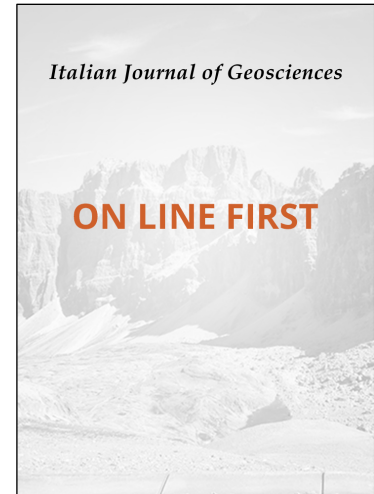


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First remains of neoginglymodian actinopterygians from the Jurassic of Monte Nerone area (Umbria-Marche Apennine, Italy)

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## First remains of neoginglymodian actinopterygians from the Jurassic of Monte Nerone area (Umbria-Marche Apennine, Italy)

MARCO ROMANO <sup>(1,2,3)</sup>, ANGELO CIPRIANI <sup>(2,3)</sup>, SIMONE FABBI <sup>(2,3,4)</sup> & PAOLO CITTON <sup>(2,3,5,6)</sup>

### ABSTRACT

Since the early nineteenth century, the structural high of Mt. Nerone in the Umbria-Marche Sabina Domain (UMS – Central/Northern Apennines, Italy) attracted scholars from all over Europe due to the wealth of fossil fauna preserved in a stunningly well-exposed Mesozoic sedimentary succession. Several geopalaeontological studies were focused on the abundant and diverse invertebrate fauna, whereas contributions dealing with Mesozoic vertebrates were to date virtually lacking. Recently, the first material referable to hybodont sharks, consisting of an articulated crushing dentition, was described from the area and referred to *Asteracanthus* cf. *A. magnus*. In this contribution, we report the first evidence of ginglymodian actinopterygians from the Upper Jurassic of Mt. Nerone. The material is represented by seven highly tritorial isolated teeth collected from three classic fossiliferous localities of the area (i.e. Pian del Sasso, Fosso Pisciarellino, I Ranchi). The general morphology of the material under study allow us to conservatively refer the teeth to the Neoginglymodi, a clade formed by Lepisosteiformes and Semionotiformes. The occurrence of durophagous organisms, to date represented by hybodont sharks and ginglymodian fishes, reveals interesting palaeoecological scenarios characterizing the pelagic carbonate platform-basin system of Mt. Nerone, which were most likely triggered by large-scale geodynamic processes. The complex submarine palaeotopography, inheritance of the Western Tethys Early Jurassic rifting, aroused the establishment of new infaunal and epifaunal communities opening up unexplored trophic niches for durophagous predators. The particular geodynamic setting of the UMS Domain, consisting of predominantly interconnected structural highs and lows, and the relative evolution of a diverse invertebrate fauna characterized by terebratulid, ostreids, limids, brachiopods, crustaceans, and gastropods, attracted both hybodontids and durophagous ginglymodians in the Tethyan Realm, influencing their dispersal during the Late Jurassic.

**KEY WORDS:** *Ginglymodian actinopterygians, Lepidotes, Late Jurassic, palaeoecology, Pelagic Carbonate Platform.*

### INTRODUCTION

Mt. Nerone is one of the largest Jurassic structural highs of the Umbria-Marche-Sabina Domain (hereafter

UMS). The Mt. Nerone area attracted scholars from all over Europe and was studied in detail since the end of the nineteenth century, due to the richness in invertebrate macrofossils, especially cephalopods, and the favorable exposure of the Mesozoic succession (e.g. ZITTEL, 1870; PRINCIPI, 1921; SCARSELLA, 1951; COLACICCHI *et alii*, 1970; CENTAMORE *et alii*, 1971; FARINACCI *et alii*, 1981; LOWRIE & ALVAREZ, 1984; IMMERZ, 1985; CECCA & SANTANTONIO, 1986; BAUMGARTNER, 1987, 1990; KÁLIN & URETA, 1987; ALVAREZ, 1989a, b, 1990; CECCA *et alii*, 1990; SANTANTONIO, 1993, 1994, 2002; CRESTA *et alii*, 1989, 1995; BARTOLINI & CECCA, 1999; MENICHINI, 1999; CHILOVI *et alii*, 2002; MORETTINI *et alii*, 2002; COCCIONI & GALEOTTI, 2003; GILL *et alii*, 2004; PASSERI & VENTURI, 2005; SPERANZA *et alii*, 2005; MARINO & SANTANTONIO, 2010; STEIN *et alii*, 2011; SANTANTONIO & CARMINATI, 2011; BARCHI *et alii*, 2012; CARMINATI *et alii*, 2013; CIPRIANI *et alii*, 2016; FABBI *et alii*, 2016a; CITTON *et alii*, 2018), to the point that it can be considered a real natural monument for palaeontology and geology *sensu lato* (SANTANTONIO, 2002).

Over the decades, several contribution have been dedicated to the study of the Mesozoic invertebrate fauna of the area, with papers focused on ammonites (CECCA *et alii*, 1987; 1990, 1994a, b, 1995; CECCA & SANTANTONIO, 1986; CRESTA & PALLINI, 1986, FARAONI *et alii*, 1995; PASSERI & VENTURI, 2005), belemnites (MARIOTTI, 2003), aulacocerids (MARIOTTI & PIGNATTI, 1993; MARIOTTI, 1994), bivalves (MONARI, 1994a, b), echinids (MARIOTTI *et alii*, 1978), corals (GILL *et alii*, 2004), crinoids (MANNI & NICOSIA, 1994; MANNI & TINOZZI, 2002), benthic (NOCCHI, 1992) and planktonic (RENZ, 1951; COCCIONI *et alii*, 2006, 2012) foraminifers, nannofossils (COCCIONI *et alii*, 1992; TREMOLADA & ERBA, 2002) and radiolarians (BAUMGARTNER, 1987, 1990). In particular, the study of the abundant ammonite faunas from the condensed deposits of Mt. Nerone Pelagic Carbonate Platform (hereafter PCP —*sensu* SANTANTONIO, 1994), pertaining to the early Pliensbachian-late Tithonian “Bugarone Group” (*sensu* GALLUZZO & SANTANTONIO, 2002; Bugarone Fm. in JACOBACCI *et alii*, 1974), led to extremely refined biostratigraphic schemes (CECCA *et alii*, 1990) allowing to identify a consistent stratigraphic gap from the early Bajocian to the early Kimmeridgian (up to 20 Ma – BARTOLINI & CECCA, 1999).

Differently, contribution on Mesozoic vertebrate fauna from the area, and from the Umbria-Marche-Sabina Domain as a whole, are extremely rare. MARIOTTI & SCHIAVINOTTO (1977) report and describe fish teeth from the Toarcian Rosso Ammonitico Fm. (Erbaense Zone) cropping out at Mt. La Pelosa (Polino, Terni, Central Italy), referring the material to *Oxyrhina* sp. MANNI *et alii* (1999) describe a tetrapod swimming-related trackway, named *Accordiichnus*

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*natans*, from Pliensbachian pelagites of Corniola Fm. cropping out on the northern side of the Burano River valley. The trackway, about 3,20 m in length, was found by Prof. Bruno Accordi (see ROMANO & NICOSIA, 2018) in the early 80's and has been referred by MANNI *et alii* (1999) to an unknown marine reptile. MARIOTTI (2003) reported a probable ichthyosaur rib from the early Kimmeridgian of Campo al Bello (Mt. Nerone). PAPARELLA *et alii* (2016) describe the first ophthalmosaurid ichthyosaur from the Upper Jurassic "Calcari a Saccocoma e aptici" Fm. (*sensu* GALLUZZO & SANTANTONIO, 2002; FABBI, 2015; CIPRIANI, 2016) of the Umbria–Marche Apennines, originally discovered on the summer of 1976 near Genga (Ancona, Marche, Italy). The specimen, *Gengasaurus nicosiai*, is characterized by a unique combination of features with respect to other ophthalmosaurids, especially with regard to the peculiar condition of the preaxial facet on the humerus, supporting the formalization of a new taxon (see PAPARELLA *et alii*, 2016).

