

NEW DATA ON THE EARLY JURASSIC BIODIVERSITY OF THE LOMBARDY BASIN (SOUTHERN ALPS, ITALY) AND THE EARLIEST RECORD OF *SPHENODUS* (CHONDRICHTHYES, NEOSELACHII)

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Abstract. At the beginning of the Jurassic, the initial stages of the rifting that preceded the opening of the Alpine Tethys led to the establishment of the Lombardy basin, characterized by a shallow water marine palaeoenvironment inhabited by highly diversified ecological communities. Macrofossil records from the whole Lower Jurassic succession of Lombardy are currently mostly confined to invertebrates. The earliest occurrence of marine vertebrates is from the Sinemurian Moltrasio Limestone of Osteno (Varese), subsequent to the Triassic/Jurassic boundary (TJB) post-crisis recovery.

Here, we describe material from the Roncola section (Roncola San Bernardo, Bergamo) of the Sedrina Limestone (upper Hettangian), consisting of a dense accumulation of crinoid skeletal remains belonging to *Balanocrinus ticinensis* Hess, 2006. Among them are three isolated neoselachian teeth assigned to the genus *Sphenodus* Agassiz, 1843.

This new discovery is significant and extends our knowledge of the biodiversity of the Lombardy basin Jurassic, mainly because these dental remains represent the earliest vertebrate macrofossils ever documented from this area after the Triassic/Jurassic boundary. *Sphenodus* (which ranges from the Sinemurian to the Danian) is a fairly ubiquitous Sinemurian neoselachian shark but this new record moves its First Appearance Datum (FAD) back to the Hettangian stage.

INTRODUCTION

The Mesozoic (Upper Triassic to Lower Jurassic) successions deposited in the South Alpine Domain (North Italy), document the evolution and the reorganization of a shallow water marine palaeoenvironment, due to the beginning of the extensional events that lead to the Liassic opening of the Alpine Tethys, identifying a subsiding area with horst and grabens known as the Lombardy Basin (Jadoul et al. 2012; Bertotti et al. 1993).

According to McRoberts (1994) the depositional model of the Lombardy Basin during the Triassic-Jurassic time interval (Fig. 1a), is comparable with that of the present-day Great Bahama Bank. Subject to an arid or semiarid climate, the broad carbonate inter-platform lagoonal system of the Lombardy Basin was not affected by the influx of terrigenous sediment; the nearest emergent landmass ran alongside the westernmost portion of the basin (Jadoul et al. 2005).

This platform (or ramp) carbonate system dominated both stratigraphic and palaeoenvironmental settings from the Rhaetian to the Early

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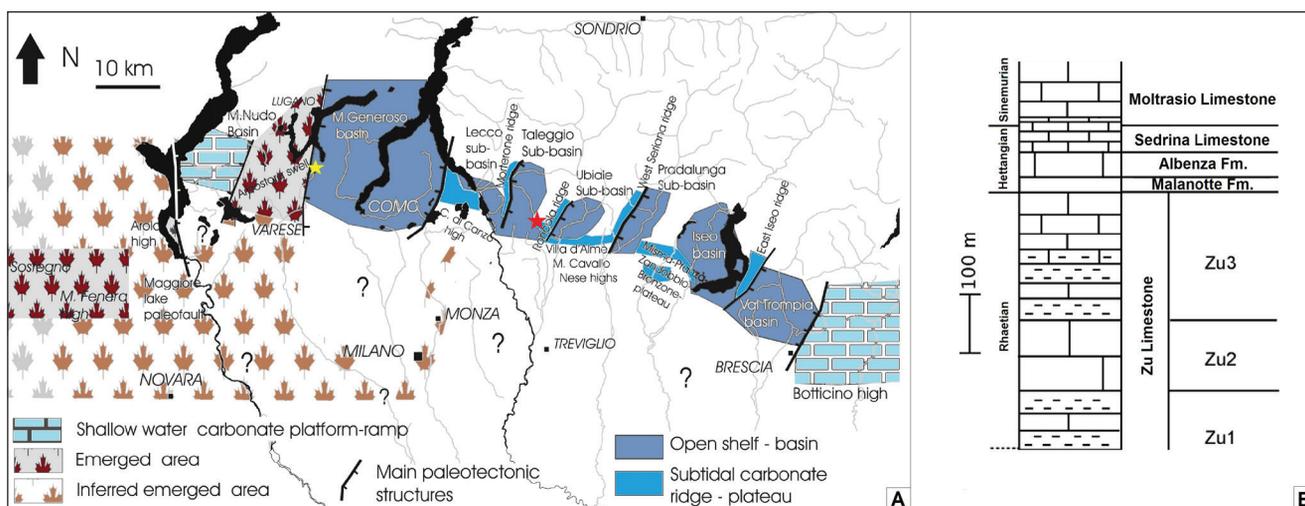


Fig. 1 - A) Paleogeographic map of the Lombardy basin during the late Hettangian-early Sinemurian (coloured and modified from Jadoul et al., 2005). The red star indicates the Roncola section and the location where the specimen under study was found. The yellow star indicates the locality of Arzo (Switzerland) where the holotype of *Balanocrinus ticinensis* was collected and described by Hess, 2006. B) Simplified stratigraphic column of Upper Triassic - Lower Jurassic succession of M. Albenza. (modified from Muttoni et al., 2010). Zu Limestone consists of alternating carbonate and shales, is divided into three members (Zu1, Z2 and Zu3) and is overlain by the micritic limestone of the Malanotte Formation (the T/J boundary is located in the lowermost part of this unit).

Sinemurian (Jadoul & Galli 2008) and experienced progressive drowning of the basinal area at the Triassic/Jurassic boundary (TJB). Rhaetian carbonate productivity was strongly reorganized in the Hettangian systems (i.e., the mid-inner to outer carbonate ramp of the Zu Limestone, the outer to carbonate ramp Malanotte Formation, the inner ramp to subtidal carbonate shelf Albenza Formation, and the open shelf Sadrina Limestone), also considering the ecological recoveries following the Triassic/Jurassic biological crisis (Sepkoski 1996; Jadoul & Doniselli 1987; Jadoul & Galli 2008; Jadoul et al. 2012). In shallow water successions, the Rhaetian/Hettangian transition is difficult to define, and the TJB was documented historically on the basis of palynological evidence (Galli et al. 2005, 2007; Muttoni et al. 2010) and with data from the calcareous nanoplankton record (Bottini et al. 2016) at the base of the Malanotte Formation (Fig. 1b).

The Malanotte Formation, which is poor in fossil contents, documents a rapid sea level rise during the Lower Hettangian, and this transgressive event provided the appropriate space for the progradation of the Albenza Formation (Jadoul & Galli 2008; Jadoul et al. 2012). A second marine transgression occurred during the Upper Hettangian, as highlighted by the lower and middle portions of the Sadrina Limestone. This event led to the establishment of an open shelf carbonate

succession (Jadoul & Galli 2008) with a regionally widespread outer platform environment which is presumed to have been deeper to the north (Jadoul & Doniselli 1987).

Marine facies associations in the Sadrina Limestone present a complete transgressive-regressive sequence: from the open shallow subtidal conditions of the lower lithozone, represented by the *Grenzbivalvenbank*, to the rapid progradation of the oolitic-bio-intraclastic sediments of the upper lithozone, represented by the *Brachiopod bank* (Bersezio et al. 2014). These marine habitats were colonized by highly diversified ecological communities as reported by Gaetani (1970), who documented a rich macrofauna from the upper Hettangian Sadrina Limestone, with some faunal differences between the lower and upper lithozones.

The lower lithozone of the Sadrina Limestone (Cenozone 1 in Gaetani 1970) can be described as an inner subtidal platform palaeoenvironment with shallow water moved by bottom currents, a muddy seafloor, well oxygenated and conditions of normal salinity. Inhabited by several benthic invertebrates, this facies is characterized by a relatively rich faunistic association (Gaetani 1970; Jadoul & Doniselli 1987; Bersezio et al. 2014), mainly represented by bivalves (*Astarte subtetragona* Münster in Goldfuss, 1840, *Chlamys dispar* (Terquem 1855), *Liostrea dumortieri* (Joly 1907), *Liostrea*

pictetiana (Mortillet 1858), ? *Nemodon* Conrad, 1869, *Parallelodon bettangiensis* Terquem, 1855, *Plagiostoma* Sowerby, 1814, *Plicatula acuminata* Terquem & Piette, 1855, *Pteria deshayesi* Terquem, 1855), which explains the nomenclatural origin of the so-called Grenzbivalvenbank, but also gastropods, (*Colostroacon avena* Terquem, 1855, *Katosira* Koken, 1892, *Mesalia Zinkeni* Dunker, 1851, *Omphaloptycha morencyana* Piette, 1856, *Promathilda sinemuriensis* Martin, 1862), and minor forms such as brachiopods, crinoids and echinoderms, benthic foraminifera, ostracods and corals (*Stylophyllum* Reus, 1854, *Stylophyllopsis* Frech, 1890).

