

Atti Mus. Civ. St. Nat. Trieste	62	2021	43-62	X 2021	ISSN: 0335-1576
---------------------------------	----	------	-------	--------	-----------------

## THE PLATYSOMIFORMES AND THE ORIGINS OF THE PYCNODONTIFORMES

LUIGI CAPASSO\*, AMANDA CANTRELL†

\*Director of the University Museum, State University “G. d’Annunzio” – Piazza Trento e Trieste, n. 1 – 66100 Chieti (Italy) – E-mail: l.capasso@unich.it

†Owner, Badlands Scientific Expeditions LLC – 24 Chamisa Loop, Edgewood, New Mexico (USA) – E-mail: amanda.cantrell@outlook.com

**Abstract** – The authors take into consideration general morphological analogies of the skeleton, coating of scales, and dentition that exist between the Pycnodontiformes and the Platysomiformes. Through analysis of new fossil samples, the authors establish that the characters showing similarities between the two groups are at least the following: (i) structure of vertebrae, (ii) post-abdominal bone, (iii) squamation reduced to bar-scale; furthermore, the structure and arrangement of the teeth is also compared between the two groups. The existence of these anatomical and structural analogies allow us to re-propose the opinion by earlier authors (Agassiz, Egerton, Young, Stensiö, Berg, Gardner) that the Paleozoic ancestors of the Pycnodontiformes would have had close anatomical, structural and ecological affinities to those of some fish close to the Platysomiformes.

**Key Words:** Pycnodonts, Origins, Platysomiformes

**Riassunto** – Gli autori prendono in considerazione le analogie morfologiche generali dello scheletro, del rivestimento di squame e della dentatura che esistono tra i Pycnodontiformi ed i Platysomiformi. Attraverso l’analisi di nuovi campioni fossili, gli autori stabiliscono che i caratteri che mostrano somiglianze tra i due gruppi sono almeno i seguenti: (i) struttura delle vertebre, (ii) osso post-addominale, (iii) squamazione ridotta a piccole barre; inoltre, tra i due gruppi viene confrontata anche la struttura e la disposizione dei denti. L’esistenza di queste analogie anatomiche e strutturali permette di riproporre l’opinione di autorevoli autori precedenti (quali Agassiz, Egerton, Young, Stensiö, Berg, Gardner), secondo cui gli antenati paleozoici dei Pycnodontiformi avrebbero avuto strette affinità anatomiche, strutturali ed ecologiche con quelle di alcuni pesci vicini ai Platysomiformi.

**Parole chiave:** Pycnodonti, Origine, Platysomiformi

### 1. – Introduction: the question of the origins of Pycnodonts

Pycnodonts represent a homogeneous group of fossil fishes, completely extinct today, that flourished from the Ladinian (Middle Triassic) (DALLA VECCHIA & CARNEVALE, 2011) to the Priabonian (Eocene) (VOSS *ET AL.*, 2019), a period of over 200 million years. During this time, Pycnodonts occupied an important position in the aquatic vertebrate fauna, extending their presence all over the world. In fact, independent of their phylogeny (NURSALL, 2010), Pycnodonts thrive in marine, brackish, and freshwater habitats; some lived in shallow reef environments, developing several of the swimming adaptations common to reef fishes; some lived a pelagic, open-water life (*Gyrodus spp.*, KRIWET & SCHMITZ, 2005); some were benthonic (*Coccodus armatus*), some cryptic (*Ichthyoceros*), and some occupied, at last temporarily, a freshwater environment (CAVIN *ET AL.*, 2020). Large orbital size suggests that some members were nocturnal (*Gyrodus hexagonus*); some served as prey (EVERHART, 2007), and some were predators of other fishes (KÖLBL-EBERT *ET AL.*, 2018 and CAPASSO, 2019); finally, most were probably armed by an anatomically

complex poisonous apparatus (CAPASSO, 2018). In summary, the Pycnodonts were a successful and significant component of the faunas and ecosystems in which they lived throughout the Mesozoic Era (NURSALL, 2010).

From an anatomical point of view, Pycnodonts represent a relatively uniform group, and were characterized by a laterally compressed body, a more or less rounded outline, posteriorly placed dorsal and anal fins, and by elongated snouts with well-developed durophagous dentition.

From a systematic point of view, Pycnodonts are a strong monophyletic group, even within the Pycnodontiformes. Despite that, they represent a well-defined monophyletic assemblage where high homoplasy was demonstrated (although somewhat unexpected in a supposedly anatomically uniform group). As demonstrated by POYATO-ARRIZA & WENZ (2002) there are puzzling combinations of primitive and derived characteristics, and convergence are especially abundant. Pycnodonts are a highly homoplastic group and reversions occur frequently.

During their over 200 million year presence around the globe, the Pycnodonts developed remarkably diverse forms, with many dozen fossil genera and hundreds of fossil species being described in the last two centuries.

Notwithstanding great attention by paleontologists, and a high number of scientific papers on the subject, the origins and reasons for the rapid extinction of these fishes remain completely obscure.

On the subject of the origins of these fishes, we should consider that NURSALL (2010) demonstrated that the fossil monophylum Pycnodontomorpha represents the final flowering of a lineage originating in a common ancestor with the crown group Teleostomorpha. This supposed common ancestor probably lived during the Early Triassic, but could go back to the Late Paleozoic (Permian or Upper Carboniferous).

The morphological characteristics that should mark this common ancestor were hypothesized by NURSALL (2010), as the differentiation between Pycnodontomorpha and Teleostomorpha was originally presumed to be concentrated in the mandibular and rostro-maxillary-ethmoid regions. But what could be the anatomical characters that distinguished the oldest ancestors of the Pycnodontiformes? And, above all, which fossil fishes from the Upper Palaeozoic could be suspected of representing relatives closest to the most ancient ancestors of the Pycnodontiformes?

In this study the authors examine in detail the anatomy of some skeletal and dental characters of the Upper Carboniferous, Permian and Lower Triassic Platysomiformes (including Bobasatraniiiformes); this is done both by taking the point of view of many ancient and authoritative authors, such as AGASSIZ, EGERTON, YOUNG, STENSIÖ, BERG, GARDINER, and also by examining new well preserved specimens recently collected and studied by the authors. The new observations, combined with the old ones, provide comparison with similar characters that are typical of Pycnodontiformes, and that should be interpretable as its precursors in the Platysomiformes.