This scarcity of contributions is partly due to a real paucity of Mesozoic vertebrate remains in the area, but perhaps also to the little importance given, over time, to isolated and very fragmentary vertebrate remains. In this context, POUÉCH *et alii* (2015) stressed that even if isolated fish remains, as bones or teeth, are very common in several Mesozoic outcrops "*paradoxically they are not systematically collected and studied*" (POUÉCH *et alii*, 2015, p. 32). The authors link this fact both to the time-consuming field processing to obtain micro-vertebrate assemblages, and to a real difficulty in determination of isolated material. However, even isolated teeth or vertebrae can consistently increase our knowledge about the faunal composition during the Mesozoic and throw new light on possible palaeoecological inferences. This is particularly crucial in a very peculiar sedimentological and biological context such as that characterizing the PCP-basin systems. Within this framework, more recently new attention has been focused on museum collections and new material from the UMS Domain, in order to describe more specimens referable to the poorly known vertebrate fauna. In particular, ROMANO *et alii* (2018a) reported the first hybodont material from the Rosso Ammonitico Formation, cropping out in the Polino area (Terni, Central Italy). The material is represented by two teeth found isolated within Toarcian red marly-limestone (Bifrons Zone) referred to the genus *Asteracanthus*, characterized by the typical crushing dentition of hybodont sharks within the Subfamily Acrodontinae. Articulated teeth, indicating an extreme crushing feeding behaviour and referred to *Asteracanthus* cf. *A. magnus*, represent the first hybodont material from the Upper Jurassic of Mt. Nerone area (CITTON *et alii*, 2018).

In the present contribution we describe the first specimens referable to neoginglymodian actinopterygians from the Upper Jurassic of Mt. Nerone area. The material was collected from three classical localities of Mt. Nerone, namely "Pian del Sasso", "Fosso Pisciarellino" and "I Ranchi" and is represented by seven isolated teeth still partly embedded in the original matrix. The new material represents the first report of ginglymodians fish from Upper Jurassic deposits of Italy, throwing new light on the diversity of this actinopterygians group in the Jurassic of northern Gondwana. Palaeoecological aspects and vertebrate-invertebrate interactions in a peculiar palaeoenvironment such as that of the Jurassic PCP-basin

system will be discussed along with the description of the specimens.

## MATERIAL AND METHODS

The studied material consists of seven isolated teeth, stored at Museo dei Fossili e dei Minerali del Mt. Nerone of Apecchio (Pesaro-Urbino, Marche, Italy). All the material has been directly analysed and measured using a digital calliper. Pictures of the specimens in the principal views were taken using a 24 Megapixel Canon EOS 750D (18 mm focal length). Fresh fractures on the samples allow to analyse the embedding pelagites, and a brief description of each lithotypes is provided below. Being the studied specimens part of the historical collections of the museum, it was not possible to chemically or mechanically treat the matrix to further prepare the material and to observe possible preserved roots portion.

In this paper the Mt. Nerone Jurassic PCP-top succession will be described adopting the lithostratigraphical nomenclature of GALLUZZO & SANTANTONIO (2002), which is here preferred to that of JACOBACCI *et alii* (1974). Essentials for this work were the papers of CENTAMORE *et alii* (1971), CRESTA *et alii* (1989) and CECCA *et alii* (1990), that describe with very high details several Jurassic stratigraphic sections of the Mt. Nerone area.

## GEOLOGICAL SETTING

The whole Mt. Nerone area falls in the Sheet 290 "Cagli" of Italian Geological Map at 1:50.000 scale (SERVIZIO GEOLOGICO D'ITALIA, 1972; JACOBACCI *et alii*, 1974) and in the Geological Maps of Marche Region at 1:10.000 scale (available online - <http://www.regione.marche.it/Regione-Utile/Paesaggio-Territorio-Urbanistica/Cartografia/Repertorio/Cartageologicaregionale10000>).

Mt. Nerone represents the northern offshoot of the Mt. Catria-Mt. Nerone regional anticline (Umbria-Marche Ridge, Northern Apennines, Italy) (Fig. 1). The Neogene-Quaternary Apennine chain building phase produced the exposure of Mesozoic and Cenozoic rocks referable to the UMS succession (e.g. CENTAMORE *et alii*, 1971; FARINACCI *et alii*, 1981; GALLUZZO & SANTANTONIO, 2002). This limestone/marl/chert-made succession records a complex Meso-Cenozoic tectono-sedimentary evolution, deeply influenced by the rifting stage that affected the Western Tethys during the Early Jurassic (e.g. SANTANTONIO & CARMINATI, 2011). This extensional phase dismembered a vast carbonate platform (Calcarea Massiccio platform – Hettangian) and caused the differentiation of several palaeogeographic domains. Shallow-water environments persisted on the footwall-blocks of Jurassic master faults up to Miocene (e.g. Latium-Abruzzi Carbonate Platform – CARMINATI *et alii*, 2013), while deeper water pelagic sedimentation characterized the hangingwall-blocks (e.g. UMS Domain), where all the initially surviving benthic carbonate factories drowned through the Sinemurian and the early Pliensbachian (MORETTINI *et alii*, 2002; PASSERI & VENTURI, 2005; MARINO & SANTANTONIO, 2010; FABBI & SANTANTONIO, 2012).

Although also the seafloor of the UMS domain was complicated by a pattern of up- and downthrown blocks (CENTAMORE *et alii*, 1971; BERNOULLI & JENKYN, 1974;



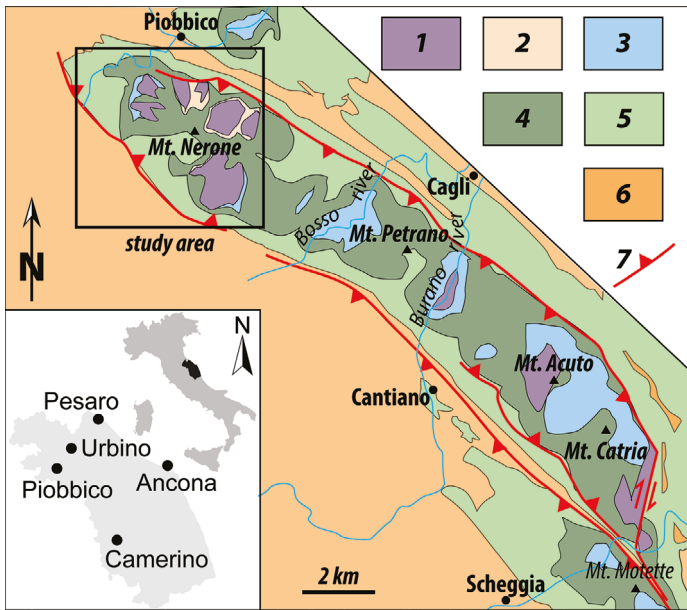


Fig. 1 - Geographical localization and simplified geological map of Mt. Nerone-Mt. Catria ridge. Legend: 1) Calcare Massiccio Fm.; 2) Bugarone Group; 3) Jurassic basinal succession; 4) Maiolica Fm.; 5) upper Lower Cretaceous-Oligocene deposits; 6) Miocene-Recent deposits; 7) main thrust faults.

FARINACCI *et alii*, 1981; SANTANTONIO, 1994; SANTANTONIO *et alii*, 1996; GALLUZZO & SANTANTONIO, 2002), from the early Pliensbachian, onwards, as said, only a genuine pelagic factory is recorded in the basin, and the intrabasinal highs became Pelagic Carbonate Platforms (PCPs – SANTANTONIO, 1994). Intrabasinal horsts and grabens were connected by submarine palaeoescarpments, resulting from the erosion of Early Jurassic fault-scarps (SANTANTONIO *et alii*, 1996; CARMINATI & SANTANTONIO, 2005), along which the pre-rift Calcare Massiccio Fm. was exposed. This rift-related architecture was progressively filled by the pelagic

succession during the Jurassic and the Early Cretaceous, albeit with evident facies and thickness variations (Fig. 2).

On the top of the structural highs (PCPs) only thin (up to 40 m) condensed and fossiliferous successions (“Bugarone Group”, Pliensbachian *p.p.*-Tithonian *p.p.* – GALLUZZO & SANTANTONIO, 2002; “Bugarone Formation” in JACOBACCI *et alii*, 1974 or “condensed series” in CENTAMORE *et alii*, 1971) were sedimented, while in the deeper adjacent basins a thick (up to 600 m), almost coeval, resediment-rich limestone-cherty successions accumulated (Corniola, Rosso Ammonitico, Calcari e marne a Posidonia, Calcari Diasprigni and Calcari ad aptici e Saccocoma Fms., Sinemurian-Tithonian *p.p.* – CECCA *et alii*, 1990; “complete series” in CENTAMORE *et alii*, 1971). Small patches of condensed units can also remarkably be sedimented along the palaeoescarpments (epiescarpment deposits - SANTANTONIO, 1993).