In the upper lithozone of the Sedrina Limestone (Cenozones 2 and 3 of Gaetani 1970) and basal layers of the succeeding Moltrasio Limestone, shallow water conditions persisted but were characterized by a deepening upward trend (Jadoul & Galli 2008). Muddy bottoms and well oxygenated water offered suitable living conditions for the benthic communities, brachiopods in particular. Oolitic sediments suggest shallow warm waters, supersaturated with calcium carbonate. In contrast with the lower lithozone, in this facies can be noted increasing differentiation in biodiversity (Gaetani 1970; Jadoul & Doniselli 1987; Bersezio et al. 2014) with faunal communities mainly represented by brachiopods (*Calcirhynchia rectemarginata* Vecchia, 1945, *Cuneirhynchia latesinuosa* Trauth, 1909, *Lobothyris ovatisi-maeformis* Bockh, 1874, *Zeilleria perforata* Piette, 1856) - hence the so-called Brachiopod bank, gastropods (*Amberleya* aff. *decorata* Martin, 1859), crinoids (*Iso-crinus* Meyer in Agassiz, 1836), bivalves (*Cardinia quadrata* Agassiz, 1845, *Gryphaea* Lamarck, 1801, *Praeonia tetragona* (Terquem 1855), *Tutcheria heberti* Terquem, 1855) and rare, badly preserved ammonoid fragments (*Schlotheimia* Bayle, 1878).

In the present work, the Roncola section of the uppermost Sedrina Limestone was investigated. According to Vialli (1959), the fossil record of this section consists of brachiopods and small-sized, badly preserved ammonites. These strata can be correlated with Cenozone 3 of Gaetani (1970), being rich in crinoid, echinoid and brachiopod clusters, and to the Lithozone D of Jadoul & Doniselli (1987), corresponding to the “Livello a selci bianche” (Italian for “white chert marker bed”; Casati 1970; Gaetani 1970). This deposit represents a mid-high energy and relatively shallow open shelf - basin paleoenvironment.

According to the earlier studies dealing with the whole Lower Jurassic succession of Lombardy, some of which date back to the mid-nineteenth century, it is apparent that macrofossil records are currently limited to elements of the invertebrate fauna. The earliest occurrence of marine vertebrates following the TJB post-crisis recovery is known so far from the western part of the Lombardy Basin, where they suddenly appear in the Sinemurian Moltrasio Limestone of Osteno (Varese). Here, vertebrates are represented by *Cosmolepis ornatus*, cf. *Pteroniscus* (Egerton 1858), *Dapedium* Leach, 1822, *Furo* Gisl, 1848, an un-named myriacanthoid (Duffin 1993), *Ostenoselache stenosoma* Duffin, 1998, *Peripeltopleurus* Bürgin, 1992, *Pholidolepis* Nybelin, 1966, *Squaloraja polyspondyla* Agassiz, 1843 and *Synechodus pinnai* (Duffin, 1987).

On the contrary, if we consider the central part of the Lombardy Basin, the earliest documented post-TJB marine vertebrate macrofossil occurrence was provided by Tintori (1977), who described several species of fishes from the Toarcian deposit of the Albenza mountain range.

The reason behind this could be closely related to the Mesozoic Marine Revolution (MMR), seen as a post-Permo/Triassic Mass Extinction Event (PTME) ecosystem readjustment expressed in the replacement of ‘Palaeozoic’ by ‘Modern’ faunas. It is probably related to the post-PTME biotic recovery. Changing predator-prey interactions were a key component of this ecosystem evolution and seem to be expressed in a sort of ecological ‘arms race’ with novel adaptations emerging in both predators and prey (for a recent summary see Cueille et al. 2020 and references therein). Explosive bursts of adaptive radiation, beginning in the Triassic, affected most invertebrate and vertebrate groups, including crinoids (Baumiller et al. 2010) and sharks (Kriwet et al. 2009), the two faunal elements described in this paper. Increasing chondrichthyan diversity began in the Late Triassic but seems to have undergone significant expansion in the Toarcian (with the appearance of batomorphs, orectolobiforms, heterodontiforms and hexanchiforms; Cappetta 2012). *Synechodontiformes*, the sister group of all living sharks (Klug 2009; Klug et al. 2009), is the only group of neoselachian sharks to cross the Triassic/Jurassic boundary. *Sphenodus*, previously recorded from Sinemurian and younger rocks, belongs to this group.

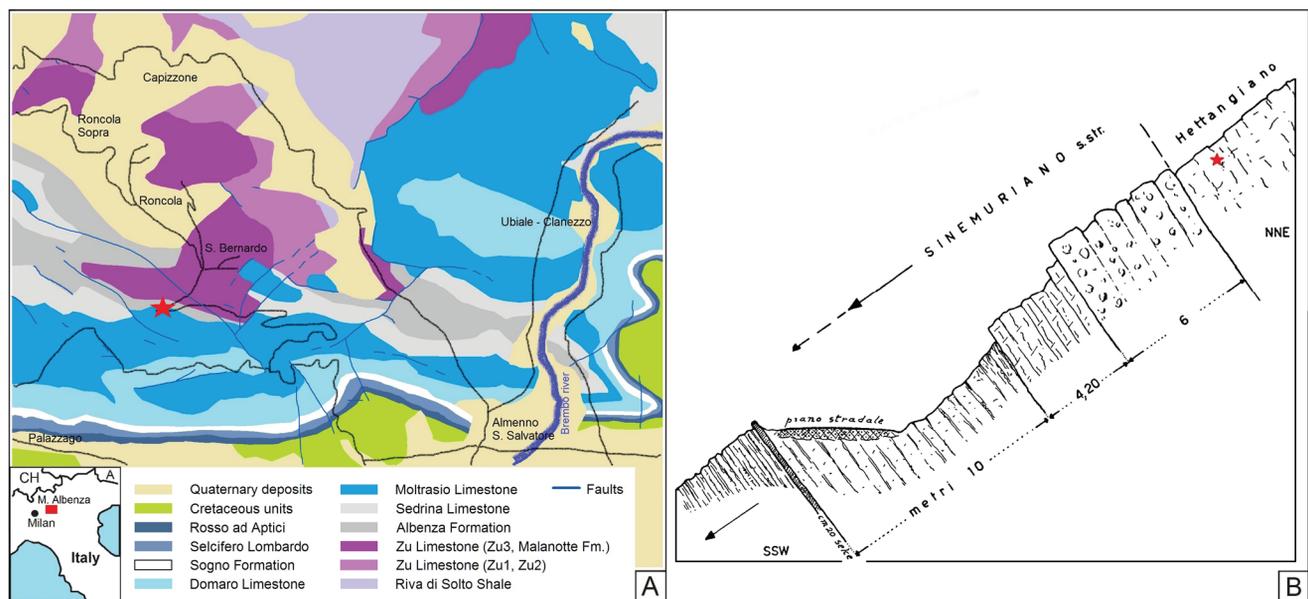


Fig. 2 - A) Simplified geological map of the studied area (modified after ISPRA, 2014). The red star indicates the position of the S. Bernardo section where sample MSNVI 044-076 was collected. B) Stratigraphy of the S. Bernardo section as reported in the work of Vialli (1959). A cut in the road (*piano stradale*) exposed the reversed strata with the Hettangian Sedrina Limestone beds overlying the Sinemurian Moltrasio Limestone.

The aim of this paper is to describe material from the Roncola section of the Sedrina Limestone, consisting of a dense accumulation of crinoid remains amongst which are three isolated neoselachian teeth which can be assigned to the genus *Sphenodus* Agassiz, 1843. These dental remains are the earliest vertebrate macrofossils documented from the Lombardy Basin following the TJB. *Sphenodus* is quite a common neoselachian shark in the Sinemurian and this discovery moves its First Appearance Datum back to the Hettangian stage. Moreover, the crinoid skeletal remains described here are identified as belonging to *Balanocrinus ticinensis* Hess, 2006. This species was previously regarded as an endemic form restricted to the upper Pliensbachian marly limestone of Arzo (Canton Ticino, Switzerland; see Fig. 1a). This new occurrence of *B. ticinensis* indicates that this genus was already present in the Lombardy Basin during the late Hettangian.

GEOGRAPHICAL AND GEOLOGICAL CONTEXT

The San Bernardo outcrop (45.764839°N, 9.553734°E) is located near the last turn of the SP172 road on the run up to the village of Roncola San Bernardo (750 metres away), on the left side of

Valle Imagna (province of Bergamo, Lombardy). It lies at an elevation of 850 metres above sea level (Fig. 2) and was discovered by a well-known local fossil collector, Luigi Torri (who also collected the fossils studied herein). The discovery of the locality was shared with Vittorio Vialli (b.1914 - †1983), paleontologist and vice-president of the Museo Civico di Storia Naturale di Milano since 1957. Vialli found this outcrop to be very interesting and praised the valuable contribution of Mr. Torri to our understanding of the paleontology of the Bergamo area and the Albenza mountain in particular (Pesenti 1977). In a series of subsequent field visits, Vialli undertook a stratigraphic analysis of the area (Vialli 1959) which is also known as the San Bernardo section.

Vialli provided detailed descriptions of the Sinemurian and Hettangian strata that were well exposed due to the sideways cut of the road, and his observations provided an important basis for the work of later authors (Gaetani 1970; Jadoul & Doniselli 1987).

According to Vialli (1959), the Hettangian strata are characterized by light brown (or “coffee and milk” grey), compact beds forming thick banks, with indistinct stratification. Rich in brachiopods and ammonites, these strata can be considered as belonging to the top of the Hettangian succession.

