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New observations on the anatomy and paleobiology of the Eocene requiem shark †*Eogaleus bolcensis* (Carcharhiniformes, Carcharhinidae) from Bolca Lagerstätte, Italy

Nouvelles observations sur l'anatomie et la paléobiologie du requin requiem de l'Éocène †Eogaleus bolcensis *(Carcharhiniformes, Carcharhinidae) du Lagerstätte de Bolca, Italie*

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ABSTRACT

Here we provide new information about the anatomy of the extinct shark †*Eogaleus bolcensis* from the early Eocene Bolca Konservat-Lagerstätte. The combination of morphological and dental characters of the three known articulated specimens and a single isolated tooth collected from the Pesciara and Monte Postale sites (e.g., head bulky with rounded snout, pectoral fins of semiplesodic type, cutting-clutching dentition, dermal denticles shell-shaped and of drag-reducing type, caudal fin accounting for one fourth of the entire body length, 135–153 vertebrae) supports the assignment of †*Eogaleus* to the family Carcharhinidae and allows us to confirm definitively its distinct taxonomic status from the sympatric carcharhiniform, the triakid †*Galeorhinus cuvieri*. Moreover, the analysis of the dermal denticle morphology and the size and maturity age estimates of the studied specimens provide new paleobiological information about †*Eogaleus*, suggesting a close association of this small top predator with the tropical shallow-water marine context hypothesized for the Bolca paleobiotopes.

RÉSUMÉ

De nouvelles informations sont fournies sur l'anatomie du requin disparu †*Eogaleus bolcensis*, du Lagerstätte de Bolca de l'Éocène inférieur. La combinaison des caractères morphologiques et dentaires des trois spécimens articulés connus et d'une unique dent isolée récoltée dans les sites de Pesciara et de Monte Postale (à savoir, tête massive avec museau arrondi, nageoires pectorales de type semiplésodique, dentition agrippante/coupante, denticules dermiques en forme de coquille et de type *drag-reducing*, nageoire caudale atteignant le quart de la longueur totale du corps, 135 à 153 vertèbres) donne du poids à l'attribution

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de †*Eogaleus* à la famille des Carcharhinidae, et nous autorise à confirmer définitivement son statut taxonomique distinct de celui du carcharhiniforme sympatrique, le triakidé †*Galeorhinus cuvieri*. En outre, l'analyse de la morphologie des denticules dermiques et l'estimation de la taille et de l'âge de maturité des spécimens étudiés fournissent de nouvelles informations paléobiologiques sur †*Eogaleus*, suggérant une association étroite de ce petit prédateur avec un environnement tropical marin de faible profondeur, comme le sont supposés les paléobiotopes de Bolca.

1. Introduction

The family Carcharhinidae Jordan & Evermann (1896), whose representatives are commonly known as requiem sharks, is a diverse group of small- to large-sized selachians (possible maximum body length of 7.4 m attained in *Galeocerdo cuvier*) within the order Carcharhiniformes Compagno (1973). These sharks primarily occur in tropical and warm-temperate waters, and are worldwide distributed in coastal and pelagic ecosystems, although some species can enter brackish or freshwaters (Compagno, 1984, 1988; Nelson et al., 2016). Although the phylogenetic relationships within the family remain largely unclear (Cappetta, 2012; but see also Naylor, 1992; Iglésias et al., 2005; etc.), several authors have recognized a set of morphological characters that are useful to distinguish requiem sharks from other carcharhiniforms, including well-developed nictitating membranes, last gills open above the base of the pectoral fins, caudal pits, absence of oro-nasal grooves, intestine with scroll valve but lacking a spiral valve, strongly asterospondylic vertebrae with secondary calcification in the shape of a Maltese cross, and shell-shaped dermal denticles of drag-reducing type (Cappetta, 2012; Compagno, 1988; Nelson et al., 2016; Reif, 1985; White, 1938). This family currently includes about 70 species in 12 living and at least eight fossil genera dating back to the Early Cretaceous (Cappetta, 2012; Guinot et al., 2014). However, the fossil record of Carcharhinidae is almost entirely represented by isolated teeth predominantly recovered in Cenozoic deposits in the North Hemisphere (e.g., Adnet et al., 2010; Cappetta, 2012; Cappetta and Case, 2016; Noubhani and Cappetta, 1997), although occurrences have been recently reported also in South America (e.g., Landini et al., 2017; Staig et al., 2015). So far, the only carcharhinid taxon represented by complete and articulated specimens is †*Eogaleus bolcensis* Cappetta (1975) recovered from the Ypresian (early Eocene) fossil fish-bearing strata of the Bolca Lagerstätte, one of the few Paleogene deposits in which chondrichthyans are exquisitely preserved. Although several recent studies contributed to our knowledge of the extraordinary paleobiodiversity and evolutionary significance of this deposit, with more than 230 described teleost species (e.g., Bannikov, 2004, 2006, 2008; Bannikov and Carnevale, 2009, 2010, 2016; Blot, 1969; Blot and Tyler, 1990; Carnevale and Pietsch, 2009, 2010, 2011, 2012; Carnevale et al., 2014, 2017; Marramà and Carnevale, 2017a, 2017b; Marramà et al., 2016a, 2016b; Monsch, 2006; Tyler and Santini, 2002), the cartilaginous fishes of Bolca have received only little attention so far (see Marramà et al., 2017a, 2017b, 2017c). Sharks from the Bolca Lagerstätte are mentioned in the literature at least since the end of the XVIII century (Volta, 1796) and are currently represented, besides †*Eogaleus bolcensis*, by several articulated skeletons of the triakid †*Galeorhinus cuvieri* (Agassiz, 1835) and by isolated teeth of the odontaspidid †*Brachycarcharias lerichei* (Casier, 1946) (Cappetta, 1975; Fanti et al., 2016; Marramà et al., 2017b, 2017c).

The goal of this paper is to provide new information about the anatomy of the requiem shark, †*Eogaleus bolcensis*. Such a revisionary analysis is necessary in order to conclusively exclude Applegate's (1978) hypothesis, who regarded it as a synonym of †*G. cuvieri* (see "Remarks" section). Moreover, new analyses of size and age estimation, as well as the study of dermal denticles provide new insights into the paleobiology and paleoecology of this Paleogene requiem shark.

2. Geological setting

The examined material comes from the early Eocene Bolca Konservat-Lagerstätte, which is located in Verona Province, northeastern Italy (Fig. 1). The preservational quality and lithological features of the slabs containing specimens MCSNV T.311, MCSNV T.414/T415 and MGP-PD 8869 C/8870 C are consistent with the lithology of the fish-bearing strata of the Pesciara site, whereas MCSNV VII.B.94 has been extracted from the strata of the Monte Postale site as previously suggested by Jaekel (1894) and Cappetta (1975).

The fossiliferous layers of the Pesciara site have been traditionally referred to the so-called 'Calcari Nummulitici', an informal unit of Eocene age widely distributed in northeastern Italy (Papazzoni and Trevisani, 2006). This succession consists of a cyclic alternation of about 20 meters of finely laminated micritic limestones (containing exquisitely preserved fishes, plants and invertebrates) and coarse-grained biocalcarenite/biocalcirudite with a rich benthic fauna. Based on their larger benthic foraminiferan content, the fish-bearing limestones of the Pesciara site were referred to the †*Alveolina dainelli* Zone, corresponding to the late Cuisian (late Ypresian, about 49 Ma; Papazzoni and Trevisani, 2006; Papazzoni et al., 2014). The results of a recent quantitative paleoecological analysis by Marramà et al. (2016c) suggested that the Pesciara fish assemblage was characterized by a sharp oligarchic structure dominated by zooplanktivorous fishes (mostly clupeoids), whereas the taphonomic features suggest that the
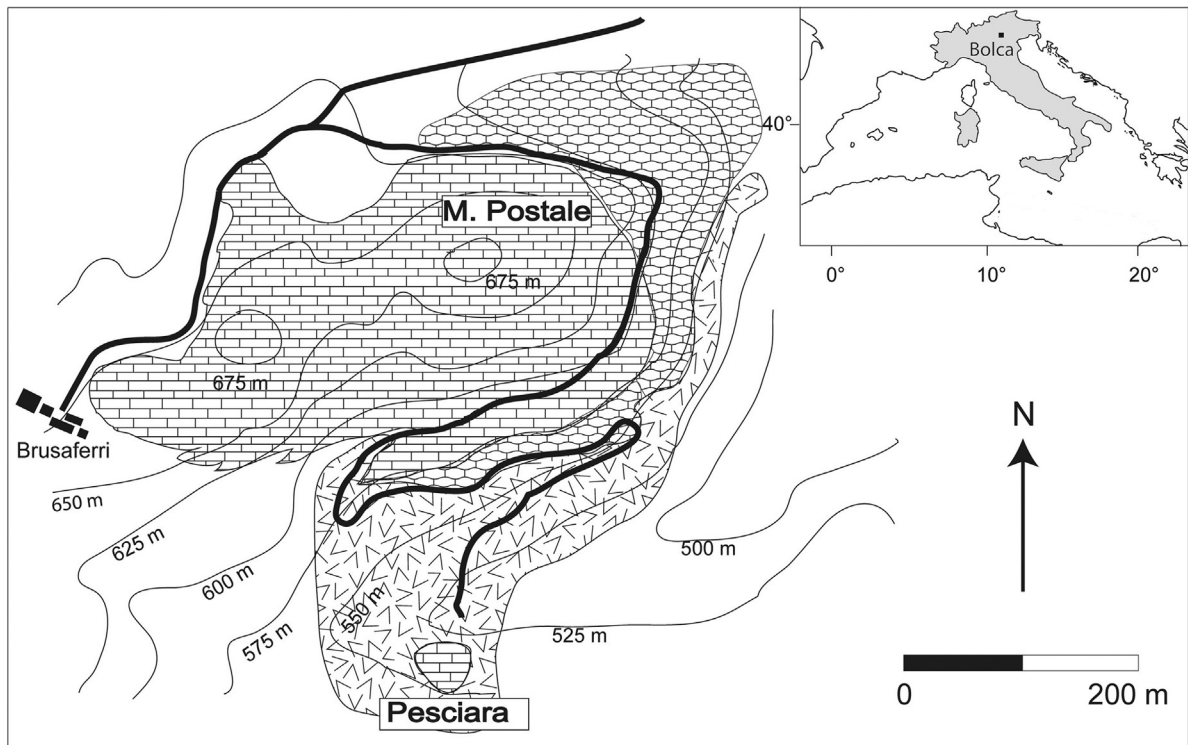
Fig. 1. Location and geological map of the Bolca area showing the Pesciara and Monte Postale sites of Ypresian age where †*Eogaleus bolcensis* Cappetta (1975) has been found.

Fig. 1. Carte géologique et de localisation de la zone de Bolca, montrant les sites de Pesciara et de Monte Postale d'âge Yprésien où a été trouvé † *Eogaleus bolcensis* Cappetta (1975). Modifié selon Marramà et al. (2016c).

Modified from Marramà et al. (2016c).

fossiliferous sediments accumulated in a shallow intraplatform basin in which anoxic conditions and the development of a biofilm at the bottom promoted the high-quality preservation of the fossils (see also Papazzoni and Trevisani, 2006).

The Monte Postale site is located about 300 m north of the better known Pesciara site, and exhibits similar age and sedimentological features, mostly comprising finely laminated micritic limestones with fish and plant remains. Papazzoni et al. (2017) recently investigated the stratigraphical relationships between the two fossiliferous deposits, suggesting that the uppermost strata of the Monte Postale should correlate with those of the Pesciara site, although the fossiliferous laminites of Pesciara appear to be slightly younger. The Monte Postale succession includes the Cretaceous Scaglia Rossa Formation up to Ypresian fossiliferous limestone, containing larger benthic foraminifera of the genus †*Alveolina* and also marine and brackish molluscs in its uppermost part (Papazzoni et al., 2014). Solid evidence of a coralgal rim, lagoonal deposits, and a fore-reef system was detected for the Monte Postale paleobiotope (Vescogni et al., 2016); this interpretation was also supported by recent paleoecological and taphonomic studies of the Monte Postale fish assemblage based on the abundance of marine and terrestrial plants, the large number of invertebrates (including abundant corals), and reef-associated fishes (Marramà et al., 2016c).

Disarticulation of fish skeletons, unimodal dispersion of the elements and bioturbation were the result of at least periodic oxic bottom conditions (Marramà et al., 2016c).

