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SOCIETÀ TOSCANA
DI
SCIENZE NATURALI

MEMORIE • SERIE A • VOLUME CXXX • ANNO 2023

Edizioni ETS

Atti Soc. Tosc. Sci. Nat., Mem., Serie A, 130 (2023)
pagg. 9-18; figg. 7; *doi: 10.2424/ASTSN.M.A.2023.02*

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LIBANOHETERODONTUS COSTAE GEN. ET SP. NOV., A NEW EXTINCT BULLHEAD SHARK (CHONDRICHTHYES: HETERODONTIFORMES), FROM THE MARINE UPPER CENOMANIAN (LATE CRETACEOUS) OF EN NAMMOURA, CENTRAL LEBANON

Abstract - L. Capasso, Libanoheterodontus costae *gen. et sp. nov., a new extinct bullhead shark (Chondrichthyes: Heterodontiformes), from the marine upper Cenomanian (Late Cretaceous) of En Nammoura, Central Lebanon.*

The author describes a new genus and a new species of *Heterodontiformes* from the marine Cenomanian of Lebanon, *Libanoheterodontus costae* gen. et sp. nov. The holotype consists of a complete adult specimen and the taxonomic diagnosis was based both on dental characters, as is almost always the case for Heterodont sharks, and on skeletal and integumentary characters. The new taxon appears to be characterized by a marked heterodonty, which also includes some very peculiar traits: (i) the presence of anterior teeth with a styliform crown, curved distally, and a semilunar root without openings and vascular canals; (ii) the presence of molariform, multicuspid posterior teeth, with distal cusp and serrated edges. Although the fish-fossil localities of Lebanon have been known for over four centuries, no remains of Heterodonts (teeth, spines of dorsal fins) have ever been found and described in them; this demonstrates the absolute rarity of these fish in the thanatocenosis context of the marine Cenomanian of Central Lebanon. The new genus *Libanoheterodontus* enriches the very scarce biodiversity of the Heterodontiformes during the Cretaceous, flanking only the genera, *Heterodontus* and *Proheterodontus*, which represent the bullhead sharks of the Cretaceous.

Key words - bullhead sharks, Cenomanian, Lebanon

Riassunto - L. Capasso, Libanoheterodontus costae *gen. et sp. nov., un nuovo squalo testa di toro estinto (Chondrichthyes: Heterodontiformes), dal Cenomaniano superiore marino (Cretaceo Superiore) di En Nammoura, Libano centrale.*

L'autore descrive un nuovo genere e una nuova specie di Heterodontiformes del Cenomaniano marino del Libano, *Libanoheterodontus costae* gen. et sp. nov. L'olotipo è un esemplare adulto completo e la diagnosi tassonomica, quindi, si è basata sia sui caratteri dentali – come quasi sempre avviene per gli squali Heterodontiformes – che su caratteri scheletrici e tegumentari. Il nuovo taxon appare caratterizzato da una marcata eterodontia, che comprende anche alcuni tratti assolutamente peculiari: (i) la presenza di denti anteriori con una corona stiliforme, ricurva distalmente, e con radice semilunare apparentemente priva di aperture e canali vascolari; (ii) la presenza di denti posteriori molariformi, multicuspidi, con cuspide distale a bordi seghettati. Sebbene le località ittiofossilifere del Libano siano conosciute da oltre quattro secoli, in esse non è mai stato rinvenuto e descritto alcun resto di Heterodontiformes (denti, spine delle pinne dorsali); ciò dimostra l'assoluta rarità di questi pesci nell'ambito della tanatocenosi del Cenomaniano marino del Libano centrale. Il nuovo genere *Libanoheterodontus* arricchisce la scarsissima biodiversità degli Heterodentiformes del Cretaceo, affiancando i due soli generi *Heterodontus* e *Proheterodontus*, che rappresentano gli unici squali testa di toro ad oggi noti nel Cretaceo.
Parole chiave - squali testa di toro, Cenomaniano, Libano

Introduction

Heterodontiformes are known from the Lower Jurassic and at least nine species still survive in present-day seas. Their first appearance dates back to the Toarcian, with the species *Heterodontus duffini* (Thies, 1983; Underwood, 2006; Hovesdt, 2018), but it has been hypothesized (Maisey *et al*., 2004) that the Heterodontiformes separated from the rest of the selaceous galeomorphs as early as the beginning of the Jurassic. From a paleogeographical point of view, all fossil evidence indicates that the Heterodontiformes originated in the Western Tethys Sea, corresponding to extant Europe (Kriwet, 2008). From a paleoecological point of view, Heterodontiformes have always represented a minor and scarce, if not rare component of marine ichthyofauna from the Jurassic to today (Nelson, 2006).
Unfortunately, the Heterodontiformes are almost exclusively known in their fossil state through their teeth (Hovestadt, 2018) which, as the name of the group implies, are characteristically heterodont. Moreover, the fossils that also include, at least in part, the remains of their exoskeleton and above all of their endoskeleton in anatomical connection, are extraordinary rare finds. This fact implies that our paleontological knowledge of the Heterodontiformes is based on a dental taxanomy whose biological meaning remains largely speculative, as we do not know the correspondence between the variability of the dental morphology and the somatic structure, that is the general anatomy of these sharks. Paradoxically, this situation makes it very difficult to study, compare and taxonomically determine the few fossil specimens preserved even with their skeleton.
According to the biodiversity reconstructed almost exclusively on the basis of tooth fossils, it has been ascertained that the number of species of Heterodontiformes of the Jurassic period was relatively high. In the Cretaceous this biodiversity was certainly greatly reduced and subsequently restricted in the Cenozoic and further reduced to only nine living species (Kriwet & Klug, 2004; Kriwet, 2008).

