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DIGITAL INVESTIGATION OF LAMNIFORM SHARK VERTEBRAE FROM THE SIBILLINI MTS. (NORTHERN APENNINES, ITALY)

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Abstract: During the sampling of a stratigraphic section along the shore of the Fiastra Lake (Carg Project - Sheet 313 "Camerino" of the Geological Map of Italy at 1:50 000 scale), a small rock boulder with partially exposed bony material was discovered at the base of a small cliff at the northern termination of the Sibillini Mts. In this area, the classical facies of Umbria-Marche stratigraphic succession are well-exposed. The Oligocene-Miocene portion of the succession is represented by the ~200 m-thick Scaglia Cinerea Formation, passing upwards to the ~100 m-thick Bisciaro Formation. The microfossil assemblage has allowed the specimen to be constrained to the lower Burdigalian. The skeletal remains were examined using a CT-SCAN, a non-invasive method that has proven to be highly performing. The analysis revealed some articulated vertebrae, deformed by lithostatic compaction, which are attributed to a shark of the order Lamniformes. Subsequently, the vertebrae were digitally isolated, extracted from the surrounding matrix, and rendered into three-dimensional prints. Through digital retro-deformation, the body length of the lamniform shark was estimated to be approximately 4 metres. Further considerations on the vertebrae allowed us to infer that the studied shark had similarities to either *Isurus oxyrinchus* Rafinesque, 1810 or *Carcharodon carcharias* Linnaeus, 1758. The development of a dead-fall microbial community likely facilitated the preservation of the vertebrae. The studied specimen represents the first occurrence of a lamniform shark in the Lower Miocene of the Umbria-Marche Domain and represents one of the very rare recorded occurrences of lamniforms from the Lower Miocene of Italy.

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INTRODUCTION

In May 2022, during the sampling of a reference stratigraphic section cropping out along the northern shore of the Fiastra Lake - in the frame of the Sheet 313 “Camerino” of the Geological Map of Italy at 1:50 000 scale - a rock boulder with odd structures was found at the base of a small (about 15 m) cliff where the boundary between Scaglia Cinerea and Bisciaro formations is exposed. The finding area is located at the northern termination of the Sibillini Mts. ridge, which is characterised by the occurrence of a thick and slightly deformed succession of the Umbria-Marche pelagic basin, spanning from the Jurassic to the Middle Miocene, which was deemed useful as a reference section for the stratigraphic setting of the Region.

A more detailed analysis in the lab revealed that the structures represented fossilised bone remains. Thus, recognizing the significance of the finding, the boulder was sampled for a thorough analysis. Given the fragile nature of the rock matrix, which started to crumble soon after recovery, a non-invasive CT-SCAN analysis was deemed the most suitable approach. This analysis allowed the investigation of the nature and orientation of the bones within the rock, not only in their surface expression but also throughout their three-dimensional development within the rock body. By digitally isolating the structures from the enclosing rock, based on their different density, it was possible to digitally extract the entire specimen from the boulder and to render it in 3D.

The five articulated vertebrae that can be confidently referred to a lamniform shark are of great interest considering that, even secondarily ossifies in the form of calcified hydroxyapatite bone (Goodrich 1930; Applegate 1967; Moss 1977; Compagno 1999), vertebral centra of sharks are very rare in the fossil record when compared with highly mineralized teeth (e.g., Cappetta 1987, 2012; Shimada 1997a, 1997b, 2005, 2007, 2008; Hamm & Shimada 2002; Underwood 2006; Whitenack & Gottfried 2010; Cook et al. 2011; Guinot et al. 2012; Ebersole & Ehret 2018). Even if shark vertebrae are less diagnostic than dental characters (Shimada et al. 2006; Frederickson et al. 2015; Kriwet et al. 2015; Welton 2015), however, if sufficiently preserved, they can provide a taxonomic attribution at least at the order level and interesting additional information, including taphonomic and palaeoenvironmental evidence. In addition, Miocene marine vertebrates are generally quite rare from the sedimentary deposits of the Central Apennines (Marsili et al. 2007).

While palaeontological studies on the Umbria-Marche Domain have focused on invertebrate fossils and microfossils due to their great abundance and diversity (see Romano et al. 2021), studies on marine vertebrates have historically been extremely rare. Recently, a new interest has been turned to fossil vertebrates from the marine deposits of the Central Apennines (Paparella et al. 2017; Romano et al. 2019a, 2019b, 2021; Citton 2019, 2021), with interesting information on the faunal composition in the Jurassic and Cretaceous and possible palaeoecological and palaeoenvironmental inferences. In this paper, we report and describe the first evidence of large shark remains in the Burdigalian of Umbria-Marche, adding new information on the marine vertebrate fauna of the Central Apennines.

Lamniform sharks in the fossil record

The monophyletic lamniform sharks (De Carvalho 1996; Shirai 1996; Martin & Naylor 1997; Naylor et al. 1997, 2012; Kriwet 2006; Kriwet et al. 2008; Jambura et al. 2019) probably appear in the fossil record in the Jurassic (Frederickson et al. 2015; Guinot & Cavin 2016; Jambura et al. 2019) although the first remains that can be assigned with certainty to the group are from the Early Cretaceous (Kriwet et al. 2008; Schmitz et al. 2010; Carrillo-Briceño et al. 2019). According to Frederickson et al. (2015), throughout evolutionary history, lamniforms are characterized by an increase in size attributable, starting from the late Early Cretaceous, to the warming of ocean temperatures, with first evolutionary radiation in the Aptian-Cenomanian (Underwood 2006; Cappetta 2012; Guinot et al. 2012; Frederickson et al. 2015; Guinot & Cavin 2016; Vullo et al. 2016; Guinot & Carrillo-Briceño 2018). Since the latest Cretaceous, the clade shows forms with an ecomorphospace completely similar to that occupied by living forms and a high diversity; after the K-Pg extinction, differently, the lamniforms show a consistent reduction both in the ecological niches occupied and in the general body dimensions (Belben et al. 2017). Globally, the faunal turnovers across the Cretaceous–Palaeogene and Eocene–Oligocene boundaries are characterized by a general replacement of lamniforms by carcharhiniforms which become the dominant shark order worldwide (Kriwet & Benton 2004; Cappetta 2012; Underwood & Gunter 2012; Sorenson et al. 2014; Maisch et al. 2015).

In Europe and Mediterranean area, Lower Miocene lamniform fossils have been described from Austria (Brzobohatý & Schultz 1971; Schultz 2013), Belgium (de Schutter & Everaert 2020), Egypt (Cook et al. 2010), France (Joleaud 1907-1912; Cappetta 1970, 1973, 1975; Goedert et al. 2017), Germany (Probst 1879, Lutzeier 1922; von Ihering 1927; Barthelt et al. 1991; Scholz & Bienert 1992; Sach & Heizmann 2001; Baier et al. 2004; Reinecke et al. 2011, 2015; Höltke 2014; Pollerspöck & Beaury 2014), Hungary (Kordos & Solt 1982; Kocsis 2007), Portugal (Zbyszewski 1949; Antunes et al. 1981), Russia (Nazarkin & Malyshkina 2012), Slovakia (Koch 1904; Holec et al. 1995), Spain (Vicens & Rodríguez-Perea 2003; Mas & Antunes 2014), and Switzerland (Leriche 1927; Fischli 1930; Bolliger et al. 1995; Jost et al. 2016). In Italy, Lower Miocene lamniform remains have been only reported from Abruzzi (Marsili et al. 2007), Piedmont (D'Erasmo 1924) and Veneto (Vardabasso 1922).