3. Material and methods

The present study is based on the three articulated specimens formerly studied by Cappetta (1975) and on new material represented by a single tooth. Specimens are housed in the collections of the Museo Civico di Storia Naturale di Verona (MCSNV) and Museo di Geologia e Paleontologia dell'Università degli Studi di Padova (MGP-PD). The articulated specimens MCSNV VII.B.94 and MGP-PD 8869 C/8870 C were examined under UV light to distinguish preserved soft tissues from grout or pigments traditionally used in the ancient restorations of the fossil fishes. Measurements of the specimens were taken to the nearest 0.1 cm and the total length (TL; from the anterior tip of the snout to the posteriormost tip of the caudal fin) is used throughout. The dermal denticles of MCSNV VII.B.94 were examined and photographed with a Scanning Electron Microscope (SEM) Jeol 6400 at the University of Vienna. Osteological and tooth terminology follows Cappetta (1975, 2012), Reif (1985), Compagno (1988) and Herman et al. (2003). Morphometric terminology follows Cappetta (1975).

The ratio between the ridge spacing on dermal denticles and their crown width is used here to hypothesize the possible paleoecology of †*Eogaleus* follows Reif (1985). The von Bertalanffy growth equation is employed to calculate the estimate age for the three specimens following the methods applied to living and fossil chondrichthyans (Allen, 1966; Chen et al., 1992; Fanti et al., 2016). The paleobiological implications of the age estimates for †*E. bolcensis* are not directly based on the absolute numerical value; they rather are based on the comparison of these values with the age at maturity of living species, in order to predict if the fossil specimens might represent sexually mature or immature individuals.

4. Systematic palaeontology

Class Chondrichthyes Huxley (1880)
Subclass Elasmobranchii Bonaparte (1838)
Order Carcharhiniformes Compagno (1973)
Family Carcharhinidae Jordan & Evermann (1896)
Genus †***Eogaleus*** Cappetta (1975)

4.1. Type species

†*Eogaleus bolcensis* Cappetta (1975).

4.2. Diagnosis

(Emended). A carcharhinid shark with bulky head and short, broad and rounded snout, not pointed or triangular; preoral length much smaller than mouth width; first dorsal fin located in front of the mid-length of the body; its base equidistant from pectoral- and pelvic-fin bases; height of first dorsal fin roughly equals the length of its base; posterior margin of first dorsal fin located well anterior to pelvic-fin insertion; second dorsal fin well-developed and inserting close to anal-fin origin and about 2/3 as high as the first dorsal fin; pectoral fin almost equals the size of first dorsal fin and containing about 18–19 radials; postero-ventral margin of caudal fin deeply incised; 135–153 vertebrae of which 50–55 monospondylous precaudal, 25–35 diplospondylous precaudals, and 60–65 caudals; gradient monognathic and marked dignathic heterodonty; about 15 tooth files per half jaw in both jaws (total row count 30/30); teeth small, not exceeding 12 mm in total height; distal cusplets on lower and upper jaw teeth; lower anterior teeth with weakly mesio-distally expanded crown and a high central cusp, slightly bent lingually; labial face strongly convex, overhanging labial face of root by a distinct bulge; distal heels of lower lateral teeth bearing up to four cusplets; teeth with marked sigmoid profile and strongly convex lingual face of cusp; upper teeth with comparatively higher and wider crown and root; distal heel high and oblique, bearing one to four strong cusplets; basal edge of root broad, not rectilinear, with a distinct and deep nutritive furrow; dermal denticles on pectoral fins rounded or subrhombic, relatively small and not ornamented; rhombic placoid scales of trunk and caudal fin bearing 5–6 prominent longitudinal ridges with ectodermal pits along their posterior edge.

4.3. Remarks

The genus †*Eogaleus* was created by Cappetta (1975) to accommodate three articulated specimens, MCSNV T.331 (holotype), MCSNV VII.B.94 and MGP-PD 8869 C/8870 C, because of their evident differences with the other carcharhiniform shark from Bolca, the triakid †*Galeorhinus cuvieri*, in body proportions, and tooth and denticle size and morphology (Cappetta, 1987, 2012; Fanti et al., 2016). Nevertheless, Applegate (1978) regarded †*G. cuvieri* as a conspecific of †*E. bolcensis* and referred both to †*Alopiopsis*. The taxon †*Alopiopsis plejodon* was created by Lioy (1865) based on a single specimen deposited in Vicenza, Italy. The diagnosis and descriptions of this taxon provided by Lioy (1865) and later by de Zigno (1874) included a total length of more than 150 cm, probably about 200 vertebrae, caudal fin about one third of the total length, and teeth defined as "completely filled inside" probably referring to the absence of a pulp cavity and therefore to the osteodont type. In any case, this set of characters does not fit with the morphological features of the three specimens of †*Eogaleus* (see Description and Discussion). Unfortunately, the holotype of †*A. plejodon* was destroyed during the Second World War (Blot, 1980; Cappetta, 1975) and the original illustrations of Lioy (1865) are unclear and difficult to interpret, making its validity and taxonomic affinities impossible to define [see Cappetta (1975) for a more detailed taxonomic history of the taxon †*Alopiopsis plejodon* Lioy (1865)]. Consequently, this taxon should be considered as *nomen dubium*.

4.4. Included species

Type species only.
†*Eogaleus bolcensis* Cappetta (1975)
(Figs. 2–9)
†*Alopiopsis plejodon* Lioy (1865): Jaekel (1894): p. 171, pl. 8
†*Eogaleus bolcensis* Cappetta (1975): p. 282, figs. 2–4, pls. 1–4 (original occurrence of name and photographs)
†*Alopiopsis plejodon* Lioy (1865): Applegate (1978): p. 55
†*Eogaleus bolcensis* Cappetta (1975); Blot (1980): p. 343
†*Eogaleus bolcensis* Cappetta (1975); Cappetta (1987): p. 122, fig. 104
†*Eogaleus bolcensis* Cappetta (1975); Frickhinger (1991): p. 185
†*Eogaleus bolcensis* Cappetta (1975); Cappetta (2012): p. 310, fig. 294
†*Eogaleus bolcensis* Cappetta (1975); Carnevale et al. (2014): p. 41
†*Eogaleus bolcensis* Cappetta (1975); Fanti et al. (2016): p. 8
†*Eogaleus bolcensis* Cappetta (1975); Marramà et al. (2017c): p. 1

4.5. Holotype

MCSNV T.331, nearly completely articulated specimen, 121.6 cm TL, Pesciara site (Fig. 2A)

Fig. 2. †*Eogaleus bolcensis* Cappetta (1975) from the Eocene Bolca Konservat-Lagerstätte. A. MCSNV T.331, holotype. B. MCSNV VII.B.94. C. MGP-PD 8869 C. Scale bars 50 mm.
Fig. 2. †*Eogaleus bolcensis* Cappetta, 1975 du Lagerstätte éocène de Bolca. A. MCSNV T. 331, holotype. B. MCSNV VII.B.94. C. MGP-PD 8869 C. Barre d'échelle = 50 mm.

4.6. Referred material

MCSNV VII.B.94, partially articulated specimen, 123.5 cm TL, Monte Postale site (Fig. 2B); MGP-PD 8869 C/8870 C, partially articulated specimen, in part and counterpart, 139.5 cm TL, Pesciara site (Fig. 2 C); MCSNV T.414/415, single isolated tooth in part and counterpart, lacking the root, Pesciara site (Fig. 3).

4.7. Type locality and horizon

Pesciara site, Bolca Lagerstätte, Italy; early Eocene, late Ypresian, middle Cuisian, SBZ 11, †*Alveolina dainelli* Zone (see Papazzoni et al., 2014).

4.8. Diagnosis

As for the genus.

4.9. Description

4.9.1. Overall body morphology

Measurements and counts for †*Eogaleus bolcensis* are summarized in Tables 1 and 2 (see also Fig. 4). The three articulated specimens examined exhibit a similar size ranging from 121.6 to 139.5 cm total length (TL), thereby suggesting similar ontogenetic ages. The holotype MCSNV T.311 and specimen MCSNV VII.B.94 are dorso-ventrally preserved in the anterior portion of the body, whereas their posterior half is exposed in lateral profile (Fig. 2A–B). On the contrary, specimen MGP-PD 8869 C/8870 C appears to be preserved in lateral view, although the arched disposition
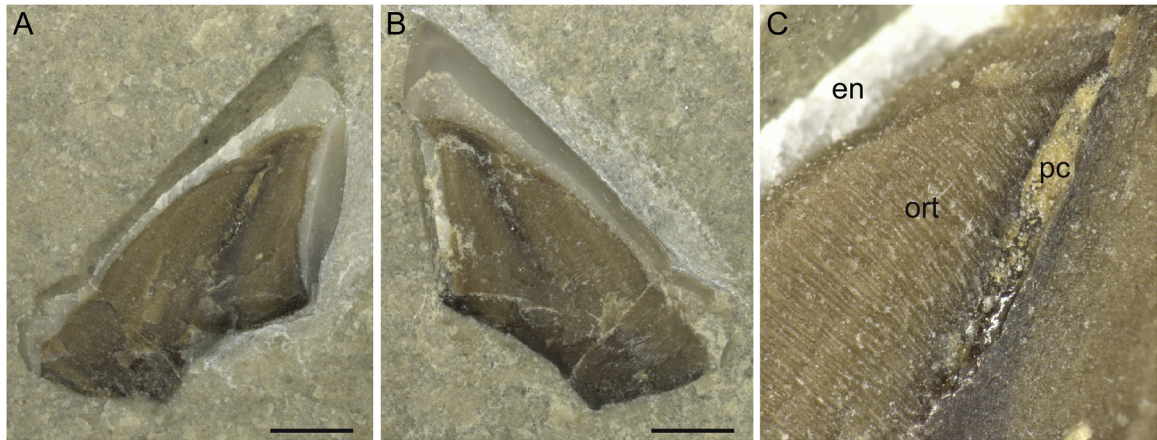
Fig. 3. †*Eogaleus bolcensis* Cappetta (1975) from the Eocene Bolca Konservat-Lagerstätte; single upper lateral tooth in part and counterpart. A. MCSNV T.415. B. MCSNV T.414. C. close up of MCSNV T.415. Scale bars 1 mm. en: enameloid; ort: orthodentine; pc: pulp cavity.

Fig. 3. †*Eogaleus bolcensis* Cappetta (1975) du Lagerstätte éocène de Bolca ; unique dent latérale supérieure en empreinte et contre-empreinte. A. MCSNV T.415. B. MCSNV T.414. C. Obturation de MCSNV T.415. Barres d'échelle : 1 mm. en : de type émail ; ort : orthodentine ; pc : cavité pulpaire.

of teeth might suggest that at least the head is dorso-ventrally flattened (Fig. 2C, 5A–B). The body of †*E. bolcensis* is elongate, gradually tapering posteriorly, but more massive than that of the Bolca triakid †*G. cuvieri*. The head is broad and bulky, as long as broad, about 18% of TL (Fig. 5). The snout is short, broad and bluntly rounded, not pointed or triangular; the preoral length is distinctly smaller than the mouth width. The mouth is ventrally positioned.

The pectoral fin is pointed, being almost of the same size as the first dorsal fin. Part of the internal skeleton is preserved in specimen MCSNV VII.B.94 showing that the pectoral fin is of semiplesodic type, with the longest radial being about 60–70% of the anterior margin length (Fig. 6); therefore, it is consistent with the pectoral fin-type that is characteristic of the family Carcharhinidae (Compagno, 1988). There are about 18–19 pectoral radials. The anterior distal radials are pointed, tapering and elongated, with the longest element being about three times the length of the longest proximal radial. Conversely, the posteriormost distal radials are shorter, subrectangular in shape, and higher than long.

The first dorsal fin originates at about 25% TL and its posterior margin is well anterior to the pelvic-fin insertion (Fig. 2). The height of the first dorsal fin more or less equals its base. The second dorsal fin is well-developed and its origin is located approximately at the same level as the anal-fin origin, at about 64% TL; the second dorsal fin is about 2/3 as high as the first dorsal fin. The pelvic-fin origin is located at about mid-length of the body (ca. 51% TL). The anal fin is slightly smaller than the second dorsal fin, with its height and base length being about 0.76 and 0.57 times those of the second dorsal fin. The posterior margin of the anal fin seems to be deeply notched in MCSNV VII.B.94.

The caudal fin is heterocercal and accounts for one quarter of the entire body length; its postero-ventral margin is deeply incised and its dorsal lobe possesses a small accessory lobe, the depth of which is about 5% TL. Undulations along the dorsal margin typical of carcharhinids (Compagno, 1988) are difficult to detect. The ventral lobe

of the caudal fin is well developed. Although Cappetta (1975) supposed the presence of a precaudal pit in MGP-PD 8869 C/8870 C, this feature cannot be unambiguously detected on the articulated specimens here studied. No sexual dimorphism can be inferred based on the presence of claspers since all specimens are poorly preserved in the pelvic region.