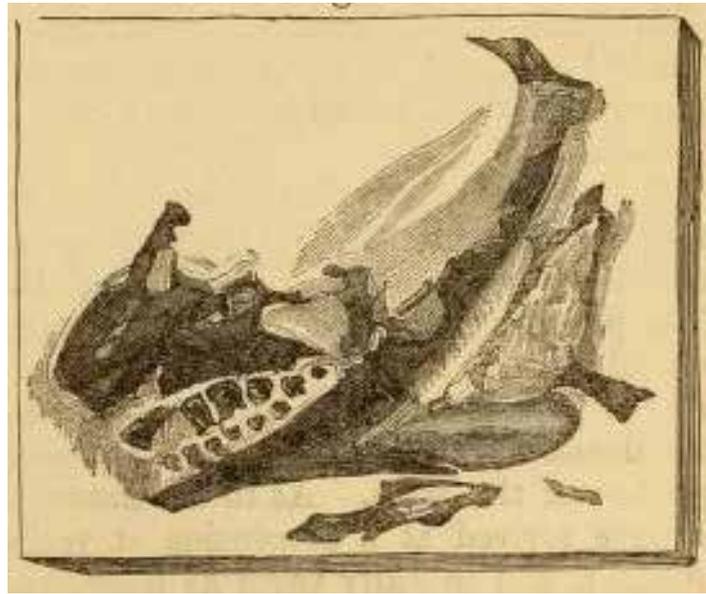
## 2. – The relationships between *Platysomus*, *Amphicentrum*, *Bobasatrania*, sister genera and Pycnodontiformes: a historical overview

*Platysomus* was established by Louis AGASSIZ (1833-43). He assigned to the genus five new species, *P. gibbosus*, *P. rhombus*, *P. striatus*, *P. macrurus* and *P. parvus*, all based on specimens from England and Germany; Agassiz placed the new genus among the “*Lepidoids*”. Moreover, Agassiz provided a reconstruction of *Platysomus* that was largely incorrect, especially regarding the post-cranial skeleton (Figure 1): no trace of the notochord was reported in this drawing, and the vertebral column appeared as a sequence of completely ossified metamers. This interpretation appears to be wrong due to the fact that all specimens examined by Agassiz had their bodies covered in scales, preventing the correct evaluation of the morphology of the vertebral column and its state of ossification. Because of the imperfect material studied by Agassiz an academic discussion about the true systematic position of the genus *Platysomus* was necessary.



**Figure 1:** Schematic reconstruction of the skeleton of *Platysomus* by Louis Agassiz, reproduced in Plate D of volume 2 of his treatise “*Reserches sur les Poissons Fossiles*”, Neuchâtel, 1833-43.

The first change in the classification of the group in which *Platysomus* belongs was proposed by Sir P. G. EGERTON (1849), who outlined the numerous affinities of the genus *Platysomus* with the Pycnodonts. On the bases of new specimens collected in the Permian magnesian limestone of the Raisby Formation of Ferryhill (Durham)



**Figure 2:** Specimen of *Platysomus* collected from the Permian magnesian limestone of the Raisby Formation of Ferryhill, Durham, UK, which allowed Sir Philip Egerton to describe in detail the anatomy of the masticatory apparatus, the morphology and arrangement of teeth in this genus of fossil fish, highlighting the analogies with the Pycnodonts. From EGERTON (1849).

(Figure 2), Sir Egerton demonstrated superposition of tooth morphology and setting, and the true nature of the emapophyses of the *Platysomus*, initially compared by Agassiz to the V-shaped sternal ribs of the Clupeiform fish. Sir Egerton communicated to Prof. Agassiz his idea that *Platysomus*, on the bases of many characters of teeth and skeleton, pertained to the Pycnodonts, and reported the answer received from Agassiz, demonstrating that Agassiz himself fully shared the observations raised by Sir Egerton, and shared the idea that the genus *Platysomus* should be considered a Pycnodont. Sir Egerton reports the text of the answer received from Louis Agassiz and we believe that this represents a very important document in the historical interpretation of the systematics of the Platysomiformes. Here is the text of Agassiz reported by EGERTON (1849):

*“I quite agree with you in the propriety of combining the genus Platysomus with the Pycnodonts; for some time past I had, indeed, been impressed with the great difference there is between that genus and the others of the family in which it stands, and I now feel that my only reason for putting it there was the heterocerqual form of tail, a character which could not fail to produce a vivid impression upon my mind when first discovered, but which I now expect to find in fishes of various families*

*in the oldest geological ages, as well as everywhere in the youngest state of our actual fishes in their embryonic growth. The teeth, as you mentioned, are conclusive evidence for placing Platysomus with the Pycnodonts. Let me now point out to you another evidence of this relation in the form of the skeleton, especially of the apophyses before the dorsal. The specimens of Platysomus in the museum in Munich show some good portion of the skeleton, and in my mind I now compare them to the skeleton of the small Pycnodus rhombus, without detecting any difference. Pray institute the comparison upon a safer ground that recollection, and let me know when you find. You know under what circumstances the fossil fishes have been worked out, and as a matter of course I must expect to see daily important additions made to the edifice of which I have only the foundation.”*

It is striking how the great authority of Louis Agassiz is nearly apologetic to Sir Egerton for not recognizing the dental and skeletal morphologies that make it necessary to classify *Platysomus* among the Pycnodonts.

John YOUNG (1866) takes up the question of the systematic position of *Platysomus*, which had become the central genus of a group of forms of the Upper Palaeozoic, and at the time was elevated to the rank of “family”. To the “family” of Platysomidae YOUNG (1866) adds a new genus, *Amphicentrum*. All of Young’s work is devoted to describing the relationships and analogies of Platysomidae with related fossil fishes, as the title of his work unequivocally demonstrates: “*On the affinities of Platysomus and allied genera.*” In the context of these complex comparisons, YOUNG (1866) shows that the new genus *Amphicentrum* is the one which, in the context of Platysomidae, demonstrates the closest and most convincing relationships with the Pycnodonts. In particular, YOUNG (1866) points the attention to the structure of the internal skeleton, both in *Amphicentrum* as well as in Pycnodonts, present a persistent notochord, “with well ossified arches”, and the conspicuous analogies in the teeth shape and arrangement; as the same YOUNG (1866) underline that the most important characteristic that serves to exclude *Amphicentrum* to the “family” of Pycnodonts is the ventral fin, that is completely absent in his new Carboniferous genus.

