A re-description of *Hensodon spinosus*, a remarkable coccodontid fish (Actinopterygii, †Pycnodontiformes) from the Cenomanian (Late Cretaceous) of Haqel, Lebanon

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Abstract

Hensodon spinosus, a rare and very peculiar pycnodontiform fish from the Upper Cenomanian limestone of the Haqel fossils quarry (Lebanon) is re-described on the basis of four new specimens. It is the only species assigned to the genus. It shares with the family Coccodontidae (*sensu* POYATO-ARIZA & WENZ, 2002) almost all its synapomorphies but is also characterized by several unique autapomorphies. The species exhibits a rounded general shape of the body, an enormous head, an extremely reduced snout with a minute mouth gash, a horny frontal showing modifications that we interpret as dimorphic sexual differences, styliform teeth, a giant occipital process with many spines on its margins and formed by the dermosupraoccipital, the parietal and the supratemporal, a prefrontal, an edentulous, unornamented, elongated rhomboid maxilla, a very massive spiny cleithrum, a big spiny post-coelomic bone, and a few elongated bar scales. All those characters award a unique impressive aspect to the fish. Remains of the original colour pattern add information about the external aspect of this remarkable fish.

Résumé

Hensodon spinosus, un pycnodonte rare et très particulier provenant des calcaires du Cénomanien supérieur de la carrière à fossiles de Haqel (Liban) est redécrit sur la base de quatre nouveaux spécimens. Il s'agit de la seule espèce du genre. Elle partage presque toutes les synapomorphies de la famille des Coccodontidae (sensu POYATO-ARIZA & WENZ, 2002) mais est aussi caractérisée par quelques autapomorphies uniques. L'espèce montre un corps de forme arrondie, une tête énorme, un museau extrêmement réduit avec une minuscule fente buccale, un frontal cornu montrant des différentes que nous interprétons comme du dimorphisme sexuel, des dents styliformes, un processus occipital gigantesque, garni d'épines sur ses bords et formé par le dermosupraoccipital, le pariétal et le supratemporal, un préfrontal, un maxillaire rhomboïde, édenté, lisse et allongé, un cleithrum très massif et épineux, un grand os postcoelomique épineux, ainsi que quelques écailles réduites et en forme de barre. Tous ces caractères donnaient un aspect tout à fait remarquable au poisson. Des restes de la coloration ajoutent des informations sur l'aspect extérieur de ce curieux poisson.

Introduction

The fish fauna collected in the past three centuries from the Upper Cenomanian limestones of the quarry of Haqel includes a large series of pycnodontiforms offering an impressive variability of forms. The most abundant pycnodontid species of all in the thanatocoenosis of Haqel is *Nursallia goedeli* (HECKEL, 1856), which is really common there. This abundance of pycnodonts revealed that the environmental conditions typical of the habitat of this area were particularly favourable to these types of fishes during Late Cenomanian times. The pycnodontiform local fauna includes also a number of rare and sometimes very rare forms, prevalently of little size, collected during the last twenty years (see e. g. FOREY *et al.*, 2003; NURSALL & CAPASSO, 2004; CAPASSO *et al.*, 2009). The interest for these rare species consists in the unusual combination of its anatomical characters that demonstrate the impressive variability of the members of the pycnodont group, despite it is considered a monophyletic group, inside the thanatocenosis of one of the most famous fossil fish localities over the world.

  HENNIG (1907) briefly described and figured one of

those rare pycnodontiform fishes from the Cenomanian of Haqel under the name *Mesodon spinosum*. Later, STEINMANN (1928) also figured the specimen as *Mesodon spinosus* HENNIG. A modern re-description has been done by KRIWET (2004) but remains very superficial because of the bad preservation of the holotype and single known specimen at that time. However, KRIWET (2004) has shown that this fish was not a *Mesodon* but belonged to a new genus for which he erected the taxon *Hensodon* located by him within the pycnodontiform family Coccodontidae.

One of us (R. N.) has recently found at the Haqel quarry four new and better preserved specimens referable to *Hensodon spinosus* (HENNIG, 1907) but showing some osteological differences between one specimen and the three others, differences due in our opinion to a remarkable sexual dimorphism.

The aim of our paper is thus to give a more complete re-description of this very peculiar pycnodontiform fish.

Material (Figs 1a, 1b; Table 1)

The material examined here consists of the following four samples, all in only one part, without counterparts, coming from the Haqel fossil quarry (see next paragraph):

(1) Specimen CLC # S.357: near complete fish (only the tip of the tail is missing), 64 mm long (but this measure did not represent the Total Length (TL), because the final part of the caudal fin is missing); the fish is seen by its left side (Fig. 1a-A). We interpret this specimen as a male because its frontal horns are bigger and its skeleton more heavily ossified than in the three following specimens, considered as female. In our opinion, the holotype described by KRIWET (2004) is also female. We do not think that there were two different but closely allied species of
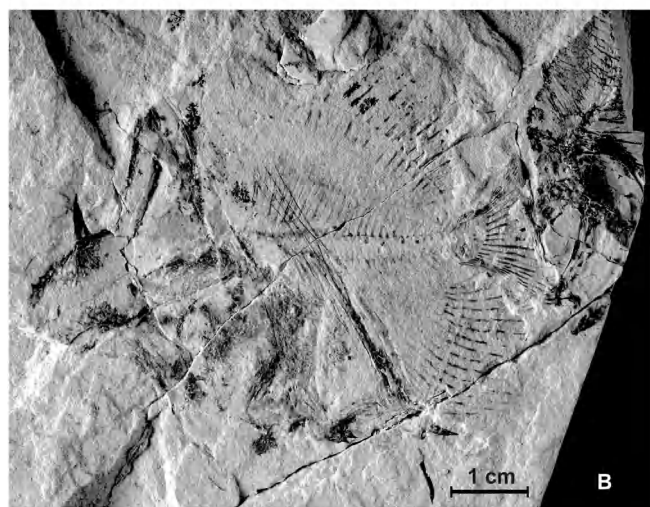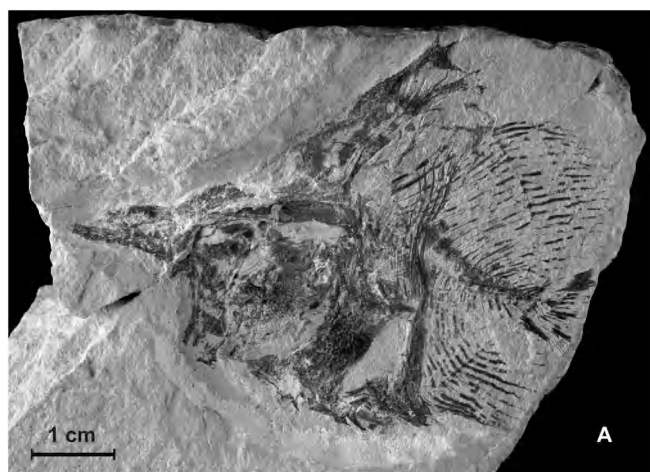

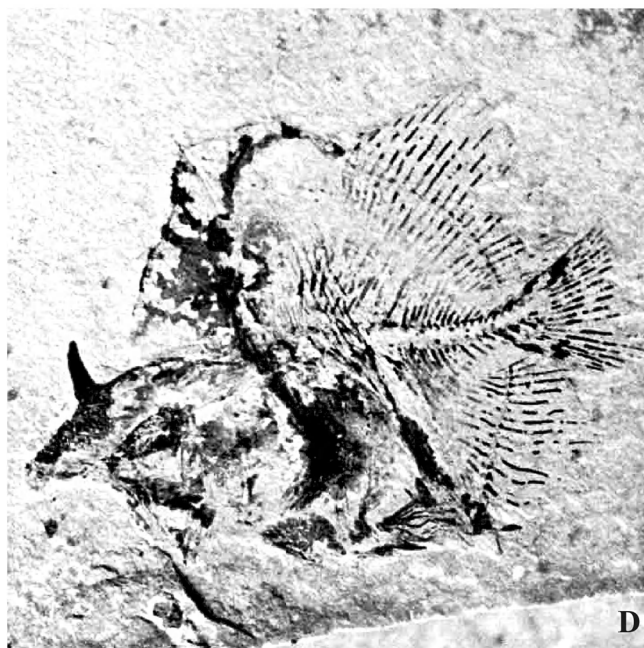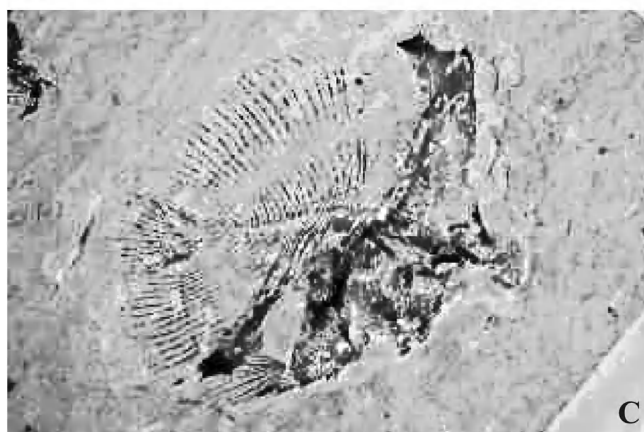Fig. 1a – *Hensodon spinosus* (HENNIG, 1907). A: CLC # S.357; B: CLC # S.718.

Fig. 1b – *Hensodon spinosus* (HENNIG, 1907). C: CLC # S.572; D: CEH # 115.

Table 1 – Main measurements (in mm) and main numeric characters of the examined samples of *Hensodon spinosus*.

Sample	TL	SL	TD	nV	nDP	nAP	nCR	nPR	nVR
CLC # S.357	---	46	49	23	21	13	29	17	7
CLC # S.718	55	50	62	25	22	16	26	10-12	7
CLC # S.572	50	47	60	23	21	16	29	---	7
CEH # 115	57	48	46	28	22	16	26	---	7

TL = total length, measured as horizontal distance between tip of pre-maxilla and the posterior limit of the caudal fin (in our case the TL is sensibly minor to the total length of the other fish, because the spines of the frontal region are not included in this measure, as these spine exceeding the anterior margin of the premaxilla); SL= standard length; TD = total (maximum) depth (measured as the greatest vertical distance of the body); nV = total number of vertebral segments; nDP = number of dorsal pterygiophores; nAP = number of anal pterygiophores; nCR = number of principal caudal fin rays; nPR = number of principal pectoral fin rays; nVP = number of principal pelvic fin rays. The sign --- indicates that the character is not visible or not countable.