The differences that can be seen in the shape of some structures (e.g., fin shape and size, robustness of the caudal fin peduncle) among specimens might be related, at least in part, to artificial historical reconstructions of part the body outlines, although we do not exclude that taphonomic biases might have led such a variation.

The skeletal structures are poorly preserved in all the specimens and their characters are difficult to define. Due to the extensive covering of grout and/or pigment used to restore all the specimens, UV light was not useful to distinguish further details of preserved bones or other tissues, with the exception of MGP-PD 8869 C/8870 C (Fig. 5A–B). In this specimen, the rostrum appears small, short and measuring about one quarter of the cranial length. As in extant carcharhiniforms (see Compagno, 1988), the rostrum is tripartite with a single medial and two lateral rostral cartilages. The nasal capsules appear ovoid and laterally expanded, with their width reaching about 1.5–2.0 times their length. The nasal apertures appear subrectangular in outline and laterally elongate. No other structures of the chondrocranium are preserved in MGP-PD 8869 C/8870 C. However, this specimen shows traces of an eye as a brown-coloured pigmented area (Fig. 5A–B). The eyeball is small, rounded in outline, located at the level of the anterior margin of the mouth, and possibly consists of a dense accumulation of lens pigments exhibiting a pattern very similar to that reported in modern and fossil sharks (Hueter et al., 2004; Vullo et al., 2016; Zigman, 1991). The palatoquadrate and Meckel's cartilage run nearly parallel to each other, and their antimeres meet at their respective symphyses with an angle of about 80–90°.
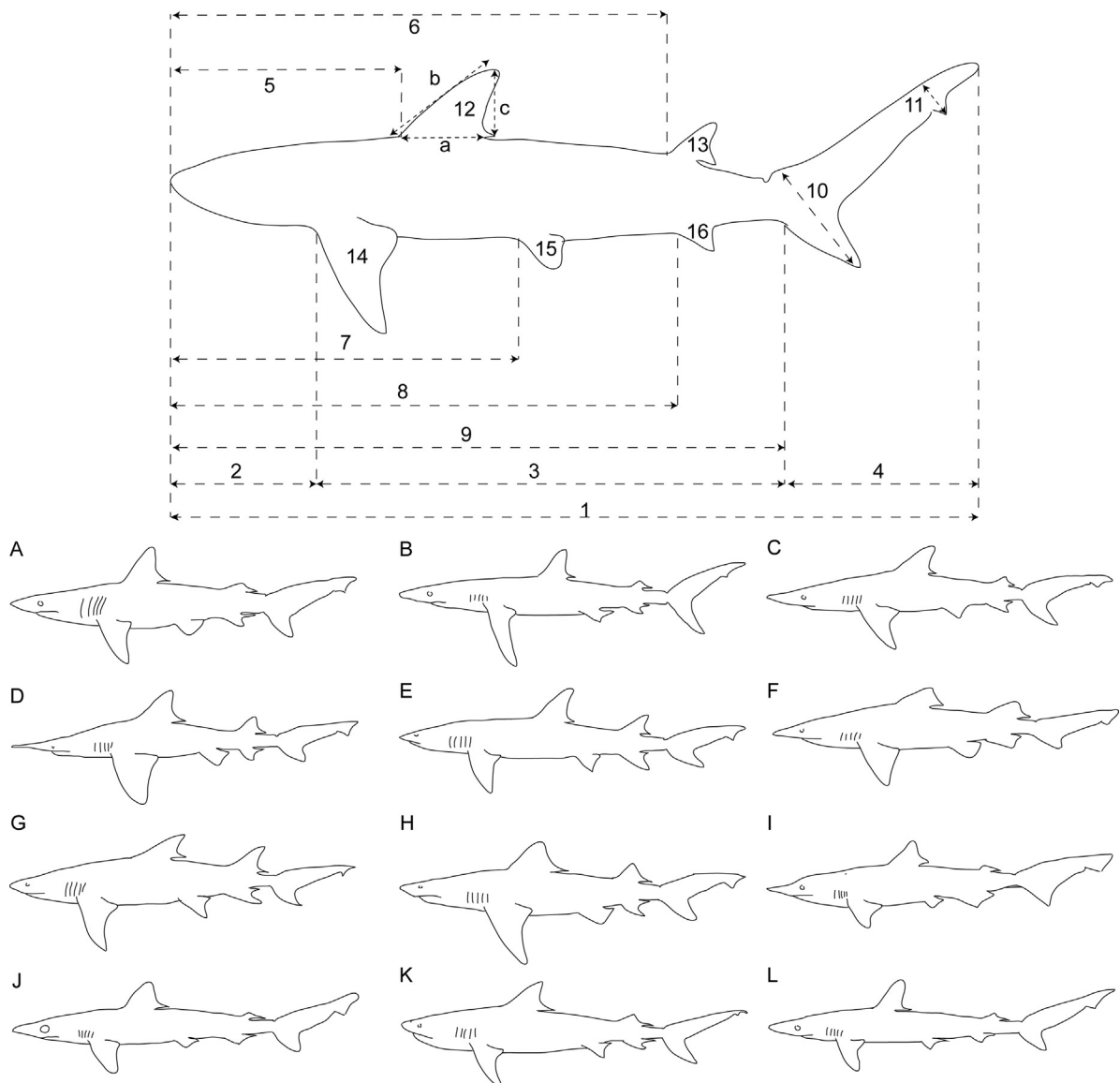
Fig. 4. Simplified outline of †*Eogaleus bolcensis* Cappetta (1975) from the Eocene Bolca Lagerstätte showing the measurements used in Table 1. The outline of †*E. bolcensis* represents the average body proportions of the three fossil specimens and is compared to the body outlines (not to scale) of extant carcharhinid genera: A. *Carcharhinus*. B. *Prionace*. C. *Nasolamia*. D. *Isogomphodon*. E. *Triaenodon*. F. *Lamiopsis*. G. *Negaprion*. H. *Glyphis*. I. *Scoliodon*. J. *Rhizoprionodon*. K. *Galeocerdo*. L. *Loxodon*. Morphometric scheme adopted from Cappetta (1975). Body outlines adopted and modified from Compagno (1984, 1988).
Fig. 4. Contour simplifié de † *Eogaleus bolcensis* Cappetta (1975) du Lagerstätte éocène de Bolca, montrant les mesures utilisées dans le Tableau 1. Le contour de *E. bolcensis* représente les proportions moyennes corporelles des trois spécimens fossiles et est comparé aux contours corporels (pas à l'échelle), des genres de carcharhinidés actuels (A à L). Schéma morphométrique adopté d'après Cappetta (1975). Contours corporels adoptés et modifiés selon Compagno (1984, 1988).

The vertebral column of †*Eogaleus* consists of about 135–153 vertebral centra; of these, 50–55 are monospondylous precaudal (35–37% of the total vertebral count), 25–35 are diplospondylous precaudals (19–23%), and 60–65 are caudals (40–44%). The vertebrae are strongly calcified, subrectangular in shape and antero-posteriorly compressed.

4.9.2. Dentition

The teeth of †*Eogaleus* are small, up to 12 mm in total height. The dentition is of cutting-clutching type and gradient monognatic. Additionally, a marked dig-nathic heterodonty is developed. Although most of the teeth are strongly displaced in all examined specimens, it is possible to recognize about 15 tooth files in each jaw half in both upper and lower jaws (total row count 30/30).

The lower anterior teeth are small, high and show a weakly mesio-distally expanded crown with a high and narrow cusp, slightly bent lingually (Fig. 7A–B). Contrary to †*Galeorhinus cuvieri*, the height of the anterior teeth is greater than the fore-aft basal length and the crown is
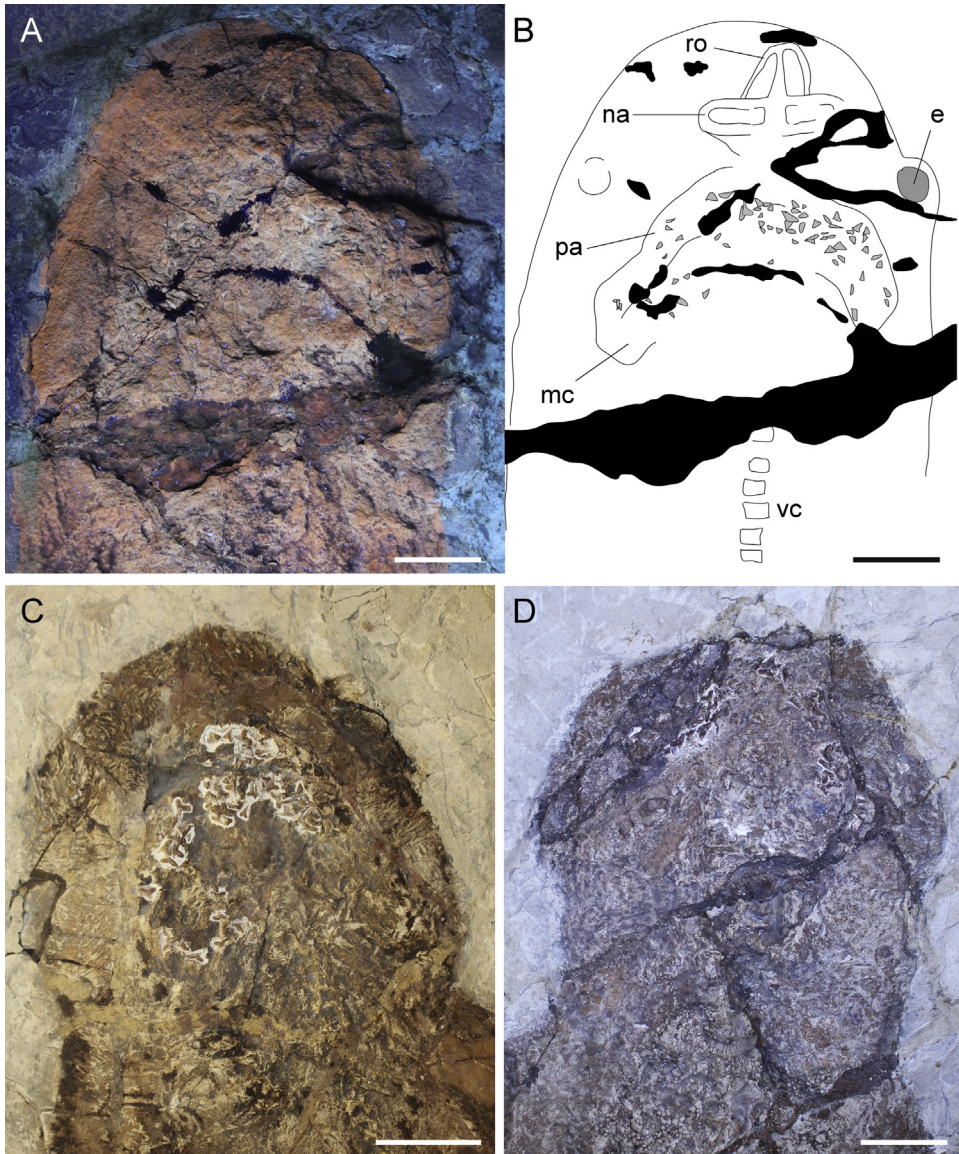
Fig. 5. †*Eogaleus bolcensis* Cappetta (1975) from the Eocene Bolca Lagerstätte; close-up of the head of A. MGP-PD 8869 C under UV light. B. Reconstruction of MGP-PD 8869 C. C. MCSNV T.311, holotype. D. MCSNV VII.B.94. Scale bars 50 mm. e: eye; mc: Meckel's cartilage; na: nasal capsule; pa: palatoquadrate; ro: rostrum; vc: vertebral centra.
Fig. 5. †*Eogaleus bolcensis* Cappetta (1975) du Lagerstätte éocène de Bolca; obturation de la tête de A. MGP-PD 8869 C sous éclairage UV. B. Reconstitution de MGP-PD 8869 C. C. MCSNV T.311, holotype. D. MCSNV VII.B. 94. Barres d'échelle 50 mm. e : oeil ; mc : cartilage de Meckel ; na : capsule nasale ; pa : palato-carré ; r : rostre ; vc : centres vertébraux.

never upturned near the tip (Fanti et al., 2016). The labial face of the crown is strongly convex and overhangs the labial face of the root by a distinct bulge. The root is low and very stout with a distinct nutritive furrow, bearing a large foramen. Cusplets are absent in the lower anterior teeth. The teeth of more lateral files possess a wider crown base and their labial face shows a low central bulb (Fig. 7C–D). The distal cutting-edge is more bent creating a notch at the distal heel that is incised in more lateral files and may bear up to four distinct cusplets. The cusp is strongly bent posteriorly and the weak mesial heel disappears. Some of the lower lateral teeth show a marked

sigmoid profile with a strongly convex lingual face of the cusp.