In 1932 the group of Platysomiformes acquired a more modern configuration, as WHITE (1932) described the new genus *Bobasatrania*, based on fossil specimens from the Lower Triassic of Madagascar. In the same year, STENSIÖ (1932) described the species *Bobasatrania groenlandica*, based on fossils found in the Triassic limestone of the eastern Greenland. Furthermore, Stensiö also attributed the species *Bobasatrania nathorsti* from the island of Spitzbergen, to the same genus, which he himself described in 1921 as belonging to the genus *Platysomus*. Finally, more recently BÖTTCHER (2014) attributed to the genus *Bobasatrania* the tooth plates described as *Colobodus hogardi* by Agassiz in 1843 (from the Muschelkalk of Lorraine, France) as well as *Colobodus scutaus* by Gervais in 1852 (from the Muschelkalk of Craillseim, Germany)(see Figure 11 B). He STENSIÖ (1932) identified and underlined all the features of *Bobasatrania*’s dental and skeletal anatomy that closely linked this genus to the Pycnodonts; in particular, STENSIÖ (1932) also emphasized some anatomical features of the cranial bones. In fact, in *Bobasatrania*

we observe a pre-operculum divided into two separate bones, one inferior and one superior, placed in front of a very reduced operculum: this structure is believed to be quite characteristic of the Pycnodontiformes.

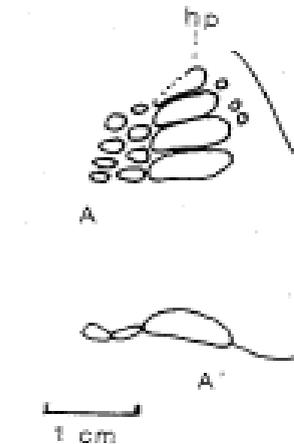
BERG (1947), in his fundamental work, redefined the order of the Pycnodontiformes by clearly pointing out the relationships, based on stringent structural analogies, between this order and the Platysomiformes (which today also include the Bobasatraniiiformes). These analogies concern, first of all, the morphology and the arrangement of the teeth, the subdivision of the pre-opercle, the general morphology of the body – flattening in the lateral sense and with a sub-circular profile – the persistence of a well-developed notochord along the vertebral column.

Finally GARDINER (1958, 1960, 1963, 1993), and GARDINER *ET AL.* (1996), related the Pycnodonts with Bobasatraniiiformes as their presumed ancestral taxon, comparing in detail, with a long series of scientific works, many anatomical characters.

This long scientific discussion, lasting for over a century among the world's leading experts on fossil fish, shows that in the Upper Carboniferous and Permian seas there lived small, flat-bodied and round-profile fish that had anatomical analogies, but probably also functional and ecological super-positions, with the Pycnodonts, whom would have existed in the Triassic, Jurassic, and most prolifically of all, during the Cretaceous time period where they rise to their maximum expansion.

### 3. – The question of possible Paleozoic Pycnodontiformes

In 1979 SÁNCHEZ & BENEDETTO describe *Archaeopycnodon riveroi* based on a specimen collected in the limestone of the so called “Palmarito Formation” outcropping near Carache, a locality between Carona and Trujillo, Los Andes, West Venezuela, and dated to the Upper Pennsylvanian-Lower Permian, as fossil remains pertaining to Pycnodontiformes fish. The new genus and species was established on a single sample representing a Pycnodont-like dentition. Notwithstanding that this report appears completely out of the chronological range of the Pycnodonts, it is important to underline that both the anatomy of the fossil remains as well as the stratigraphic location of the rock that includes it, are absolutely convincing. On the stratigraphic point of view, one of the authors (Dr. Gianluigi Benedetto) was a great expert of geology in Venezuela, applied to the “División Exploraciones” of the “Ministerio de Energía y Minas” of the Venezuela Government. On the morphological point of view, the pictures that the authors present are absolutely convincing. We have little doubt that the described specimen represents a left pre-articular, with four series of rounded teeth, of a typical Pycnodontiformes, despite the articular region being missing (Figure 3). Unfortunately, nearly half a century has passed since this discovery and no new specimens have been collected to support the presence of Pycnodonts in the Upper Carboniferous of South America.



**Figure 3:** Schematic drawing of the pycnodont-like dentition of *Archaeopycnodon riveroi* SÁNCHEZ & BENEDETTO (1979), found in the limestone of the Palmarito Formation, near Carache, Los Andes, Venezuela, and dated to the Upper Pennsylvanian–Lower Permian (modified from SÁNCHEZ & BENEDETTO, 1979).

### 4. – Triassic and Jurassic forms

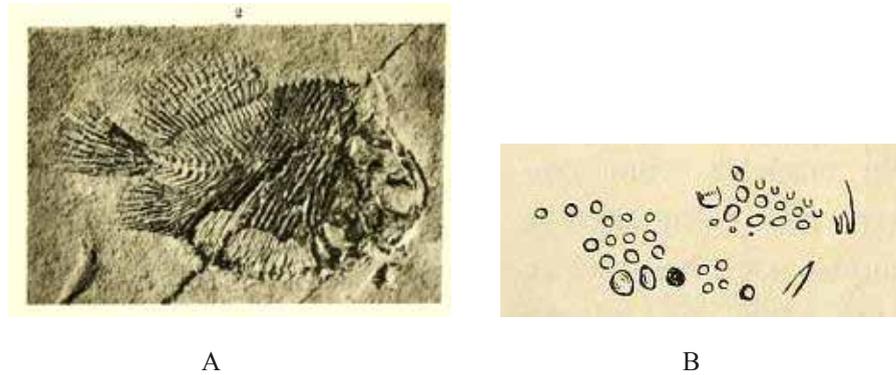
The unquestionably oldest Pycnodontiform appears during the Ladinian (Middle Triassic) with a series of fossil fish, more or less synchronic, and distributed in North and Central Europe. The first fossils pertaining to the Pycnodontiformes consist of both complete skeletons and isolated dentitions. From a palaeoenvironmental point of view, all these Triassic Pycnodontiformes are known from marine deposits of both the northern Tethys margin (what is now northern Italy and Austria), and from the epicontinental sea deposits of France, Belgium and Luxembourg.

There are five or six formal species of Pycnodonts that appear in nearly the same time (Norian); we briefly describe them in chronological order of publication.

*Gyrodus milinum* was described by J. HENRY (1876) from Rhetian (Upper Triassic) limestone of Grozon (Jura department in the Franche-Comté), France, and consists of isolated teeth. Specimens were collected in association with a typical Upper Triassic fauna, composed especially by molluscs and corals, indicating a reef environment. More recently these teeth were interpreted as possibly pertaining to Colobodontids or Perleidids (DELSATE & KRIWT, 2004), but direct examination of the material was not conducted.

