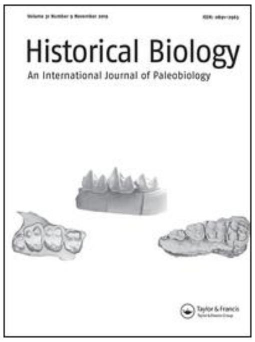

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ARTICLE

Jurassic neoselachian sharks from the Mt Nerone Pelagic Carbonate Platform (Umbria-Marche Apennine, Italy): a further constrain for the palaeoecology related to PCP systems

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ABSTRACT

The Mt Nerone area hosts a Jurassic-Cretaceous Pelagic Carbonate Platform (PCP)-basin succession in the Umbria-Marche Domain (Central Italy). Despite being studied thoroughly on sedimentological and geological aspects, wide-spectrum palaeocological studies are currently missing for this peculiar setting. While several studies on the invertebrate fauna of PCP system are available, the vertebrate fauna remained for a long time mostly unknown. Recently a renewed interest has been directed to vertebrate remains of the region. To date, an articulated dentition and some other tooth fragments of hybodont sharks and neoginglymodian actinopterygians have been described from the Jurassic of the Mt Nerone area. These taxa indicate the existence of diverse durophagous ecological niches available for durophagous fauna in the PCP system, linked to the abundant hard-shelled invertebrate fauna inhabiting the structural highs. In the present contribution we report and describe remains of neoselachians Synechodontiformes from five localities of the Mt Nerone area. The new material, represented by several isolated teeth and referred to as *Sphenodus* spp., testifies an additional trophic level for the Jurassic palaeoecology in the Umbria-Marche Domain, throwing new light on the peculiar PCP-basin ecosystem.

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Orthacodontidae; palaeoecology; *Sphenodus*; Umbria-Marche-Sabina Domain; Bugarone group

Introduction

The Mt Nerone Pelagic Carbonate Platform (hereafter PCP *sensu* Santantonio 1993, 1994) is proving to be a feasible observatory for a more inclusive understanding of the vertebrate/invertebrate palaeocommunities that inhabited Jurassic seas and structural highs within PCP-basin systems of the Umbria-Marche-Sabina (hereafter UMS) Domain. The invertebrate components of the Mt Nerone fauna were largely studied, as testified by a huge number of papers (e.g. Mariotti et al. 1978; Cecca and Santantonio 1986; Cresta and Pallini 1986; Baumgartner 1987, 1990; Cecca et al. 1987, 1990, 1994a, 1994b, 1995; Conti and Monari 1992; Mariotti and Pignatti 1993; Manni and Nicosia 1994; Mariotti 1994, 2003; Monari 1994a, 1994b; Faraoni et al. 1995; Manni and Tinozzi 2002; Tremolada and Erba 2002; Gill et al. 2004; Passeri and Venturi 2005; Fabbi et al. 2019; Cipriani et al. 2019a). On the other side, recently discussed tooth material (Citton et al. 2019; Romano et al. 2019a), along with a probable ichthyosaur rib reported from Kimmeridgian condensed deposits of Campo al Bello (Mariotti 2003), represent the only current formally described vertebrate record of the area. The fish material consists of a partial, articulated dentition and few tooth fragments of hybodont sharks referred to *Asteracanthus* cf. *A. magnus* (Citton et al. 2019), and several teeth of neoginglymodian actinopterygians showing a greater affinity to the genus *Scheenstia* (Romano et al. 2019a).

This record, substantial when considering that the remaining vertebrate record of the whole UMS Domain is represented by few other known specimens (i.e. tetrapods, ichthyosaurs and fish – Mariotti and Schiavinotto 1977; Manni et al. 1999; Paparella et al. 2017; Romano et al. 2018), resulted in acquiring further information about both the faunal composition and the palaeoecology of a fragmented environment such as that characterising PCP-basin systems.

Hybodont sharks and neoginglymodian actinopterygians were representatives of the nektonic fauna adopting two distinct typologies of durophagous feeding behaviour, mainly catching infaunal and epifaunal hard-shelled invertebrates such as large bivalves (i.e. limids and ostreids), echinoderms, gastropods, crustaceans and other hard-shelled invertebrates dwelling the sea-floor, as well as possibly cephalopods living in the water-column (see Citton et al. 2019; Romano et al. 2019a). The occurrence of durophagous sharks and fishes in the Jurassic of the UMS Domain has been related to immigration into new settled submarine environments and the flourishing of benthic communities as eco-biological response to large scale geodynamic phenomena (i.e. the Early Jurassic rifting – Romano et al. 2018). Similarly, Cuny and Benton (1999) proposed that the first major radiation and diversification of neoselachians was related to the Rhaetian transgression and the settling of shallow epicontinental marine conditions over Western Europe.

The census of the vertebrate fauna from Mt Nerone is further enriched by other isolated neoselachian teeth historically collected from well-known fossiliferous localities of the area, which are reported here (Figure 1). The material consists of nine isolated teeth partially embedded in the matrix, which alternatively consists of highly fossiliferous wackestone to packstone of the condensed Jurassic succession. Based on few characters of the tooth crown, the teeth presented here are referred to the clade Synechodontiformes (Chondrichthyes, Neoselachii). The Jurassic was a crucial period for the radiation of

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Supplemental data for this article can be accessed here.

