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RESEARCH ARTICLE

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Hybodont dentition from the Upper Jurassic of Monte Nerone Pelagic Carbonate Platform (Umbria-Marche Apennine, Italy) and its ecological implications

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Here we describe a number of articulated teeth of a hybodont shark from Upper Jurassic deposits of the Monte Nerone Pelagic Carbonate Platform, in the Umbria-Marche-Sabina Palaeogeographic Domain (Northern Apennines, Central Italy). The material has been referred to as *Asteracanthus* cf. *A. magnus*, a quite well-known taxon already reported from Middle to Upper Jurassic deposits of Europe. Teeth indicate an extreme crushing feeding behaviour, suggesting as putative prey both infaunal and epifaunal hard-shelled invertebrates dwelling the sea-floor, such as large bivalves, brachiopods, gastropods as well as vagile crustaceans. The finding represents, to date, the first formal report of hybodont shark in the Umbria-Marche-Sabina Domain, throwing further light on the ecology within Pelagic Carbonate Platform settings, and on the occurrence of *Asteracanthus* in the Late Jurassic of the Western Tethys.

KEYWORDS
hybodont shark, Late Jurassic, palaeoecology, Pelagic Carbonate Platform, Umbria-Marche-Sabina Domain

1 | INTRODUCTION

Hybodont sharks were the dominant group of chondrichthyans during the Triassic and Early Jurassic, declining in diversity from the Middle Jurassic up to their extinction close to the Cretaceous-Palaeogene boundary (Rees & Underwood, 2005, 2008). This decline, mostly in marine palaeoenvironments, was deemed a consequence of increasing competition due to the latest Triassic radiation and further diversification of neoselachian sharks and rays, as well as teleost actinopterygians (Underwood, 2006). On the contrary, a great Early Cretaceous diversity among hybodont sharks was reported in marginal marine settings up to lagoon and freshwater palaeoenvironments, where neoselachians were rare, if not absent (Cappetta, Buffetaut, Cuny, & Suteethorn, 2006; Cuny, 2012; Cuny et al., 2004; Cuny, Suteethorn, Kamha, & Buffetaut, 2008; Cuny, Suteethorn, Kamha, Buffetaut, & Philippe, 2006; Patterson, 1966; Rees & Underwood, 2005; Underwood, 2006; Underwood & Rees, 2002).

Here, we describe and discuss the first finding of a hybodont shark in the Umbria-Marche-Sabina (hereafter UMS) Domain, within the Western Tethyan palaeoecological/palaeoenvironmental framework presently recorded in the Central and Northern Apennines. The specimen was collected as loose material (43° 34′ 01.59″ N, 12° 31′ 03.41″ E), exposed in Upper Jurassic deposits cropping out crossing the well-known (Alvarez, 1989a, b; Cecca, Cresta, Pallini, & Santantonio, 1990; Centamore, Chiocchini, Deiana, Micarelli, & Pieruccini, 1971; Immerz, 1985; Santantonio, 1993, 1994; Zittel, 1870) Monte Nerone Pelagic Carbonate Platform (hereafter PCP—sensu Santantonio, 1994), in the Northern Apennines, on the north-northeastern slope of Monte Nerone, facing the Infernaccio gorge ("Sezione dell'Infernaccio"—Cecca et al., 1990; Centamore et al., 1971). The area, about 1,200 m a.s.l. and 1,5 km SE of the village of Piobbico (PU), can be easily reached along the mountain road that start from Acquanera locality, along the "Strada Provinciale 82 - Rocca Leonella", and ends at the Monte Nerone summit (1,525 m a.s.l.; Figure 1).

In the text that follows, we describe the new material referable to the hybodont genus *Asteracanthus*, also discussing its ecological implications for the Umbria-Marche-Sabina Domain.

2 | MATERIAL AND METHODS

The shark material consists of five teeth in anatomical connection (two groups consisting of three and two teeth, respectively), and some fragments encased in the carbonate matrix. The specimen, whose size is about 13 × 6 × 4 cm, is presently deposited at Museo Universitario di Scienze della Terra, Sapienza University of Rome and labelled as MPUR NS 167.1 (MPUR NS: Museo di Paleontologia University di Roma, Nuova Serie; Figure 2). The specimen was scanned at the Museum für Naturkunde Berlin using X-ray computed tomography (phoenix|X-ray nanotom s) at 130 kV, 240 μA for 1,400/360° projections/segment of the multiscan, and an exposition timing of 750 ms/projection. The specimen was scanned at a magnification ratio of ×1.54100859 and an effective voxel size of 0.03244628 mm as well as an additional calibration value of 0.5780. A 0.5 mm cu filter was used to compensate for the high current. Cone beam reconstruction out of 1,400 saved 16bit—tagged image files was performed using datos|x-reconstruction software (GE Sensing and Inspection Technologies GmbH phoenix|X-ray). The multiscan was merged, and all scans were visualized and segmented in VG Studio Max 3.0.

A thin section of the sample was prepared, both for observing microfacies and dental structure and for micropalaeontological analysis to fix the relative age of the specimen. The thin section is presently deposited at Museo Universitario di Scienze della Terra and labelled as MPUR NS 167.2.

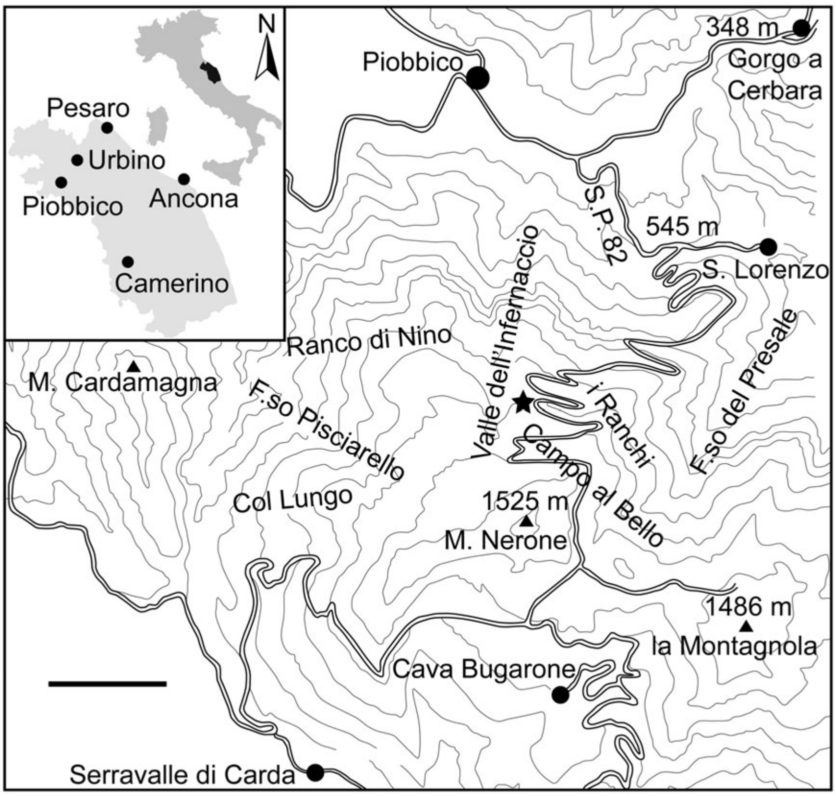

FIGURE 1 Location map of "Infernaccio" stratigraphical section in the Monte Nerone area. Black star indicates the site where the discussed material was found (43° 34′ 01.59″ N, 12° 31′ 03.41″ E). Spacing of contour lines equals to 100 m altitude. Scale bar equals to 1 km