These strata have an E-W orientation and broadly exposed in the Bergamo province (Bersezio et al. 2014). Such strata were defined by Francani (1967) as the Sadrina Limestone. This lithostratigraphic unit includes a succession of bioclastic limestones (sometimes dolomitized), and oolitic or marly limestones with chert nodules, grey to black in colour. Several authors have recognized different lithozones (Francani 1967; Gaetani 1970; Jadoul & Doniselli 1987) in the Sadrina Limestone. The upper oolitic-bioclastic lithozone is made up of calcarenites and calcirudites, that are often rich in fossils (highly silicified bivalves, brachiopods and crinoids). This lithozone contains a highly fossiliferous level also known as the “brachiopod bank” (Rassmuss 1912).

MATERIAL AND METHODS

Specimen history

Luigi Torri (b.1904- †1996) was a well-known fossil collector. His contribution to the geological and paleontological knowledge of Mount Albenza was important, as before his discoveries this territory was considered to be a barren region as far as fossils were concerned. Cited in several scientific papers, six fossil species currently bear his name (Pesenti 1977). He was in contact with several representatives of the scientific community, among whom it is worth mentioning Ardito Desio (b.1897-†2001), Vittorio Vialli and mgr Marino Colombo (b.1917- †1987). The latter served as director of the Museo di Storia Naturale “Antonio Stoppani”, Venegono Inferiore (VA) from 1946 to 1964 (Gentili 1999) and *inter alia*, he also commissioned Mr. Torri to sample and build up the stratigraphic succession of Mount Albenza for educational purpose (for details see Jaselli 2020). Due to the friendship between them, in the 1960s, Mr. Torri personally collected and donated the specimen described in the present study to mgr Colombo. This sample is still housed in the collection of the Museo di Storia Naturale “Antonio Stoppani” (hereinafter referred to as the MSNVI) under accession number MSNVI 044-076.

Materials

MSNVI 044-076 consists of a ca. 215 x 150 mm block of light grey bioclastic calcarenite from the upper lithozone of the Sadrina Limestone, S. Bernardo section of M. Albenza, dated to the upper Hettangian.

The Upper lithozone of the Sadrina Limestone consists of oolitic-bioclastic calcarenites, affected by a diffuse silicification process and very rich in crinoid and other bioclasts, often piled up in banks (“Livello a selci bianche” (Casati 1970; Gaetani 1970)) contrasting with the basal layers of the succeeding lower Moltrasio Limestone (Sinemurian), which are characterized by better stratified and fine dark grey limestones with black chert.

The rock block studied here comprises a dense pile of silicified and disarticulated isocrinid remains (all belonging to the same genus) resembling a crinoid bank. Among them can be easily recognized the presence of three isolated neoselachian shark teeth as well as isolated echinoid spines.

SYSTEMATIC PALAEOLOGY

Class **CRINOIDEA** Miller, 1821

Subclass **ARTICULATA** von Zittel, 1879

Order **Isocrinida** Sieverts-Doreck, 1952

Family Isocrinidae Gislén, 1924

Subfamily Balanocrininae Roux, 1973

Genus *Balanocrinus* Agassiz in Desor, 1845

Type species: *Pentacrinites subteres* Goldfuss, 1831

Balanocrinus ticinensis Hess, 2006

Fig 3A-U

Material: MSNVI 044/076, a block of light grey bioclastic calcarenite comprising a dense pile of crinoid ossicles, mainly represented by isolated columnals (nodals and internodals), and a few pluricolumnals, almost entirely internodals (mainly composed of 2-3 columnals, the longest fragment comprising 6 columnals without any nodal), very few nodals (5) in comparison, one radial, one primibrachial and several secundibrachials.

Description

Moderate to long isocrinid. Even if the noditaxal length is unknown (as no complete noditaxi have ever been found), only five nodals were identified among hundreds of nodals present in this assemblage. This low nodal/internodal ratio strongly suggests moderate to long noditaxes.

Stem: columnal diameters range between 1.14 mm and 3.5 mm (2.4 mm on average). The outline of the columnals is sub-pentalobate (Fig. 3E) or pentagonal (Fig. 3I) to sub-pentagonal (Fig. 3F), or circular (Fig. 3S) to sub-circular (Fig. 3B). Ornamentation of the latera shows some variability, ranging from smooth cylindrical (Fig. 3L), and even weakly concave in some cases (Fig. 3R), to weakly tuberculate (Fig. 3D), from single tubercles to tubercles arranged and fused in a weak median irregular ridge (Fig. 3T). The nodal height is about 134% of the internodal height. Nodal diameters range between 1.3 mm and 2.9 mm (2.4 mm on average). Cirral scar width is between 0.46 to 0.96 mm (0.74 mm on average). Cirral scars are rounded or slightly oval and proportionately moderate (*sensu* Simms 1989) with a width of 29% to 36% (33% on average) of nodal diameter and a height of about 57% to 87% (74% on average) of nodal height (distal lip excluded). The cirrus socket is not deeply sunken but directed outward and slightly upward. The distal lip is well developed, prominent, and may overreach the lower margin (Fig. 3A). Cupules are weak-

ly developed above the cirral scar of nodals (Fig. 3O). The central pore of the cirral scar divides a transverse ridge which is thickened at each end (Fig. 3O). Articulation between nodal and infranodals is cryptosymplectial (Fig. 3O). Columnal articulation is symplectial with an arrangement of the crenulae which is peculiar to this genus (Fig. 3E). Marginal crenulae length increases toward the radials; adradial crenulae of adjacent petals are mostly fused in a typical V-shape and decrease in size toward the lumen but sometimes they are weakly developed or indiscernible (Fig. 3A, 3C); the petal outline is elliptical or pyriform. A few columnars (internodals) feature well-developed intercolumnal fossulae (Fig. 3H, 3Q), or show an inflated latus (Fig. 3R).

Cup: the cup and primibrachials are represented by only a small number of specimens, all of which are heavily weathered, compromising confident identification; however, considering the fact that this assemblage of ossicles seems to be monospecific, these elements are assigned to the same species. One weathered and isolated radial can be observed in aboral view; the outline is pentagonal, the upper margin slightly concave, and the lower margin bowl-shaped; the radial is wider than high, and no other characters are discernible. A high, stretched basal ring seems to be fused with the uppermost columnal, basal and radials (Fig. 3U). The poor state of preservation precludes any further diagnosis or meaningful measurement.

Brachials: just one primibrachial and a few secundibrachials have been identified but their assignment cannot be made with confidence because of being obscured by the surrounding matrix. These ossicles all feature a smooth or slightly granular surface. Among them can be recognized a primibrachial (Fig. 3P) with a smooth proximal (muscular facet) and certain secundibrachials which have a proximal facet without a pinnule socket (Fig. 3N), a distal (syzygy) facet with typical V-shaped ridges and furrows radiating from the axial canal without a pinnule socket (Fig. 3G), and a synostiosial facet pinnule which is socket-free (Fig. 3M).

Taxonomic remarks

Ranging from the Middle Triassic (Anisian; Hagdorn 2011) to the Lower Cretaceous, *Balanocrinus* is the longest-lived of all isocrinids (Hess & Gale 2010). This genus appears in the Triassic fossil record and is believed to have evolved from *Isocri-*

nus by pedomorphic progenesis (Hunter & Clark 2009; Simms 1988, 1989). Either way, Hess (2013b) considered debatable Triassic and Upper Cretaceous occurrences thus narrowing the confirmed range of this genus as being from the Early Jurassic (Sinemurian) to the Lower Cretaceous (Albian).

Among the Jurassic crinoids, the genus *Balanocrinus* is quite common and includes several species that have been described from several geological formations and locations (Klikushin 1982, 1992; Hess 2013a, 2013b, Krajewski et al. 2019); these species are mainly diagnosed on the pattern of their flexible ligamentary articulation (symplectial).

Variability in columnal outline and ornamentation are common in isocrinids (Hess 2006) and morphological variations along the stem (i.e. proximal to distal) can be expected. This variance might wrongly suggest that the specimens belong to multiple taxa. For this reason, several new species (featuring little difference in morphology) have been erected on the basis of very few specimens, referencing rather restricted portions of the column (Hess 2013b). In order to avoid this potential pitfall, the herein described specimen was compared with numerous species already described in literature, and above all, with reported occurrences from Lower Jurassic strata.

Balanocrinus antiquus de Loriol, 1887 (*nomen dubium* according to Simms 1989) seems to be the only balanocrinid found in Hettangian deposits, but the species merely shows morphological similarity with a balanocrinid symplectial and is presumed to be a remnant of a Triassic lineage (Simms 1989, 2011).

Simms (1989) also described five balanocrinid species from the Lower Jurassic, distributed in Sinemurian to Lower Toarcian rocks: *B. quiaiosensis* de Loriol, 1891; *B. subteroides* Quenstedt, 1858; *B. gracilis* Charlesworth, 1847 and *B. solenotis* Simms, 1989. All these species feature smooth latera, devoid of any ornamentation. Therefore, none of them resembles our specimens except for *B. moniliferus* Münster in Goldfuss, 1831, characterized by ornamented latera and short noditaxi made up of 4-5 columnals. MSNVI 044/076 lacks any complete noditaxi but, considering the ratio between nodals and internodals, the expectation is that a moderately-long one was present.

