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A new species of *Gladiopycnodus* (Coccodontoidea, Pycnodontomorpha) from the Cretaceous of Lebanon provides new insights about the morphological diversification of pycnodont fishes through time

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ABSTRACT

The Coccondontoidea is a distinctive superfamily of pycnodont fishes characterized by a series of derived characters, including thick and well-ossified cranial bones supporting horns and spines and a hypertrophied pectoral girdle sutured to the skull forming a sort of cephalo-torax. A new distinctive coccodontoid species, *Gladiopycnodus byrnei* n. sp., is described from the Cenomanian locality of Hjoûla, Lebanon. This new species exhibits a unique combination of features that clearly support its inclusion within the coccodontoid family Gladiopycnodontidae, including an extremely elongate snout forming a sword-shaped rostrum, thick dermal bones ornamented with rounded tubercles, large supracleithrum and cleithrum extensively sutured to the skull, and irregularly imbricated scales covering the entire body. The new taxon differs from type species *G. karami* by

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having different meristic counts and body proportions, dermal bones strongly ornamentated, skull roof with partially fused bones, scales ornamented with small tubercles, and rounded scales covering the caudal peduncle absent. The presence of pectoral fins in our exquisitely well-preserved specimen allowed us to redefine the morphology of the genus *Gladiopycnodus*, also modifying the diagnosis of the family. In order to interpret the patterns of morphospace occupation and quantify the morphological diversification of pycnodonts through time, the geometric morphometric approach was used. The morphospace analysis revealed that a significant increase in morphological disparity of pycnodonts during the Late Cretaceous was related, at least in part, to the appearance of the representatives of the superfamily Coccodontoidea. The rapid evolutionary radiation of these well-armored pycnodonts was interpreted as an adaptive solution in response to the large predatory-prey escalation in the context of the Mesozoic Marine Revolution.

Keywords: Cenomanian; Cretaceous; *Gladiopycnodus byrnei* n. sp.; Hjoûla in Lebanon; morphospace analysis

1. Introduction

Pycnodontomorpha constituted a high successful monophyletic group of actinopterygian fishes that comprise about 40 genera and more than 600 nominal species, most of them exclusively based on isolated dentition (e.g., Kriwet, 2001a, 2005). They were usually small- to medium-sized fishes, with a deep and laterally compressed body and highly specialized feeding apparatus (e.g., Kriwet, 2001b, 2005), being characterized by a notable functional and ecological flexibility (Poyato-Ariza, 2005). Their fossils have worldwide distribution and were found mostly in shallow

marine deposits, although some authors (e.g., Longbottom, 1984; Poyato-Ariza et al., 1998) suggest that pycnodonts may have colonized also brackish or freshwater habitats. The successful evolutionary history of pycnodonts ranges from the middle Norian to the middle Eocene, encompassing approximately 175 million years (Tintori, 1981; Longbottom, 1984).

Traditionally, all pycnodont fishes were included within the order Pycnodontiformes (e.g., Nursall, 1996; Poyato-Ariza & Wenz, 2002). Their systematic position has been successively reanalyzed and all of them have been included in the superorder Pycnodontomorpha, which was considered to be the sister-group of the Teleostei (Nursall, 2010). More recently, based on a cladistic analysis, Poyato-Ariza (2015) concluded that pycnodonts represent the sister-group of the Halecostomi (Holostei+Teleosteomorpha) and, therefore, the most basal group among neopterygian fishes. Following Nursall (2010), Pycnodontomorpha comprises the orders Gyrodontiformes, which includes the families Mesturidae and Gyrodontidae, and Pycnodontiformes (new usage for the former Pycnodontoidei), which includes all the remaining clades.

Pycnodontiforms are well-represented in the marine Cenomanian Lebanese fossiliferous localities Hâqel, Hjoûla and En Nammoûra, from which these fishes were studied since the XIX century (e.g., Pictet, 1850; Davis, 1887; Hay, 1903; Forey et al., 2003; Poyato-Ariza & Wenz, 2005; Capasso et al., 2009). New material from these localities allowed the introduction of the new superfamily Coccodontoidea, which includes the highly specialized representatives of the families Coccodontidae, Gebrayelichthyidae, Gladiopycnodontidae and Trewavasiidae (Taverne & Capasso, 2013, 2014a, b). All these distinctive pycnodonts share unique synapomorphies, including a fusiform body, antero-posteriorly or dorso-ventrally elongated, thick and well-ossified dermal bones ornamentated with tubercles, horns and spines, and a hypertrophied pectoral girdle strongly fused to the skull and forming a sort of cephalo-torax (Taverne & Capasso, 2013). These features make their body plan very different from the generalized rounded deep-bodied pycnodonts. The representatives

of the superfamily Coccodontoidea were found exclusively in Cenomanian localities and therefore they contribute enormously to the taxonomic and morphological exuberance that pycnodont fishes experienced during the Late Cretaceous. Although the remarkable Late Cretaceous species diversity of pycnodonts was already reported by some authors (e.g., Poyato-Ariza, 2005; Poyato-Ariza & Martín-Abad, 2013), morphological diversity (i.e., disparity; Foote, 1992) was never analyzed through a quantitative approach.

In this paper, a new species of *Gladiopycnodus* is described from the Cenomanian of Hjoûla, Lebanon based on a single exquisitely preserved specimen. The fossil shows a series of diagnostic features that allow us to re-describe the genus by amending the diagnosis of the family Gladiopycnodontidae. Moreover, we applied the landmark-based geometric morphometrics (Bookstein, 1991; Rohlf & Marcus, 2003; Zelditch et al., 2004) in order to interpret the patterns of morphospace occupation, quantifying the morphological diversification of pycnodont fishes through time.

2. Geological Setting

The Upper Cretaceous Fossil-Lagerstätte of Hjoûla, together with those of Hâqel, and En Nammoûra, Lebanon, has been celebrated for its exceptionally preserved fossils, particularly fishes, since the Middle Ages (Roger, 1946). The superbly preserved specimen documented herein was collected from the Cenomanian deposit of Hjoûla, north of Beirut, close to the Lebanese coast (Fig. 1). The fossiliferous laminated limestone of Hjoûla (as well as those of Hâqel) were deposited in small and restricted basins possibly representing sinkholes formed by tectonic activity at the outer margin of the continental shelf, along the south-western margin of the Tethys (e.g., Hückel, 1970; Hemleben & Swinburne, 1991). The fossiliferous deposits pertain to the Sannine Limestone, a 650

m thick, finely laminated to massive carbonate sequence that originated in a tropical neritic setting. Based on the fish fauna, Patterson (1967) hypothesized a mid-Cenomanian age for the fossiliferous strata. An Early Cenomanian age was proposed by Hückel (1970) and Saint-Marc (1974), while Hemleben (1977) suggested a late Cenomanian age on the basis of the planktonic foraminifera. More recently, Wippich and Lehmann (2004) confirmed a late Cenomanian age based on the presence of the heteromorphic ammonite *Allocrioceras* cf. *annulatum*, a species typical of the lower upper Cenomanian *Sciponoceras gracile* Zone of the Western Interior of the United States of America, thereby suggesting an age of about 94 Ma (see Grandstein et al., 2004).