FIGURE 2 Teeth-bearing specimen NS 167.1 from the "Infernaccio" stratigraphical section (Monte Nerone area). Scale bar equals to 3 cm [Colour figure can be viewed at wileyonlinelibrary.com]

A three-dimensional photogrammetric model of the specimen was made using a 24 Megapixel Canon EOS 750D (18 mm focal length). The software used to build a photogrammetric model is Agisoft PhotoScan Pro, already successfully applied both in the geological and palaeontological field (e.g., Breithaupt, Matthews, & Noble, 2004; Cipriani, Citton, Romano, & Fabbi, 2016; Citton et al., 2017; Citton, Nicolosi, Carluccio, & Nicosia, 2016, Citton, Nicosia, Nicolosi, Carluccio, & Romano, 2015; Díaz-Martínez, González, & De Valais, 2017; Fabbi, Romano, Citton, & Cipriani, 2016; Lomax, Falkingham, Schweigert, & Jiménez, 2017; Mallison & Wings, 2014; Pesci et al., 2016; Petti et al., 2008; Romano, Brocklehurst, & Fröbisch, 2017; Romano & Citton, 2016). A 3D PDF of the obtained model is provided in the Supplementary Information.

3 | GEOLOGICAL SETTING

The Monte Nerone area belongs to the UMS Domain in Central and Northern Apennines, where a well-known Upper Triassic-to-Neogene stratigraphic succession is exposed (Centamore et al., 1971; Cipriani, 2016; Colacicchi, Passeri, & Pialli, 1970; Donatelli & Tramontana, 2014; Fabbi, 2015; Fabbi & Santantonio, 2012; Farinacci, 1967; Farinacci, Mariotti, Nicosia, Pallini, & Schiavinotto, 1981; Galluzzo & Santantonio, 2002; Pierantoni, Deiana, & Galdenzi, 2013). In particular, the Jurassic-Cretaceous stratigraphy of Monte Nerone area was extensively studied in the past (e.g., Cecca et al., 1990 and references therein).

In the area throughout the UMS Domain, Jurassic sedimentation was strictly controlled by a submarine palaeotopography inherited by a strong Early Jurassic extensional phase (Bernoulli, 1967; Bertotti, Picotti, Bernoulli, & Castellarin, 1993; Centamore et al., 1971; Colacicchi et al., 1970; Farinacci et al., 1981; Santantonio & Carminati, 2011).

Since the late Hettangian, this extensional phase fragmented the vast "Calcare Massiccio" carbonate platform, producing a complex setting of structural highs and lows, where the drowning of the carbonate platform and the consequent onset of pelagic sedimentation occurred differently and diachronically. In the hanging-wall blocks of Jurassic normal faults, characterized by very rapid tectonic subsidence, the termination of shallow-water carbonate production occurred as soon as the early Sinemurian (Passeri & Venturi, 2005). The structural highs, by contrast, remained at very low bathymetry, so that the carbonate factories remained active until the early Pliensbachian (*ibex* Biozone—Morettini et al., 2002), when their drowning occurred simultaneously in the whole UMS Domain, possibly due to marine water environmental perturbations (Marino & Santantonio, 2010). From the early Pliensbachian to Early Cretaceous, the whole UMS Palaeogeographic Domain was dominated by pelagic sedimentation which slowly filled the basin up to blanket the palaeotopographic gaps, albeit with local exceptions (see Cipriani, 2016, 2017; Fabbi, Citton, Romano, & Cipriani, 2016). The structural lows were filled by some hundred metres-thick successions, whereas on the structural highs the same time span was covered by some tens to some metres-thick condensed successions, in settings commonly known as "Pelagic Carbonate Platforms" (Catalano, Channel, D'Argenio, & Napoleone, 1976; Santantonio, 1993, 1994; see also Flügel, 2010 for a brief critical revision of the nomenclature of condensed pelagic carbonates). Rocks pertaining to this depositional context are, by definition, characterized by condensed facies and, with regard to stratigraphic nomenclature, are referred to as the "Bugarone Group" following Cecca et al. (1990) and Galluzzo and Santantonio (1994, 2002; but see Centamore et al., 1971 for a different nomenclatural assessment). This lithostratigraphic unit encompasses a time span ranging from the late Pliensbachian to the Tithonian and includes a major late Bajocian–early Kimmeridgian stratigraphic gap (Cecca, Cresta, Pallini, & Santantonio, 1985).

3.1 | Geology of Monte Nerone

Monte Nerone was a flat-topped PCP (Santantonio, 1994), albeit with local exceptions (see below), characterized by an up to 40-m-thick late Pliensbachian to early Tithonian succession with typical features of condensed pelagic facies association (facies association A of Santantonio, 1993). According to Santantonio (1993), the northern sector of the Monte Nerone PCP, from which the vertebrate remains under study came from, passed from a flat-topped setting (PCP type 1 of Santantonio, 1994) to a low-angle ramp-like depositional environment in the Middle Jurassic. This newly formed architecture was probably related to a late Aalenian (Cecca et al., 1990) syn-sedimentary extensional perturbation, that caused a stepping of the northern PCP margin, a minor tilting of the northern hanging-wall block and the formation of a depocenter towards the south (perched basin at stepped PCP margin of Santantonio, 1994). This instability triggered sediments sliding, as suggested by soft-sediment deformations in Aalenian deposits of the "Infernaccio" stratigraphical section (Cecca et al., 1990), where S-dipping scars and S-verging slumps (retrodeforming the Miocene orogenic deformations) permit to recognize the existence of a S-dipping palaeoslope. Moreover, the syn-sedimentary tilting would provide the accommodation space for a cherty unit wedging between early Bajocian and early Kimmeridgian condensed deposits (Santantonio, 1993), which sounds unusual for PCP successions that are anywhere chert-free. The same applies to gravity-driven deposits, usually absent in PCP-top condensed succession according to Santantonio (1993). Indirect evidence for Middle Jurassic tectonics comes from the Gorgo a Cerbara area (north-eastern part of Monte Nerone) also, where slumps embedded in Aalenian basinal pelagites of the thicker hanging-wall block succession (Calcari e marne a Posidonia Fm.) were recognized.

3.2 | Biostratigraphical constraints

The study specimen was found by one of the authors (P.C.) as loose material near the top of Monte Nerone. Thus, the exact stratigraphic position of the sample in the exposed succession is unknown. A thin section of the sample was produced for microscopical analysis, involving part of a tooth (Figure 3, discussed below) and the embedding pelagites. Texturally, the microfacies of the encasing limestone is a pervasively dolomitized, burrowed, bioclastic mudstone/wackestone. The sample include biomarkers, which can be used to determine the age of the sediment encasing the shark teeth, in order to put the sample in a well-constrained stratigraphic context.