From the upper Pliensbachian (Domerian) calcareous mudstones and marlstones of Arzo (Ticino, Switzerland), Hess (2006) has described a

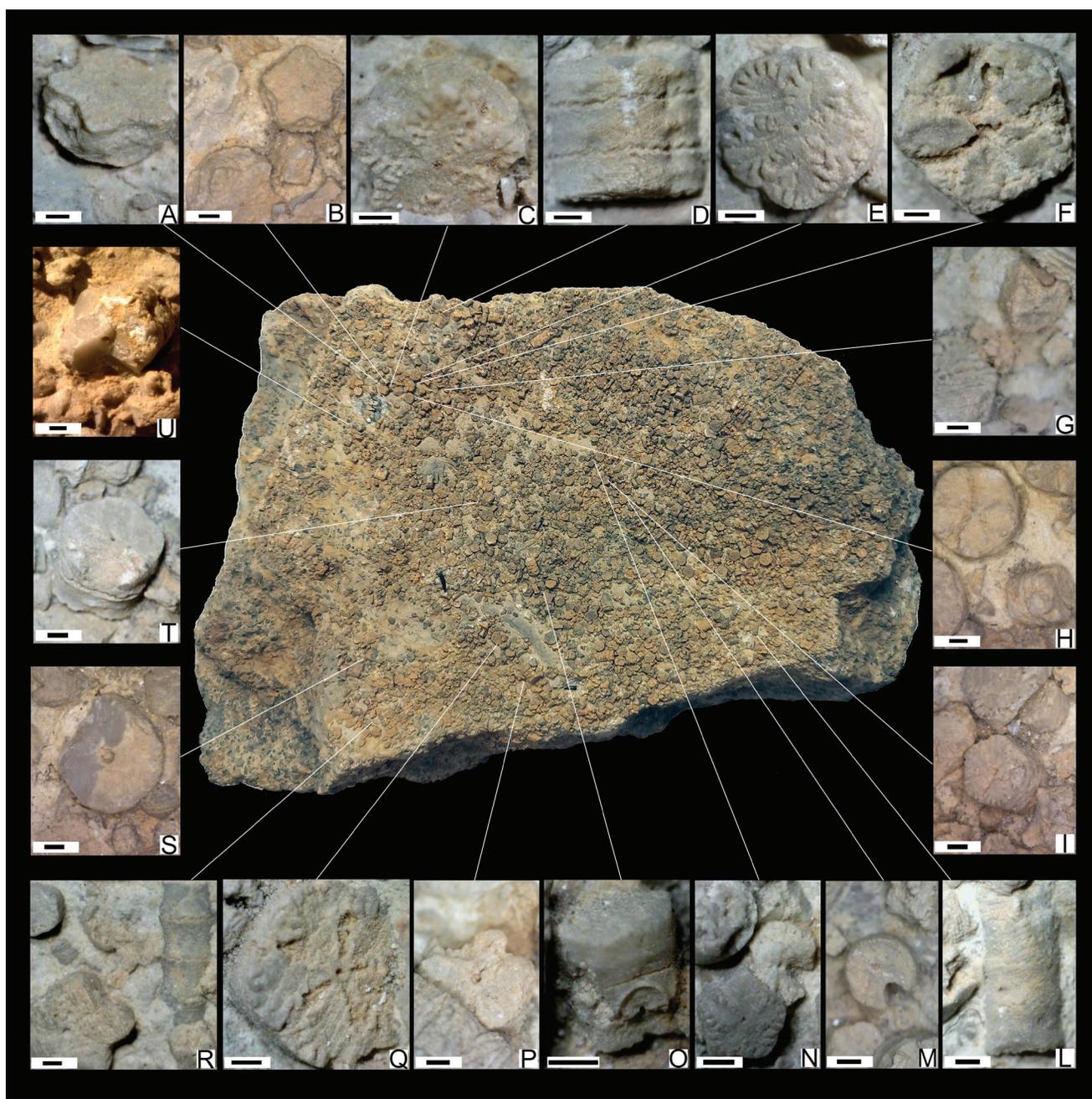


Fig. 3 - *Balanocrinus ticinensis*, upper Hettangian, Roncola San Bernardo (Bergamo, Italy). A-B-C) Nodal with proximal symplectial facet and latera with well-developed cirrus socket. D) Weakly ornamented (single tubercles) pluricolumnal latera. E) Sub-pentalobate internodal with rather deep areola. F) Weathered sub-pentagonal internodal. G) Secundibrachial, distal (syzygy) facet without pinnule socket. H) Symplectial facet of internodal with intercolumnal fossulae. I) Symplectial facet of pentagonal internodal. L) Lateral view of a pluricolumnal (four internodals) with weakly concave latera. M) Secundibrachial, synostosal facet pinnule socket free. N) Secundibrachial (proximal facet without a pinnule socket) and a sub-pentagonal internodal symplectial. O) Lateral view of pluricolumnal (nodal and supranodal) with well-developed cirrus socket. P) Primibrachial smooth proximal (muscular facet). Q) Columnal facet with well-developed intercolumnal fossulae. R) Lateral view of a pluricolumnal (four internodals) with concave latera. S) Smooth facet of a circular internodal. T) Symplectial facet of a weakly ornamented (tubercles fused in a weak median irregular ridge), sub-pentalobate pluricolumnal. U) Lateral view of an high basal ring (seemingly fused by the top most columnal, basal and radials). Scale bars = 0.5 mm.

rich and diversified crinoid fauna, raising also the species *Balanocrinus ticinensis* Hess, 2006. Due to its distinctiveness, the large number of ossicles collected, and a comparison with previously reported Early Jurassic balanocrinids, Hess (2006) regarded it

as an endemic species not formerly reported from elsewhere.

The Lombardy specimens are compatible with *B. ticinensis* as can be seen from the description (see above). However, some minor differences are

noted between the Italian and the Swiss materials:

(1) Simms (1989) considers a noditaxi length where the number of columnals is in the range of 10–25 as being moderate. Hess (2006) was unable to find a complete noditaxi of *B. ticinensis* and estimated it as comprising a length of about ten columnals. The Lombardy specimens have also failed to yield a complete noditaxi, and the low number of nodals found in respect of the internodals suggests a moderate or maybe a long (>25 columnals) noditaxal length. This feature remains questionable for both these occurrences until complete noditaxi are found for this taxon.

(2) Low proximal columnals with tubercles fused in a sharp median ridge as described by Hess (2006) cannot be positively recorded in the Lombardy specimens, but their presence cannot be excluded due to the nature of the accumulation (a pile of ossicles embedded in rock matrix instead of single sieved and isolated articula). Weakly tuberculate latera can be clearly recognized in our sample (Hess 2006, pl. 23, fig. 11); these perfectly match those present in Fig. 3D, sometimes fused together to form a weak irregular median ridge.

(3) Cirral scar height is 70% of the nodal height (lip excluded) in *B. ticinensis* and 74% in the Lombardy specimen. This is a minimal and probably insignificant difference, especially since the nodals figured by Hess (2006, fig. 16) are identical to those illustrated in Fig. 3A.

Therefore, according to the morphological characters described, the crinoid remains embedded in sample MSNVI 044/076 fully match the diagnosis of *Balanocrinus ticinensis* and can be assigned with confidence to that taxon. The aforementioned minor differences can be interpreted as part of the range of intraspecific variation as also shown in living populations of crinoids.

Remarks on palaeoecology and taphonomy

The monotaxic crinoid assemblage described herein is the remnant of a colony of organisms that inhabited the marine floor of the Lombardian basin after the Triassic–Jurassic extinction event. Piles of balanocrinid articula and ossicles densely carpet the bedding surface, thus documenting a high density of individuals that successfully colonized the same benthic environment. Often, these mass occurrences are monospecific as these organisms commonly lived in dense aggregations (Hess 2013b).

Widely distributed in shallow and deep water environments, *Balanocrinus* can be considered the most successful genus of Jurassic stalked crinoid (Hess 2013b). Extant stalked crinoids prefer to attach on to hard substrates, but *Balanocrinus* was able successfully to colonise muddy seafloors (de Loriol 1887; Hess 1975, 2006; Simms 1989; Thuy et al. 2011) as well as hardgrounds by anchoring to the sea bottoms via their cirri.

It is also common for isocrinids to relocate and find suitable microhabitats depending on: (1) the availability of suitable substrates; (2) the presence of suitable current flow to supply their feeding filtration fan; (3) the need to protect against benthic predators (Stiller 2011, and references therein; Hess 2013b).

Simms (1986) argued that benthic crinoids seem to be facies-dependent. Hess (2013b) later indicated that articulated, well preserved balanocrinid remains are found in muddy seafloor deposits, whereas they are disarticulated when associated with hardgrounds. This is also the case for the sample studied here, where the skeletal remains are disarticulated and embedded in bioclastic calcarenites of the upper lithozone of the Sedrina Limestone, which testify to a depositional environment typical of an open subtidal platform.