Hensodon living in the same marine Late Cretaceous environment at Haqel.

(2) Specimen CLC # S.718: near complete fish, with TL = 50 mm; the fish shows its left side (Fig. 1a-B).

(3) Specimen CLC # S.572: near complete fish on a limestone slab with many fractures, with TL = 55 mm; the fish shows its right side (Fig. 1b-C).

(4) Specimen CEH # 115: near complete fish, with TL = 57 mm; the fish shows its left side (Fig. 1b-D).

CLC: Public collection of fossil fish called *Luigi Capasso Collection*, Registered by the Italian Ministery of Cultural Heritage, with Protocol STRAP n. 21 of the 20.01.2000 – Situated in via d`Aragona, 12 – 66100 Chieti (Italy); complete list of the *Luigi Capasso Collection* is available upon request to the quoted postal address, or throught the "Italian Government – Ministery of Cultural Heritage – Soprintendenza Archeologica dell'Abruzzo – Via dei Tintori, 1 – 86100 Chieti (Italy)".

CEH: Collection of Dr. Roy Nohra, stored at the Expo Haqel, Main Road, Haqel, Lebanon.

Location and preservation of fossils (Figs 2, 3)

The specimens described herein are preserved in lagerstätten, formed by fine-grained (micritic), finely laminated plattenkalk of the Haqel quarry.

The little village of Haqel lies in northern Lebanon, in the district of Jbel, province of Jabal Loubnan, on the eastern slope of Mount Lebanon, near the head of the Haqel River valley, 700 m above sea level. Haqel is a small village, with about 775 inhabitants in 70 houses (Fig. 2). The only quarry open in this region is on the left (South) wall of the valley near the source of the Haqel River, about 1 km East of the village, at

an altitude of 700 m. The site of the quarry extends for ca. 3000 square metres (Fig. 3). At the same level on the opposite wall of the valley the prevalent outcrop is of massive sterile limestone in the upper levels; but recently an excavation made by the family Abi Saad identified near the same formation, and apparently the same fossil fishes at the bottom of the sterile limestone also on the right (North) side of the Haqel River quarry. Nazih Nohra began to work at Haqel in 1964. The quarry continues until now to be an abundant source of fossils. Today, only two families are active in the fossil quarry: chiefly the Nohra family of Haqel, less frequently the Saad family of Byblos. Extraction is manual, but extension of a power cable from the village to the quarry by the Nohra family enables collectors to use an electric cutter to reduce the weight of the blocks containing fossils.

The composition of the Haqel flint is: $CaCO_3 \approx 75\%$; $SiO_2 \approx 20\%$; remainder mostly clay minerals (HÜCKEL, 1970). The limestone is well stratified (Fig. 3C). The strata are variably inclined downward, from 25 to 50 degrees to the West, but inclination is highly variable both in angle and direction. In addition, stratification is very irregular, as many micro-faults and curved strata are often present (Figs 3A, B). Chert is present in lenses and nodules, varying from few centimetres to 50 cm or more in diameter without concentric structure, often of irregular shape. The thickness of lamination is also very variable from a few millimetres to 50 cm. The thickest strata are usually sterile (Fig. 3B). The colour is also impressively variable from a pale yellow to a brown-beige, to grey and near black.

Haqel, in particular among Lebanese fossil localities, has an abundant preserved ichthyofauna. In fact the limestone of this restricted area probably represents one of the richest deposits of fossil fish in the world. Mass
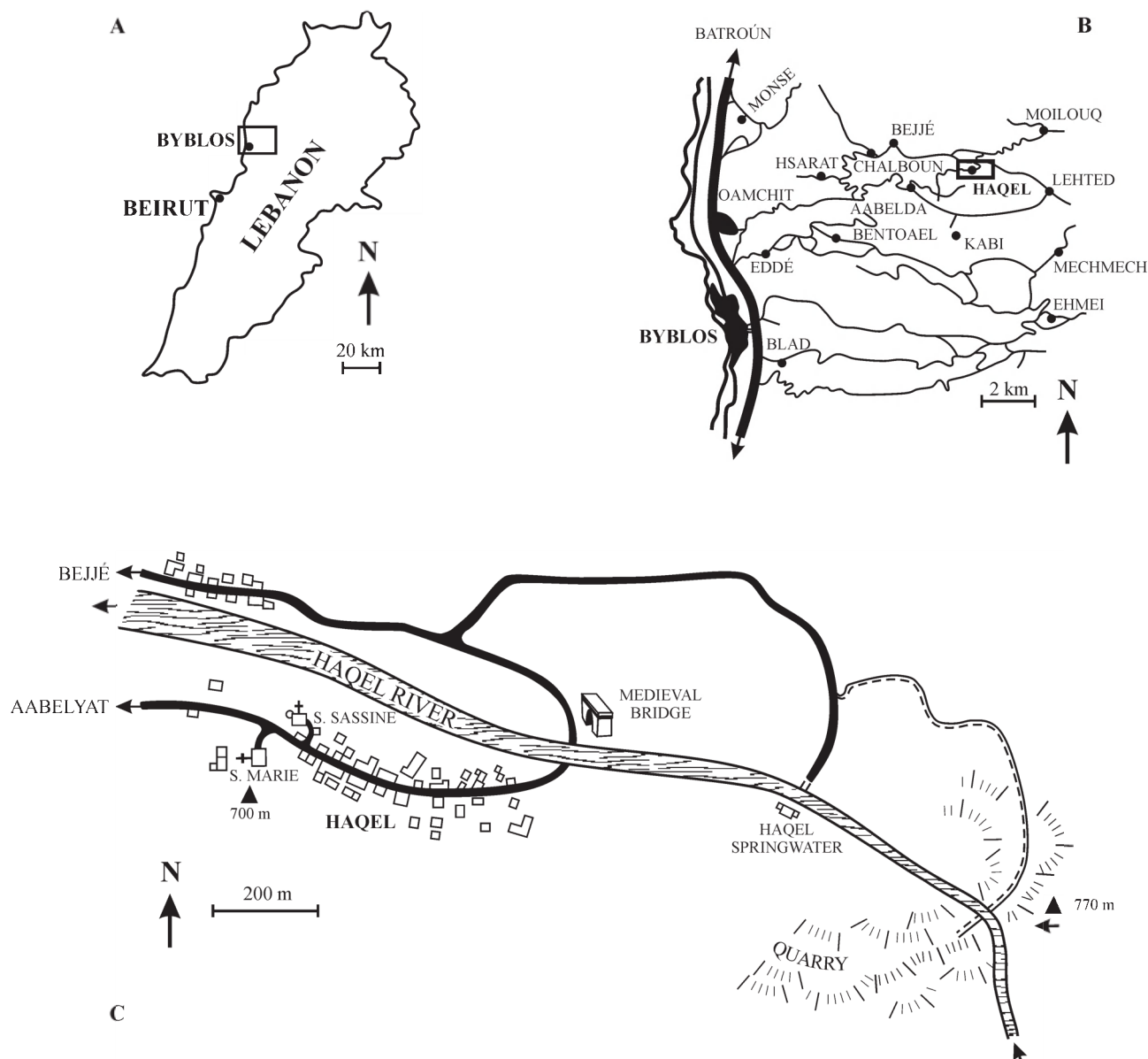
Fig. 2 – Geographic position of the Haqel fossils quarry.

mortality layers are relatively frequent; multiple fish slabs are regularly found in this locality. It is impossible to obtain very large slabs because the laminations of the richest strata are distorted, and cherty deposits are frequent. As already said, fishes are the most common fossils, but crustaceans are also frequent, and plants, reptiles, echinoderms, insects and birds are also present as rare finds (listed in decreasing order of frequency) (GAYET *et al.*, 2003). Bits and pieces of fossils are often seen in different layers at the edges of blocks, which are not cut square. FOREY *et al.* (2003) recorded 55 genera and 69 species of fishes in Haqel deposits, but this number is increased in the last two years, compared to 47 genera and 58 species in nearby Hajula, and 25 genera and 30 species in En Nammoura, although it

must be kept in mind that these figures will change with further collection and description. Five (9%) of 56 species of actinopterygians described by FOREY *et al.* (2003) from Haqel are pycnodontiform fishes, all of which are highly derived.

HÜCKEL (1970) described the probable conditions of deposition at Haqel, with concentration of sediments in small basins, influenced by tectonic activity causing slippage at shelf margins. HEMLEBEN (1977) invoked the probability of biological toxicity ("red tides") and oxygen deficiency in the mortalities recorded at Haqel. Fishes are the most common and noticeable fossils at the sites, usually complete with scales (HÜCKEL, 1970). HEMLEBEN (1977) noted that 87% of fishes oval in shape lay in a stable position on their

side, but that 13% were found lying on their back or belly. Often the fish are strongly arched, with head and tail raised, and sometimes a telescoping of the vertebrae (HÜCKEL, 1970). The four specimens described here are generally not badly deformed. However, the specimen CLC # S.357 seems to be a little compressed in supero-

Fig. 3 – Three aspects of the extant situation and works for fossils extraction at the Haqel quarry.

inferior direction. The Haqel fish layers have been defined as Cenomanian V, in the analysis of HÜCKEL (1970).

The actual quarries that produce the new specimens of *Hensodon spinosus* are shown in Figure 3.

Systematic paleontology

Class Osteichthyes HUXLEY, 1880
Subclass Actinopterygii COPE, 1887
Division Halecostomi REGAN, 1923
sensu PATTERSON, 1973
Order Pycnodontiformes BERG, 1937
Suborder Pycnodontoidei NURSALL, 1996
Family Coccodontidae BERG, 1940
sensu POYATO-ARIZA & WENZ (2002)
Genus *Hensodon* KRIWET, 2004

Type species: *Hensodon spinosus* (HENNIG, 1907)

Hensodon spinosus (HENNIG, 1907)
Figs 4 - 21

Description
General shape (Figs 4-6)
Hensodon spinosus is a pycnodontid of little dimension, between 5 to 10 cm of total length. The fish is disc-shaped and laterally compressed, with a very short abdominal region. The head and the pectoral girdle are enormous in comparison with the body, representing a little more than the half of the entire fish. The snout is short, with a reduced mouth gash. The frontal region bears big horns. A very large occipital horny process exists in the post-frontal region. Many large bones of the skull are spongy, allowing the big head to be lighter than with internally solid bones. The pectoral girdle is spiny. The maximum body depth corresponds to the posterior margin of the post-frontal osseous process, with a mean of the ratio SL (standard length)/TD (maximum body depth) = 87.3 (see Table 2) (as the Total Length is the horizontal distance between the tip of the premaxilla and the posterior limit of the caudal fin, in our case the TL is sensibly minor to the total length of the other fish, because the spines of the frontal region are not included in this measure, as these spine exceeding largely the anterior margin of the premaxilla).