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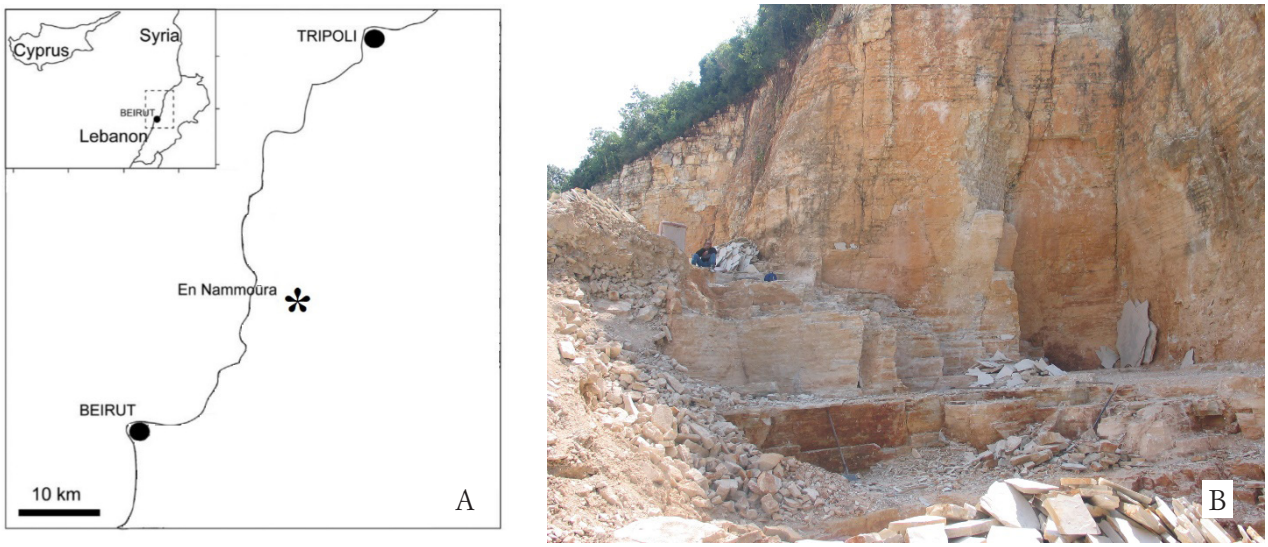


Figure 1. A: The asterisk indicates the geographical position of the En Nammoura deposit in Central Lebanon (schematic); B: The limestone quarry near En Nammoura where the find described in this paper was found (photo September 1994).

In this context, the specimen described in this paper represents an exceptional find, as it is one of very few complete fossils of Heterodontiformes, with an entire and well-preserved skeleton in anatomical connection, and refers to the Late Cretaceous, an epoch for which the biodiversity of Heterodontiformes was quite minimal.

Material and methods

The material described in this paper refers to specimen no. # S-482, belonging to the "Luigi Capasso Public Collection" (LCPC). This is a Public Collection that was established two centuries ago, and is protected by the Italian State. It is legally registered by two Decrees of the Ministry for Cultural Heritage, such as the no. 14, dated October 11, 1999, and no. 6259-A, dated April 29, 2020, both according to Italian law 1089/39 for the protection of the National Cultural Heritage. The specimens of this Collection were publicly-accessible for studies on the basis of the Article 30 of Italian law N ° 42/2004.
Specimen LCPC # S-482 was collected during the mid past century in a limestone quarry located just North of the village of En Nammoura, in Central Lebanon (Fig. 1), a location described in detail by Capasso (2017). The limestone outcroppings in this locality are part of the Sannine Limestone Formation, dated to the upper Cenomanian (Late Cretaceous), and were deposited in a marine environment with warm and shallow waters, close to the coast line (Capasso, 2017).
Specimen LCPC # S-482 was examined macroscopically, and was observed and documented, also photographically, using a Wild M 8 Leica reflected light binocular microscope, illuminated with both normal light and ultraviolet light.
As regards the description and nomenclature of skeletal anatomy, strict reference was made to data that was reported and codified in the unsurpassed works of Daniel (1914; 1915), and in the works by Casier (1947; 1961) concerning teeth anatomy.

Systematic Paleontology

Class **Chondrichthyes** Huxley, 1880
Subclass **Elasmobranchii** Bonaparte, 1838
Cohort **Euselachii** Hay, 1902
Subcohort **Neoselachii** Compagno, 1977
Order **Heterodontiformes** Berg, 1940
Family **Heterodontidae** Gray, 1851
Libanoheterodontus gen. nov.

Type species. *Libanoheterodontus costae* sp. nov.
Derivation of name. The name of the new genus refers to the name of the Nation in which the holotype was collected, Lebanon.
Diagnosis. The only shark pertaining to the family Heterodontidae, both living and fossil, which possesses anterior teeth with a styliform, needle-like crown, strongly curved distally, and a single semilunar root, without apparent vascular holes and/or channels.

Libanoheterodontus costae gen. et sp. nov.
Figure 2
Diagnosis. Small heterodont shark, with pelvic fins inserted immediately behind the first dorsal fin and supported by elongated and rectilinear basipterygium; anterior spines of the dorsal fins consisting of ossified

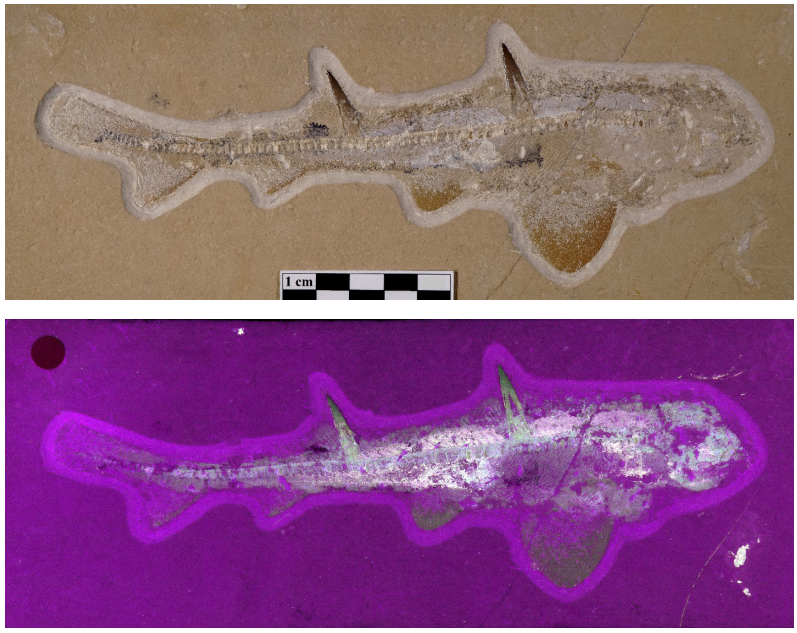


Figure 2. *Libanoheterodontus costae* gen. et sp. nov., holotype. From the marine upper Cenomanian (Late Cretaceous) Sannine limestone of En Nammoura, Central Lebanon.

cartilage before any vascularization; palatoquadrate/mandibular joint in which the hyomamdibola also participates. Heterodonty with at least three dental types: (i) anterior teeth monocuspid, with semicircular root and almost needle-like crown, curved with distal concavity; (ii) lateral teeth with a characteristic crown with a central V-shaped cusp and two minor lateral cusplets and in which the lingual root shown the vascular opening; (iii) posterior molariform teeth with 6 cusplets, with densely serrated distal edge of the distal cusplet, and with the lingual root showing the vascular openings and canals.

