

EVIDENCE OF OPPORTUNISTIC FEEDING BETWEEN ICHTHYOSAURS AND THE OLDEST OCCURRENCE OF THE HEXANCHID SHARK *NOTIDANODON* FROM THE UPPER JURASSIC OF NORTHERN ITALY

GIOVANNI SERAFINI¹, JACOPO AMALFITANO², MIRIAM COBIANCHI³,
BEATRICE FORNACIARI¹, ERIN E. MAXWELL⁴, CESARE ANDREA PAPAZZONI^{1*},
GUIDO ROGHI⁵ & LUCA GIUSBERTI²

¹Dipartimento di Scienze Chimiche e Geologiche, Università degli Studi di Modena e Reggio Emilia, Via Campi 103, I-41125 Modena, Italy. E-mail: gio94jp@gmail.com, beatrice.fornaciari@unimore.it, papazzoni@unimore.it

²Dipartimento di Geoscienze, Università degli Studi di Padova, Via Gradenigo 6, I-35131 Padova, Italy. E-mail: jacopo.amalfitano@phd.unipd.it, luca.giusberti@unipd.it

³Dipartimento di Scienze della Terra e dell'Ambiente, Università degli Studi di Pavia, via Ferrata 1, I-27100, Pavia, Italy. E-mail: miriam@unipv.it

⁴Staatliches Museum für Naturkunde Stuttgart, Rosenstein 1, 70191 Stuttgart, Germany. E-mail: erin.maxwell@smns-bw.de

⁵Istituto di Geoscienze e Georisorse, CNR, Via Gradenigo 6, 35131 Padova, Italy. E-mail: guido.roghi@igg.cnr.it

*Corresponding author.

To cite this article: Serafini G., Amalfitano J., Cobiانchi M., Fornaciari B., Maxwell E.E., Papazzoni C.A., Roghi G. & Giusberti L. (2020) - Evidence of opportunistic feeding between ichthyosaurs and the oldest occurrence of the hexanchid shark *Notidanodon* from the Upper Jurassic of Northern Italy. *Rin. It. Paleontol. Strat.*, 126(3): 629-655.

Keywords: Taphonomy; scavenging; Ophthalmosauridae; Hexanchidae; Kimmeridgian; UV-light.

Abstract. In 2016, two fossil marine reptiles were re-discovered in the collections of the Museo Civico di Storia Naturale di Verona. Originally recovered near Asiago, Vicenza province (northern Italy) from an outcrop of the Rosso Ammonitico Veronese Fm. (Middle-Upper Jurassic), they were never described. Morphological analysis carried out under UV-light allowed enhancing contrast with the surrounding matrix and better identifying some anatomical details. Both specimens consist of partially articulated postcranial elements from two distinct ichthyosaurs, including vertebrae, ribs, and some fragmentary elements of the appendicular skeleton. The first specimen V7101 is here tentatively assigned to Ophthalmosauridae based on a combination of features shared with other taxa in this family, such as the regionalization of the vertebral column. Taphonomical analysis suggests a long exposure of the carcass on the sea floor before burial; two teeth of the hexanchiform shark *Notidanodon* found near the ribcage could indicate scavenging. An ichthyosaur tooth most probably not belonging to the same specimen was found stuck on a rib and can also be attributed to scavenging – the first ever record of this interaction between two ichthyosaurs. The second specimen V7102 is represented by a poorly preserved partial vertebral column and is here referred to Ichthyosauria indet. due to the absence of taxonomically significant characters. Calcareous nannofossil data and microfacies analyses allow us to assign both specimens to the basal Kimmeridgian. This makes the two *Notidanodon* teeth associated with V7101 the oldest recorded occurrence of this genus.

INTRODUCTION

Ichthyosaurs were a highly successful group of marine reptiles that inhabited the Mesozoic oceans from the Early Triassic (Olenekian) to the early Late Cretaceous (Cenomanian) (Motani

1999; Sander 2000; McGowan & Motani 2003). The order Ichthyosauria is known for its striking morphological adaptation to an aquatic environment, reflected in a fish-like body plan. Although the palaeobiology of the group is relatively well known (mostly from few exceptionally preserved genera from Konservat-Lagerstätten), the phylogenetic position of ichthyosaurs within amniotes

Received: March 30, 2020; accepted: July 08, 2020

and their ingroup relationships are more problematic. Conservative skeletal morphology imposed by hydrodynamic constraints and evolutionary convergence make apomorphies difficult to detect (Maisch 2010). Nevertheless, ichthyosaurs and their closest relatives are now generally recognized as neodiapsids (Motani et al. 2015; Benton 2015) and major divergences within the order are supported in most recent phylogenetic analyses (Ji et al. 2016; Moon 2017). The evolution of the order is fairly well understood, especially for Late Triassic–Early Jurassic taxa, when the body plan was refined to its iconic tuna-like shape (Motani 1999, 2009). Ichthyosaurs appear to have become morphologically homogeneous during the Late Jurassic and Cretaceous, and only some cranial and appendicular characters appear to be useful as diagnostic features (Maisch 2010; Dick & Maxwell 2015).

The fossil record of Upper Jurassic ichthyosaurs is excellent and is mainly represented by a series of globally distributed Lagerstätten (Bardet et al. 2014). In the part of Europe formerly comprising the western Tethys, key localities include the upper Kimmeridgian–Tithonian Kimmeridge Clay of the UK (yielding the taxa *Ophthalmosaurus*, *Brachypterygius* and *Nannopterygius*; Moon & Kirton 2016, 2018), and the Tithonian lithographic limestones of southern Germany (yielding *Aegirosaurus*, and potentially also additional genera). However, the Oxfordian–lower Kimmeridgian fossil record of ichthyosaurs in Europe is much more fragmentary. Material from the Oxfordian of the UK has been referred to *Ophthalmosaurus* sp. (Danise et al. 2014) and *O. icenicus* (Moon & Kirton 2016), and a specimen from European Russia has also been referred to *O. icenicus* (Arkhangelsky et al. 2018). Indeterminate Oxfordian ichthyosaurian remains have been reported from France and Poland (Buffetaut & Thierry 1977; Tyborowski et al. 2018). Aside from these reports, no other material diagnostic to the generic level is known from the western Tethys, and it is likely that, globally speaking, taxonomic diversity is being underestimated for this interval (Benson et al. 2010). Given the scarcity of ichthyosaurian remains from the western Tethys, documenting even fragmentary occurrences from this interval becomes very significant.