Blanketing of PCP-basin systems was completed with the deposition of Maiolica Fm. (Tithonian *p.p.*- early Aptian), albeit with “local” exceptions (CIPRIANI, 2016; FABBI *et alii*, 2016b). From the Cretaceous to the Miocene, hemipelagic and pelagic deposits progressively evolved to marly and finally siliciclastic deposits as a result of the Apennine orogeny.

THE MT. NERONE PELAGIC CARBONATE PLATFORM

Mt. Nerone was a Jurassic morphostructural high, flanked by relatively deep-water basins (Burano-Bosso, Biscubio and Pieia basins - CENTAMORE *et alii*, 1971; CECCA *et alii*, 1990; SANTANTONIO & CARMINATI, 2011). Mt. Nerone represents one of the widest PCPs of the UMS Domain, being its top at least 15 km<sup>2</sup> broad. The platform interior, the PCP-edges and the basin-margins are spectacularly exposed along the slopes and the valleys that incise the mountain, allowing to appreciate facies and thickness changes of a PCP-basin system in natural transects.

The “backbone” of Mt. Nerone is made of Calcare Massiccio Fm., exposed for hundreds of meters in the

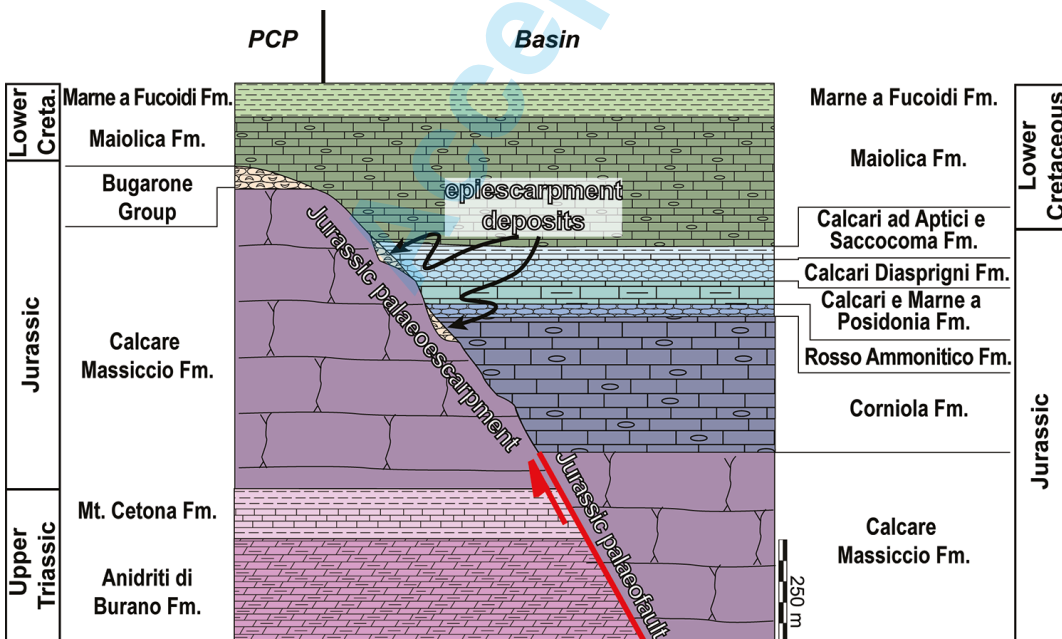


Fig. 2 - Simplified scheme of the Mesozoic stratigraphic setting of PCP-basin system in the UMS Domain.

deep-incised Infernaccio, Presale and Giordano valleys. This unit is made of peritidal carbonates bearing numerous supratidal facies (reddish and pisolitic levels, palaeokarst structures). The uppermost part of this formation is represented by the "Calcare Massiccio B" member (CITA *et alii*, 2007; Calcare Massiccio B in CENTAMORE *et alii*, 1971). This lithosome is made of a mix of both benthic (coated grains) and pelagic (mud with radiolarians and sponge spicules) factories and represents the drowning succession of Calcare Massiccio carbonate platform on the horst-blocks (MARINO & SANTANTONIO, 2010). The thickness of Calcare Massiccio Fm. is more than 600 m.

The definitive demise of benthic production and the onset of pure pelagic deposits is represented by the Bugarone Group (early Pliensbachian-Tithonian *p.p.*). Type-localities of the Bugarone Group are Campo al Bello, Infernaccio and Fosso Bugarone (see CENTAMORE *et alii*, 1971 and CECCA *et alii*, 1990 for a detailed description of these localities). This lithostratigraphic unit is up to 40 m thick. The oldest formation of the Bugarone Group is the Corniola-equivalent Fm. (early Pliensbachian-early Toarcian), made of well-bedded grey limestones rich in cephalopods (*Atractites* sp., ammonites), echinoderm fragments and siliceous sponge spicules. The Corniola-equivalent Fm. is about 12 m thick and its top is marked by a mineralized and fossiliferous hard-ground on which rests the Rosso-Ammonitico-equivalent Fm. (Toarcian *p.p.*). This unit is composed by are nodular, yellowish marls and marly limestones rich in ammonites and thin-shelled bivalves. The Rosso Ammonitico-equivalent Fm. is up to 9 m thick and pass upward to the Bugarone inferiore Fm. (Toarcian *p.p.*-early Bajocian), which consists of well bedded, nodular, dolomitized limestones pale orange to yellow in colour. Soft-sediment deformations characterize the Aalenian deposits of Infernaccio section (CECCA *et alii*, 1990), probably triggered by synsedimentary tectonic instability (ROMANO *et alii*, 2018a). The Bugarone inferiore Fm. is rich in ammonites and thin-shelled bivalves, and in the Bajocian facies occurs "thick-shelled" *Globuligerina oxfordiana* (*sensu* GIOVAGNOLI & SCHIAVINOTTO, 1987). The Bugarone inferiore Fm. is up to 12 m-thick, and the upper boundary coincides with a fossiliferous hard-ground. In the Bugarone quarry, CECCA *et alii* (1984, 1985) identified between the Bugarone inferiore and the Bugarone superiore Fms. an important stratigraphic gap ranging from the early Bajocian to the early Kimmeridgian (CRESTA *et alii*, 1989; CECCA *et alii*, 1990; BARTOLINI & CECCA, 1999). This main gap characterizes several PCP-top condensed successions of UMS Domain and causes the paraconformable juxtaposition of the two units. Exceptionally, interlaid between the Bugarone inferiore and superiore Fms. is a siliceous lithosome eteropic to the basinal Calcari Diasprigni Fm. The condensed succession of Mt. Nerone represents one of these exceptions. In fact, locally occur pinched-out radiolarian-rich facies (radiolarites) interposed between Bajocian and Kimmeridgian deposits (Campo al Bello, I Ranchi, Presale and Infernaccio sections in CENTAMORE *et alii*, 1971 and CECCA *et alii*, 1990). BAUMGARTNER (1990) analysed the Mt. Nerone radiolarites and suggested a Callovian-Kimmeridgian age for these deposits.

The youngest unit of the Bugarone Group is the Bugarone superiore Fm. (early Kimmeridgian-late Tithonian), made of well-bedded, dolomitized, nodular,

cephalopod-rich and glauconitic limestones. "Thin-shelled" globuligerinids (*sensu* GIOVAGNOLI & SCHIAVINOTTO, 1987) characterize the Kimmeridgian deposits of the unit, and associated are *Saccocoma* sp., crinoids and brachiopods. Pennular corals were also reported from this unit (GILL *et alii*, 2004). The Bugarone superiore Fm. is up to 4 m thick and pass upward to the dolomitized, whitish facies of Maiolica Fm. The material presented and described in this contribution was collected from three different localities of the Mt. Nerone area, namely Pian del Sasso, Fosso Pisciarelllo and I Ranchi (Fig. 3).

#### PIAN DEL SASSO

This locality is on the southern slopes of Mt. Nerone, about 1 km N of Pieia village. Here, the south-eastern (in present day coordinates) edge of Mt. Nerone PCP and the uppermost tract of an ESE-dipping palaeoescarpment are spectacularly exposed. In the westernmost part, the Calcare Massiccio Fm. pass upward to the Bugarone Group that is 16 m thick (CENTAMORE *et alii*, 1971) (Fig. 4). Moving towards E, the Bugarone Groups thins to a pair of meters and is overlapped by the Maiolica Fm. The Bugarone group rests on the Calcare Massiccio Fm. affected by several neptunian dykes. Laterally, the same Calcare Massiccio Fm. surface shows morphological irregularities filled by thin veneers of condensed facies (mainly Tithonian in age) in the form of epiescarpment deposits. Both the Calcare Massiccio and the epiescarpment deposits are overlapped by the Maiolica Fm.