Skull, teeth and hyoid skeleton (Figs 7-10, 12)
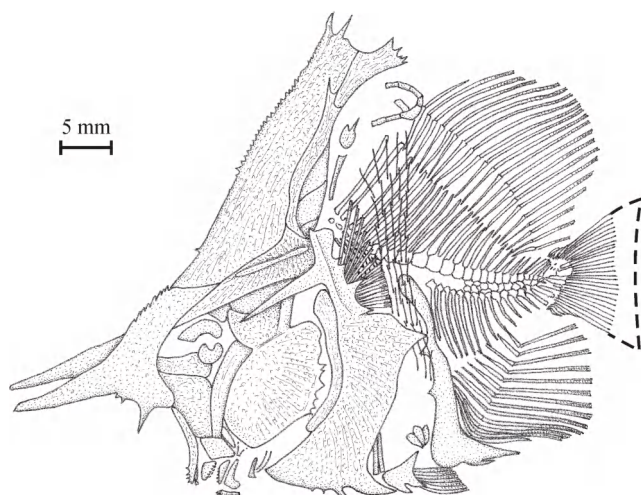The two frontals are large and horny bones. They protrude, forming so not only the frontal region but also

Fig. 4 – *Hensodon spinosus* (HENNIG, 1907). Reconstruction of the entire fish based on the supposed male specimen CLC # S. 357.
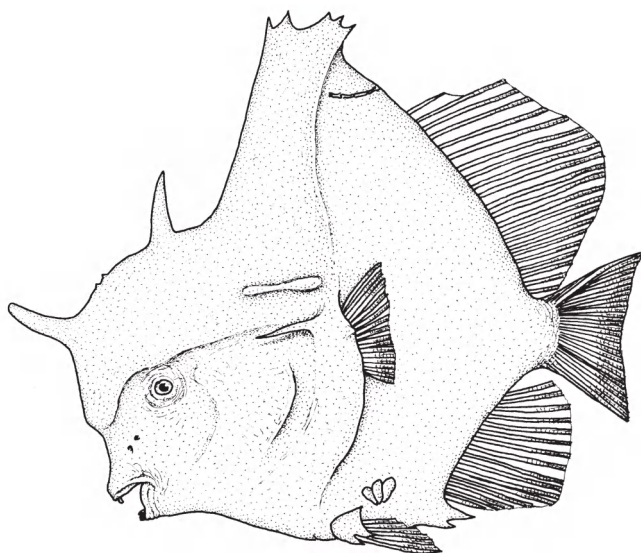

Fig. 6 – *Hensodon spinosus* (HENNIG, 1907). Reconstruction of the entire living fish. The supposed female pattern.

the anterior part of the skull. There are two patterns of frontal region and horns, very probably representing a sexual dimorphism. In specimen CLC # S.357, the frontals are rather narrow above the orbit. They support two huge, elongate, anteriorly directed conic horns, with a pointed pit, one on each frontal. Above that horn, the frontal margin exhibits a series of eight small spines, contributing to determine a serrated aspect on the superior margin of the frontal. Ventrally, at the base of the big horn, there are two other smaller spines. As already said, we interpret that morphology as the male pattern. In the holotype, the frontal exhibits two smaller horns, one dorsally, the other more ventrally (HENNIG, 1907: fig. 3; KRIWET, 2004: fig. 1, 3). We think that
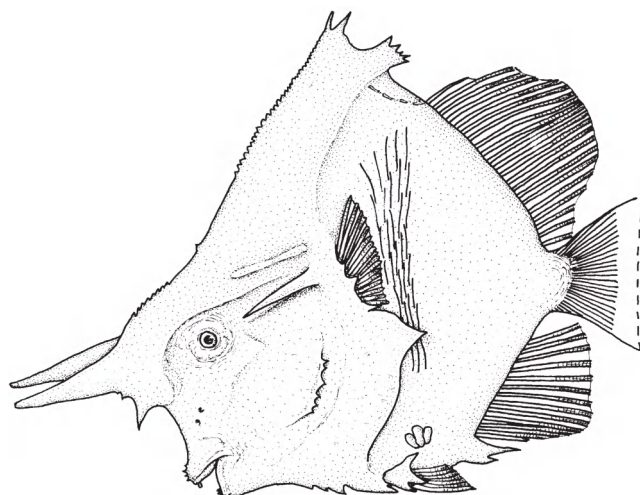

Fig. 5 – *Hensodon spinosus* (HENNIG, 1907). Reconstruction of the entire living fish. The supposed male pattern.

is the female pattern. In specimen CLC # S.572, the horny region of the frontal is lost, while samples CLC #S.718 and CEH # 115 have preserved the upper part of the frontal, with the dorsal horn, but have lost the lower part of the bone, with the ventral horn. These last three specimens also show that the frontal is much broader above the orbit in the supposed female fishes than in the male.

KRIWET (2004: fig. 3) described on the holotype a horizontally elongate parietal (= postparietal in KRIWET's text) behind the frontal. This bone bears the same sort of horn as on the frontal. HENNIG (1907: fig. 3) figured the same structure. Our own observations show that the parietal offers a quite different shape and is not horny. KRIWET's horny "parietal" simply is a fragment of one of the two frontals posteriorly displaced by the fossilisation.

Behind the frontal, the crown of the skull develops a gigantic tower-like occipital process, like the one of *Trewavasia carinata* (DAVIS, 1887) and *Ichthyoceros spinosus* GAYET, 1984, two other Late Cretaceous coccodontid fishes from Lebanon (GAYET, 1984: fig. 1 and 2; NURSALL & CAPASSO, 2008: fig. 5), but still much higher. The very large dermosupraoccipital forms

Table 2 – Value of the ratio SL/ TD in described samples of *Hensodon spinosus*.

Sample	SL	TD	Ratio
CLC # S.357	46	49	93.9
CLC # S.718	50	62	80.6
CLC # S.572	47	60	70.3
CEH # 115)	48	46	104.3
Mean			87.3

the anterior part of the process, while its posterior part is constituted ventrally by the thin but very deep parietal, and dorsally by the supratemporal (= extrascapular). The long anterior margin of the dermosupraoccipital is serrated and its superior margin bears two well-developed spines. This serration is less pronounced in the supposed female samples than in specimen CLC # S.357. The dorsal margin of the supratemporal also bears a few spines. This character is the same in both presumed sexes but the anterior margin of the process follows the frontal profile in the supposed male fish (CLC # S.357) while it forms a marked angle with the frontal profile in our three female specimens and in the holotype (KRIWET, 2004).

The dermopterotic is very long but not high and it bears a long horizontal crest. Its acuminate anterior
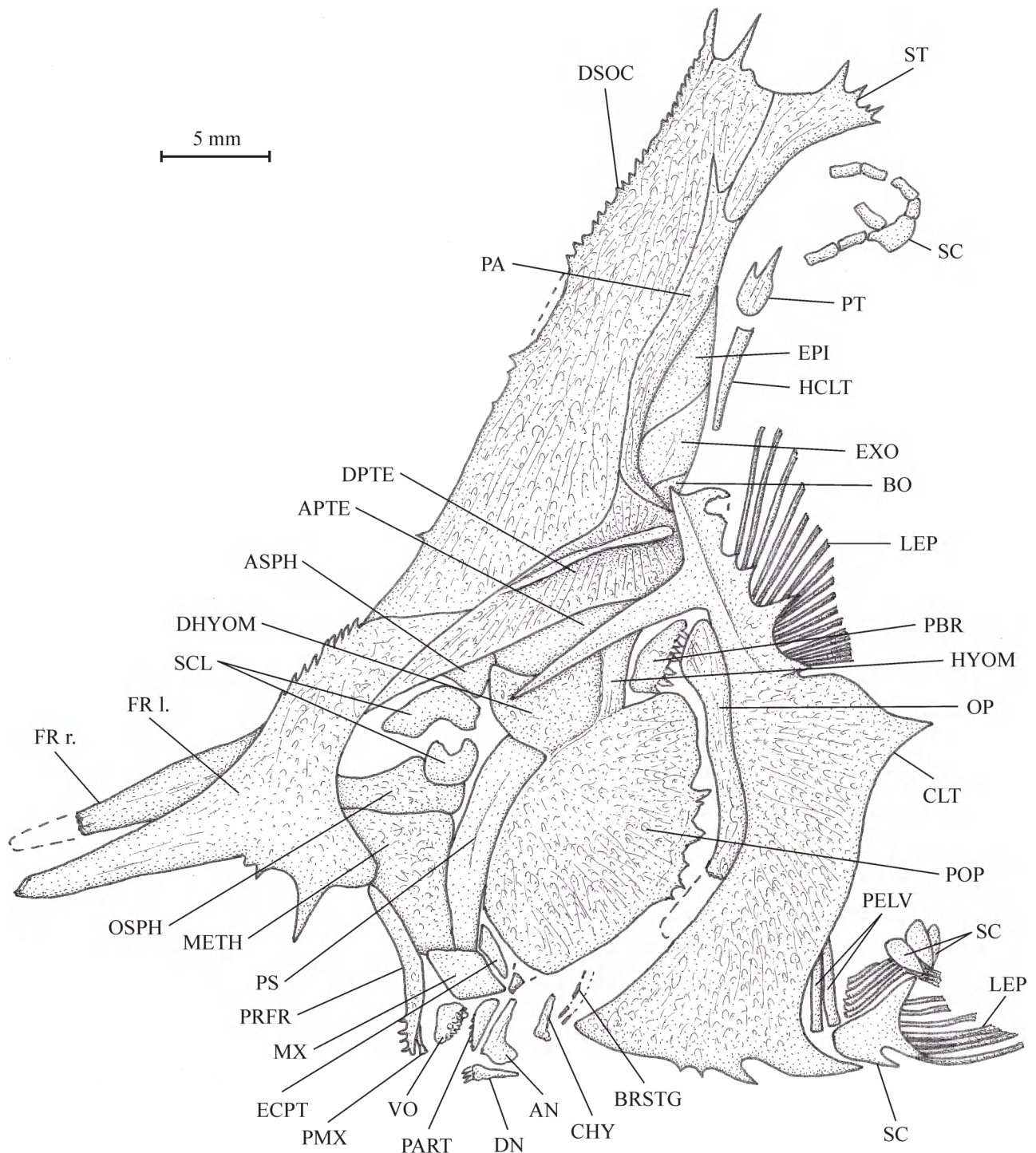
Fig. 7 – *Hensodon spinosus* (HENNIG, 1907). The skull and girdles of the supposed male specimen CLC # S.357.