3. Material and Methods

The present study is based on a single well-preserved and completely articulated specimen from the fossiliferous layers of Hjoûla, Lebanon, which currently is housed in the Dipartimento di Scienze della Terra of Università degli Studi di Torino, Italy (MGPTPU). The fossil was prepared through the acid transfer method following the procedure proposed by Toombs and Rixon (1959) and examined with a Leica M80 stereomicroscope equipped with a camera lucida drawing arm. Measurements were made to the nearest 0.1 mm using a dial caliper. Osteological terminology primarily follows Nursall (1996, 2010), Poyato-Ariza & Wenz (2002), Nursall & Capasso (2008) and Taverne & Capasso (2013). The generic term “pycnodont” is used herein to indicate all the representatives of the clade Pycnodontomorpha as proposed by Nursall (2010). Standard length (SL) is used throughout.

In order to analyze the morphospace occupation of Pycnodontomorpha and to quantify the morphological diversity through time, we used the landmark-based geometric morphometric approach (Zelditch et al., 2004). The list of species examined for this study contains 57 species

(including *Gladiopycnodus byrnei* n. sp.) ranging in age from Late Triassic (Norian) to early Eocene, for which the entire morphology of the body is known (Table S1). Although a few specimens were examined and photographed in numerous collections, a majority of these were taken from published images (photographs or specimen drawings; Table S1). A total of 17 landmarks and 21 semi-landmarks were digitized using the software package TPSdig 2.05 (Rohlf, 2005) following the scheme applied in some studies about the shape variation in modern or extinct fishes (Fig. S1). The landmark coordinates were translated, rotated and scaled at unit centroid size by applying a Generalized Procrustes Analysis (GPA) to minimize the variation caused by location, orientation and size (Zelditch et al., 2004) and performed through the software package TPSrelw (Rohlf, 2003). A principal component analysis (PCA) was then performed on the new landmark coordinates (Procrustes coordinates) to obtain the relative warp (RW). RW axes are vectors describing the maximum variation of specimen shape compared to the consensus configuration (mean shape). The two-dimensional morphospace of each assemblage was defined using the area inside the minimum convex polygon including all taxa (i.e., convex hull; Cornwell et al., 2006) and built on the RW axes explaining over 5% of the morphological variation (Zelditch et al., 2004). Deformation grid plots show changes in shape along the axes (Fig. S2).

The quantitative morphospace occupation was analyzed performing two non-parametric tests: the PERMANOVA (Anderson, 2001) was used to the test similarities in the group centroid positions, whereas the ANOSIM (Clarke, 1993) was employed to test the degree of overlap between different clades or periods. Euclidean distances were chosen as distance measure for both tests and statistical significance was calculated along all RW axes with 9,999 random permutations.

The distribution of the data set in the multidimensional space (i.e., patterning, Tuset et al., 2014) was visualized through Kernel-density plots, which provide a direct visual image of taxon distribution. Moreover, the Ripley's *K* function (Ripley, 1979) was used to describe the

clusterization of points (taxa) in the morphospace. Convex hull areas and all patterning analyses are based on the morphospaces built on the first two RW axes.

The morphological disparity was calculated as sum of variances because it is relatively insensitive to differences in sample size (Ciampaglio et al., 2001). To assess statistical significant increase or decrease in disparity between two consecutive periods we calculate the t-statistic using Monte Carlo permutations following the method outlined in Zelditch et al. (2004). Partial disparity of each clade (e.g., family) was also calculated to assess the contribution of each lineage to the overall disparity (Table S6).

Statistical and disparity analyses were performed using the software package PAST 3.08 (Hammer et al., 2001). Additional details on dataset list and morphospace analyses are given in the Supplementary material.

4. Results

4.1 Systematic paleontology

Division Halecostomi *sensu* Patterson, 1973

Superorder Pycnodontomorpha Nursall, 2010

Order Pycnodontiformes *sensu* Nursall, 2010

Superfamily Coccodontoidea Taverne and Capasso, 2013

Family Gladiopycnodontidae Taverne and Capasso, 2013

Diagnosis (emended): Antero-posteriorly elongate coccodontoids with long snout forming a rostrum extending anteriorly to the lower jaw; anterior tip of the rostrum formed by the long and

broad prefrontal only; premaxilla long, broad, toothless and articulated with the ventral margin of the prefrontal; pectoral fin surrounded posteriorly by the expanded posterior process of the cleithrum; body entirely covered with small flake-like scales.

Gladiopycnodus Taverne and Capasso, 2013

Type species: Gladiopycnodus karami Taverne and Capasso, 2013.

Diagnosis (emended): Gladiopycnodontid with extremely elongate snout forming a horizontal and sword-shaped rostrum, measuring about the half of head length; anterior tip of the prefrontal pointed; all dermal bones ornamented with rounded tubercles; subtrapezoidal frontals antero-posteriorly elongated; extrascapulars posteriorly elongated and reaching the dorsal fin origin; predorsal scutes absent; cleithrum supporting an anterior ventral limb and a large process extending posteriorly beyond the pectoral fin; reduced pelvic girdle; nuchal horn absent; dorsal fin located in the posterior half of the body and composed by short isolated rays forming a series of finlets; caudal fin with a convex posterior border; large paired dorsal scutes along the dorsal margin of the body between the extrascapulars and the tail; body completely covered with small subromboidal scales, dorso-ventrally elongated and irregularly imbricated; ventral scutes reduced to a single small pelvic plate and a very large sword-like and pointed anal plate extending posteriorly well beyond the distal caudal fin margin.

Gladiopycnodus byrnei n. sp.

Figs. 2–5

Holotype. MGPTPU 130335, nearly complete well-preserved articulated specimen, 50.8 mm SL (Fig. 2).

Diagnosis. Small sized *Gladiopycnodus* that differs from *G. karami* by having the following combination of characters: skull roof with partially fused frontals, parietals and dermosupraoccipital; parietals subtriangular in shape; small, narrowed, and dorso-ventrally elongated opercle; pectoral fin with 16 rays; 14 paired dorsal scutes; dorsal fin with about 14 rays; caudal fin with 24 rays; scales ornamented with tubercles smaller than those characteristic of the dermal bones; rounded scales covering the caudal peduncle absent; head length about 50% SL; maximum body depth about 25% SL.

Etymology. Species named in honour of the American musician and composer David Byrne.

Horizon and locality. Sannine Limestone, Hjoûla, Lebanon; Cenomanian, Upper Cretaceous, about 94 Ma.