*Eomesodon hoferi* was described by GORJANOVIC-KRAMBERGER (1905) from the Norian limestone of Hallein, near Salzburg (Austria). This species represents the first

complete Pycnodontiformes described and illustrated through both the dentition, and cranial and post-cranial skeleton (Figure 4). Additional remains of the same species were also collected in Triassic limestone of the Val Brembana, Lombardy (North Italy)(TINTORI, 1981).



**Figure 4:** A: The first photographic reproduction of a Pycnodont, which refers to the first description of a Pycnodont from the Triassic, *Mesodon hoeferi*, collected near Salzburg, Austria, and published by Professor Dragutin Gorjanovic-Kramberger in 1905. B: detail of the dentition.

*Brembodus ridens* and *Gibbodon cenensis* are two species collected in the Norian (Upper Triassic) limestone of Cene, Lombardy (TINTORI, 1981); *Brembodus ridens* is known through a quantity of very well preserved material representing the best studied of the Triassic Pycnodonts. *Gibbodon cenensis* is known through three specimens preserved as articulated, more or less complete individuals.

In the so-called “Dolomia di Forni”, an Upper Norian (so-called “Alaunic” stage) dolomitic outcropping in a locality along the right bank of the Seazza stream and a few kilometers south of the village of Preone (province of Udine, north-eastern Italy), some excavations conducted in 1988 by the Friulian Museum of Natural History of Udine have produced complete specimens of Pycnodonts (Figure 5). These specimens are of a small size (about 3.5 cm in total length), are not well preserved, and have been attributed to the genus *Gibbodon*, but are currently subject to anatomical and systematic study (DALLA VECCHIA, 2012).

A single tooth of a undetermined pycnodont was described by CUNY & RAMBOER (1991) from the Upper Triassic limestone of Saint-Nicolas-de-Port, in the Meurthe-et-Moselle département, in north-eastern France.

Isolated teeth and dentitions are known, but not described, from the so called *Rhaetic Rocks* outcropping at the Aust Cliff, near the end of the Bristol Channel. These Pycnodont remains are part of a fossil assemblage that includes shark and

fish teeth, scales and coprolites, fragments of Ichthyosaur and Plesiosaur bones, and invertebrate fossils, including clams and oysters (as reported by DELSATE & KRIWET, 2004).

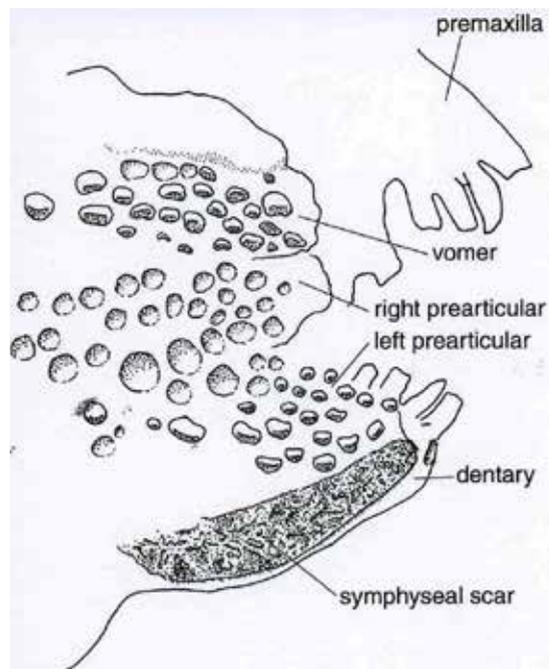


**Figure 5:** An undetermined Pycnodontiformes collected in the “Dolomia di Forni” near Preone (province of Udine, north-eastern Italy), dated to the upper Noric. Total length = 3.5 cm. Friulian Museum of Natural History, no. 13810. Courtesy of Dr. Giuseppe Muscio.

The “*Val Garza species*” represents a undescribed species of Pycnodont, collected in the Norian deposits of Val Garza, near Brescia, North Italy. This primitive Pycnodontiform is represented by eight specimens, all more or less incomplete, that were reported, but not described by BRUNETTI *ET AL.* (2001). Brunetti declared that a description was in progress, but approximately 20 years has passed and this very important species remains almost unknown today, except for the brief description and figures published by NURSALL (2010).



A



B

**Figure 6:** B: The so-called “*Val Garza species*”, the oldest Pycnodont known today, from the Lower Norian of Val Garza, Brescia, northern Italy. Museo Civico di Storia Naturale di Brescia, n. VG04. Courtesy of Dr. Paolo Schirolli. B: detail of the dentition.

Isolated teeth and a complete prearticular dentition of a undetermined species of Pycnodontiform was collected in the Norian sands of Habay-la-Vieills, Belgium and described by DELSATE & KRIWET (2004).

Isolated teeth and a partial dentition of an undetermined species of Pycnodontiform was collected in the Norian dolomitic marls of Medernach, Luxembourg and described by DELSATE & KRIWET (2004).

The Early and Middle Jurassic fossil records of pycnodontiforms in the aftermath of the Triassic-Jurassic mass extinction event is, by comparison, scarce. As reported by STUMPF *ET AL.* (2020), just two species have been described from the Early Jurassic. At least twelve nominal species have been described from the Middle Jurassic, most represented by isolated vomerine and prearticular dentitions, rendering their identification difficult. Consequently, most of the Early and Middle Jurassic Pycnodontiformes species are dubious and its need of revision. Despite the scarcity of published Jurassic specimens, we assume that Early and Middle Jurassic Pycnodonts were widespread, existing in nearly all of the marine environments, and that preservational or collection bias is to blame for the lack of specimens in the fossil record.

Since the Triassic Pycnodontiformes come from marine deposits of both the northern Tethys margin (what is now northern Italy and Austria), and from epi-continental sea deposits (what is now France, Belgium and Luxembourg), we assume that the origin of the Pycnodontiformes is geographically localized in correspondence of Tethys, and its epi-continental basins. During the Early and Middle Jurassic, despite the fact that the number of published genera are limited, the Pycnodontiformes spread: in fact, in addition to remaining endemic in the Tethys basin, they are found in the fossil state at south of the Tethys, just to Congo (TAVERNE, 2019), as well as at east of the Tethys, just to Thailand (CAVIN, *et al.*, 2007).