Derivation of name. The name of the new species is dedicated to the famous Italian physician and paleontologist Oronzo Gabriele Costa (1789-1867), who was one of the founders of Paleo-ichthyology and discovered many new paleontological deposits in Southern Italy, in addition to describing hundreds of new species of fossil fishes. Moreover, he was among the first to import into Europe and to describe fossil fish from the Cretaceous of Haqel and Shael Alma quarries, Lebanon.

Holotype. The specimen LCPC # S-482, a complete fish, with TL = 213 mm (Fig. 2).

Age. The upper Cenomanian, Late Cretaceous.

Type-locality and horizon. En Nammoura, Central Lebanon; Sannine Marine Limestone Formation (Walley, 1997).

Description. The holotype is a whole fish, without any missing parts, preserved on a whole limestone slab and without fractures. Nevertheless, it is a poorly preserved specimen: the exoskeleton, consisting of a dense coat of smooth dermic denticles, is well preserved while the endoskeleton, almost completely cartilaginous, is poorly preserved. In fact, since the skeleton of the specimen described here is composed of cartilage, it is certainly the cause of this poor and incomplete conservation. In addition, the anatomical limits between the individual bones are indistinct and difficult to follow, even with the aid of a microscope, and the surface of many of the skeletal elements, including those of the skull, is calcified into tiny mineralized denticles called tesserae. It is the presence of these calcified and therefore perfectly preserved superficial structures which hinders an acceptable view of the anatomy of the underlying cartilage skeleton. Despite these limitations, some skeletal characters are present and can be described, as reported in the following lines.

The neurocranium is less conserved and only a few structures emerge from it (Figs. 3A and B). Anteriorly, in the upper part of the anterior extremity of the muzzle, an almost oval cartilage nucleus is visible which corresponds to the olfactory, or nasal capsules (NC). In the posterolateral part of the skull, at the superior-posterior extremity, there is a second thick-walled hemispherical structure, which corresponds to the auditory capsule (AC). Between the olfactory capsule (anteriorly) and the auditory capsule (posteriorly), a vast and elongated socket opens, leaning against the dorsal profile of the head, i.e. the orbital cavity (OC). As in living heterodonts, this orbital cavity is bounded by a few structures raised up to the cranial surface: overhanging the orbit is the broad superorbital crest (SOC), from the anterior part of which arises the preorbital process (PROP), and from the posterior the postorbital process (POP); inferiorly, the base of the orbit continues towards the palatoquadrate cartilage (PQC). Posterior to the auditory capsule the presence of the occipital condyles (OCC) is clearly evident, which connect the neurocranium to the first metamer of the vertebral column (I-vb).

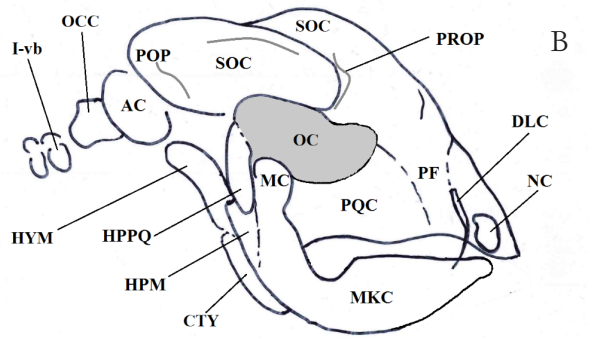


Figure 3. *Libanoheterodontus costae* gen. et sp. nov., holotype. A: Cephalic region; B: interpretation scheme of the single cartilages and anatomical structures in topographical relationship between them (also interpreted with the aid of illumination with UV light). AC: auditory capsule; CTY: ceratohyoid cartilage; MC: mandibular condyle; DLC: dorsal labial carilages; HPM: hyal process (mandibular part); HPPQ: hyal process (palatoquadrate part); HYM: hymandibular cartilage; I-vb: first vertebral body; MKC: Meckel's cartilage; NC: nasal capsule; OC: orbital cavity; OCC: occipital condyle; PF: palatal fossa; POP: postorbital process; PQC: palatoquadrate cartilage; PROP: preorbital process; SOC: superorbital crest.

As for the splanchnocranium, the bones deriving from the first branchial arch are quite prevalent. The upper part of this arch is the palatoquadrate cartilage (PQC), which is a massive, sturdy skeletal piece, closely connected to the neurocranium and spaced from the nasal capsule by a blunt notch, called the palatal fossa (FT). The lower part of the first branchial arch is represented by the mandibular cartilage, or Meckel's cartilage (MKC); this too is a robust, sinuous skeletal piece, with its ascending branch reinforced by a robust, almost vertical process, the hyal process (HPM), which continues upwards until it reaches the joint line with the palatoquadrate. The palatoquadrate cartilage is antero-posteriorly longer than the mandibular cartilage. Posteriorly and dorsally, the palatoquadrate includes a robust cartilage crest, the hyal process (HPPQ), which continues downwards after crossing the rhyme of the palatoquadrate/mandible joint and with the similar process located on the ascending branch of the mandible (HPM). The mandibular cartilage is a remarkably robust segment, with increased thickness from front to back.

The articulation between the palatoquadrate and mandible is complex, composed of two parts: the anterior one is composed of a madibular condyle (MC) which is tightened with a corresponding cocket in the lower face of the palatoquadrate; the posterior part consists of a slot of the superior margin of the ascending branch of the mandible where the hyal process of the palatoquadrate fits.

Thin cartilage with an almost filamentous yet robust and sinuous appearance, connects the anterior part of the palatoquadrate to the mandible, at the level of the palatine fossa, bridging the gap in the mouth: the dorsal labial cartilage (DLC). Of the second branchial arch, observation only included: (i) the hyomandibula (HYM), placed immediately behind the palatoquadrate-mandibular joint, and shaped like a dorsoventral elongated cartilage; and (ii) the ceratohyoid (CTY), located immediately below the angle of the mandible and shaped like a slender half-moon-shaped cartilage. In our specimen no traces of cartilagineous rays supporting gill septa seem to be preserved (even in living species the presence of gill-rays is extremely variable, as demonstrated by Daniel, 1914).