Geological setting

The northern Sibillini Mts. are located in the Central Apennines fold and thrust belt (Fig. 1), which resulted from the deformation of two Mesozoic-Cenozoic palaeogeographical domains: the Umbria-Marche-Sabina and Latium-Abruzzi. These domains were part of the passive margin of Adria (Parotto & Praturlon 2004). The study area falls within the Umbria-Marche-Sabina Domain, which experienced pelagic sedimentation since the Early Jurassic due to the Western Tethys rift (Bernoulli 1967; Centamore et al. 1971; Santantonio & Carminati 2011; Fabbi & Santantonio 2012; Santantonio et al. 2022). The latter led to the fragmentation and drowning of substantial portions of the supra-regional Calcare Massiccio carbonate platform (Passeri & Venturi 2005; Santantonio & Carminati 2011). From the Early Jurassic to the Palaeocene, sedimentation was dominated by calcareous muds with a significant silica fraction, resulting in a thick succession of pelagic limestones with cherts, along with subordinate marlstones and claystones (Pierantoni et al. 2013; Fabbi 2015; Cipriani 2016). Since the Eocene, a general increase in terrigenous supply led to the decrease in chert content, as recorded by the transition from Scaglia Rossa, Scaglia Variegata and Scaglia Cinerea formations (Fig. 1c) (sheets 280 "Fossombrone" and 302 "Tolentino" of the Geological Map of Italy at 1:50 000 scale - Servizio Geologico d'Italia 2009, 2016). In the earliest Miocene, a recovery of the carbonate factory joined with an increase in siliceous content (as shown by diffuse chert layers and nodules), is recorded by the Bisciaro Formation (Fig. 1c). Palaeoecological perturbations led to this "carbonate event", and the increase of silica in the seawater was related to strong volcanic activity, as also recorded by several volcaniclastic levels within the Bisciaro (Guerrera et al. 2015). Since the Middle Miocene, the advancing Apennine chain caused the flexure of the foreland and the deepening of the basin, resulting in the sedimentation of the hemipelagic facies of the Schlier Formation and the development of the Laga foredeep basin, which hosted a >3000 m-thick turbidite succession (Milli et al. 2007).

The chain building occurred through the eastward migration of thrust systems, which produced an arcuate mountain ridge (Royden et al. 1987; Calamita & Deiana 1988; Patacca et al. 1992; Carminati & Doglioni 2012; Pierantoni et al. 2013). The Olevano-Antrodoco-Sibillini Mts. Thrust is one of the major thrust fault systems of the Central Apennines and produced the overthrusting of the Umbria-Marche-Sabina stratigraphic units on the foredeep deposits of the Laga formation (Pierantoni et al. 2005; Cosentino et al. 2010; Calamita et al. 2012; Curzi et al. 2021). After the compressional tectonic phase, due to the opening of the Tyrrhenian back-arc basin, the E-verging accretionary wedge was affected by Quaternary extensional tectonics (Patacca et al. 1992; Doglioni 1995; Doglioni et al. 2006; Stendardi et al. 2020).

The Fiastra section

Along the northern shore of the Fiastra Lake, and the Fiastrone River, a ca. 1 km-thick succession, encompassing the Pliensbachian to Langhian time span, is exposed (Fig. 1b, d). This succession is at the backlimb of the hanging wall anticline of the Sibillini Mts. thrust (resulting in the Sibillini Mts. ridge), and is about WSW-dipping with dip angles less than 30°. The Kimmeridgian-

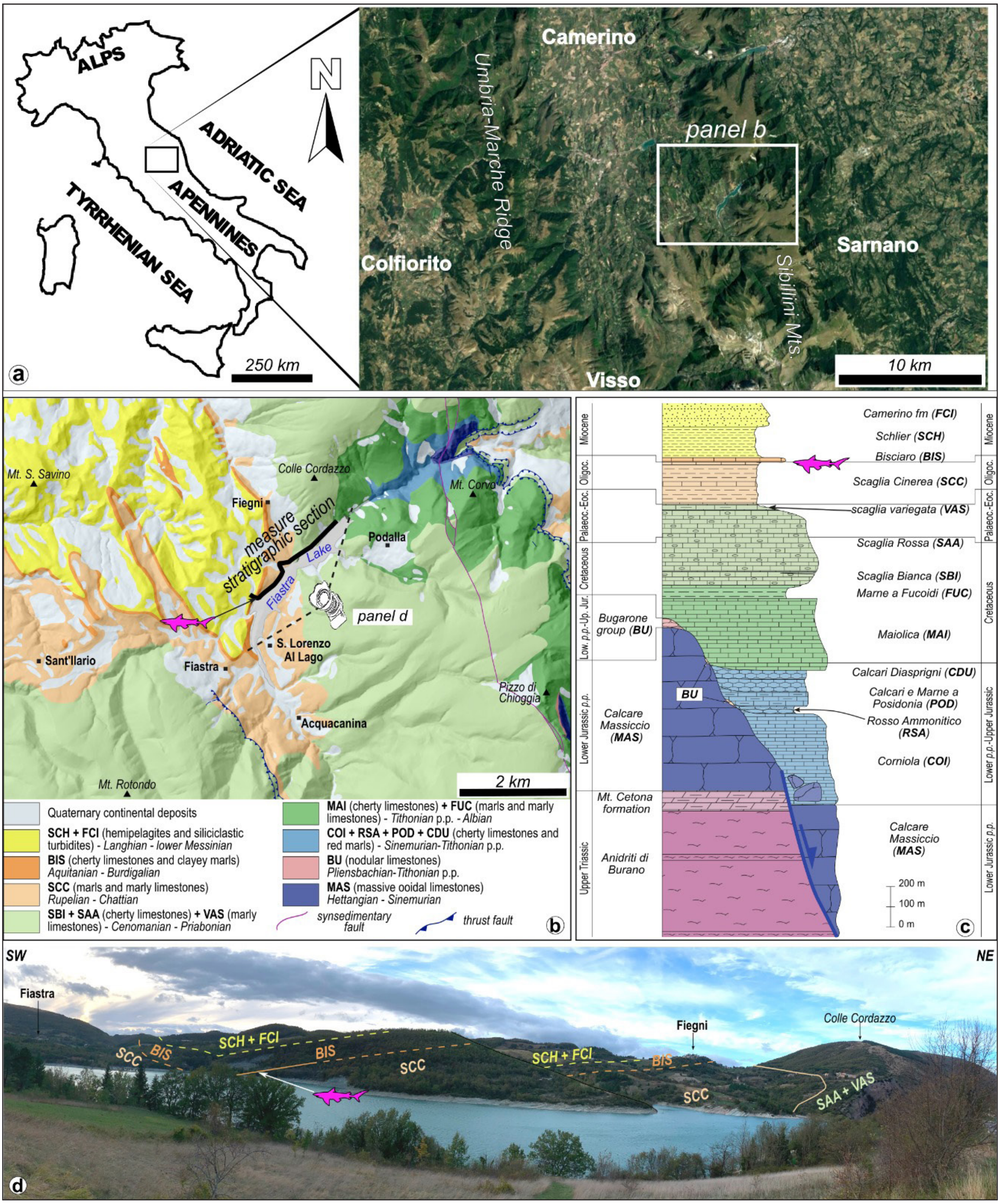


Fig. 1 - a) Geographic localisation of the study area (modified from Google Earth Pro); b) simplified geological map of the Fiastra Lake area. For acronyms of lithostratigraphic units please refer to panel c; c) stratigraphic scheme of the Upper Triassic-Miocene succession of the Umbria-Marche-Sabina Domain (modified from Curzi et al. 2023); d) panoramic view of the Northern Fiastra Lake bank, where the stratigraphic section was measured and the study vertebrate remains were found (discovery site arrowed). For acronyms, please refer to panel c.

Langhian interval has been sampled for becoming a reference section for the Geological Sheet 313 “Camerino”. Approximately 400 samples were collected for micro and nannofossil analyses,

Fig. 2 - a) Field view of the finding site of the study material; b, c) top and lateral views, respectively, of the sample MUST 1/SF/2024. Scale bar 10 cm.

showing the key litho-biostratigraphic features of the Umbria-Marche Domain.

The Oligocene-Miocene portion of the succession is particularly well-exposed. The about 200 m-thick Scaglia Cinerea consists of calcareous marlstones, marlstones, and clayey marlstones, organised in medium-thin beds, grey-greenish in colour with occasional reddish intervals at the base of the unit. Noteworthy, dm-thick nummulitid-rich calcarenites are also present. This unit is latest Priabonian to earliest Aquitanian in age. The Scaglia Cinerea is overlain by the Bisciaro, which is about 100 m-thick (in this sector of the Sibillini Mts.). This formation is made up of alternations of dark-grey to hazelnut marly and siliceous limestones, bearing beds up to 60 cm in thickness and black chert nodules and ribbons, with cm to dm-thick grey marlstones and clayey marlstones. In addition, the Bisciaro contains several volcaniclastic levels, with the lowest one ("*Raffaello*" level – 21.9 Ma) marking the boundary with the Scaglia Cinerea (Coccioni & Montanari 1994), whereas Petti & Falorni (2007) indicate the occurrence of carbonate beds in a clay-dominated succession as a lithostratigraphic marker for differentiating the two units. The age of the Bisciaro is considered Aquitanian *p.p.* to Burdigalian *p.p.*

Material and Methods

The studied specimen (Fig. 2) is included in an erratic boulder (23 x 15.5 x 8.5 cm in size) that was found near the boundary between the Scaglia Cinerea and the Bisciaro formations. Thin sections and smear slides were prepared from the clast matrix in order to recover valuable data on its relative age as well as taphonomy. For these purposes, we investigated the calcareous nannofossils and micropalaeontological assemblages, and the microfacies.