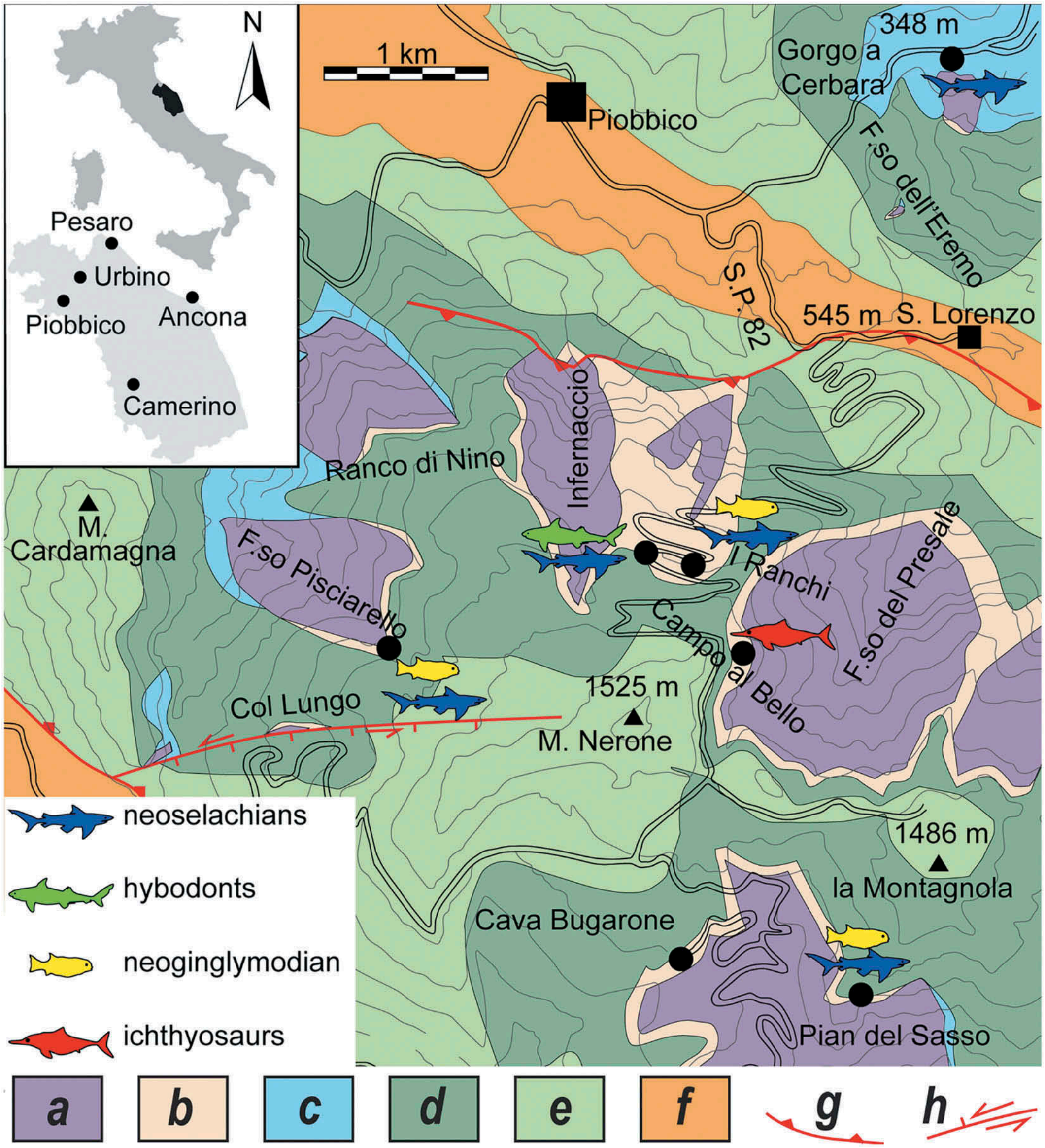

Figure 1. Geographical and geological localisation of the Mt Nerone area. The provenance of neoselachian teeth is reported, as well as the sites of other vertebrate remains found on the Mt Nerone slopes. Hybodonts are from Citton et al. (2019), neoginglymodian are from Romano et al. (2019a) and ichthyosaurs are from Mariotti (2003). Spacing of contour lines in the geological map equals 100 m altitude. Legend: (a) Calcare Massiccio; (b) Bugarone group; (c) Jurassic basinal succession; (d) Maiolica; (e) upper Lower Cretaceous-Oligocene deposits; (f) Miocene-recent deposits; (g) main thrust faults; (h) left-lateral transtensive fault.

neoselachian sharks, when most groups appeared for the first time in the fossil record (Klug 2010 and references therein). During this period also Synechodontiformes, which appeared in the Late Palaeozoic, also diversified into a great number of different forms and ecological roles. Within Synechodontiformes, the material here reported and described is referred to as *Sphenodus* spp., which indicates slender, maybe fast-swimmer neoselachian sharks equipped with a tearing-type dentition.

Material and methods

Nine isolated teeth were analysed first-hand, measured using digital calliper and photographed with a digital camera. Lithological features, as well as macro- and micropalaeontological content of the teeth-bearing rock samples were also analysed in order to constrain the material to the Jurassic lithostratigraphic framework of UMS Domain and determine a relative age, respectively. The lithostratigraphic nomenclature for PCP condensed successions of Galluzzo and Santantonio (2002) (i.e. Corniola-equivalent, Rosso Ammonitico-equivalent, Bugarone inferiore and Bugarone superiore formations as parts of the Bugarone Group) was preferred to the classification of Jacobacci et al. (1974) and Fabbi (2015). For a comprehensive description of the stratigraphical sections refer to Centamore et al. (1971), Cresta et al. (1989) and Cecca et al. (1990). Nomenclature of PCP type margins and related deposits follows Santantonio (1993) and the synthesis provided by Santantonio et al. (2017).