The lower edge of the palatoquadrate cartilage and the upper edge of the mandible feature many teeth which are placed inside superficial furrows. Unfortunately, in our specimen almost all the teeth have detached from their natural position and have undergone, even if minimal, translations. Moreover, many teeth may have been lost perhaps during the preparation of the delicate fossil (Fig. 4A), though many are still preserved and give an acceptable description of the characters of the teeth of this heterodont shark.

The teeth are characteristically heterodont and at least three dental types with very distinct morphologies were identified: the anterior, lateral and posterior teeth. Fossil remains of the symphyseal teeth (with characteristic bilateral symmetry of the crown and root) are apparently missing. Anterior teeth are rather small, higher than wide, and range from 0.9 to 1.2 mm in height. Their crown is unicuspid and the cusp is elongated, tapered, sinuous, almost needle-like and strongly curved distally. The root is massive, expanded, semicircular in shape apparently without vascular holes or channels (Figs. 4B and C). The lateral teeth, placed in the arch between the anterior and posterior ones, are considerably more voluminous, with a triangular and erect main cusp and two lateral cusplets, which are joined at the base of the main cusp and converge slightly towards it. The height of the

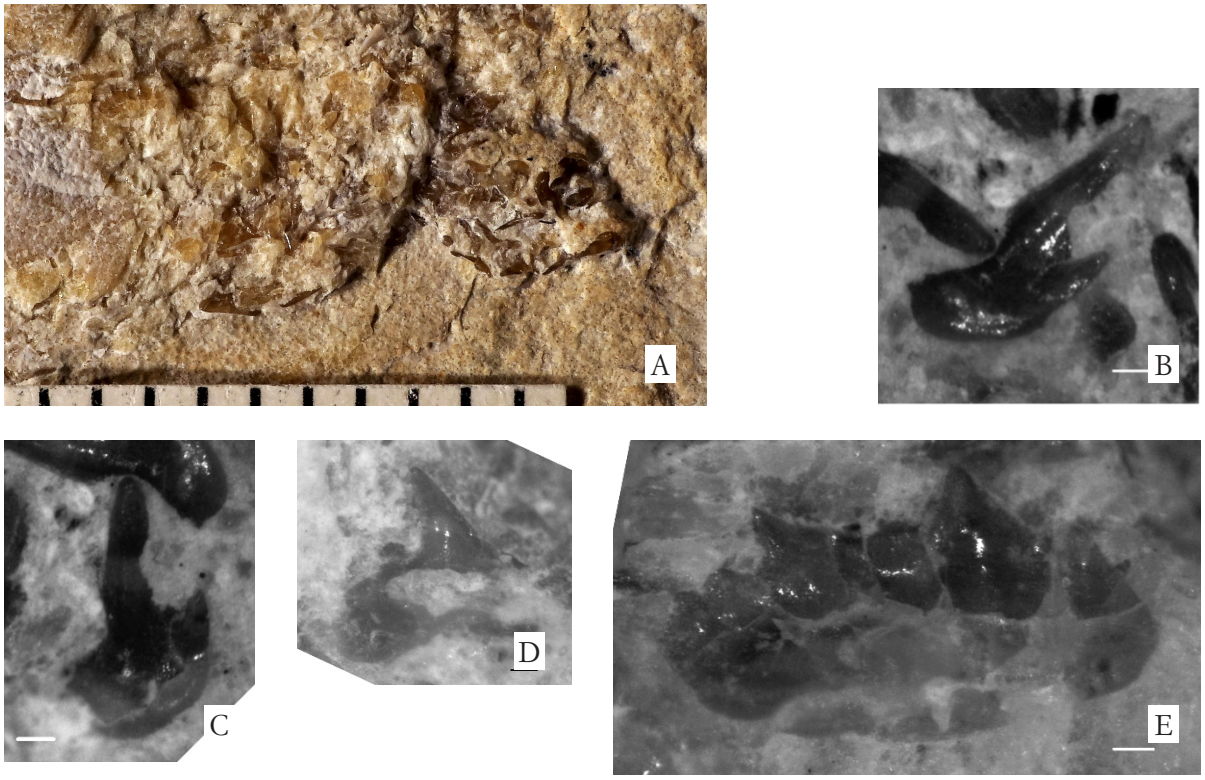


Figure 4. *Libanoheterodontus costae* gen. et sp. nov., region of the mouth with the remains of the dentition; A: a single tooth remained in place, but small translations occurred due to initial taphonomic phenomena (millimeter scale); B and C: two lower anterior teeth, monocuspid, with semicircular root and almost needle-like crown, curved with distal concavity; D: a lateral (median) tooth with a characteristic crown with a central V-shaped cusp and two minor lateral cusplets (the lingual root shown the vascular opening); E: a posterior molariform tooth with 6 cusplets: note the densely serrated distal edge of the distal cusplet (the lingual root shown the vascular opening and canals). Metric scale = 1 mm.

main cusp is significantly greater than that of the lateral cusplets. These teeth have a variable length between 1.0 and 1.3 mm and a variable height between approximately 0.9 and 1.3 mm. The crown has a triangular shape, with a slightly convex mesial margin and a slightly concave distal margin. The root is wide, expanded and has a large vascular opening in its center, the medio-lingual foramen (Fig. 4D), and as a whole the root is V-shaped with a bulbous root-lobe junction. Finally, the posterior teeth are larger than the anterior and lateral ones and they are wider than their height. They range between 1.5 to 1.9 mm in length, and 0.8 to 0.9 mm in height. They are molariform-like teeth, which show a number of sharp cusplets ranging between 6 to 7 and are different from each other, both in general morphology and in height with respect to the collar. The general shape of these cusplets is approximately triangular, with a very pointed apex and with approximately straight or convex walls, while only the mesial profile of the more mesial cusplet appears slightly concave. The distal edge of the most distal cusplet is finely serrated (Fig. 4E), while the highest cusplet is the second followed by the fourth. The root is more expanded than the crown and the line of the dental collar is well defined, undermined, and sinuous. The root, positioned in the center of its labial face, is pierced by a large foramen, which appears to be connected to two other foramina which are observed in the labial face of the root (Fig. 4E). As regards the topographical distribution of the heterodonty, the morphological transition between anterior, lateral and posterior teeth is nearly continuous, and this progressive change is partially illustrated in Fig. 5.

