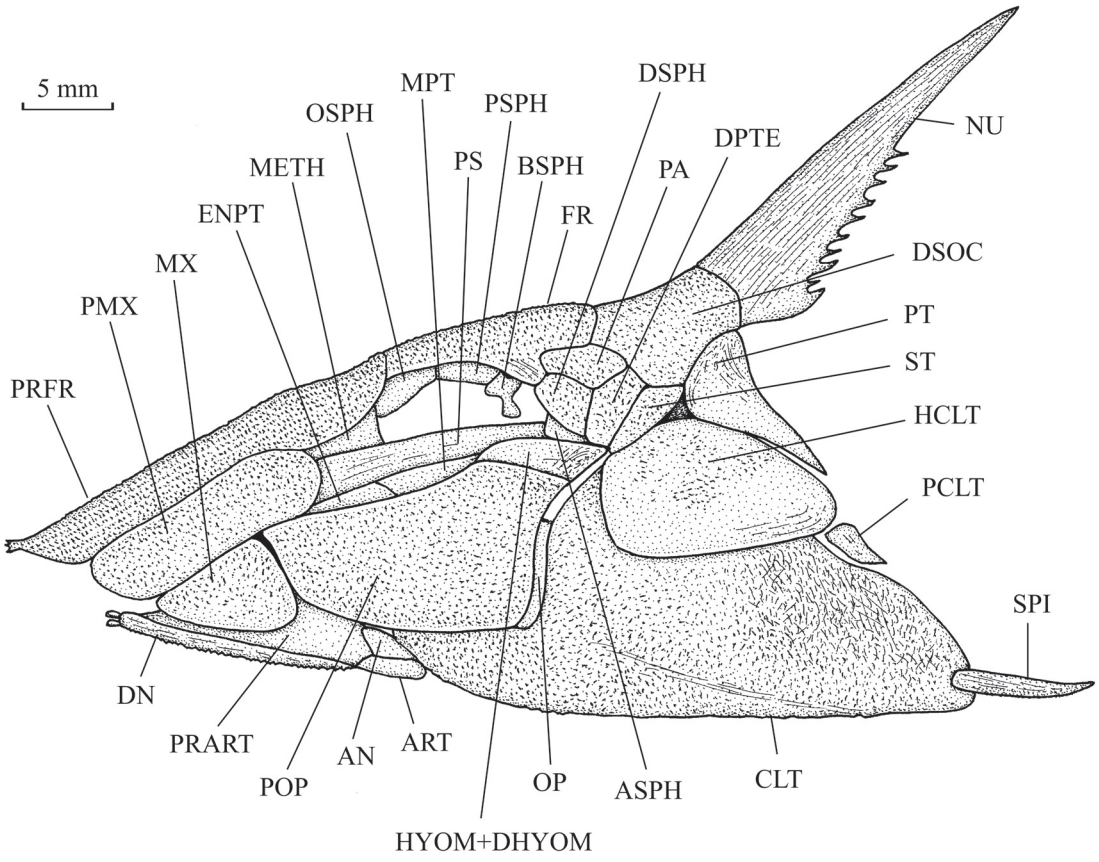

Fig. 6. *Joinvillichthys lindstroemi* (Davis, 1890). Reconstruction of the skull and the pectoral girdle based on holotype, NRM PZ P. 2073, and samples IRSNB N° P 9276, CLC S-138 and CLC S-324. The scale refers to sample CLC S-138.

The long, pointed rostrum slightly outpaces the lower jaw and is formed by two large paired bones, the prefrontal and the premaxilla. The anterior tip of the prefrontal bears two or three very small spines. Posteriorly, the bone reaches the orbit level. Only the most posterior part of the mesethmoid is visible. The vomer is completely hidden by the premaxilla. However, a small anterior fragment of the premaxilla is lost on sample CLC S-138 and a part of the vomer is visible. The bone bears small, rounded molariform teeth that are irregularly ranged.

The frontal is short, not curved and slightly broader posteriorly than anteriorly. The posterior portion of the frontal outpaces the level of the orbit. The posterior lateral part of the skull roof is formed on each side by four small bones, the parietal, the dermosphenotic, the dermopterotic and the supratemporal. The dermosphenotic partly covers the autosphenotic. The dermopterotic is deeper than long. The supratemporal is sutured to the dermopterotic and does not reach the parietal. The dermosupraoccipital occupies the median posterior part of the skull roof. This large bone is sutured with the frontal, the parietal, the dermopterotic and the supratemporal. A long pointed nuchal horn is fixed to the dermosupraoccipital. This horn is ornamented with long and thin striations and bears a series of spines on its posterior border.

Sample IRSNB N° P 9276 clearly shows the orbitosphenoid, the pleurosphenoid and the basisphenoid in the orbit. The three bones are pressed against the frontal. The orbitosphenoid reaches anteriorly the mesethmoid. The small basisphenoid is divided in a dorsal meningost and a short ventral belophragm.

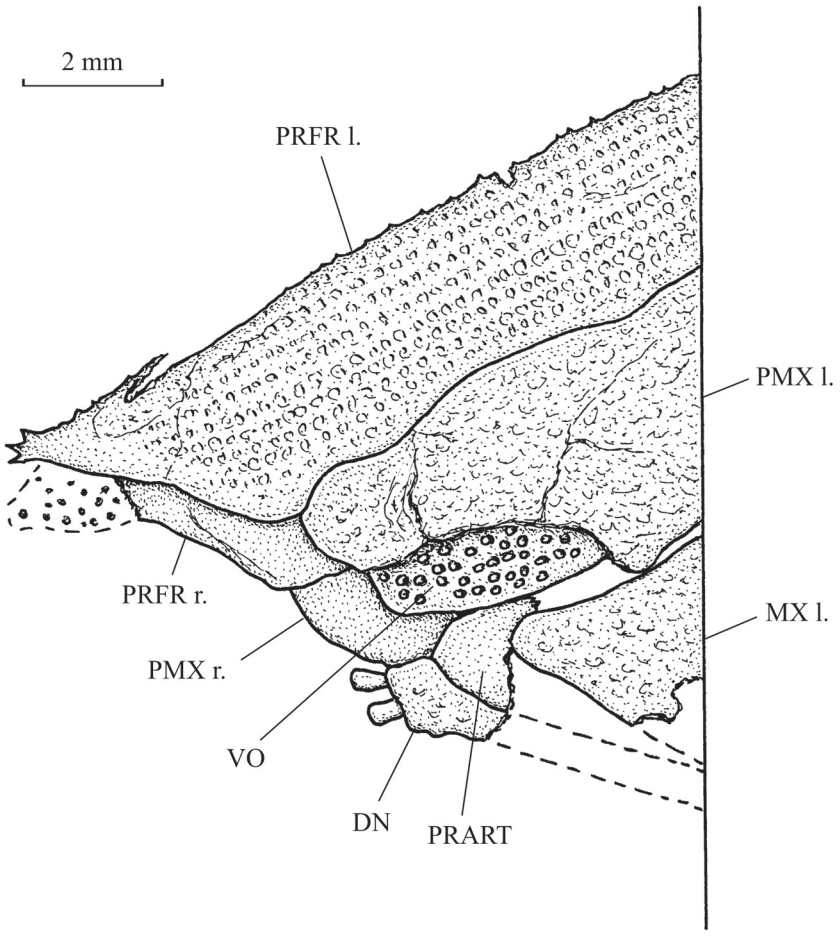

Fig. 7. *Joinvillichthys lindstroemi* (Davis, 1890). Vomerian region of sample CLC S-138.

The parasphenoid is very long, almost straight, but it does not reach the posterior border of the skull that is occupied by the basioccipital, as seen on the same specimen. Sample P 9276 also shows the very small prootic with a large foramen for the trigeminal nerve (V) in its anterior border.

The anterior margin of the metapterygoid and the entopterygoid is visible between the preopercle and the parasphenoid. The quadrate and the symplectic remain hidden by the preopercle and the cleithrum.

The premaxilla and the maxilla compose the upper jaw. As in other pycnodontomorph fishes, there is no supramaxilla. The broad, long and toothless premaxilla is located below the prefrontal to which it is sutured by its upper margin. The maxilla is large, toothless and triangle-shaped. The lower jaw comprises the dentary, the prearticular, the angular and the articular. The articulation with the quadrate is located at the level of the anterior border of the orbit. The prearticular is the largest bone of the series but is partly covered by the maxilla and the preopercle. The teeth of the prearticular are not visible. The articular and the angular are small bones. The dentary bears two incisiform teeth and is reduced to its ventral branch. Its lower margin is denticulated.

The orbit is large and longer than deep. No orbital bone is preserved, except the dermosphenotic that is sutured to the frontal, the parietal and the dermopterotic. Fragments of a sclerotic bony ring are visible on the holotype.

The hyomandibula-dermohyomandibula and the preopercle are sutured together. The exposed part of the hyomandibula-dermohyomandibula is much smaller than the greatly enlarged preopercle. The opercle is a long and very thin bone wedged between the preopercle and the cleithrum.

Small fragments of branchial bones with a few long and acuminate branchiospines are visible on sample IRSNB N° P 9276.