extremity overhangs the orbit in the male specimen. In our three female samples, the dermopterotic is a little shorter and less acuminate. The dermopterotic and the frontal serve as the basis of the tower-like occipital process. Between the dermopterotic and the big anterior dorsal spine of the cleithrum, specimen CLC # S.357 shows the print of the autopterotic. On the same specimen, below the anterior part of the dermopterotic and just behind the orbit, a small autosphenotic is visible.
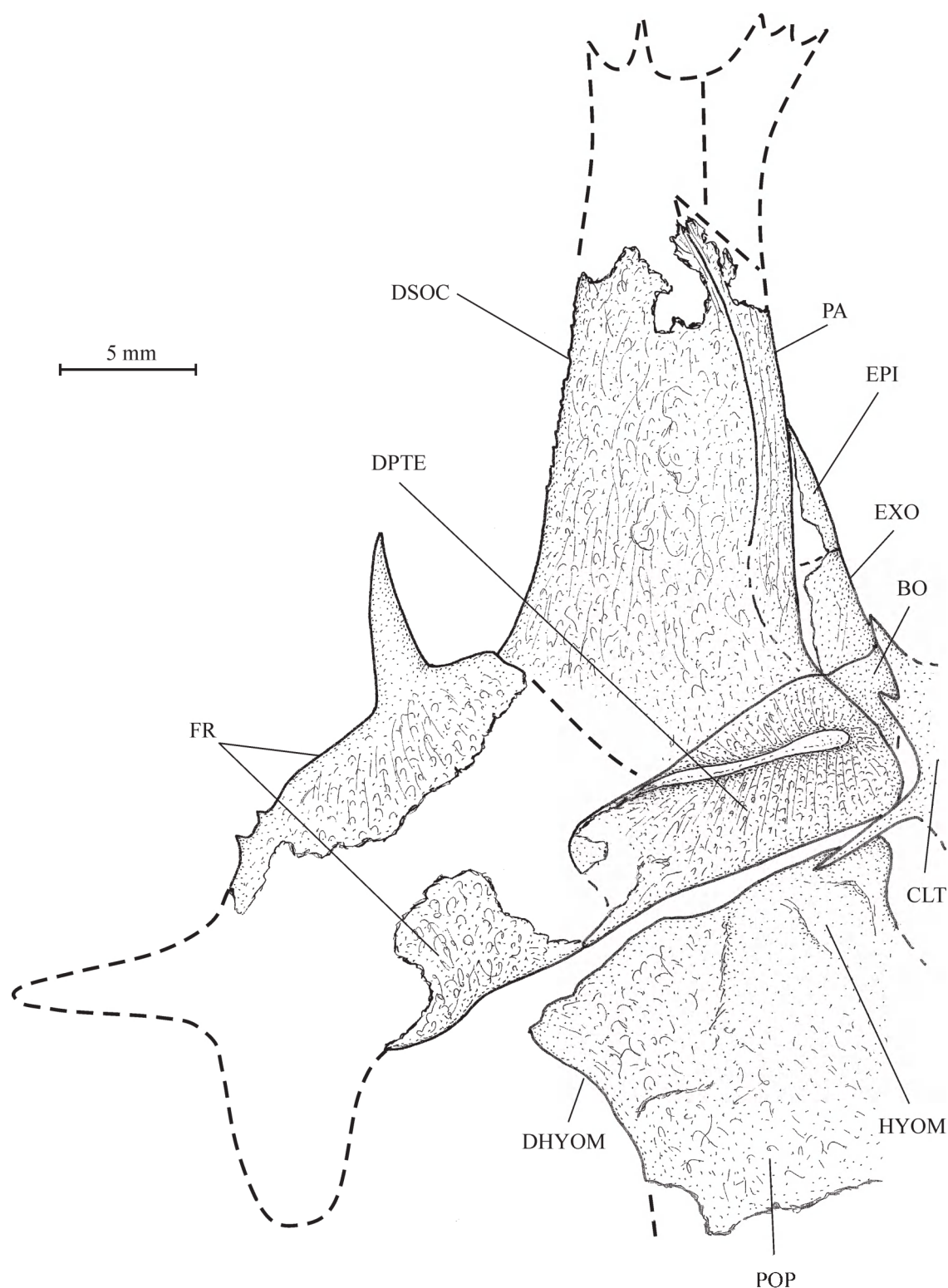

Fig. 8 – *Hensodon spinosus* (HENNIG, 1907). Part of the skull of the supposed female specimen CLC # S.718.

The ethmoid complex consists of the dermal prefrontal and the endochondral mesethmoid. The prefrontal is well preserved on specimen CLC # S.357. It is a long and thin bone located just under the basis of the frontal and before the mesethmoid, partly covering the premaxilla. There are four small spines on the lower part of the anterior margin of the bone. Such a prefrontal exists in a few pycnodontiform fishes. It is a paired dermal bone of the ethmoid region perhaps homologue with the laterodermethmoid. The mesethmoid is a large and massive bone contacting the frontal and the prefrontal anteriorly and resting on the parasphenoid posteriorly.

The parasphenoid is preserved as an imprint in all specimens. It is a broad and curved bone. Its antero-ventral extremity is not very well distinguishable

Fig. 9 – *Hensodon spinosus* (HENNIG, 1907). Upper part of the occipital process with bony spines in specimen CLC # S.357.

because that part of the bone is covered by the maxilla. The anterior-superior margin serves as a basis for the orbit.

The infraorbital series is preserved neither in our specimens nor in the holotype (KRIWET, 2004: fig. 3). These bones were perhaps absent in *Hensodon*. Two well-developed sclerotic bones are present. Both are semi-lunar in general shape. The dorsal one is longer than the ventral.

A large orbitosphenoid is present just below and before the ventral sclerotic bone. It contacts the frontal anteriorly and the mesethmoid ventrally.

The vomer is reduced, with its dorsal margin in contact with the ventral margin of the parasphenoid. It is impossible to decide the number of vomerine teeth, but these teeth seem to be arranged in longitudinal series. The tooth shape seems to be conic, styliform in the anterior elements, but the posterior teeth seem to have a clavate aspect, such as semi-spherical, but pedunculate, similar in general shape to the typical vomerian and dental teeth in *Trewavasia carinata* (NURSALL & CAPASSO, 2008: fig. 5, 9, 10).

The jaws are very reduced and located on the ventral margin of the head. Only the lower part of the thin premaxilla is visible behind the prefrontal. One prehensile, conic, styliform tooth is present on each premaxilla. The maxilla is large, rhomboid in general shape, edentulous, with an unornamented external surface. Sometimes, the bone is overlapping the posterior part of the vomer. The dentary is little developed. Three conic teeth are present. The prearticular is delicate, short, near triangular in general shape. Only one series of prearticular teeth seems to be present, implanted only on the occlusal margin of the bone, but we are unable to decide definitively if others teeth are really absent from the inside surface of the prearticular. These teeth, presumably arranged in a unique series, can be observed in negative on the matrix of the fossils, and we can be sure that the general shape is conic, with well-developed pits, styliform. No traces of typical rounded teeth are visible on the prearticular in any sample. There is a long angular below the prearticular. The articular is not visible.

Only the condylar part of the quadrate is preserved. Above the quadrate and between the maxilla and the preopercle, the postero-ventral part of a small ectopterygoid is also visible.

The space between the parasphenoid and the cleithrum is occupied by three bones, a very large ventral ornamented preopercle, a smaller antero-dorsal ornamented dermhyomandibula and a still smaller but more robust postero-dorsal hyomandibula. These three
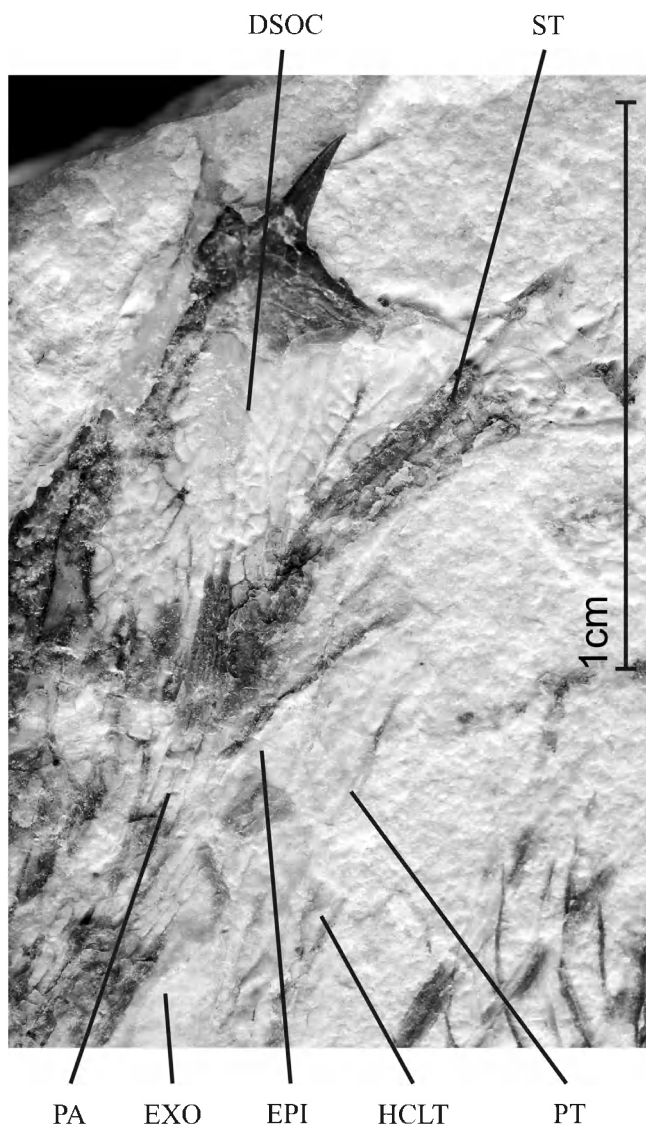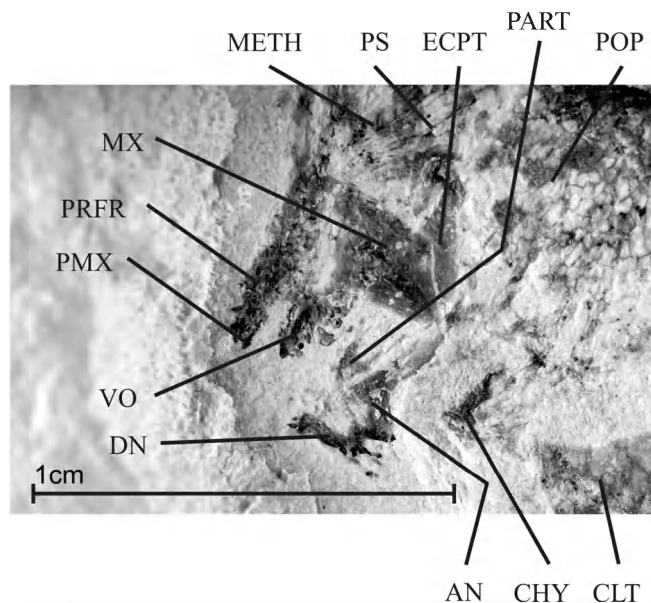
Fig. 10 – *Hensodon spinosus* (HENNIG, 1907). Mouth region of specimen CLC # S.357.