##### 5. – Additional specimens suggest a relationship between the Pycnodontiformes and Late Pennsylvanian Platysomiformes

A series of new specimens of *Amphicentrum jurgenai* ZIDEK 1992, were recently collected by one of us (A.C.) in the world-famous Kinney Quarry Lagerstätte, Manzanita Mountains, New Mexico USA. The Kinney Quarry is positioned stratigraphically low in the Tinajas Member of the Atrasado Formation, and is dated to the Late Pennsylvanian (middle Missourian) by LUCAS *et al.* 2011. This locality is one of the most studied and best known sites for collecting exceptionally well preserved Late Pennsylvanian fish specimens anywhere in the world. The Platysomiform genera formally described from Kinney include *Platysomus*, *Amphicentrum* and *Bobasatrania*. Thin laminations and the fine-grained texture of sediments, coupled with near-perfect mineralization of the fossil bones, make viewing even the most minute details of fossils skeletons from the Kinney Quarry possible.



**Figure 7:** Detail of the vertebral column of *Amphicentrum jurgenai* from the late Pennsylvanian of the Manzanita Mountains, New Mexico, U.S.A., to show the absence of ossified vertebral centra (photo by L.Capasso).



**Figure 8:** Specimen of *Chirodus (Amphicentrum) cf. C. persanae* from the Stark Shale Member of the Dennis Formation, Nebraska (U.S.A.). This specimen almost completely lost its flake cover during the tanatocoenosis process, which highlights the skeleton. Note the presence of a large post-coelomatic bone (asterisks). Courtesy of Dr. John Hedley, The Natural Canvas Company, San Mateo, California, U.S.A. (photo by L.Capasso).



**Figure 9:** Detail of the covering of flakes in the dorsal region of a specimen of *Amphicentrum jurgenai* from the late Pennsylvanian of the Manzanita Mountains, New Mexico, U.S.A.. The scales are reduced to scale-bars, and are thin and short, twisted in on themselves and embracing one to the other, to form direct dies back-ventrally. (photo by L.Capasso).

In addition, we consider a single specimen of *Chirodus (Amphicentrum) cf. persanae*, collected in the Hansen Quarry, Papillon, Nebraska (U.S.A.). The specimen was recovered from the Stark Shale Member of the Dennis Limestone and is dated to the Late Pennsylvanian (HATCH & LEVENTHAL, 1992; AKANDI, 2008). It is particularly interesting because, for taphonomic reasons, the individual completely lost its squamation, showing the internal structure of the skeleton.

The new specimens documented here serve to demonstrate a series of anatomical details, never before recognized, that corroborate the relationship between the Platsomiformes and the Pycnodontiformes. In particular, we consider the following three characters: (i) the structure of the vertebrae and its apophysis, (ii) the post-abdominal bone, and (iii) the squamation reduced to simple bar-shaped scales.

*Structure of vertebrae* – *Amphicentrum* is characterized by the persistence of a well-developed notochord. Our observation demonstrates the absence of vertebral centra, but rather, well perichondrally ossified neural arches and basiventralia. Each centra appears to have a rhomboid shape, strictly connected with the dorsal and ventral apophysis (Figure 7). The notochordal space is very large, a character not observed by AGASSIZ (1933-43)(see Figure 1).

*Post-abdominal bone* – A robust bone close posteriorly to the abdominal cavity in *Amphicentrum* is developed vertically and parallel to the last ribs (Figure 8). This bone lifts the ventral profile of the fish posterior the anus with a special shaped scale (post-anal scale).

*Squamation reduced to bar-shaped scales* – The dermal scales in *Amphicentrum* are reduced to very thin, dorso-ventrally elongated bony bar-shaped scales (Figure 9). These scales are near monomorphic, near circular in middle transversal section, and fusiform. These bar-shaped scales are arranged in a dorso-ventrally oriented series starting from each side of the dorsal ridge. Each bar-shaped scale is in contact with the superior scale (except for the more dorsal scales), and with the inferior scale one (except for the more ventral ones). A notable overlapping exists between one scale with the other along the same dorso-ventral series, and no strict contact exist between each anterior scale with the posterior one, and vice-versa (Figure 9). These scales cover nearly the entire dorsal half of the body.

#### **6. – Analysis of the anatomical characters of Platysomiformes interpretable as possible precursors of similar characters in the Pycnodontiformes, and their functional, ecological and evolutionary significance**

Between Platysomiformes and Pycnodontiformes there are clearly relevant anatomical differences, mainly in the structure and arrangement of the bones of the skull, both of the dermocranium and the internal skull. These differences are profound and recent computer-assisted phyletic analysis techniques have provided great phylogenetic value. Nonetheless, it cannot be omitted that modern Cladistic analysis is based on characters selected by analysts and which, once established, are often not visible in many of the available fossil specimens leading to a large quantity of fossil remains being excluded from analysis. Cladistic analysis can only contribute, with limited information, to the understanding of the clade, its structure and its relationships, including evolutionary ones. Therefore, the purpose of the discussion that we present here is only to address the question of the structural analogies between Platysomiformes and Pycnodontiformes on an exclusively morphological basis, being fully aware of the limits of this comparison, but equally not wanting to underestimate the value of the analogies which, in the already largely speculative field of research into the origins of the Pycnodonts, have great circumstantial value.

Various ancient and some modern authors (for example: GARDINER *ET AL.* 1996) consider the main morphological characteristics relating the Platysomiformes to the Pycnodontiformes to be the general body shape and the structure of the dentition. A laterally flattened and round-shape profile is a morphology that first appeared during the Late Carboniferous in some marine fish. Preceding these new round and flattened fish, the marine ichthyofauna was composed of spindle-shaped fish, representing the only body pattern present in the pelagic fish of the Paleozoic era. Slowly, this

innovative morphology spread and was adopted by an increasing number of genera in the Upper Carboniferous and Permian (MICKLE & BADER, 2009).

Numerous paleontological studies dedicated to the subject have shown that, in pelagic fish, a fusiform body morphology allows excellent speed and quick release performance in swimming, but is associated with poor maneuverability. On the contrary, fish with a flattened body and a rounded profile are actually slower in swimming, but they have great maneuverability (BACKLE, 2004). The latter function being very useful in the reef environment where, due to confined spaces, it is more important to maneuver to conquer safe and protected areas, rather than competing with predators by moving away from the reefs using swimming sprint and speed (WALKER *ET AL.*, 2013).

Platysomiformes were some of the first pelagic fish to adopt a flat and round-shaped profile, and all the major genera that adopted this schema rapidly conquered a relevant position as important components of the characteristic fish fauna of the Upper Paleozoic reefs (MICKLE & BADER, 2009). *Platysomus*, *Amphicentrum*, *Cheirolepis*, *Bobasatrania*, *Ecrineosomus*, *Ebanauqua*, are the major representatives of this strategy, and were successful over a very long time, between the Middle Carboniferous to the Middle Triassic Periods.