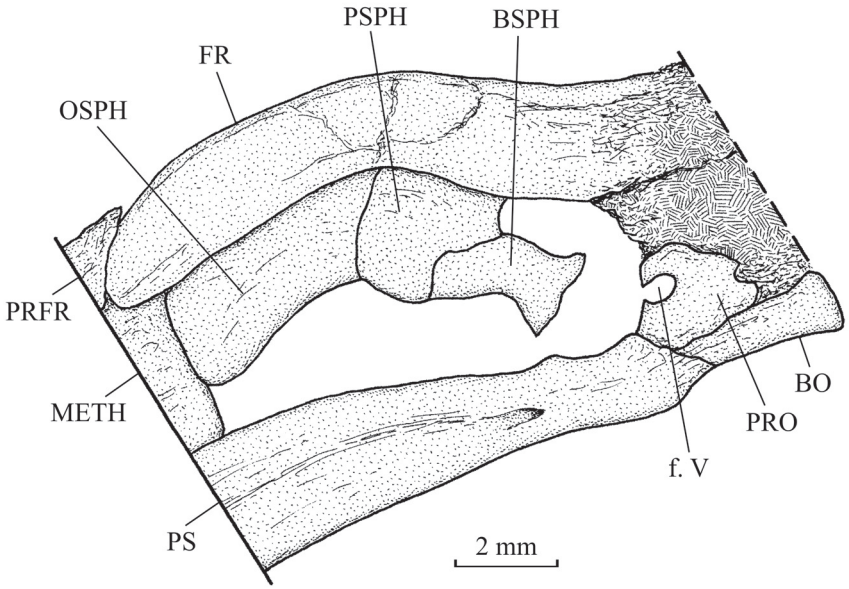

Fig. 8. *Joinvillichthys lindstroemi* (Davis, 1890). Orbital region of sample IRSNB N° P 9276.

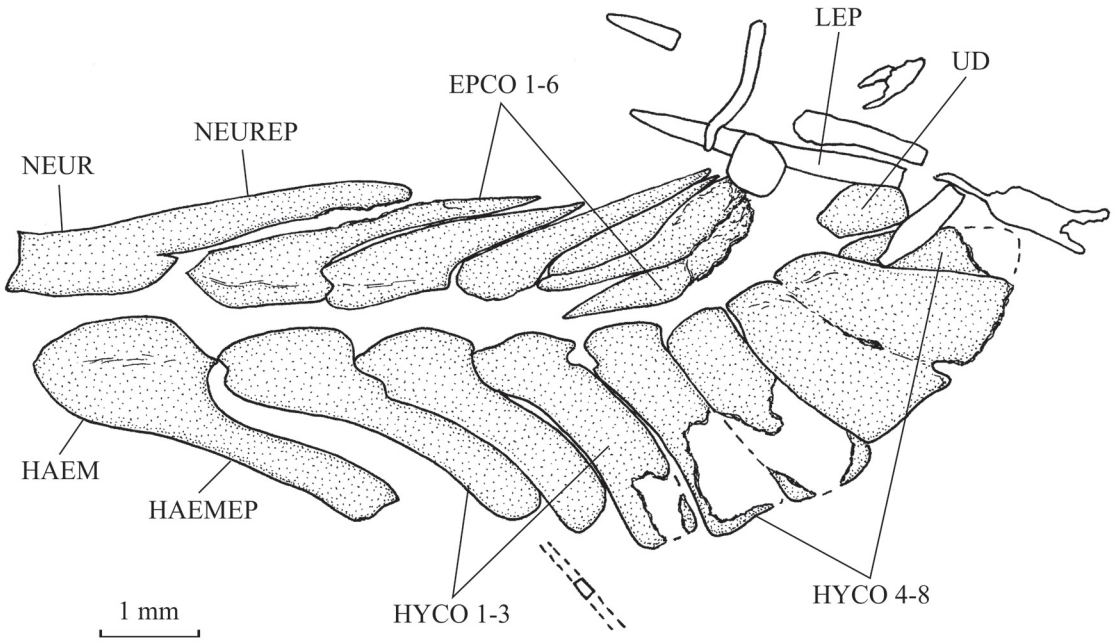

Fig. 9. *Joinvillichthys lindstroemi* (Davis, 1890). Caudal skeleton of sample IRSNB N° P 9276.

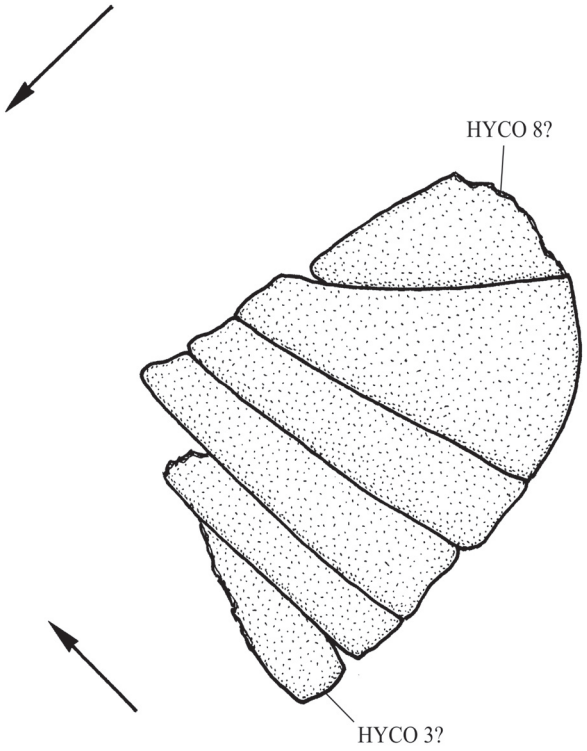

Fig. 10. *Joinvillichthys lindstroemi* (Davis, 1890). Hypochordal elements of sample CLC S-138. The arrows indicate the position of the most external dorsal and ventral procurrent ray of the caudal fin.

2. The girdles (Figs 4–6)

As in all Gladiopycnodontidae, the enlarged pectoral girdle is closely associated to the skull, forming a sort of cephalo-thorax. The dermal bones are ornamented with small tubercles. The postemporal rests on the large ovoid hypercleithrum (= supracleithrum) and is articulated with the dermosupraoccipital by its broad anterior border. Its posterior extremity is acuminate. The cleithrum is enormous, with a well developed anterior branch and a very wide posterior process. There is a small postcleithrum. The pectoral fin is replaced by a long and thin spine that is decorated with a few ridges and tubercles. The spine is articulated on the rear of the cleithral posterior process.

No trace of a pelvic girdle is visible. It is possible that reduced pelvic bones and fins were present but hidden by the gigantic cleithral posterior process. Such a situation exists in other gladiopycnodontid fishes (Taverne & Capasso 2013: figs 8, 18).