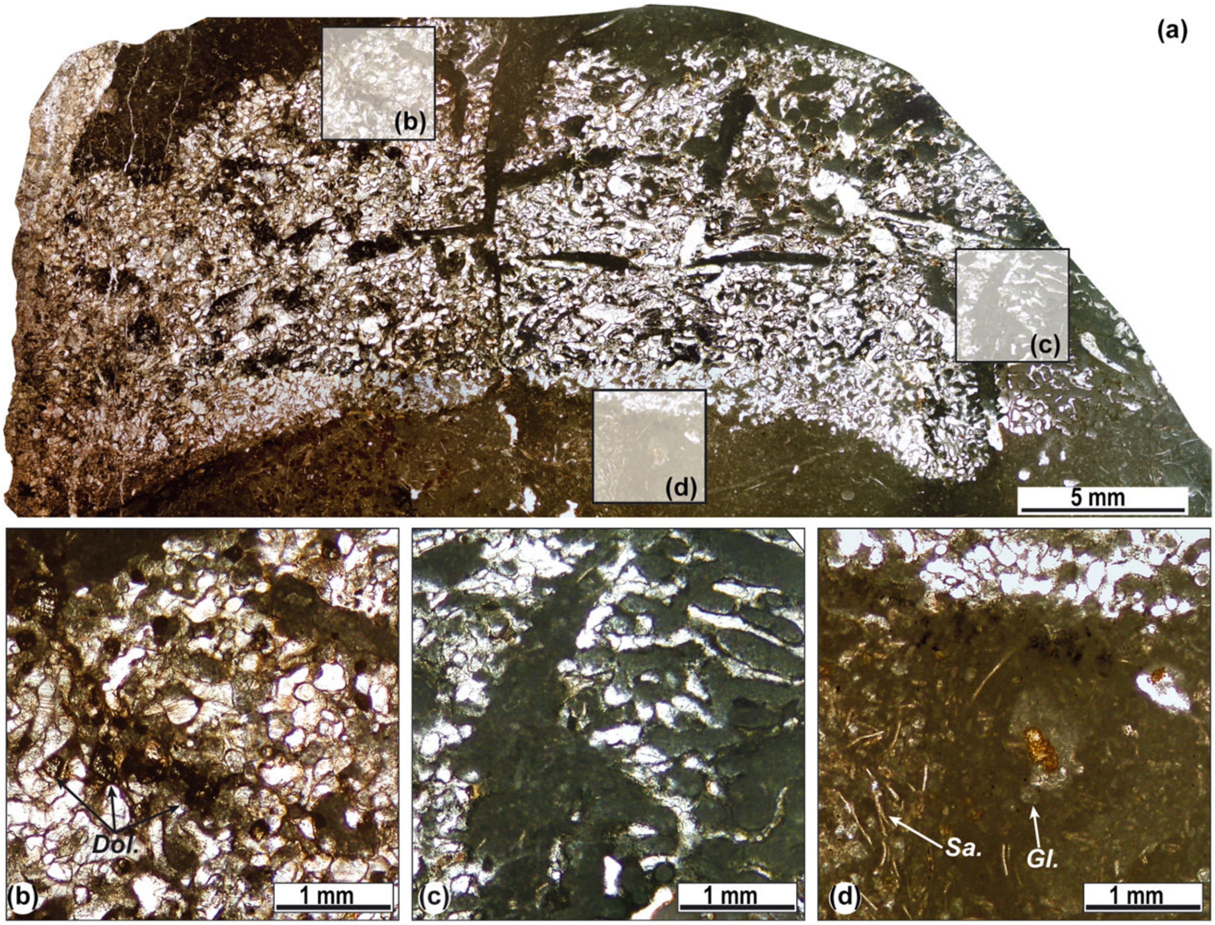

FIGURE 3 Thin section (NS 167.2) microphotographs of the study specimen. (a) Panoramic view of the thin section. The sample is dominated by the tooth, embedded in partially dolomitized lime mud and associated with pelagic fauna. (b,c) Details of the tooth, where the vascularization of the dentine is appreciable. The vascular canals are filled by carbonate mud, locally replaced by dolomite crystals (*Dol.*). (d) Particular of the teeth-embedding pelagites; the microfacies is dolomitized bioclastic mudstone-to-wackestone with vertebrate remains. The pelagic fauna is represented by fragments of *Saccocoma* (*Sa.*) and by specimens of *Globuligerina oxfordiana* (*Gl.*) [Colour figure can be viewed at wileyonlinelibrary.com]

These fossil remains are represented by fragments of crinoids belonging to the genus *Saccocoma* and by the thin-shelled (sensu Giovagnoli & Schiavinotto, 1987) "pelagic" foraminifer *Globuligerina oxfordiana* (Figure 3d). The ecological event represented by the mass occurrence of the genus *Saccocoma* is dated, at a regional scale, to the latest early Kimmeridgian (Paparella, Maxwell, Cipriani, Roncacè, & Caldwell, 2016 and references therein). Two species of *Saccocoma* characterize the Upper Jurassic stratigraphic record of the Western Tethys: *Saccocoma tenella* and *Saccocoma vernioryi* (Manni & Nicosia, 1994). The study deposits contain abundant *S. tenella*, while *S. vernioryi* is absent. While *S. tenella* characterizes all the stratigraphic distribution of the "pelagic" crinoids (latest early Kimmeridgian–late Tithonian), *S. vernioryi* is only recorded from the lower to middle Tithonian in the Central and Northern Apennines (Manni & Nicosia, 1984). Moreover, chitinoidellids are absent in our thin-section; according to Andreini, Caracuel, and Parisi (2007) and Lakova and Petrova (2013), the chitinous forms appear all over the Tethys in the latest early Tithonian. These data, coupled with the presence of *Globuligerina oxfordiana* that characterizes the Bajocian and Kimmeridgian facies of the UMS basin, allow to constrain the age of the teeth to the late early Kimmeridgian–earliest early Tithonian (Figure 4). This would make the occurrence of the specimen coincident with the deposition of the "Bugarone superiore Fm." on the PCP-tops or of the "Calcari ad aptici e *Saccocoma* Fm." in the basins (Galluzzo & Santantonio, 2002). The Upper Jurassic deposits outcropping at the Infernaccio stratigraphical section (Cecca et al., 1990) are mainly represented by nodular, intensely dolomitized and bioturbated mudstones/wackestones, resulting in places very rich in terebratulid brachiopods, ammonites, and bivalves, mainly in centimetric to millimetric fragments. A sketch of the stratigraphical column of the Infernaccio section is reported in Figure 5.

4 | SYSTEMATIC PALAEONTOLOGY

The taxonomy used in this paper is based on Guinot, Cappetta, and Adnet (2014).