Remarks. The family Gladiopycnodontidae was created by Taverne & Capasso (2013) based on five specimens from Hâqel, Lebanon, sharing unique derived characters among pycnodonts. These features include a long rostrum formed by prefrontal only and extending anteriorly well in front of the lower jaw, premaxilla long, broad and toothless and a body entirely covered by small, imbricated scales. Taverne & Capasso (2013) also recognized the loss of the pectoral fin and its replacement with a pectoral spine articulating with the cleithrum as one of the main diagnostic features of the family Gladiopycnodontidae. Among the available specimens three new genera and species of pycnodonts (*Gladiopycnodus karami*, *Monocerichthys scheuchzerii* and *Rostropycnodus gayeti*) were recognized (Taverne & Capasso, 2013). Subsequently, the same authors included *Joinvillichthys lindstroemi* (previously referred to as "*Coccodus*") within the family, as well as two additional species based on several specimens from Hâqel and Hjoûla (*Joinvillichthys kriweti* and *Pankowskichthys libanicus*; Taverne & Capasso, 2014a). Based on an inadequate explanation, the

same authors (Taverne & Capasso, 2014c) referred the coccodontid *Ichthyoceros spinosus* to the family Gladiopycnodontidae, although the holotype clearly exhibits a pectoral fin (Gayet, 1984). More recently, based on some character of the skull roof and the pectoral girdle, *Stenoprotome hamata* Hay, 1903, previously referred to Saurichthyidae, was included within the family Gladiopycnodontidae (Taverne et al., 2015). Although the available material of *Stenoprotome hamata* clearly exhibits some fin rays in the position of the pectoral fin, these elements were considered as pertaining to the pelvic fins, and their unusual displacement due to the taphonomic biases (Taverne et al., 2015). The new exquisitely preserved specimen from Hjoûla described herein clearly belongs to the family Gladiopycnodontidae. However, the obvious presence of a pectoral fin formed by 16 rays and the concurrent absence of a pectoral spine in *Gladiopycnodus byrnei* suggests that the inadequate preservation of the specimens described by Taverne and Capasso (2013, 2014a) prevented the recognition of the pectoral fin, whose apparent absence was erroneously regarded as a diagnostic character of *Gladiopycnodus*, and, more generally, of the whole family. The recognition of the pectoral fin in the new species documented herein permitted to redescribe some dermal bones previously incorrectly interpreted. Taverne & Capasso (2013) recognized the hypertrophy of the pectoral girdle as a synapomorphy of the family, describing a dorso-ventrally elongate and laterally narrowed cleithrum in *Gladiopycnodus karami*. The massive cleithrum of *Gladiopycnodus byrnei*, instead, is in agreement with those of the other representatives of the superfamily Coccodontoidea and also with those of the other genera of the family Gladiopycnodontidae. Taverne & Capasso (2013) described a very large preopercle bearing a ventral process in *G. karami* whose shape and position are very similar to those of the cleithrum of *Gladiopycnodus byrnei*. Moreover, Taverne & Capasso (2013) indicated the presence of large extrascapulars (= supratemporals of Taverne & Capasso, 2013) sutured with dermosupraoccipital, the parietals and the posttemporal as diagnostic character of the superfamily Coccodontoidea.

Unlike the other gladiopycnodontid genera, this feature was not recognized in *Gladiopycnodus karami*. The new species *Gladiopycnodus byrnei*, instead, exhibits this character, even if the extrascapulars are greatly developed and reach the dorsal fin origin showing a condition similar to that of the coccodontoid *Trewavasia carinata* (Nursall & Capasso, 2008) in which the evident pair of extrascapulars has been erroneously re-interpreted as a unique dermosupraoccipital by Taverne & Capasso (2014c). The sword-like and posteriorly directed structure that extends posteriorly the distal end of the caudal fin shared by *Gladiopycnodus byrnei* and *G. karami* was interpreted by Taverne & Capasso (2013) as a modified first anal-fin ray. We propose that this element represents a modified ventral keel scute. All pycnodonts share the presence of ventral keel scales along the belly, which are modified and reduced to two or three large plates in more derived pycnodonts as in the Trewavasiidae (Poyato-Ariza & Wenz, 2002; Nursall & Capasso, 2008).

Measurements (as percentage of SL). Total length (including the prefrontal rostrum and anal plate) = 127.1; total length (including the prefrontal rostrum and excluding the anal plate) = 105.1; head length (including the prefrontal rostrum) = 59.1; length of the prefrontal rostrum (distal tip to the lower jaw level) = 30.9; maximum body depth (coinciding to the head depth) = 26.0; prepectoral distance = 56.3; predorsal distance = 73.9; dorsal-fin base length = 25.8; anal plate length (including the spine) = 48.2; caudal peduncle depth = 4.1.

Description. The body is fusiform and notably antero-posteriorly elongate (Fig. 2), its depth is about ¼ of SL. The head is contained less than two times in SL. All dermal bones (cranial, pectoral girdle, scales and plates) are well-ossified and ornamented with small tubercles. The pectoral girdle is strongly sutured with the skull forming a sort of cephalo-torax. The sword-shaped rostrum is prominent and horizontally directed, projecting well anterior to the tip of the lower jaw. Small rhomboidal and strongly imbricated scales cover the entire body. Ventral keel scales are reduced to two large modified pelvic and anal plates; the latter is very large, sword-shaped and

projects posteriorly well-behind the caudal fin terminating into a pointed tip. The dorsal fin is located in the posterior half of the body. There are no predorsal scutes. The caudal fin is externally symmetric with a convex posterior margin.

The dermatocranium is consistent with that of the other coccodontoid fishes (Fig. 3). The snout is formed by a single unpaired large prefrontal, sword-shaped, horizontally directed and distally pointed; it is the largest bone of the skull, projecting anteriorly well beyond the anterior end of the lower jaw, its length measuring about 75% of head length. The frontals are large with a subtrapezoid shape; these suture medially with each other, and with the prefrontal anteriorly. The parietals are small and subtriangular in shape without any trace of a peniculated process. The dermopterotic is small, irregular in shape and marks the posterior border of the orbit. According to Taverne & Capasso (2013), this bone is partially fused with the dermosphenotic in *Gladiopycnodus*. The autosphenotic is expanded postero-ventrally to the frontal, whereas the long straight parasphenoid can be recognized anteriorly to it. The dermosupraoccipital is large and semicircular; its anterior margin appears to be convex, whereas the posterior border is almost straight. Frontals, parietals and dermosupraoccipital seem to be partially fused together (Fig. 4). The extrascapulars (= supratemporals of Taverne & Capasso, 2013) are the posteriormost paired elements of the skull roof; they are antero-posteriorly elongated and subtrapezoid in shape; they are sutured to each other medially, and anteriorly with the posterior margin of the dermosupraoccipital. Like in the coccodontoid *Trewavasia carinata*, the extrascapulars extend posteriorly reaching the origin of the dorsal fin, forming a post-cephalic structure that functionally replaces the predorsal keel scutes (Nursall & Capasso, 2008). Unlike *Trewavasia*, the posterior margin of the extrascapulars in *Gladiopycnodus* does not define the dorsal apex, and the maximum body depth is located at the level of the suture between the extrascapulars and the dermosupraoccipital. Because of the

taphonomic shift of the skull roof toward the right side of the fish, it is very difficult to describe the elements of the circumorbital series as well as the endocranial elements.

The jaws are well-preserved although slightly dislocated from their original position. The edentulous maxilla is small, drop-shaped; its anteriormost region is pointed, whereas its posterior margin is much more expanded; there is no evidence of tubercles on its external surface and the ornamentation consists of antero-posteriorly directed ridges. The dentary is the largest element of the jaws; it is antero-posteriorly elongate, expanded anteriorly and more narrow posteriorly with a concave dorsal margin and concave ventral margin. The prearticular is elongate and its ventral margin articulates entirely with the dorsal margin of the dentary; the coronoid process is weakly developed and emerges at about mid length of the prearticular. Since the anterior margins of both dentary and prearticular are hidden under the maxilla, it is difficult to check the presence of teeth on both the dentary and prearticular. Taverne & Capasso (2013) described molariform prearticular teeth in *Gladiopycnodus karami*; similar teeth were likely present also in *Gladiopycnodus byrnei*. The angular is antero-posteriorly elongated, expanded posteriorly, and subtriangular in shape; it sutures with the postero-dorsal margin of the prearticular; the quadrate-angular junction cannot be observed, hidden by the large preopercle. The articular is small and sutures with the posterior margin of the dentary.