Upper antero-lateral teeth have high and wide crowns and roots, robust and oblique cusps that become more bent, wide and flat laterally in the series (Fig. 8). The mesial cutting edges are less concave than in lower lateral teeth. There is no differentiated mesial heel. The base of the mesial cutting edge of some teeth may bear some irregular weakly developed serrations. The distal heel is higher than in lower teeth, oblique and bearing up to four rather strong cusplets. The basal face of the root is broad and flat, with a distinct and deep nutritive furrow.
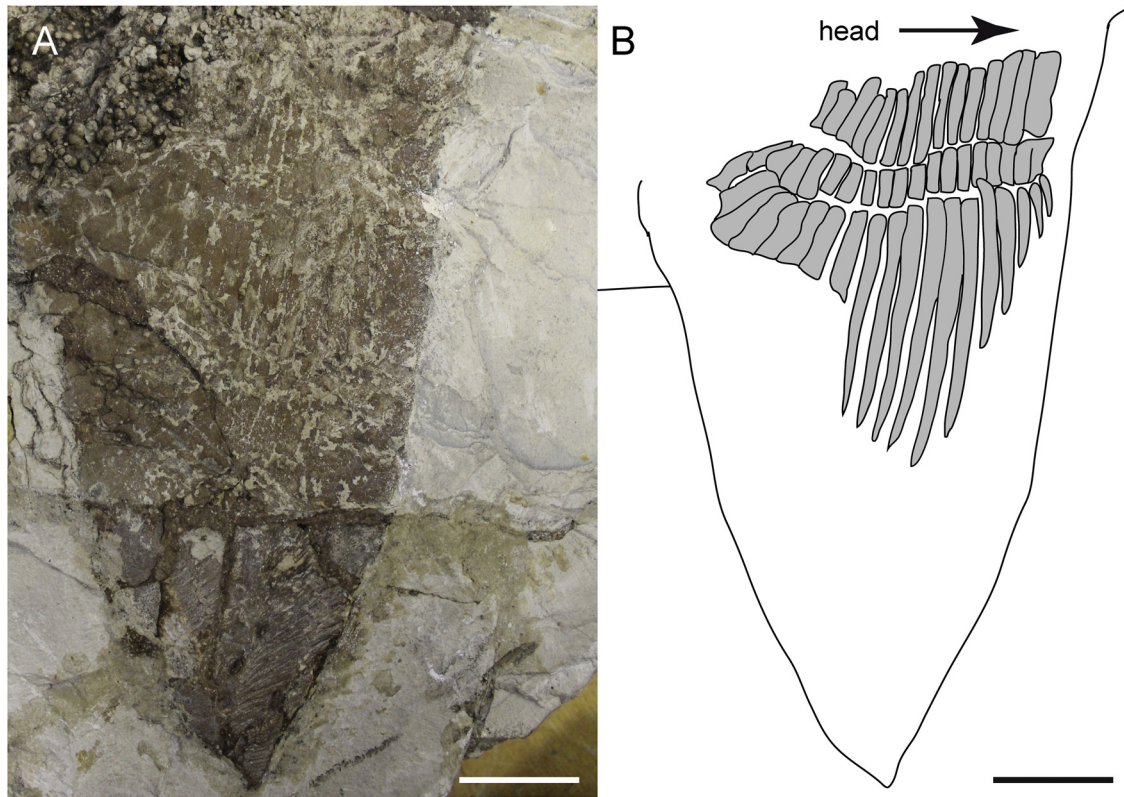
Fig. 6. Pectoral fin of †*Eogaleus bolcensis* Cappetta (1975) from the Eocene Bolca Lagerstätte. A. MCSNV VII.B.94. B. Reconstruction of the radials. Scale bars: 20 mm.
Fig. 6. Nageoire pectorale de †*Eogaleus bolcensis* Cappetta (1975) du Lagerstätte éocène de Bolca. A. MCSNV VII.B.94. B. Reconstitution des rayons. Barres d'échelle : 20 mm.

Most of these characters can be also recognized in the single isolated tooth MCSNV T.414/415 (Fig. 3). Although the specimen is incomplete, lacking the root and distal heel, a strongly bent main cusp with a broad base having with weak serrations at the base of the mesial cutting edge is recognizable. The specimen shows its internal structure, useful to detect the tooth histology of †*E. bolcensis*. The presence of a prominent coat of orthodentine surrounding a wide pulp cavity clearly indicates that the tooth represents a functional tooth of orthodont type, resembling the condition of most of the Carcharhiniformes (Compagno, 1988; Herman et al., 2003). This excludes its assignment to the odontaspidid †*Brachycarcharias* from Bolca characterized by teeth of osteodont type (Marramà et al., 2017b), whereas the bulky crown and the absence of an upturned crown tip distinguishes from the sympatric carcharhiniform †*Galeorhinus cuvieri*.

4.9.3. Dermal denticles

We sampled three loci with preserved dermal denticles in specimen MCSNV VII.B.94 (Fig. 9). The placoid scales of †*E. bolcensis* are consistent with the typical carcharhinid morphology being shell-shaped, of drag-reducing type (White, 1938; Reif, 1985). Their shape and size vary considerably depending on the body regions. The leading edge of the pectoral fins (Fig. 9A) is characterized by small dermal denticles (250–300 μm in diameter), rounded or slightly rhomboidal in shape, without cusp and with a rounded posterior margin. The crown is not ornamented and the ridges are apparently absent. The dermal denticles of the ventral lobe of the caudal fin (Fig. 9B–C) are closely imbricated, larger (about 500 μm wide) and characterized by a more complex structure. They are rhombic in outline with a crown usually as long as wide, ornamented with six prominent longitudinal ridges extending over the entire length of the crown. The ridges are well spaced from each other (ca. 80–90 μm). The two central ridges are slightly stronger and more pronounced than the lateral ones. The ectodermal pits are present along the posterior edge (Fig. 9C). The shape and size of the dermal denticles of the trunk (Fig. 9D) are similar to those of the caudal fin although they can support up to five ridges, some of which bifurcate at least once and with their posterior margins more pointed than that of the caudal fin denticles.

Following the method of Reif (1985), the ratio between ridge spacing (ca. 80–90 μm) and denticle diameter (ca. 500 μm) of †*E. bolcensis* falls within the range of the living *Carcharhinus amblyrhincos*, *C. melanopterus*, and *C. plumbeus* (Fig. 10), which are considered near-shore species characterized by moderate swimming speed (Compagno, 1984; Reif, 1985).
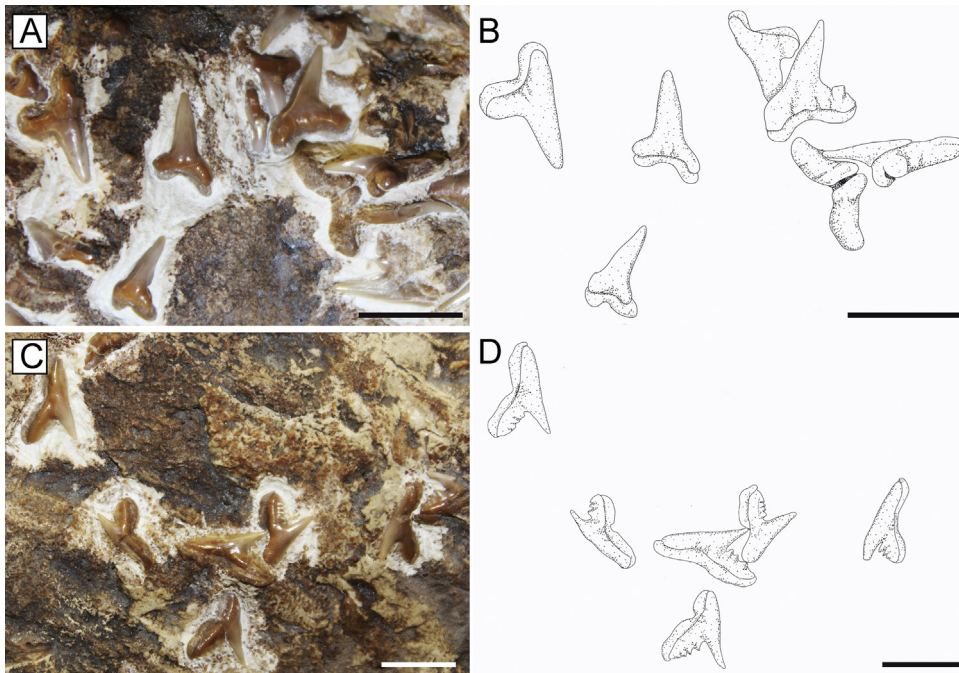
Fig. 7. †*Eogaleus bolcensis* Cappetta (1975) from the Eocene Bolca Lagerstätte. A–B. Lower anterior and C–D. Lower lateral teeth of MCSNV T.311. Scale bars: 10 mm.
Fig. 7. †*Eogaleus bolcensis* Cappetta (1975) du Lagerstätte éocène de Bolca. A–B. Dents antérieures inférieures. C–D. Dents latérales inférieures de MCSNV T.311. Barres d'échelle : 10 mm.

Table 1
Measurements of the three specimens of †*Eogaleus bolcensis* Cappetta (1975) from the Eocene Bolca Lagerstätte. See also the morphometric scheme in Fig. 3, which is adapted from Cappetta (1975).
Tableau 1
Mesures des trois specimens de †*Eogaleus bolcensis* Cappetta (1975) du Lagerstätte éocène de Bolca. Voir aussi le schéma morphométrique de la Fig. 3, issu de Cappetta (1975).

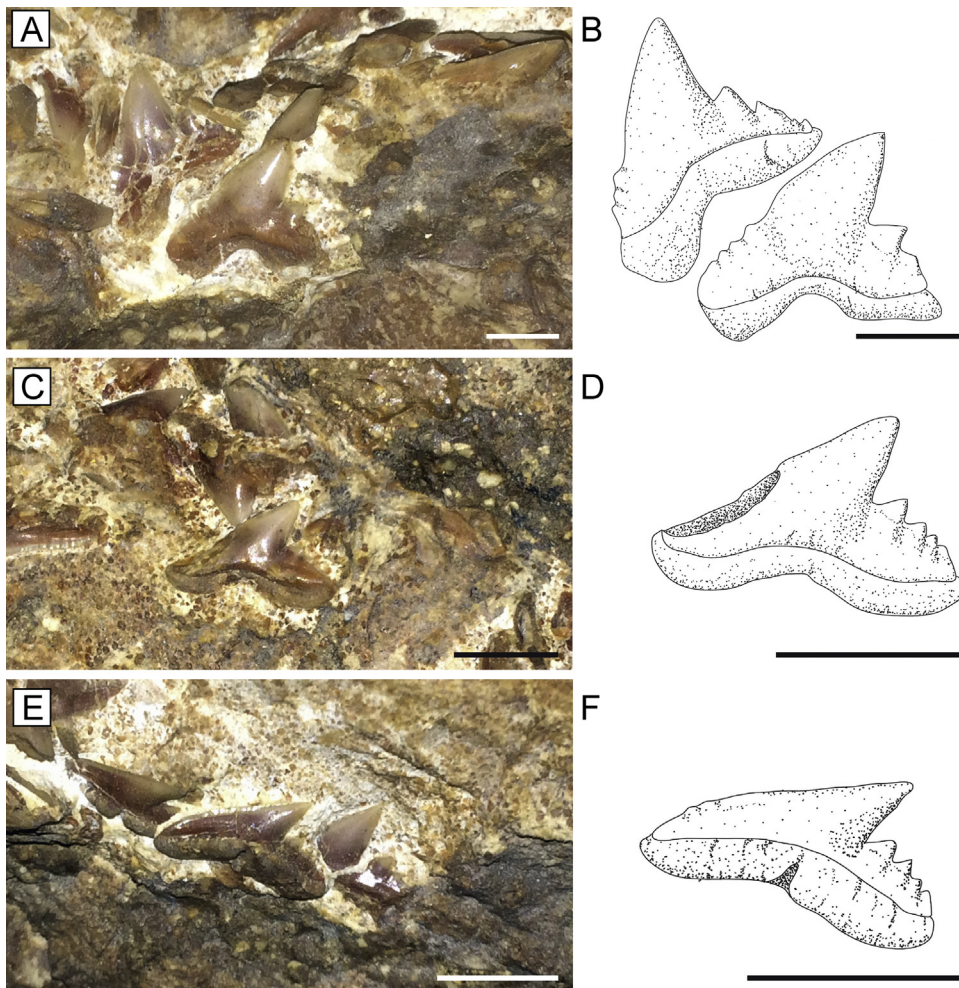| Measurements	MCSNV T.311		MCSNV VII.B.94		MGP-PD 8870		Mean % TL
	cm	% TL	cm	% TL	cm	% TL	
1	121.6	100.0	123.5	100.0	139.5	100.0	100.0
2	20.0	16.4	21.1	17.1	27.6	19.8	17.8
3	70.6	58.1	71.7	58.1	78.2	56.1	57.4
4	31.5	25.9	32.1	26.0	33.6	24.1	25.3
5	31.5	25.9	24.6	19.9	42.9	30.8	25.5
6	81.5	67.0	75.6	61.2	89.2	63.9	64.1
7	60.3	49.6	63.4	51.3	74.2	53.2	51.4
8	75.9	62.4	77.2	62.5	91.4	65.5	63.5
9	91.1	74.9	92.2	74.7	105.7	75.8	75.1
10	22.0	18.1	19.1	15.5	?	?	16.78
11	?	?	5.9	4.8	6.6	4.7	4.75
12a	9.9	8.1	?	?	14.2	10.2	9.16
12b	18.1	14.9	?	?	19.2	13.8	14.32
12c	14.2	11.7	?	?	9.9	7.1	9.39
13a	6.6	5.4	10.9	8.8	7.7	5.5	6.6
13b	11.1	9.1	15.4	12.5	8.7	6.2	9.3
13c	9.4	7.7	9.1	7.4	6.2	4.4	6.5
14a	11.2	9.2	14.0	11.3	?	?	10.3
14b	17.7	14.6	20.3	16.4	14.4	10.3	13.8
14c	12.4	10.2	15.3	12.4	?	?	11.3
15a	6.2	5.1	7.6	6.2	7.0	5.0	5.4
15b	7.3	6.0	7.8	6.3	6.4	4.6	5.6
15c	5.8	4.8	6.4	5.2	4.5	3.2	4.4
16a	6.3	5.2	5.9	4.8	7.1	5.1	5.0
16b	6.0	4.9	7.3	5.9	6.4	4.6	5.1
16c	4.8	3.9	3.9	3.2	5.4	3.9	3.7