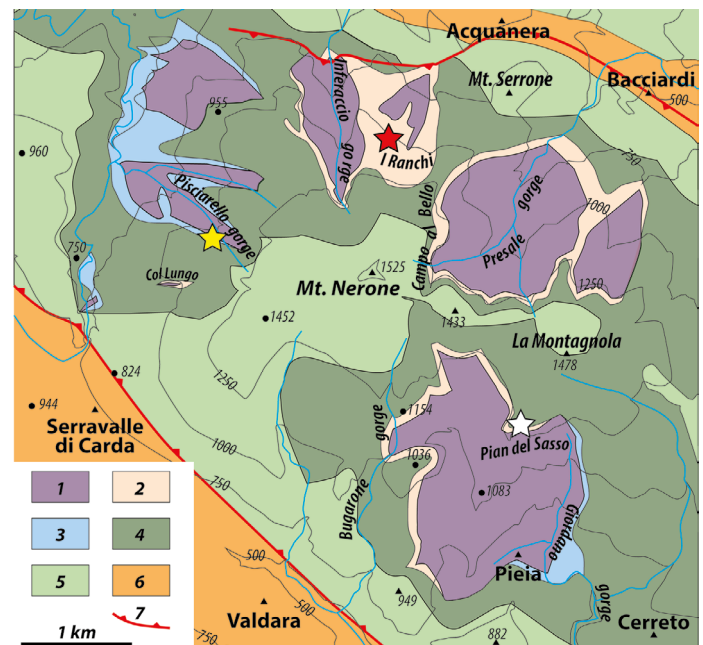


Fig. 3 - Simplified geological map of the Mt. Nerone area. The yellow star represents the teeth collected from the Fosso Pisciarelllo section (D295-B; D295-E; D295-G); the red star indicates the teeth sampled from the I Ranchi section (D295-C; D295-D; D295-F); the white star indicates the Pian del Sasso section, from which the tooth D295-A was collected. Legend: 1) Calcare Massiccio Fm.; 2) Bugarone Group; 3) Jurassic basinal succession; 4) Maiolica Fm.; 5) upper Lower Cretaceous-Oligocene deposits; 6) Miocene-Recent deposits; 7) main thrust faults.

## FOSSO PISCIARELLO

The incision of Pisciareello stream displays the western edge of Mt. Nerone PCP. Here a less than 10 m-thick, extremely fossiliferous succession of the Bugarone Group rests directly on the Calcare Massiccio Fm. The condensed succession of Fosso Pisciareello is one of the thinner of Mt. Nerone and allowed to enlarge the stratigraphic range of the Bugarone group to the Berriasian, due to the very condensed features of Maiolica-type facies (CECCA *et alii*, 1990) (Fig. 4).

## I RANCHI

The I Ranchi section is exposed along the mountain road that connect the Piobbico village to the mountaintop of Mt. Nerone. Here the Bugarone Group resting above the Calcare Massiccio Fm. reaches a thickness of more than 40 m. Characteristic of this sector of PCP-succession is the occurrence of up to 6 meters of Calcari Diasprigni Fm. interposed between the Bugarone inferiore and Bugarone superiore Fms. (CECCA *et alii*, 1990) (Fig. 4).

## THE TEETH-BEARING ROCK SAMPLES

The matrix in which the specimens are embedded ranges from mudstone-wackestone to wackestone, sometimes pseudonodular (e.g. specimen D295-A) or bioclastic (e.g. specimen D295-E) varying in colour from whitish to pale yellow/orange, hazelnut, grey and pale brown. The associated fauna comprises radiolarians,

benthic forams, fragments of *Saccocoma* sp. ranging from scarce to abundant, small “thin-shelled” *Globuligerina oxfordiana*, fragments of molluscs, aptychi (*Lamellaptychus* sp. in D295-B and D295-G), embryos of and macroscopic ammonites (?Lithoceratidae and Phylloceratidae, respectively in specimens D295-A and D295-D) and undeterminable bioclastic debris. Ammonites show characteristic pseudo-shells made of calcite as a result of dissolution and replacement of originally aragonitic shells. Pseudo-shells show also a greenish colour due to authigenic glauconite minerals. On the whole, the above reported features allow us to refer the rock samples to the Bugarone superiore Fm. The occurrence of small, “thin-shelled” globuligerinids (specimens D295-C, D295-E, D295-F) suggest a Kimmeridgian age for these deposits. Taphonomic condensation and very low sedimentation rates are suggested by a tooth resting directly on an ammonite shell (specimen D295-A).

Ganoid scales of ginglymodians are not associated with the teeth samples, albeit scales of ginglymodians embedded in Upper Jurassic pelagites are stored at Museo dei Fossili e dei Minerali del Mt. Nerone of Apecchio. Unfortunately, the inaccurate collection of the specimens not allows to correlate the occurrence of ginglymodian scales with the levels from which the study teeth were sampled.

## SYSTEMATIC PALAEOONTOLOGY

The taxonomy used in this paper is based on LÓPEZ-ARBARELLO & SFERCO (2018) and POUÉCH *et alii* (2015), after

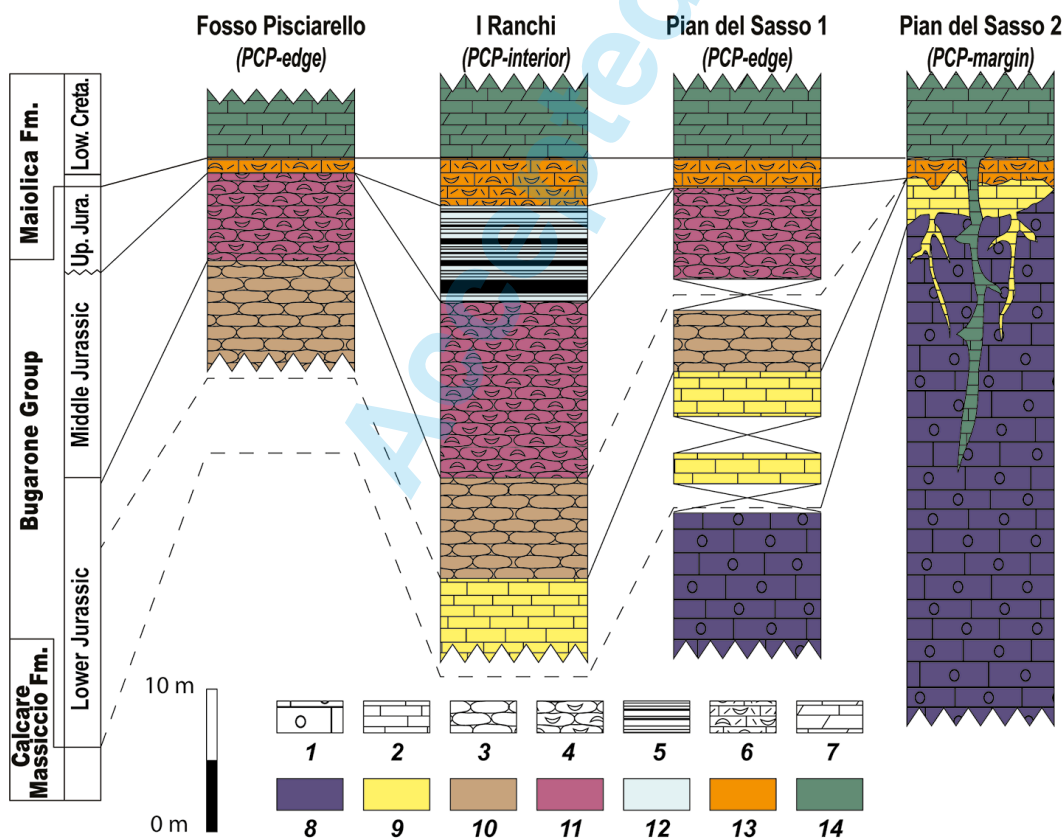


Fig. 4 - Jurassic to Lower Cretaceous stratigraphic sections of Fosso Pisciareello, I Ranchi and Pian del Sasso localities (modified from CENTAMORE *et alii*, 1971 and CECCA *et alii*, 1990). Legend: 1) massive, peloidal limestone; 2) well-bedded peloidal limestone; 3) nodular marly limestone; 4) nodular, 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 inferiore Fm.; 12) Calcari Diasprigni Fm.; 13) Bugarone superior Fm.; 14) Maiolica Fm.



the major systematic revision of ginglymodian fishes based on phylogeny by LÓPEZ-ARBARELLO (2012).