Class	Chondrichthyes Huxley, 1880
Subclass	Elasmobranchii Bonaparte, 1838
Cohort	Euselachii Hay, 1902
Superfamily	Hybodontoidea Owen, 1846
Family	Acrodontidae Casier, 1959
Genus	*Asteracanthus* Agassiz, 1837
Species	*Asteracanthus* sp. cf. *A. magnus* Agassiz, 1838

Figures 2, 3 and 6, 7

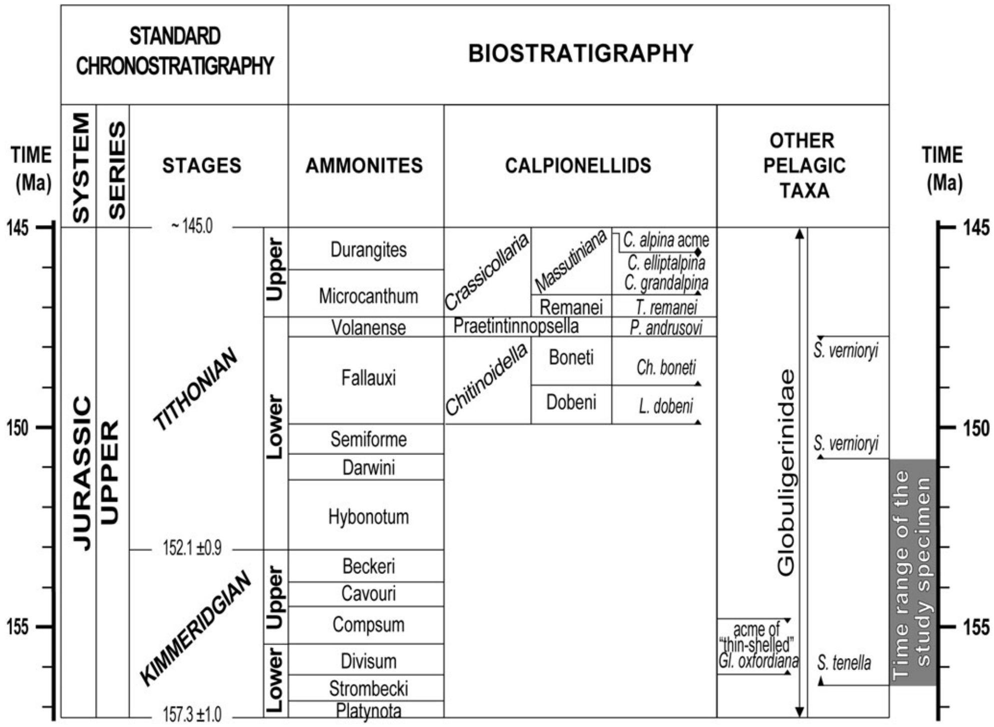

FIGURE 4 Chrono- and biostratigraphic scheme of the Upper Jurassic in Western Tethys realm. Ammonites' biozones are correlated with calpionellids biozones and other pelagic taxa that characterize the stratigraphic record of the study area (modified from Hardenbol et al., 1998)

4.1 | Description

The sample is a light grey to whitish mudstone bearing teeth both exposed on a surface and partially included in the carbonate mud. Teeth seem to be in the original articulated pattern and are arranged exposing the occlusal surface, so as the ornamentation of the crown is observable (Figure 6a,c,e).

Two of the largest teeth (i.e., Teeth 2 and 3 of Figure 6a–d) have a flat occlusal surface with a mostly rectangular outline in occlusal view, whereas in Tooth 1 the occlusal surface is slightly domed (Figure 6e,f). The ornamentation is finely reticulate, densely pitted, and without any trace of a clear occlusal crest. The smaller teeth (Teeth 4 and 5 in Figure 6a–d) are at a distance ranging from 2.5 to less than 1 cm from the largest ones; they are ovoid in occlusal view and characterized by the same finely reticulate ornamentation. They lack the occlusal crest, observed in the largest ones. Another tooth is preserved on the surface but a large portion, subtriangular in morphology (as obtainable from the impression left in the matrix), was lost, and a small part is covered by sediment, so that only a vertical section of the crown can be observed on the sample (Tooth 6, Figure 6c,d).

In thin section, the tooth structure presents alveolar-shaped vascularized osteodentine, reticulate setting of dentinal tubules (Figure 7b,c), with large vascular canals filled by pelagic mud (Figure 3b,c; see also pl. 5, Figure 4, 10 in Rees & Underwood, 2008).

Based on this general description of the teeth, the material under study is tentatively referred to as *Asteracanthus* cf. *A. magnus* (see Rees & Underwood, 2008, for a comprehensive description of characters among different species within the genus *Asteracanthus*). According to Rees and Underwood (2008), the Family Acrodontidae Casier, 1959, in which the genus *Asteracanthus* Agassiz, 1837 is included, gathers hybodont sharks equipped with a crushing dentition. With respect to some other species within the genus, taking into account only the characters we were able to observe and excluding taxa based on fin spines (e.g., *A. acutus* Agassiz, 1837; *A. semisulcatus* Agassiz, 1837; *A. granulosus* Egerton, 1854; *A. semiverrucosus* Egerton, 1854; *A. verrucosus* Egerton, 1854; *A. aegyptiacus* Stromer, 1927—see Rees & Underwood, 2008, p. 132), we can exclude: (a) *Asteracanthus medius*, because lateral teeth referred to this species commonly exhibit a more pronounced domed morphology; (b) *Asteracanthus ornatissimus*, due to its unique ornamentation, characterized by a complex pattern of enameloid folds, and prominent occlusal crest, which is displayed by all teeth regardless of their position; and (c) *Asteracanthus tenuis* and *A. longidens* (see Rees & Underwood, 2008, p.137, for the taxonomical assessment of these two taxa), due to the asymmetrically situated domed areas on the occlusal surface, lacking in the material here described.

One of the most complete articulated dentition referred to as *Asteracanthus* is the holotype of *A. medius* Owen, 1869 (in Rees & Underwood, 2008, Figure 3, p. 136) from Bathonian deposits of northern France, which constitutes a reference for reconstructing the dentitional pattern of other *Asteracanthus* species, as it can be observed. Recently, a quite complete and articulated dentitional pattern has been described by Rigal and Cuny (2016), on the basis of the specimen MPV.2010.3.44 (Paléospace, Palaeontological Museum of Villers-sur-Mer) from the Bathonian of Normandy. Rees and Underwood (2008) based their description of *A. medius* on the material from the Bathonian of northern France and *A. ornatissimus* on the material from the Callovian of southern England (specimens not figured in the same paper). According to the same authors, the dentitional pattern of *Asteracanthus* would consist of two rows of relatively high anterior