Fig. 8. †*Eogaleus bolcensis* Cappetta (1975) from the Eocene Bolca Lagerstätte. A–B. Upper antero-lateral. C–D. Lateral. E–F. Lateralmost teeth of MCSNV VII.B.94. Scale bars: 5 mm.
Fig. 8. †*Eogaleus bolcensis* Cappetta (1975) du Lagerstätte éocène de Bolca. A–B. Dents antéro-latérales supérieures. C–D. Dents latérales. E–F. Dents les plus latérales de MCSNV VII.B.94. Barres d'échelle : 5 mm.

4.9.4. Age and maturity estimation

The three specimens of †*E. bolcensis* have a similar body size ranging from 121.6 to 139.5 cm total length (TL), suggesting similar ontogenetic ages of the individuals. Based on literature data (Table 3) the von Bertalanffy growth curves of some of the living carcharhinids indicate rather large age ranges for the three specimens of †*E. bolcensis*: 0.7–12.8 years for MCSNV T.311, 0.7–15 years for MCSNV VII.B.94, and 1.2–19.2 years for MGP-PD 8869 C/8870 C. The comparison of the age at maturity of living taxa with the age of each fossil specimen would suggest that they represent sexually immature individuals. However, some exceptions occur when †*Eogaleus* body sizes are compared with *Isogomphodon oxyrhynchus*, *Triaenodon obesus*, *Carcharhinus amblyrhynchos*, *C. melanopterus*, *C. sorrah*, and *C. plumbeus*, suggesting that the fossil specimens (and, in particular, the comparatively larger MGP-PD 8869 C/8870 C) possibly represent sexually mature individuals.

5. Discussion

5.1. Comparisons

The analysis of the material referred to †*Eogaleus bolcensis* has revealed the presence of several characters that unquestionably support the assignment of this selachian to the carcharhiniform family Carcharhinidae, and consequently its exclusion from the families to which other Bolca Lagerstätten selachians were assigned. In particular, the typical carcharhinid characters of †*E. bolcensis* include semiplesiodic pectoral fins (aplesodic in the triakid *Galeorhinus*), dentition of cutting-clutching type with orthodont teeth with low roots (osteodont, of tearing type and teeth with high roots in the odontaspidid †*Brachycarcharias*), dermal denticles shell shaped, of drag-reducing type (lanceolate or teardrop shaped in †*G. cuvieri*). Other carcharhinid characters, such as the vertebrae of
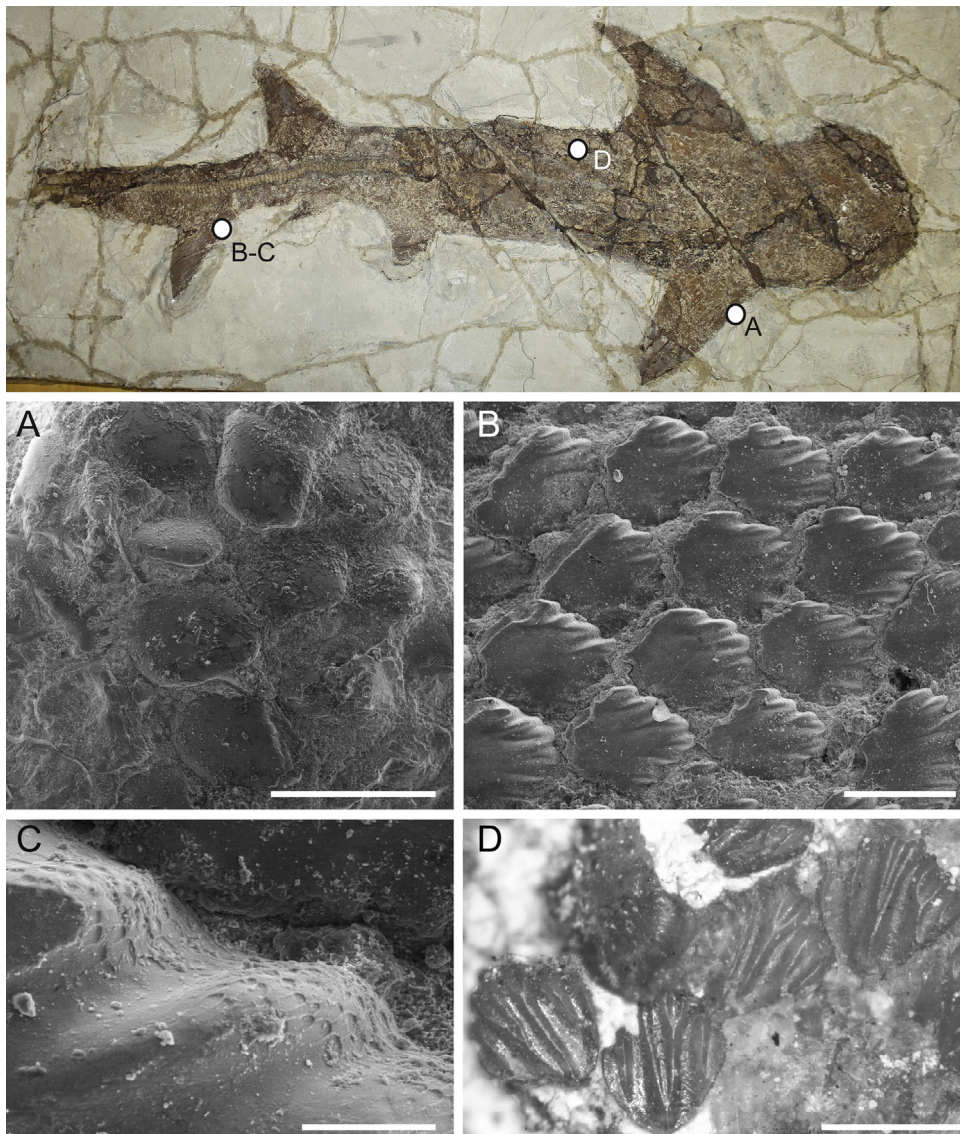
Fig. 9. The specimen MCSNV VII.B.94 showing the areas where dermal denticles were sampled. A–C. SEM micrographs. D. Image from Leica MZ12 stereomicroscope photographed with a 3D digital microscope Keyence VHX-1000D 3D. Dermal denticles were sampled from A. Anterior margin of pectoral fin. B–C. Anterior margin of the ventral caudal-fin lobe. D. Trunk. Scale bars in A, B, D are 500 μm; scale bar in C is 50 μm.

Fig. 9. Spécimen MCSNV VII.B.94 montrant les zones où les denticules dermiques ont été échantillonnés. A–C. microphotos au microscope électronique à balayage. D. image obtenue au stéréomicroscope Leica MZ12, photographiée au microscope digital 3D Keyence VHX-1000 3D. Les denticules dermiques ont été échantillonnés à partir : A, de la marge antérieure de la nageoire pectorale ; B–C, de la marge antérieure du lobe de la nageoire caudale ventrale. D, du tronc. Barres d'échelle pour A, B, D = 500 μm ; barre d'échelle pour C = 50 μm.

asterospondylic type with secondary calcification having the characteristic shapes of a Maltese crosss and caudal pits (Compagno, 1984, 1988; White, 1938) are difficult to detect in the examined material. Moreover, in †*E. bolcensis* the presence of a pectoral fin having almost the same size as the first dorsal fin, the caudal fin which occupies one quarter of the entire body length, and the vertebral number ranging between 135 and 153 allow us to definitively exclude any possible alignment to the triakid †*Galerorhinus cuvieri* (that on the contrary has pectoral fins with a surface that is approximately twice that of the first dorsal fin, a caudal fin occupying a third of TL, and 200–213 vertebrae;

Cappetta (1975); Fanti et al. (2016)), thereby providing a conclusive argument against the taxonomic hypothesis of Applegate (1978).

†*Eogaleus* can be separated from modern carcharhinids by its unique combination of meristic features (see Table 2). In particular, the total number of tooth rows (30/30) is useful to distinguish it from *Galeocerdo, Isogomphodon, Lamiopsis*, and *Loxodon*. The number of vertebrae of †*Eogaleus* (135–153) separates this extinct genus from *Galeocerdo, Lamiopsis, Nasolamia, Negaprion, Prionace* and *Triaenodon*, whereas the low number of pectoral radials (18–19) of †*E. bolcensis* appears to be unique among carcharhinids,

Table 2
Selected meristic features used to discriminate †*Eogaleus bolcensis* Cappetta (1975) from other living carcharhinid genera.
Tableau 2
Caractéristiques méristiques sélectionnées, utilisées pour différencier † *Eogaleus bolcensis* Cappetta (1975) des autres genres de carcharhinidés actuels. Les données sont issues de Compagno (1988).

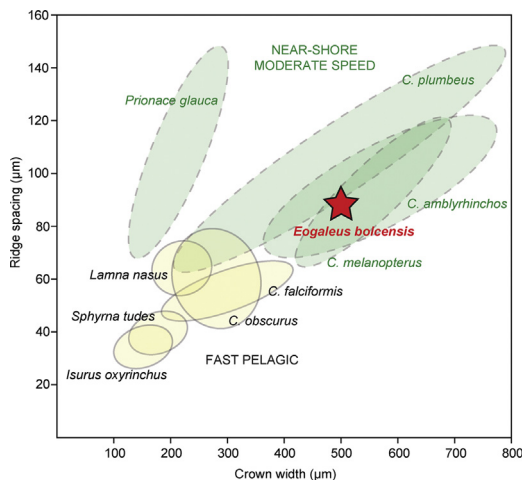| Genus	Tooth rows	Head width/Head length ratio	Vertebrae	% monospondylous precaudal v.	% diplospondylous precaudal v.	% diplospondylous caudal v.	Pectoral radials
Carcharhinus	24–37/23–35	0.55–0.81	97–244	23.3–36.4	8.3–28.2	40.8–57.7	22–34
†*Eogaleus*	30/30	1.00	135–153	34.6–37.0	18.5–23.3	40.0–44.4	18–19
Galeocerdo	18–26/18–25	0.94	216–234	25.2–27.8	19.2–21.3	52.9–54.5	23
Glyphis	27–37/26–34	0.80	149–217	31.1–32.3	18.7–24.9	42.9–50.0	25
Isogomphodon	49–61/49–56	0.45	147–158	30.3–33.3	14.7–15.7	51.0–53.7	30
Lamiopsis	39–43/37–41	0.76	174–179	28.7–29.6	25.2–27.7	44.3–45.2	25
Loxodon	25–28/24–28	0.62	148–191	24.2–28.6	22.0–28.5	46.3–50.3	24
Nasolamia	27–30/24–28	0.52	176–182	28.1–28.9	19.2–19.3	51.7–52.4	?
Negaprion	27–33/27–33	0.91	197–227	33.0–36.1	24.3–27.6	36.8–41.8	25
Prionace	24–31/25–34	0.51	239–252	32.3–37.4	24.3–26.9	37.9–41.9	29
Rhizoprionodon	23–30/21–28	0.65	121–170	20.9–30.1	19.4–30.5	43.1–56.1	22–25
Scoliodon	25–33/24–34	0.60	148–171	27.3–33.0	31.4–38.5	31.6–36.6	22–23
Triaenodon	?	0.85	208–218	30.3–33.2	27.5–31.9	36.6–40.9	24–25

Data from Compagno (1988).