Given the great fragility of the recovered block containing the osteological material, non-invasive CT-SCAN analysis was conducted to digitally reconstruct the vertebrae incorporated into the original matrix. Specifically, a medical CT scanner was used which, even having a lower resolution and scanning energy than Micro CT scanners and synchrotron CT, offers the advantage of being able to accommodate large samples, with the ability to acquire volumes of up to 70 cm in diameter with excellent image quality both in terms of spatial resolution and contrast. Furthermore, the most recent equipment allows the post-processing of the acquired data, the application of artifact reduction algorithms, the analysis of the volumes and substances present in the acquired scans (spectral

Philips Ingenuity - Acquisition Protocols	
Protocol 1: HighRes spiral acquisition	**Protocol 2:** HighRes sequential acquisition
– Detectors 16 X 0,625 mm	– Detectors 16 X 0,625 mm
– kV 140	– kV 140
– mA 425	– mA 331
– Rt 1,5s	– Rt 1,5s
– Pitch 0,66	– Contiguous
– Acq FOV 250 mm	– Acq FOV 250 mm
– Recon 1 mm	– Recon 1,5 mm
– DistFact 0,5 mm	– DistFact 0,75 mm
– Brain Smooth (UA), enhancement 0, -5, -1	– Brain Smooth (UA), enhancement 0, -5, -1
– Standard (B), enhancement 0, -5, -1	– Standard (B), enhancement 0, -5, -1
– Y-detail (YB) enhancement 0, +5, +1	– Y-detail (YB) enhancement 0, +5, +1

Tab. 1 - CT-SCAN acquisition protocols.

imaging), as well as the reconstruction of images on all planes of space both in Multi Planar Reconstruction (MPR) and Maximum Intensity Projection (MIP), Minimum-intensity projection (MinIP) and Volume Rendering Technique (VRT) modes, therefore both flat and three-dimensional images. These images, in particular the MPR and VRT, allow an in-depth analysis of the materials under examination as well as offering the possibility of reproducing the acquired specimens with 3D printers at the desired dimensions.

Specifically, for the radiological analysis of the specimen in question, a Philips Ingenuity multi-detector CT equipment was used which acquires 64 layers of 0.625 mm thickness with each rotation of the RX-detector tube system.

The biggest obstacle in producing images of specimens is the presence of CT beam hardening artifacts, i.e. due to the absorption of low-energy radiation when passing through materials with a high atomic number. These appear as radial striae in the image and occur when very high-density structures are present (unburned bone fragments, metal jewelry, stones), immersed in less dense material. To overcome this problem, an acquisition technique defined as Hard-X-ray with high material penetration power is used, associated with the application of specific reconstruction algorithms.

The acquired volume was then reprocessed to produce a series of images (data set) suitable for the type of analysis required by applying specific processing algorithms (Kernel), thus obtaining the images from which important information was obtained. In particular, 9 series of images were produced, 3 for each Kernel used by applying a further enhancement algorithm to each one, for the Smooth and Standard Kernels negative values for the Y-detail positive values. From the data sets obtained it was possible to produce images of the specimen as a whole, as well as the measurement of volumes, dimensions, and densities.

To obtain the above-mentioned images, the specimen was studied using two acquisition protocols (Tab. 1), one in spiral mode and one in sequential mode, both with 250 mm of FOV using only 16 detectors to reduce the size of the radiant beam on the Z axis by increasing thus the spatial and contrast resolution.

The image series from the CT-SCAN were then imported and processed using Mimics Research 21.0 and 3-Matic Research 21.0. Measurements were conducted using Amira 5.4.5. Other images used in the figures were created using the open-source software MeshLab. The current reference material has been imported from the online Morphosource database and includes the CT-SCAN of a portion of the vertebral column of *Squalus acanthias* Linnaeus, 1758 3DAS:0002 (http://n2t.net/ark:/87602/m4/375585) and a complete scan of a juvenile specimen of *Carcharodon carcharias* Linnaeus, 1758 LACM: 43805-1 (http://n2t.net/ark:/87602/m4/545335).

Retrodeformation of the digitally reconstructed vertebral material was performed by using the sculpting tools of Blender 3.4. The first and the second vertebra in the preserved portion of the vertebral column were individually sliced and extracted using Mimics. An STL 3D file was then exported for each of the two vertebrae and imported into Blender.

Based on the general anatomy and mechanical behaviour of shark vertebrae (Ingle et al. 2018), retrodeformation of the two bones, along with the original specimen, was based on the following three

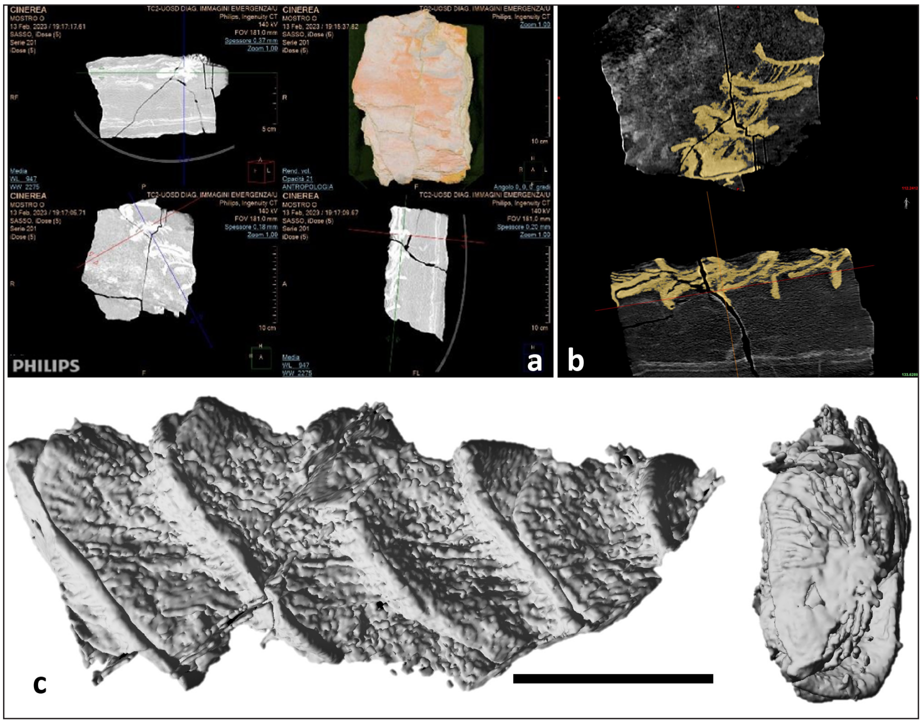


Fig. 3 - a) Visualization of reconstruction and analysis planes during acquisition at CT-SCAN. b) CT-SCAN of the sample MUST 1/SF/2024: axial section (above) and sagittal section (below); c) Digital cast of MUST 1/SF/2024: lateral view (left) and frontal view (right). Scale bar 5 cm.

Tab. 2 - Total length calculated at death, birth, and age 7 of specimen MUST 1/SF/2024, based on different equations. Abbreviations: FL, fork length; PCL, precaudal length; TL, total body length.

Reference	EQ	Results: at death		birth	maturity	r^2
Cailliet et al. (1985)	TL=35.9+5.7*VD	TL=	400,7	106,7	250,7	0,9
Gottfried et al. (1996)	TL=22+5.8*VD	TL=	393,2	94,1	240,6	0,97
Wintner and Cliff (1999)	PCL=(VD/10+0.284)/0.0188	PCL=	355,5	81,2	215,6	0,96
	TL=5.207+1.251*PCL	TL=	450,0	106,8	274,9	
Natanson (2001)	FL=21.0+11.8*VR	FL=	398,6	94,3	243,3	0,94
	TL=(FL+0.06)/0.94	TL=	424,1	100,4	258,9	
		mean TL=	417,0	102,0	256,3	0,9425

assumptions: i) the anterior and posterior faces of the centra were made as much circular as possible, keeping the radius constant; ii) the birth ring was kept in the middle of the face and his centre was also considered the centre of the outermost ring; iii) the anteroposterior thickness of both centra was kept as preserved in the original specimen since apparently the shear that deformed it acted only in the dorsoventral and mediolateral direction.