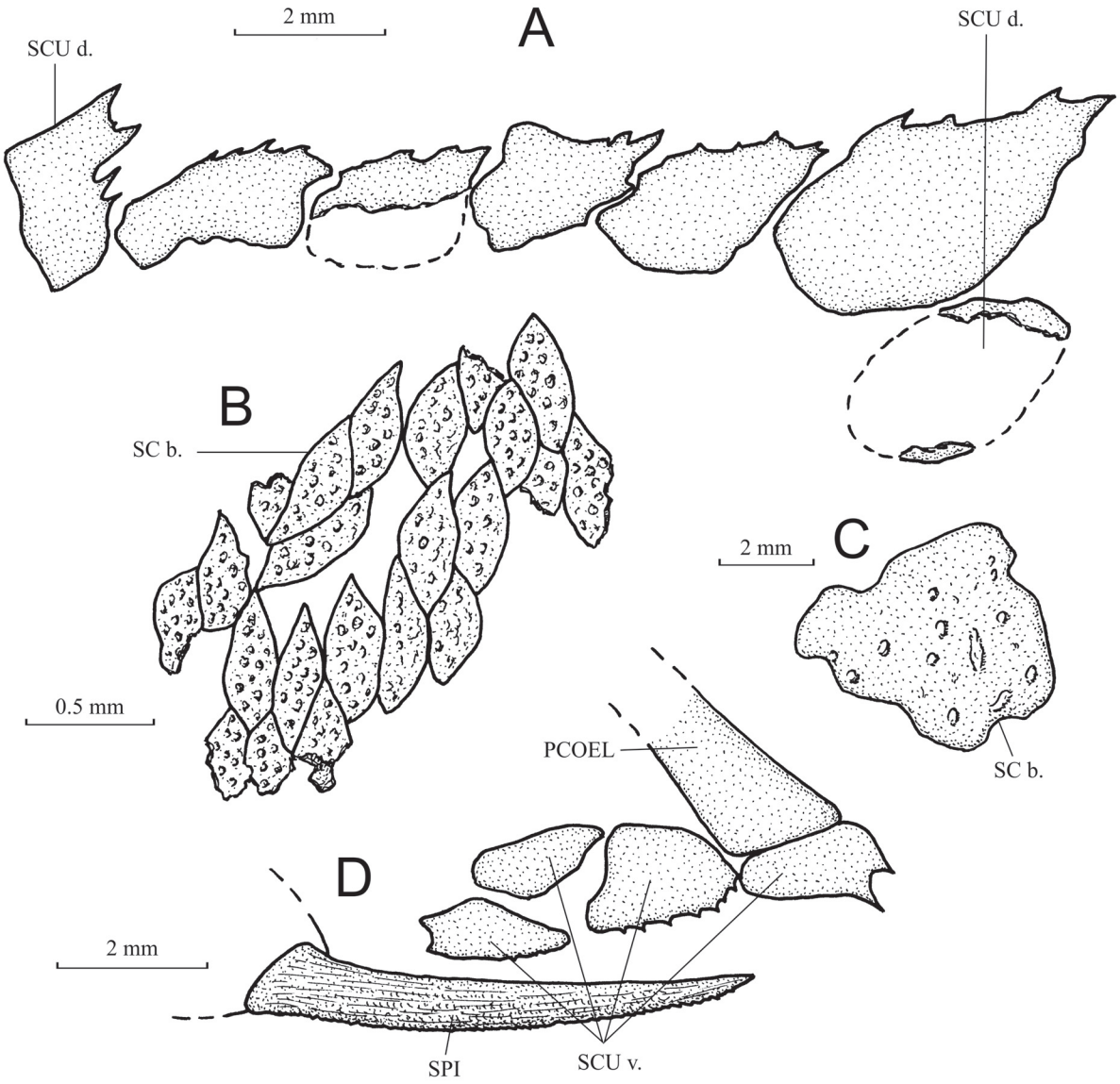

Fig. 11. *Joinvillichthys lindstroemi* (Davis, 1890). **A**. Dorsal ridge scutes of sample IRSNB N° P 9276. **B**. Anterior flake-like body scales of sample CLC S-138. **C**. Posterior scute-like body scale of sample CLC S-138. **D**. Ventral keel scutes of sample CLC S-138.

3. The axial skeleton (Fig. 4)

As in most Gladiopycnodontidae, the trunk is fusiform and not deep-bodied. Sample IRSNB N° P 9276 has lost the scales on the body and so the well preserved axial skeleton is completely accessible. The vertebrae are constituted by the dorsal and ventral arcocentra. They surround almost completely the notochord. There are 17 neural spines before the epichordal elements and 10 haemal spines before the hypochordal series. Before the level of the dorsal fin, the neural spines are long and narrow. Posteriorly, the neural spines are much shorter but also a little broader. The haemal spines are short and broad. The number of ribs is not determinable but ribs are present under the cleithral posterior process, as seen on sample CLC S-138. The last ribs are very short. The postcoelomic bone is backwardly oriented and is articulated with the ventral arcocentrum preceding the one bearing the first haemal spine. The bone is broader ventrally than dorsally.

4. The dorsal and anal fins (Fig. 4)

The dorsal and anal fins are short and located in the middle of the body length. There are 8 or 9 dorsal pterygiophores and also 8 or 9 anal pterygiophores, each of them bearing a ray. The first dorsal and anal ray is spiny. The other rays are segmented.

5. The caudal skeleton (Figs 9–10)

Sample IRSNB N° P 9276 presents the best preserved caudal skeleton. The caudal peduncle is long and includes 5 or 6 vertebral segments. There are 6 epichordals and a least 8 hypochordals. The hypochordals are broader than the long, thin and pointed epichordals. In specimen IRSNB N° P 9276, the sixth and seventh hypochordals are moderately broadened and partly fused together. In sample CLC S-138, the sixth and seventh hypochordals are not fused and the broadening only exists on the seventh element.

The caudal fin has a convex posterior margin (Poyato-Ariza & Wenz 2002: fig. 36B) and contains 17 or 18 principal caudal rays. There are a few procurrent rays in each lobe.

6. Squamation (Fig. 11)

The body is entirely covered by scales ornamented with tubercles and imbricated one into another. Anteriorly, these scales are very small, flake-like and they extend on the cleithral posterior process. Posteriorly to the median fins, these scales are a much larger, irregular and scute-like shaped.

Between the nuchal horn and the dorsal fin, the dorsal ridge is composed by 7 to 9 scutes with a spiny upper margin.

The ventral keel contains at least 4 scutes. The first three are located in the cloacal region. The posterior one of these three has a spiny lower margin. A fourth spiny scute is associated with the ventral extremity of the postcoelomic bone.

Joinvillichthys kriweti sp. nov.

urn:lsid:zoobank.org:act:B8C4822F-44CA-4776-8455-452C5DBDCA1C

Figs 12-16

Diagnosis

Joinvillichthys with a body depth equal to 46.0 % of the standard length. A dorsal prominence present on the frontal. Maxilla elongated. Large parietal. Dermosupraoccipital sutured to the parietal and not to the dermopterotic. Dermopterotic much longer than deep. Small dermosphenotic. Comma-shaped opercle. Anterior ventral branch of the cleithrum lost. Broad and short pectoral spine articulated on the ventral margin of the cleithral posterior process. Caudal fin double emarginated.

Etymology

The name of the new species is dedicated to Dr Jürgen Kriwet (Vienna) who has greatly improved our knowledge of the pycnodontiform fishes.

Holotype

LEBANON: sample CLC S-137, a complete specimen from Haqel (Fig. 12), total length: 91 mm.

Paratype

LEBANON: sample AMNH 4517a (3698) and counterpart, an incomplete specimen from Hgula (Hay 1903: pl. 29, fig. 1); only the head and the beginning of the body are preserved, length: 63 mm.

Formation and locality

Marine Upper Cenomanian, Haqel and Hgula, Lebanon.

Morphometric data (Fig. 13)

The morphometric data are given in % of the holotype standard length (76 mm)

Length of the head (dermosupraoccipital included) ..... 54.2 %
Length of the cephalo-thorax (cleithrum included) ..... 75.3 %
Depth of the head (without the nuchal horn) ..... 43.8 %
Length of the nuchal horn ..... 27.7 %
Maximum depth of the body (just behind the nuchal horn) ..... 46.0 %

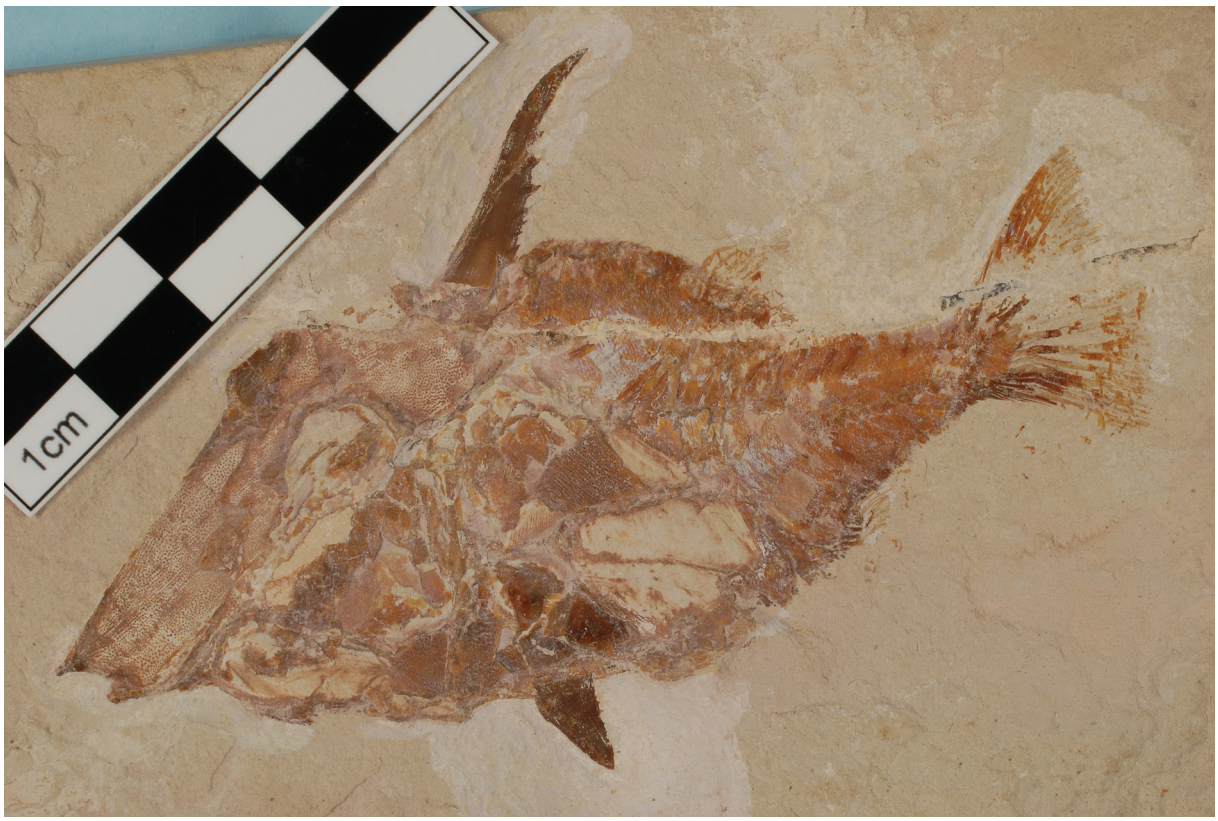

Fig. 12. *Joinvillichthys kriweti* gen. et sp. nov. Holotype, CLC S-137.