The opercular series is reduced to the preopercle and opercle; there is no evidence of both the interopercle and suborpercle. The opercle is small, narrow and dorso-ventrally developed, and articulates with the dermalized upper portion of the hyomandibula (i.e., dermohyomandibula). The preopercle is large, almost ovoid in outline, lying ventrally to the orbit. As in other derived pycnodonts (Nursall, 1996; Poyato-Ariza & Wenz, 2002), the preopercle is in close contact postero-dorsally with a small portion of the dermohyomandibula. The other elements of the suspensorium and the hyoid apparatus are not clearly recognizable.

As in the other representatives of the superfamily Coccodontoidea, the pectoral girdle of *Gladiopycnodus byrnei* is sutured to the skull, forming a sort of cephalo-torax (Taverne & Capasso, 2013, 2014a). The cleithrum is massive and hypertrophied, forming the largest element of the pectoral girdle; the ventral margin of the cleithrum bears a crescent-shaped and pointed anterior process, extending anteriorly in the gular region; moreover, a large posterior process of the cleithrum surrounds posteriorly the pectoral fin, which emerges from the pectoral sinus and contains about 16 distally segmented rays (Fig. 5). The supracleithrum (= hypercleithrum of Taverne & Capasso, 2013) is large and subtriangular in shape; it articulates with the dorsal margin of the cleithrum, whereas its anterior margin is in contact with the dermopterotic. An isolated bony element, ornamented and lying dorsally to the supracleithrum is interpreted herein as the posttemporal.

As in *Trewavasia carinata*, the predorsal scutes are absent due to the large extrascapulars that reach the dorsal-fin origin. The ventral keel scales are reduced to two large ventral plates. The pelvic plate is the smaller, subtriangular in shape, and ornamented with tubercles; it lies between the posterior tip of the cleithrum and the anterior margin of the anal plate. The anal plate is very large, sword-shaped, and projecting well-behind the posterior margin of the caudal fin; the surface of the anal plate is ornamented with small tubercles, which gradually merge posteriorly forming horizontal ridges that cross antero-posteriorly the plate. At least two small spines can be observed along the dorsal margin of the anal plate.

The body is entirely covered with small dorso-ventrally elongated subrhomboid scales; the scales are irregularly imbricated and ornamented with small tubercles. Unlike in *Gladiopycnodus karami*, there are no rounded scales covering the caudal peduncle. The dorsal margin of the body, from the posterior margin of the extrascapulars to the caudal fin, is covered by a continuous series

of 14 large paired modified scales ornamented with tubercles. These scutes decrease in size posteriorly and cover the base of the dorsal fin.

The dorsal fin lies in the posterior half of the body just posterior to the extrascapulars; it consists of about 14 short rays each arising from the junction between two adjacent paired dorsal scutes; in the specimen described herein only the non-segmented proximal portion of each ray is visible. The caudal fin is externally symmetrical, not forked, with a convex posterior margin and contains about 24 principal rays; there are also five dorsal plus five ventral procurrent rays. The anal and pelvic fins and the pelvic girdle are not exposed, hidden under the anal and pelvic plates.

4.2 Morphospace analysis of Pycnodontomorpha

The relative warp analysis produced 57 RW axes with the first three together explaining about 78% of the variation. The morphospace occupation of Pycnodontomorpha is shown in Fig. 6. The first axis (44.2% of variance) describes the ratio between the body depth and the standard length, showing that, like other fish groups (e.g., Claverie & Wainwright, 2014), elongation is the main axis of the body shape variation in Pycnodontomorpha; in particular, negative scores are related to extreme deep-bodied pycnodonts (e.g., gebrayelichthyids) whereas in positive values lie fusiform and antero-posteriorly elongate shapes (e.g., coccodontids). The RW2 (21.6%) describes the distance from the pelvic to the anal fin; taxa with long pelvic-anal fin distance are on negative values (e.g., gebrayelichthyids) whereas pycnodonts with short pelvic-anal fin distance lie on positive scores (e.g., most of pycnodontids). The RW3 (11.8%) describes the correlation between the head size with respect to the rest of the body; in particular, negative scores are related to taxa with large head and short body (e.g., gladiopycnodontids), whereas on positive values lie pycnodonts with relatively small head and large body (e.g., gyrodontiforms).

The statistical significance at clade-level morphospace occupation (Fig. S3) is provided by the non-parametric tests; the PERMANOVA (Table S2) indicates that pycnodont lineages have different group centroids ($F=12.0$, $p<0.001$), whereas the ANOSIM (Table S4) shows that clades are significantly different ($R=0.71$, $p<0.001$). Based on morphospace plotted on the first two RWs, the center of morphospace is occupied by taxa with a generalized rounded deep-bodied morphology around the consensus shape, such as "brembodontids", pycnodontids, gyrodontiforms and trewavasiids, which provide a reduced contribution to the overall morphological diversity (Fig. S3A). Conversely, the extreme shapes lying on peripheral regions are defined by taxa with an extremely dorso-ventrally elongated body such as the gebrayelichthyids, or antero-posteriorly elongated body such as the gladiopycnodontids and coccodontids. An exception within the Coccodontidae is represented by *Hensodon spinosus*, which is characterized by a generalized rounded body, thereby lying around the consensus shape. Based on morphospace built on RWs 1 and 3 (Fig. S3B), the extreme shapes are defined, other than gebrayelichthyids, coccodontids and gladiopycnodontids, also by taxa with a relatively small head and large body (e.g., all *Gyrodus* species), or by taxa with a large head and small body (e.g., *Ichthyoceros spinosus* and *Gibbodon cenensis*).

The representatives of the family Pycnodontidae show the broadest area due primarily to the wider range of morphologies, although they lie around the consensus shape. The Kernel density and Ripley's K plots of the overall morphospace show that taxa appear significantly aggregated around the center where lie taxa with generalized deep-bodied morphology (Fig. S4). In the clade-level analysis, only Pycnodontidae shows a significant aggregated pattern, due to the high number of taxa lying around the consensus shape; representatives of the Coccodontidae clusterize at long distances on the periphery of the morphospace where lie most of their species, whereas gebrayelichthyids, gladiopycnodontids and gyrodontiforms show a randomized taxon distribution.

Coccodontidae shows the highest morphological disparity among the different lineages, due at least in part to the presence of both extreme (e.g., *Coccodus*) and generalized (e.g., *Hensodon*) morphologies (Table S6). Moreover, Coccodontidae, Gladiopycnodontidae and Pycnodontidae together provide almost 90% of the contribution to the morphological variation (Table S6).