bones are more or less ankylosed together. An ankylosis of the cranial bones in this anatomical region is typical of the family Coccodontidae, according to the POYATO-ARIZA & WENZ (2002: 162). The dermhyomandibula is semi-lunar and thus quite distinguishable from the preopercle in the male sample CLC # S.357 but is in complete continuity with the preopercle in the female specimen CLC # S.718. The posterior margin of the preopercle exhibits some small spines in specimen CLC # S.357. It seems that our three supposed female
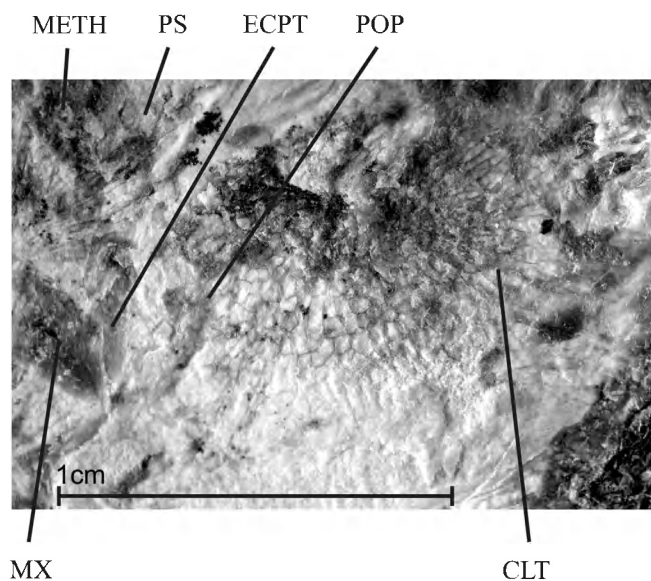

Fig. 11 – *Hensodon spinosus* (HENNIG, 1907). Part of the preopercle and the cleithrum in specimen CLC # S.357, showing the polygonal aspect of the bone surface.

samples and the holotype (KRIWET, 2004: fig. 3) do not possess such preopercular spines.

The opercle is a very narrow bony lamina inserted between the posterior margin of the preopercle and the anterior margin of the cleithrum.

Three endocranial bones are clearly visible as prints in the region of the origin of the vertebral column, just behind the parietal, on specimen CLC # S.357. They have also let some bony traces on specimen CLC # S.718. We interpret these three bones as the basioccipital, the exoccipital and the epiotic.

A boomerang-shape ceratohyal occupies the region immediately back to the prearticular, and supports two little and thin branchiostegal rays partly preserved.

A pharyngeal bone supporting 5 to 8 teeth is present immediately in front of the anterior margin of the cleithrum, just behind the hyomandibula (Fig. 12). These teeth are well visible in the specimens CLC # S.357 and CLC # S.572, and seem to be arranged in one series. The shape of these pharyngeal teeth is quite variable, but many of these teeth have a large root, with
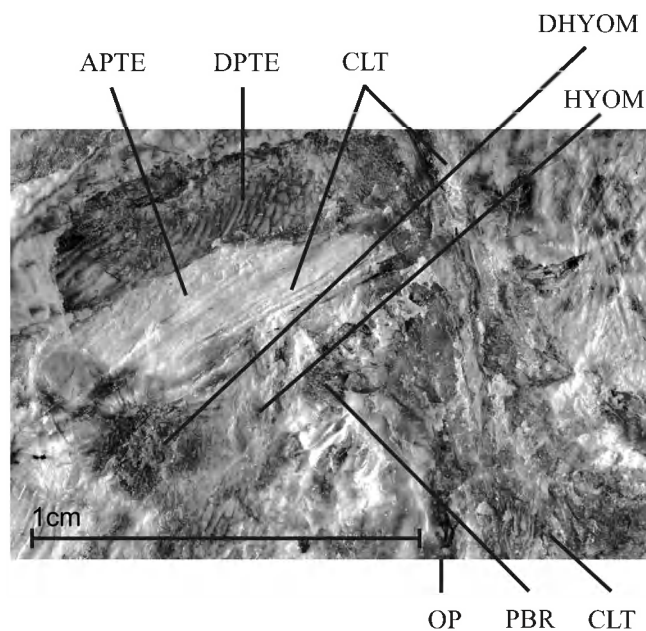

Fig. 12 – *Hensodon spinosus* (HENNIG, 1907). Part of the skull and pectoral girdle in specimen CLC # S. 357, showing the toothed pharyngeal bone.

an elliptic profile, and the crown is inserted on a pole and appears hooked.

Pectoral girdle and fins (Figs 6, 7, 9, 11-13)
Specimen CLC # S. 357 exibits a small posttemporal, with a broad basis and a spiny apex, and a small rod-like supracleithrum. The posttemporal is also visible on specimen CLC # S.718.

The cleithrum is enormous and represents the most

important bone in the skeletal anatomy of this species. It is extended from the ventral margin of the fish to the ventral border of the tower-like occipital process. In the supposed male subject CLC # S.357, the cleithrum is sensibly more robust, with many elongated and robust spines. Despite that, the number and general arrangement of the spines and the general shape of the bone is exactly the same in both presumed sexes. However, the three supposed female individuals present a cleithrum generally more delicate. The cleithrum is composed by strong bone, with a surface structured in polygonal figures (Fig. 11). It shows two major limbs vertically oriented. The upper branch is short and supports a very long acuminate anterior spine, which reaches the orbital region. But this position is probably due to the fossilization and to the compression of the limestone strata. We think that the original position of this spine, as well as some possible others spines of this region, was directed laterally or antero-laterally, as suggested in the reconstruction proposed in Fig.11. The upper limb also exhibits a long dorsal spine and three to four smaller spines on the posterior margin. The lower branch of the cleithrum is much larger. A big spine is inserted at the dorsal part of its posterior margin. The ventral margin of the cleithrum supports 4 spines directed inferiorly and posteriorly, the last one being the biggest. The anterior margin of the cleithrum is concave and spine-less. The posterior margin is quite different in the ventral and in the dorsal limbs. In the ventral limb, the posterior margin is slightly convex. The posterior margin of the dorsal limb is near right. As all our samples are fossilized laterally, we are unable to verify if there is a bone bar connecting the cleithra of both sides as in *Coccodus* PICTET, 1850 (KRIWET, 2005: fig. 61).

The pectoral fin is located high on the body. It emerged from the middle part of the posterior margin of the cleithral upper limb and is short and broad. The pectoral radials are not visible. In sample CLC # S.357, the pectoral fin possesses 17 rays which are divided immediately after their origin. These divided rays are directed backward and upward. They are reaching the anterior margin of the post-coelomic bone because of the shortening of the abdominal portion of the body. They are crossing the level of the characteristic bunch of the bar scales of the squamation (see below). Specimen CLC # S.718 exhibits only 10 to 12 pectoral rays but the fin is probably incomplete.

Pelvic girdle and fins, and anal region (Figs 6, 7, 14)
Immediately after and partly hidden by the ventral part of the cleithral posterior margin, there is a pair of small
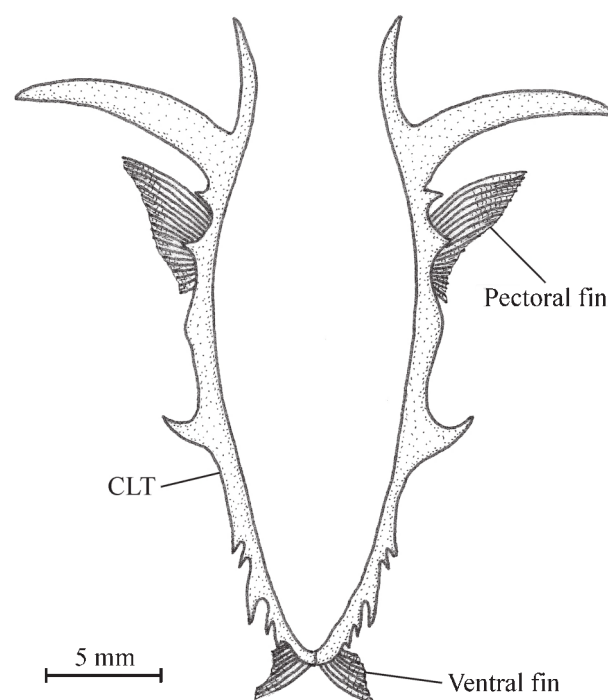

Fig. 13 – *Hensodon spinosus* (HENNIG, 1907). Hypothetical reconstruction of both cleithra in the anterior view. In the scheme also the pectoral and pelvic fins of both sides are reported.

rod-like and vertically oriented pelvic bones. In all the samples, each pelvic fin exhibits 7 well-developed and elongated principal rays, which reach the post-coelomic bone and so close completely the inferior margin of the visceral cavity. A large ventral scale with one dorsal and two ventral spines covers the basis of the fin. This pelvic scale seems similar to only the posterior portion of the last piece of the pelvic plate series, typical of *Trewavasia carinata* (GAYET, 1984: fig. 8; NURSALL & CAPASSO, 2008: fig. 5). Three other smaller lenticular scales are located above the big spiny scale, just before the post-coelomic bone. They occupy the anatomical region of the cloaca. The median plate is the biggest and the others two, probably lateral, are smaller and shorter. These thin plates are completely identical to the anal laminae described in *Trewavasia carinata* by NURSALL & CAPASSO (2008: 151).