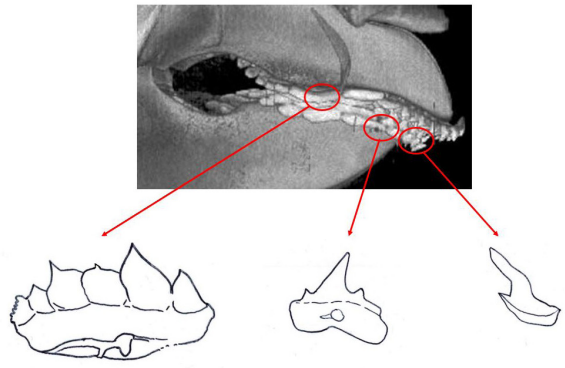


Figure 5. *Libanoheterodontus costae* gen. et sp. nov. Diagram showing the topographical variations of heterodonty.

The vertebral column is composed of 83 vertebral bodies: 48 of which are pre-caudals and 35 caudals. Vertebrae from 16th to 18th support the base of the anterior spine of the first dorsal fin, while those from 40th to 42th support the base of the anterior spine to the second dorsal fin. The first vertebra in the column is connected by the occipital condyles of the cranium (Fig. 3B), and the second through to the eighth vertebrae have well developed ribs growing from their basiventrals. In fact, it is very likely that a number of later vertebrae also have ribs, but the dense and thick coating of dermal denticles prevents the axial skeleton from being seen in this area (immediately above the pectoral fin). The visible ribs are stocky and short, slightly arched with posterior concavity, very short and with a pointed apex.
In the anterior section, and up to the height of the first dorsal fin, the vertebral bodies have an almost quadrangular profile, with a length approximately equal to their height; posteriorly they have a more rectangular profile, being taller than long. Each vertebral metamer consists of a strong centrum upon which a large interdorsal (intercalary) platerests, which is wedge-shaped between the apophyses that make up the neural arches. In the posterior portion of the vertebral column, behind the first dorsal fin, the sequence of neural arches/inderdorsal plates is tightened, and the cartilaginous pieces are closely attached to each other, so as to constitute a continuous neural cord, leaning against the dorsal margin of the sequence of the vertebral centers (see Fig. 7C). Haemapophyses become evident only starting from the caudal pedicel (see Fig. 7D).
The pectoral fin is wide, expanded, with a softly rounded margin, 30 mm long and 21 mm high, with a uni-lobed shape and with a semi-elliptical inferior and posterior profile. The pectoral fin originates close to the skull, immediately behind the skeletal elements pertaining to the gill arches, and ends approximately in correspondence to the beginning of the first dorsal fin. Its surface is completely covered by the tesserae of the skin denticles; at the base of the fin, in its anterior part, the skin covering is raised due to the presumable presence of the cartilaginous pieces that make up the skeleton of the pectoral girdle which, however, are not visible.
The pelvic fin is small, 21 mm long and 11 mm high. It develops approximately in correspondence to the middle between the two dorsal fins: it begins at the rear of the first dorsal fin and ends approximately at the beginning of the second dorsal fin. At the anterior margin of the base of the pelvic fin there is a skeletal element in the shape of a thin, slender bar, arranged in a longitudinal direction, which corresponds to the basal cartilage of the pelvic girdle (basipterygium). Also this fin appears completely covered by a thick layer of denticles which prevents a view of the underlying radials.
The two dorsal fins are characteristic of the heterodonts and, as we have seen, they are both preceded by a strong anterior spine, which connects directly to the neural arches of the corresponding vertebrae. An observation under the stereo-microscope of both the anterior spines of the dorsal fins revealed that these spines have an absolutely compact structure; no trace of vascular channels is present at their base nor in their internal structure, as far as the natural rupture lines go (Figs. 6A and B). Therefore, these spines are shown to be made up of completely calcified and completely avascular cartilage. The first dorsal fin begins approximately at the end of the pectoral fin, while the second is placed in correspondence to the joint between the pelvic fin and the anal fin. The first dorsal fin is constituted by a large anterior spine, overall 24 mm high and 8 mmwide at its base, and protrudes about 15 mm on its anterior side from the dorsal cutaneous margin of the fish, and about 9 mm on the posterior side (Fig. 6A). The spine is followed by a skin flap, completely covered with dermal denticles of a near triangular shape, thus projecting the spine backwards for about 12 mm. No cartilage elements are visible between the anterior spine and the soft part of the fin (basal pieces), as the area is covered by the skin denticles. The second dorsal fin is smaller: the spine is 21 mm high and about 6 mm wide at its base and protrudes about 12 mm on its anterior side from the dorsal cutaneous margin of the fish, and about 7 mm on the posterior side (Fig. 6B). This spine is followed by a cutaneous flap, completely covered by dermal denticles, triangular in shape, which extends to form the dorsal profile of the fish, projecting the spine backwards for about 10 mm. Also in this case, no cartilage elements are visibly leaning against the posterior margin of the spine (basal pieces), as the area is covered by dense skin denticles.
Finally, the anal fin is a soft structure with a clearly triangular profile. It is completely covered by a thick layer of dermal denticles which appears reinforced along the anterior margin, so as to form a sort of robust fold, thicker towards the base, covered by robust and large denticles, which tapers below (Fig. 6C). The posterior margin, on the other hand, appears blurred, covered by more slender and minute denticles. The anal fin develops in the region placed posteriorly at the end of the second dorsal fin, and has an overall length of 17 mm and a height of 7 mm approximately.
The tail fin is characteristically bilobed. The lower lobe is completely ventral and develops as a gently rounded margin fold, while the superior lobe receives the last codal vertebrae. The supporting skeleton of the tail fin is represented by the ventrally prolonged haemal arches, but no trace of any cartilaginous extensions of these haemal arches is visible, since the covering of cutaneous denticles is continuous and thick also in this area, so as to give the tail fin a homogeneous appearance.