The material, labelled as D296-A to D296-I, is presently stored at ‘Museo dei Fossili e dei Minerali del Monte Nerone’ of Apecchio (PU, Marche – Central Italy), and constitutes part of the historical collection of the same institution; for this reason the original matrix was not chemically or mechanically treated to prepare the material. The teeth were collected from five different localities of the Mt Nerone area, namely ‘I Ranchi’ (specimen D296-A), ‘Pian del Sasso’ (specimen D296-B), ‘Gorgo a Cerbara’ (specimens D296-C, D296-E, D296-F, D296-G, D296-H), ‘Infernaccio’ (specimen D296-D) and ‘Fosso Pisciarello’ (specimen D296-I) (see Romano et al. 2019a; Figure 2).

Geological setting

The UMS Domain hosts an Upper-Triassic to Neogene limestone/marl/chert-made stratigraphic succession (e.g. Farinacci 1967; Colacicchi et al. 1970; Centamore et al. 1971; Farinacci et al. 1981; Galluzzo and Santantonio 2002; Bollati et al. 2012; Fabbi and Santantonio 2012; Donatelli and Tramontana 2014; Fabbi 2015; Cipriani 2016, 2019). Pelagic/hemipelagic deposits follow shallow-water limestones as a result of the drowning of a vast peritidal carbonate platform (Calcare Massiccio carbonate platform). Hettangian normal faults, related to the rifting stage affecting the Western Tethys during the Early Jurassic (e.g. Santantonio and Carminati 2011), were mainly responsible for this drowning and produced a complex physiography of the seafloor made of horsts and grabens/halfgrabens (Centamore et al. 1971; Bernoulli and Jenkyns 1974; Farinacci et al. 1981; Santantonio 1994; Santantonio et al. 1996; Galluzzo and Santantonio 2002; Di Francesco et al. 2010; Cipriani et al. 2016, 2019b). On the structural lows, pelagic sedimentation replaced the benthic carbonate factory by the earliest Sinemurian (Passeri and Venturi 2005) and a thick (up to 600 metres), resediment-rich, cherty limestone succession accumulated up to the Tithonian *p.p.* (‘complete series’ in Centamore et al. 1971; see also Cecca et al. 1990). On the horst blocks, the benthic carbonate factory persisted up to the early Pliensbachian (Morettini et al. 2002; Marino and Santantonio 2010), when the definitive drowning switched the intrabasinal structural highs to Pelagic Carbonate Platforms (Santantonio 1993, 1994). Here a condensed, discontinuous and fossiliferous succession sedimented from the Pliensbachian *p.p.* to the Tithonian *p.p.* (Bugarone Group), with a major late Bajocian-early Kimmeridgian stratigraphic gap (about 16 Myrs – Cecca et al. 1985). The complex submarine macrotopography was evened out in the earliest Cretaceous by the deposition of the (typical Tethyan) calpionellid limestones of the Maiolica formation (Tithonian *p.p.*-earliest Aptian in age; e.g. Gill et al. 2004), albeit with local exceptions (Cipriani 2016, 2017, 2019; Fabbi et al. 2016; Cipriani and Bottini 2019a, 2019b). From the Early Cretaceous to the Miocene, sedimentation progressively evolved from hemipelagic and pelagic to marly and finally siliciclastic as result of the Apennine orogeny (e.g. Pierantoni et al. 2013).

The Jurassic of the Mt Nerone PCP

Mt Nerone constitutes the northern offshoot of the Mt Catria-Mt Nerone regional anticline in the Umbria-Marche Ridge (Northern Apennines, Italy) and represents one of the widest PCPs of the UMS Domain, preserving at a seismic scale the main features of a PCP-basin system. During the Jurassic the Mt Nerone PCP was a flat-topped PCP (PCP type 1 of Santantonio 1994) experienced synsedimentary normal faulting in the late Aalenian that caused local tilting of the PCP-top (Cecca et al. 1990).

PCP condensed succession is represented by the Bugarone Group (lower Pliensbachian-Tithonian *p.p.*), which reaches a maximum thickness of about 40 metres (Cecca et al. 1990). This unit occurs on the top of the PCP, overlying directly and in stratigraphic concordance the shallow-water limestones of the Calcare Massiccio, or can lay unconformably on the Calcare