A true cloacal vestibule did not exist in *Hensodon spinosus*, because the ventral ridge scales are absent and the ribs very shortened. For this reason no bone elements contribute to identify an anal region which was surely developed immediately in front of the post-coelomic bone.

Axial skeleton (Figs 4, 15-17)
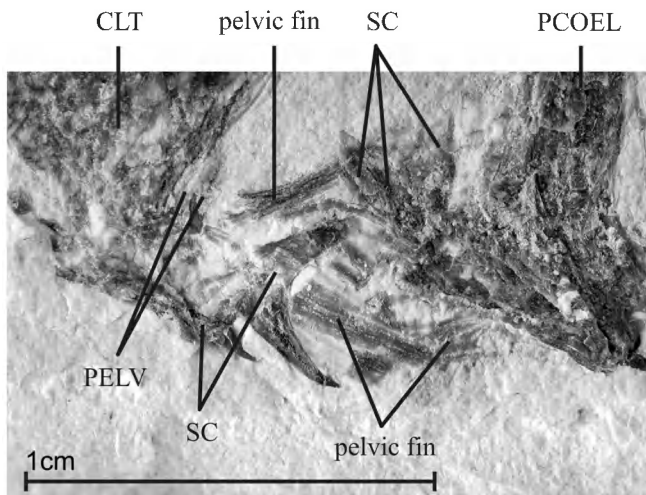In the caudal region, the vertebral column corresponds

Fig. 14 – *Hensodon spinosus* (HENNIG, 1907). The pelvic region in specimen CLC # S. 357.

to the general axis of the fish body. More anteriorly, it rises slowly, but in the most anterior part of the fish the vertebral column rises more rapidly and reaches, more or less, the level of the big occipital process. When referred to the number of neural spines, including the epichordal elements, one can count from 23 to 28 vertebral segments.

The dorsal and ventral arcocentra are more developed in the presumed male sample CLC # S.357 than in the three other samples. These arches are interlocking with their successive neighbours through a very simple contact, consisting in only one pointed zygapophysis (Fig. 17), sometimes in both the pre- and postzygapophysis. The arcocentra surround the nothocord only very partially, except in the caudal region of the specimen CLC # S.357.

There are 28 to 31 neural spines, including the epichordal elements. At first sight, the first spines seem to be not connected with the neural arches (see also KRIWET, 2004: 528) but this observation is erroneous. Indeed, an examination under high magnification microscopy of specimen CLC # S.718 shows that each of these apparently autogenous neural spines is connected to the correspondent neural arch by two or three very thin and delicate but long bony lamellae (Fig. 15). Some traces of these lamellae are also visible on sample CLC # S.357. The successive neural spines, as well as all the haemal spines, are flange-less, except for a few caudal neural spines of specimen CLC # S.357 which bear an anterior wing-like expansion.

In all samples we examine here, we found reduced ribs, very short, thin and occupying only the superior quart of the visceral cavity, just at the same level of
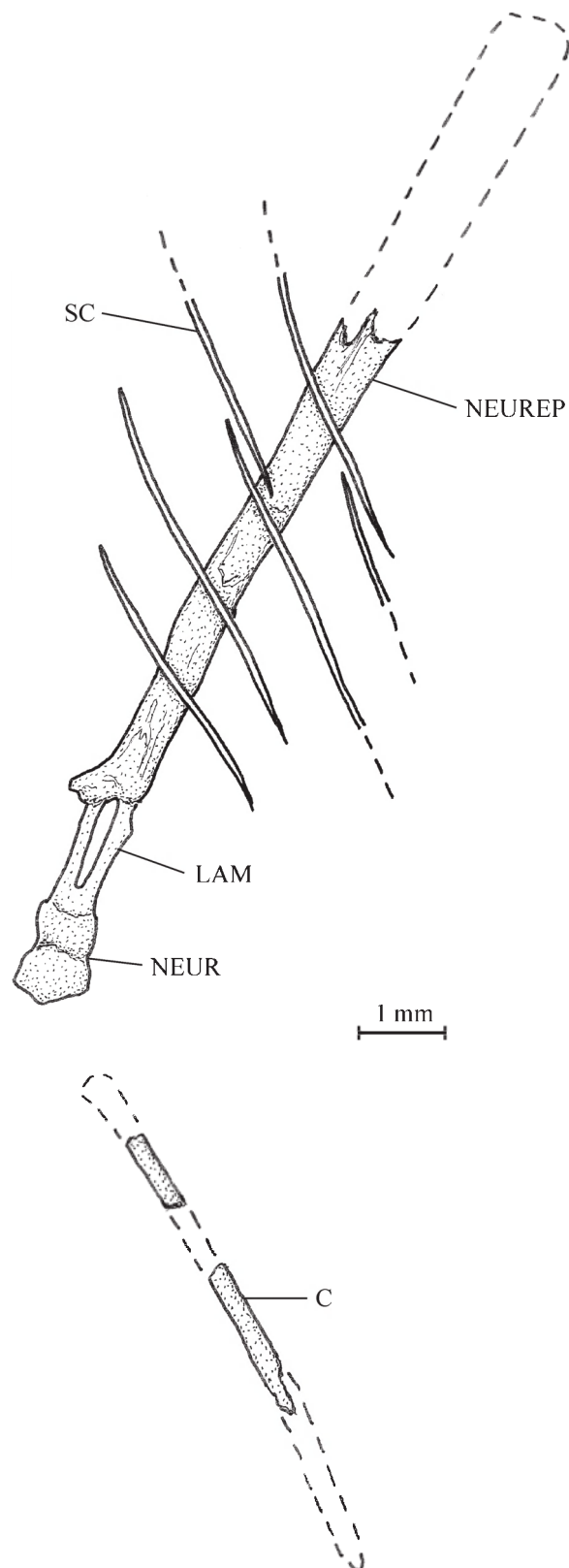

Fig. 15 – *Hensodon spinosus* (HENNIG, 1907). Specimen CLC # S.718. The fifth neural spine connected to the neural arch by two very thin and delicate bony lamellae, and the first reduced rib.
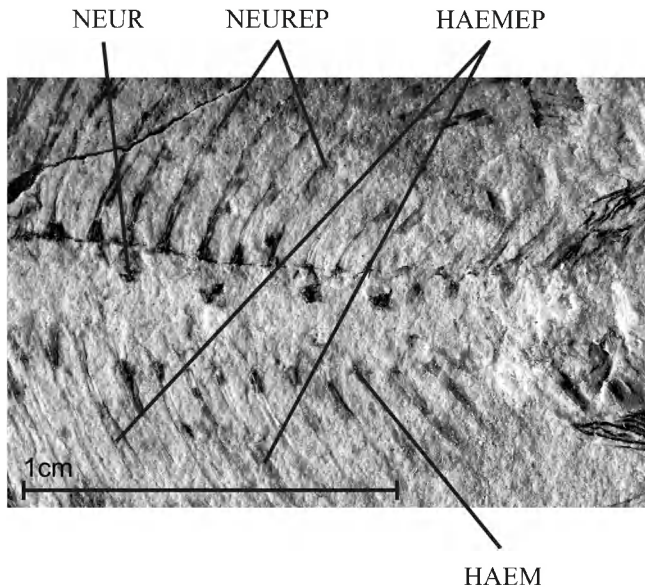
Fig. 16 – *Hensodon spinosus* (HENNIG, 1907). The middle part of the vertebral column in the presumed female specimen CLC # S. 718, showing the partially uncovered notochord.

the pectoral fin. For this reason, we think that these bones were vestigial in *Hensodon spinosus*, as the greatest part of the visceral cavity is perfectly empty in all our samples. Only in specimen CLC # S.572, we documented a mass that occupies the centre of the visceral cavity, and that can represent the remains of the digestive trait content.

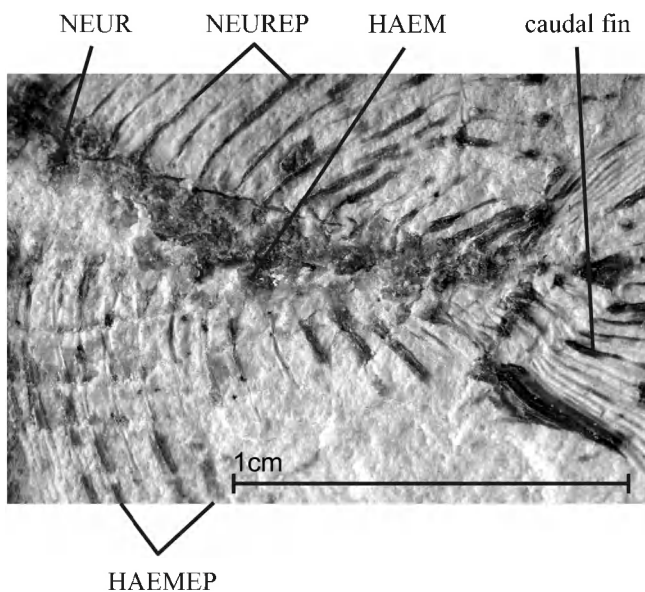There are about a dozen of haemal spines preceding

Fig. 17 – *Hensodon spinosus* (HENNIG, 1907). The posterior part of the vertebral column in the presumed male specimen CLC # S.357, showing the bony covered notochord.

the hypochordal elements. These spines only exist in the caudal part of the fish.

Another very relevant bone in the anatomy of the skeleton of our species is the post-coelomic bone (Fig. 4). In both presumed male and female individuals this bone is robust, despite that in the supposed females it seems to be more delicate. The post-coelomic bone is sinuous and stays in contact with the first haemal spine as well as with the first anal axonosts. It extends from the ventral profile of the fish and reaches the inferior border of the vertebral column. The ventral part is expanded, clave-shaped, and its ventral margin develops two big spines. The relevant dimensions of these post-coelomic spines are near the same in both presumed sexes. In the supposed male CLC # S.357, two other small spines are present on the anterior margin of the bone, facing the abdominal cavity.