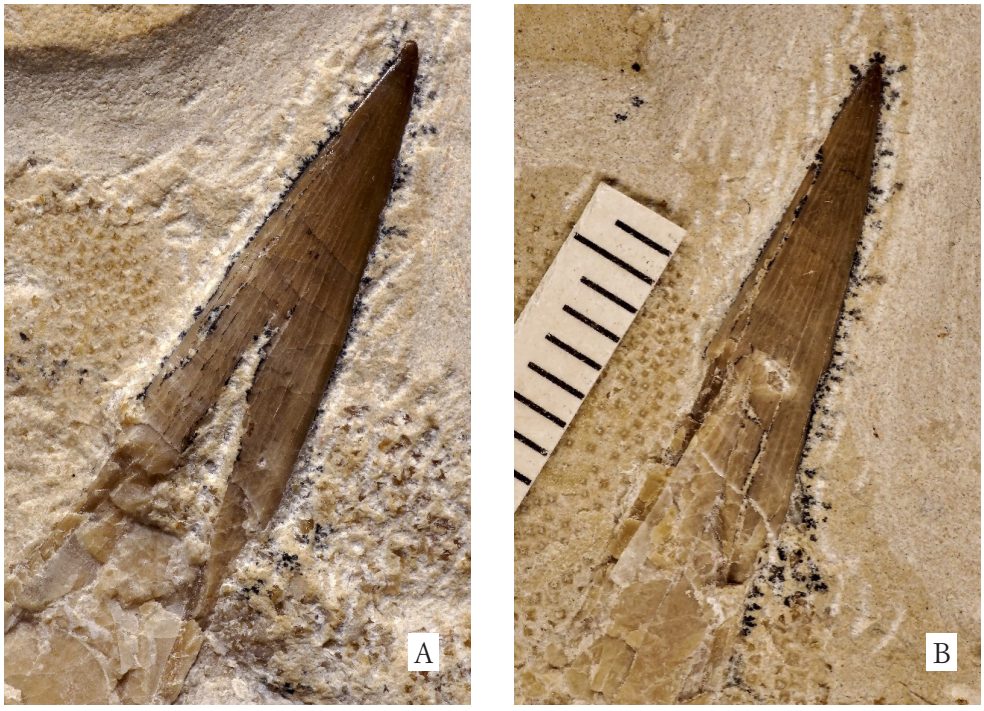
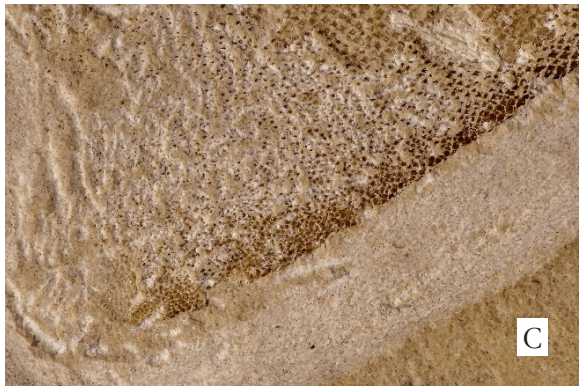


Figure 6. *Libanoheterodontus costae* gen. et sp. nov., holotype. A: anterior spine of the first dorsal fin; B: anterior spine of the second dorsal fin; C: anterior margin of the anal fin.

The external covering is completely made up of cutaneous denticles, called tesserae, which vary in shape and size depending on their position on the body of fish. The tesserae have mostly a rhomboid shape, and the larger ones correspond to the soft area above the visceral cavity (Fig. 7A). Tesserae of smaller dimensions, but with the same profile, cover the cephalic region (Fig. 6B), and also those that cover the skin in the region immediately anterior to the anal fin, though slightly smaller in size, but equally rhomboid in shape (Fig. 7C). Finally, the tesserae that cover the fins are rhomboid and of variable dimensions (Fig. 7D), while the tesserae that form a sort of dorsal keel and are located at the dorsal edge of the fish have a completely different morphology: they are larger, with a polygonal profile, equipped with numerous acute, almost thorny edges, and partially overlap each other (Fig. 7E). This dorsal keel is interrupted by two anterior spines of the two dorsal fins, which emerge from the dorsal profile of the fish, and are preceded and followed by skin folds, that constitute the body of the dorsal fins and are covered with more minute tesserae, but always with a rhomboid profile (see Figs. 6A and B).



Observations and comparisons

From a taxonomic point of view, as well as on the basis of the presence of two dorsal fins both preceded by robust spines, and of a marked heterodonty, with sharp-crowned anterior teeth and molariform posterior teeth, I assigned the described specimen to the family Heterodontidae. In addition, the characters that led us to attribute the described specimen to a genus very close to the genus *Heterodontus* are the following: (i) the dental characters, with particular regard to the morphology of both the anterior teeth (with a sharp crown) and of the posterior ones (molariform, but with cusplet still preserved and well evident); (ii) the morphology, position and extension of the fins, both of the even ones (paddlelike) and of the uneven ones, both of the dorsal ones, which cover the base of the anterior spines, and of the anal (characteristically heterocercial), whose tip is an undifferentiated (fused) mass; (iii) the anterior spines of the two dorsal fins are constituted by completely avascular calcified cartilage. In particular, as reported in the diagnosis of the new genus, this specimen is the only representative, both