The resulting retrodeformed models were employed for quantitative analysis and anatomical description, detailed in the results section. To facilitate visual inspection, the original specimen, its retrodeformed model, and the first and second centra, along with their retrodeformed models, were 3D printed.

Files were sliced in Cura 5.2.2, and printing was carried out utilizing an Artillery Sidewinder x2 3D printer, in white PLA, with a 0.2 layer thickness at 60 mm/s. The 3D printed models (Fig. 3) were then deposited in the MUST (Museo Universitario di Scienze della Terra) collections for further study.

To estimate the body size of specimen MUST 1/SF/2024 we used the largest centrum (vertebra 2) preserved. By assuming this vertebra is the largest belonging to the individual, we can obtain at least the minimum body length that the specimen should have reached at death. To do so, we used the equations calculated by Cailliet et al. (1985), Gottfried et al. (1996), Wintner & Cliff (1999), and Natanson (2001) (Tab. 2). The same has been done for the body length at birth (ring 1 diameter equals 12.4 mm) and at maturity (ring 7, diameter equals 37.7 mm).

BIOSTRATIGRAPHY AND MICROFACIES ANALYSIS

The microfossil content (Fig. 4a-c) extracted from the matrix embedding the specimen include sponge spicules, radiolarians, planktonic forams

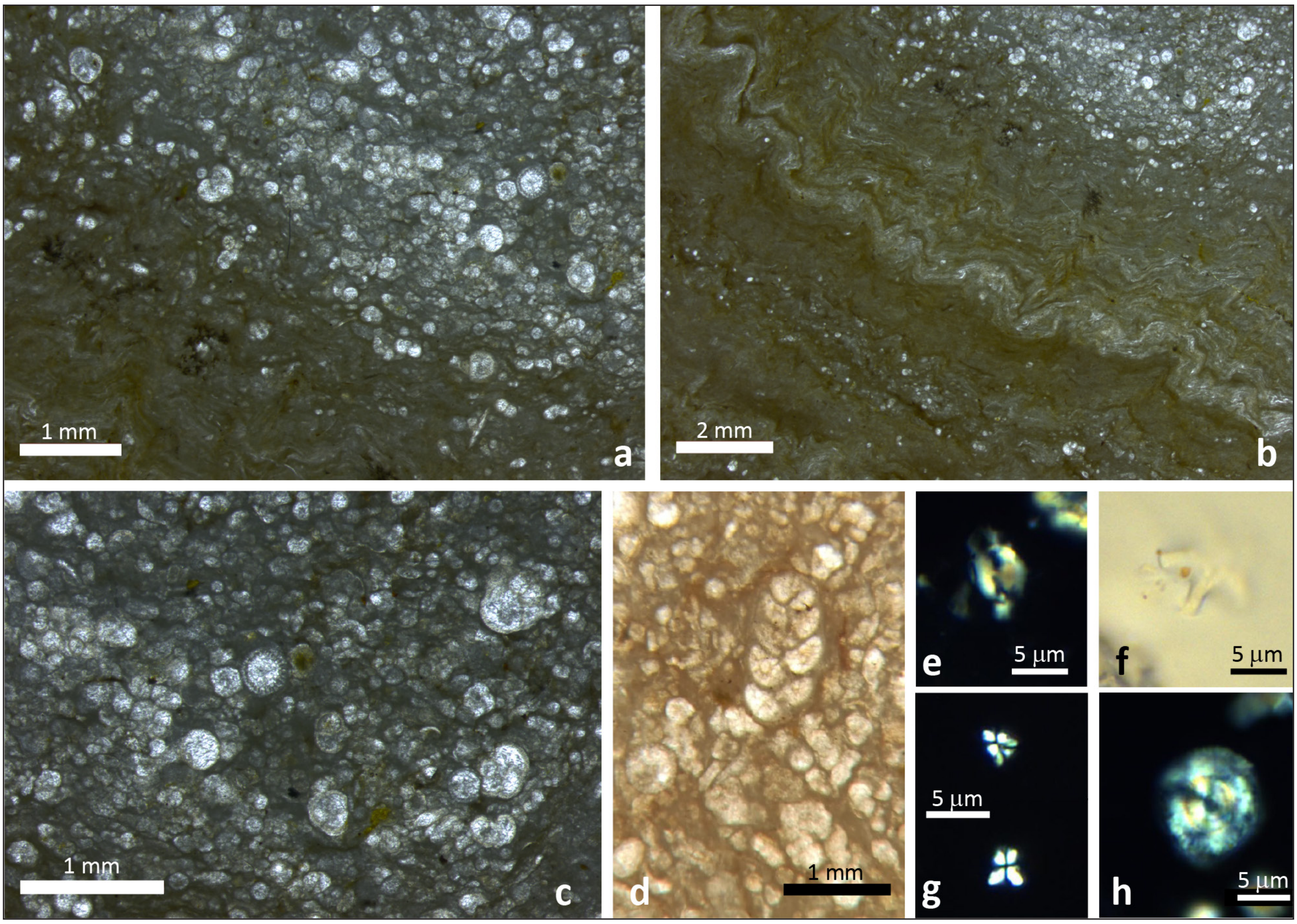


Fig. 4 - Selected microfacies, micro- and nannofossils from MUST 1/SF/2024. a) Thin section view of the glauconitic planktonic-rich facies with microbial laminae at the lower left side; b) stereoscopic view of the same thin section as in (a) with marked wavy microbial domed laminae; c) facies detail of the glauconitic planktonic-rich assemblage composed of foraminifera and radiolarians; d) indeterminate biserial benthic foraminifera; e) *Helicosphaera carteri*; f) *Discoaster druggii*; g) *Sphenolithus disbelemnos*; h) *Coccolithus miopelagicus*.

(*Globorotalia* sp., *Globigerinoides* sp., *Catapsydrax* sp.) of hemipelagic environment, along with some biserial foraminifera, that commonly occur in bathyal settings during the Early Miocene (Smart & Thomas 2006; Beldean et al. 2010).

The calcareous nannofossil assemblage (Fig. 4e-h) is well-preserved and includes *Coccolithus miopelagicus* Bukry, 1971, *Sphenolithus disbelemnos* Fornaciari & Rio, 1996, *Discoaster druggii* Bramlette & Wilcoxon, 1967, *Helicosphaera carteri* (Wallich, 1877) and other taxa. It can be referred to the MNN2b biozone (Burdigalian) due to the presence of *S. disbelemnos* and *H. carteri,* and the absence of *H. euphratis* Haq, 1966 and *S. belemnos* Bramlette & Wilcoxon, 1967 (Di Stefano et al. 2023). The data suggest an age interval for our sample bracketed between ~ 19.35 and 19.12 Ma (Fig. 5), therefore the studied lamniform specimen should be placed in the lower-middle part of the Bisciaro.

Facies analysis in thin section displays a glauconitic packstone with large amounts of radiolarians and planktonic foraminifera. The matrix closely embedding the vertebrae is instead interestingly characterised by a texture of superimposed thin filamentous laminae made of fine, lithified sediment (Fig. 4a, b). In a closer thin section view, a wavy morphology composed of dark-brown laminae, resembling filamentous bacteria, alternates irregularly with other brighter (likely dissolved) laminae (Fig. 4b). The general aspect strongly recalls biogenic activity (encrusting and binding) and sediment trapping. This suggests the occurrence of in-situ benthic precipitation of bio-laminated microbially induced sedimentary structure, which can be classified as a domed microbial mat (Flugel 2010; Noffke 2021). The position further indicates that such has grown next to or above the vertebral material, forming an encrusting community on the overall or some portions of the skeletal material. Furthermore, the occurrence of planktonic microfossils embedded into the wavy microbialites (Fig. 4) suggests growth and superimposition of bacterial laminae while receiving hemipelagic sedimentation. Therefore, these insights point out that microbialites have most likely formed over sunken, articulated, vertebrae of a shark carcass, in a deep-water marine bottom (see discussion in "taphonomic remarks" chapter).