The record of post-Triassic ichthyosaurs from Italy is very poor, especially if compared

with the abundant and well-preserved fossils from the Italian side of the Triassic Monte San Giorgio site (Reposi 1902; Dal Sasso & Pinna 1996; Brinkmann 1997). All post-Triassic ichthyosaurs found in Italy to date come from the Upper Jurassic and Lower Cretaceous, with no published occurrences of Lower–Middle Jurassic ichthyosaurs (Paparella et al. 2016). Historically, the first Jurassic ichthyosaur discovered in Italy was the tip of a rostrum (V7158) from the Tithonian of Campo Retrato, near Erbezzo (Verona province), reported but never fully described by De Zigno (1883) and De Stefani (1883). Other Upper Jurassic records include fragmentary and undescribed specimens found in the Rosso Ammonitico Veronese Formation (hereafter referred as RAV Fm.) from the Altopiano di Asiago (Bizzarini 2003; see below), and to the holotype of *Gengasaurus nicosiai* (Fastelli & Nicosia 1980; De Marinis & Nicosia 2000; Paparella et al. 2016). This specimen, found in 1976 near Genga (Ancona province, Central Apennines), consists of a disarticulated skull, pectoral girdle, and semi-articulated vertebral column, and represents the most complete post-Triassic ichthyosaur skeleton from Italy to date. The Cretaceous ichthyosaur record from Italy is almost entirely limited to the Northern Apennines, with several fragmentary fossils from the provinces of Modena and Bologna (Sirotti & Papazzoni 2002; Serafini et al. 2017, 2019). Among them are five platypterygiine rostrum fragments, a humerus and some vertebrae. The only Cretaceous specimen from outside the Northern Apennines is an upper Albian platypterygiine rostrum fragment found at Tregnago (Lessini Mountains of Verona province), described by Fornaciari et al. (2017).

Here we describe two specimens from the Upper Jurassic of the Altopiano di Asiago (Vicenza province), recently re-discovered in the collections of the Museo Civico di Storia Naturale di Verona. These specimens represent a notable addition to the Italian record of Upper Jurassic ichthyosaurs. The aim of this study is the detailed description of the two fossils, their taxonomic assignment, taphonomic analysis and age determination based on analysis of calcareous nannofossils.

The taphonomic analysis also provided new information about ichthyosaur deadfalls, in particular about the mobile scavenger stage (e.g., Smith et al. 2015).

GEOLOGICAL AND PALAEOLOGICAL CONTEXT

The specimens were found at Monte Interrotto (Fig. 1A–B) about 3.5 km NW from Asiago in the Altopiano di Asiago (Vicenza province). The Altopiano di Asiago is located in the Southern Alps, northeastern Italy, an Adria-vergent fold and thrust belt derived from the retrowedge collision and inversion of the Adria Tethyan passive margin (Picotti & Cobianchi 2017). During the Early Jurassic, this area was part of a wide carbonate platform, the Trento Platform, bordered by the Lombardian Basin to the west and by the Belluno Basin to the east. This palaeogeographic unit is represented by a thick shallow-water carbonate succession (the Calcari Grigi and San Vigilio Groups; Hettangian–Aalenian), capped by a thin succession (up to 30 m) of pelagic reddish Middle–Upper Jurassic limestones, commonly nodular and rich in ammonites: the Rosso Ammonitico Veronese Formation (e.g., Martire 1996; Massari & Westphal 2011). The latter records the drowning of the Trento Platform and its transformation into a current-swept plateau (the ‘Trento Plateau’, a complex horst block) with greatly reduced pelagic sedimentation (a few millimetres per kyr), and frequent stratigraphic gaps (Massari & Westphal 2011). The RAV has been subdivided by Martire et al. (2006) into three formalized members (Fig. 1C), the reference section of which crops out in the Kaberlaba Quarry on the Altopiano di Asiago. The lower unit (Rosso Ammonitico Inferiore, RAI; upper Bajocian–lowermost upper Callovian) is generally massive and apparently not nodular with stromatolites at its base and a scarce macrofauna. It is capped by thinly bedded planar-parallel to flaser-bedded limestones, locally with red chert nodules and lenses, belonging to the upper Callovian–middle Oxfordian Rosso Ammonitico Medio (RAM). The equivalent of the RAM in the Belluno Basin (Belluno and Feltre areas) is the Fonzaso Formation (Bosellini & Dal Cin 1969), the thickness of which varies from 20 to 80 metres (e.g., Cobianchi 2002; Martire et al. 2006). The third member of the RAV, the Rosso Ammonitico Superiore (RAS; middle Oxfordian to upper Tithonian), is the most characteristic lithologically and mainly consists of nodular marly limestones, rich in ammonites. Geographically, this is the most continuous member, showing essentially the same features throughout

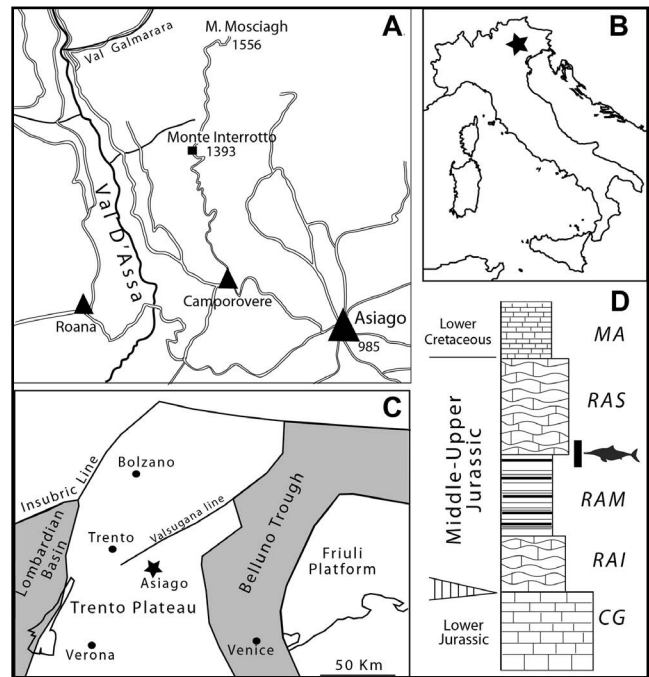


Fig. 1 - A–B) Location map of the Monte Interrotto; C) main structural elements of the Southern Calcareous Alps during Jurassic; D) the Jurassic and Lower Cretaceous stratigraphic succession (simplified) of the Asiago area. CG=Calcari Grigi Group; RAI= Rosso Ammonitico Inferiore; RAM= Rosso Ammonitico Medio; RAS= Rosso Ammonitico Superiore; MA=Maiolica.

the Trento Plateau (Martire et al. 2006). The Mesozoic succession of the Trento Plateau ends with three Cretaceous calcareous pelagic formations: the thinly bedded, white to greyish micritic cherty limestones of the Maiolica (MA) and Scaglia Variegata Alpina (SVA), capped by the pink-reddish marly limestones of the Upper Cretaceous Scaglia Rossa (SR).

The fauna of RAV and its associated marine tetrapod record

The macropalaeontological content of the RAV is characterized by a variety of invertebrates including ammonites, aptychi, rhyncholites, belemnites, nautiloids, bivalves, gastropods, brachiopods, echinoderms (mainly crinoids and echinoids) and solitary corals (e.g., Laub 1994; Martire 1996; Martire et al. 2006). With the exception of the ammonites, which have been intensively studied since the 19th century as part of biostratigraphic investigations (e.g., Sarti 1993), the macrofauna is still in need of review and in-depth analysis. Remains of vertebrates from the RAV are scarce and are mainly represented by fish teeth (both osteichthyans and chondrichthyans; see an overview in Sirna et al.