Fig. 10. Scatter plot showing the correlation between crown width and ridge spacing in dermal denticles of selected pelagic fast swimming (full line) and near-shore of moderate speed (dotted line) selachians. Adopted and modified from Reif (1985). Note that †*E. bolcensis* falls in the clouds of correlation of near-shore moderate speed sharks. The "C." species belong to *Carcharhinus*.
Fig. 10. Diagramme montrant la corrélation entre la largeur de la couronne et l'espacement des crêtes dans les denticules dermiques de sélaciens pélagiques nageant vite (ligne pleine) et de sélaciens nageant à vitesse modérée près des rivages (ligne en tireté). Adopté et modifié d'après Reil (1985). On notera que †*E. bolcensis* se place dans les champs de corrélation des requins nageant à vitesse modérée près des rivages. Les espèces « C » appartiennent à *Carcharhinus*.

usually possessing a higher number of radials. Moreover, †*Eogaleus* can be distinguished from other early Eocene carcharhinids for its unique combination of dental characters. For example, teeth of *Galeocerdo*, collected from Ypresian deposits of northern Africa (Cappetta, 2012; Noubhani and Cappetta, 1997) are larger (up to 30 mm), with the apex strongly bent lingually and with always strongly serrated mesial and distal heels; in addition, the crown apex is only slightly bent, there is no mesial heel and weak ser-

rations are sometimes present on mesial cutting edge in †*Eogaleus*. The teeth of *Rhizoprionodon*, which were also recognized in lower Eocene deposits of Morocco (Cappetta, 2012; Noubhani and Cappetta, 1997), are very small (less than 4 mm) and usually without cusplets, the main cusp of upper teeth is narrower and the basal edge of the root is almost rectilinear (Cappetta, 2012; Compagno, 1988). The anterior teeth of †*Eogaleus* can be easily distinguished from those of the Palaeocene to Oligocene †*Abdounia* for the absence of large and tall lateral cusplets. The labial face is almost flat in the teeth of †*Abdounia* and the crown does not overhang the labial face of the root (the labial face is convex in †*Eogaleus* and the crown overhangs the labial face of root). Furthermore, the distal and mesial heels of the upper teeth of †*Abdounia* are usually characterized by the presence of up to three strong cusplets, whereas up to four lower cusplets are present only on the distal heel in the upper teeth of †*Eogaleus* (see also Cappetta (1980, 2012)). Although the upper lateral teeth of †*Eogaleus* may resemble those of the early Eocene to middle Miocene †*Physogaleus*, the basal edge of the root is almost rectilinear in the latter genus, and the anterior and lower antero-lateral teeth are strongly medio-distally compressed and may bear a single cusplet on the distal heel (the basal edge of the root is not rectilinear and the cusp is more erected in upper teeth, whereas the cusplets are absent in lower anterior teeth of †*Eogaleus*; see also Cappetta (1980, 2012)). However, these differences are very slight, and teeth of †*Eogaleus bolcensis* might resemble those of the Eocene species of †*Physogaleus* (including the type species †*P. secundus*). If we interpreted such differences as interspecific variation within a single genus, then †*Physogaleus* Cappetta (1980) would be a junior synonym of †*Eogaleus* Cappetta, 1975. When erecting the genus †*Physogaleus*, Cappetta (1980) did not mention the genus †*Eogaleus* in his discussion and comparisons. Furthermore, the isolated occurrence of the skeleton-based genus †*Eogaleus* (only known from northern Italy) within the Ypresian palaeobiogeographic distribution area of the widespread tooth-based genus †*Physogaleus* (known from

Europe, North America, North Africa, and Near East; see e.g., Cappetta (2012)) might support such a hypothesis.

Isolated teeth of †*Eogaleus* have been also reported from the early Eocene of Camba Shale, India (Rana et al., 2004) and from the late Eocene of Wulagen Formation, northwestern China (Li, 1997). However, in our opinion these occurrences should be regarded as doubtful. The teeth figured by Rana et al. 2004, fig. 2 are very small in size (about 2–3 mm), the crown of the upper lateral teeth is strongly distally bent and the base of the root is clearly rectilinear. The lateral teeth referred to †*E. bolcensis* by Li, 1997, fig. 6K–L) were almost not described, and the morphology of the single tooth figured in the paper, which is characterized by tall and rounded cusplets on the distal heel, is clearly not comparable with that of †*Eogaleus*.

5.2. Paleobiological remarks

Reif (1985) separated modern selachians into six ecological groups based on the morphology of their squamation, presence of ridges and their spacing. According to this classification, dermal denticles characterized by parallel ridges on the crown with inter-spaces wider than 80 μm are typical of near-shore hunters characterized by a moderate speed during swimming (e.g., *Galeorhinus galeus*, most of the *Carcharhinus* species, *Galeocerdo cuvier*), whereas denticles with ridges that are closely arranged with spaces of 40 and 80 μm between the ridges are typical of fast pelagic sharks (e.g., *Isurus oxyrhinchus*, *Lamna nasus*, *Carcharodon carcharias*, *Sphyrna lewini*).

The parallel ridges present in the denticles of the trunk and caudal fin of MCSNV VII.B.94 are widely spaced from each other and the ratio between ridge spacing and denticle diameter falls within the range of *Carcharhinus amblyrhynchos*, *C. melanopterus*, and *C. plumbeus* (Fig. 10), which are considered near-shore species with a moderate swimming speed (Compagno, 1984; Reif, 1985). In this perspective, we can hypothesize that †*Eogaleus* possibly had a similar life style. This is also suggested by the presence of the typical ornamentation of the ectodermal pits on the posterior edge of the caudal fin and trunk dermal denticles in our samples. Ectodermal pits typically occur along the posterior margin of placoid scales in near shore sharks with moderate swimming speed like *Carcharhinus plumbeus*, *Prionace glauca*, and *Galeorhinus galeus*, whereas they appear uniformly distributed along the entire surface of the denticles in fast swimming pelagic sharks like *Sphyrna* (Reif, 1985). These structures, along with the particular shell-shaped morphology of the placoid scales, seem to have a drag-reducing function in both ecological groups, whereas ectodermal pits appear to be almost totally absent in deep-sea species, pelagic sharks characterized by low swimming speed, and demersal taxa living on rocky, sandy or muddy substrates (Reif, 1985).

Moreover, considering that the ratio between ridge spacing and crown width of †*Eogaleus bolcensis* falls within the range of *Carcharhinus amblyrhynchos*, *C. melanopterus* and *C. plumbeus* (Fig. 10), the size of the fossil specimens fitted with the von Bertalanffy curves of these three *Carcharhinus* species (see Table 3) suggests that the individuals of †*E. bolcensis* from Bolca may have already reached the age of maturity, representing adult or subadult individuals. *Carcharhinus amblyrhynchos*, *C. melanopterus* and *C. plumbeus* are actually some of the smallest living carcharhiniform species (up to 2.4 m) that are very common in coastal inshore tropical waters (mostly in the Indo-Pacific) often associated with coral reefs and shallow lagoons with depths of only a few metres (Chin, 2013; Compagno, 1984; McAuley et al., 2006). These selachians are active, social predators feeding on reef bony fishes, in particular small fishes less than 30 cm long, but also on squids, octopuses, crabs, lobsters and shrimps (Compagno, 1984).

The range of body sizes of the †*E. bolcensis* individuals described herein is consistent with the relatively small size of the other Bolca selachians. The triakid †*Galeorhinus cuvieri* is known from several completely articulated specimens ranging from 54 to 92 cm which are interpreted as juvenile individuals (Fanti et al., 2016). The small sand tiger shark †*Brachycarcharias lerichei* is known from several isolated teeth belonging to juvenile and adult individuals whose estimated body size might have ranged between 62 and 171 cm (Marramà et al., 2017b). In this perspective, the small size of †*E. bolcensis* specimens, probably representing adult or subadult individuals, supports the hypothesis of Marramà et al. (2017b) who suggested that the presence of small shark species like †*B. lerichei* and juvenile individuals of †*G. cuvieri* in the Bolca paleobiotopes might be related to the competitive advantage of juveniles and small shark species in having access to relatively competitor-free trophic niches and food resources (see also Castro, 1993; Motta, 2004; Simpfendorfer and Milward, 1993), which were probably unavailable for larger top predators. In this context, sand/sea-grass beds, open sea, lagoon, and coral reefs concurred to create heterogeneous habitats in which small zooplanktivorous fishes, mainly represented by clupeoids (see Marramà and Carnevale, 2015a, 2015b, 2016, 2018) constituted one of the main trophic resources for most predators including †*E. bolcensis*. Similar paleoecological settings are also known from other Eocene tropical shallow contexts like the middle to late Eocene Midawara Formation in Egypt, in which the higher levels of the trophic chain were also occupied by small cosmopolitan shallow-water specialized feeders on small nectobenthic prey, such as small triakids and carcharinids, all considered as generalist feeders focusing on small active preys (Underwood et al., 2011).

6. Conclusions

The new anatomical observations on the Eocene shark †*Eogaleus bolcensis* presented herein definitively confirm its attribution to the family Carcharhinidae and its different taxonomic status from the sympatric carcharhiniform †*Galeorhinus cuvieri*. Moreover, the age estimations and the analysis of the morphology of the dermal denticles have provided new insights into the paleoecology of this Paleogene requiem shark, confirming its affinities with the tropical shallow waters of the Bolca paleobiotopes.

The Paleogene was marked by a diversification of the carcharhiniform sharks that involved members of the family Carcharhinidae around the Palaeocene/Eocene boundary and that has been associated with the decline of

Table 3

Age estimates for the three specimens of †*Eogaleus bolcensis* Cappetta (1975) from the Eocene Bolca Lagerstätte using the von Bertalanffy functions of living carcharhinid species. In some cases, it was not possible to detect an estimate because the specimens of †*E. bolcensis* are larger than the maximum length (L_∞) of the original population.

Tableau 3

Estimations d'âge pour les trois spécimens de † *Eogaleus bolcensis* Cappetta (1975) du Lagerstätte éocène de Bolca, utilisant les fonctions de von Bertalanffy des espèces actuelles de carcharhinidés. Dans certains cas, il n'a pas été possible de proposer une estimation, car les spécimens de † *E. bolcensis* sont plus grands que la longueur maximum (L_∞) de la population d'origine.

Taxon	Sex	k	L_∞	t_0	Age at maturity	Age of MCSNV T.311	Age of MCSNV VII.B.94	Age of MGP-PD 8870
Carcharhinus amblyrhynchos	C	0.05	229.2	−7.51	7.3	7.6	8.0	11.3
Carcharhinus brachyurus	C	0.0385	384.8	−3.477	16.5	6.4	6.6	8.2
Carcharhinus brevipinna	M	0.203	257.4	−1.709	7.9	1.4	1.5	2.1
Carcharhinus brevipinna	F	0.151	288.2	−1.988	7.8	1.6	1.7	2.4
Carcharhinus falciformis	C	0.148	216.4	−1.76	6.0	3.8	4.0	5.2
Carcharhinus leucas	C	0.076	285	−3	16.0	4.3	4.5	5.8
Carcharhinus limbatus	C	0.28	171	−1.5	6.0	2.9	3.1	4.5
Carcharhinus longimanus	C	0.103	341.7	−2.7	4.5	1.6	1.7	2.4
Carcharhinus longimanus	C	0.099	284.9	−3.4	7.0	2.2	2.3	3.4
Carcharhinus melanopterus	C	0.251	158.5	2	5.6	7.8	8.0	10.5
Carcharhinus plumbeus	C	0.04	239.6	−4.9	15.0	12.8	13.2	16.9
Carcharhinus sorrah	F	0.34	123.9	−1.9	2.5	9.8	15.0	?
Carcharhinus sorrah	M	1.17	98.4	−0.6	?	?	?	?
Galeocerdo cuvier (Atlantic)	C	0.107	440	−2.35	10.0	0.7	0.7	1.2
Galeocerdo cuvier (Gulf of Mexico)	C	0.184	388	−1.13	7.5	0.9	1.0	1.3
Isogomphodon oxyrhynchus	C	0.12	171.4	−2.612	6.0	7.7	8.0	11.4
Loxodon macrorhinus	C	0.41	84.2	−2.2	1.6	?	?	?
Negaprion brevirostris	C	0.057	317.65	−2.302	12.2	6.2	6.3	7.8
Prionace glauca	M	0.18	282	−1.35	15.0	1.8	1.9	2.4
Prionace glauca	F	0.13	310	−1.77	15.0	2.1	2.1	2.8
Rhizoprionodon lalandii	C	0.301	78.1	−1.463	2.6	?	?	?
Rhizoprionodon porosus	C	0.171	112.99	−1.751	3.3	?	?	?
Rhizoprionodon terraenovae	C	0.359	108	−0.98	3.5	?	?	?
Scoliodon laticaudus	F	0.358	71.5	−0.59	1.7	?	?	?
Scoliodon laticaudus	M	0.4046	67.6	−0.59	1.3	?	?	?
Scoliodon laticaudus	C	0.2731	75.5	−0.5664	?	?	?	?
Triaenodon obesus	F	0.05	207.8	−9.8	9.0	7.8	8.2	12.5
Triaenodon obesus	M	0.1	150.9	−6.6	9.0	9.8	10.5	19.2