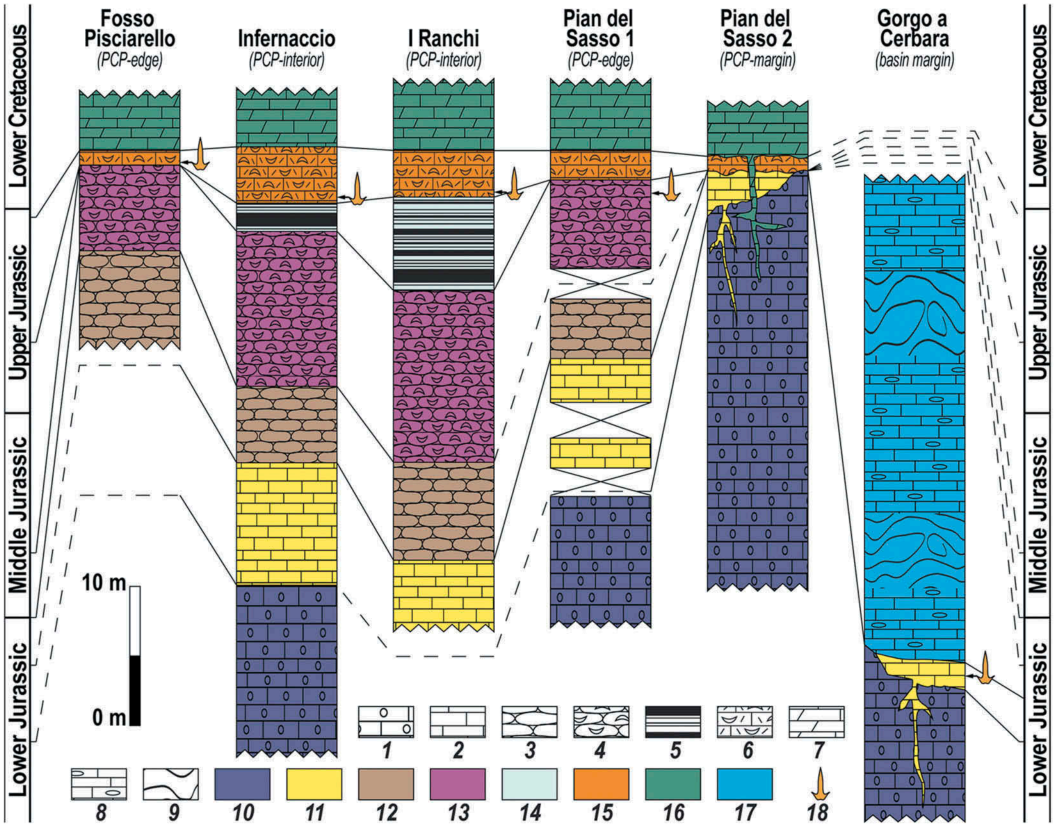

Figure 2. Jurassic to Lower Cretaceous stratigraphic sections of Fosso Pisciarello, Infernaccio, I Ranchi, Pian del Sasso and Gorgo a Cerbara localities (modified from Centamore et al. 1971; Cecca et al. 1990). Legend: (1) massive, peloidal limestone; (2) well-bedded pelagic limestone; (3) nodular marly limestone; (4) nodular, bioclastic limestone; (5) chert and cherty limestone; (6) bioclastic limestone; (7) dolomitised limestone; (8) cherty limestone; (9) slumped interval; (10) Calcare Massiccio; (11) Corniola-equivalent; (12) Rosso Ammonitico-equivalent; (13) Bugarone inferiore; (14) Calcari Diasprigni; (15) Bugarone superiore; (16) Maiolica; (17) Corniola; (18) neoselachian teeth.

Massiccio as epi-escarpment deposit (Galluzzo and Santantonio 2002). At Monte Nerone, the Calcare Massiccio is mainly composed of peritidal carbonates testifying numerous supratidal facies. In its uppermost portion, the unit is characterised by the co-occurrence of benthic and pelagic factories, overall representing the drowning succession of the carbonate platform on the horst blocks (Marino and Santantonio 2010; see also Centamore et al. 1971; Petti et al. 2007).

The four formation-rank units of the Bugarone Group are (from older to younger): the Corniola-equivalent (COE – lower Pliensbachian-lower Toarcian), the Rosso Ammonitico-equivalent (RAE – Toarcian *p.p.*), the Bugarone inferiore (BUI – Toarcian *p.p.*-lower Bajocian) and the Bugarone superiore (BUS – lower Kimmeridgian-upper Tithonian). A geological description of the localities producing the material under study is provided in Appendix 1.

Lithostratigraphy and age of the study material

The neoselachian tooth material, embedded in its rocky matrix, is shown in Figure 3. Specimens D296-C, D296-E, D296-F, D296-G and D296-H (Figure 3(c,e,–h)) are associated to a hazelnut to pinkish mudstone/floatstone, ammonite-rich matrix with frequent glauconite-rich nodules. The associated fauna consists of radiolarians, benthic foraminifers (ophtalmidids in specimen D296-C), siliceous sponge spicules, crinoid fragments, brachiopods (terebratulids in specimen D296-H), ammonite embryos and ostracods (specimen D296-C). Ammonite shells, among which *Fuciniceras* sp. and *Tropidoceras* sp. (specimen D296-E), are often oxidised and pyritised, sometimes characterised by goethite pseudomorph. Stromatolithic-like, iron-rich structures such as *Frutexites* were also observed (specimen D296-F). These features enable us to refer specimens D296-C, D296-E, D296-F, D296-G and D296-H to condensed facies of the COE. These specimens were collected from the epi-escarpment facies resting unconformably on the Calcare Massiccio at Gorgo a Cerbara. Here the NW-facing Jurassic escarpment of the Mt Nerone PCP is exposed (Marino and Santantonio 2010; Romano et al. 2019b), and unconformably covered by the upper Pliensbachian basin-filling pelagites of the Corniola formation (Kälin and Ureta 1987; Cecca et al. 1987, 1990; Cresta et al. 2002).

Specimen D296-B (Figure 3(b)) is embedded in a bioclastic, ammonite-rich, hazelnut nodular wackestone, containing small gastropods, thin-shelled bivalves and thick-shelled *Globuligerina oxfordiana* (*sensu* Giovagnoli and Schiavinotto 1987). Overall, the rock sample can be confidently referred to the BUI.