1994). Marine reptiles are exceedingly rare in the RAV, but some interesting findings have been recorded since the 18th century from the Altopiano di Asiago area. The first discovery consisted of a skull of a marine crocodylomorph recovered at Treschè Conca in 1787 and formally ascribed to ‘*Steneosaurus barettoni*’ by Omboni (1890). The specimen was recently assigned to *Metriorhynchoidea incertae sedis* by Cau (2019), and its phylogenetic relationships remain unresolved. De Zigno (1883) reported the presence of some alleged plesiosaurian vertebrae from the RAV at Cesuna; a recent revision of the material led to the recognition of a vertebra with a chimerical association of a plesiosaurian neural arch and a crocodylomorph centrum (Cau & Fanti 2016). A second metriorhynchoid crocodylomorph is represented by a fragmentary mandible recovered in the early 1990s from the RAI in the Valbella Quarry at Sasso D’Asiago (Bizzarini 1996; Cau 2014, 2019). Later, Bizzarini (2003) reported the presence of badly preserved cranial and vertebral elements of an alleged ophthalmosaurid in a RAV block also coming from Valbella Quarry at Sasso D’Asiago and used for the construction of a dam in the Lagoon of Venice. The block preserving this specimen has been removed from the dam and is presently housed in the Museo Civico della Laguna Sud at Chioggia (Venice province). Other bone fragments of an alleged ichthyosaur found at Cima del Porco (Altopiano di Asiago) reported by Bizzarini (2003) remain unfigured and undescribed. Finally, Cau & Fanti (2014) described the first Italian articulated plesiosaurian skeleton from the RAM of Kaberlaba Quarry (Asiago, Vicenza province). The specimen was ascribed to Pliosauridae; Cau & Fanti (2016) later erected the taxon *Anguanax zignoi* based on this material.

MATERIAL AND METHODS

History and preservation of the study specimens

The material under study consists of two specimens, V7101 and V7102, both found in June 1904 according to the museum archive, and housed since then in the collections of the Museo Civico di Storia Naturale di Verona (MCSNV). Neither of them has been described or even cited in the literature, making this study the first official report

of these specimens. According to the scarce documentation accompanying the fossils, they were both found in the RAV Fm. at Monte Interrotto (Asiago, Vicenza province) and preliminarily examined by the geologist Enrico Nicolis (1841–1908).

The two specimens appear to have undergone some preparation, as shown by the different pieces of matrix held together by concrete and by the wooden frame enclosing both slabs. Moreover, chisel marks are visible around some bones. No further information could be retrieved regarding the specimens, although they were once part of the old museum exhibit. A shark tooth detached from slab V7101 is also labelled with the same catalogue number and it is presently housed in a different section of the Museum collections. The original position of the tooth on the slab V7101 is indicated by its impression, clearly visible on the matrix beneath the ichthyosaur ribcage.

Due to osteological, taphonomical and palaeoecological similarities, V7101 was compared with MSVG 39617, the holotype of *Gengasaurus nicosiai* (see Paparella et al. 2016). The latter specimen was found at Camponocchie, near Genga (Ancona province) in rocks of the upper Kimmeridgian–basal Tithonian “*Calcari ad Aptici e Saccocoma*” Formation, and currently housed in the Museo Speleopaleontologico ed Archeologico di Genga.

Osteological analysis

Study of V7101 and V7102 was initially carried out under natural light in the Museo Civico di Storia Naturale di Verona. Measurements were taken to the nearest millimetre with a digital calliper. Due to the quality of preservation, only the following vertebral elements were measured: centrum height (CH), centrum length (CL), centrum width (CW, just for one vertebra), neural arch height (NaH) neural arch length (NaL), neural spine height (NsH) and neural spine length (NsL) (Fig. 2A–B). High-resolution pictures were taken with a Nikon D810 camera with Nikon macro lens 60 mm micronikkor f/2.8 and a 3D rendering of the two slabs based on the high overlap between pictures was accomplished using photogrammetry. A digital three-dimensional map featuring the height differences across the slabs was produced with the software Agisoft Photoscan© (Supplementary Fig. S1). In order to identify anatomical details invisible under natural light and to better distinguish

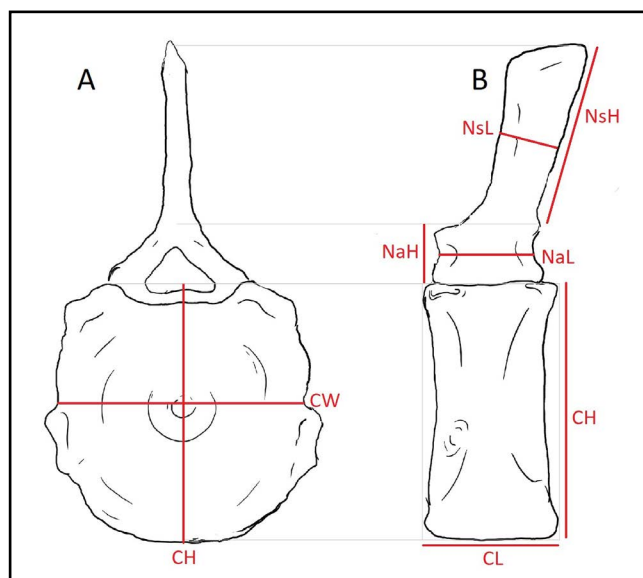


Fig. 2 - Sketch showing vertebral measurements. CH, centrum height; CL, centrum length; CW centrum width; NaH, neural arch height; NaL, neural arch length; NsH, neural spine height; NsL, neural spine length.

the skeletal material from the matrix and from the concrete, the two specimens were exposed to ultraviolet (UV) light. UV-induced fluorescence was obtained for two different UV ranges: two 26W Wood lamps for the UV-A range ($\lambda = 360$ nm) and one 15 W germicide lamp for the UV-C range ($\lambda = 254$ nm). The two specimens were separately exposed to UV-A and to UV-A and UV-C combined. Photographs under UV-A and UV-C combined give a strong greenish colour due to the lack of a visible-wavelength screen on the germicide lamp, which also emits a pale green light in the visible range. The three UV lamps were part of a custom design expressly built for this study: the lamps were fixed to a wooden table perpendicular to the slabs and placed on a cardboard frame in order to keep out the external light and to protect the operator from UV-C radiation.

Micropalaeontological analysis of the matrix

Two sets of matrix samples were extracted from each specimen for micropalaeontological and petrographic analyses. One set of samples was prepared in order to analyse the calcareous nannofossils according to the smearing technique (Bown & Young 1998). Analyses were performed using a polarized light microscope under a magnification of 1250X. Nannofossil assemblages were semi-quantitatively

estimated by counting all the nannoliths recorded in 300 fields of view. Relative species abundances are reported as: A = abundant, at least 1 individual every 1–10 observation fields; C = common, 1 individual every 1–10 observation fields; F = frequent, 1 individual every 10–30 observation fields; R = rare, 1 individual every > 30 observation fields. Biostratigraphy is described with reference to the biozonation by Casellato (2010). A second set of matrix samples was used to produce two thin sections for the microfacies analysis. The samples were embedded in epoxy resin (Hardrock 554) to keep the material cohesive during cutting. The two sections were polished to 30 μm thickness and observed under a polarized optical microscope.