Data for living species taken from Prabhakaran Nair (1976), Compagno (1984), Branstetter (1987), Branstetter and Stiles (1987), Branstetter et al. (1987), Brown and Gruber (1988), Devadoss (1998), Walter and Ebert (1991), Seki et al. (1998), Castro et al. (1999), Lessa et al. (1999, 2000), Skomal and Natanson (2002), Chin (2013), Oshitani et al. (2003), Joung et al. (2005), McAuley et al. (2006), Robbins (2006), Lessa et al. (2009), and Gutteridge et al. (2013). k: growth coefficient (rate of change in length increment); L_∞: mean maximum length for the population; t_0: hypothetical postnatal length; C: male and female combined; F: female; M: male. Ages are in years.

a large part of the medium to large-sized, fast-swimming Cretaceous top predators (Cappetta, 2012; Friedman and Sallan, 2012; Kriwet and Benton, 2004) and their diversification promoted by shallow coral reef settings (Sorenson et al., 2014). In this perspective, †*Eogaleus* might be considered, along with †*Abdounia, Carcharhinus, Galeocerdo,* †*Physogaleus* and *Rhizoprionodon*, another participant to the opportunistic ecological replacement in marine high trophic levels experienced by Carcharhinidae in the context of the adaptive fish radiation in the aftermath of the end-Cretaceous extinction.

References

Adnet, S., Cappetta, H., Tabuce, R., 2010. A middle-late Eocene vertebrate fauna (marine fish and mammals) from southwestern Morocco; preliminary report: age and palaeobiogeographical implications. Geol. Mag. 147, 860–870.

Agassiz, L., 1835. Revue critique des poissons fossiles figurés dans l'Ittiolitologia Veronese. Petitpierre et Prince, Neuchâtel.

Allen, K.R., 1966. A method of fitting growth curves of the von Bertalanffy type to observed data. J. Fish. Res. Board. Can. 23, 163–179.

Applegate, S.P., 1978. Phyletic studies. Part. I. Tiger sharks. Univ. Nal. Auton. Mexico Inst. Geol. Rev. 2, 55–64.

Bannikov, A.F., 2004. Fishes from the Eocene of Bolca, northern Italy, previously classified with the *Chaetodontidae* (*Perciformes*). St. Ric. Giac. Terz. Bolca 10, 55–74.

Bannikov, A.F., 2006. Fishes from the Eocene of Bolca, northern Italy, previously classified in the *Sparidae, Serranidae* and *Haemulidae* (*Perciformes*). Geodiversitas 28, 249–275.

Bannikov, A.F., 2008. Revision of the atheriniform fish genera *Rhamphognathus Agassiz* and *Mesogaster Agassiz (Teleostei)* from the Eocene of Bolca, northern Italy. St. Ric. Giac. Terz. Bolca 9, 65–76.

Bannikov, A.F., Carnevale, G., 2009. A new percoid fish from the Eocene of Monte Bolca, Italy: *Hendrixella grandei* gen. & sp. nov. Swiss J. Geosci 102, 481–488.

Bannikov, A.F., Carnevale, G., 2010. Bellwoodilabrus landinii, a new genus and species of labrid fish (*Teleostei: Perciformes*) from the Eocene of Monte Bolca. Geodiversitas 32, 201–220.

Bannikov, A.F., Carnevale, G., 2016. †*Carlomonnius quasigobius* gen. et sp. nov.: the first gobioid fish from the Eocene of Monte Bolca, Italy. Bull. Geosci 91, 13–22.

Blot, J., 1969. Les poissons fossiles du Monte Bolca classés jusqu'ici dans les familles des *Carangidae*, *Menidae*, *Ephippidae*, *Scatophagidae*. St. Ric. Giac. Terz. Bolca 2, 1–522.

Blot, J., 1980. La faune ichthyologique des gisements du Monte Bolca (Province de Verone, Italie). Catalogue systématique présentant l'état actuel des 160 recherches concernant cette faune. Bull. Mus. Hist. Nat. Paris 2, 339–396.

Blot, J., Tyler, J.C., 1990. New genera and species of fossil surgeon fishes and their relatives (*Acanthuroidei, Teleostei*) from the Eocene of Monte Bolca, Italy, with application of the Blot formula to both fossil and Recent forms. St. Ric. Giac. Terz. Bolca 6, 13–92.

Bonaparte, C.L.J.L., 1838. Selachorum tabula analytica. Nuov. An. Sci. Nat. 2, 195–214.

Branstetter, S., 1987. Age and growth-estimates for blacktip, *Carcharhinus limbatus*, and spinner, *C. brevipinna*, sharks from the northwestern Gulf of Mexico. Copeia, 964–974.

Branstetter, S., Stiles, R., 1987. Age and growth estimates of the bull shark, *Carcharhinus leucas*, from the northern Gulf of Mexico. Environ. Biol. Fishes 20, 169–181.

Branstetter, S., Musick, J.A., Colvocoresses, J.A., 1987. A comparison of the age and growth of the tiger shark, *Galeocerdo cuvier*, from off Virginia and from the northwestern Gulf of Mexico. Fish. Bull 85, 269–279.

Brown, C.A., Gruber, S.H., 1988. Age assessment of the lemon shark, *Negaprion brevirostris*, using tetracycline validated vertebral centra. Copeia, 747–753.

Cappetta, H., 1975. Les Sélaciens éocènes du Monte-Bolca. I–Les Carcharinidae. St. Ric. Giac. Terz. Bolca 2, 279–305.

Cappetta, H., 1980. Modification du statut générique de quelques espèces de sélaciens crétacés et tertiaires. Palaeovertebrata 10, 29–42.

Cappetta, H., 1987. Handbook of Paleoichthyology. In: 3B - Chondrichthyes II – *Mesozoic* and *Cenozoic Elasmobranchii*. Gustav Fischer Verlag, Stuttgart.

Cappetta, H., 2012. Handbook of Paleoichthyology - Chondrichthyes – *Mesozoic* and *Cenozoic Elasmobranchii*: Teeth. Verlag Dr. Friedrich Pfeil, München.

Cappetta, H., Case, G.R., 2016. A selachian fauna from the Middle Eocene (Lutetian, Lisbon Formation) of Andalusia, Covington County, Alabama, USA. Palaeontogr. Abt. A 307, 43–103.

Carnevale, G., Pietsch, T.W., 2009. An Eocene frogfish from Monte Bolca, Italy: the earliest skeletal record for the family. Palaeontology 52, 745–752.

Carnevale, G., Pietsch, T.W., 2010. Eocene handfishes from Monte Bolca, with description of a new genus and species, and a phylogeny of the family *Brachionichthyidae* (*Teleostei: Lophiiformes*). Zool. J. Linn. Soc. 160, 621–647.

Carnevale, G., Pietsch, T.W., 2011. Batfishes from the Eocene of Monte Bolca. Geol. Mag. 148, 461–472.

Carnevale, G., Pietsch, T.W., 2012. †*Caruso*, a new genus of anglerfishes from the Eocene of Monte Bolca, Italy, with a comparative osteology and phylogeny of the teleost family Lophiidae. J. Syst. Palaeontol. 10, 47–72.

Carnevale, G., Johnson, G.D., Marramà, G., Bannikov, A.F., 2017. A reappraisal of the Eocene priacanthid fish *Pristigenys substriata* (De Blainville, 1818) from Monte Bolca, Italy. J. Paleontol. 91, 554–565.

Carnevale, G., Bannikov, A.F., Marramà, G., Tyler, J.C., Zorzin, R., 2014. The Pesciara-Monte Postale Fossil-Lagerstätte: 2. Fishes and other vertebrates. In: Papazzoni, C.A., Giusberti, L., Carnevale, G., Roghi, G., Bassi, D., Zorzin, R. (Eds.), The Bolca Fossil-Lagerstätte: a window into the Eocene world. Rendiconti della Società Paleontologica Italiana 4, Modena, pp. 37–63.

Casier, E., 1946. La faune ichthyologique de l'Yprésien de la Belgique. Mem. Mus. R. Hist. Nat. Belg 104, 1–267.

Castro, J.I., 1993. The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Environ. Biol. Fishes 38, 37–48.

Castro, J.I., Woodley, C.M., Brudek, R.L., 1999. A preliminary evaluation of the status of shark species. Food and Agriculture Organization of the United Nations Food & Agriculture Org. FAO, Rome.

Chen, Y., Jackson, D.A., Harvey, H.H., 1992. A comparison of von Bertalanffy and polynomial functions in modelling fish growth data. Can. J. Fish. Aquat. Sci. 49, 1228–1235.

Chin, A., 2013. The biology and ecology of the blacktip reef shark *Carcharhinus melaopterus* (Quoy & Gaimard, 1824) and implications for management [PhD thesis, James Cook University].

Compagno, L.J.V., 1973. Interrelationships of living elasmobranchs. Zool. J. Linn. Soc. 53, 15–61.

Compagno, L.J.V., 1984. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniformes. FAO species catalogue 4, 251–655.

Compagno, L.J.V., 1988. Sharks of the order Carcharhiniformes. Princeton University Press, New Jersey.

Devadoss, P., 1998. Growth and population parameters of the spade nose shark, *Scoliodon laticaudus* from Calicut coast. Indian J. Fish. 45, 29–34.

Fanti, F.-, Minelli, D., Larocca Conte, G., Miyashita, T., 2016. An exceptionally preserved Eocene shark and the rise of modern predatory-prey interaction in the coral reef food web. Zool. Lett. 2, 246, http://dx.doi.org/10.1186/s40851-016-0045-4.

Frickhinger, K.A., 1991. Fossilien Atlas: Fische. Mergus, Melle.

Friedman, M., Sallan, L.C., 2012. Five hundred million years of extinction and recovery: a Phanerozoic survey of large-scale diversity patterns in fishes. Palaeontology 55, 707–742.

Guinot, G., Cappetta, H., Adnet, S., 2014. A rare elasmobranch assemblage from the Valanginian (Lower Cretaceous) of southern France. Cretaceous Res 48, 54–84.

Gutteridge, A.N., Huveneers, C., Marshall, L.J., Tibbetts, I.R., Bennett, M.B., 2013. Life-history traits of a small-bodied coastal shark. Mar. Freshwater Res. 64, 54–65.

Herman, J., Hovestadt-Euler, M., Hovestadt, D.C., 2003. Tooth vascularization and phylogenetic interpretation. Bull. Inst. R. Sci. Nat. Belg. Biol. 73, 5–26.

Hueter, R.E., Mann, D.A., Maruska, K.P., Sisneros, J.A., Demski, L.S., 2004. Sensory biology of elasmobranchs. In: Carrier, J.C., Musick, J.A., Heithaus, M.R. (Eds.), Biology of sharks and their relatives. CRC Press, Boca Raton, pp. 325–368.

Huxley, T.H., 1880. On the application of the laws of evolution to the arrangement of the Vertebrata and more particularly of the Mammalia. Proc. Zool. Soc. London, 649–662.

Iglésias, S.P., Lecointre, G., Sellos, D.Y., 2005. Extensive paraphylies within sharks of the order Carcharhiniformes inferred from nuclear and mitochondrial genes. Mol. Phylogenet. Evol. 34, 569–583.

Jaekel, O., 1894. Die eocänen Selachier vom Monte Bolca: ein Beitrag zur Morphogenie der Wirbelthiere. Verlag J. Springer, Berlin.

Jordan, D.S., Evermann, B.W., 1896. The fishes of North and Middle America, a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the isthmus of Panama. Part. I. Bull. U.S. Natl. Mus. 47, 1–1240.