Intact, articulated fossil crinoids imply death having either been caused, or immediately followed, by sudden burial. This quite rare occurrence prevents crinoids from undergoing rapid decay and subsequent disarticulation of their skeletal components. By contrast, marine currents and the activities of scavengers or bacterial decay of soft tissues are responsible for the rapid disarticulation of crinoid skeletons (Meyer 1971, Liddell 1975). This is mainly because the skeletons of echinoderms are formed by complexes of calcitic ossicles that rapidly disarticulate when the organism dies. Donovan (1991) reported that, in normal oxygenated conditions, complete post-mortem disarticulation of crinoids occurs within a couple of weeks after death. Experiments performed by Gorzelak & Salamon (2013) demonstrate that initial disintegration in crinoids takes place after two hours, equivalent to ca. 1 km of transport (with this method, crinoid specimens were put in a tumbling barrel with a speed around 0.135 m/s time equivalent to ca. 0.5 km of transportation per one hour. According to this model two hours are equivalent to 1 km) and com-

plete disarticulation was achieved after 408 hours (ca. 204 km of transport). The disarticulation grade depends on the associated current energy, style of post-mortem transport, and time elapsed between death and physical disturbance.

The high degree of disarticulation present in sample MSNVI 044/076 suggests long-term exposure on the sea bed. The degree of preservation of these specimens cannot help in determining the extent of transportation that has taken place.

Class **CHONDRICHTHYES** Huxley, 1880
 Subclass **ELASMOBRANCHII** Bonaparte, 1838
 Cohort **Euselachii** Hay, 1902
 Subcohort **Neoselachii** Compagno, 1977
 Superorder **Squalomorphii** Compagno, 1973
 Order **Synechodontiformes** Duffin & Ward, 1993
 Family Orthacodontidae Glikman, 1957
 Genus *Sphenodus* Agassiz, 1843
 Type species: *Sphenodus longidens* Agassiz, 1843

Sphenodus helveticus De Beaumont, 1960

Sphenodus cf. *helveticus*

Fig. 4A-F

Material: MSNVI 044-076, a block of light grey bioclastic calcarenite with three isolated central cusps, here designated as (A), (B) and (C).

Description

The block exposes three isolated crowns (Fig. 4A-F). One of these, designated tooth C (Fig. 4A-B) is fragmentary and shows little detail other than an ornament comprising well-developed vertical ridges. The other two cusps (teeth A and B; Fig. 4C-E and Fig. 4F respectively) are more complete and can be described in more detail.

Tooth A (Fig. 4C-E) is an isolated cusp exposed in oblique labial view. The maximum height of the upright, sharply-pointed cusp is around 5.7 mm, and the mesio-distal width at the preserved base is 1.46 mm. The cusp is fairly gracile, with slight sigmoidal flexure in lateral view. The cutting edges are prominent, equally sharp on both the mesial and distal sides (so far as can be told) and best developed in the apical half of the cusp. No torsion in the long axis of the cusp seems to be present. The labial face of the cusp is rather more flattened than the more deeply convex lingual face. Both faces of

the cusp are ornamented with a series of relatively coarse, mostly non-bifurcating vertical ridges. Most of these ridges originate from the cusp base (a few are added just above it), are regularly spaced mesio-distally, and ascend the labial face of the cusp to a point approximately half-way to the cusp apex. Not all the ridges reach this point labially; some terminate around 35% of the way up the cusp. Only the most central ridge of the labial face bifurcates basally. The ridges on the lingual face of the crown are partly obscured by matrix but, so far as can be told, ascend to a similar point on the cusp and have a similar density. The cusp is almost symmetrical and probably comes from an anterior position in the dentition.

Tooth B (Fig. 4F) is also an isolated cusp and is the smaller of the two specimens. It measures approximately 3.3 mm in height and 1.01 mm in mesiodistal width across the base. Exposed in labial view, the cusp is less symmetrical than in specimen A; it is slightly inclined distally (about 12 degrees from the vertical). This suggests that it originates from a slightly more lateral position in the dentition than specimen A. The cutting edges are symmetrically disposed and very well developed, especially half-way up the cusp, which is not so sharply pointed as in specimen A. The labial face of the cusp appears to lack ornamentation; this face is slightly flattened, smooth and does not possess vertical ridges. There is a slightly flattened area toward the base of the cusp.

Taxonomic remarks

Sphenodus is a genus of neoselachian shark that has been the subject of considerable debate, and whose definition and relationships are still a matter of some conjecture. Originally raised by Agassiz for *Lamna* (*Sphenodus*) *longidens* Agassiz (1843, vol. 3, p. 298, pl. 37, figs. 24-29), based on isolated cusps from the Upper Jurassic (Oxfordian) of several localities in Bavaria, subsequent publications saw a large number of species being established, mostly on the basis of isolated complete and partial teeth. This has led to a proliferation of species names; most workers agree that much synonymy probably exists amongst the described material, and that the genus is due for critical re-evaluation (e.g. Duffin & Ward 1993, p. 58; Rees 2000, p. 416; Guinot et al. 2014, p. 61). Part of the problem centres around the fact that, whilst a single tooth might be designated

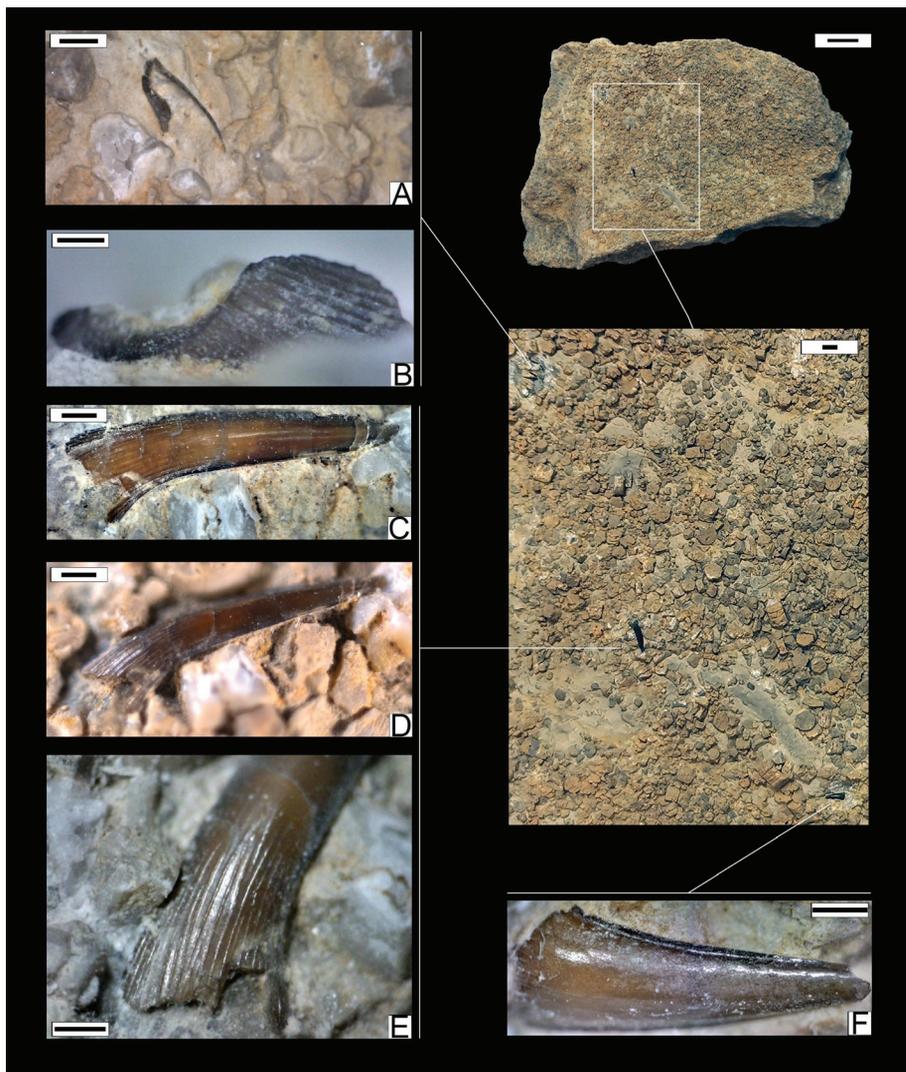


Fig. 4 - *Sphenodus* cf. *helveticus*, upper Hettangian, Roncola San Bernardo (Bergamo, Italy). A) Fragmented tooth C. Scale bar = 1 mm. B) closer view of ridges on fragmented tooth C (lingual view). Scale bar = 0.2 mm.; C-E) Tooth A. Scale bar = 0.5 mm; F) Tooth B. Scale bar = 1 mm. This figure also indicates the locations of the teeth on Specimen MSNVI 044-076 in global (scale bar = 2 cm) and detailed view (scale bar = 2 mm). C-D) latero-labial view. E-F) labial view.

as a holotype, our understanding of tooth-based selachian species requires an appreciation of the heterodonty (which might be considerable) shown through the dentition. This might involve changes in tooth morphology in a single jaw (monognathic heterodonty), between the upper and lower jaws (dignathic), between the sexes (gynandric), or with age (ontogenetic). Whilst a full analysis of the heterodonty is not needed to define a selachian taxon based on teeth, modern workers try to incorporate some consideration of it when erecting new species or making comparisons with other species. The assignment of the status of a new species to specimens in older literature did not always take heterodonty into account, leading to confusion in the definition of extinct taxa in numerous cases. Fortunately, a few specimens of *Sphenodus* from Konservat Lagerstätten contain complete or partial dentitions from which aspects of the heterodonty can be discerned and, potentially, applied to the genus

as a whole (e.g. Wagner 1862; Böttcher & Duffin 2000). Initial attempts to clarify the status of certain nominal species of *Sphenodus* have met with only limited success (Cusumano et al. in press).