The same procedures (thin sections and smear slides) were carried out for four rock samples collected by some of us during a field survey on Monte Interrotto in March 2019 (see below). The samples were taken according to their similarity with the facies observed in the slabs under study.

Institutional abbreviations

MCSNV, Museo Civico di Storia Naturale di Verona; MSVG, Museo Speleopaleontologico ed Archeologico di Genga, Ancona, Marche, Italy.

Lithostratigraphic assignment and petrographic analysis of V7101 and V7102

The two fossils are preserved in slabs consisting of thin-irregularly bedded reddish marly limestones, in association with aptychi and ryncholites. The lithology is compatible with that of the non-cherty facies of the RAM as reported by Martire (1996) and more similar to the reddish beds of the upper part of Fonzaso Formation (“*Aptychen schiefer*”) in the Feltre area (Della Bruna & Martire 1985). However, the thin sections from the rocks embedding V7101 and V7102 revealed that the microfacies consists of a packstone densely rich in saccocomid remains (Fig. 3A-B). Saccocomids (e.g., *Saccocoma* and *Crassicoma*; Hess 2002) are a group of stemless pelagic crinoids, frequently reported in the Upper Jurassic deposits of the Tethyan Realm, with a widespread acme during the Tithonian (Benzagagh et al. 2015). The peculiar microfacies dominated by elements of *Saccocoma* has been reported so far by Martire (1996) and Martire et al. (2006) in the Asiago area only in the Rosso Ammonitico Superiore (RAS).

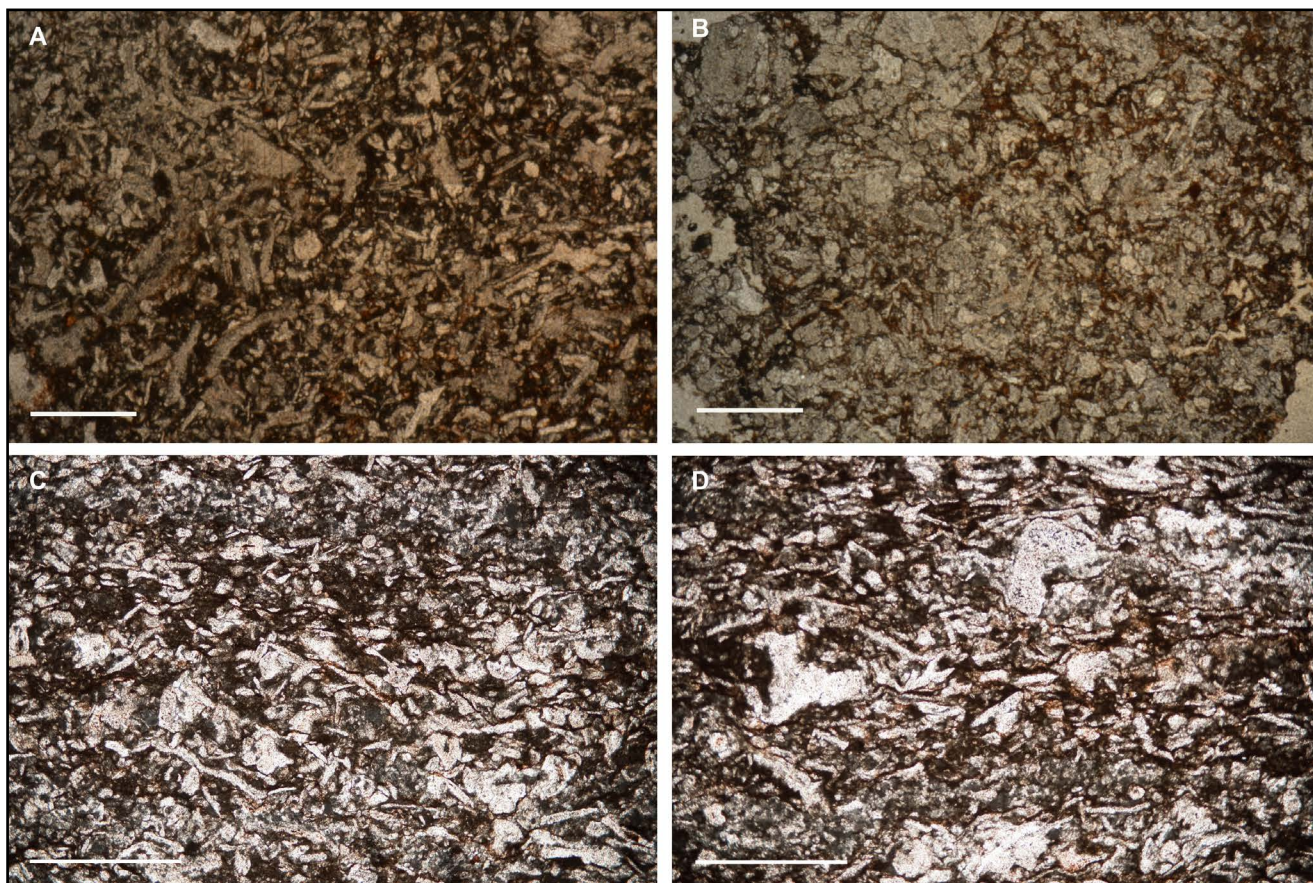


Fig. 3 - Thin sections of the matrix of V7101 (A) and V7102 (B). Thin sections from samples collected at Monte Interrotto: sample MT3 (C) and sample MT4 (D). Scale bars represent 1 mm.

Martire (1996, fig. 4) reported a simplified log of a 10 m-thick succession of the RAV at Monte Interrotto, showing all the three members of the RAV with the RAM represented only by a cherty thinly bedded/subnodular facies. Because of the discrepancies between the lithology of the fossils and literature data about the Monte Interrotto succession, we carried out a field survey in March 2019. The RAV succession at Monte Interrotto crops out on the western slope (Barbieri & Grandesso 2007), and blocks were extracted during the second half of the 19th century for the construction of a military fort on the top of the mountain. Despite the dense vegetation cover, RAI and RAS deposits still partly crop out, whereas the RAM in between is completely covered by vegetation and was observed only in debris likely derived from quarrying activity. Such rock debris frequently contains aptychi, belemnites and rhyncholites, and shows a lithology identical to the V7101 and V7102 slabs. The microfacies of four samples (MT1–MT4) collected from the debris is the same as that of the studied fossils

and consists of a saccocomid packstone (Fig. 3C-D), confirming the provenance of the fossils from the same deposits. No cherty limestones were observed among the RAM debris. Moreover, the lower beds of the RAS observed at Monte Interrotto show an alternation of nodular reddish limestones with thinly bedded reddish marly limestones identical to the samples of the debris and to the lithology of V7101 and V7102, suggesting a transitional contact between the Middle and Upper member of the RAV. Based on all available evidence, we infer that the ichthyosaurs come from this so far undescribed “atypical” RAM saccocomid-dominated facies, or possibly from the RAM-RAS transition.