Dorsal and anal fins (Figs 4, 18)

The dorsal fin corresponds in its general shape to the type E-anteriorly rounded of POYATO-ARIZA & WENZ (2002: fig. 34). There are 21 to 22 pterygiophores and the same number of dorsal rays. The first ray is unsegmented, pointed and shorter than the others, which are segmented and branched. The last rays become again shorter. The first pterygiophore is a little shorter than the following elements, which are more elongated. The last pterygiophores gradually shorten towards the tail. The basal tips of the pterygiophores are in connection with the neural spines. There is only one pterygiophore, or occasionally two, inserted between two successive neural spines.
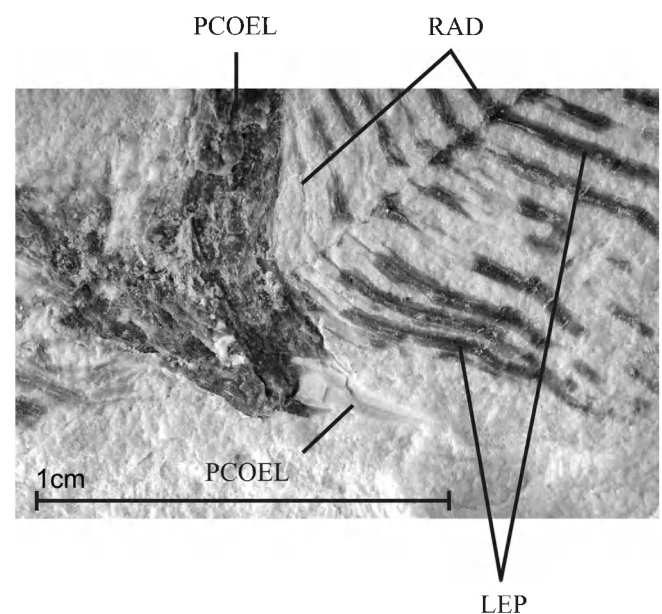

Fig. 18 – *Hensodon spinosus* (HENNIG, 1907). The beginning of the anal fin in specimen CLC # S.357.

The anal fin is also of the type E-rounded (ibid., 2002: fig. 34). There are 13 to16 anal pterygiophores, each of which bearing one ray. Here also, the first ray is unsegmented, pointed and shorter than the following rays, which are segmented and branched. The first six pterygiophores rest on the post-coelomic bone. The first pterygiophore is a little short. All the successive pterygiophores are longer but those close to the tail decrease in length. A little triangular space exists between the posterior margin of the anal fin and the ventral margin of the caudal one. Only one axonost is inserted in the space between two successive haemal spines.

Caudal skeleton and fin (Figs 14, 15)
The caudal pedicle is very short because the posterior

ends of both anal and dorsal fins are in close contact with the caudal fin.

The specimen CLC # S.357 exhibits four epichordal elements (= neural spines) and eight hypochordal elements (= haemal spines and hypurals) sustaining the caudal fin. The specimen CLC #S. 718 also shows four epichordal elements but only the anterior margin of the fourth piece in preserved in this sample. There are eight or nine hypochordal elements and perhaps more. Indeed, a large space devoid of any bony fragment exists above the last hypural. All the hypochordal elements are characterized by a moderate enlargement, except the seventh one in sample CLC # S.357 and the eighth one in sample CLC # S.718. The third and the fourth hypocordal pieces present a beginning of ankylosis in sample CLC # S.357 and the sixth and the seventh
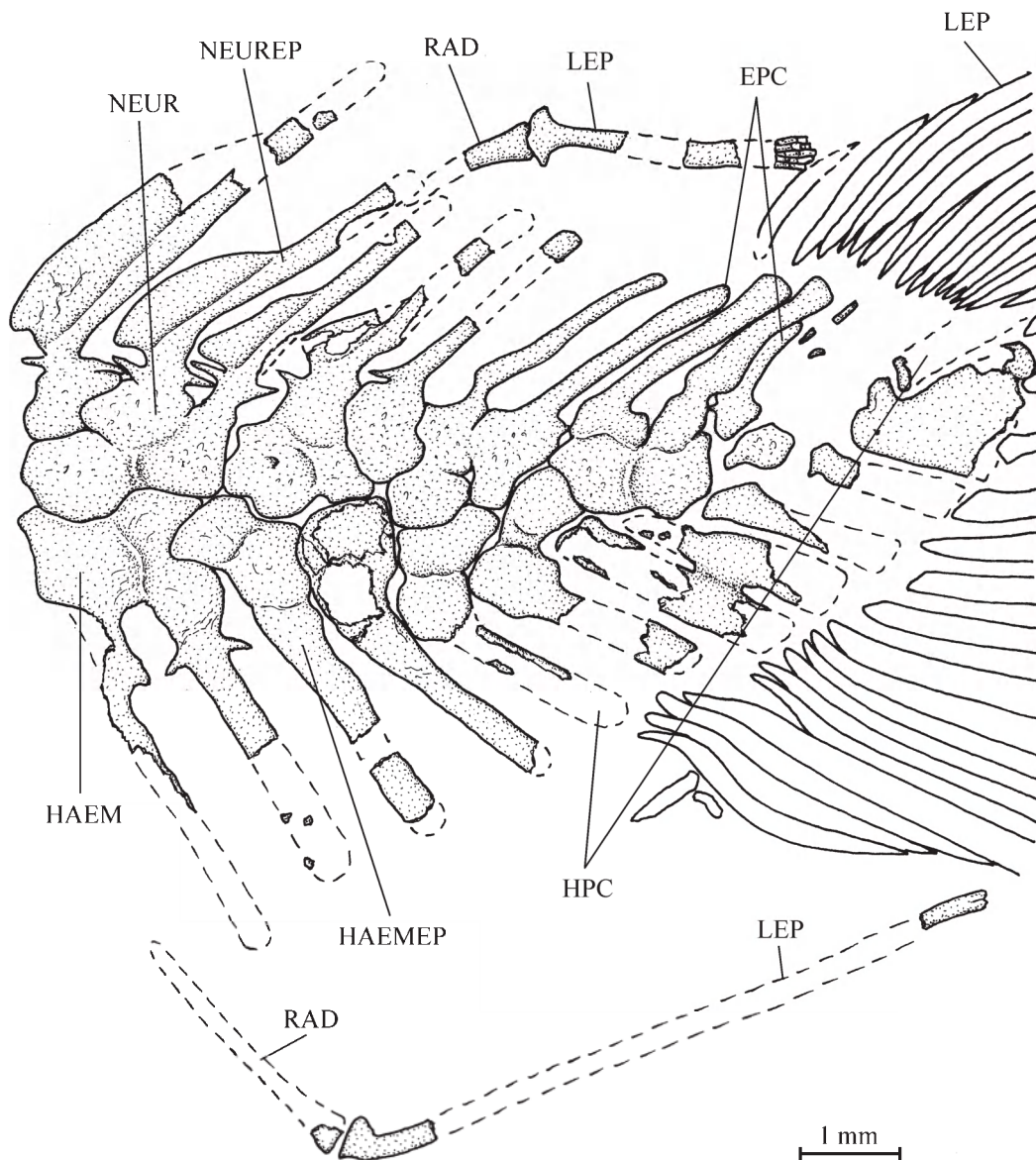

Fig. 19 – *Hensodon spinosus* (HENNIG, 1907). The caudal skeleton in the presumed male specimen
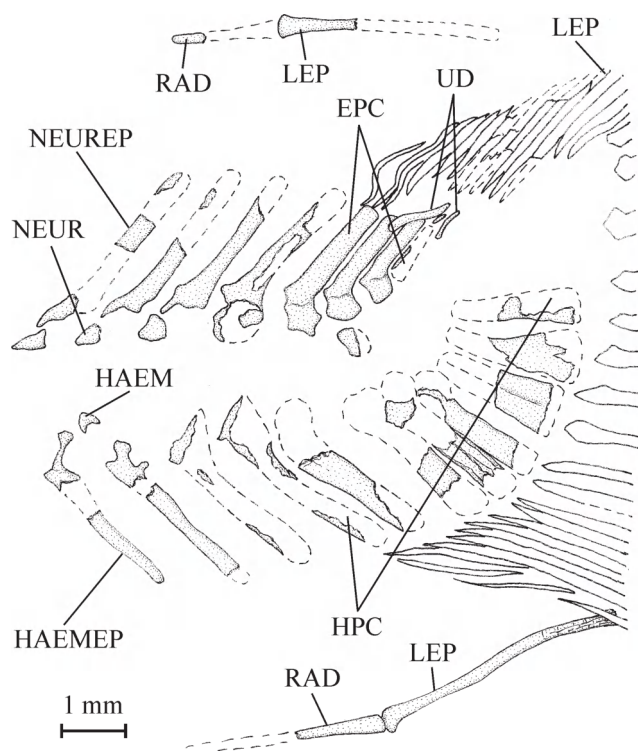CLC # S.357.

Fig. 20 – *Hensodon spinosus* (HENNIG, 1907). The caudal
skeleton in the presumed female specimen CLC #
S.718.

are completely ankylosed in sample CLC # S.718.
Specimen CLC # S.357 possesses three vey small
bony remains behind the last neural spine that could be
remains of an urodermal. Sample CLC # S.718 has one
narrow urodermal displaced above the last neural spine.
Two very small bony fragments behind this urodermal
could be the last remains of a second urodermal. There
is an important differences concerning the last neural
and haemal arches between the two sexes. In the three
supposed female specimens, these arches are small
and the notochord is uncovered. In the supposed male
sample CLC # S.357, the last neural and haemal arches
present wing-like expansions that cover completely the
notochord and some arches are ankylosed together.

The distal border of the caudal fin is slightly concave.
There are from 26 to 29 principal rays in the caudal fin
and a few dorsal and ventral procurrent rays.

Squamation (Figs 4-6, 21)
No dorsal ridge and no ventral keel are present. The
scales of the median line are completely missing.
However, in specimen CLC # S.357, two series of
some small rod-like elements are present at the level
of the dorsal midline, backward to the posterior margin

of the occipital process (Fig. 4). Posteriorly, these
elements meet a thin more or less circular bony plate
perforated on the centre and located just before the first
dorsal pterygiophore. These pieces are probably the
neurodermic remains of the scales bearing the right and
left upper lateral lines (NURSALL, 1999, fig. 8; KRIWET,
2005, fig. 1B). Some traces of such lateral line scales
are also visible on sample CLC # S.718.