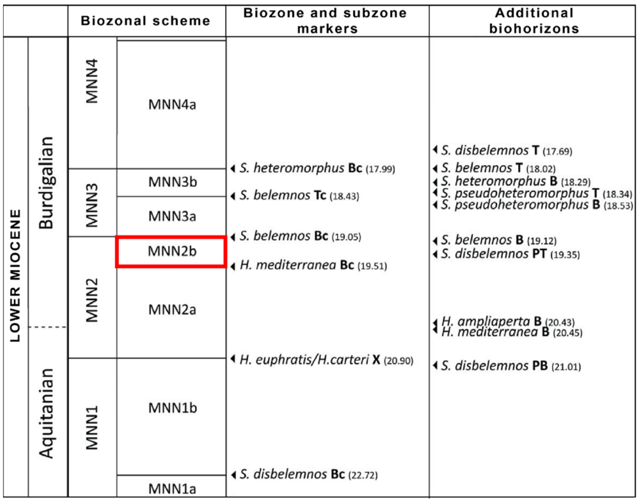


Fig. 5 - Lower Miocene calcareous nannofossil biozones; the range of the studied specimen is indicated in the red rectangle (modified after Di Stefano et al. 2023).

SYSTEMATIC PALAEONTOLOGY

Class CHONDRICHTHYES Huxley, 1880
Subclass ELASMOBRANCHII Bonaparte, 1838
Infraclass **Neoselachii** Compagno, 1977
Superorder **Galeomorphii** Compagno, 1973
Order **Lamniformes** Berg, 1958
Lamniformes indet.

Material: MUST 1/SF/2024; five vertebral centra embedded in the matrix (Figs. 2, 3).

Locality: Northern shore of the Fiastra Lake, Sibillini Mts., Central Apennines, Italy (Figs. 1, 2).

The CT-SCAN carried out on the rock sample MUST 1/SF/2024 has revealed a morphology in the sagittal, axial, and coronal sections inconsistent with the normal inclusions present within the rock. Repetitive elements have been identified along the entire structure, with secondary elements having run longitudinally throughout its entire length (Fig. 3b).

A digital cast has been obtained from the structure highlighted in the rock (Fig. 3c). The cast clearly shows that the shape can be attributed to a partially preserved section of the vertebral column, which has been highly deformed mostly by compaction during diagenesis (Fig. 3c).

Two of the most diagnostic and representative vertebrae were subsequently isolated, then retro-deformed (Fig. 6). The vertebrae exhibit an amphicoelous condition, consisting in two biconcave conical structures converging at the centre of the vertebral body, attributable to a selachimorph. The two ends are longitudinally connected by thin structures arranged parallel to the axis of the vertebra and interpreted as the external margin of the thin, closely spaced, and radially-oriented plates (lamellae) typical of lamniform sharks (e.g., Morse et al. 2022). An analysis of the thickness of different vertebral areas has shown that these skeletal elements are overall light, with the thickest region being the most reduced, identified exclusively in the cones (Fig. 7).

The morphology and distribution of bone thickness show that the vertebral body is composed of two different macrostructures, including the double cone and the longitudinal lamellae. The coronal section of the two retro-deformed vertebrae has provided a good projection of the radial orientation of the lamellae (Fig. 8a, b).

Vertebra 1, in particular, shows a highly branched pattern of the radially developing outline of the lamellae (Fig. 8c). In this case, it is possible to distinguish a clear asterospondylic radial condition (Ridewood 1921) with four types of lamellae, from a simple to a four-branched branching. Gaps are also distinguishable as empty spaces that have separated bundles of lamellae. The gaps represent the spaces where vertebral arches have been inserted (Ridewood 1921) and do not show traces or rudiments of additional lamellae in their empty spaces. Despite the strong deformation due to diagenesis, the preservation of vertebra 1 allowed the identification of up to ten growth rings (Fig. 9).

Although the vertebral growth seems to follow a constant pattern (Fig. 9b), the analysis of the reciprocal distance between the various growth rings has led to the distinction, at a different level of detail, of two different phases of development,

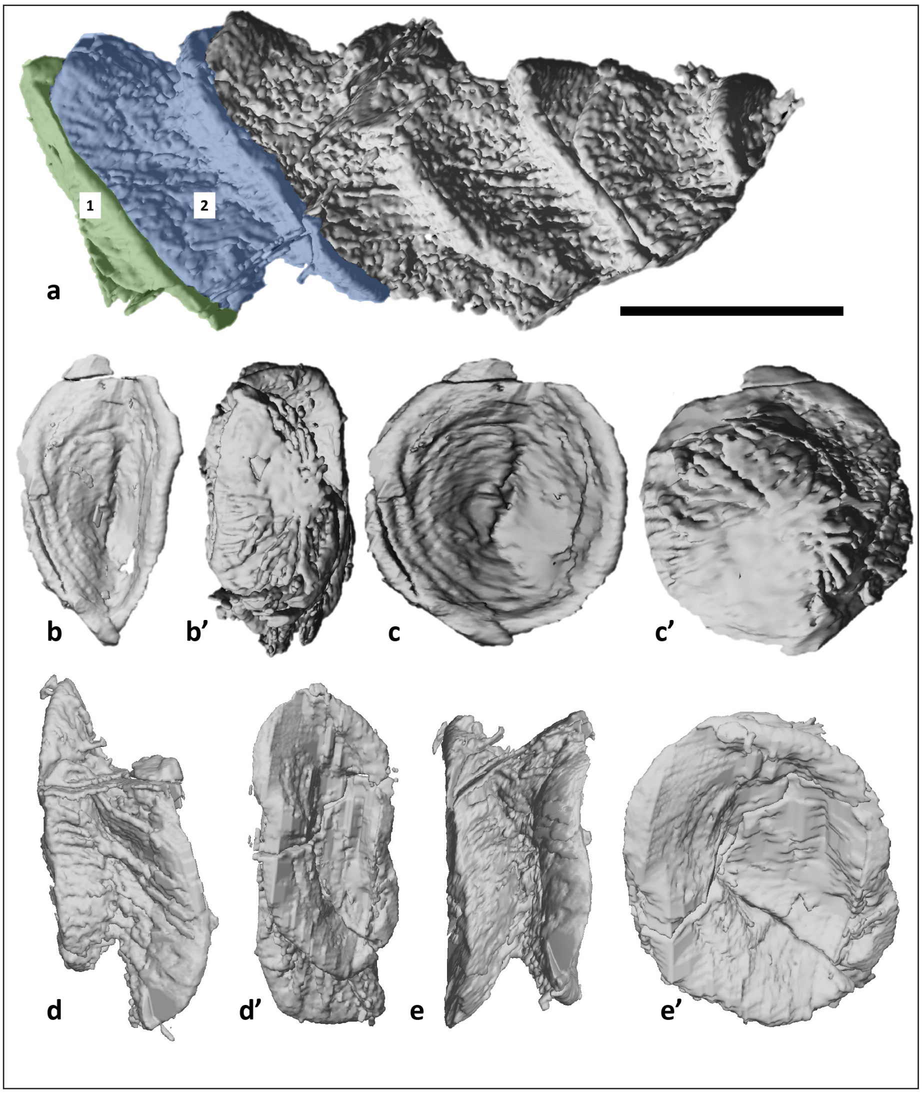


Fig. 6 - Digital cast of diagnostic vertebrae. a) Position of diagnostic vertebrae; b, b’) frontal and posterior view, respectively, of the vertebra 1 (compressed); c, c’) frontal and posterior view, respectively, of the vertebra 1 (retro-deformed); d, d’) lateral and frontal view, respectively of the vertebra 2 (compressed); e, e’) lateral and frontal view, respectively of the vertebra 2 (retro-deformed). Scale bar 5 cm.

in which a rapid increase is recognizable up to the seventh ring, then slowing down until the last ring (Fig. 9c).