De Beaumont (1960) was the first to review this genus, and when Duffin & Ward (1993) suggested that *Sphenodus* belonged in the Family Orthacodontidae as part of the Order Synchodontiformes they listed 28 nominal species contained within it, ranging from the Lower Jurassic (Sinemurian) to the Lower Cenozoic (Danian). Guinot et al. (2014, p. 61) stated that *Sphenodus* embraces “about 30 nominal species” but give its range as Bajocian (Middle Jurassic) to Danian. The reason for this contraction in the proposed range of the genus is concern over whether some of the earlier species originally assigned to *Sphenodus* actually belong in the genus or not. The oldest member of genus, as traditionally defined, is *Sphenodus helveticus*, raised by de Beaumont (1960) for isolated teeth from the Sinemurian

of Arzo in Switzerland. Cappetta et al. (1993, p. 599) commented that the type material of *S. helveticus* contained teeth of both *Sphenodus* and *Paraorthacodus*. This point was picked up by Rees (2000, p. 416) who commented that ‘as *Sphenodus* is probably the sister-group of the palaeospinacids (Duffin & Ward 1993), it is likely that early forms would have a morphology approaching that of some early palaeospinacids’. Cappetta (2006, p. 103) then transferred the species *helveticus* to *Paraorthacodus*, but later (Cappetta 2012, p. 101) seemed to retain it in *Sphenodus*. Cappetta (2012, p. 102) presented the most recent summary of the two genera as a whole and indicated the differences between them as *Sphenodus* possessing a less well developed pseudopolyaulacornhize root, and a central cusp which is higher and sharper with better-defined cutting edges (a feature which he considers to be autapomorphic for the genus). Note, however, that Klug et al. (2009, p. 110) include the presence of a well-developed cutting edge in their diagnosis of *Paraorthacodus*.

Considering these rather poorly defined characters in respect of the Hettangian teeth described above, unfortunately no judgement can be made concerning root vascularisation as the roots are missing. The cutting edges in the Lombardy specimens are evenly developed on mesial and distal sides of the cusp and are clearly well defined (Fig. 4D-F). Some later species of *Sphenodus* show asymmetric development of the cutting edges and torsion of the cusp about its long axis (Böttcher & Duffin 2000), but these features are not present in all members of the genus (e.g. Cappetta 2012, fig. 88; de Beaumont 1960). Tooth A seems to be sharply pointed (Fig. 4C) as in teeth of both *Sphenodus* and *Paraorthacodus* (Böttcher & Duffin 2000 figs 11, 13 pls. 1-2; Klug et al. 2009, fig. 7). Unfortunately, the fact that the Hettangian material comprises only isolated central cusps precludes calculating a cusp height to tooth width ratio, which is one means of judging relative cusp height. In terms of absolute size, it is true that some later species of *Sphenodus* are very high-crowned with central cusps measuring 35 mm or more (e.g. in *S. longidens*, which ranges from the Bajocian to the Aptian). Cusp height in the Hettangian material falls within the size range of that described for *Sphenodus macer* Quenstedt, 1851 (Middle Oxfordian to Late Kimmeridgian) and for which the full dentition is known (Böttcher & Duffin 2000). The Lombardy material also shows the

presence of a slight sigmoidal flexure to the central cusp in lateral view, a character noted to be commonly developed in teeth of *Sphenodus* (Cappetta 2012, p. 100). Thus, we conclude that the Hettangian teeth described above fall within the diagnosis of the genus *Sphenodus*.

The presence of vertical ridges toward the base of the central cusp is a feature also found in teeth of *Sphenodus helveticus*, originally described by de Beaumont for isolated teeth from the Upper Sinemurian (Lotharingian regional stage) of Arzo (Switzerland; de Beaumont 1960 fig. 3) which is also the type locality of *Balanocrinus ticinensis*. The development and extent of these ridges is similar in the two samples, leading us to designate the Hettangian teeth *Sphenodus* cf. *helveticus*. In other species of the genus, such ridges are commonly reduced or, more commonly, absent altogether (e.g. Duffin & Ward 1993 text-fig. 1; Böttcher & Duffin 2000; Citton et al. 2019).

Discussion

The question arises as to whether there is any palaeoecological significance to the association of isolated sharks’ teeth and crinoid debris on the same bedding plane at this locality. Does the association represent part of a food chain, or is it the consequence of sedimentological and taphonomic factors alone? The question is not easily answered with confidence but is discussed below.

Balanocrinus is a stalked suspension-feeding crinoid which most commonly occurs in monospecific aggregations, often reflecting high density populations exploiting muddy sea floors (Hess 2013b, p. 43). The San Bernardo sample comprises an abundance of disarticulated, mostly isolated skeletal elements lying on the bedding surface. The bulk of the material is made up of isolated columnals with occasional short lengths of articulated pluricolumnals also being found. Parts of the cup and brachial skeletons are also disarticulated and much less common than the columnals. Representational disparities like this have long been suspected as being due to some form of taphonomic bias, especially the possibility of selective predation (Baumiller & Gahn 2003). Possessing bodies comprising a high proportion of calcareous skeletal components, the low nutrient returns for crinoids has suggested that predation pressure on them is likely to be low. This seems to be true for extant crinoids (Meyer &

Ausich 1983, p. 380). When it comes to the fossil record, predation of crinoids is even less well understood. There is some direct evidence of predation by fishes during the Palaeozoic; the Permian petalodont *Janassa bituminosa* Schlotheim 1820, for example, has had crinoid brachial fragments reported as stomach contents (Malzahn 1968, p. 83), while Zangerl & Richardson (1963, p. 142) recorded crinoid columnals in a coprolitic mass, probably produced by a chondrichthyan from the Pennsylvanian of Illinois. We are not aware of any other evidence for predation on crinoids by chondrichthyans.

The sharply-pointed, relatively high-cusped teeth armed with well-developed cutting edges in *Sphenodus* belong to a tearing-type dentition. This, together with the body form known from articulated material described from the Late Jurassic of Nusplingen (Böttcher & Duffin 2000), suggests that *Sphenodus* was an active pelagic predator, probably feeding at the surface or in mid-water column. The tooth morphology implies feeding on nekton such as fishes and cephalopods (Citton et al. 2019) rather than on benthonic organisms. Thus, it is most likely that the association between the teeth of *Sphenodus* and the skeletal fragments of *Balanocrinus* is due to chance rather than indicating part of an ancient food chain. Moreover, considering the relatively poor preservation of these incomplete teeth (lacking cusp apices and roots) at least minimal transportation by marine currents or other external event cannot be excluded. Taking into account the fact that the upper lithozone of the Sedrina Limestone offered suitable living conditions for *Balanocrinus*, it can be speculated that these crinoids were autochthonous, being deposited in their immediate living environment, where they were associated with allochthonous shark teeth.

CONCLUSIONS

The discovery of new material from the upper Hettangian Sedrina Limestone of Roncola San Bernardo, documents the presence of marine vertebrates in the Lombardy Basin in the wake of the TJB biotic crisis. This is significant, because even if their presence in this shallow water environment might have been assumed, it was never reported in earlier studies. This is also true for the balanocrinid skeletal remains (*Balanocrinus ticinensis*), which docu-

ment a new and earlier occurrence than previously reported, and which was formerly considered to be an endemic species.

Both of these finds extend our knowledge of the diversification of ecological communities in the Early Jurassic South Alpine Domain. Future research and hopefully the discovery of new material could improve upon the results of the present work.

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REFERENCES

- Agassiz J.L.R. (1833–1843) - Recherches sur les poissons fossiles. 3, Neuchâtel, viii + 390 + 32 pp., Atlas with 82 pls.
- Agassiz J.L.R. (1836) - Prodrôme d'une Monographie des Radiaires ou Echinodermes. *Mémoires de la Société des Sciences naturelles de Neuchâtel*, 1: 168-199.
- Baumiller T.K. & Gahn F.J. (2003) - Predation on Crinoids. In: Kelley P.H., Kowalewski M. & Hansen T.A. (Eds) - Predator-Prey Interactions in the Fossil Record: 263-278. Kluwer Academic/Plenum Publishers, New York.
- Baumiller T.K., Salamon M.A., Gorzelak P., Mooi R., Charles G. Messing C.G., & Gahn F.J. (2010) - Post-Paleozoic crinoid radiation in response to benthic predation preceded the Mesozoic marine revolution. *Proceedings of the National Academy of Sciences*, 107(13): 5893-5896.
- Beaumont G. de (1960) - Contribution à l'étude des genres *Orthacodus* Woodw. et *Notidanus* Cuv. (Selachii). *Mémoires Suisses de Paléontologie*, 77: 1-46.
- Bersezio R., Bini A., Gelati R., Ferliga C., Rigamonti I. & Strini A. (2014) - Note illustrative della Carta Geologica d'Italia alla scala 1:50.000: Foglio 097 "Vimercate". Servizio Geologico D'Italia, 293 pp.
- Bertotti G., Picotti V., Bernoulli D. & Castellarin A. (1993) - From rifting to drifting: tectonic evolution of the South-Alpine upper crust from the Triassic to the Early Cretaceous. *Sedimentary Geology*, 86: 53-76.
- Bonaparte C.L.J. (1838) - Selachorum tabula analytica. *Nuovi Annali Scienze naturali*, (1)2: 195-214.
- Bottini C., Jadoul F., Rigo M., Zaffani M., Artoni C. & Erba E. (2016) - Calcareous nannofossils at the Triassic/Jurassic boundary: stratigraphic and paleoceanographic characterization. *Rivista Italiana di Paleontologia e Stratigrafia*, 122(3): 141-164.
- Böttcher R. & Duffin C.J. (2000) - The neoselachian shark *Sphenodus* from the Late Kimmeridgian (Late Jurassic) of Nusplingen and Egesheim (Baden-Württemberg, Germany). *Stuttgarter Beiträge zur Naturkunde. Series B*, 283: 1-31.