The dermal body squamation consist in a very
characteristic series of only four or five rows of bar
scales assembled in a bunch situated immediately back
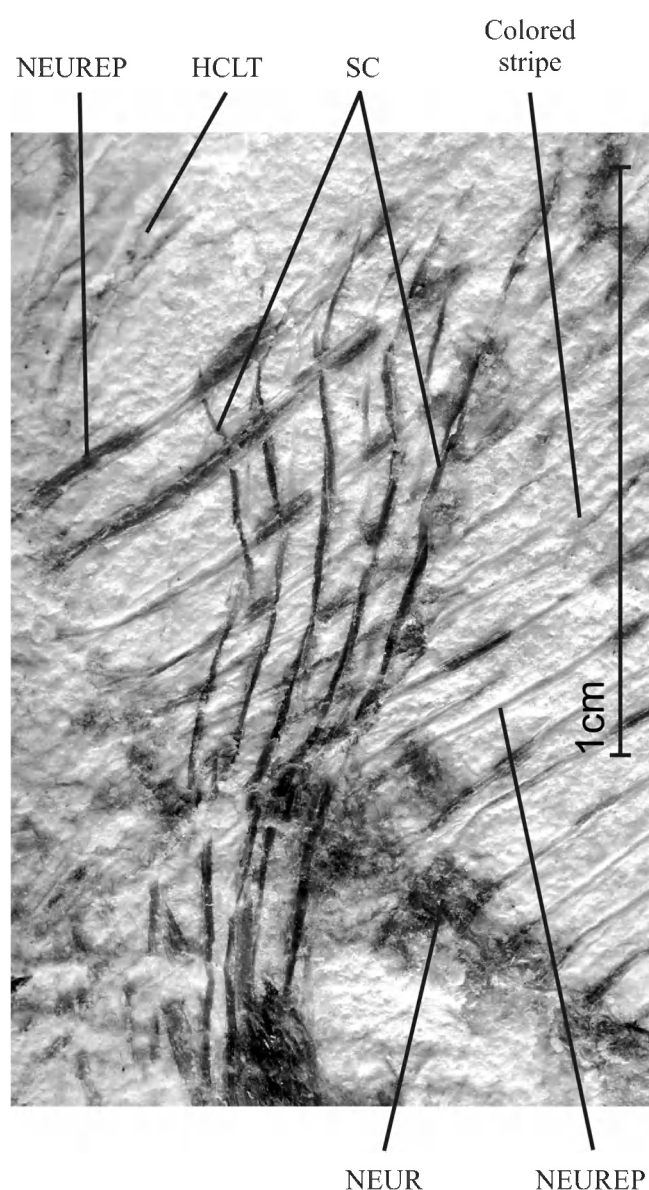of the cleithrum, and extending from the region where

Fig. 21 – *Hensodon spinosus* (HENNIG, 1907). The
filiform elements composing the bar scales of the
squamation and a small part of the two colored
longitudinal stripes of the dorsal region in specimen
CLC # S.357.

the dorsal fin begins to the posterior wall of the visceral cavity. No contacts are visible between both the dorsal and ventral ends of these bar scales and the dorsal and ventral margins of the fish. Each bar scale is constituted by a series of stringed short filiform elements, arranged in a single row, overlapping one to other for a relevant trait. 8 to 12 single filiform elements contribute to form each single scale bar row (Fig. 21). This type of squamation did not correspond to any type described in previous known pycnodonts.

Non osseous remains (Fig. 21)
The specimen CLC #S.572 shows possible remains of colour pattern. In fact two stripes of yellow-brown colour are extended by the posterior margin of the occipital process to the end of the dorsal fin (Fig. 21). No bone structures are visible on these stripes, never under very high magnification, and this seem to be consistent in order to interpret these stripes as remains of the original colour pattern of the fish.

Near the centre of the visceral cavity of the same specimen, a mass of remains is visible. That seems to be fossil traces of the contents of the intestinal tube of the fish. The examination under high magnification microscopy show no details of possible microscopic structures linked to digestion of hard tissues of animal origins (bones, shells, etc.).

Discussion and comparisons

All the osteological characters observed on our samples demonstrate unequivocally that *Hensodon spinosus* is a true Pycnodontiformes. It exhibits practically all the synapomorphies used by NURSALL (1996), POYATO-ARIZA & WENZ (2002) and KRIWET (2005) to define this order.

Within Pycnodontiformes, *Hensodon* seems to be more closely related to the Coccodontidae (including the Trewavasiidae of NURSALL, 1996), a Lebanese fish family also comprising the genera *Coccodus* PICTET, 1850, *Trewavasia* WHITE & MOY-THOMAS, 1941 and *Ichthyoceros* GAYET, 1984.

POYATO-ARIZA & WENZ (2002) define the Coccodontidae by nine characters to which they add eleven other characters with an ACCTRAN analysis. Unfortunately we are unable to apply completely *Hensodon* within the synapomorphic scheme set up by these authors, because some of the characters they used are difficult or impossible to see in our specimens. We can note, however, that their characters 4[0] (ventral apex absent), 10[1] (prefrontal present), 18[0]

(supratemporal not fused to parietal), 36[1] (vomerine teeth with a circular to subcircular contour), 53[1] (arcocentra surrounding nothocord partially), 59[1] (hypochordal elements in caudal endoskeleton enlarged), 63[1] (hypertrophied spines on cleithrum), 66[1] (20 to 29 dorsal axonosts) and 70[0] (10 to 19 anal axonosts) are present in *Hensodon* near the same expressions supposed to be typical of the family Coccodontidae by these two authors. *Hensodon* also shares a great part of the synapomorphies proposed by NURSALL (1996) to characterize the Coccodontidae, i. e. his characters 60 (the body is without scales [apertate]; the scales are vestigial in *Hensodon* but a few ones still exist), 61 (dorsal ridge and ventral keel scales are lacking), 62 (strong, vertical, occipital spine) and 66 (the ribs are short and not alate). *Hensodon* also exhibits some apomorphies typical of the Trewavasiidae according to NURSALL (1996), i. e. his characters 56 (one or more frontal spine anterior to orbit) and 59 (preoperculum and cleithrum spinose).

Hensodon differs from the other members of the Coccodontidae by several specialized characters, for instance its very reduced jaws, its dentary without ventral osseous expansions, its styliform teeth (perhaps arranged in only one ridge) on the prearticular, its edentulous, unornamented, elongated rhomboid maxilla, its enormous frontal appendixes (with possible sexual dimorphism), its small spines on the upper border of the frontal, the gigantic development of its occipital process, its very large cleithrum, ornamented with an enormous antero-dorsal spine and smaller spines on the posterior and ventral margins, the loss of the ventral keel scales, the loss of the dorsal keel scales and the presence of a few vestigial body scales of peltate type (see also KRIWET, 2004: fig. 1-3). All these autapomorphies attest that *Hensodon* deserves its peculiar generic status within the family.

If we try to determine the exact systematic position of *Hensodon* within the Coccodontidae we can see that *Hensodon*, *Trewavasia*, *Ichthyoceros* share some characters not present in *Coccodus*: (1) a deep, short and more or less rounded body, with a very short abdominal region, (2) a small ventrally directed mouth, (3) a large horny frontal, (4) a very big occipital process and (5) the presence of body scales more or less developed (GAYET, 1984: fig. 1, 2, pl. 2, fig. 1, pl. 3, fig. 1, 2; KRIWET, 2004: fig. 1-3; NURSALL & CAPASSO, 2008: fig. 3, 5). On the contrary, *Coccodus* exhibits an elongated body, with a long abdominal region, a large anteriorly directed mouth, no frontal horns and a completely nude body (DAVIS, 1887: pl. 30, fig. 1; WOODWARD, 1895: pl. 16, fig. 4; KRIWET, 2005: fig. 4).

On the other hand, *Trewavasia* and *Ichthyoceros* present at least two apomorphies differing from *Hensodon*: (1) the lower margin of the dentary is ornamented with irregular osseous expansions and (2) the development of very large, lozenge-shaped, spiny scales covering all the body and the caudal pedicle (GAYET, 1984: fig. 1, 2, 4-6, pl. 2, fig. 1, 4, 5, pl. 3, fig. 1, 2; KRIWET, 2004: fig. 4; NURSALL & CAPASSO, 2008: fig. 5, 6, 10).

In the phylogenic hypothesis of the Coccodontidae (*sensu* POYATO-ARIZA & WENZ, 2002), *Hensodon* is hypothesized to have an advance position in relation to *Coccodus*, and a basal position in relation to *Trewavasia* and *Ichthyoceros*.

It is to be noted that NURSALL (1996) has restricted the Coccodontidae to only *Coccodus* and has erected the new family Trewavasiidae for *Trewavasia* and *Ichthyoceros*. But POYATO-ARIZA & WENZ (2002) and KRIWET (2004) did not accept this innovation and they have maintained a family Coccodontidae comprising all the genera, an opinion followed in our present paper. However, we think that the apomorphies shared by *Hensodon*, *Trewavasia* and *Ichthyoceros*, but absent in *Coccodus*, are important enough to justify at least the grouping of these three genera in a subfamily Trewavasiinae.

Conclusions

Hensodon represents a very peculiar pycnodontiform fish with a presumed remarkable sexual dimorphism. This genus pertains to the Coccodontidae family (*sensu* POYATO-ARIZA & WENZ, 2002) and shares some synapomorphies with *Trewavasia* and *Ichthyoceros* but not present in *Coccodus*. *Hensodon* exhibits several autapomorphies, which totally confirm the erection of this peculiar genus by KRIWET (2004).

Acknowledgements

Key to the abbreviations

AN: angular
APTE: autopterotic
ASPH: autosphenotic
BO: basioccipital
BRSTG: branchiostegal ray
C: rib
CHY: ceratohyal
CLT: cleithrum
DHYOM: dermhyomandibula
DN: dentary
DPTE: dermopterotic
DSOC: dermosupraoccipital
FR: frontal
ECPT: ectopterygoid
EPC: epichordal elements (= neural spines supporting the caudal fin)
EPI: epiotic (= epioccipital)
EXO: exoccipital
HAEM: haemal arch (= ventral arcocentrum)
HCLT: hypercleithrum (= supracleithrum)
HAEMEP: haemal spine
HPC: hypochordal elements (= haemal spines supporting the caudal fin + hypurals)
HYOM: hyomandibula
LAM: thin bony lamellae connecting the neural spine to the neural arch
LEP: fin ray
METH: mesethmoid
MX: maxilla
NEUR: neural arch (= dorsal arcocentrum)
NEUREP: neural spine
OP: opercle
OSPH: orbitosphenoid
PA: parietal
PART: prearticular
PBR: pharyngeal bone
PCOEL: postcoelomic bone
PELV: pelvic bone
PMX: premaxilla
POP: preopercle
PRFR: prefrontal (= laterodermethmoid)
PS: parasphenoid
PT: posttemporal
RAD: pterygiophore
QU: quadrate
SC: scale
SCL: sclerotic bones
ST: supratemporal (= extrascapula)
UD: urodermal
VO: vomer
l.: left
r.: right

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