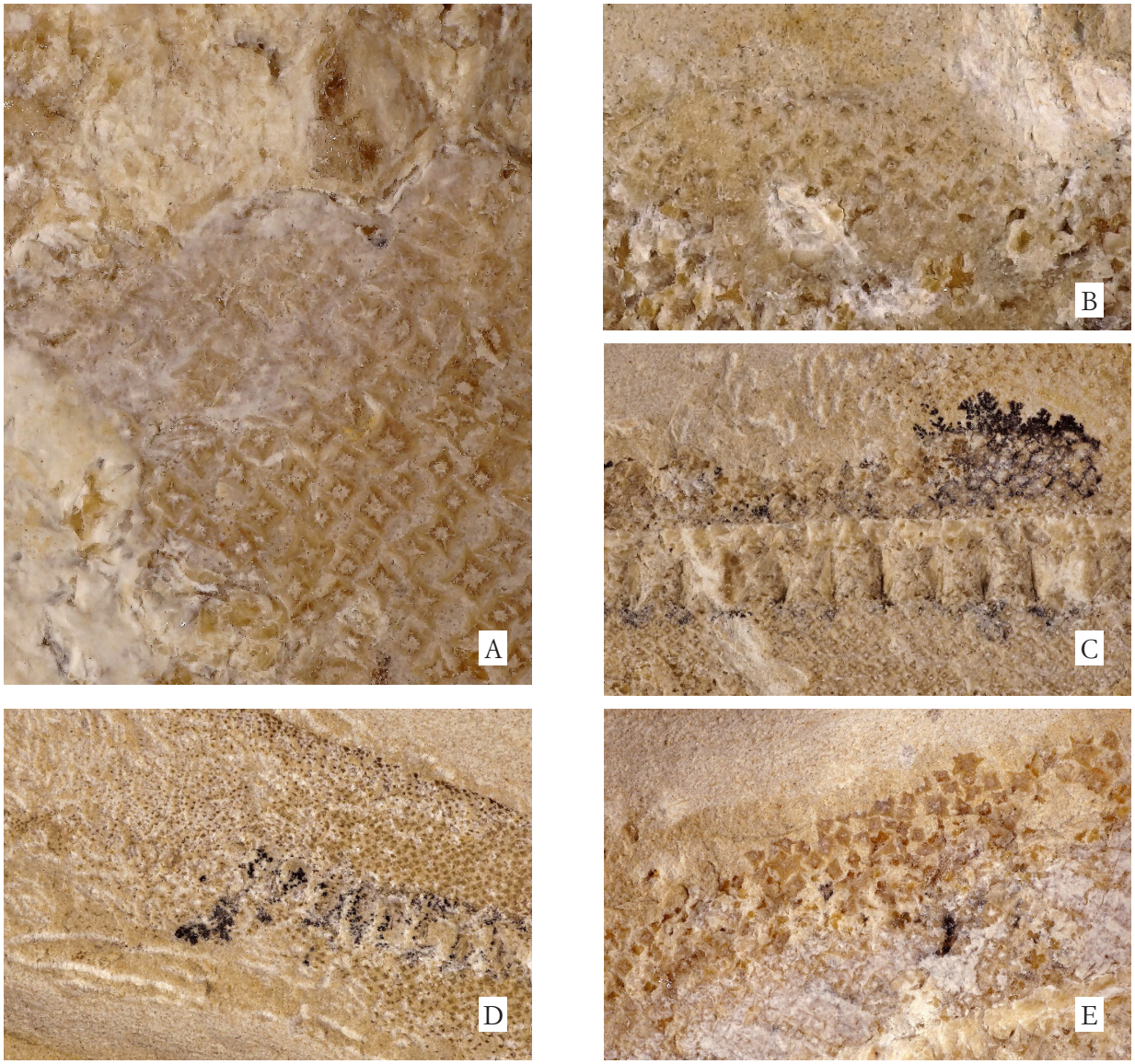


Figure 7. *Libanoheterodontus costae* gen. et sp. nov., holotype. Skin lining. A: cutaneous denticles in the region overlying the visceral cavity, just below the vertebral column; B: cutaneous denticles in the cephalic region overlying the palatoquadrate/mandibular joint area; C: cutaneous denticles in the region of the body at the level of the anal fin, just behind the second dorsal fin; D: cutaneous denticles in the region of the base of the upper lobe of the caudal fin; E: cutaneous denticles of the dorsal keel in the stretch between the two dorsal fins.

living and fossil, of the family Heterodontidae to possess anterior teeth with a unicuspid crown, of styliform morphology, almost needle-like, curved distally, supported by a wide root semilunar in appearance and apparently devoid of openings and vascular channels. We will recall how the absence of vascular channels, according to the large comparative studies carried out by Casier (1947; 1961) refer to teeth immersed in gums and vascularized through the dense gingival vascular network. Unfortunately, in our specimen no teeth referable to elements of the siphysis region are preserved. All this led us to suppose that the anterior teeth with a styliform crown were implanted very anteriorly and could potentially be mobile and prehensile. This conforms to both the morphology of the lower part of the root (softly and completely rounded), and to the absence of vascular foramina (which indicate their total immersion in the soft gingival tissues). Overall, the heterodonty demonstrated in the new genus described here could fit within the heterodontic shark teething model that Hovestadt (2018) called "Morphotype 1", and which is the same model that Reif (1976) called "portusjacksoni- type", with three distinct dental types, in addition to symphyseal teeth.

The Heterodontiformes were already present in the Jurassic, and the genera *Heterodontus* and *Proheterodontus* were already present in the Lower Jurassic, as demonstrated by Eastman (1914), Meisey (1982), and Kriwet & Klug (2004).
The following fossil genera and species belonging to the Cretaceous and to the family Heterodontiformae which have been described up to now, are mainly based on a few teeth or very often a single tooth: *Acrodus cretaceous*, *Acrodus emmonsi*, *Acrodus humilis*, *Acrodus polydyctios*, *Acrodus rugosus*, *Cestracion canaliculatus*, *Cestracion falcifer*, *Cestracion sulcatus*, *Cestracion upnikensis*, *Ginglymostoma lithuanica*, *Gonphodus agassizi*, *Heterodontus boussioni*, *Heterodontus carerens*, *Heterodontus creamridgensis*, *Heterodontus granti*, *Heterodontus havreensis*, *Heterodontus laevis*, *Heterodontus lepagei*, *Heterodontus lonzeensis*, *Heterodontus maisierensis*, *Heterodontus paucicarinata*, *Heterodontus polonicus*, *Heterodontus tuberculatus*, *Paracestracion pectinatus*, *Platyacrodus unicus*. However, the accurate revision recently carried out by Hovestadt (2018) mainly demonstrated that almost all of the species cited need a thorough systematic revision and moreover many of them are certainly not valid from a taxonomic point of view. Moreover, of the seven genera cited in literature for the Cretaceous, only the following two remain valid: *Heterodontus* and *Proheterodontus*, having all the others fallen into the synonymy of these two.
The vascularization of the roots of the lateral teeth in *Libanoheterodontus* is of the hemiaula corhizian type, i.e. it corresponds to the hemiaulacorhizid root type described by Casier (1947), such as the V-shaped root with a bulbous root-lobe junction. This trait brings the new genus *Libanoheterodontus* closer to the genus *Heterodontus*. To distinguish the new genus with respect to both *Heterodontus* and to *Proheteroduntus*, however, the following relevant charactersremain: (i) the absolutely peculiar morphology of the anterior teeth, and (ii) the multicuspid morphology of the posterior teeth. This combination of dental traits is absolutely characteristic of the new genus *Libanoheterodontus*.