- Cappetta H. (1987) - Chondrichthyes II. Mesozoic and Cenozoic Elasmobranchii. In: Schultze H.P. (Ed.) - Handbook of Paleichthyology, 3B. Gustav Fischer Verlag, Stuttgart, 193 pp.
- Cappetta H. (2006) - Elasmobranchii Post-Triadici (Index specierum et generum). *Fossilium Catalogus. 1. Animalia*, Pars 142: 1-472.
- Cappetta H. (2012) - Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth. In: Schultze H.P. (Ed.) - Handbook of Paleichthyology, 3E: 512 pp. Verlag Dr. Friedrich Pfeil, München.
- Casati P. (1970) - Alcuni aspetti della silicizzazione di calcari oolitici della Lombardia e del Veneto. *Natura*, 61: 197-211.
- Charlesworth E. (1847) - New species of *Pentacrinus* in the Lias of Yorkshire. *London Geological Journal*, 2(96): 131-132.
- Citton P., Romano M., Fabbi S. & Cipriani A. (2019) - Jurassic neoselachian sharks from the Mt Nerone Pelagic Carbonate Platform (Umbria-Marche Apennine, Italy): a further constrain for the palaeoecology related to PCP systems. *Historical Biology*, doi.org/10.1080/08912963.2019.1699920
- Compagno L.J.V. (1973) - Interrelationships of living elasmobranchs. In: Greenwood P.H., Miles R.S. & Patterson C. (Eds) - Interrelationships of Fishes 1: 15-61. *Zoological Journal Linnean Society*.
- Compagno L.J.V. (1977) - Phyletic Relationships of Living Sharks and Rays. *American Zoologist*, 17: 303-322.
- Cueille M., Green E., Duffin C.J., Hildebrandt C. & Benton M.J. (2020) - Fish and crab coprolites from the latest Triassic of the U.K. and evidence for the origins of the 'Modern' ecosystem. *Proceedings of the Geologists' Association*, 131 (6): 699-721.
- Cusumano A., d'Arpa C. & Duffin C.J. (in press) - Taxonomic revision of the genus *Sphenodus* in the Jurassic collections of the "G.G. Gemmellaro" Geological Museum (Palermo, Sicily). *Bollettino della Società Paleontologica Italiana*.
- Desor E. (1845) - Résumé de ses études sur les crinoïdes fossiles de la Suisse. *Bulletin de la Société des Sciences naturelles de Neuchâtel*, 1: 211-222.
- Donovan S.K. (1991) - The taphonomy of echinoderms: calcareous multi-element skeletons in the marine environment. In: Donovan S.K. (Ed.) - The processes of fossilization: 241-269. Belhaven Press, London.
- Du Y., Chiari M., Karádic V., Nicora A., Onoue T., Pálffy J., Roghi G., Tomimatsu Y. & Rigo M. (in press) - The asynchronous disappearance of conodonts: New constraints from Triassic-Jurassic boundary sections in the Tethys and Panthalassa. *Earth-Science Reviews*.
- Duffin C.J. (1987) - *Palaeospinax pinnai* n. sp., a new palaeospinacid shark from the Sinemurian (Lower Jurassic) of Osteno (Lombardy, Italy). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 128: 185-202.
- Duffin C.J. (1998) - *Ostenoselache stenosoma* n. g. n. sp., A new neoselachian shark from the Sinemurian (Early Jurassic) of Osteno (Lombardy, Italy). *Paleontologia Lombarda*, 9, 39 pp.
- Duffin C.J. & Patterson C. (1993) - I Pesci Fossili di Osteno: una Nuova Finestra sulla Vita del Giurassico Inferiore. *Paleocronache*, 2: 18-38.
- Duffin C.J. & Ward D.J. (1993) - The Early Jurassic Palaeospinacid sharks of Lyme Regis, southern England. *Service géologique Belgique, Professional Paper*, 264: 53-102.
- Gaetani M. (1970) - Faune Hettangiane della parte orientale della provincia di Bergamo. *Rivista Italiana di Paleontologia*, 76 (3): 355-442.
- Galli M.T., Jadoul F., Bernasconi S.M. & Weissert H. (2005) - Anomalies in global carbon cycling and extinction at the Triassic/Jurassic boundary: evidence from a marine C-isotope record. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 216 (3-4): 203-214.
- Galli M.T., Jadoul F., Bernasconi S.M., Cirilli S. & Weissert H. (2007) - Stratigraphy and palaeoenvironmental analysis of the Triassic-Jurassic transition in the western Southern Alps (Northern Italy). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 244 (1-4): 52-70.
- Gentili E. (1999) - Il Museo scientifico-naturalistico Antonio Stoppani e gli altri beni culturali del Seminario di Venegono. In: Morando C. (Ed.) - I luoghi del patrimonio: 87-102. Ed. Franco Angeli.
- Gislén T. (1924) - Echinoderm Studies. *Zoologiska Bidrag*, 9, Uppsala, 330 pp.
- Glikman L.S. (1957) - O geneticheskoy svyazi semeystv Lamnidae i Odontaspidae i novykh rodakh verkhnemelovykh lamnid. [Genetic relations of the Lamnidae and Odontaspidae and new genera of lamnids from the Upper Cretaceous]. *Trudy Geologicheskogo muzeja Imeni A. P. Karpinskogo/Akademija Nauk SSSR*, 1: 110-117.
- Goldfuss G.A. (1826-1833) - Petrefacta Germaniae, Divisio prima. Divisio secunda. Radiariorum reliquiae: 115-221 [Echinodermata]. Arnz & Co., Düsseldorf, 252 pp.
- Gorzela P. & Salamon M.A. (2013) - Experimental tumbling of echinoderms - Taphonomic patterns and implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 386: 569-574.
- Guinot G., Cappetta H. & Adnet S. (2014) - A rare elasmobranch assemblage from the Valanginian (Lower Cretaceous) of southern France. *Cretaceous Research*, 48: 54-84.
- Hagdorn H. (2010) - Triassic: the crucial period of post-palaeozoic crinoid diversification. *Swiss Journal of Paleontology*, 130: 91-112.
- Hay O.P. (1902) - Bibliography and catalogue of the fossil Vertebrata of North America. *Bulletin of the United States Geological Survey*, 179: 1-168.
- Hess H. (1975) - Die fossilen Echinodermen des Schweizer Juras. Seesterne, Schlangensterne, Seelilien, Seeigel, See walzen. Veröffentlichungen aus dem Naturhistorischen Museum Basel, 8: 1-130.
- Hess H. (2006). Crinoids from the Lower Jurassic (Pliensbachian) of Arzo, southern Switzerland. *Schweizerische paläontologische Abhandlungen* 126, 143 pp.
- Hess H. & Gale A.S. (2010) - Crinoids from the Shenley Limestone (Albian) of Leighton Buzzard, Bedfordshire, UK. *Journal of Systematic Palaeontology*, 8 (3): 427-447.
- Hess H. (2013a) - *Balanocrinus* and other crinoids from Late Jurassic mudstones of France and Switzerland. *Swiss Journal of Paleontology*, 133: 47-75.
- Hess H. (2013b) - *Balanocrinus* (Crinoidea) from the Jurassic:

- species concept, reconstruction, ontogeny, taphonomy and ecology. *Swiss Journal of Palaeontology*, 133: 35-45.
- Hunter A.W. & Clark N.D.L. (2009) - The discovery of *Isocrinus* cf. *robustus* from the Lias Group (Lower Jurassic) near Dunrobin Castle, Sutherland, Scotland. *Proceedings of the Geologists' Association*, 120: 76-78.
- Huxley T.H. (1880) - On the Application of the Laws of Evolution to the Arrangement of the Vertebrata, and more particularly of the Mammalia. *Proceedings of the Zoological Society of London* 1880: 649-662.
- ISPRA (2014) - Foglio 097 Vimercate. Carta Geologica d'Italia alla scala 1: 50.000.
- Jadoul F. & Doniselli T. (1987) - La successione del Lias Inferiore di Morterone (Iecchese). *Memorie della Società Italiana di Geologia*, 32: 49-66.
- Jadoul F., Calabrese L., Galli M.T. & Gnaccolini M. (2005) - Stratigraphy of Rhaetian to Lower Sinemurian carbonate platforms in western Lombardy (Southern Alps, Italy): paleogeographic implications. *Rivista Italiana di Paleontologia e Stratigrafia*, 111: 285-303.
- Jadoul F. & Galli M.T. (2008) - The Hettangian shallow water carbonates after the Triassic/Jurassic biocalcification crisis: the Albenza Formation in the western Southern Alps. *Rivista Italiana di Paleontologia e Stratigrafia*, 114: 453-470.
- Jadoul F., Galli M.T., Muttoni G., Rigo M. & Cirilli S. (2012) - The late Norian-Hettangian stratigraphic and paleogeographic evolution of the Bergamasc Alps. Escursione pre congresso Geitalia, VI meeting FIST - Rimini, 2007. *Geol.F. Trips*, Vol. 4 No.1.1 (2012), 55 pp., 22 figs. (DOI10.3301/GFT.2012.01).
- Jaselli L. (2020) - Luigi Torri e la Serie Stratigrafica del Monte Albenza, nel Museo Scientifico Naturalistico "Antonio Stoppani". *Rivista del Museo civico di Scienze Naturali "E. Caffi" di Bergamo*, 32: 85-90.
- Klikushin V.G. (1992) - Taxonomic survey of fossil isocrinids with a list of the species found in the USSR. *Geobios*, 15(3): 299-325. *Annales de Paléontologie*, 105: 63-73.
- Klikushin V.G. (1992) - Iskopaemye morskie lilii pentakrinidy i ikh rasprostranenie v CCCP. [Fossil pentacrinid crinoids and their occurrence in the USSR]. *Leningradskaja Paleontologicheskaja Laboratorija (Sankt Peterburg)*: 358 pp.
- Klug S. (2009) - Monophyly, phylogeny and systematic position of the †Synchodontiformes (Chondrichthyes, Neoselachii). *Zoologica Scripta*, 39: 37-49.
- Klug S., Kriwet J., Böttcher R., Schweigert G. & Dietl G. (2009) - Skeletal anatomy of the extinct shark *Paraorthacodus jurensis* (Chondrichthyes; Palaeospinacidae), with comments on synchodontiform and palaeospinacid monophyly. *Zoological Journal of the Linnean Society*, 157: 107-134.
- Krajewski M., Olchowy P. & Salamon M.A. (2019) - Late Jurassic (Kimmeridgian) sea lilies (Crinoidea) from central Poland (Łódź Depression). *Annales de Paléontologie*, 105: 63-73.
- Kriwet J., Kiessling W. & Klug, S. (2009) - Diversification trajectories and evolutionary life-history traits in early sharks and batoids. *Proceedings of the Royal Society B*, 276: 945-951.
- Liddell W.D. (1975) - Recent crinoid biostratigraphy. *Geological Society of America Abstracts with Programs*, 7: 1169.
- Loriol P. de (1882-89) - Paléontologie française, ou description des fossiles de la France, Sér. 1, Animaux invertébrés. Terrain Jurassique: 11, Crinoïdes. Ed. G. Masson, Paris, 1207 pp.
- Loriol P. de (1891) - Description de la faune jurassique du Portugal. *Commission Géologique du Portugal, Travaux*, 2: 1-179.
- Malzahn E. (1968) - Über neue Funde von *Janassa bituminosa* (Schloth.) im niederrheinischen Zechstein. *Geologisches Jahrbuch*, 85: 67-96.
- McRoberts C.A. (1994) - The Triassic-Jurassic ecostratigraphic transition in the Lombardian Alps, Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 110: 145-166.
- Meneghini G. (1867-1881) - Monographie des fossiles appartenant au calcaire rouge ammonitique de la Lombardie et de l'Apennin de l'Italie centrale. In: Stoppani A. (Ed.) - Paléontologie Lombarde. Milano, 293 pp.
- Meyer D.L. (1971) - Post-mortem disintegration of Recent crinoids and ophiuroids under natural conditions. *Geological Society of America Abstracts with Programs*, 3: 645-646.
- Meyer D.L. & Ausich W.I. (1983) - Biotic Interactions among Recent and among Fossil Crinoids. In: Tevesz M.J.S. & McCall P.J. (Eds) - Biotic Interactions in Recent and Fossil Benthic Communities: 377-427. Springer, Boston.
- Miller J.S. (1821) - A Natural History of the Crinoidea, or Lily-Shaped Animals: with observations on the genera, Asteria, Euryale, Comatula & Marsupites. Bristol, 276 pp.
- Muttoni G., Kent D.V., Jadoul F., Olsen P.E., Rigo M., Galli M.T. & Nicora A. (2010) - Rhaetian magneto-biostratigraphy from the Southern Alps (Italy): constraints on Triassic chronology. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 285 (1-2): 1-16.
- Oppel A. (1856) - Die Juraformation Englands Frankreichs und Südwestlichen Deutschlands. *Abdruck des Württembergischen naturwissenschaftlichen Jahrbuchs*, 12-14: 1- 857.
- Pesenti G. (1977) - Luigi Torri il geologo di Caprino. *La Domenica del Popolo*, 57(28): 16-17.
- Pinna G. (1967) - Découverte d'une nouvelle faune à crustacés du Sinémurien inférieur dans la région du lac Ceresio (Lombardie, Italie). *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 106: 183-185.
- Pinna G. (1985) - Exceptional preservation in the Jurassic of Osteno. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, 311: 171-180.
- Quenstedt F.A. (1858) - Der Jura. Laupp, Tübingen, 842 pp.
- Rees J. (2000) - Neoselachian sharks from the Callovian-Oxfordian (Jurassic) of Ogdorzieniec, Zawiercie Region, southern Poland. *Palaeontology*, 53(4): 887-902.
- Roux M. (1981) - Echinodermes: Crinoïdes Isocrinidae. Résultats des campagnes Musorstom I, Philippines (18-28 mars 1976). *Mémoires ORSTOM*, 91: 477-543.
- Schlothem, E.F. von (1820) - Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreichs der Vorwelt. Becker, Gotha, 437 pp.

- Sieverts-Doreck H. (1952) - Articulata. In: Moore R.C., Lalicker C.G. & Fischer A.G. (Eds): *Invertebrate fossils*: McGraw-Hill, New York, 766 pp.
- Sepkoski J.J.Jr. (1996) - Patterns of Phanerozoic extinction: A perspective from global data bases. In: Walliser O.H. (Ed.) - *Global events and event stratigraphy in the Phanerozoic*: 35-51. Springer, Berlin.
- Simms M.J. (1986) - Contrasting lifestyles in Lower Jurassic crinoids: a comparison of benthic and pseudopelagic isocrinida. *Palaeontology*, 29(3): 475-493.
- Simms M.J. (1988) - Patterns of evolution among Lower Jurassic crinoids. *Historical Biology*, 1: 17-44.
- Simms M.J. (1989) - British Lower Jurassic crinoids. Monograph of the Palaeontographical Society, London, Publication 581, 103 pp.
- Simms M.J. (2011) - Stereom microstructure of columnal latera: a character for assessing phylogenetic relationships in articulate crinoids. *Swiss Journal Palaeontology*, 130: 143-154.
- Rasmuss H. (1912) - Zur Geologie der Val Adrara. *Zeitschrift Deutsche Geologische Gesellschaft*, 64: 322-341.
- Stiller F. (2011) - An early isocrinid sea lily from the middle to late Anisian boundary (Middle Triassic) of South-West China - Evidence for a Far-East tethyan origin of the family Isocrinidae. *Palaeontology*, 54(6): 1415-1433.
- Stoppani A. (1857) - *Studi geologici e paleontologici sulla Lombardia*. Turati, Milano, 461 pp.
- Thuy B., Gale A.S. & Reich M. (2011) - A new echinoderm Lagerstätte from the Pliensbachian (Early Jurassic) of the French Ardennes. *Swiss Journal of Palaeontology*, 130: 173-185.
- Tintori A. (1977) - Toarcian fishes from the Lombardian Basin. *Bollettino della Società Paleontologica Italiana*, 16(2): 143-152.
- Vialli V. (1959) - Ammoniti sinemuriane del M. Albenza (Bergamo). *Memorie della Società Italiana di Scienze Naturali*, 12: 143-188.
- Wagner J.A. (1862) - Monographie der fossilen Fische aus den lithographischen Schiefern Bayerns. I. Plakoiden und Pyknodonten. *Abhandlungen der Mathematischen Physikalischen Classe der königlich bayerischen Akademie der Wissenschaften*, 9: 277-352.
- Wiedenmayer F. (1963) - Obere Trias bis mittlerer Lias zwischen Saltrio und Tremona (Lombardische Alpen). Die Wechselbeziehungen zwischen Stratigraphie, Sedimentologie und syngenethischer Tektonik. *Eclogae Geologicae Helvetiae*, 56: 529-640.
- Zangerl R. & Richardson E.S. (1963) - The paleoecological history of two Pennsylvanian black shales. *Fieldiana: Geological Memoir* 4, 352 pp.
- Zittel K.A. von. (1876-1880) - *Handbuch der Paläontologie*, Band 1, *Palaeozoologie*, Abt. 1, 765 pp.