Subclass Actinopterygii COPE, 1887  
 Series Neopterygii REGAN, 1923  
 Super Division Holostei *sensu* GRANDE, 2010  
 Division Ginglymodi *sensu* GRANDE, 2010  
 Neoginglymodi LÓPEZ-ARBARELLO & SFERCO, 2018

*Material*: seven isolated teeth referable to the Neoginglymodi LÓPEZ-ARBARELLO & SFERCO, 2018 (clade formed by Lepisosteiformes + Semionotiformes) (Figs. 5-8)

#### TAXONOMIC REMARKS

The tritorial sub-circular button-like teeth analysed in this contribution are very reminiscent, in the overall morphology, of those classically referred to several species of the genus *Lepidotes* described in the literature (i.e. *L. mantelli* AGASSIZ, 1833, *L. fittoni* AGASSIZ, 1833, *L. laevis* AGASSIZ, 1837, *L. maximus* WAGNER, 1863, *L. decoratus* WAGNER, 1863, *L. degenhardtii* BRANCO, 1885). However, in the recent phylogenetic analysis of ginglymodian fishes, LÓPEZ-ARBARELLO (2012) considered the genus *Lepidotes* as one of the largest taxonomic ‘wastebasket’ for Mesozoic actinopterygians (see also DEESRI *et alii*, 2016). In fact, the results of the cladistics analysis, performed on 37 taxa, recognize as monophyletic *Lepidotes* just few Early Jurassic species from central Europe (i.e. *Lepidotes gigas* AGASSIZ, 1832 and *Lepidotes semiserratus* AGASSIZ, 1836). Differently, many of the species ascribed to the genus made *Lepidotes* paraphyletic and posit in the same group

with *Scheenstia zappi* LÓPEZ-ARBARELLO & SFERCO, 2011 (LÓPEZ-ARBARELLO, 2012), while many others are referred to Callipurbeckiidae. This result in the topology, based on six unambiguous synapomorphies and very high Bremer and Bootstrap supports, led LÓPEZ-ARBARELLO (2012) to refer the old name “*Lepidotes*” *mantelli* AGASSIZ, 1833, “*Lepidotes*” *laevis* AGASSIZ, 1837, “*Lepidotes*” *maximus* WAGNER, 1863, “*Lepidotes*” *decoratus* WAGNER, 1863, “*Lepidotes*” *degenhardtii* BRANCO, 1885 and “*Lepidotes*” *hauchecornei* BRANCO, 1885 to the new combinations *Scheenstia mantelli* LÓPEZ-ARBARELLO 2012, *S. laevis* LÓPEZ-ARBARELLO 2012, *S. maximus* LÓPEZ-ARBARELLO 2012, *S. decoratus* LÓPEZ-ARBARELLO 2012, *S. degenhardtii* LÓPEZ-ARBARELLO 2012 and *S. hauchecornei* LÓPEZ-ARBARELLO 2012. Differently, the species with a Late Jurassic (Kimmeridgian) to the Early Cretaceous (Hauterivian-Barremian) occurrence, characterized by a very strong tritorial dentition, must be referred to the genus *Scheenstia*. However, tritorial teeth are also known in Late Jurassic callipurbeckiids as *Macrosemimimus lennieri* (SAUVAGE, 1893) and other species referred to *Lepidotes*, which have not been revised yet (e.g., “*Lepidotes*” *leedsii*, “*Lepidotes*” *latifrons* – JAIN & ROBINSON, 1963). For this reason, in the present paper we prefer to conservatively refer the material to the clade Neoginglymodi (Lepisosteiformes + Semionotiformes, see LÓPEZ-ARBARELLO & SFERCO, 2018), although a close affinity with the teeth characterizing the genus *Scheenstia* is stressed and discussed in the text; in addition, the genus *Scheenstia* is tentatively used in this contribution as a possible model for ecological and paleoenvironmental reconstruction of the peculiar Jurassic PCP setting.

#### DESCRIPTION

*Specimen D295-A* – The tooth is flat and sub-circular in general outline (Figs. 5, 8A-A1) showing a typical translucent cap of acrodine (see POUÉCH *et alii*, 2015), and a maximum diameter equal to 17,63 mm. In lateral view, the specimen results gently domed, with a height of the glassy crown equal to 7,98 mm. The gently domed occlusal surface show just very moderate trace of wearing. The occlusal surface is simple, showing no carina or superficial ornamentation.

*Specimen D295-B* – The isolated tooth, with a translucent cap of acrodine, is sub-circular in outline (Figs. 6A, 8B-B1) with a maximum diameter slightly lower than D295-A, and equal to 12,78 mm. In lateral view, the tooth is characterized by a quite rounded lateral margin, with a glassy crown 6,74 mm in height. Differently from D295-A, the occlusal surface results essentially flat in lateral view (Fig. 8B1), thus indicating a substantial wearing of the tooth. No superficial ornamentation or carina are observable in the preserved occlusal surface. From dorsal view, some small pits are observable close to the crown margin, probably representing damage of the tooth crown made by mechanical impact with hard shells.

*Specimen D295-C* – The tooth is sub-circular and is smaller than D295-B, with a maximum diameter of 9,06 mm and is characterized by a classical translucent cap of acrodine (Figs. 7A, 8C-C1). In lateral view the margins are rounded, and the crown height is equal to 4,33 mm. The glassy crown result gently domed in lateral view, with a condition intermediate between the one characterizing the



Fig. 5 - Specimen D295-A. Note the flat and sub circular outline of the tooth showing a translucent cap of acrodine and a simple occlusal surface, without carina and ornamentation. AM, Ammonite. Scale bar is 2 cm.



Fig. 6 - A) Specimen D295-B. Note the sub-circular outline of the tooth with a translucent cap of acrodine and a flat occlusal surface indicating a substantial wearing of the tooth. B) Specimen D295-E. Note the circular outline and the quite flat top of crown. C) Specimen D295-G. Note the circular outline of the tooth with simple occlusal surface. Scale bars are 2 cm.

specimens D295-A and D295-B. Wearing of the occlusal surface is moderate; in dorsal view, on the crown margin, some longitudinal short scars are observable, probably referable to wear traces caused by mechanical contact with hard shells. The wear along the occlusal margin of the crown is not uniform, with a small flat area, facing upward and laterally, indicating a major wearing in this region of the tooth. The occlusal surface lack any kind of carina or other superficial ornamentations.

*Specimen D295-D* – The tooth, showing a translucent cap of acrodine, is sub-circular in outline even if resulted slightly more developed along a major diameter equal to 13,25 mm, with general dimension comparable to the specimen D295-B (Figs. 7B, 8D-D1). In lateral view the glassy crown results quite compressed with a height of 5,34 mm. The occlusal surface in dorsal view is essentially flat, indicating a substantial wearing of the tooth, comparable to the condition characterizing the specimen D295-B. On the lateral side of the crown a small flat area is observed, facing laterally and upward, that indicate also a lateral wearing of the tooth in addition to the one characterizing the occlusal surface. No carina or superficial ornamentations characterize the tooth occlusal surface.

*Specimen D295-E* – The tooth is almost perfectly circular in dorsal view, with a diameter of 8,19 mm. As for the other specimen, the lateral portion of the glassy crown (translucent cap of acrodine) is rounded in lateral view, and the top of the crown results quite flat indicating a moderate wearing (Figs. 6B, 8E-E1). The occlusal surface is simple, lacking any kind of ornamentation or carina. The height of the crown in lateral view is equal to 3,62 mm.

*Specimen D295-F* – The tooth is the smallest in size within the material here described, and shows an almost circular outline in dorsal view, with a diameter equal to 6,54

mm and a classical translucent cap of acrodine (Figs. 7C, 8F-F1). In lateral view the crown profile is consistently domed, with a total height of 3,53 mm. The lateral border of the glassy crown is different with respect to the simple rounded one characterizing the other specimens described, being more restricted at the base of the preserved crown, and wider in the upper margin. The well pronounced domed occlusal surface indicate very little or absence of wearing for the tooth. No carina or superficial ornamentation characterize the occlusal surface.