The temporal analysis of pycnodontomorph morphospace (Fig. 7) shows that there are no significant differences in terms of morphospace occupation (PERMANOVA: $p>0.05$; ANOSIM: $p>0.05$; see Tables S3 and S5) or disparity (Student's t: $p>0.05$) between two consecutive time intervals from Late Triassic to the Early Cretaceous. During this period pycnodonts keep a generalized rounded deep-bodied body plan and lie near to center of morphospace. The Late Cretaceous experienced an explosive morphological diversification as shown by the significant peak of morphological disparity coupled with the highest morphospace occupation in terms of area. This significant increase in disparity is also reflected in standard statistical tests (Student's t: -5.96, $p<0.0001$). This is primarily due to the appearance of new body plans corresponding to the new morphologies exhibited by the Cenomanian representatives of the families Coccodontidae, Gladiopycnodontidae and Gebrayelichthyidae. After the end-Cretaceous mass extinction and until the Eocene, when they become extinct, both morphospace occupation and disparity reduced to the levels before the explosive radiation of the Late Cretaceous. The significant drop in disparity between Late Cretaceous and Paleogene is again reflected by statistical tests (Student's t: 5.52, $p<0.0001$). Pycnodonts return to their generalized rounded deep body, near the center of morphospace, and these fishes do not experience any new morphological diversification.

5. Discussion

The distinctive Cenomanian pycnodont *Gladiopynodus byrnei* n. sp. from the fossiliferous strata of Hjoûla, Lebanon, was part of an evolutionary history that started in the late middle Norian and terminated in the middle Eocene, reaching its apex in terms of morphological diversification in the Cenomanian (Late Cretaceous). The redefinition of the genus *Gladiopycnodus* and of the family Gladiopycnodontidae was the initial stimulus to analyze the morphological diversification of pycnodonts through the time using a quantitative approach. The bizarre morphology of this new taxon and its allies is very different from the basic body plan of most pycnodonts, placing it on peripheral area of morphospace together with the other Cenomanian gladiopycnodontids, gebrayelichthyids and coccodontids (see Fig. 6). The extreme shapes of these representatives of the Coccodontoidea substantially contributed to the Late Cretaceous (mostly Cenomanian) morphospace expansion and remarkable peak of disparity.

The morphological diversification of pycnodonts during the Late Cretaceous was characterized by the proliferation of new anatomies and, at least in part, to the exploitation of new ecological strategies (Poyato-Ariza, 2005; Poyato-Ariza & Martín-Abad, 2013). *Gladiopycnodus* exhibits an unusual body plan that does not seem to reflect any ecological counterpart in modern fish lineages. The presence of a rigid armored trunk, a long anterior rostrum counterbalancing the posterior sword-shaped anal plate result in a peculiar gestalt that is in some ways reminiscent to that of the modern centriscoid fishes (macroramphosids and centriscids; see Bannikov & Carnevale, 2012), and of the closely related Late Cretaceous gasterorhamphosids (Sorbini, 1981). These modern fishes often swim in a vertical position with the snout downwards primarily by sculling the pectoral fins, due to the presence of rigid bony plates on the body (see Stewart & Roberts, 2004). They usually feed on zooplankton and small benthic organisms that are preyed on with the modified long and tubular mouth (e.g., Clarke, 1984). The long dorsal spine characterizing the morphology of these syngnathiform fishes likely represents a defensive adaptation. Because of a certain similarity

in the body design, we suggest that *Gladiopycnodus* probably had a similar lifestyle, with the long anterior rostrum and anal spine acting as defensive structures.

The taxonomic exuberance coupled with the high morphological diversity that characterizes the Late Cretaceous (mostly Cenomanian) history of pycnodonts (see Poyato-Ariza & Martín-Abad, 2013) may largely reflect the rapid appearance of new different ecological strategies. The representatives of the superfamily Coccodontoidea (including coccodontids, trewavasiids, gebrayelichthyids, and gladiopycnodontids), were exclusive of this interval, and may provide new insights into the rapid Cenomanian appearance of new body plans and morphological innovations, some of which with a probable defensive function. A large part of the morphological innovations characterizing this clade (strongly ossified dermal bones, pectoral girdle structurally integrated to the skull forming a cephalo-torax, ornamented cranial bones and scales bearing horns and spines) likely evolved as anti-predatory structures.

Up to now, all the representatives of the superfamily Coccodontoidea showing morphological exuberance occur at a single point in space and time (Cenomanian of Lebanon). Although such a diversification could be interpreted as a local radiation due to restrained paleoecological or paleobiogeographical conditions (Cavin, 2008), we cannot exclude the collecting and taphonomic biases as the major causes leading such an apparently localized occurrence (Sansom, 2015; Sansom et al., 2015). Therefore, this geographically restricted morphological radiation could be interpreted in the context of a global macroevolutionary phenomenon.

Cavin et al. (2007) evidenced that diversification rates of several fish lineages were triggered by global scale events coincident with an increase in the oceanic crust activity and oceanic volcanism. The impact of these changes on the marine environment might have caused an increase in the sea level and the temperature of the marine surface. During the Cretaceous, a remarkable increase in both sea level and temperature occurred since the Aptian reaching their maximum in the

Cenomanian (Gale, 2000). Cavin et al. (2007) suggested that sea temperature is always positively correlated to the diversification rate of most fish lineages, and Cavin & Forey (2007) demonstrated that a vast radiation of several lineages of actinopterygian fishes occurred during the Cenomanian. Moreover, because all the Cenomanian Tethyan localities share a large part of their taxa (Forey et al., 2003), Cavin et al. (2007) hypothesized that the Tethys may have been a Cretaceous center of origin for many fish groups. The broad Cretaceous diversification of several fish taxa may have allowed the exploitation of new ecological and trophic resources and feeding strategies, primarily associated with the modification of their jaw apparatus and with the increasing in body maneuverability (see Rosen, 1982). Some of these changes were probably associated with the so-called Mesozoic Marine Revolution, a protracted event characterized by predation and biological disturbance (Vermeij, 1977). Even though this dramatic event has been primarily associated with a substantial increase in bioerosion and bioturbation, the clearest evidences of the change in the nature of biological interactions are best seen in predator-prey interactions (Vermeij, 1977, 1987; Harper, 2003). Several groups of benthic invertebrates, including gastropods, bivalves and brachiopods, gradually developed a number of structural features of their shells to increase resistance to crushing and simultaneously evolved a series of defensive structures (e.g., spines) on its surface (see Stanley, 1977; Vermeij, 1977; Vörös, 2010). Vermeij (1977) evidenced that these ecological changes represent an adaptive solution of the benthic prey, in response to the large increase in predatory pressure during the Late Cretaceous, and suggested that the predatory escalation led the evolution of adaptive defensive morphological and behavioral adaptation (Vermeij, 1987).

The conchiferous benthic faunas were not the only organism to adopt adaptive solutions to the increase in predatory strategies. Starting in the Cenomanian, also other groups of fishes as acanthomorphs evolved a suite of morphological features (dorsal-, anal-, and pelvic-fin spines,

ossified and dense scale covering and thick cranial bones, often ornamented with horns and spines; Patterson, 1964; Tyler & Sorbini, 1996; González-Rodriguez et al., 2013) that have been recently interpreted in terms of a rapid evolution of adaptive anti-predatory features (Chen et al., 2014).

In this perspective, the explosive Cenomanian radiation of pycnodonts, with the first appearance of the well-armored representatives of the superfamily Coccodontoidea, which greatly contribute to the expansion of morphospace of Pycnodontomopha in the Late Cretaceous, can be considered another example of the rise and evolution of defensive morphological adaptations that characterized neopterygian fishes in the context of the Mesozoic Marine Revolution.