Calcareous nannofossils, *Saccocoma acme* and age calibration of V7101 and V7102

In order to better constrain the stratigraphical position and age of the fossils, samples from both specimens (V7101 and V7102) were analysed for their calcareous nannofossil content. Unlike what usually occurs in the RAV, sample assemblages dis-

play frequent to common nannoliths, even though these are poorly preserved, being heavily selected by diagenesis. *Watznaueria* spp. dominate the assemblages both for stratigraphic reasons and because they are dissolution-resistant species (e.g., Roth 1981, 1984) selectively preserved in nodular limestones rich in pressure-solution structures, as is the RAV facies (Fig. 4).

Sample V7101 contains common *Watznaueria* aff. *W. manivitae* (Fig. 4C), frequent specimens of *W. manivitae*, *W. manivitae* large (Figure 4F) and *W. communis* (Fig. 4A, D), and rare *Watznaueria britannica*, *W. barnesiae*, *Cyclagelosphaera* sp., and *Lotharingius hauffii* (Fig. 4B). Casellato (2010) documented the Last Occurrence (LO) of *L. hauffii* within the Subzone NJT13b (middle–upper Oxfordian) but considers it an event requiring further investigation, and indeed, Cobianchi (2002) observed this species in Kimmeridgian samples. Based on the absence of both *L. sigillatus* and *Faviconus multicolumnatus*, V7101 should be ascribed to the Subzone NJT13b (Casellato 2010) of middle-late Oxfordian age.

Sample V7102 displays an acme (common occurrence) of *Watznaueria manivitae*, *W. aff. manivitae* (Fig. 4E–G), *W. manivitae* large (Figures 4J–K), and *W. communis* (Figure 4I). Rare specimens of *Watznaueria britannica* (Fig. 4H), *W. barnesiae* and *Cyclagelosphaera* sp. (Fig. 4L) are also recorded. Chiri et al. (2007) documented this acme in the Kimmeridgian, below the First Occurrence (FO) of *Zenhrabdotus embergeri*, but Pittet & Mattioli (2002) and Bartolini et al. (2003) documented an acme of *W. manivitae* in the uppermost Oxfordian–lower Kimmeridgian interval. Casellato (2010) suggested that the FO of *Faviconus multicolumnatus* could be used to approximate the Oxfordian/Kimmeridgian boundary; this species was not observed in our samples. Therefore, sample V7102, referable as lowest biostratigraphic assignment to the NJT13b subzone (Casellato 2010), is certainly not older than middle–upper Oxfordian, and for the high relative abundance of *Watznaueria manivitae* and *W. aff. manivitae*, can be ascribed to the lower Kimmeridgian.

The nannofossil assemblages of the two samples display the same taxonomic composition; the only difference is the greater relative abundance of *W. manivitae* and *W. aff. manivitae* in V7102. This difference could be related to a small difference in age, with V7102 being slightly younger than V7101 or, alternatively, to a local difference in species abun-

dance driven by bioturbation, sediment winnowing by currents or zonal early diagenetic dissolution.

In order to verify the age of the two specimens, four samples (MT1–MT4) collected directly *in situ* at Monte Interrotto were analysed for their nannofossil content. The biostratigraphic data obtained are fully consistent with those obtained from the matrix of the studied specimens. High relative abundance of *W. manivitae* and *W. aff. manivitae* was recorded also in the best-preserved samples of Monte Interrotto, suggesting even for these an early Kimmeridgian age.

The analysis of the microfacies, both on samples from the matrix of V7101 and V7102 and from the samples collected at Monte Interrotto, revealed a packstone with abundant saccocomids. Saccocomids range from the middle Oxfordian to the upper Tithonian, with a widespread Tethyan acme in the Tithonian (e.g., Benzaggagh et al. 2015). In the Kaberlaba RAV type-section at the Altopiano di Asiago, *Saccocoma* is recorded and abundant from the basal part of RAS (lithozone 8; Martire et al. 2006), where it is the main bioclastic component of both nodules and embedding clay-rich matrix up to the upper Tithonian beds. According to Martire et al. (2006), the base of the RAS at Kaberlaba is latest early Kimmeridgian in age. However, it must be emphasized that the beginning of the RAS in the Asiago area differs from section to section, spanning the middle Oxfordian to lower Kimmeridgian (Martire 1996; Martire et al. 2006). Unfortunately, no detailed data on the microfacies of sections containing middle–upper Oxfordian basal beds of the RAS at Asiago are available. In the Lessinian area, Clari et al. (1984) recorded *Saccocoma* associated with abundant *Globochaete alpina* in the basal beds of the RAS, ascribable to the middle–upper Oxfordian, but no data on its abundance are recorded. In the Belluno Basin, some *Saccocoma* beds have been reported in a number of sections from an interval spanning the Kimmeridgian (e.g., Cobianchi 2002; Picotti & Cobianchi 2017). Outside the Southern Alps, in the Umbria Marche Apennines the mass occurrence of the genus *Saccocoma* is dated to latest early Kimmeridgian (Citton et al. 2019). In a Rosso Ammonitico succession of western Sicily, Savary et al. (2003) recorded the first occurrence of *Saccocoma* in the middle Oxfordian beds, followed by the first massive occurrence of *Saccocoma* in a lower Kimmeridgian packstone and a subsequent high abun-