*Specimen D295-G* – The isolated tooth results circular in outline in dorsal view, with a diameter of 9,48 mm. In lateral view the tooth differs substantially with respect to the other specimen described, showing a very well pronounced domed occlusal portion, pyramidal in shape (Figs. 6C, 8G-G1). The top of the pyramidal glassy crown is truncated showing a small flat area, probably linked to very moderate wearing. The occlusal surface is simple, without any ornamentations or carina. The tooth crown height in lateral view is equal to 5,21 mm.

#### REMARKS

Overall, distinctive features such as i) the greater width of the crown with respect to the height; ii) the broad shape of the crown with a very blunt conical termination; iii) a thin enamel with respect to non-tritorial taxa; and iv) a various degree of wear of the teeth, absent in non tritorial forms, allow us to ascribe the studied material to the category 'extremely tritorial dentition' by JAIN (1983).

The specimen D295-A resembles the tooth figured by CUNY *et alii* (2010, figures A1, A2, p. 420) from the Early Cretaceous of Kut Island (Gulf of Thailand), and referred



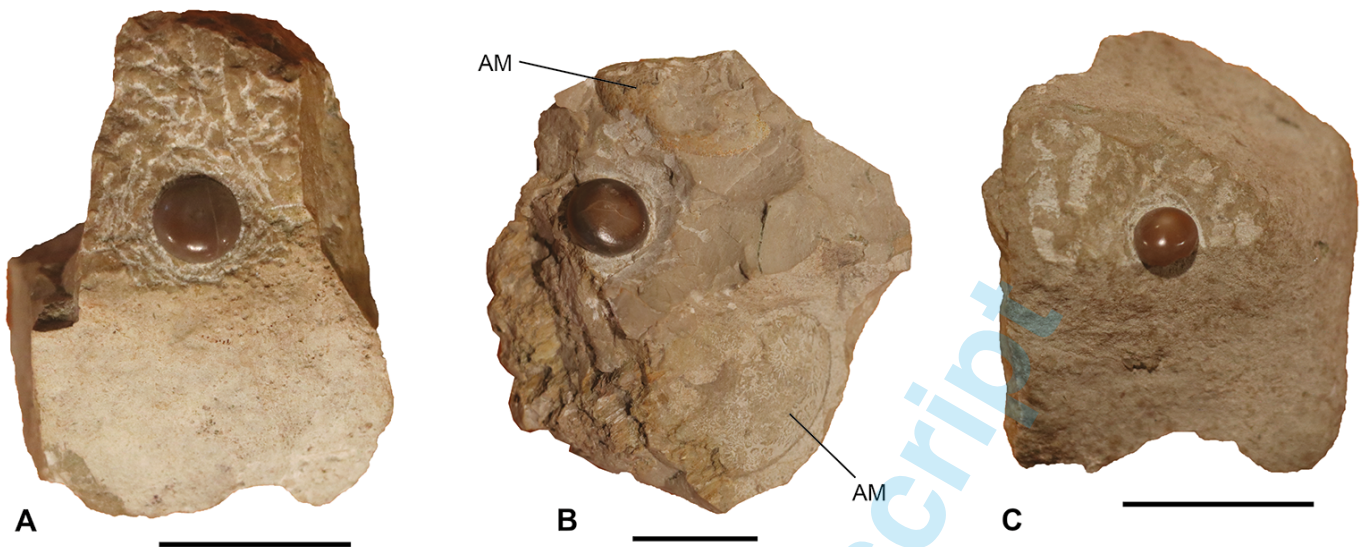


Fig. 7 - A) Specimen D295-C. Note the sub-circular outline of the tooth and the classical translucent cap of acrodine. The occlusal surface lack any kind of carina or other superficial ornamentations. B) Specimen D295-D. Note the sub-circular outline of the tooth and the classical translucent cap of acrodine. No carina or superficial ornamentations characterize the tooth occlusal surface. C) Specimen D295-F. The tooth shows an almost circular outline in dorsal view and a translucent cap of acrodine. No carina or superficial ornamentation characterize the occlusal surface. AM, Ammonite. Scale bars are 2 cm.

by the authors to "*Lepidotus*" sp. The specimen is also very similar to the teeth figured by ETHERIDGE & WILLETT (1889, plate XV, p. 358) and referred to as "*Lepidotus*" *maximus*.

The specimen D295-B is very reminiscent of the teeth figured by ALVARAGO ORTEGA *et alii* (2014, figure 8 3-4, p.12) and ascribed by the authors to as *Scheenstia* sp. The specimen D295-D is quite similar to the material of ALVARAGO ORTEGA *et alii* (2014, figure 8 3-4, p.12), even if the specimen here described shows a more intense wearing, with an almost flat occlusal surface.

The specimen D295-C is similar to the tritorial tooth reported by GARRISON *et alii* (2007, figure 22E, p. 484) from the Lower Cretaceous Cedar Mountain Formation (Mussentuchit Wash, Utah) and referred to as '*Lepidotus*' sp.

The specimen D295-F is quite similar to the teeth figured by POUÉCH *et alii* (2015, figure 4B, p. 38) referred by the authors to as *Scheenstia mantelli*, even if the specimen here described does not show a preserved root.

The specimen D295-G shows a similar apical wear flat surface to those referred to *Scheenstia* from the Oxfordian-Early Kimmeridgian of Mexico (ALVARAGO-ORTEGA *et alii*, 2014). A classic conical domed cusp when unworn is considered by SWEETMAN *et alii* (2014) typical of splenials, pterygo-palatines, and vomerine teeth in the genus *Scheenstia*. The general globular morphology (crowns not clearly larger than deep) indicates that the specimen cannot be classified as a real molariform tooth according to BERMUDEZ-ROCHASA & POYATO-ARIZA (2015). A similar tooth is figured by CUNY *et alii* (2010, figures C1, C2, p. 420) from the Early Cretaceous of Kut Island (Gulf of Thailand) and referred by the authors to "*Lepidotus*" sp., even if the tooth from Thailand seem to be characterized by a more marked and developed terminal papilla.

Tritorial teeth are described by SHRÖDER *et alii* (2012) for Late Jurassic (Kimmeridgian-early Tithonian) *Macrosemimimus fegerti* SHRÖDER *et alii*, 2012 and *M. lennieri* (SAUVAGE, 1893). According to the Authors,

these specimens present comparable dentition features with the genus *Scheenstia*, as highly tritorial teeth and morphological adaptation of mouths (i.e. a single vomer, the deep lower jaw with a deep symphysis and a very deep angular with concave posterior border) to a durophagous diet. On the basis of the description of LÓPEZ-ARBARELLO & SFERCO (2011), the phylogenetic analysis and the discussion reported by LÓPEZ-ARBARELLO (2012), and considering the strong tritorial dentition in the analysed material and its Late Jurassic occurrence in the Mt. Nerone Area, we conservatively refer all the specimens to the clade Neoginglymodi LÓPEZ-ARBARELLO & SFERCO, 2018, with a great affinity to the genus *Scheenstia*.

## DISCUSSION AND CONCLUSIONS

### STRATIGRAPHICAL DISTRIBUTION OF GINGLYMODIAN ACTINOPTERYGIANS

Ginglymodian actinopterygians have been the subject of several recent contributions both in term of taxonomy, phylogenetic analysis, ecology, macroevolutionary studies and description of new taxa (e.g. CAVIN & SUTEETHORN, 2006; TINTORI & LOMBARDO, 2007; LOMBARDO & TINTORI, 2008; CAVIN, 2010; GRANDE, 2010; FOREY *et alii*, 2011; LÓPEZ-ARBARELLO & ALVARADO ORTEGA, 2011; CAVIN *et alii*, 2013; LÓPEZ-ARBARELLO, 2012; GIBSON, 2013a, b; DEESRI *et alii*, 2014, 2016; POUÉCH *et alii*, 2015; LÓPEZ-ARBARELLO & WENCKER, 2016). The two main clades of ginglymodians are: i) the extinct Semionotiformes, that include *Semionotus*, and ii) Lepisosteiformes, including *Lepidotus* and the gars (see LÓPEZ-ARBARELLO, 2012). These taxa are registered worldwide and are well known in the Late Jurassic of Europe (LÓPEZ-ARBARELLO & WENCKER, 2016). The early occurrence for the group results Middle Triassic for the semionotiforms and