Predorsal length ..... 76.6 %
Basal length of the dorsal fin ..... 9.8 %
Preanal length ..... 80.4 %
Basal length of the anal fin ..... 6.4 %
Depth of the caudal peduncle ..... 9.8 %

Osteology

1. The skull (Fig. 14)

The general morphology of the skull is rather close to that of *Joinvillichthys lindstroemi* and the cranial dermal bones also are ornamented with small tubercles. However, there are many small differences in the head skeleton of the two fishes. Thus the description that follows will principally emphasize these differences.

The skull is shorter and deeper than in *Joinvillichthys lindstroemi*. Its depth, from the upper margin of the dermosupraoccipital to the lower margin of the cleithrum, is equal to 83 to 86 % of its length, from the tip of the snout to the basis of the nuchal horn.

The rostrum lengthening is less pronounced. The prefrontal is broader and has a very sinuous suture with the frontal. Its anterior tip also bears very small spines but is less outpacing of the lower jaw level. The frontal is broader but does not outpace posteriorly the level of the orbit. The bone bears a small dorsal prominence. The dermosupraoccipital is longer and is sutured to the parietal and the supratemporal but not with the dermopterotic. The parietal is considerably larger. The dermopterotic is longer but much thinner. The supratemporal is sutured to the parietal and reaches the dermopterotic at only one point. As in *Joinvillichthys lindstroemi*, the long nuchal horn is supported only by the dermosupraoccipital.

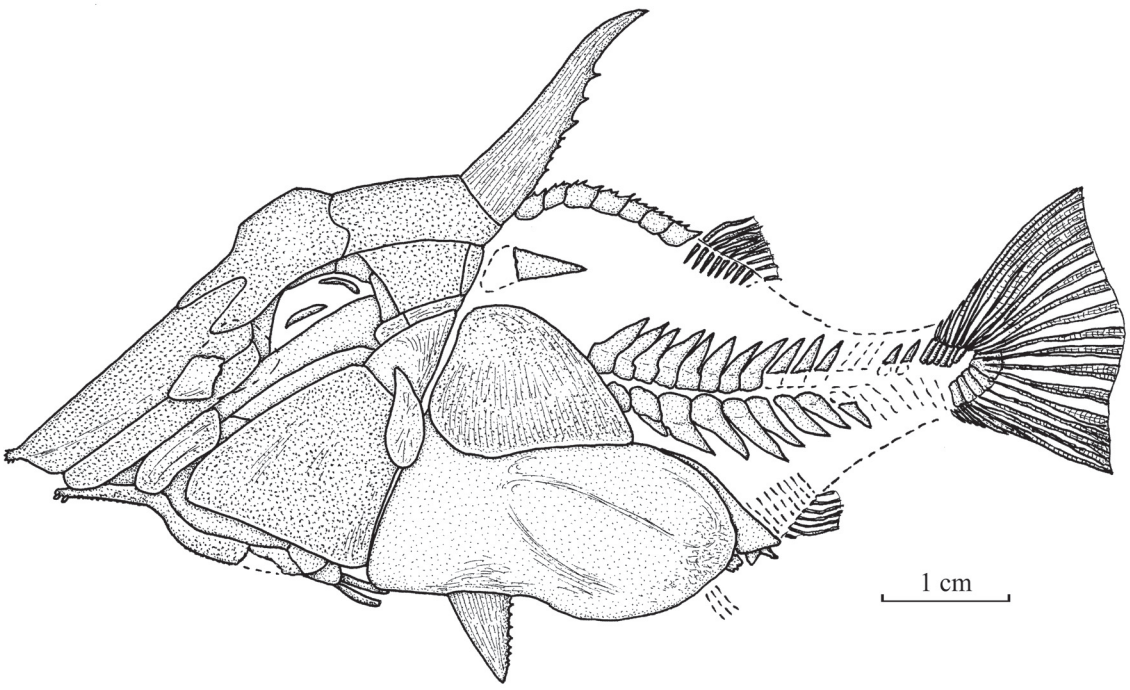

Fig. 13. *Joinvillichthys kriweti* gen. et sp. nov. General reconstruction based on holotype, CLC S-137.

The orbitosphenoid and the pleurosphenoid are present in the orbit, just below the frontal, but the basisphenoid is not visible.

The toothless premaxilla is longer and narrower. The toothless maxilla also is narrower and more elongate. The lower jaw is composed with the same bones but is longer. The dentary bears two small incisiform teeth and its ventral margin is denticulated. The articulation with the quadrate is located at the level of the posterior border of the orbit.

A fragment of a large first infraorbital is preserved on the suture between the prefrontal and the premaxilla. The sclerotic ring is visible in the orbit.

The hyomandibula and the preopercle are sutured together. The exposed part of the hyomandibula-dermohyomandibula is larger than in *Joinvillichthys lindstroemi* but still much smaller than the considerably enlarged preopercle. The opercle is broader and comma-shaped, with the sharp end dorsally located. A part of the anterior ceratohyal and two small branchiostegal rays are visible behind the lower jaw.

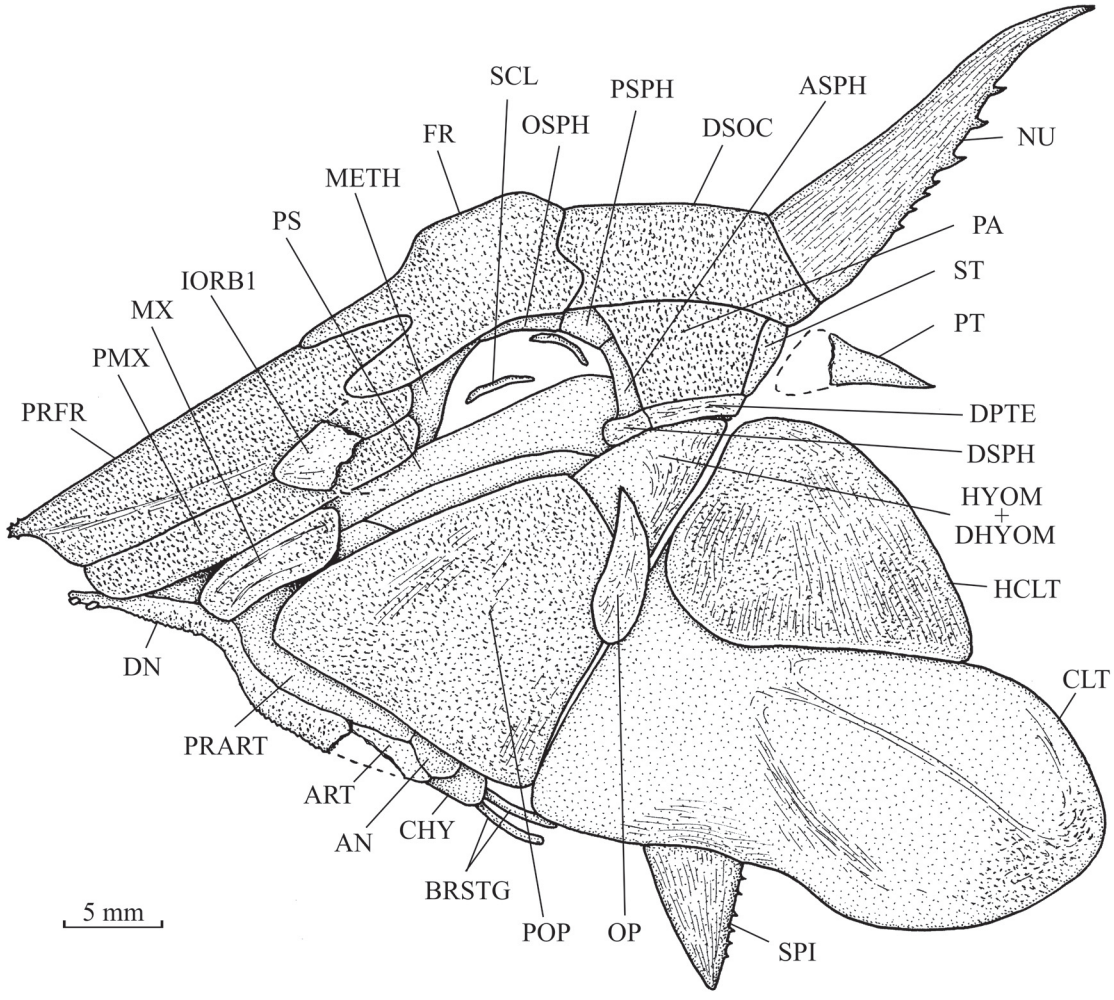

Fig. 14. *Joinvillichthys kriweti* gen. et sp. nov. Reconstruction of the skull and the pectoral girdle based on holotype, CLC S-137.

2. The girdles (Figs 14, 16)

The bones of the gigantic pectoral girdle have the same size and shape as in *Joinvillichthys lindstroemi*. However, two important differences exist. The anterior ventral branch of the cleithrum is lost. No postcleithrum is visible, but that is perhaps due to the fossilization. The pectoral spine is shorter, much broader and is not articulated with the rear of the cleithrum but more anteriorly on its lower margin.