Joung, S.-J., Liao, Y.-Y., Liu, K.-M., Chen, C.-T., Leu, L.-C., 2005. Age, growth, and reproduction of the spinner shark, *Carcharhinus brevipinna*, in the Northeastern waters of Taiwan. Zool. Stud. 44, 102–110.

Kriwet, J., Benton, M.J., 2004. Neoselachian (*Chondrichthyes, Elasmobranchii*) diversity across the Cretaceous-Tertiary boundary. Palaeogeogr. Palaeoclimatol. Palaeoecol. 214, 181–194.

Landini, W., Collareta, A., Pesci, F., Di Celma, C., Urbina, M., Bianucci, G., 2017. A secondary nursery area for the copper shark *Carcharhinus brachyurus* from the late Miocene of Peru. J. South Am. Earth Sci. 78, 164–174.

Lessa, R., Marcante Santana, F., Renato, P., 1999. Age, growth and stock structure of the oceanic whitetip shark, *Carcharhinus longimanus*, from the southwestern equatorial Atlantic. Fish. Res. 42, 21–30.

Lessa, R., Santana, F.M., Batista, V., Almeida, Z., 2000. Age and growth of the daggernose shark, *Isogomphodon oxyrhynchus*, from northern Brazil. Mar. Freshwater Res. 51, 339–347.

Lessa, R., Santana, F.M., De Almeida, Z.S., 2009. Age and growth of the Brazilian sharpnose shark, Rhizoprionodon lalandii and Caribbean sharpnose shark, R. porosus (Elasmobranchii Carcharhinidae) on the northern coast of Brazil (Maranhão). Pan-Am. J. Aquat. Sci. 4, 532–544.

Li, G.-Q., 1997. Elasmobranchs from the lower Tertiary of the Western Tarim Basin. China, and their biostratigraphic significance. Palaeoworld 7, 107–136.

Lioy, P., 1865. Sopra alcuni avanzi di plagiostomi fossili del Vincentino e specialmente sull Alopiopsis plejodon Lioy (*Galeus cuvieri Ag.*). Atti Soc. Ital. Sci. Nat., Mus. Civ. Stor. Nat. Milano 8, 398–405.

Marramà, G., Carnevale, G., 2015a. The Eocene sardine †*Bolcaichthys catopygopterus* (Woodward, 1901) from Monte Bolca, Italy: osteology, taxonomy, and paleobiology. J. Vert. Paleontol. 35, e1014490 https://doi.org/10.1080/02724634.2015.1014490.

Marramà, G., Carnevale, G., 2015b. Eocene round herring from Monte Bolca, Italy. Acta Palaeontol. Pol. 60, 701–710.

Marramà, G., Carnevale, G., 2016. An Eocene anchovy from Monte Bolca, Italy: The earliest known record for the family Engraulidae. Geol. Mag. 153, 84–94.

Marramà, G., Carnevale, G., 2017a. Morphology, relationships and paleobiology of the Eocene barracudina †*Holosteus esocinus* (Aulopiformes, Paralepididae) from Monte Bolca, Italy. Zool. J. Linn. Soc. 181, 209–228, http://dx.doi.org/10.1093/zoolinnean/zlw029.

Marramà, G., Carnevale, G., 2017b. *Eoalosa janvieri* gen. et sp. nov., a new clupeid fish (Teleostei, Clupeiformes) from the Eocene of Monte Bolca, Italy. Paläontol. Z., http://dx.doi.org/10.1007/s12542-017-0378-0.

Marramà, G., Bannikov, A.F., Tyler, J.C., Zorzin, R., Carnevale, G., 2016c. Controlled excavations in the Pesciara and Monte Postale sites provide new insights about the paleoecology and taphonomy of the fish assemblages of the Eocene Bolca Konservat-Lagerstätte, Italy. Palaeogeogr. Palaeoclimatol. Palaeoecol. 454, 228–245.

Marramà, G., Carnevale, G., Engelbrecht, A., Claeson, K.M., Zorzin, R., Fornasiero, M., Kriwet, J., 2017c. A synoptic review of the Eocene (Ypresian) cartilaginous fishes (*Chondrichthyes: Holocephali, Elasmobranchii*) of the Bolca Konservat-Lagerstätte, Italy. Paläontol. Z., http://dx.doi.org/10.1007/s12542-017-0387-z.

Marramà, G., Claeson, K.M., Carnevale, G., Kriwet, J., 2017a. Revision of Eocene electric rays (Torpediniformes, Batomorphii) from the Bolca Konservat-Lagerstätte, Italy, reveals the first fossil embryo in situ in marine batoids and provides new insights into the origin of trophic novelties in coral reef fishes. J. Syst. Palaeontol., http://dx.doi.org/10.1080/14772019.2017.1371257.

Marramà, G., Engelbrecht, E., Carnevale, C., Kriwet, J., 2017b. Eocene sand tiger sharks (Lamniformes, Odontaspididae) from the Bolca Konservat-Lagerstätte, Italy: palaeobiology, palaeobiogeography and evolutionary significance. Hist. Biol., http://dx.doi.org/10.1080/08912963.2017.1341503.

Marramà, G., Garbelli, C., Carnevale, G., 2016a. A morphospace for the Eocene fish assemblage of Bolca, Italy: a window into the diversification and ecological rise to dominance of modern tropical marine fishes. Boll. Soc. Paleontol. Ital. 55, 11–21.

Marramà, G., Garbelli, C., Carnevale, G., 2016b. A clade-level morphospace for the Eocene fishes of Bolca: patterns and relationships with modern tropical shallow marine assemblages. Boll. Soc. Paleontol. Ital. 55, 139–156.

Marramà, G., Carnevale, G., 2018. Eoalosa janvieri gen. et sp. nov., a new clupeid fish (Teleostei, Clupeiformes) from the Eocene of Monte Bolca. Italy. Paläontol. Z. 92, 107–120, http://dx.doi.org/10.1007/s12542-017-0378-0.

Monsch, K.A., 2006. A revision of scombrid fishes (Scombroidei, Perciformes) from the middle Eocene of Monte Bolca, Italy. Palaeontology 49, 873–888.

McAuley, R.B., Simpfendorfer, C.A., Hyndes, G.A., Allison, R.R., Chidlow, J.A., Newman, S.J., Lenanton, R.C.J., 2006. Validated age and growth of the sandbar shark, *Carcharhinus plumbeus* (Nardo 1827) in the waters off Western Australia. Environ. Biol. Fish. 77, 385–400.

Motta, P.J., 2004. Chapter 6 – Prey capture behavior and feeding mechanics of elasmobranchs. In: Musick, J.A., Carrier, J.C., Heithaus, M.R. (Eds.), Biology of sharks and their relatives. CRC Press, Boca Raton, pp. 153–209.

Naylor, G.J.P., 1992. The phylogenetic relationships among requiem and hammerhead sharks: inferring phylogeny when thousands of equally most parsimonious trees result. Cladistics 8, 295–318.

Nelson, J.S., Grande, T.C., Wilson, M.V.H., 2016. Fishes of the world, 5th ed. Wiley, Hoboken.

Noubhani, A., Cappetta, H., 1997. Les Orectolobiformes, Carcharhiniformes et Myliobatiformes (*Elasmobranchii, Neoselachii*) des bassins de phosphate du Maroc (Maastrichtien–Lutétien basal). Systématique, biostratigraphie, évolution et dynamique des faunes. Palaeo. Ichthyol. 8, 1–327.

Oshitani, S., Nakano, H., Tanaka, S., 2003. Age and growth of the silky shark *Carcharhinus falciformis* from the Pacific Ocean. Fish. Sci. 69, 456–464.

Papazzoni, C.A., Trevisani, E., 2006. Facies analysis, palaeoenvironmental reconstruction, and biostratigraphy of the "Pesciara di Bolca" (Verona, northern Italy): an early Eocene Fossil-Lagerstätte. Palaeogeogr. Palaeoclimatol. Palaeoecol. 242, 21–35.

Papazzoni, C.A., Carnevale, G., Fornaciari, E., Giusberti, L., Trevisani, E., 2014. The Pesciara-Monte postale Fossil-Lagerstätte: 1. Biostratigraphy, sedimentology and depositional model. In: Papazzoni, C.A., Giusberti, L., Carnevale, G., Roghi, G., Bassi, D., Zorzin, R. (Eds.), The Bolca Fossil-Lagerstätte: a window into the Eocene world. Rendiconti della Società Paleontologica Italiana 4, Modena, pp. 29–36.

Papazzoni, C.A., Fornaciari, E., Giusberti, L., Vescogni, A., Fornaciari, B., 2017. Integrating shallow benthic and calcareous nannofossil zones: the lower Eocene of the Monte Postale section (northern Italy). Palaios 32, 6–17.

Prabhakaran Nair, K., 1976. Age and growth of the yellow dog shark *Scoliodon laticaudus* Muller and Henle from Bombay waters. J. Mar. Biol. Assoc. India 18, 531–539.

Rana, R.S., Kumar, K., Singh, H., 2004. Vertebrate fauna from the subsurface Cambay Shale (Lower Eocene), Vastan Lignite Mine, Gujarat. India. Curr. Sci. 87, 1726–1733.

Reif, W.E., 1985. Squamation and ecology of sharks. Cour. Forsch. Inst. Senckenberg 78, 1–255.

Robbins, W., 2006. Abundance demography and population structure of the grey reef shark (*Carcharhinus amblyrhynchos*) and the white tip reef shark (*Triaenodon obesus*) (Fam. Carcharhinidae) [PhD Thesis, James Cook University].

Seki, T., Taniuchi, T., Nakano, H., Shimizu, M., 1998. Age, growth and reproduction of the oceanic whitetip shark from Pacific Ocean. Fish. Sci. 64, 14–20.

Simpfendorfer, C.A., Milward, N.E., 1993. Utilisation of a tropical nursery area by sharks of the families Carcharhinidae and Sphyrnidae. Environ. Biol. Fishes 37, 337–345.

Skomal, G.B., Natanson, L.J., 2002. Age and growth of the blue shark. Prionace glauca, in the North Atlantic Ocean. Col. Vol. Sci. Pap. ICCAT 54, 1212–1230.

Sorenson, L., Santini, F., Alfaro, M.E., 2014. The effect of habitat on modern shark diversification. J. Evol. Biol. 27, 1536–1548.

Staig, F., Hernández, S., López, P., Villafaña, J.A., Varas, C., Soto, L.P., Carrillo-Briceño, J.D., 2015. Late Neogene elasmobranch fauna from the Coquimbo Formation. Chile. Rev. Bras. Paleontol. 18, 261–272.

Tyler, J.C., Santini, F., 2002. Review and reconstructions of the tetraodontiform fishes from the Eocene of Monte Bolca Italy, with comments on related tertiary taxa. St. Ric. Giac. Terz. Bolca 9, 47–120.

Underwood, C.J., Ward, D.J., King, C., Antar, S.M., Zalmout, I.S., Gingerich, P.D., 2011. Shark and ray faunas in the middle and late Eocene of the Fayum area, Egypt. Proc. Geol. Assoc. 122, 47–66.

Vescogni, A., Bosellini, F.R., Papazzoni, C.A., Giusberti, L., Roghi, G., Fornaciari, E., Dominici, S., Zorzin, R., 2016. Coralgal buildups associated with the Bolca Fossil-Lagerstätten: new evidence from the Ypresian of Monte Postale (NE Italy). Facies 62, 21.

Volta, G.S., 1796. Ittiolitologia Veronese del Museo Bozziano ora annesso a quello del Conte Giovambattista Gazola e di altri gabinetti di fossili veronesi. Stamperia Giuliari, Verona.

Vullo, R., Guinot, G., Barbe, G., 2016. The first articulated specimen of the Cretaceous mackerel shark *Haimirichia amonensis* gen. nov. (*Haimirichiidae* fam. nov.) reveals a novel ecomorphological adaptation within the Lamniformes (*Elasmobranchii*). J. Syst. Palaeontol 14, 1003–1024, http://dx.doi.org/10.1080/14772019.2015.1137983.

Walter, J.P., Ebert, D.A., 1991. Preliminary estimates of age of the bronze whaler *Carcharhinus brachyurus* (Chondrichthyes: Carcharhinidae) from southern Africa, with a review of some life history parameters. S. Afr. J. Mar. Sci. 10, 37–44.

White, E.G., 1938. Interrelationships of the Elasmobranchs with a key to the order Galea. Bull. Am. Mus. Nat. Hist. 74, 25–138.

Zigman, S., 1991. Comparative biochemistry and biophysics of elasmobranch lenses. J. Exp. Zool. 256, 29–40.

de Zigno, A., 1874. Catalogo ragionato dei pesci fossili del calcare Eoceno di M. Bolca e M. Postale. Stabilimento Tipografia Grimaldo e C, Venice, Italy.