In addition to Platysomiformes, other types of fish, such as *Dapedium*, adopted the same body pattern and occupied the same ecological niches. The main difference between *Dapedium* and the various genera that represent Platysomiformes are in the squamation. *Dapedium* has ganoin scales, a substance similar to enamel (ZYLBERBERG *ET AL.*, 1997), very resistant and very compact; the individual scales are very robust and are strongly connected to each other, forming an almost tenacious armor, effectively protecting the fish from attack. This, however, represented a protective scheme that many paleontologists have defined “archaic”, that is, a heavy armor, which limited the movements of the fish, slowing down swimming speed and reducing maneuverability (WEBB, 1984). The *Dapedium* were remarkably successful and developed throughout the Jurassic period, but paleontological evidences clearly indicates that their heavy scaling did not serve to protect them from all predators. In fact, some predators likely specialized specifically in the capture the *Dapedium* and did it successfully. This being inferred from the large amount of *Dapedium* flakes found in the coprolites of many marine reptiles (such as the Ichthyosaurs) (BUCKLAND, 1835) and from the presence of regurgitalites composed of clusters of *Dapedium* scales expelled by reptiles that fed on these fish during the Jurassic period (Figure 10).

Platysomiformes adopted the same body structure, but with a much lighter squamation than *Dapedium*. The scales are mainly bony, that is, they consisted of a porous and light substance. In this context, the new observations we report here suggest that by the Upper Carboniferous some forms of Platysomiformes had already adopted a squamation made up of very light, filiform bony scales. In the *Amphicentrum jurgenai*, as we have shown, this squamation is reduced to such an extent that it closely resembles the bar-shape scales of the more advanced Pycnodontiformes.



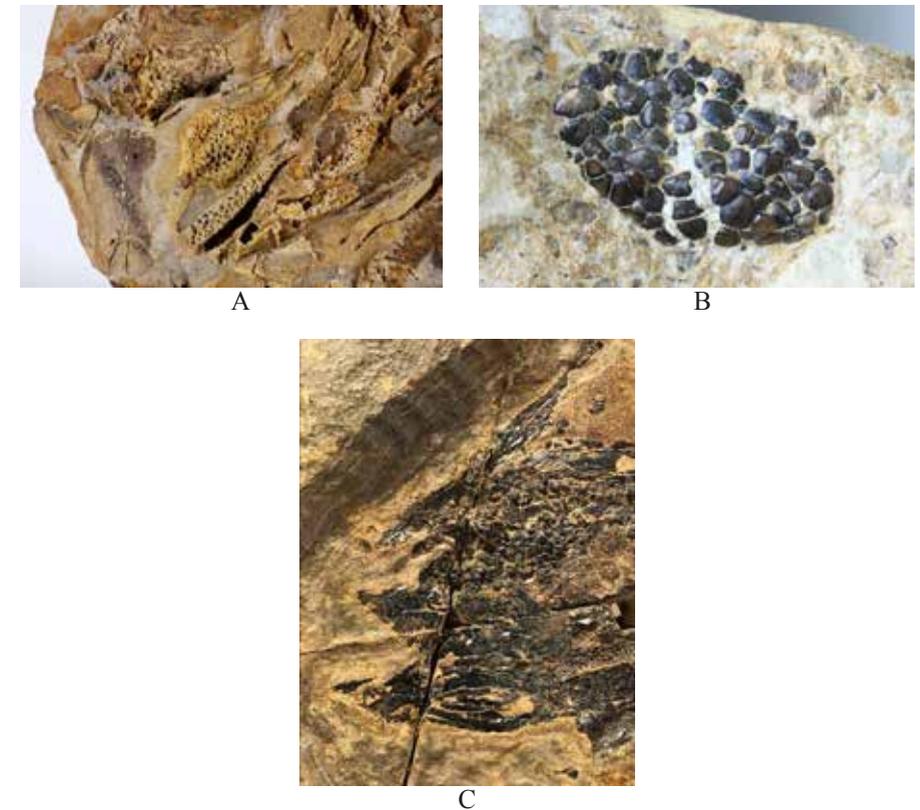
**Figure 10:** Ichthyosaur regurgitation composed almost exclusively of ganoid flakes of *Dapedium sp. ind.*; from the Jurassic of Lyme Regis, England (photo by L.Capasso).

In this context of data, we hypothesize that some Platysomiformes had lightened their squamation as to make the maneuverability of their body in the narrow spaces of the cliffs even more efficient, adding the advantage of having a very lightened, and therefore easier, body to move in a quick swim, without losing muscle strength moving a heavy ballast. Certainly this anatomical scheme, with its resulting greater functional efficiency, could have exposed these fish more to their predators, but equally certainly it was a successful body-plan, since it was then adopted and perfected by the Pycnodontiformes, beginning in the Late Triassic. CAPASSO (2018) hypothesized that Pycnodontiformes employed part of their lightened squamation as a poisonous organ, likely used as an additional defense mechanism.

Two anatomical structures and functional potentialities of Late Carboniferous Platysomiformes precede, but will later characterize, the Pycnodontiformes: the general shape of the body (additionally the posterior position of the dorsal and anal fins) and a very lightened squamation composed by modern-type, osseous scales. These anatomical structures could be linked to the same new requirements of functional anatomy, deriving from the adopted laterally flattened body structure and the circular profile with median fins posteriorly positioned, and the presence of a post-abdominal bone.

The post-abdominal bone is present in both Platysomiformes and Pycnodontiformes, and has the specific function of strengthening the posterior edge of the abdominal

cavity. In fish that have a particularly flattened general body shape, the thickness of the musculature of the codal pedicel is very small. Also, the movement of lateral fluctuation of the tail produces traumatism that tend to separate the musculature of the right side from that of the left side, which are clearly separated both from the hemapophysis of the caudal vertebrae, and from the axonostei of the codal fin (BLAKE, 2004). In living Zeiform fishes, for example, this bone is very well developed and is an anatomical expression characteristic of a laterally flattened fish (BERG, 1947). Many Pycnodontiformes possess this characteristic skeletal element (POYATO-ARIZA & WENZ, 2002), which is also present in all the Bobasatraniiiformes (*Bobasatrania*, *Ecrineosomus*, *Ebanaqua*). We observe the presence of post-abdominal bones in the *Amphicentrum* specimens published here, whose skeletons are almost completely void of a scaly coating allowing for detailed examination of the internal anatomy.