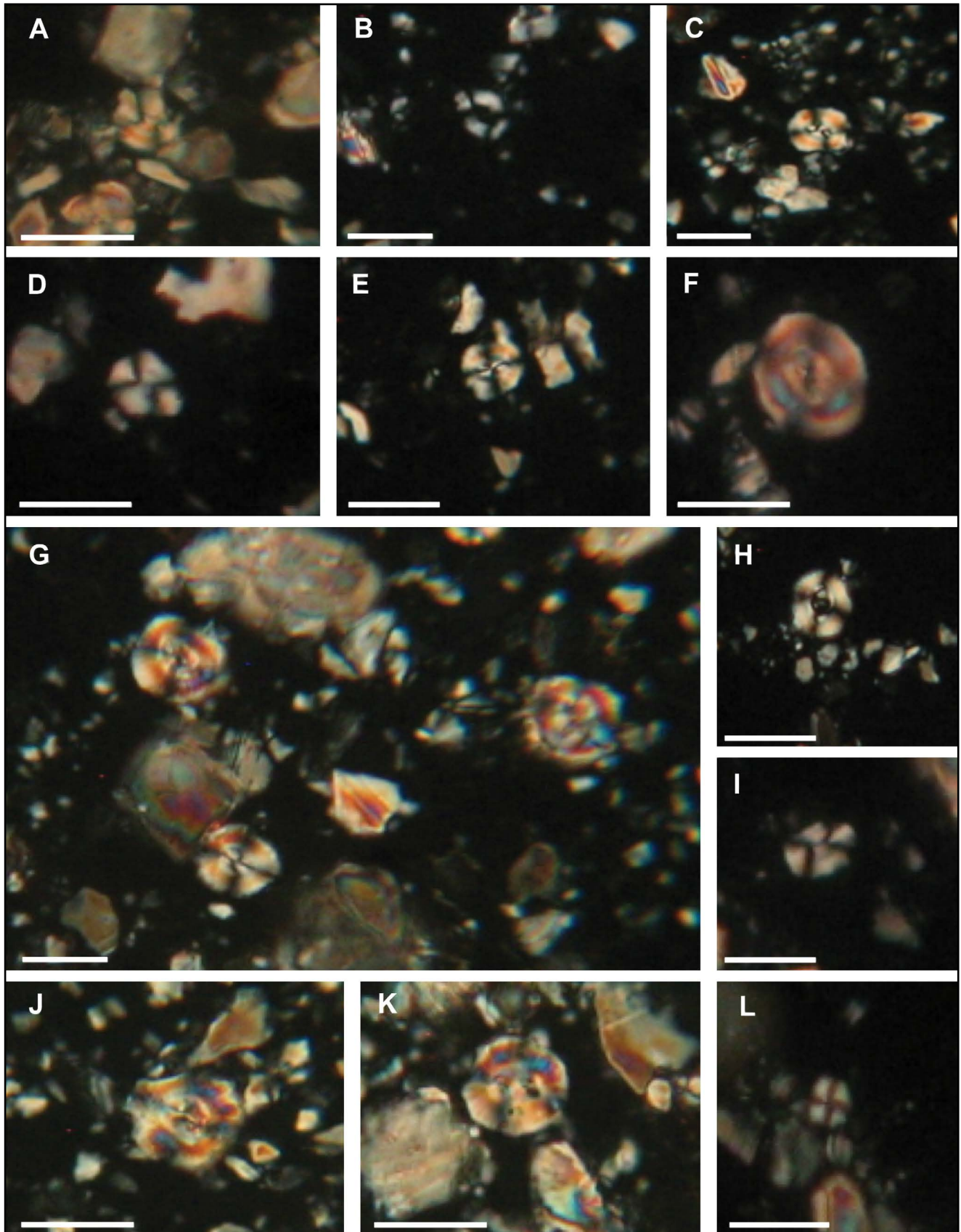


Fig. 4 - Nannoliths and calcareous nannoplankton in smear slide from V7101 and V7102 matrix: A, D) *Watznaueria communis*, sample V7101; B) *Lotharingius bauffi*, sample V7101; C) *Watznaueria* aff. *manivitae*, sample V7101; E) *Watznaueria* aff. *manivitae*, sample V7102; F) *Watznaueria manivitae* (large), sample V7101; G) *Watznaueria* aff. *manivitae* and *W. manivitae* Acme, sample V7102; H) *Watznaueria britannica*, sample V7102; I) *Watznaueria communis*, sample V7102; J-K) *Watznaueria manivitae* (large), sample V7102; L) *Cyclagelosphaera* sp., sample V7102. Scale bars represent 10 μ m.

dance in the lower Tithonian. Based on available literature data, saccocomids appeared in the middle Oxfordian, with some local acmes first recorded in the Kimmeridgian, followed by a widespread acme in the Tithonian. Although the abundance of sand-sized *Saccocoma* in the RAS varies because of changes in currents or productivity on the Trento Plateau (see Ogg 1981), it appears clear from what is reported above that saccocomids are abundant only in the Kimmeridgian–Tithonian RAV beds.

Based on all the considerations above, the occurrence of the *Saccocoma* acme in both V7101 and V7102 suggests that they possibly belong to the same stratigraphic interval. The slight difference between the nannofossil assemblages in these two samples, i.e. the absence of the *Watznaueria manivittae* acme in the V7101, is more likely due to a preservation bias, rather than at a different age. In conclusion, the saccocomid acme observed in both samples and the *Watznaueria manivittae* acme preserved only in V7102, suggest, respectively, that V7101 and V7102 are the same age and that they can be ascribed to the lower Kimmeridgian.

SYSTEMATIC PALAEOONTOLOGY

SPECIMEN V7101

Order **Ichthyosauria** Blainville, 1835

Clade **Parvipelvia** Motani, 1999

Clade **Thunnosauria** Motani, 1999

Family **Ophthalmosauridae** Baur, 1887

Fig. 5–9A

Description. V7101 is represented by a fairly complete anterior axial skeleton and possible fragments of appendicular elements. The slab measures 120 x 80 cm and the skeleton is approximately 110 cm in length (Fig. 5A). The skeleton is highly flattened and heavily eroded to the cancellous bone, with just a few elements (especially on the posterior end) looking three-dimensional and complete. This is visible on the 3D depth map of the slab surface (Supplementary Fig. S1). Despite the poor preservation, the skeleton is still semi-articulated, with the left portion of the ribcage close to anatomical position. The orientation of the neural spines allows identification of the anterior part of the column to the left of the slab.

The preserved vertebral column consists of 26 vertebrae (Fig. 5B), most of them in lateral section. The anteriormost preserved centrum is also the only recognizable vertebra in anterior view (Fig. 6A–B): the centrum is well-preserved and slightly eroded, with the central concavity still visible and left diapophysis and parapophysis still close to the corresponding ribs. This is the only centrum where width can be measured, and the floor of the neural canal is visible. The general shape of this vertebra is typical of the ichthyosaurian anterior dorsal region. After a few fragmentary centra, the following vertebrae in lateral view are relatively complete and the outline of centrum, neural arch and neural spine is visible and measurable (Fig. 6C). Unfortunately, the ventral part of this first anterior set of vertebral centra is missing due to a crack between it and the underlying ribcage. The middle section of the torso, after the ninth vertebra, is much more fragmentary and individual centra become difficult to see. The elements in this region appear broken and are difficult to count under natural light. Neural spines are generally high, rectangular, and start to be fragmented just like the centra in the middle part of the column; shortly after, they start to be lost towards the posterior part of the column. The posterior centra appear much more complete and three-dimensionally preserved (Fig. 6D). From centra v20 to v26, centrum length (CL) and centrum height (CH) can be measured more accurately. A 27th vertebra could also be present based on a small bone fragment after v26. However, due to its small size and uncertain identification, we preferred to exclude it from the numeration. UV-induced fluorescence allowed visualization of vertebral details invisible under natural light as well as previously unobserved structures (Fig. 7A–B): centra in the middle section of the column became individually outlined under both UV-A and UV-C. Vertebral surfaces show a strong contrast from the surrounding matrix, and ossified elements overlapping the centra become visible, for example the neural arches. Close to the left side of the first vertebra, the outline of another partial centrum in frontal view is visible only under UV-A light. The structure is crossed by a fracture in the matrix filled with concrete, preventing its identification under natural light, and even under ultraviolet the fluorescence is very weak. We decided to number this vertebra as v0 because the element could just be a cast or the posterior sliced surface of v1. UV light