A small pelvic girdle is present. Indeed, a part of a vertically oriented pelvic bone is visible under a broken part of the cleithrum.

3. The axial skeleton (Fig. 13)

The trunk is fusiform but proportionally deeper than in *Joinvillichthys lindstroemi*. The axial skeleton is incomplete. Three vertebral segments are missing near the caudal peduncle. There are 16 neural spines (the three missing ones included) before the epichordal series. Only 8 haemal spines are preserved. The total number of haemal spines must be around 12 or 13. The neural and haemal spines are short but broad. The neural and haemal arches surround almost completely the notochord. No ribs are visible. The postcoelomic bone is well developed and backwardly oriented.

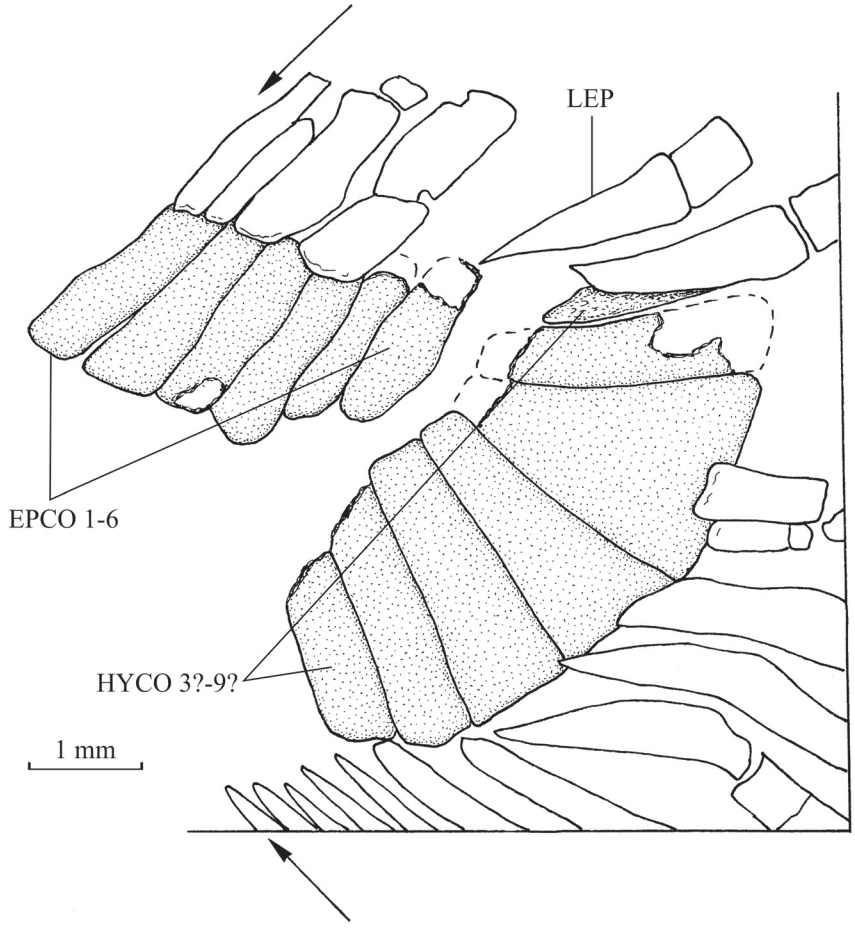

Fig. 15. *Joinvillichthys kriweti* gen. et sp. nov. Caudal skeleton of holotype, CLC S-137. The arrows indicate the positions of the most external dorsal and ventral procurrent rays of the caudal fin.

4. The dorsal and anal fins (Fig. 13)

The short dorsal and anal fins are located at the mid-length of the body. There are 9 pterygiophores and 9 rays in the dorsal fin. The anal fin contains 7 rays, but the number of anal pterygiophores is not determinable. The first dorsal and anal ray is spiny. The other rays are segmented.

5. The caudal skeleton (Fig. 15)

The caudal skeleton of the holotype is partly preserved. There are 6 short and broad epichordals and 7 hypochordals. However, one or two anterior hypochordals are missing, so the complete series must be composed of 8 or 9 elements. The fifth preserved hypochordal is strongly enlarged. No urodermal is visible, but the region where theses bones are usually present is not preserved.

The caudal fin is double emarginated (Poyato-Ariza & Wenz 2002: fig. 36E) and contains 19 principal segmented caudal rays, the 2 external being pointed and the 17 others branched. There are 6 ventral and at least 4 dorsal procurrent rays.

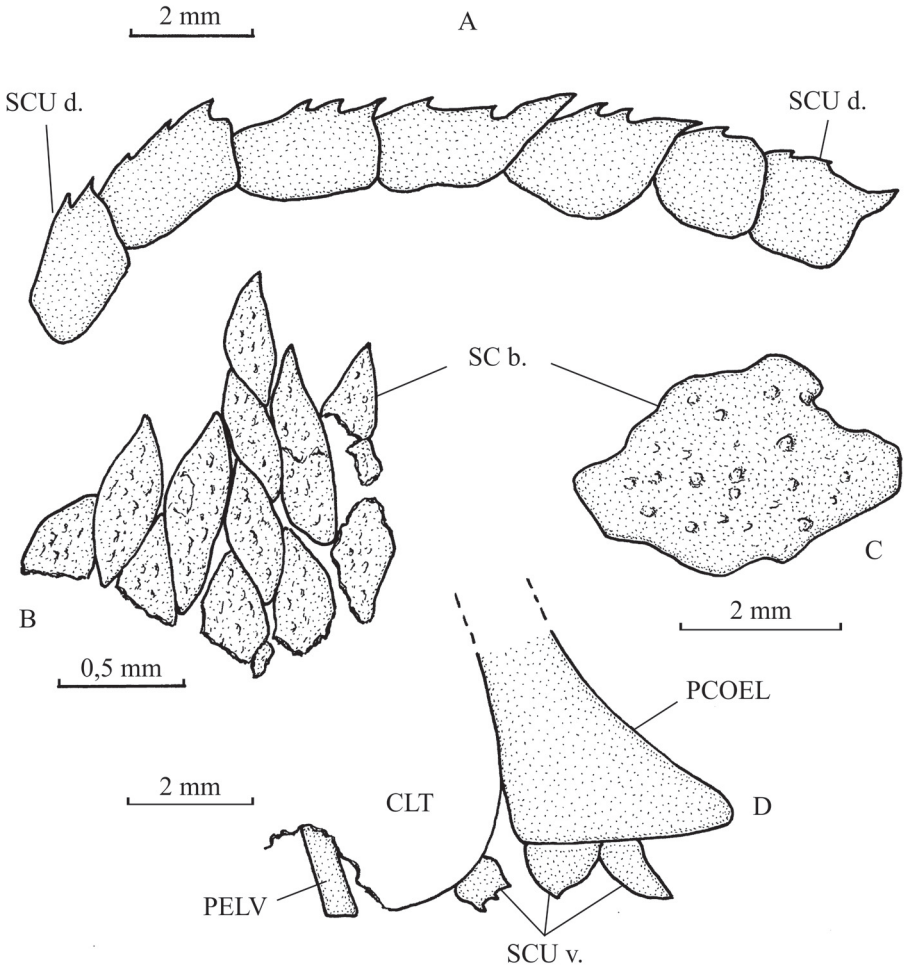

Fig. 16. *Joinvillichthys kriweti* gen. et sp. nov. Holotype, CLC S-137. **A**. Dorsal ridge scutes. **B**. Anterior flake-like body scales. **C**. Posterior scute-like body scale. **D**. Ventral keel scutes.

6. Squamation (Fig. 16)

The squamation is the same as in *Joinvillichthys lindstroemi*. There are 7 spiny scutes in the dorsal ridge and at least 3 spiny scutes in the ventral keel. The two posterior ventral scutes are associated with the ventral margin of the postcoelomic bone. The body scales are slightly ornamented with tubercles. Anteriorly, they are small and flake-like. Posteriorly, there are much larger, irregular and scute-like shaped.

Pankowskichthys gen. nov.

urn:lsid:zoobank.org:act:6C6C231C-40DC-4AD6-9250-2FD72E4EDC1B

Type species: *Pankowskichthys libanicus* gen. et sp. nov. (by monotypy)

Diagnosis

As for the species (monospecific genus).

Etymology

The name of the new genus is dedicated to Mark Pankowski (Rockville, Maryland, U.S.A.), who generously offered the holotype of *Pankowskichthys libanicus* gen. et sp. nov. to the Royal Belgian Institute for Natural Sciences (IRSNB).