Specimens D296-A, D296-D and D296-I (Figure 3(a,d,i)) are associated with pale grey to greenish, strongly glauconitic wackestone to packstone. Radiolarians, small thin-shelled *Globuligerina oxfordiana*, aptychi, ammonite embryos and crinoid fragments referable to the genus *Saccocoma* sp. constitute the associated fauna. Specimen D296-D preserves the external mould of a perisphinctid ammonite. These rock samples can be referred to the upper Kimmeridgian facies of the BUS.

Results

Systematic palaeontology

We followed the systematic schemes of Duffin and Ward (1993), Böttcher and Duffin (2000) and Klug (2010).

Class: Chondrichthyes Huxley, 1880
Subclass: Elasmobranchii Bonaparte, 1838
Cohort: Euselachii Hay, 1902
Subcohort: Neoselachii Compagno, 1977
Superorder: Squalomorphii Compagno, 1973
Order: Synechodontiformes Duffin and Ward, 1993 *sensu* Klug (2010)
Family: Orthacodontidae Glikman, 1957
Genus: *Sphenodus* Agassiz, 1843
Type species: *Lamna longidens* Agassiz, 1843
Age and locality: Oxfordian, Mont Vohaye (Switzerland)

Sphenodus spp.
Figures 3, 4

Description

The material is represented by nine single tooth-crowns and, in few cases, by fragmentary remains (Figure 4).

Specimen D296-A is a fragmentary tooth of about 1 cm in height. The base and the apex of the crown are missing (Figure 4(a)).

Specimen D296-B is quite worn-out and measures 10.26 mm in height and 4.87 mm in maximum width. The external surface of the crown is smooth both on the labial and lingual (partially observable) faces. The crown is slender, slightly sigmoidal and shows a sharply pointed apex. Cutting edges are quite well-developed. Secondary cusps are not present (Figure 4(b–d)).

Specimen D296-C measures 13.86 mm in height and 6.03 mm in width and has a smooth external surface. The crown is gently curved in its proximal portion, while it is straight in the central and distal portions, including the pointed apex. Cutting edges are quite evident in the proximal and central portions of the crown, while they are much less marked distally. Compared to the specimen D296-B, the crown appears on the whole less flattened labio-lingually (Figure 4(e–f)).

Specimen D296-D is 14.61 mm in height and 2.89 mm in width, is fragmented and quite worn-out, lacking both the crown base and the cusp region. The tooth surface is smooth. The crown has a slender, sigmoidal profile with not very well-developed cutting edges. Labio-lingual flattening can be observed on the section left by the broken off tip of the tooth (Figure 4(g,h)).

Specimen D296-E measures 26.86 mm in height and 4.47 mm wide. The crown base is only preserved in its most distal part. On the whole, the crown appears quite slender and similar to specimen D296-C in the weak labio-lingual flattening. Cutting edges are weakly developed. The tooth surface is characterised by weak ornamentation composed of parallel striae of about 4 mm in length located at the most proximal portion of the lingual face, close to the crown base and parallel to the tooth long axis. The rest of the crown is smooth. As in specimen D296-C, the crown is proximally curved and straight from its central portion towards the apex. The cusp is missing (Figure 4(i,j)).

Specimen D296-F, which is different from the other specimens, is low-crowned, 12.55 mm in height and 5.66 mm in width. A larger surface of the crown base is observable, which seems wider than other specimens, but its proximal portion is missing, preventing the observation of the complete morphology. The crown is straight and gently inclined towards the lingual side; its surface shows parallel striae developed on the whole tooth length. The cusp is pointed (Figure 4(k)).

Specimen D296-G is 18.09 mm in height and 4.87 mm in width. The external surface is smooth. The crown is slender, blade-like, straight and labio-lingually flattened. Cutting edges are weakly developed and the cusp is sharply pointed (Figure 4(l,m)).

Figure 3. (a) Specimen D296-A (Bugarone superiore). (b) Specimen D296-B (Bugarone inferiore). (c) Specimen D296-C (Corniola-equivalent). (d) Specimen D296-D (Bugarone superiore). (e) Specimen D296-E (Corniola-equivalent). (f) Specimen D296-F (Corniola-equivalent). (g) Specimen D296-G (Corniola-equivalent). (h) Specimen D296-H (Corniola-equivalent). (i) Specimen D296-I (Bugarone superiore). Scale bar equals 1 cm.

Specimen D296-H is 17.64 mm in height and 4.36 mm in width. The crown, which exhibits a smooth external surface, is slightly sigmoidal. On the labial face, in the proximal portion of the tooth, two shallow depressions can be observed. As in the previous specimen, cutting edges are weakly developed and the cusp is sharply pointed (Figure 4(n–o)).

Specimen D296-I is 24.02 mm in height and 5.82 mm in width. The crown is smooth, straight, with prominent cutting edges and a sharply pointed cusp. The labio-lingual flattening is also marked. A small portion of the crown base seems to be preserved and it appear to be slightly expanded (Figure 4(p,q)).