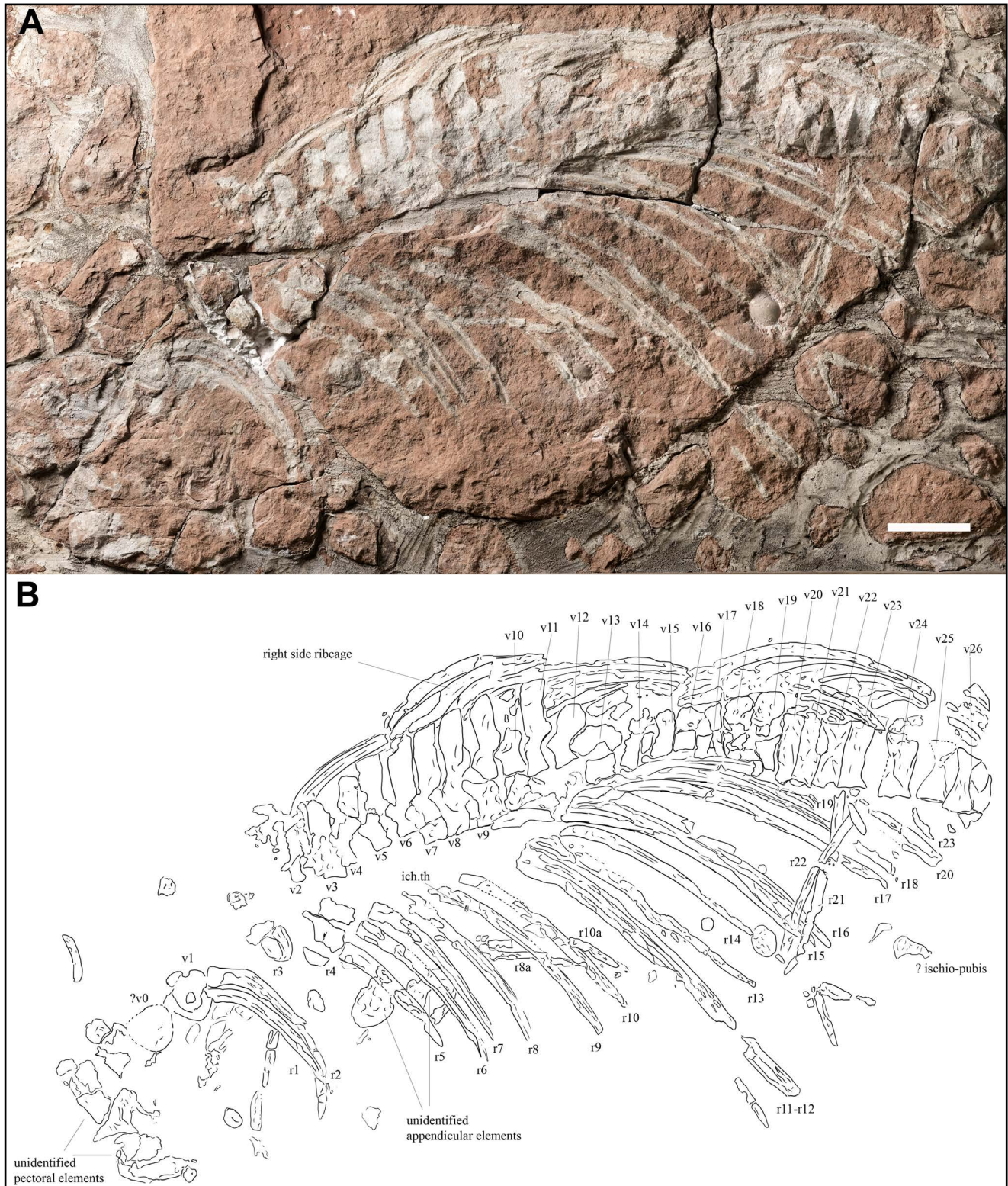


Fig. 5 - Overview of V7101 under natural light A) with interpretive line drawing B). Abbreviations: v, vertebra; r, rib; ich.th, ichthyosaur tooth. Scale bar represents 10 cm.

also emphasizes the differences between compact and cancellous bone in the vertebral column: the most represented bone tissue is the cancellous one, even in the more complete and three-dimensional

vertebrae, and only a few centra show a layer of compact bone (v1, v13–v19).

The left side of the ribcage shows 23 ribs, most of them still close to or even articulating with