Pankowskichthys libanicus gen. et sp. nov.

urn:lsid:zoobank.org:act:F3762EEA-A774-4377-9D4D-8E9DF3E28EE7

Figs 17-21

Diagnosis

Gladiopycnodontid with the elongate prefrontal forming a long, acuminate rostrum greatly outpacing the lower jaw level. Long frontal with a weakly developed dorsal prominence. Large parietal. Small dermopterotic. Orbitosphenoid present and separated from the mesethmoid. Premaxilla rather short, toothless, with a hook-like anterior process, and sutured by its upper margin to the prefrontal. Small, toothless triangular maxilla. Dentary curved and bearing 2 incisiform teeth. Hypertrophied trapezoid preopercle covering the cheek. Exposed part of the hyomandibula-dermohyomandibula much smaller than the preopercle. Extremely long nuchal horn, with a spiny posterior margin, and resting on both the dermosupraoccipital and the parietal. Dermosphenotic narrow. Pectoral girdle closely associated to the skull, forming a cephalo-thorax. Cleithrum hypertrophied, with a long, pointed, ventral branch. Hypercleithrum hypertrophied. Small posttemporal. Very short and broad pectoral spine articulated on the ventral margin of the cleithrum. Long dorsal fin, beginning just behind the nuchal horn. Short anal fin with 7 rays. A very broad hypural plate present in the hypochordal series. Body entirely covered by large, scute-like scales. A short, ventral spine articulated on the postcoelomic bone.

Etymology

The species name refers to Lebanon.

Holotype

LEBANON: sample IRSNB P 9278, a complete and well preserved specimen from Hgula (Fig. 17), total length: 41 mm.

Formation and locality

Marine Upper Cenomanian, Hgula, Lebanon. The species has also been found at Haqel (Gayet *et al*. 2012: 87).

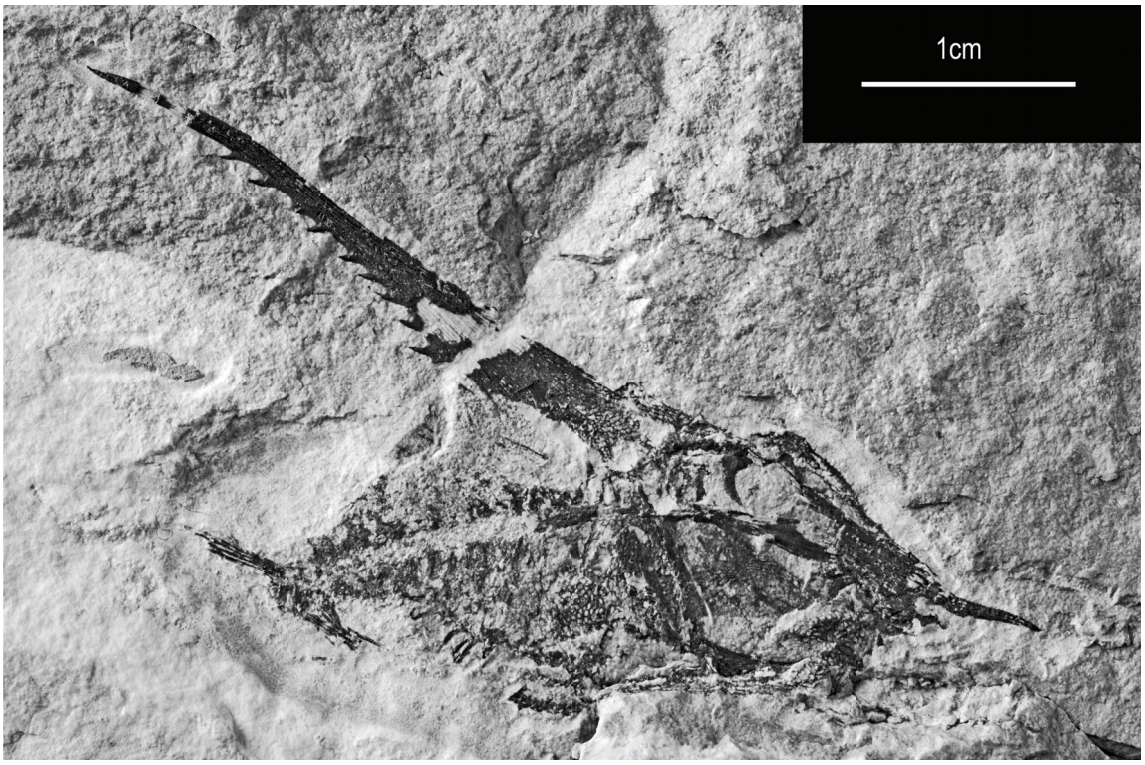

Fig. 17. *Pankowskichthys libanicus* gen. et sp. nov. Holotype, IRSNB P 9278.

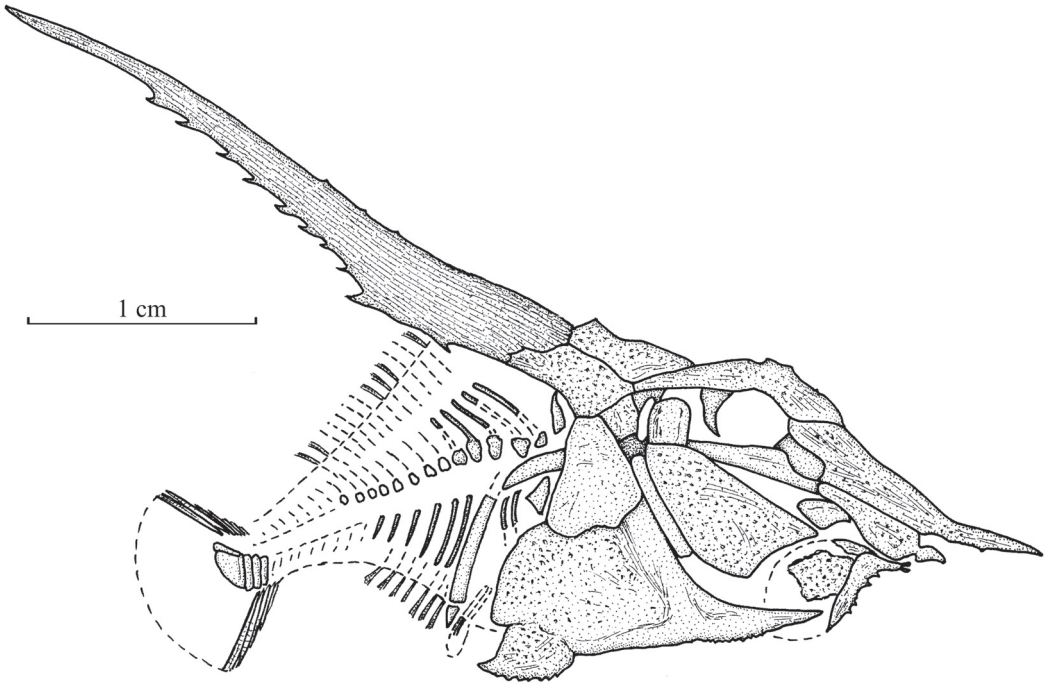

Fig. 18. *Pankowskichthys libanicus* gen. et sp. nov. General reconstruction based on holotype, IRSNB P 9278.

Morphometric data (Fig. 18)

The morphometric data are given in % of the standard length of the holotype (36 mm).

Length of the head (dermosupraoccipital and parietal included) ..... 73.1 %
Length of the cephalo-thorax (cleithrum included) ..... 72.5 %
Depth of the head (without the nuchal horn) ..... 42.4 %
Length of the nuchal horn ..... 83.5 %
Maximum depth of the body (just behind the nuchal horn) ..... 35.4 %
Predorsal length ..... 82.6 %
Basal length of the dorsal fin ..... 20.3 %
Preanal length ..... 75.9 %
Basal length of the anal fin ..... 8.9 %
Depth of the caudal peduncle ..... 8.5 %

Osteology

1. The skull (Fig. 19)

The head and the pectoral girdle are closely associated, forming a cephalo-thorax that is gigantic when compared to the body size. This character and the feeble ossification of the axial skeleton probably indicate that the concerned sample is a juvenile fish. The dermal bones are ornamented with tubercles, alveoli and thin ridges.