Remarks

Few morphological characters of the tooth crown, such as the sigmoid curvature of some specimens, the prevailing absence of ornamentation, and the overall size of the specimens support their attribution to the genus *Sphenodus*. As can be observed in some published specimens referred to this genus (e.g. some teeth from the

Figure 4. (a) Specimen D296-A (Bugarone superiore). (b, d) Specimen D296-B (Bugarone inferiore). (e, f) Specimen D296-C (Corniola-equivalent). (g, h) Specimen D296-D (Bugarone superiore). (i, j) Specimen D296-E (Corniola-equivalent). (k), Specimen D296-F (Corniola-equivalent). (l, m) Specimen D296-G (Corniola-equivalent). (n, o) Specimen D296-H (Corniola-equivalent). (p, q) Specimen D296-I (Bugarone superiore). Scale bar equals 1 cm.

late Kimmeridgian of Germany in Böttcher and Duffin 2000), teeth are upright with sharply pointed cusps and defined cutting edges; moreover, they do display a very weak to absent ornamentation and are characterised by a wide base. Comparable features in some of our specimens could be inferred looking at the proximal, expanded portion of the crown, in respect to the general tapered outline of the cusp. Nevertheless, it should be noticed that characters of the tooth crown are not highly diagnostic for taxonomical nor systematical purposes. As stressed by Klug (2010), tooth crown morphology is dependent on feeding adaptations and looses systematical value since similar morphologies could be convergently developed in different neoselachian lineages exploiting a similar trophic niche. Moreover, neoselachian sharks display ontogenetic and sexual variations in several tooth characters (e.g. Underwood and Ward 2008). On the other hand, tooth roots are taxonomically and systematically significant (Klug 2010); among Synechodontiformes, for example, Klug et al. (2009) stressed that taxa referred to this clade possess a characteristic pseudopolyaulacorhize vascularisation pattern of the root (even if differently developed depending on tooth position) and a root depression on the labial face for open nutritive grooves.

The specimen D296-F (Figure 4(k)) is low-crowned and could represent one of the lateral teeth, as observed for example in *Sphenodus macer* (Böttcher and Duffin 2000) but also in other neoselachians, such as the galeomorph *Palaeocarcharias stromeri* de Beaumont 1960 (Duffin 1988; see also Jambura et al. 2019 for a recent hypothesis about the phylogenetic position of *P. stromeri*) and hybodont sharks such as *Hybodus* Agassiz 1837 (e.g. Martill 1985; Maisey 1987; Delsate 1995; Rees and Underwood 2008). In addition, our material did not allow to establish with certainty if the other teeth belonged to the upper or lower jaws (see the variation in tooth morphology described by Martill 1985, based on Jurassic teeth from the Oxford Clay of England; Böttcher and Duffin 2000).

Within the genus *Sphenodus* many species were erected (de Beaumont 1960; Duffin and Ward 1993) and subsequently synonymised or considered as being dubious (Kriwet et al. 2006). Three Jurassic species are considered valid by Böttcher and Duffin (2000), namely *S. longidens* Agassiz 1843, *S. macer* (Quenstedt 1851) and *S. nitidus* Wagner 1862, described from the Upper Jurassic of southern Germany. We adopted the review of Böttcher and Duffin (2000) to further discuss the studied material. Taking into account only tooth crown characters, the main features distinguishing *Sphenodus* species are size, type and position of cutting edges, torsion of the cusp and direction of the medial side of the tooth (Böttcher and Duffin 2000, Tab., p. 1).

Sphenodus longidens has extremely high and slender cusps, up to 44 mm in height (Böttcher and Duffin 2000) and are slightly S-shaped in lateral view. Cutting edges are well-developed, starting abruptly above the crown-root junction and running along the whole margin of the crown. Cusps are lingually inclined and lack any type of ornamentation (Rees 2010).

Sphenodus macer is the smallest of the Jurassic species of *Sphenodus*, displaying a maximum tooth height of 18 mm, including the root. Central cusps are upright in mesial teeth and distally inclined in lateral ones (Böttcher and Duffin 2000). Central cusps in *S. macer* are characterised by cutting edges on both sides. According to Böttcher and Duffin (2000), the overall size is the main diagnostic feature to distinguish *S. macer* from *S. longidens*. The latter taxon displays central cusps greater than 20 mm in height and, similarly to *S. nitidus*, cusps are more arched labially (Böttcher and Duffin 2000), differently from *S. macer* in which the labial face of the cusps is generally flat. Moreover, *S. macer* shows with respect to both *S. longidens* and *S. nitidus* a lesser degree of cusp's distal inclination, absence or very weak torsion of the cusp, absence of narrow root in anterior teeth, and symmetrical cutting edges (differently from what is observed in *S. nitidus*) (Böttcher and Duffin 2000).

Sphenodus nitidus displays teeth with a maximum height of about 22 mm. Central cusps of symphyseal teeth are upright in labial view and with two cutting edges. Central cusps of other teeth are inclined distally; they show a strong torsion around the longitudinal axis and asymmetrical cutting edges, which are, together with a sigmoidal profile of the cusps (Böttcher and Duffin 2000), an important features distinguishing *S. nitidus* from *S. longidens* and *S. macer*. *Sphenodus nitidus* also differs from *S. longidens* by the opposite direction of torsion (Böttcher and Duffin 2000).

As stressed by Cappetta (2012), a reliable attribution can be reached only on the basis of complete specimens, so a species-level attribution of the material under study is prevented. Our specimens are similar to some published specimens of *Sphenodus* sp., among which ZPAL P. 15.3 (Rees 2012), L08255t and L08257t (Rees 2000), NMV 88 (Kanno et al. 2017).