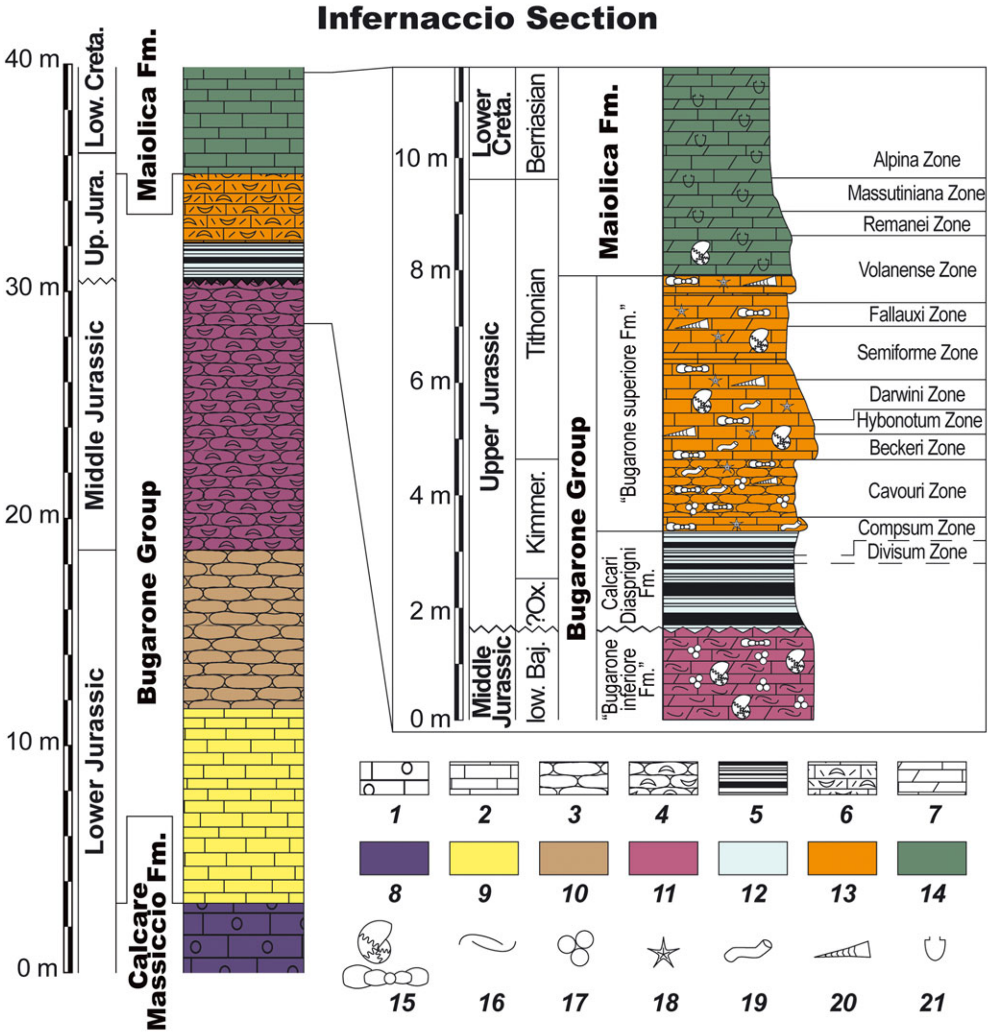

FIGURE 5 Jurassic-to-Lower Cretaceous simplified stratigraphy of the Infernaccio section (modified from Cecca et al., 1990). (1) Massive, peloidal limestone; (2) well-bedded pelagic limestone; (3) nodular marly limestone; (4) nodular, bioclastic limestone; (5) chert and cherty limestone; (6) bioclastic limestone; (7) dolomitized limestone; (8) Calcare Massiccio Fm.; (9) "Corniola-equivalent Fm."; (10) "Rosso Ammonitico-equivalent Fm."; (11) "Bugarone inferior Fm."; (12) Calcari Diasprigni Fm.; (13) "Bugarone superior Fm."; (14) Maiolica Fm.; (15) ammonites; (16) thin-shelled bivalves; (17) *Globuligerina oxfordiana*; (18) *Saccocoma* sp.; (19) burrows; (20) belemnites; (21) calpionellids [Colour figure can be viewed at wileyonlinelibrary.com]

teeth, characterized by well-developed occlusal crests and tapered lateral extremities; two rows of enlarged, rectangular laterals lacking the occlusal crests; and two rows of smaller, rounded teeth with flat or slightly domed occlusal surface, plus a symphyseal row. However, following Rigal and Cuny (2016), for specimen MPV.2010.3.44, which has been assigned to *A. magnus*, only one row of posterior teeth is present at least on the lower jaw; a condition similar to the Early Jurassic species *Asteracanthus smithwoodwardi* from Switzerland (Peyer, 1946). Thus, the general dental formula for MPV.2010.3.44 would be S-A1-A2-L1-L2-P for the lower jaw and A1-A2-L1-L2-P for the upper jaw. Therefore, the authors argue that in contrast to the similarity between *A. magnus* and *A. medius* found by Rees and Underwood (2008), the general pattern in the two species is quite different. *A. magnus* is characterized by strongly arched anterior teeth, with the first lateral tooth being much shorter than the second one. In contrast, the first and second lateral teeth are more or less the same length in *A. medius*. *A. magnus*, however, has just one row of posterior teeth. That said, according to Rigal and Cuny (2016), the overall dentition in *A. magnus* is more comparable with that characterizing *Asteracanthus smithwoodwardi*. Additionally, Rigal and Cuny (2016) state that, in the description of the specimen of *A. magnus*, the first lateral teeth have been misidentified as the anterior ones; Rigal and Cuny (2016) suggest that misidentification of the tooth position in several specimens are potentially one reason for the rarity of front teeth for *A. magnus* from the classical collection of the Natural History Museum of London.

According to the reconstruction of the holotype of *A. medius* and the specimen MPV.2010.3.44 referred to *A. magnus*, the largest teeth are most likely all lateral teeth belonging to the same row (tentatively the second lateral one, considering the rectangular and only slightly convex morphology), whereas the smaller, ovoid ones, represent teeth of the posterior row, considered as single following the description by Rigal and Cuny (2016). Still, on the basis of the specimen MPV.2010.3.44 assigned by Rigal and Cuny (2016) to *A. magnus*, the subrectangular lateral teeth are, in occlusal view, slightly convex in the lower jaw and slightly concave in the upper jaw. Based on these