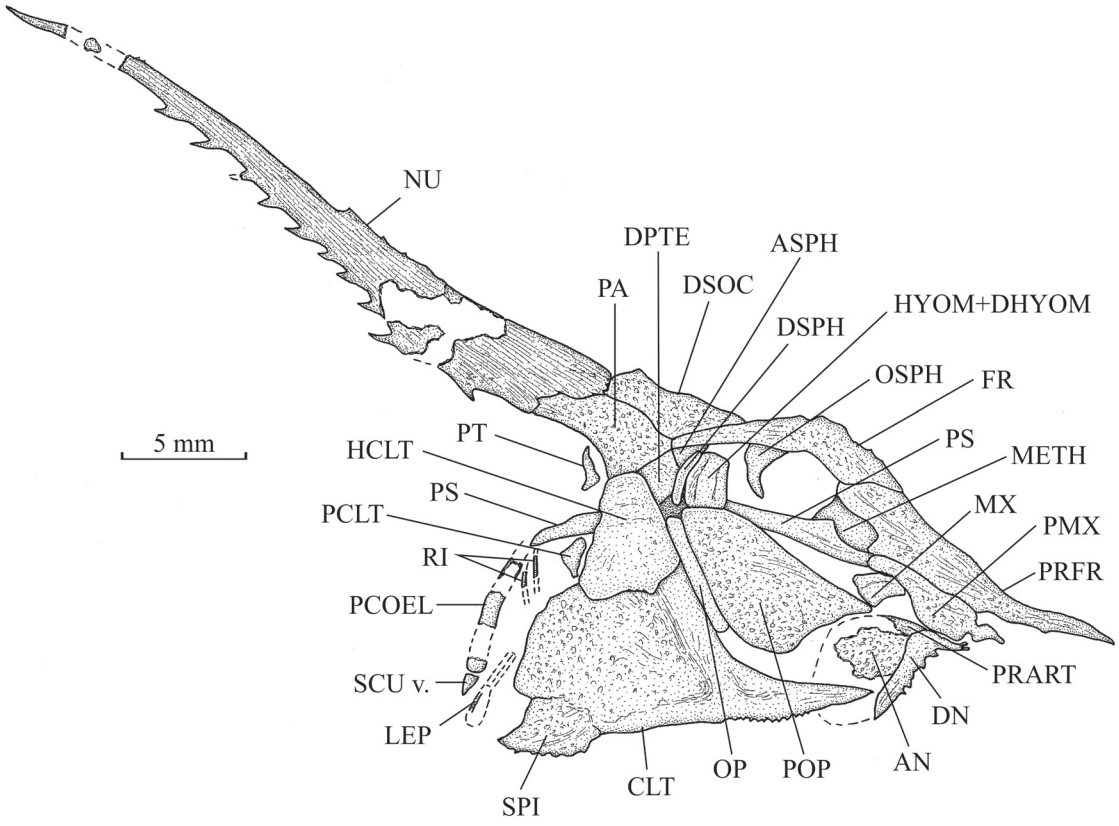

Fig. 19. *Pankowskichthys libanicus* gen. et sp. nov. Reconstruction of the skull and the pectoral girdle based on holotype, IRSNB P 9278.

The rostrum is longer than in *Joinvillichthys* gen. nov. It is formed by the acuminate anterior extremity of the prefrontal. This rostrum greatly outpaces the lower jaw level. The preorbital length, rostrum included, represents 54.5 % of the total length of the head. The prefrontal is long, anteriorly pointed and rather broad posteriorly, hiding completely the vomer and a great part of the mesethmoid.

The frontal is narrow, rather long and exhibits a weakly developed median protuberance located just above the orbit. The elongate posterior part of the frontal extends far behind the orbit, under the dermosupraoccipital ventral margin, and reaches the parietal. The dermopterotic is small but the dermosupraoccipital and the parietal are large bones that protrude posteriorly. The small autosphenotic is located in front of the dermopterotic and just below the posterior extremity of the frontal. An extremely long nuchal horn with a spiny posterior margin is articulated on both the parietal and the dermosupraoccipital.

The parasphenoid is very long, straight and toothless. Its posterior extremity greatly outpaces the rear of the skull. The orbitosphenoid is separated from the mesethmoid. No other endocranial bone of the braincase and no bone of the palato-quadrate arch are visible.

The premaxilla and the maxilla are toothless. There is no supramaxilla. The premaxilla is long but much shorter than the prefrontal, to which it is sutured by its upper margin. This premaxilla exhibits a small, anterior hook-shaped process, a broad anterior part and a much narrower posterior region. The premaxilla does not contribute to the rostrum. The small, triangular maxilla is located below the posterior part of the premaxilla. The dentary, reduced to its ventral branch, is well developed. It bears two very small, incisiform teeth. Its posterior part forms a right angle with its anterior extremity. Its lower margin is spiny. The angular is a rather large bone. Only a very small part of the prearticular is visible. The articular is not preserved.

The orbit is wide. The long and very thin dermosphenotic is placed against the autosphenotic and the dermopterotic. No other bone of the orbital series is present.

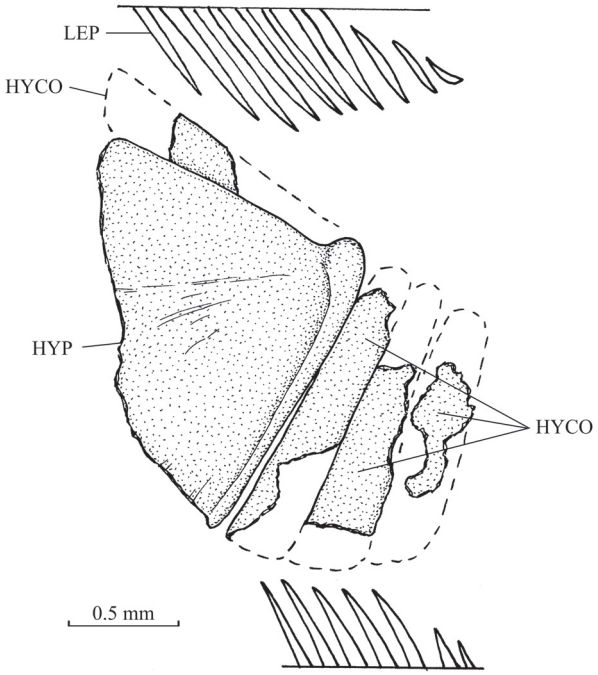

Fig. 20. *Pankowskichthys libanicus* gen. et sp. nov. Caudal skeleton of holotype, IRSNB P 9278.

The hyomandibula and the preopercle are sutured together. The exposed part of the hyomandibula-dermohyomandibula is deeper than broad but much smaller than the hypertrophied, trapezoid-shaped preopercle that covers the cheek. The opercle is a long, rod-like bone pressed between the preopercle and the pectoral girdle.

2. The girdles (Figs 18–19)

The hypertrophied pectoral girdle is pressed against the skull. The bones are ornamented with tubercles, alveoli and thin ridges. The gigantic cleithrum possesses a long, narrow and pointed ventral branch, with a serrated lower margin, and a very broad posterior process. The hypercleithrum (= supracleithrum) is a large bone, broader ventrally than dorsally. A small, triangular posttemporal, with an acuminate upper extremity, is located near the parietal. A small postcleithrum is visible behind the hypercleithrum. The pectoral fin is replaced by a short but very broad spine that is articulated and partly fused to the ventral margin of the wide cleithral posterior process.

A fragment of a pelvic ray is visible a little before the postcoelomic bone. The pelvic bones are not preserved.

3. The axial skeleton (Fig. 18)

The axial skeleton is poorly ossified. Only the first thirteen vertebral segments are partly preserved. The complete vertebral axis probably contained a little less than twenty segments. Well developed neural arches are present but the haemal arches are not visible. Thus, the notochord is not surrounded by the arches. The first neural and haemal spines are long and the last ones very short. Fragments of ribs are visible. The postcoelomic bone is broad but rather short.

4. The dorsal and anal fins (Fig. 18)

The dorsal fin has a rather long basis and begins just behind the nuchal horn. The number of rays and pterygiophores is unknown. The anal fin has a shorter basis and contains 7 rays. Traces of at least 5 anal pterygiophores are visible.

5. The caudal skeleton (Fig. 20)

The caudal skeleton is incompletely preserved. Only the hypochordal series is present with 5 elements. The fourth hypochordal is greatly enlarged, forming a very broad hypural plate. This plate probably results from the fusion of several hypochordals. The epichordals and the urodermals are not known.

Only a part of the caudal fin is present.

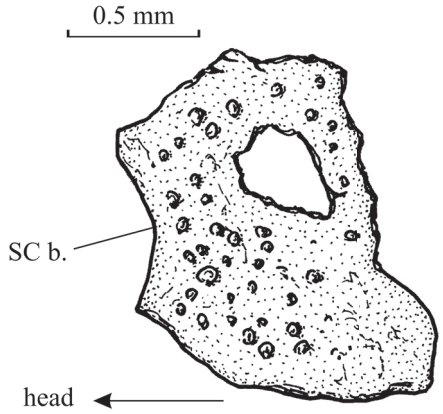

Fig. 21. *Pankowskichthys libanicus* gen. et sp. nov. A scute-like body scale of holotype, IRSNB P 9278.

6. Squamation (Fig. 21)

The squamation is badly preserved. However, some fragments and prints of scales are visible on the entire body. These scales are large, scute-like, irregularly shaped and ornamented with tubercles and alveoli.

A small spine is articulated on the ventral extremity of the postcoelomic bone.

Discussion

1. *Joinvillichthys* gen. nov. and *Pankowskichthys* gen. nov. within Neopterygii

Joinvillichthys gen. nov. and *Pankowskichthys* gen. nov. share a few very peculiar characters: (1) there is a dermosupraoccipital, (2) the maxilla is plate-like and toothless, (3) the supramaxillae are lost, (4) the mesethmoid is very long and includes the lateral ethmoids, (5) a dermohyomandibula is fused with the hyomandibula, (6) the hyomandibula is sutured to the preopercle, (7) the preopercle is greatly hypertrophied, trapezoid in shape and it covers a great part of the cheek, (8) the opercle is severely reduced, (9) the subopercle and interopercle are lost, (10) the parasphenoid is elongate and toothless, (11) the pelvic girdle is reduced, (12) a postcoelomic bone is present and (13) the neural and haemal arches do not fuse together. Within Neopterygii, the association of these thirteen characters states is found only in the Pycnodontomorpha, a superorder recently erected by Nursall (2010) for the former Pycnodontiformes and to which the two new genera can be allocated.