Following the morphological and dimensional characters provided by Böttcher and Duffin (2000), additional considerations can be made in regards of some studied specimens. Specimen D296-I might be considered more similar to *S. longidens* for its size, the mostly straight central cusp, the absence of ornamentation and symmetry of cutting edge. Specimens D296-B, D296-C, D296-G and D296-H might be considered more comparable to *S. macer* than to the other species, even if D296-G and D296-H are larger than the overall size indicated by Böttcher and Duffin (2000). No firm indication of the torsion of the cusp in the material under study can be provided, even if it appears to be overall very weak.

Discussion and conclusions

The chondrichthyan material from the Jurassic of Monte Nerone is referred to as *Sphenodus* spp.

The chondrichthyan record from Europe is very rich and diverse and consists of a huge amount of material coming from different facies. The record is mostly represented by teeth. While skeletons are preserved under exceptional conditions, being mostly cartilaginous, teeth have intrinsically more chances of preservation, being continuously replaced throughout life, and possessing a very resistant three-layered enameloid (i.e. the external hypermineralised tissue making the tooth, see Cappetta 1987, 2012; Cuny et al. 2001; Cuny and Risnes 2005).

Neoselachians remains were reported from inner shelf carbonates and shallow marine settings (e.g. Pliensbachian of Denmark – Rees 1998 – and Sweden – Rees 2000; Bathonian of England – Young 1982; Kimmeridgian of Switzerland – Leuzinger et al. 2017; Tithonian of France – Candoni 1995), restricted settings (‘*plattenkalke*’-type facies, e.g. Tithonian of Germany – Schweizer 1964; the Nusplingen and Solnhofen *lagerstätten* – Wagner 1862; Leidner and Thies 1999; Kriwet and Klug 2004 and reference therein; Klug and Kriwet 2008; Kimmeridgian of France – Saint-Seine 1949), marginal marine settings with reduced salinity (e.g. Kimmeridgian of Germany – Duffin and Thies 1997), and open marine settings from several deposits of different ages, namely (i) Early Jurassic (e.g. Sinemurian of northern Italy – Duffin 1987, 1998; Toarcian of Belgium – Delsate and Lepage 1990; Germany – Thies 1989); (ii) Middle Jurassic (e.g. Aalenian of Germany – Thies 1983; Bathonian of southern and central England – Underwood and Ward 2004b; Callovian of England – Thies 1983; Martill 1991; Poland – Rees 2012); (iii) Late Jurassic (e.g. Kimmeridgian of England – Underwood 2002; France – Candoni 1995); and (iv) Early Cretaceous (e.g. Hauterivian of England – Underwood et al. 1999; Schmitz et al. 2010). Outside Europe, neoselachians were reported from all the continents, namely from Africa (e.g. Cuny et al. 2012), South America (e.g. Otero et al. 2013) and North America (e.g. Waldman 1971; Johns et al. 1997; Cuny et al. 2001; Underwood and Cumbaa 2010), Asia (e.g. Thies 1982; Goto et al. 1996; Kanno et al. 2017), Oceania (e.g. Rozefelds 1993) and Antarctica (e.g. Kriwet 2003).

The Neoselachii (Chondrichthyes) is a monophyletic clade comprising sharks, rays and skates. Most of the Palaeozoic and Triassic neoselachian-like sharks did not pass the Triassic/Jurassic boundary (Kriwet et al. 2009) and neoselachians were represented by few lineages by the Early Jurassic (Kriwet and Klug 2008), greatly diversifying during the Toarcian (Kriwet et al. 2009). During pre-Toarcian times, neoselachian diversity was quite low in northwest Europe, with a relatively high occurrence of palaeospinacids, hexanchids and agaleids (Delsate and Duffin 1994; Johns et al. 1997; Rees 1998, 2000; Stumpf and Kriwet 2019). Although some