**Figure 11:** Mouth region with detail showing the dental morphology in *Bobasatrania mahavavica* from the Triassic of Madagascar (A); *Bobasatrania scutata* tooth superior plate from the Middle Triassic of southern Germany (B); and in *Platysomus schultzei* from the Carboniferous of New Mexico (C) (photos by L.Capasso).

We conclude that common characters between the Pycnodontiformes and the Platysomiformes demonstrate a functional convergence between the two groups. The post-abdominal bone is the adaptation, deriving from the need to adopt a more appropriate swimming model for fish with flat, rounded bodies with very posterior dorsal and anal fins. Thorough study of analogies in the morphology and structure of the dentition, mentioned several times by previous workers, are warranted. We note that although Pycnodontiformes tooth arrangement is different from Platysomiform tooth arrangement, dental morphology is widely variable (Figure 11) and it clearly shows that both groups fed on hard foods and shared a similar if not the same ecological niche.

## 7. – Conclusion

Pycnodontiforms represent a highly derived group of Actinopterygii, whose oldest representatives are certainly found in the Upper Triassic, but whose origins – together with those of the Neopterygians in general – represent the origin of the modern Teleostei and certainly rest somewhere in the Permian or Upper Carboniferous. The Platysomiformes of the Upper Carboniferous were among the first fish to adopt a deep-bodied, laterally compressed and nearly circular outline, with posteriorly positioned dorsal and anal fins. They also possessed a durivorous dentition and occupied an ecological niche in reef habitats, attributes later shared by the Triassic Pycnodonts. A series of anatomical characteristics and their functional implications presented in this paper demonstrate that many analogies exist between Platysomiformes and Pycnodontiformes: general body shape, posteriorly positioned fins, very lightened squamation, and post-abdominal bone. All this suggests that the presumed Paleozoic ancestors of the precursor of the Pycnodontiformes had to be anatomically and systematically close to the Platysomiformes, a newly emerging model of Neopterygian fish.

## 8. – Additional Note

The fossil specimens examined and described in this work belong to the “Capasso Public Collection”. The CAPASSO Public Collection is legally registered by a decree of the Ministero per i Beni e le Attività Culturali under the date of October 11th 1999, following the disposition of the Italian law 1089/39. The specimens of this collection were also subject to prescription in order of conservation and availability to the studies on the basis of the article 30 of the Italian law N° 42/2004. The fossil specimens examined and described in this work are the following six, the provenance of which is described in detail in the text and in the figures indicated below:

Figure 7: CPC # S-1872 *Amphicentrum jurgenai*

Figure 8: CPC # S-1950 *Chirodus cf. persanae*

Figure 9 and Figure 11 B: CPC # S-1832 *Amphicentrum jurgenai*

Figure 10: CPC # S-777 *Ichthyosaurus undetermined*

Figure 11 A: CPC # S-1899 *Bobasatrania mahavavica*

Figure 11 B: CPC # S-1946 *Bobasatrania scutata*.

*Lavoro consegnato il 12/04/2021*

## QUOTED BIBLIOGRAPHY

- AKANBI, O.T., 2008, *Paleoclimate and geochemical variation of the Stark Shale Member, Dennis Formation (Missourian), Mid-Continental North America*. Thesis in Geosciences, Texas Tech. University.
- BERG, L.S., 1947, Classification of fishes, both recent and fossil. *Travaux de l'Institut Zoologique de l'Académie des Sciences de l'URSS*, **5** (2): 1-345.
- BLAKE, R.W., 2004, Fish functional design and swimming performance. *Journal of Fish Biology*, **65** (5): 1193-1222.
- BRUNETTI, M., LOMBARDO, C., SCHIROLLI, P. & TINTORI, A., 2001, The new early Norian fish fauna from Garza Valley (Brescia – N. Italy). – In Tintori, A. (Editor), Abstract Book, III: *International Meeting of Mesozoic Fishes: Systematic, Paleoenvironments and Biodiversity*: 13; Milano (Unimi).
- BÖTTCHER, R., 2014, Phylloodont tooth plates of *Bobasatrania scutata* (Gervais, 1852) (Actinopterygii, Bobasatraniiiformes) from the Middle Triassic (Longobardian) Grenzbonebed of southern Germany and eastern France, with an overview of Triassic and Palaeozoic phylloodont tooth plates. *N. Jb. Geol. Paläont. Abh.*, **274** (2-3): 291-311.
- BUCKLAND, W., 1835, On the discovery of coprolites or fossil faeces in the Lias at Lyme Regis, and in other formations. *Transactions of the Geological Society of London (Second Series)*, **3**: 223-236.
- CAPASSO L., 2018, The flank bar-scales in Pycnodontiformes, Berg (1937): morphology, structure, evolutionary significance, and possible functional interpretation as venom apparatus. *Bollettino del Museo Civico di Storia Naturale di Verona, Geologia Paleontologia Preistoria*, **42**: 21-42.
- CAPASSO, L., 2019, Palaeontological evidence of piscivorous habits of some Pycnodonts from the Middle Cenomanian of Lebanon. *Thalassia Salentina*, **41**: 89-108.
- CAVIN, L., DEESRI, U. & SUTEETHORN, V., 2009, The Jurassic and Cretaceous bony fish record (Actinopterygii, Dipnoi) from Thailand. In: BUFFETAUT, E., CUNY, G., LE LOEUFF, J. & SUTEETHORN, V. (Eds), Late Palaeozoic and Mesozoic Ecosystems in SE Asia. *Geological Society, London, Special Publications*, **315**: 125-139.
- CAVIN, L., GARCIA, G. & VALENTIN, X., 2020, A minute freshwater pycnodont fish from the Late Cretaceous of southern France: Palaeoecological implications. *Cretaceous Research*, **106**.
- CUNY, G. & RAMBOER, G., 1991, Nouvelles données sur la faune et l'âge de Saint-Nicolas-de-Pont. *Rev. Paléobiol.*, **10**: 60-78.
- DALLA VECCHIA, F.M., 2012, *Il Friuli 215 milioni di anni fa – gli straordinari fossili di Preone, finestra su un mondo scomparso*. Comune di Preone Editor, pp. 1-224.
- DALLA VECCHIA, F. & CARNEVALE, G., 2011, Ceratodontoid (Dipnoi) calvarial bones from the Triassic of Fuseum, Carnic Alps: The first Italian lungfish. *Italian Journal of Geosciences (Bollettino della Società Geologica Italiana)* **130** (1): 128-135.
- DELSATE, D. & KRIWET, J., 2004, Late Triassic pycnodont fish remains (Neopterygii, Pycnodontiformes) from the German basin. *Eclogae geol. Helv.*, **97**: 183-191.
- EGERTON, SIR P.G., 1949, Palichthyologic Nore. No. 2 – On the Affinities of the Genus *Platysomus*. *Quarterly Journal of the Geological Society of London*, **5**: 329-332.
- EBERT M., KÖLBL-EBERT M., LANE J.A., 2015 – Fauna and Predator-Prey Relationships of Ettlting, an Actinopterygian Fish-Dominated Konservat-Lagerstätte from the Late Jurassic of Southern Germany. *Plos One*, DOI: 10.1371/journal.pone.0116140
- GARDINER, B.G., 1958, The affinities of the Pycnodontidae – XV. *Internat. Congr. Zool., Sept. V, Paper 7*: pp 3.