Nursall (2010) divided the Pycnodontomorpha into two orders, the Gyrodontiformes for the families Mesturidae and Gyrodontidae and the Pycnodontiformes as a new usage for the former Pycnodontoidei. Species belonging to the Gyrodontiformes have two dermosupraoccipitals, a dentary with dorsal and ventral branches, styliform teeth on the premaxilla and the dentary, small bony tesserae covering the snout, the cheek and the gular region, while they also lack tubular infraorbitals. Species belonging to the Pycnodontiformes possess only one dermosupraoccipital, a dentary reduced to its ventral branch, incisiform teeth on the premaxilla and the dentary and true infraorbitals even when a few bony tesserae are preserved on the cheek or in the gular region. Thus, the osteological characters of *Joinvillichthys* gen. nov. and *Pankowskichthys* gen. nov. refer these two fish genera to the Pycnodontiformes and not to the Gyrodontiformes.

The two new Lebanese genera present three remarkable apomorphies. The prefrontal and the premaxilla combined or the prefrontal alone form a long rostrum that extends more or less beyond the lower jaw level. The upper margin of the toothless premaxilla is sutured to the lower margin of the elongate and broadened prefrontal. The pectoral fin is lost and replaced by a strong pectoral spine articulated on the cleithrum. These three characters only exist in the family Gladiopycnodontidae (Taverne & Capasso 2013) and not in any other pycnodontiform lineage.

2. *Joinvillichthys* gen. nov. and *Coccodus*

As was stated above, *Joinvillichthys lindstroemi* was originally ranged by Davis (1890) in *Coccodus*, a Late Cretaceous specialized pycnodontiform genus from Lebanon. This generic attribution was explicitely contested by Poyato-Ariza & Wenz (2002: 145). A short comparison between the two concerned genera is thus useful. The data on *Coccodus* hereafter mentioned come from Pictet (1850), Davis (1887), Hay (1903), Poyato-Ariza & Wenz (2002), Kriwet (2005) and principally from our own observations (Taverne & Capasso 2014).

Coccodus exhibits a normal pycnodontiform snout, with a long, toothed premaxilla overlying a narrow prefrontal. There is no rostrum, the upper and lower jaws being located at the same level. The dermosupraoccipital bears a large horn and develops a short posterior process, but there is no nuchal

horn. The teeth on the vomer and the prearticular are typically pycnodontiform, *i. e.*, large, molariform and ranged in regular rows. The preopercle is not very wide and does not cover completely the ventral branch of the hyomandibula. There is a normal pectoral fin with soft rays. Such a skeleton greatly differs from that of *Joinvillichthys lindstroemi*.

These important cranial and pectoral differences clearly show that *Joinvillichthys lindstroemi* cannot be reported to *Coccodus*.

3. The validity of *Joinvillichthys kriweti* gen. et sp. nov.

Joinvillichthys kriweti gen. et sp. nov. is similar to *J. lindstroemi*. However, the two species differ in many morphological and osteological details. *Joinvillichthys kriweti* gen. et sp. nov. has a deeper head and a deeper body. Many bones have different shapes and sizes in the two species. This is the case, for example, for the frontal, the parietal, the dermosupraoccipital, the dermopterotic, the dermosphenotic, the premaxilla, the maxilla, the preopercle, the opercle, the exposed part of the hyomandibula-dermohyomandibula, the cleithrum and the pectoral spine. *Joinvillichthys kriweti* gen. et sp. nov. also exhibits a double emarginated caudal fin, whereas *J. lindstroemi* has a caudal fin with a convex posterior margin. These differences amply justify the erection of the new species, *Joinvillichthys kriweti* gen. et sp. nov.

4. The validity of *Pankowskichthys* gen. nov.

Pankowskichthys gen. nov. and *Joinvillichthys* gen. nov. possess the same basal anatomy but they greatly differ in the details of their skeleton. Almost all the bones of the cranium, the jaws and the pectoral girdle of the two fishes exhibit different shapes and sizes.

Some differences between the two genera could be owing to allometry and ontogenetic growth, for instance, the length of the nuchal horn, the respective proportions of the cephalo-thorax and body, and the development of the neural and haemal arches.

Other osteological differences, however, are not allometric:

(1) The frontal is sutured with the dermopterotic in *Pankowskichthys* gen. nov. That is not the case in *Joinvillichthys* gen. nov.
(2) The premaxilla of *Pankowskichthys* gen. nov. bears a well developed, anterior hook-like process. Such a process is absent on the premaxilla of *Joinvillichthys* gen. nov..
(3) *Joinvillichthys* gen. nov. has a short dorsal fin located in the middle of the back, far from the nuchal horn. *Pankowskichthys* gen. nov. has a longer dorsal fin reaching the nuchal horn.
(4) A series of dorsal ridge scutes is present in *Joinvillichthys* gen. nov., but these are absent in *Pankowskichthys* gen. nov.
(5) A greatly hypertrophied hypural plate is present in the caudal skeleton of *Pankowskichthys* gen. nov. In *Joinvillichthys* gen. nov. and in the other gladiopycnodontid genera, some hypochordals are broadened but never hypertrophied.
(6) The body is entirely covered by scute-like scales in *Pankowskichthys* gen. nov. In *Joinvillichthys* gen. nov., the greatest part of the body is covered by flake-like scales and the scute-like scales are only present in the tail region.

Pankowskichthys gen. nov. also shares with the more specialized gladiopycnodontid genera a series of apomorphies not present in *Joinvillichthys* gen. nov.:

(1) An anal spine is associated with the postcoelomic bone. This spine is short in *Pankowskichthys* gen. nov. and in one still undescribed genus of the family (pers. obs.). This spine is very large in *Rostropycnodus* and in another undescribed genus (pers. obs.), and becomes really gigantic in *Gladiopycnodus* (Taverne & Capasso 2013: figs 2, 18, 20). In *Joinvillichthys* gen. nov., as in *Monocerichthys*, the most primitive genus of the family, only postcloacal scales are present at the

level of the postcoelomic bone, as normally in pycnodontid fishes (Taverne & Capasso 2013: figs 8, 12).

(2) The pectoral spine is shortened but considerably broadened and more or less fused with the cleithrum in *Pankowskichthys* gen. nov. and in a few other specialized genera (Taverne & Capasso 2013: fig. 19). In *Joinvillichthys* gen. nov., the pectoral spine is longer, thinner and simply fixed to the cleithrum.

(3) The rostrum is elongated and becomes acuminate in *Pankowskichthys* gen. nov. and the more evolved genera of the family, the lower jaw remaining rather short. This elongation reaches its maximum in *Gladiopycnodus* and *Rostropycnodus* (Taverne & Capasso 2013: figs 3, 19). In *Joinvillichthys* gen. nov., as in *Monocerichthys*, the rostrum outpaces the lower jaw level only slightly (Taverne & Capasso 2013: fig. 9).

(4) The nuchal horn is fixed to the dermosupraoccipital and the parietal in *Pankowskichthys* gen. nov. and in the more specialized genera having retained a nuchal horn (pers. obs.). In *Joinvillichthys* gen. nov., as in *Monocerichthys*, the parietal is not involved in the cranial articulation of the nuchal horn (Taverne & Capasso 2013: fig. 9).

Such a number of differences, and especially the apomorphies shared with the more evolved genera of the family, makes it unreasonable to consider *Pankowskichthys* gen. nov. as a juvenile specimen of *Joinvillichthys* gen. nov. and justifies the creation of a unique new genus for the former fish.

5. *Joinvillichthys* gen. nov. and *Pankowskichthys* gen. nov. within Gladiopycnodontidae

Joinvillichthys gen. nov. and *Pankowskichthys* gen. nov. are rather primitive gladiopycnodontid fishes. Indeed, they preserved the nuchal horn that was lost in the more evolved members of the family (Taverne & Capasso 2013: figs 3, 19) and they had not acquired the frontal horn and the strong anal spine present in some advanced genera (Taverne & Capasso 2013: figs 2, 4, 18–20).

The skull and pectoral girdle of *Joinvillichthys* gen. nov. are not very different from those of *Monocerichthys*. The rostrum is a little more elongate and more acuminate in the new genus and its nuchal horn is a little longer and rests only on the dermosupraoccipital, with no implication of the supratemporal or posttemporal. *Joinvillichthys* gen. nov. also possesses dorsal ridge and ventral keel scutes, in opposition to *Monocerichthys* that lacks these structures (Taverne & Capasso 2013: fig. 8). The presence of scute-like scales in the caudal region of *Joinvillichthys* gen. nov. is another apomorphic character absent in *Monocerichthys*, in which only small, flake-like scales cover the entire body (Taverne & Capasso 2013: fig. 14).

Pankowskichthys gen. nov. is more apomorphic than *Monocerichthys* and *Joinvillichthys* gen. nov., as seen in section 4 of the present discussion.

The phylogeny within the Gladiopycnodontidae will be studied in a forthcoming paper, which includes the description of four other genera of this family (Taverne & Capasso, in prep.).

Acknowledgments

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