The application of body length estimation formulas shown in Table 2 to the size of the retro-deformed vertebra 2 (Fig. 6) allows to estimate the

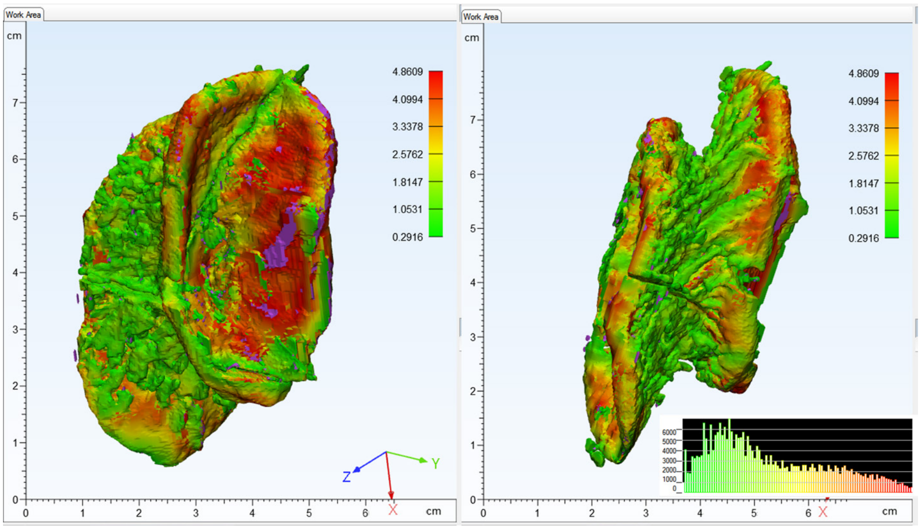


Fig. 7 - Thickness analysis in vertebra 2. False colour scale: mm.

Fig. 8 - Outline of the radial pattern of lamellae. a) Vertebra 2, midline section; b) vertebra 1, section proximal to the edge of the cone; c) silhouette of the asterospondylic pattern in vertebra 1.

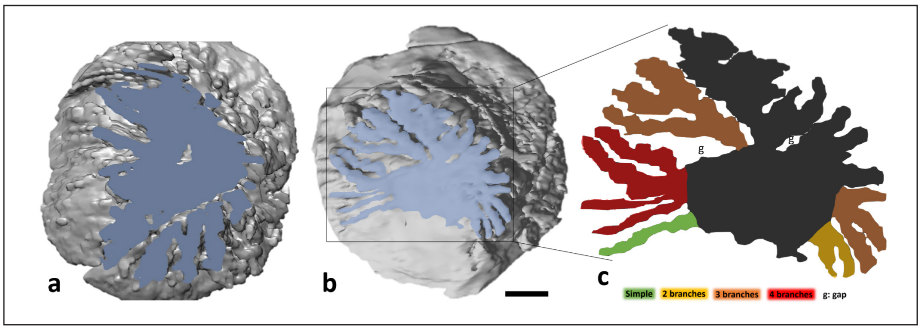
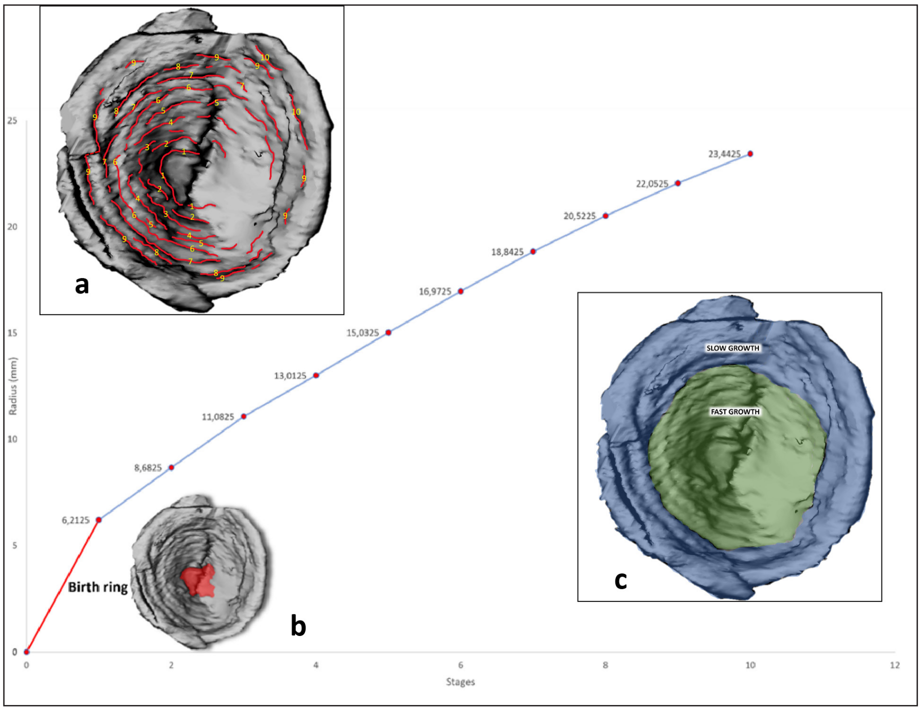


Fig. 9 - a) Annual bands in vertebra 1; b) ontogenetic development: x-axis: annual bands (stages); y-axis: radius of the vertebra; c) different phases of development based on the growth ring distances.



body length of the individual, which might have reached an average length of approximately 4 m (393.2-450 cm), with an estimated average length at maturity of 256 cm and length at birth of about 102 cm (Fig. 9b).

DISCUSSION

In this contribution, we present and describe the first large lamniform vertebrae from the Burdigalian of the Central Apennines. The five vertebrae, digitally isolated from the original limestone block thanks to the CT-SCAN technique, although quite deformed are in close contact, probably representing a short portion of articulated vertebral column. Considering that the block was found isolated on the outcrop, however, it cannot be excluded that the preserved and fossilized portion was originally more complete, before the erosion of the productive outcrop. However, it must be considered that a very common process in current fish and cetaceans is the progressive disarticulation of drifting carcasses, with portions of the body that can detach and reach the bottom with the progressive decay of muscles and connective tissues (Schäfer 1972). These processes make the presence of even very incomplete marine vertebrate specimens very frequent in the fossil record (e.g., Reisdorf et al. 2012; Boessenecker et al. 2014; Schmeisser McKean & Gillette 2015; Serafini et al. 2023). A similar possible explanation has been proposed by Serafini et al. (2023) to interpret eight imbricated or coin-stacked lamniform vertebrae from the abyssal Upper Cretaceous of the Northern Apennines (Italy).

Considering that the highly mineralized teeth have a very high fossilization potential, forming a large part of the shark fossil record, the most dia-

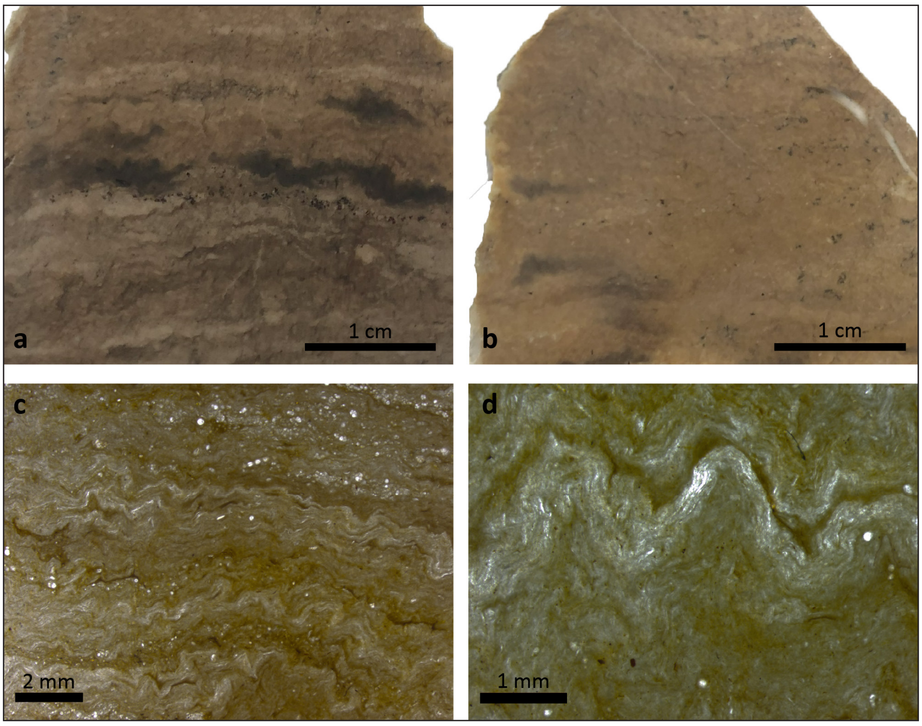


Fig. 10 - Close-up views of the domed microbial laminae embedding the vertebrae: a) and b) are obtained from polished slabs; c) and d) are obtained from thin sections. In (c) and (d), note the alternating dark and brighter thinner laminae, as well as the occurrence of plankton remains trapped within the laminae.

gnostic taxonomic characters even in lamniforms are largely based on tooth morphology. However, also being rare due to their cartilaginous composition (Compagno 1999; Dean & Summers 2006) and less diagnostic for taxonomy, especially if not associated with teeth (Shimada et al. 2006; Frederickson et al. 2015), the fossil shark vertebrae allow attribution in many cases at least at the order level, and can also provide other interesting and more solid information than that obtained from the teeth on the total length of the individual, ontogenetic state and age of the individuals (Frederickson et al. 2015). Furthermore, compared to the teeth, more or less complete portions of vertebral columns in fossil sharks can provide important additional palaeoecological and taphonomic information (e.g., Shimada 1997a; Blanco-Piñón et al. 2005; Newbrey et al. 2015; Amalfitano et al. 2017, 2019, 2022; Romano et al. 2021; Serafini et al. 2023).