6. Conclusions

In this paper we described a new species of *Gladiopycnodus* from Cenomanian of Lebanon. The excellent preservation of the specimen allowed the reinterpretation of the peculiar morphology of this genus, and to revise the diagnosis of the family Gladiopycnodontidae. Its osteological analysis was the initial input to analyze, through the geometric morphometrics, the morphospace configuration of pycnodont fishes through time. The Late Cretaceous increase in morphospace occupation and morphological disparity of Pycnodontomorpha was related, at least in part, to the first appearance of the representatives of the superfamily Coccodontoidea (that includes the new taxon documented herein). The adaptive radiation of these well-armored pycnodonts was linked to develop of anti-predatory features and interpreted in the context of the global macroevolutionary phenomenon known as Mesozoic Marine Revolution.

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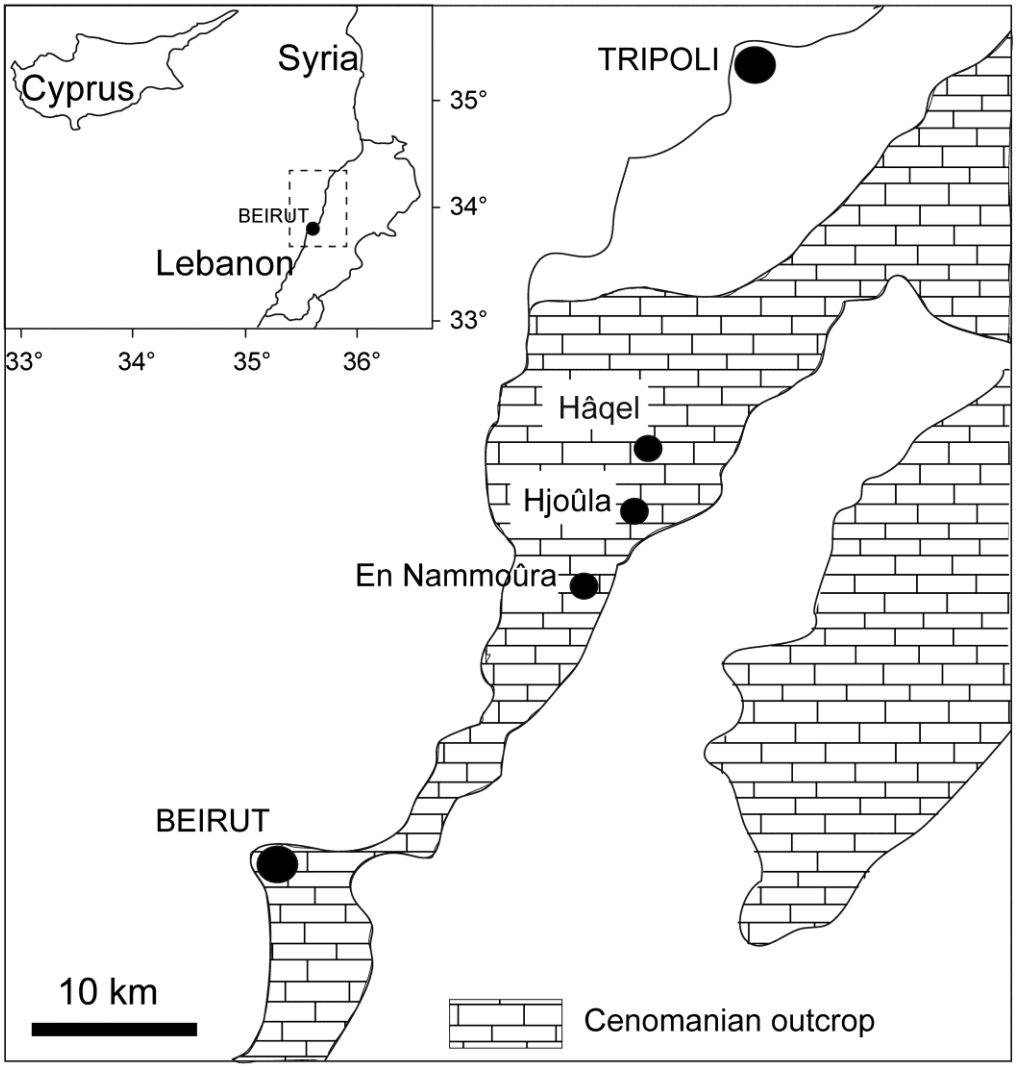
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Lebanon
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33°
TRIPOLI
Hâqel
Hjoûla
En Nammoûra
BEIRUT
10 km
Cenomanian outcrop

Fig. 1. Location map of the Cenomanian fossiliferous localities of Lebanon (modified from Forey et al., 2003). Geographic coordinates of Hjoûla: 34°07'55"N, 35°44'49"E.

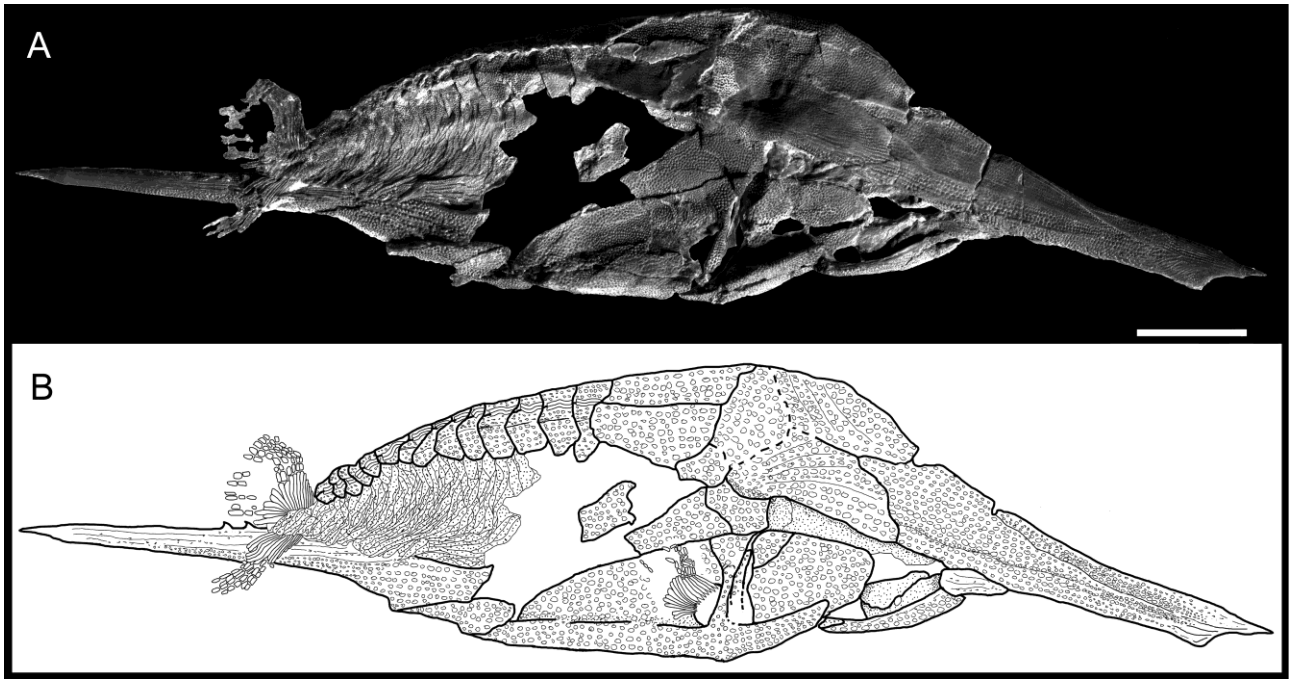

Fig. 2. *Gladiopycnodus byrnei* n. sp. from the Cenomanian of Hjoûla, Lebanon. A) Holotype, MGPTPU130335; B) Interpretative reconstruction. Scale bar 5 mm.