- GARDINER, B.G., 1960, A revision of certain actinopterygian and coelacanth fishes, chiefly from the Lower Lias- *Bull. Brit. Mus. (Natural History), Geol.*, **4** (7): 239-384.
- GARDINER, B.G., 1963, Certain palaeoniscoid fishes and the evolution of the snout in actinopterygians. *Bull. Bri. Mus. (Nat. Hist.), Geology*, **8** (6): 255-325.
- GARDINER, B.G., 1993, Osteichthyes: basal actinopterygians. In: BERTON, M.J. (Ed.): *The Fossil Records*, **2** (35): 611-619. London, Chapman & Mall Publishers.
- GARDINER, B.G., MAISEY, J.G. & LITTLEWOOD, D.T.J., 1966, Interrelationships of basal neopterygians. In: STIASSNY, M.L.J., PARENTI, L.R. & JOHNSON, G.D. (Eds.): *Interrelationships of Fishes*. pp 117-146. Academic Press, San Diego.
- GORJANOVIC-KRAMBERGER, K., 1905. Die obertriadische Fischfauna von Hallein in Salsburg. *Beiträge zur Paläontologie Österreichs Ungarns und des Orients*, **18**: 123-224.
- HATCH, J.R. & LEVENTHAL, J.S., 1992, Relationship between inferred redox potential of the depositional environment and geochemistry of the Upper Pennsylvanian (Missourian) Stark Shale Member of the Dennis Limestone, Wabouncee Country, Kansas, USA. *Chemical Geology*, **99**: 65-82.
- HENRY, J., 1876, L'Infralias dans le Franche-Comté. *Soc. Émul. Doubs*, **10**: 285-476.
- MICKLE, K.E. & BADER, K., 2009, A new platysomid from the Upper Carboniferous of Kansas (USA) and remarks on the systematics of the deep-bodies lower actinopterygians. *Acta Zoologica*, **9** (Suppl. 1): 211-219.
- NURSALL J.R., 1996, The phylogeny of pycnodont fishes. In Arratia, G. and Viohl, G. (Eds.): *Mesozoic Fishes, Systematics and Palaeoecology*: 125-152. Verlag Dr. Friedrich Pfeil, München.
- NURSALL J. R., 1999b, The pycnodontiform bauplan: The morphology of a successful taxon. In ARRATIA, G. & SCHULTZE, H.-P. (Eds): *Mesozoic Fishes 2 – Systematics and Fossil Record*, 189–214. München: Verlag Dr. Friedrich Pfeil.
- NURSALL, J.R., 2010, The case for pycnodont fishes as the fossil sister-group of teleosts. In: Nelson, J.S., Schultze, H.-P. & Wilson, M.V.H. (Eds.): *Origin and Phylogenetic Interrelationships of Teleosts*. Verlag Dr. Friedrich Pfeil, München; pp 37-60.
- POYATO-ARIZA, F.J. & WENZ, S., 2002, A new insight into pycnodontiform fishes. *Geodiversitas*, **24** (1): 139-248.
- SÁNCHEZ, T.M. & BENEDETTO, G., 1979, Una dentición de tipo pycnodontiforme del Paleozoico de los Andes de Venezuela. *GEOS, Revista Venezolana de Ciencias de la Tierra*, **25**: 13-18.
- STENSIÖ, E., 1932, Triassic Fishes from East Greenland collected by the Danish expeditions in 1929-1931. *Meddelelser om Grønland*, **83**(3): 1-305.
- STUMPF, S., ANSORGE, J., PFAFF, C. & KRIWET, J., 2020, Early Jurassic diversification of Pycnodontiform fishes (Actinopterygii, Neopterygii) after the end-Triassic extinction event: evidence from a new genus and species, *Grimmenodon aureum*. *Journal of Vertebrate Paleontology*, **37** (4): 1-14.
- TAVERNE, L., 2019, A horny pycnodont fish (Pycnodontiformes) in the continental Middle Jurassic (Stanleyville Formation) of the Democratic Republic of Congo. *Geo.-Eco.-Trop.*, **43**: 25-34.
- TINTORI, A., 1981, Two new Pycnodonts (Pisces, Actinopterygii) from the Upper Triassic of Lombardy (N. Italy). *Riv. It. Paleont. Strat.*, **86**: 795-824.
- VOSS, M., ANTAR, M.S.M., ZALMOUT, I.S., GINGERICH, P.D., 2019, Stomach contents of the archaeocete *Basilosaurus isis*: Apex predator in oceans of the late Eocene. *PLoS ONE* **14**(1): e0209021. <https://doi.org/10.1371/journal.pone.0209021>
- WALKER, J.A., ALFARO, M.E., NOBLE, M.M. & FULTON, C.J., 2013, Body Fineness Ratio as a Predictor of Maximum Prolonged-Swimming Speed in Coral Reef Fishes. *PLoS ONE*, **8** (10).
- WHITE, E.I., 1932, On a new Triassic fish from North-east Madagascar. *Journal of Natural History*, **10**: 80-83.
- WEBB, P.W., 1984, Form and function in fish swimming. *Scientific American*, **251**: 58-68.
- YOUNG, J., 1866, On the affinities of *Platysomus* and allied genera. *Quarterly Journal of the Geological Society of London*, **22**: 301-317.
- ZYLBERBERG, L., SIRE, J.-Y. & NANJI, A., 1997, Immunodetection of amelogenin-like protein in the ganoine of experimental regenerating scales of *Calamoichthys calabaricus*, a primitive actinopterygian fish. *The Anatomical Record*, **249** (1): 86-95.