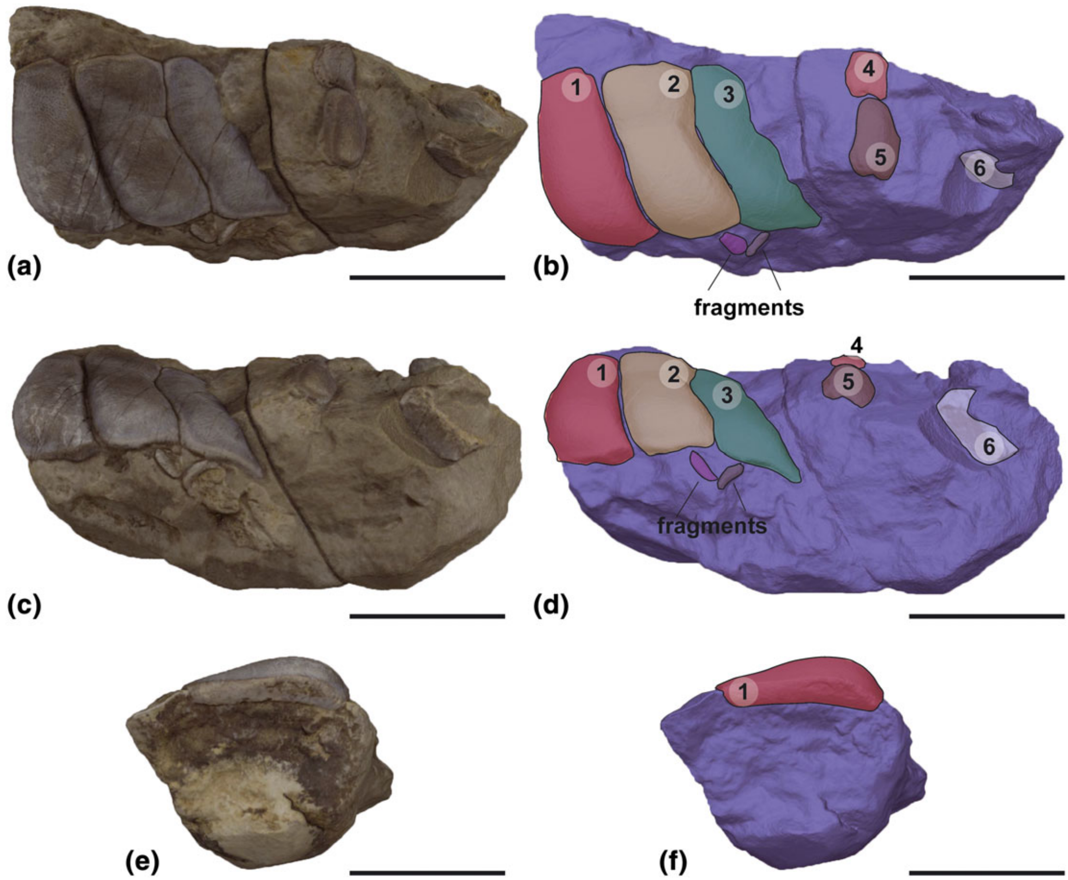

FIGURE 6 Photogrammetric textured (a,c,e) and solid (b,d,f) model of the analysed specimen in apical (a,b), labial (c,d), and lingual (e,f) views. In blue is the embedding pelagites. Arabic numerals indicate tooth positions (see text). Scale bars equal to 5 cm [Colour figure can be viewed at wileyonlinelibrary.com]

indications (and on the relative position of the posterior subcircular teeth), the specimen described here could be referred to the left lower jaw of the animal.

The identification of the anatomical position of the partial tooth preserved on the surface (Tooth 6 in Figure 6a–d) is more problematic; despite this, due to its subtriangular morphology that is observed from the tooth cast preserved on the rock sample (see pl. 5, Figure 1, p. 135 in Rees & Underwood, 2008), it could possibly be assigned to a more anterior position in the tooth row.

Nevertheless, considering the holotype of *A. medius* as a reference for the general arrangement of the dentition in genus *Asteracanthus*, the current mutual orientation between teeth series 1–3 and 4–5 does not match the orientation that would be dictated by the anatomy, as it is known from the fossil record. The major axes of the crowns of series 1–3 and 4–5 are roughly subparallel instead of being perpendicular to each other, probably stressing a post-mortem and a preburial slight displacement (i.e., low energy currents; soft-ground bioturbators) of smaller elements.

Regarding the phylogenetic relationships within the Hybodontoidea, after the classical works by Cappetta (1987), Maisey (1982, 1989), and Maisey, Naylor, and Ward (2004), the most complete and recent phylogeny is Rees (2008). This analysis is based essentially on characters in the dentition, as teeth are among the material that is more easily preserved in the fossil record. Thus, only a few characters of the fin spine and cephalic spine are additionally used in this phylogeny. In the topology by Rees (2008, p. 218, Figure 1), *Asteracanthus* comes out as the sister taxon of *Palaeobates*, and the two taxa together form the sister group of *Acrodus*. The node containing the three taxa is assigned to the subfamily Acrodontinae, within the family Hybodontidae. Such node (Node 12, see Rees, 2008, p. 218, Figure 1) is supported by a crushing dentition with enlarged lateral teeth and complex ornamentation, a shared synapomorphy of the group. The sister group *Asteracanthus* + *Palaeobates* (Node 13) is supported by asymmetrical lateral teeth, interlocking teeth characterized by flat crown, massive root showing well defined foramina and a reticulate ornamentation. Within Acrodontinae, *Acrodus* is autapomorphic in showing cusps in anterior teeth, porous root and symmetrical enlarged lateral teeth (Node 14); *Palaeobates* is autapomorphic for its narrow lateral teeth, whereas *Asteracanthus* is autapomorphic for its wide lateral teeth, a reduced number of tooth files, and fin spines characterized by tubercles along the anterior side. According to Rees (2008), the Acrodontinae group need a further investigation and a re-evaluation of the clade in future is necessary.

In addition to the Acrodontinae, the family Hybodontidae includes also the subfamily Hybodontinae (see Rees, 2008), made by the clade *Hybodus* + *Egertonodus*, and an unnamed family made by *Planohybodus* + (*Secarodus* + *Priohybodus*). The whole group of Hybodontidae in addition to the basal taxon of uncertain affinity *Lissodus*, made up the sister group of the family Lonchidiidae,