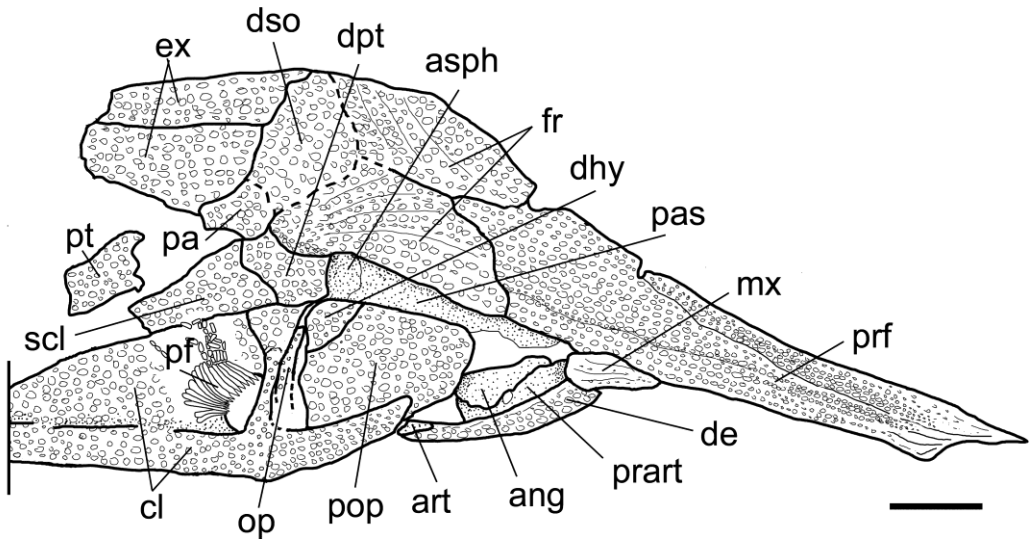

Fig. 3. *Gladiopycnodus byrnei* n. sp. Reconstruction of the head and associated pectoral girdle, right side, lateral view. Scale bar 2 mm. Abbreviations: ang, angular; art, articular; asph, autosphenoid; cl, cleithum; de, dentary; dhy, dermohyomandibula; dpt, dermopterotic; dso, dermosupraoccipital; ex, extrascapulars; fr, frontals; mx, maxilla; op, opercle; pa, parietal; pas, parasphenoid; pf, pectoral fin; pop, preopercle; prart, prearticular; prf, prefrontal; pt, posttemporal; scl, supracleithrum.

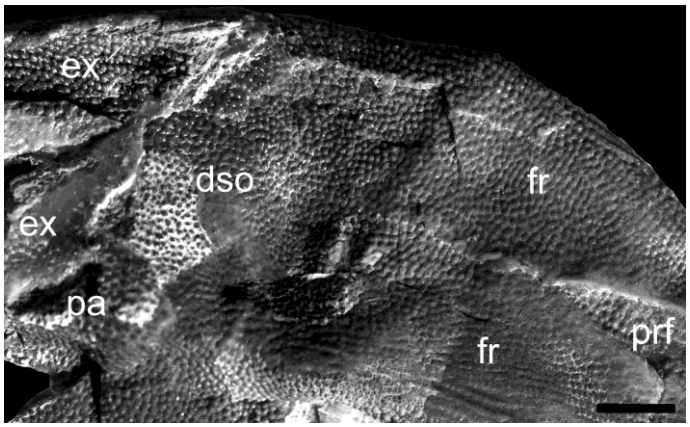

Fig. 4. *Gladiopycnodus byrnei* n. sp. Detail of the skull roof showing the fusion of some dermatocranial elements. Scale bar 1 mm. Abbreviations: dso, dermosupraoccipital; ex, extrascapulars; fr, frontals; pa, parietal; prf, prefrontal.

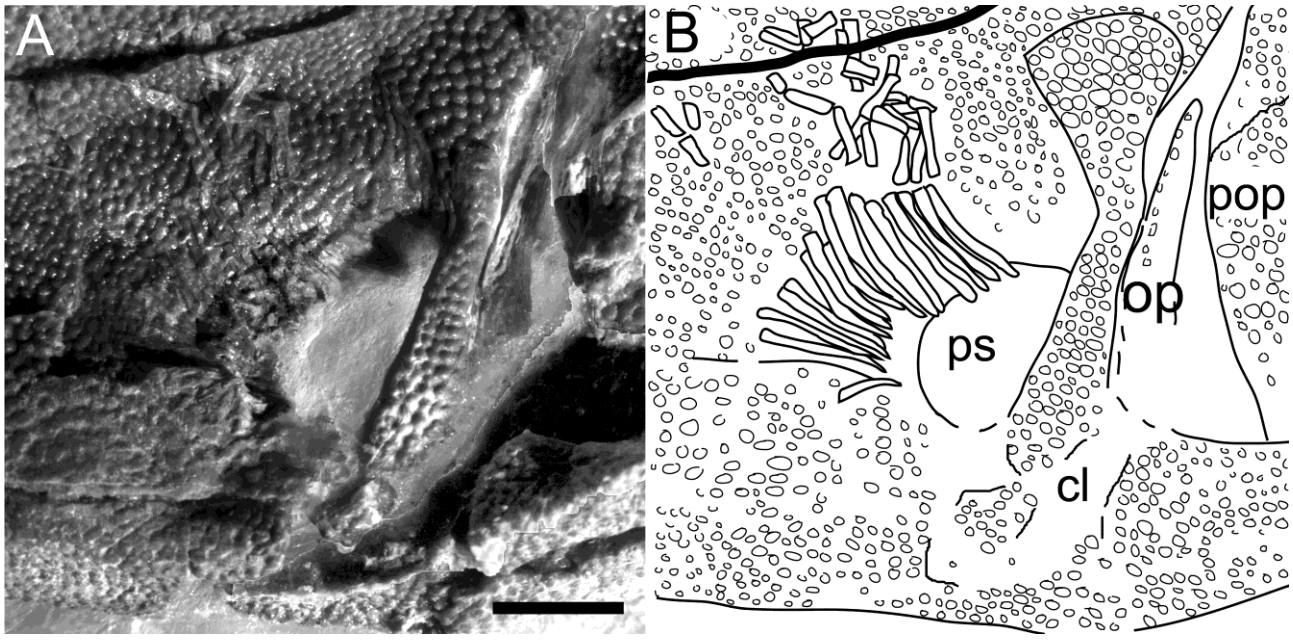

Fig. 5. *Gladiopycnodus byrnei* n. sp. Detail of the right pectoral fin and girdle, lateral view. A) Holotype, MGPTPU130335; B) Interpretative reconstruction. Scale bar 1 mm. Abbreviations: cl, cleithrum; op, opercle; pop, preopercle; ps, pectoral sinus. Note the strong ornamentation made in rounded tubercles on the dermal bones, and the large cleithrum supporting ventrally an anterior limb and a large posterior process surrounding posteriorly the pectoral fin.