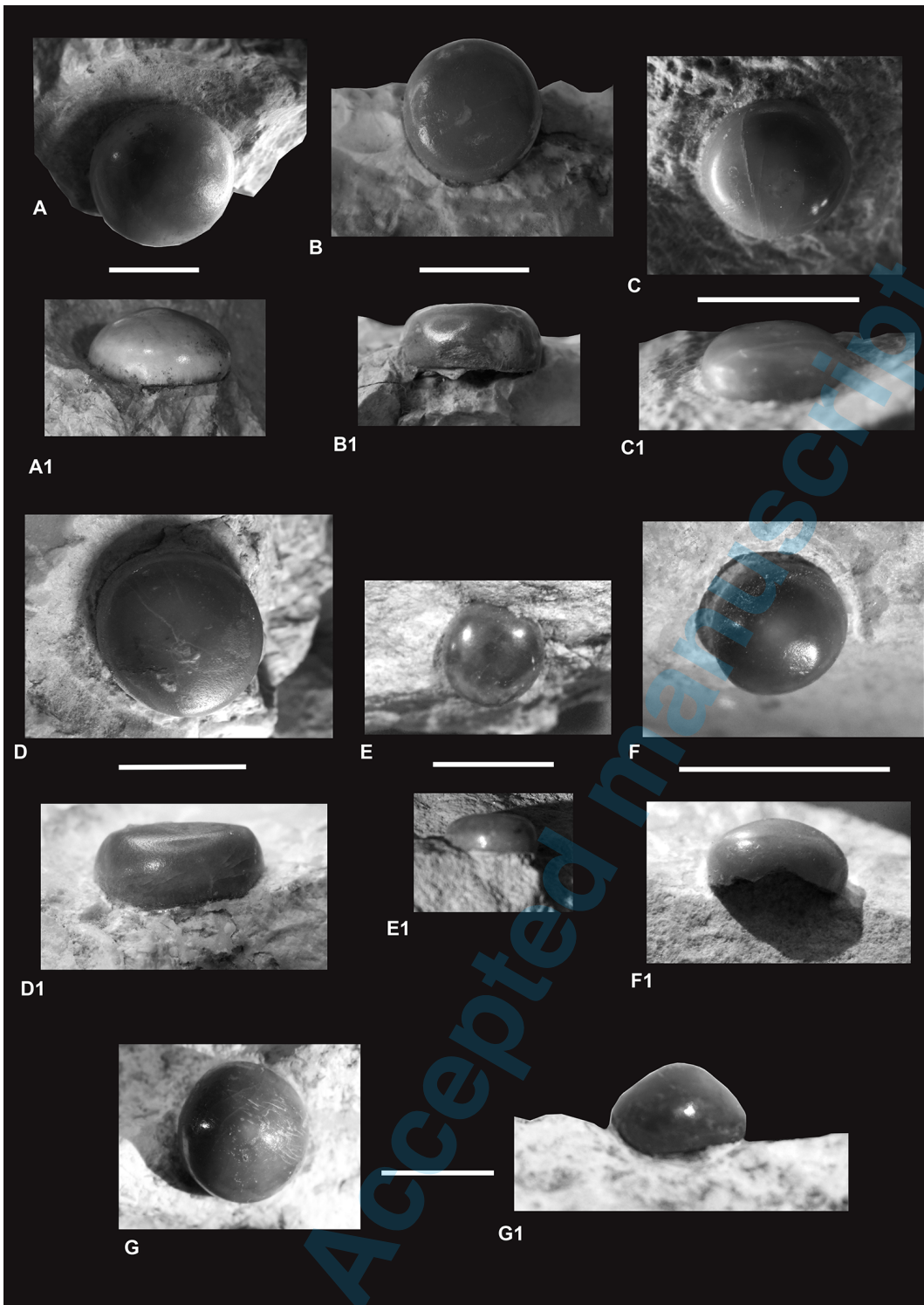


Fig. 8 - Ginglymodian actinopterygians teeth from the Mt. Nerone area. A, A1) Specimen D295-A in dorsal and lateral view, respectively. In A1 note the gently domed occlusal surface with very moderate trace of wearing. B, B1) Specimen D295-B in dorsal and lateral view, respectively. In B1 note the quite rounded margin and the essentially flat occlusal surface, indicating a substantial wearing of the tooth. C, C1) Specimen D295-C in dorsal and lateral view, respectively. In C note the moderate wearing and the longitudinal short scars probably referable to wear traces caused by mechanical contact with hard shells; in C1 note the gently domed glassy crown, intermediate between the one characterizing the specimens D295-A and D295-B. D, D1) Specimen D295-D in dorsal and lateral view, respectively. In D note the flat occlusal surface indicating a substantial wearing of the crown; in D1 note the lateral watering of the tooth. E, E1) Specimen D295-E in dorsal and lateral view, respectively. F, F1) Specimen D295-F in dorsal and lateral view, respectively. In F1 note the domed profile of the crown indicating little or absent wearing of the tooth. G, G1) Specimen D295-G in dorsal and lateral view, respectively. In G1 note the well domed, pyramidal occlusal surface with a very moderate wearing. Scale bars are 2 cm.

Early Jurassic for the lepisosteiforms (LÓPEZ-ARBARELLO & WENCKER, 2016). In particular, the genus *Sangiorgioichthys* TINTORI & LOMBARDO, 2007 from the Middle Triassic of Tethys represents the oldest 'semionotiform' known to date (see CHEN *et alii*, 2014).

In Italy, semionotiform fishes (*Sangiorgioichthys aldae* - TINTORI & LOMBARDO, 2007) were described from the upper Ladinian (Middle Triassic) Upper Meride Limestone of Mt. San Giorgio area, in the Switzerland-Italy boundary. One of the best-known actinopterygians ichthyofaunal

assemblage comes from the Calcare di Zorzino (Zorzino Limestone, middle Norian, Late Triassic) in the Bergamo Prealps, Northern Italy (TINTORI, 1981, 1983, 1990, 1995, 1996, 1998; TINTORI & RENESTO, 1983; TINTORI & LOMBARDO, 1996; LOMBARDO & TINTORI, 2005, 2008). The very rich ichthyofauna has been crucial to throw new light on variety and diversity of bony fishes during the Norian, testifying the passage from a palaeopterygians dominated 'primitive' fauna, to a more advanced one, characterizing a first major radiation of neopterygians (see TINTORI, 1998; LOMBARDO &



TINTORI, 2005). A crucial aspect for the pervasive radiation of neopterygians at the end of the Triassic was the appearance of specialized durophagy within the clade, an evolutionary radiation testified by the ichthyofauna of the Zorzino Limestone (LOMBARDO & TINTORI, 2005). This key innovation in the diet allow neopterygians to access for the first time to a new huge source of food represented by molluscs, crustaceans and echinoids, before inaccessible due to strictly anatomical constrains (see LOMBARDO & TINTORI, 2005). A morphometric analysis by BELLWOOD & HOEY (2004), analysing feeding in Mesozoic fishes from a functional perspective, demonstrate quantitatively that significant durophagy in actinopterygians started in the Norian, as already suggested by TINTORI (1998).

Specimens of semionotiform fishes referred to the genus *Lepidotes* sp. were reported from Lower Cretaceous (Barremian) ichthyoliths levels of Capo d'Orlando (Castellammare di Stabia, Naples, Italy) (BRAVI & DE CASTRO, 1995) and are currently stored in the Centro Musei delle Scienze Naturali di University of Naples. Several specimens of *Lepidotes* sp. were also found in the lower Albian "Calcari ad ittioliti di Pietraraja" *sensu* BRAVI (1994) (see also CARANNANTE *et alii*, 2006 for further litho-biostratigraphic data).

With regard to the Jurassic, the material described in this contribution and showing great affinities to the genus *Scheenstia* represent the first evidence of Upper Jurassic Ginglymodian actinopterygians from Italy. Remains of the genus *Scheenstia* as cranial bones, teeth or scales have been reported from England (Wealden Group of the Isle of Wight - MAIDMENT *et alii*, 2017; SWEETMAN *et alii*, 2014; SWEETMAN, 2016), France (Cherves-de-Cognac - POUECH *et alii*, 2015), Germany (Schamhaupten - LÓPEZ-ARBARELLO & SFERCO, 2011; KONWERT, 2016), Mexico (Tlaxiaco Basin - ALVARADO-ORTEGA *et alii*, 2014), and NW Switzerland (Porrentruy Platform - LEUZINGER *et alii*, 2017). Moreover, also almost all the classically Late Jurassic and Early Cretaceous material from Europe referred to *Lepidotes*, and now ascribed to the genus *Scheenstia* (see above) should be added to this list.