The five vertebral centra studied here found in articulation show, once digitally retrodeformed, a fairly constant diameter with a maximum value of 6.4 cm and a mostly circular section. This character could allow us to attribute the portion of the vertebral column to the precaudal region, typically characterized by sub-circular centra, while in lamniformes the centra of the caudal region are greatly elongated dorsally-ventrally (Shimada & Cicimurri 2005; Shimada et al. 2006). From a taxonomic perspective, the asterospondylic condition observed in the studied specimen is limited to the superorder Galeomorphi, with two types that can be distinguished: the radial type and the maltese cross type (e.g., Cappetta 1987). The radial asterospondylic pattern is typical of the orders Lamniformes and Orectolobiformes (White 1937; Cappetta, 1987). According to Ridewood (1921), the condition expressed by orectolobiforms is simpler and characterised by thicker and less branched lamellae if compared to those of lamniforms (Ridewood 1921). In the case of the vertebral column MUST 1/SF/2024, the projection of the lamellar pattern in Figure 8 shows how the branching of the lamellae ranges from a simple single branch to four branches, with highly irregular interlamellar spaces (Ridewood 1921). In this perspective, the vertebral column MUST 1/SF/2024 can be confidently attributable to a lamniform shark. Another noteworthy detail in Figure 8 is the complete absence of diagonal lamellae within the identified gaps. The reduction or absence of diagonal lamellae is a characteristic of the families Lamnidae and Odontaspididae (Ridewood 1921), and this feature contributes to a secure attribution of MUST 1/SF/2024 within the Lamniformes, in one of the two families.

The size of the growth rings in vertebra 2 (Fig. 9) clearly shows a differential development before and after the seventh year of age, coinciding with the achievement of sexual maturity, during which the energy of somatic growth is channeled into gonadal development (Carlander 1969). The birth size estimate of MUST 1/SF/2024, when compared to living lamniforms, is similar to that expressed by the white shark *Carcharodon carcharias* (110 cm, Uchida et al. 1987). However, there are significant differences between these species in terms of the age at which they reach maturity, which is slower in *C. carcharias*, estimated to be around 8-10 years at lengths of 3.6-4.3 m (Cailliet et al. 1985), and faster for MUST 1/SF/2024, at around 7 years and a length of 2.6 m. In this perspective, the estimates at maturity of MUST 1/SF/2024 are more comparable to those of the Mako shark (*Isurus oxyrinchus* Rafinesque, 1810) having age at maturity of 7 - 8 years and length at maturity of 275 – 293 cm (Newbrey et al. 2015).

If compared with the data in the fossil record, the characteristics of MUST 1/SF/2024 closely resemble Cretaceous species such as *Archaeolamna kopingensis* (Davis, 1890) (birth ring 5.5 mm, Newbrey et al. 2015) and *Cardabiodon ricki* Siverson, 1999 (Cenomanian – Turonian, Newbrey et al. 2015), the latter showing the closest similarity, with a birth ring radius of 3.5 – 6.6 mm and maturity at 5 - 7 years. Different values are found for another Cretaceous species known as *Cretoxyrhina mantelli* Agassiz, 1843, significantly larger, with a birth ring of 11.3 mm and an estimated birth length greater than 1.2 m (Shimada 2008). Values for the large Cenozoic sharks (see Shimada et al. 2017 for a discussion on the taxonomic status of the Family Otodontidae) such as *Otodus obliquus* Agassiz, 1843 (birth ring 8.4 – 10.4 mm) and *Otodus megalodon* Agassiz, 1843 (birth ring 16.6 mm) are far away, resulting in birth sizes of 97 - 120 cm for *O. obliquus* and over 1.9 m for *O. megalodon* (Frederickson et al. 2015). This evidence seems to align the biology of MUST 1/SF/2024 with that of living sharks of the Family Lamnidae.

Taphonomic Remarks

From a taphonomic point of view, the vertebral centra, as already stressed above, are quite deformed, with the major axis of compression perpendicular to the bedding surface. This element indicates that the deformation can be largely linked to compaction due to simple lithostatic weight during diagenesis.

An interesting taphonomic evidence observed both by eye and on the microscope is the presence of a domed microbial mat encrusting portions of the vertebral material (Figs. 4, 10). Occurrence of microbial mats on sunken carcasses is known from modern and fossil ecosystems of the so-called ‘whale-fall’, documented from cetacean remains slowly decomposing in deep water bottoms (Allison et al. 1991; Goedert et al. 1995; Deming et al. 1997; Smith & Baco 2003). Once a large marine vertebrate falls on the seafloor it becomes a consistent entrance of organic matter in the deep sea, exploited by at least three successional ecological stages called i) mobile-scavenger stage; ii) enrichment opportunist stage, and iii) sulphophilic stage. The last one is the longest-lived and includes the occurrence of sulfur-oxidizing bacteria growing on the bones by feeding sulfide from lipids secreted by the carcass (see Smith & Baco 2003 for further information). Although traces can be found in fossil whale-falls, including shells of cold-seep chemosymbiotic molluscs (Goedert et al. 1995), it is unclear in the literature whether comparable ecological stages alternate also on other, non-whale remains, such as sharks.

Marine vertebrate ‘dead-fall’ (*sensu* Higgs et al. 2014) have also been described for Mesozoic marine vertebrates (Martill 1987; Hogler 1992; Kaim et al. 2008; Danise et al. 2014; Dick 2015; Maxwell et al. 2022; Serafini et al. 2024), largely marine reptiles however with a possible case also in Cretaceous lamniforms (Serafini et al. 2023). Danise et al. (2014) describe a dead-fall community in ichthyosaurs from a Late Jurassic shelf setting of the upper Oxfordian Sandsfoot Formation (Dorset, UK). In this case, for example, the early ‘mobile-scavenger’ and ‘enrichment-opportunist’ stages were not followed by the ‘sulphophilic stage’; differently, microbial mats developed on the bones than attracting mat-grazing invertebrates, with echinoids among the most abundant (Danise et al. 2014). Serafini et al. (2023) report a peculiar dead-fall community characterized by the putative association of a medium-sized anacoracid shark and an ichthyosaur from the deep-water sediments of the Cenomanian of the Northern Apennines. While the ichthyosaur specimen shows a clear presence of pyrite connected to the microbial decomposition of the organic matter that impregnated the vertebrae (via mobilization of S-bearing compounds), such evidence of sulphophilic stage has not been observed in the vertebrae of the anacoracid shark. However, the authors report the presence in the block containing the shark vertebrae

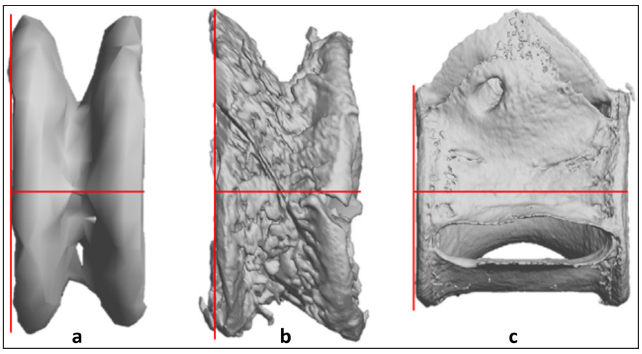


Fig. 11 - Vertebra height/length ratio of: a) *Carcharodon carcharias*, Lamniformes; b) MUST 1/SF/2024; c) *Squalus acanthias*, Squaliformes (outgroup). Height/length ratio: *C. carcharias*=2.40; MUST 1/SF/2024= 2.27; *S. acanthias* = 1.

of possible traces of locomotion and feeding left by arthropods (*Taenidium* borrows) which, according to the authors, could be indicative of an enrichment opportunistic stage (Serafini et al. 2023).