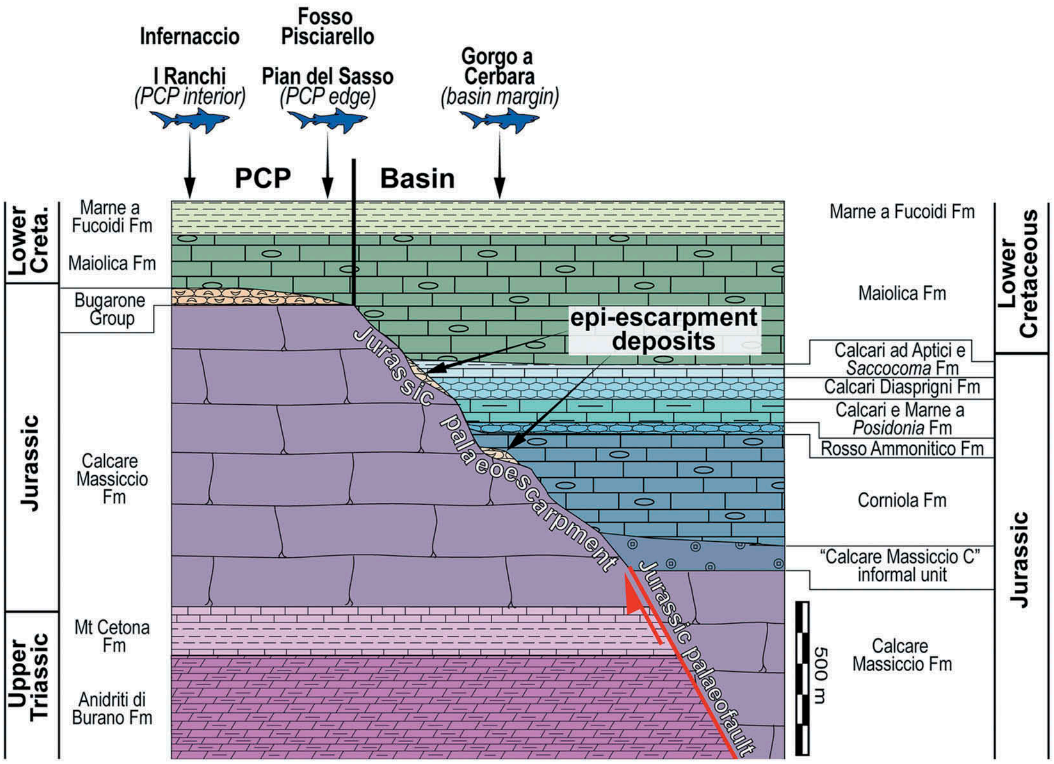

Figure 5. Simplified scheme of the Mesozoic stratigraphic setting of PCP-basin systems in the UMS Domain. Reported are the localities and the palaeogeographic settings where the study specimens were collected.

diversification already arises during the Pliensbachian (Stumpf and Kriwet 2019), since the Toarcian, favoured by altered palaeogeographic and palaeoecological conditions, greatly diversified faunas dominated by Synechodontiformes, Orectolobiformes and bathoids occurred (Delsate and Lepage 1990; Delsate and Thies 1995; Underwood and Ward 2004a, 2004b).

Within Neoselachii, the monophyletic, globally distributed, extinct clade Synechodontiformes is the sister-group to all living sharks probably representing a member of the stem lineage (Klug 2010; but see Maisey et al. 2004 for a contrasting hypothesis). Synechodontiformes is also considered the only neoselachian clade to have crossed the Triassic/Jurassic boundary (Kriwet et al. 2009), extending from the Cisuralian to the Palaeocene (Klug 2010). According to the scheme of Klug (2010, and references therein), the clade Synechodontiformes is characterised by a high-degree of polytomies, due to the paucity of cranial and post-cranial remains (Klug 2010) and comprises up to date four families, namely the Orthacodontidae Glikman 1957, the Pseudonotidanidae Underwood and Ward 2004a, the Palaeospinacidae Regan 1906 and the Paraorthacodontidae Klug 2010.

Slender, piercing teeth with sharp cutting edges and a very weak to absent ornamentation constitute the material under study and indicate a tearing-type dentition (*sensu* Cappetta 1987). This dental-type, which is not represented in bathoids, characterises fishes dwelling in different environments, from the coastal to the epi-pelagic and pelagic domain. It is characterised by numerous functional rows and teeth with tapered cusps and sharp cutting edges; the main central cusp can be associated to lateral, smaller cusplets (Cappetta 1986). Such dental type is reported since the Triassic and is well-represented during Jurassic and Early Cretaceous times in Synechodontiformes orthacodontids among which *Sphenodus* (Cappetta 1986).

Based on the most representative and rich faunas, neoselachian sharks have been described as facies-specific (Underwood 2002; Underwood and Ward 2004a, 2004b among others), with entire taxonomic groups being present in specific settings and absent in others. Synechodontiformes, for example, seem to be absent from lagoonal palaeoenvironments (Underwood and Ward 2004a) but are part of the typical chondrichthyan association of open marine settings, in association with hybodonts, heterodontiforms, orectolobiforms, protospinacids, hexanchids, scyliorhinids, and chimaeroids (Underwood 2002).

The material from the Mt Nerone PCP indicates stem neoselachians inhabiting open marine settings characterised by intrabasinal morpho-structural highs surrounded by deeper-water environments. Neoselachians were active pelagic predators, as suggested by the body structure outlined by Böttcher and Duffin (2000), catching on fishes, smaller sharks and probably cephalopods from mid- to surface water. In this context, *Sphenodus* has been considered as the possible first pelagic predator among Jurassic neoselachians (Rees 2012), probably in competition with early hexanchiforms (Thies 1983).

The highest part of the Mt Nerone PCP (i.e. PCP top) was not deeper than 230–240 m (Gill et al. 2004) in the Late Jurassic, and could reach less than 50 of depth as confirmed by the occurrence of reef corals embedded in pelagic deposits (Cipriani et al. 2019a). The association of neoselachian sharks with hybodonts and tritorial actinopterygians implies a stable benthic fauna on the structural highs. Jurassic PCP most probably constituted a physical structure in which various ecological niches became available for new members of the benthic community, attracting hybodonts and neoginglymodian actinopterygians, while marine predators, among which ichthyosaurs as possible top carnivores, adopted a large variety of feeding strategies exploiting a diverse suite of food resources. The finding of neoselachians teeth in both the PCP-top and epi-escarpment deposits (Figure 5) confirms that these sharks were active predators on and surrounding morphostructural highs (see also Cusumano et al. 2015, mentioning *Sphenodus* in condensed facies of the Upper Jurassic of Sicily). The studied material allows to add a new element for the palaeoecological reconstruction of the Mt Nerone PCP, which can be regarded as a natural laboratory and a case example for understanding the Jurassic complexities of the PCP-basin systems from the whole UMS Domain (Cresta et al. 2002). Further studies, along with new specimens from this site and others Jurassic Pelagic Carbonate Platforms will allow in the future to refine the census of the faunas and deepen the understanding of the palaeoecological dynamics within these fossil morphostructural highs.

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No potential conflict of interest was reported by the authors.

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