In general, the fossil record of neoginglymodians in the Jurassic of northern Gondwana is really poorly represented, with few known productive localities and material requiring a taxonomic review in light of recent phylogenetic analyzes and major systematic revisions (e.g. LÓPEZ-ARBARELLO, 2012; LÓPEZ-ARBARELLO & SFERCO, 2018). As already stressed by LÓPEZ-ARBARELLO (2004), African Jurassic ichthyofaunas are in general very poorly studied and scarce. The best known material for the Upper Jurassic comes from the central Gondwana Tendaguru outcrops, with the upper Saurian Bed (Tithonian) providing abundant material of *Lepidotes tendaguruensis*, and *Lepidotes* sp.

Strictly concerning the northern Gondwana margin, Jurassic neoginglymodian remains are known from the following few occurrences: *Lepidotes* sp., Techout Formation (Bathonian), Tunisia (FARA *et alii*, 2002); Lepisosteiformes indet., Anoual Formation (Bathonian), Morocco (HADDOUNI *et alii*, 2016); *Lepidotes* sp., El Mers Formation (Middle Bathonian - Late Bathonian), Morocco (LAPPARENT, 1955); *Lepidotes* sp., Lourinhã Formation (Late Kimmeridgian), Portugal (ESCASO *et alii*, 2008); *Lepidotes* sp., Lourinhã Formation (Late Kimmeridgian - Early Tithonian), Portugal (LAPPARENT & ZBYSZEWski, 1951); *Lepidotes* sp., Foz do Arelho locality (Late Kimmeridgian),

Portugal (LAPPARENT & ZBYSZEWski, 1957); *Lepidotes* sp., Alcobaça Formation (Kimmeridgian), Portugal (BRAUCKMANN, 1978); *Lepidotes* sp. and Semionotiformes indet., Alcobaça Formation (Late Oxfordian - Late Kimmeridgian), Portugal (PÉREZ-MORENO *et alii*, 1999); *Lepidotes* sp., Cabaços Formation (Oxfordian), Portugal (THULBORN, 1975). Considering this scarcity of findings, the new material described in the present paper from central Italy sheds new crucial light on the occurrence of the Jurassic neoginglymodian on the northern margin of Gondwana.

#### HABITAT

Actinopterygii (ray-finned fishes) can be considered as the most successful clade of aquatic vertebrates, which colonized all the possible environments from strictly marine to brackish and freshwater realms (GUINOT & CAVIN, 2018). In their recent ecological study through time based on a huge dataset (777 terminal taxa), GUINOT & CAVIN (2018) show empirically a strong dominance of habitat shifts, from the marine environment towards other realms, whereas colonization of mixed environments and marine realms starting from freshwater groups results quite scarce in the fossil record of actinopterygian. Within the Ginglymodi, GUINOT & CAVIN (2018) recognize two shifts from marine towards freshwater, one represented by the genera *Sinolepidotus*, *Neolepidotes* and *Lepidotyle*, and a second one represented by lepisosteiforms (*sensu* LÓPEZ-ARBARELLO, 2012), with the exception of basal-most *Lepidotes* and *Scheenstia* typical of a marine habitat. In the Cretaceous, the great part of lepisosteiforms were characterized by freshwater environment, with the exception of few brackish forms (GUINOT & CAVIN, 2018).

*Scheenstia mantelli* is considered to be typical of a fresh to brackish environment (POUECH *et alii*, 2014, 2015). However, according to POUECH *et alii* (2015), ginglymodians in the Jurassic and Cretaceous occurred in different depositional environments, and the genus *Scheenstia* include species known both from brackish deposits (e.g. *S. degenharditi* and *S. hauchecornei* from the 'Wealden' of Germany) and from marine deposits as *S. maximus* and *S. decoratus* from Solnhofen (Germany) and *S. laevis* from Cerin (France). Thus, environmental demands of *Scheenstia* can be considered compatible with open sea conditions characterizing the structural high of Mt. Nerone area during the Late Jurassic.

#### PALAEOECOLOGY

*Scheenstia mantelli* is characterized by styliform teeth in the jaw, and by addition rows of gradually more tritorial teeth in medial position (LÓPEZ-ARBARELLO & EMILIA SFERCO, 2011). The teeth disposed in the more internal part of the mouth are button-like, wider than taller (LÓPEZ-ARBARELLO & EMILIA SFERCO, 2011). According to SWEETMAN *et alii* (2014) *Scheenstia* shows both crushing and nipping dentition. Classical tritorial teeth, sub circular and domed occur on the vomer, pterygo-palatines and coronoid; differently, teeth of the premaxilla, maxilla and dentary, even being sub-circular in section, result taller in proportion and slenderer (SWEETMAN *et alii*, 2014). According to this description based on almost complete specimen, the button-like tritorial teeth



presented in this contribution could be referred to a medial position within the mouth, probably covering the pterygo-palatines, coronoidal or vomerine regions. However, in the almost complete specimens of *Scheenstia maximus* from the well-known Upper Jurassic Solnhofen limestone (Germany) described by JAIN (1984, referred to as *Lepidotes maximus*), strongly tritorial dentition characterize also the premaxillae (two strongly tritorial teeth), dentary, coronoid as well as the whole palate. Considering the large size of the specimens described herein, the Late Jurassic occurrence, and the fact the *Scheenstia maximus* is described only for strictly marine environments, the great affinity of the new described teeth with *S. maximus* is noteworthy.

The described tritorial dentition indicates a marked durophagous diet in the specimen here described. Several infaunal and epifaunal hard-shelled invertebrates have been described from the Mt. Nerone area that could represent a source of food for the ginglymodian actinopterygians. Among those are limid bivalves (*Limea* sp., see MONARI, 1994a), and ostreid (e.g., *Lopha solitaria*, MONARI, 1994a; *Praexogyra quiricensis*, MONARI, 1994b). In addition, gastropods, crustaceans, and terebratulid brachiopods could represent potential prey dwelling the sea-floor in the Late Jurassic. Durophagous ginglymodians as *Scheenstia* could also feed in small ammonoids, very abundant in the PCP-top condensed deposits of Mt. Nerone, as suggested for example by LÓPEZ-ARBARELLO *et alii* (2016) for *Ticinolepis crassidens* from the upper Besano Formation (Canton Ticino, Switzerland). The bioclastic debris identified in the microfacies embedding the teeth could be the result of feeding of crusher predators. Being in a pelagic setting, on the top of morphostructural high, characterized by very low-energy conditions, the occurrence of abundant microscopic fragments of bioclasts has been mainly referred to biological activity of durophagous eaters (CITTON *et alii*, 2018).

Similar consideration based on a mollusc-dominated diet has been recently proposed by CITTON *et alii* (2018) for the first occurrence of the hybodont *Asteracanthus* cf. *A. magnus* from the Mt. Nerone area. The new data, thus, could indicate the possible coexistence and competition for the same kind of potential hard-shelled invertebrate prey for the Late Jurassic of the PCP system in the Umbria-Marche Sabina Domain. A similar association of durophagous fishes with both hybodont and Neoginglymodi feeding in shelly molluscs is reported by SWEETMAN *et alii* (2014) for freshwater community from the Lower Cretaceous Wessex Formation (Wealden Group, Barremian) of the Isle of Wight (southern England). In this case the molluscan assemblage is dominated by unionid bivalves but also with the occurrence of few viviparid and extremely rare physid gastropods (see SWEETMAN *et alii*, 2014).

As already stressed for the evolution of cyrtocrinid crinoids (MANNI & NICOSIA, 1996; ROMANO *et alii*, 2016; 2018b) evolutionary radiations could be linked to large scale geodynamic phenomena in the UMS Domain, as the formation of submarine fault-scarps that connected the hanging-walls with the tops of structural highs. As reported in ROMANO *et alii* (2018a), the complexity of the Jurassic submarine palaeotopography with deeper basins and PCPs *sensu* SANTANTONIO (1994) could led to the exploration of new infaunal and epifaunal communities and, thus, also to new unexplored trophic niches for durophagous organisms. It follows that, as already suggested for the

recently described hybodontids from the UMS Domain (CITTON *et alii*, 2018; ROMANO *et alii*, 2018a), the pattern of structural highs and lows of the UMS Domain and the consequent evolution of invertebrate fauna (terebratulid, ostreids, limids, brachiopods, crustaceans and gastropods), most likely attracted both hybodontids and durophagous ginglymodians in the Tethyan Domain, influencing their dispersal during the Late Jurassic.

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