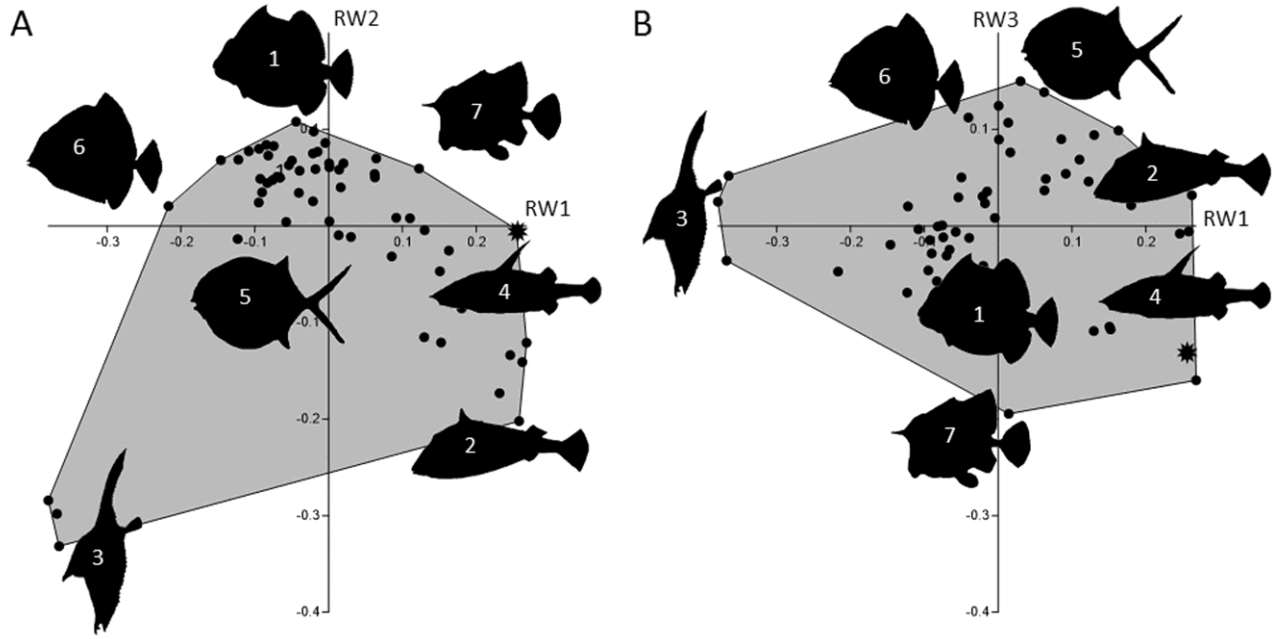

Fig. 6. Morphospace of Pycnodontomorpha plotted on the first three RW axes together accounting for over 78% of overall variance. A) Overall convex hull plotted on RW1 and RW2; B) Overall convex hull plotted on RW1 and RW3. The star marks the peripheral position of *Gladiopycnodus byrnei* n. sp. on morphospace. The silhouettes correspond to some representatives approximating the position of each clade on morphospace (see Supplementary material for detailed clade-level morphospace occupation): 1, *Brembodus ridens* ("Brembodontidae"); 2, *Coccodus armatus* (Coccodontidae); 3, *Gebrayelichthys uyenoi* (Gebrayelichthyidae); 4, *Joinvillichthys lindstroemi* (Gladiopycnodontidae); 5, *Gyrodus hexagonus* (Gyrodontiformes); 6, *Akromystax tilmachiton* (Pycnodontidae); 7, *Trewavasia carinata* (Trewavasiidae).

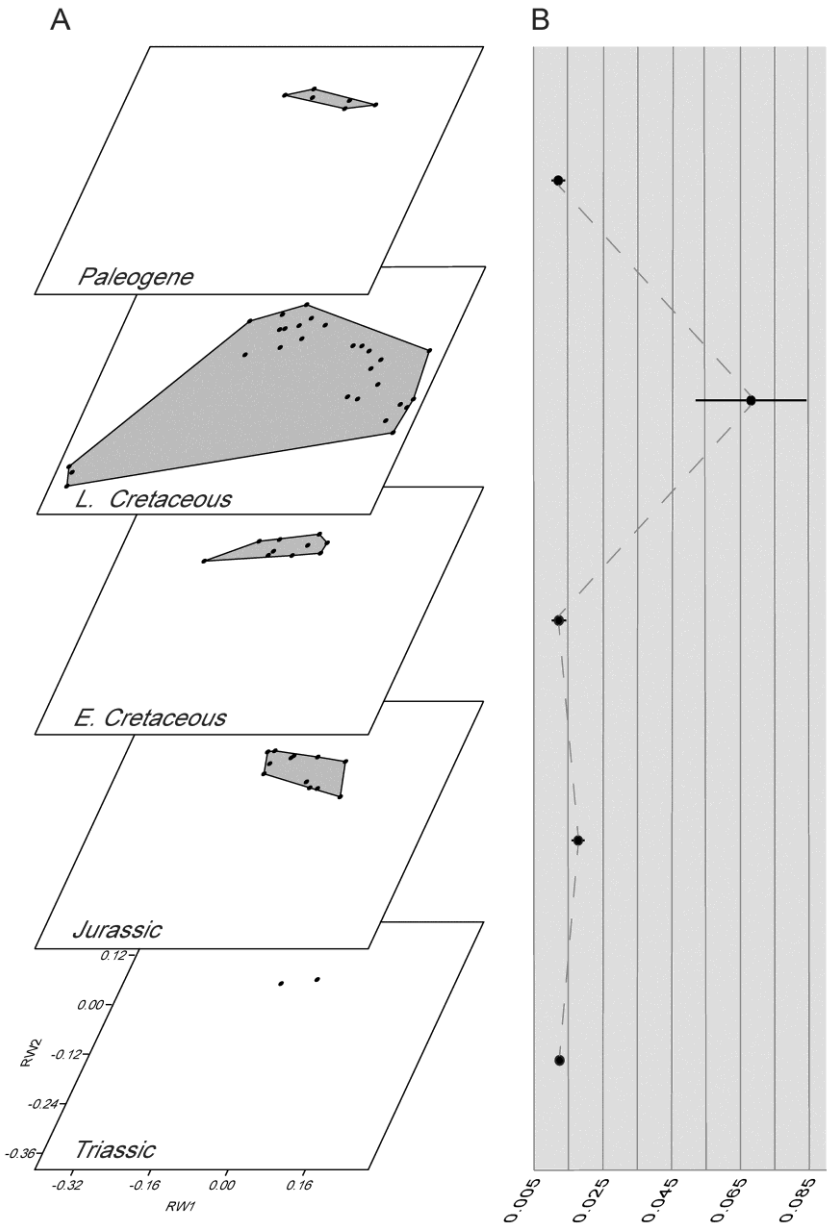

Fig. 7. Temporal patterns of morphological diversification of Pycnodontomorpha. A) Morphospace occupancy during pycnodont evolutionary history. B) Morphological disparity of pycnodonts expressed as sum of variances of the first ten RW axes. Error bars represent the confidence interval calculated as ±1 standard deviations generated from 999 bootstrap pseudoreplicates. Note the explosive morphological radiation in the Late Cretaceous (mostly Cenomanian) coupled with the significant peak in disparity.