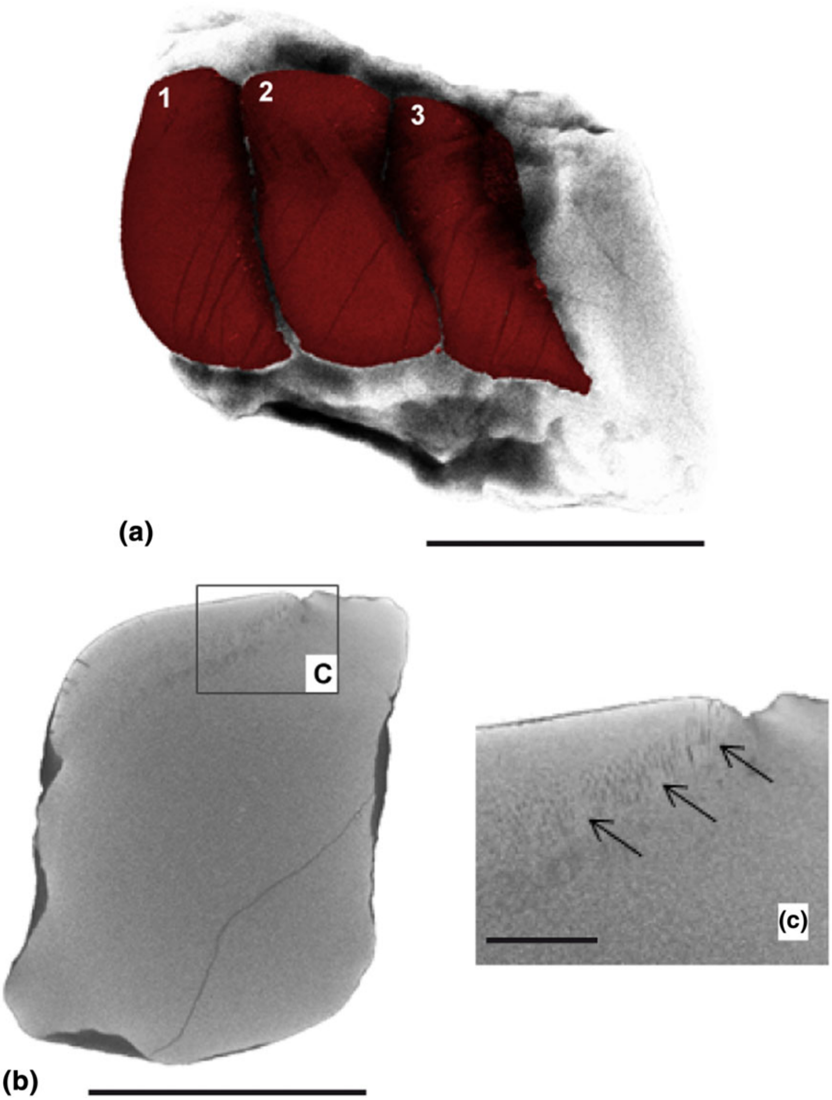

FIGURE 7 CT-scan images of specimen NS 167.1. (a) Teeth 1–3 in occlusal view. (b) Section passing through Tooth 1. (c) Detail of the Tooth 1 alveolar-shaped structure with reticulate setting of foramina and vascular canals (arrows). Scale bars equal to 5 cm in a and b and 2 cm in c [Colour figure can be viewed at wileyonlinelibrary.com]

represented by a big and unique unresolved politomy among the taxa *Lonchidion*, *Vectiselachos*, *Hylaeobatis*, and *Parvodus*.

5 | DISCUSSION

The genus *Asteracanthus* is reported from several Early to Middle and Late Jurassic deposits of England, France, Germany, Portugal, Switzerland, Northern Italy (Tre Venezie area), North Africa (see Fischer, 2008), Luxembourg, Thailand, and Japan and has therefore a cosmopolitan distribution in the Jurassic of the Tethys. The oldest occurrence of the genus (*Asteracanthus* cf. *A. reticulatus*) was reported from the Middle Triassic of Monte San Giorgio (Switzerland) by Rieppel (1981). Underwood (2002) described different groups of sharks, among which hybodonts, and rays from Upper Jurassic sediments of various localities of Dorset (Kimmeridge Clay). Kriwet and Klug (2004) described a fragmentary dorsal fin-spine referred to as *A. ornatissimus* from the Kimmeridgian of Bavaria. Vignaud et al. (1994) mentioned the occurrence of different species within the genus *Asteracanthus*, of various ages from the north-eastern border of Aquitaine Basin (France), namely, (a) *A. reticulatus* and *A. magnus* (Aalenian–Bajocian and Bathonian, in Sauvage, 1900); (b) *A. ornatissimus* and *Asteracanthus* sp. (Callovian, in Brunet, 1969); (c) *A. reticulatus* (Kimmeridgian, in Glangeaud, 1896), and *Asteracanthus* aff. *A. lepidus* (Kimmeridgian, in Sauvage, 1900). Cuny, Suteethorn, and Kamha (2005), Cuny et al. (2007), and Cuny, Srisuk, Khamha, Suteethorn, and Tong (2009) reported teeth referable to *Asteracanthus* sp. from the Tithonian Huai Hin Formation (Pha Dang Zinc Mine, Tak Province) to Khlong Min Formation (Mab Ching, Nakhon Si Tammarat Province, Middle to Late Jurassic) in Thailand. Regarding Portugal, Kriwet (1998) described a single fin spine with typical star-like tubercles referred to as *Asteracanthus biformatus* Kriwet, 1995, from the Late Jurassic underground coal mine of Guimarota (near the village of Leiria, Central Portugal). Goto (1994) described *Asteracanthus somaensis* Yabe, 1902 from the Nakanosawa Formation of the Soma Group, Oxfordian to Kimmeridgian in age (Tomizawa, Soma City, Fukushima Prefecture, Japan), and a lateral tooth referred to as *Asteracanthus* sp. from the black shale deposits of the Niranohama Formation of the Shizukawa Group, Hettangian in age (Niranohama, Shizukawa-cho, Motoyoshi-gun, Miyagi Prefecture, Japan). Takakuwa and Gunma Fossil Club (2011) reported an *Asteracanthus* tooth from the Lower Jurassic of Gunma Prefecture, and Delsate (1992) described two teeth attributed to *Asteracanthus* sp. from Luxembourg, from the lower Bajocian (*Hyperlioceras discites* Zone) of Prënzebierg.

About the Italian records of hybodont sharks, Sirna, Dalla Vecchia, Muscio, and Piccoli (1994) reported several specimens ascribed to *Asteracanthus* from the Tre Venezie region in Northern Italy (Table 1). However, Sirna et al. (1994) stress that the material from the Tre Venezie Area is affected by serious systematic problems, with dubious attributions. Nevertheless, a complete review of the material from northern Italy is beyond the scope of the present contribution.

The specimen here described constitutes, definitively, the first fossil remain referred to hybodont sharks formally published from the UMS Domain in Italy, although other material, which will be further discussed in a dedicated paper, was already found in rocks having different ages from Central and Northern Apennines (U. Nicosia, personal communication).

Hybodont sharks dominated a wide range of ecological niches, displaying, from a morpho-functional standpoint, teeth able to cut, clutch, grasp, pierce, and crush, adopting very different lifestyles according to many different dentition patterns that are known in the fossil record (see Cuny et al., 2004; Rees & Underwood, 2005, 2008). In the literature, durophagous feeding attitude is classically associated with low diet diversity and very powerful bite forces (see Clifton & Motta, 1998; Huber, Eason, Hueter, & Motta, 2005; Wainwright, 1988). According to Aguirre, Herrel, Van Damme, and Matthysen (2003), durophagous taxa were morphologically segregated in relation to the specific range of bite forces; this, in turn, leads to a segregation in relation to the possible prey that can be consumed. Thus, the evolution of durophagy would result in a relative niche specialization and consequent reduction in the competition between taxa (Huber et al., 2005).

The teeth described in this paper do fit the dentition pattern that Cappetta (1986) called “Type broyeur”, a pattern where the dentition consists of polygonal teeth (i.e., rectangular or hexagonal) with domed or flat occlusal surface, deemed typical of extreme crushing feeding behaviour, and assumed to be characterizing Jurassic hybodont sharks feeding on the seafloor (Cappetta, 1986). Another dental pattern, the “Type agrippeur-broyeur” (Cappetta, 1986) is distinguished on the basis of anterior cuspidate teeth, associated with lateral ones with flat occlusal surface (i.e., “broyeur” type) and assumed to characterize a similar feeding strategy.