Conclusion

Libanoheterodontus costae gen. et sp. nov., represents a new extinct bullhead shark which, due to its dental and skeletal characters, certainly belongs to the family Heterodontidae. The presence of some very peculiar and completely unpublished dental characters justifies the establishment of the new genus: (i) styliform anterior teeth, equipped with a semilunar root without openings or vascular canals and (ii) molariform, multicuspid posterior teeth, with the presence of serration on the more distal cusp. In addition to these dental characters, on which the taxonomy of fossil heterodontes is largely based, the specimen described here also shows some skeletal and covering features of cutaneous denticles that are quite rare for most of the genera and fossil species: (i) hymandibula that takes part at the joint between palatoquadrate and mandible, (ii) small and semilunar ceratohyoid cartilage, (iii) dorsal fin spines composed of completely avascular calcified cartilage, (iv) skin denticle lining composed of monomorphic tesserae with a rhomboid profile, (v) dorsal keel composed of polygonal profile tesserae, equipped with multiple spines which overlap one another.
Libanoheterodontus costae gen. et sp. nov. demonstrates its most stringent anatomical affinities with the genus *Heterodontus*, to which both the total avascularization of the spines of the dorsal fins, as well as the structure of the roots of the lateral teeth are united, which possess a vascularization of the hemiaula corhizian type.
Libanoheterodontus costae gen. et sp. nov., is a small species that probably lived in a benthic environment. It represents the first report of bullhead sharks in the marine Cenomanian of Lebanon, demonstrating the absolute rarity of these fish within the very rich Cenomanian ichthyofauna of the Sannine limestone of Central Lebanon. In fact, during the last four centuries of palaeontological excavations in the region, no remains of heterodontes had been reported, not even in the form of teeth or above all of spines of the dorsal fins, which also represent very robust, extremely characteristic and easy to determine fossils.
Finally, the new genus *Libanoheterodontus* enriches the very scarce biodiversity of the Heterodontiformes during the Cretaceous, flanking the only two known genera, *Heterodontus* and *Proheterodontus*, which represent the bullhead sharks of the Cretaceous.

Acknowledgements

The author thanks Donatella and Luciano Lullo, who took the photographs illustrating this article. Moreover, the author thanks Prof. Ruggero D'Anastasio who took the photos of the teeth of the specimen described in this article, using a stereomicroscope.

REFERENCES

Capasso L., 2017. The history and the situation of the world famous fossil fish quarries in Lebanon. *Bollettino del Museo Civico di Storia Naturale di Verona (Geologia, Paleontologia, Preistoria)* 41: 53-76.

Casier E., 1947. Constitution et evolution de la racine dentaire des Elasmobranchii II. Étude comparative des types. *Bulletin de l'Institut royal des Sciences naturelle de Belgique* 23(14): 1-28.

Casier E., 1961. Trasformations des systèmes de fixation et de vascularisation dentaire dans l'évolution des sélaciens du sous-ordre de Squaliformes. *Bulletin de l'Institut royal des Sciences naturelle de Belgique* 65(2): 1-61.

CIAMPAGALIO C.N., CICIMURRI D.J., EBERSOLE J.A., RUNYON K.E., 2013. A Note on Late Cretaceous Fish Taxa Recovered from Stream Gravels at Site AGr-43 in Greene County, Alabama. *Bulletin of the Alabama Museum of Natural History* 31(1): 84-97.

DANIEL J.F., 1914. The anatomy of *Heterofontus francisci*: 1 – The exoskeleton. *University of California Publications, Zoology* 13: 147-186.

DANIEL J.F., 1915. The anatomy of *Heterofontus francisci*: 2 – The endoskeleton. *University of California Publications, Zoology* 14: 447-493.

EASTMAN C.R., 1914. Catalog of the fossil fishes in the Carnegie Museum, Part IV. *Memoires of the Carnegie Museum* 6: 389-449.

HOVESTADT D.C., 2018. Reassessment and revision of the Heterodontidae (Chondrichthyes: Neoselachii) based on tooth morphology of extant taxa. *Palaeontos* 30: 1-73.

KRIWET J., 2008. A new species of extinct bullhead sharks, *Paracestracion viohli* sp. nov. (Neoselachii, Heterodontiformes), from the Upper Jurassic of South Germany. *Acta Geologica Polonica* 58: 235-241.

KRIWET J., KLUG S., 2004. Late Jurassic selachians (Chondrichthyes, Elasmobranchii) from southern Germany: Re-evaluation on taxonomy and diversity. *Zitteliana* A 44: 67-95.

KRIWET J., NUNN E.V., KLUG S., 2009. Neoselachians (Chondrichthyes, Elasmobranchii) from the Lower and Lower Upper Cretaceous of north-eastern Spain. *Zoological Journal of the Linnean Society* 155: 316-347.

MAISEY J.G., NAYLOR G.J.P., WARD D.J., 2004. Mesozoic elasmobranches, neoselachian phylogeny and the rise of modern elasmobranch diversity. In: Arratia G., Tintori A. (eds), *Mesozoic Fishes 3 – Systematics, Paleoenvironments and Biodiversity*: 17-56. Dr. Friedrich Pfeil, Munich.

MEYER R.L., 1974. *Late Cretaceous elasmobranchs from the Mississippi and east Texas embayments of the Gulf Coastal Plain*. Ph.D. Dissertation, Southern Methodist University, Dallas (TX), 419 pp.

NELSON J.S., 2006. *Fishes of the world*. 4th ed., Hoboken, John Wiley & Sons, 610 pp.

REIF W.E., 1976. Morphogenesis, pattern formation and function of the dentition of *Heterodontus* (Selachii). *Zoomorphologie* 83(1): 1-47.

SUMMERS A.P., KETCHAM R.A., ROWE T., 2004. Structure and function of the horn shark (*Heterodontus francisci*) cranium through ontogeny: development of a hard prey specialist. *Journal of Morphology* 260: 1-12.

THIES D., 1983. Jurazeitliche Neoselachier aus Deutschland und S- England. *Courier Forschungsinstitut Senckenberg* 58: 1-117.

UNDERWOOD C.J., 2006. Diversification of the Neoselachii (Chondrichthyes) during the Jurassic and Cretaceous. *Paleobiology* 32: 215-235.

WALLEY C.D., 1997. The Lithostratigraphy of Lebanon: a review. *Lebanese Science Bulletin* 10(1): 1-20.

(ms. pres. 15 gennaio 2023; ult. bozze 15 ottobre 2023)