Regarding the here studied shark vertebrae, the development of an encrusting bacterial community most likely reduced the possibility of ablation before final burial, playing a pivotal role in keeping vertebrae in anatomical connection. This evidence also indicates that the skeleton was not immediately buried by the sediment but must have remained exposed on the surface for at least the time necessary for all soft tissues to decay and for the development of the preserved microbial mat. One possibility is that the portion of the vertebral column was partially buried in the sediment, preventing it from disarticulating on the seabed, with an exposed portion where microbial encrustations developed.

Which kind of shark was the studied specimen?

The size proportions of the vertebrae of MUST 1/SF/2024 are consistent with those of various lamnid taxa (Figs. 6, 11). Vertebral proportions are not strictly linked to phylogenetic lines but rather adhere more to ecological adaptations (Buchholtz & Schur 2004; Romano et al. 2021). The vertebrae of MUST 1/SF/2024 are highly compressed, with a high height/length ratio (=2.27), and a strong morphometric convergence has been found with the high height/length ratio of *C. carcharias* (=2.40) (Fig.11).

According to several authors (Shimada 1997a, 1997b, 2007; Shimada & Cicimurri 2005), sub-circular vertebral centra are typical of fusiform pelagic sharks, while vertebrae with a general dorsal-ventrally flattened outline characterize true benthic sharks. Furthermore, the presence of numerous compressed vertebral centra, as observed in the vertebrae under study, is typical of carangiform swimmers (Newbrey et al. 2015), i.e., sharks which exhibit great maneuverability despite being moderately fast. Differently, relatively long vertebral centra would be typical of sharks with thunniform swimming mode, characterized by higher swimming speeds (Newbrey et al. 2015). Highly compressed vertebrae, with a high height/length ratio, provide considerable flexibility to the column, especially in the caudal region which is more subject to deformation being the main propulsive structure (Buchholtz & Schur 2004). The morphology of the vertebrae of MUST 1/SF/2024, similar to that of *C. carcharias*, presents particularly rounded edges which, together with the relative proportions, further facilitates the reciprocal movement of the vertebrae in the column, increasing its flexibility. The elasticity conferred to this type of vertebral column allows for a carangiform swimming shape (Fig. 12), which offers a good compromise between high-speed performance and maneuverability in water (Di Santo et al. 2021).

It is therefore highly likely that MUST 1/SF/2024 exhibited similar performance to those shown by other lamniforms such as *C. carcharias*, in an effective adaptation probably for certain trophic habits, such as the active hunting of large prey.

CONCLUSIONS

In this contribution, we report and describe the first large lamniform vertebrae from the Lower Miocene (MNN2b nannofossils biozone - lower Burdigalian, ~19.35-19.12 Ma) of the Central Apennines. The study confirms CT-SCAN methods and digital post-processing as invaluable for analysing fragile materials without causing irreversible damage. The approach used has allowed us to digitally extract the vertebrae in their current condition and digitally retrodeform them to study the general structure and attempt a possible estimate of the length of the individual in life. This pro-

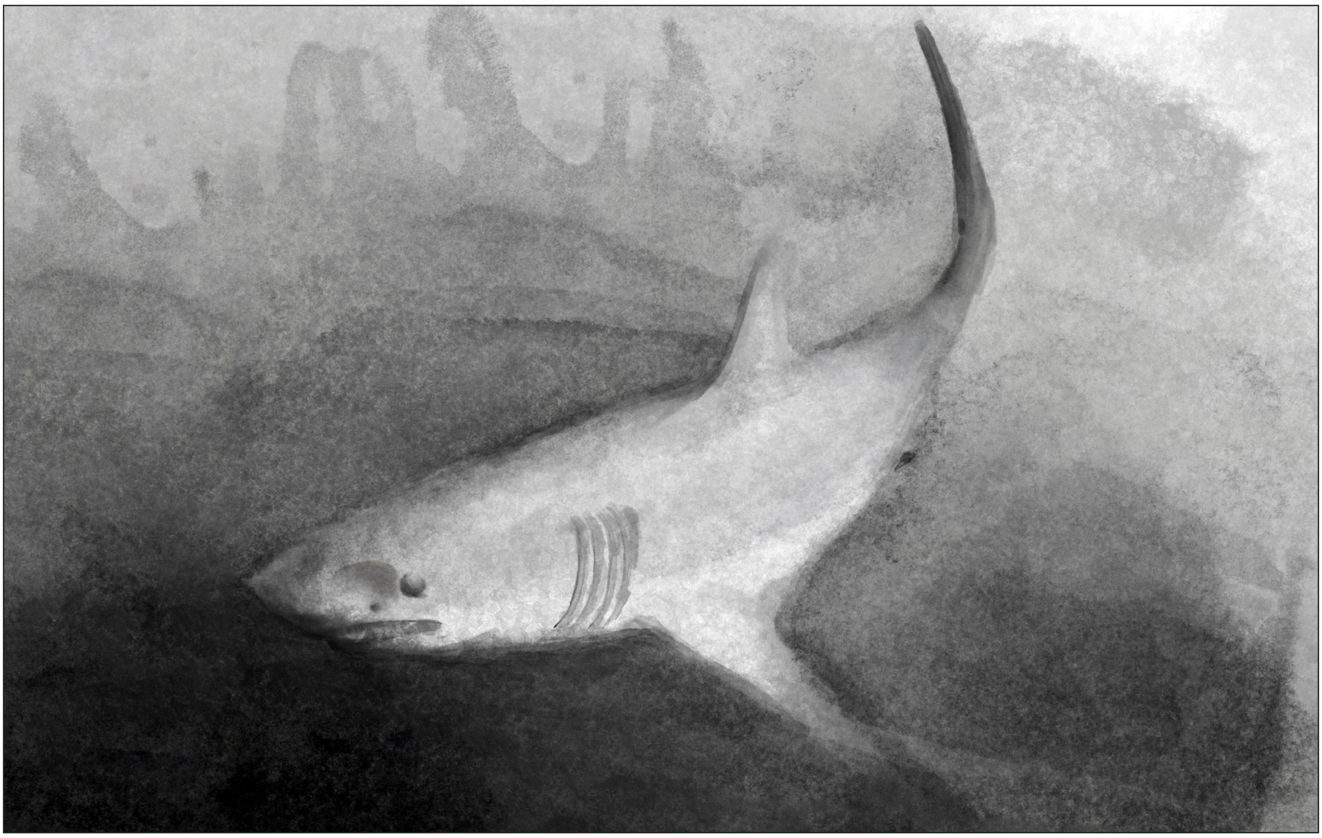


Fig. 12 - Artistic representation of the studied shark (drawing by A. Moscarella).

cess was also facilitated by the possibility of 3D printing both the original specimen and the model after retrodeformation. The characters observable in the vertebral centra thanks to this approach and in particular the projection of the lamellar pattern and reduction or absence of diagonal lamellae, have allowed a solid attribution to Lamniformes, with greater affinity with the families Lamnidae and Odontaspididae.

The detailed analysis of the reciprocal distance between the various growth rings in the best-preserved centra led to the identification of a faster first phase of development up to the seventh ring, followed by a slower phase up to the last observable ring. The count of 10 preserved rings leads to a minimum conservative estimate for the specimen of at least 10 years, with an age maturity at 7-8 years, comparable with that of the Mako shark (*Isurus oxyrinchus*).

Due to their essentially articulated arrangement and the congruity of the absolute dimensions, all the centra refer to the same portion of the vertebral column. In particular, the short structure of the centra would indicate that the vertebrae come from the pre-caudal portion and therefore can be used as sufficiently plausible proxies for the possible estimate of the total length of the shark in life. The largest preserved centrum with a diameter of 6.3 cm provided an average length of about 4 m, an estimate to be considered as a minimum value since the centrum with the largest diameter was not necessarily preserved. The presence of sub-circular and consistently compressed anteroposteriorly vertebrae is typical of fusiform pelagic sharks with a carangiform swimming mode, providing considerable flexibility to the column with a good compromise between high-speed performance and maneuverability.

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