A scavenging strategy on carcasses has also been proposed for the hybodont sharks of the Oxford Clay Fm. by Martill and Hudson (1991) and Martill, Taylor, and Duff (1994), indicating a possible opportunistic life style for these sharks (see also Wahl, 2005). This lifestyle is also suggested by Rees and Underwood (2008) for hybodontids of the Oxford Clay. The morphology and preservation of the teeth described herein do not allow a more detailed interpretation of a possible feeding strategy. *A. magnus* was reported from several different facies of the English Jurassic, both from carbonate shelf palaeoenvironments (i.e., grainstone shelves, shoal complexes, and shoreface carbonates, in addition to *Asteracanthus tenuis* and medium to large, sharply pointed toothed taxa: e.g., *Egertonodus duffini* and *Planohybodus grossiconus*), from lagoonal and restricted facies (i.e., mudstones with shelly faunas of fully marine to moderate salinity palaeoenvironments) and from open marine settings (Rees & Underwood, 2008). Dromart et al. (2003) describe *Asteracanthus* as a tolerant taxon of several palaeoenvironments whose depth did not exceed a hundred metres. Furthermore, Leuzinger, Kocsis, Billon-Bruyat, Spezzaferri, and Vennemann (2015) found an unusual isotopic signal in some teeth referred to *Asteracanthus* from the Kimmeridgian of Porrentruy (Swiss Jura), that potentially indicated an euryhaline ecology for such durophagous sharks, at least for reproduction. According to Leuzinger et al. (2015), *Asteracanthus* juveniles probably lived at the beginning of their life, in lagoons and estuaries, to get away from predators such as the bony fish *Caturus* or crocodiles.

The open marine setting fits very well with PCP/basin systems of the UMS basin, although considering the invertebrate fauna known and described from Monte Nerone and presently recorded in the rocks of Central and Northern Apennines raises the question about the presence of potential prey living on the Late Jurassic sea-floor, ostreid (e.g., *Lopha solitaria*—Monari, 1994a; *Praexogyra quiricensis*—Monari, 1994b), and limid (*Limea* sp.—Monari, 1994a) bivalves and terebratulid

TABLE 1 Material referred to *Asteracanthus* from the Tre Venezie area (Italy) after Sirna et al. (1994)

Taxon	Locality	Stored at	Age	Described in
Asteracanthus sp.	Cortina d'Ampezzo, Rifugio Cantore		Carnian	Leonardi (1945)
Asteracanthus tridentinus	Trento (Pila Quarry, S. Martino Quarry)		Tithonian	D'Erasmo (1922, 1927)
Asteracanthus ornatissimus	Trento (Pila Quarry, S. Martino Quarry)		Tithonian	D'Erasmo (1922, 1927)
Asteracanthus sp.	Rovereto	Civic Museum of Rovereto	Jurassic	Muscio, personal observation in Sirna et al., 1994
Asteracanthus cf. *A. longidens*	Garda area (San Vigilio locality), San Vigilio Oolite Fm.—“*Ludwigia murchisonae* Limestone”	Palaeontological Museum of the Padua University, De Zigno Collection	Aalenian	Bassani (1888); D'Erasmo (1922)
Asteracanthus tenuis	Selva di Progno (Val d'Illasi), San Vigilio Oolite Fm.—“Ludwigia murchisonae Limestone”	Civic Museum of Natural History of Pavia	Aalenian	Bassani (1888); D'Erasmo (1922)
Asteracanthus tridentinus	Roverè Veronese	Civic Museum of Natural History of Verona, Nicolis Collection	Tithonian	Bassani (1888); D'Erasmo (1922); De Zigno (1883)
Asteracanthus aff. *A. tenuis*	Roverè Veronese	Civic Museum of Natural History of Verona, Nicolis Collection	Tithonian	Bassani (1888); D'Erasmo (1922); De Zigno (1883)
Asteracanthus ornatissimus	Vette Feltrine (Belluno province), San Vigilio Oolite Fm.—“*Harpoceras bifrons* Limestone”	Palaeontological Museum of the Padua University	Toarcian	D'Erasmo (1922)

brachiopods. Some gastropods and crustaceans make up the most probable prey as well. In addition, the large *Asteracanthus* could potentially have also fed on ammonites present in the uppermost part of the water column, as suggested, for example, by Martill et al. (1994) and Dromart et al. (2003). In particular, Martill et al. (1994) linked the numerous angular fragments of ammonite shells from the Jurassic Oxford Clay Fm. to a predation by fishes characterized by durophagous dentitions, among which *Asteracanthus*, *Lepidotes*, *Heterostrophus*, and *Mesturus* totally excluding a damage due to simple attrition. The Italian PCP-top condensed deposits ("Bugarone Group"), where the study specimen *Asteracanthus* was found "Bugarone superiore Fm.", are characterized by extremely abundant broken fragments of calcite-shelled (mainly bivalves) and aragonite-shelled replaced by diagenetic calcite molluscs (usually ammonite phragmocones). Arresting features in the "Bugarone superiore Fm." are characterized by the occurrence of pennular corals (Gill, Santantonio, & Lathulière, 2004; Nicosia & Pallini, 1977). The presence of zooxanthellate corals, recognized in several PCP-top and basin-margin condensed successions, allows to constrain the palaeobathymetry for the top of Late Jurassic intrabasinal highs to not deeper than 230–240 m (see Gill et al., 2004 for further information). Even though a shallower depth could be admitted (100–150 m), the sedimentological and palaeobathymetric framework likely led to the exclusion of some kind of damage from attrition only. Therefore, a feeding strategy involving extensive crushing by durophagous fishes cannot be totally ruled out.

According to Wahl (2005), the presence of abundant medium-size predators such as small plesiosaurs and ichthyosaurs may have represented a competitive exclusion for the nonreptilian vertebrate such as durophagous sharks, bringing their presence to a minimum. Considering that material referred to ichthyosaurs is known from the UMS Domain (see Paparella et al., 2016), including material precisely from the Kimmeridgian of Monte Nerone area, the extreme poverty of hybodont remains found in this domain could fit such an ecological explanation.

6 | CONCLUSIONS

Two short series of articulated teeth, belonging to the same individual and referred to as *Asteracanthus* cf. *A. magnus*, were here described from Upper Jurassic deposits of the Monte Nerone Pelagic Carbonate Platform, in Northern Apennines. Considering that the great part of *Asteracanthus* material is represented by loose and isolated teeth material (see Rees & Underwood, 2008), the new articulated specimen is quite important.

The studied hybodont shark remains are the first to be formally described from the Jurassic of Central and Northern Apennines and represent the first occurrence of the genus in the Late Jurassic of the Western Tethys, also confirming the occurrence of the taxon in the Late Jurassic on European scale.

Palaeobathymetric data provided by zooxanthellate corals from PCP settings also allow to model the in-depth *Asteracanthus* outreach that could probably have exceeded 100 m, thus, increasing the range discussed by Dromart et al. (2003). The material indicates an extreme crushing feeding strategy. Dominant hybodont sharks feed were most likely large bivalves, echinoderms, and other hard-shelled invertebrate dwelling the sea-floor of the flat-topped to low-angle ramp-type PCP of Monte Nerone, as suggested by the abundance of the fragmented sea shelly deposits in the deeper portion of the basin, even if a predation of ammonites and other cephalopods in the superficial water column cannot be totally excluded.

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