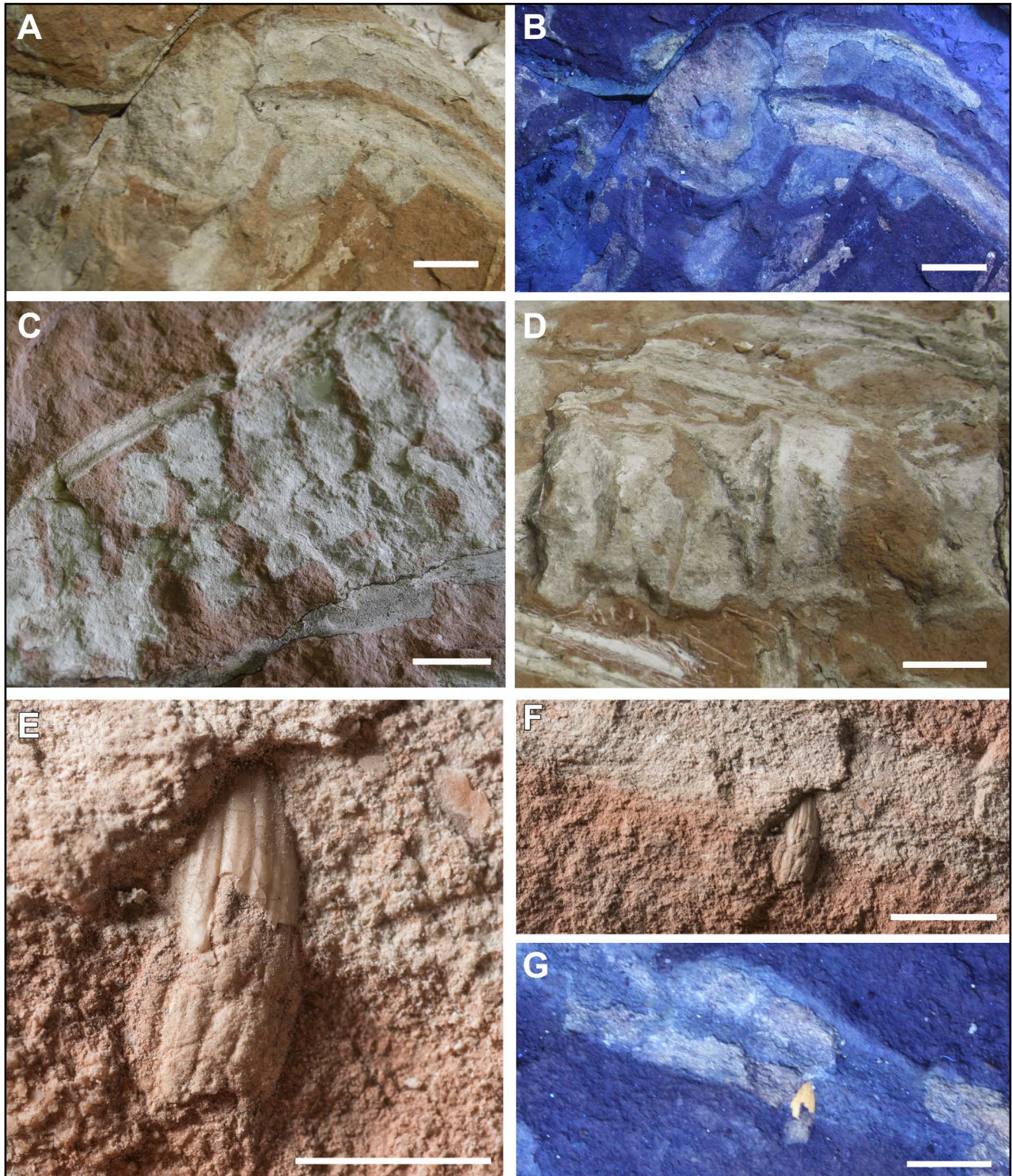


Fig. 6 - Details of V7101. Anteriormost preserved vertebra (v1) under natural A) and UV-A light B). C) Articulated anterior neural arches and neural spines; D) Posterior centra. Ichthyosaur tooth piercing the rib of the specimen under natural E, F) and UV-A light G). Scale bars represent: 2 cm in (A-B, D), 5 cm in (C, E) and 1 cm (F-G).

the vertebral column. The right part of the ribcage is visible above the vertebral column, with the individual ribs merged together into a continuous surface. For this reason, only the ribs on the left side

were numbered. As with the vertebrae, the costal elements are better preserved in the posterior part of the specimen (Fig. 8A), whereas the anterior ones show deeper erosion and higher fragmentation.

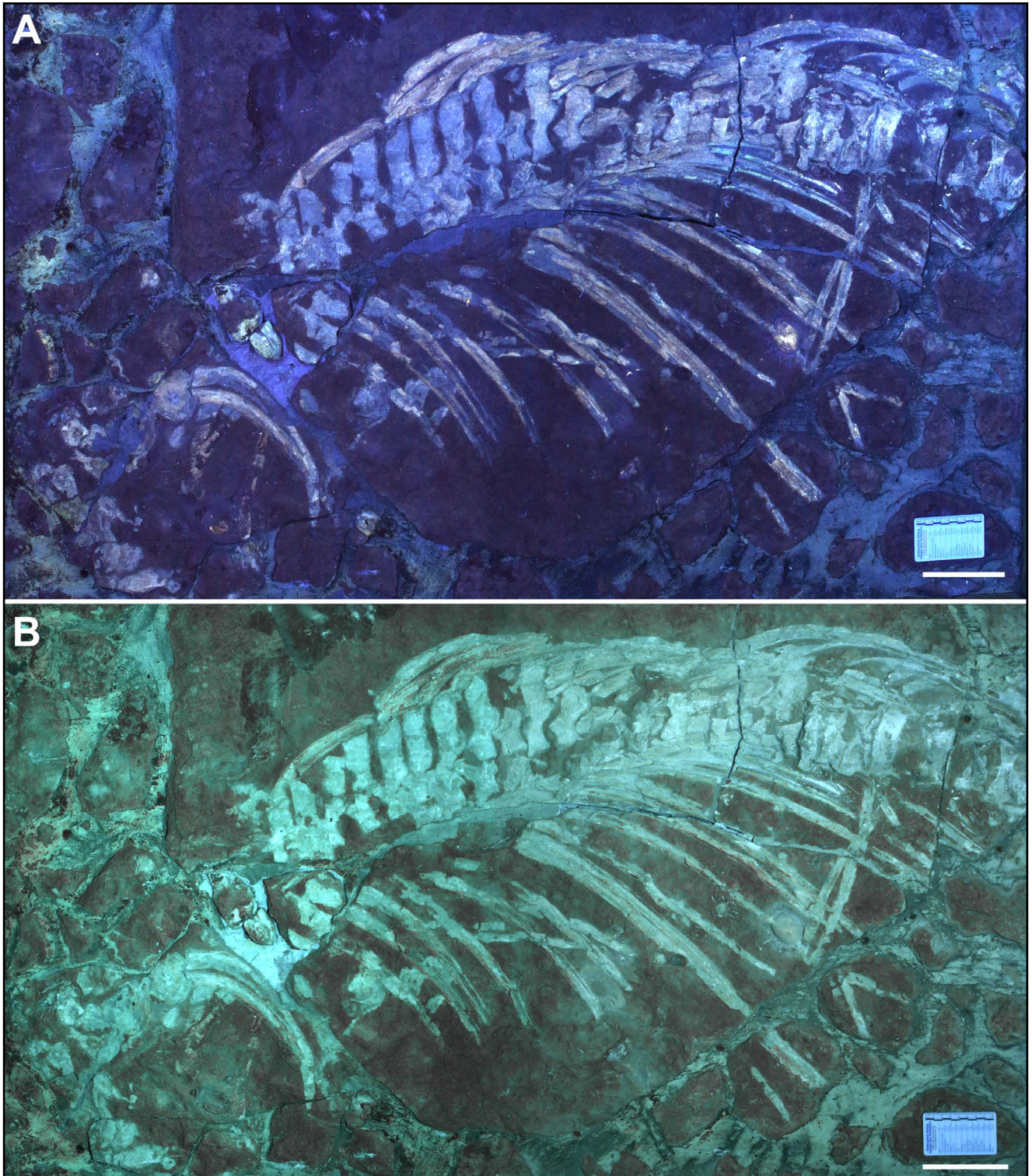


Fig. 7 - V7101 under UV-A light A). V7101 under UV-C and UV-A light B). Scale bars represent 10 cm.

Ribs are bicapitate, with capitulum and tuberculum (where visible) of similar proportions and show a deep longitudinal groove. This feature, shared by many thunnosaurian ichthyosaurs (McGowan & Motani 2003; Fischer et al. 2013), gives to the rib a distinctive “8” shape in cross section. Under UV

light, the longitudinally grooved appearance of the ribs is clearly visible, as well as the bicapitate articulation with the vertebral column. The compact bone appears to be better represented in the costal elements than in the vertebrae; its discontinuous presence on both sides of the ribcage reflects

the different pattern of erosion of the skeleton as well as histological and biomechanical differences between vertebral elements and ribs.

On the ninth rib, a small tooth appears to be stuck with the tip in the bone tissue (Fig. 6E-G and Supplementary Fig. S2). The tooth consists of the crown, featuring enamel ornamented with well-developed coarse longitudinal ridges (Fig. 6E), and a partial root. The acellular cementum is missing, and the root shows infolding of the dentine. Based on the thickness and ornamentation of the enamel at the base of the crown, the tooth is from a marine reptile rather than a fish. Among Jurassic marine reptiles, the presence of plicidentine allows us to differentially diagnose the tooth as belonging to an ichthyosaur (Edmund 1969; Sander 2000). Under UV light, the enamel reacts as the most fluorescent tissue on the skeleton (followed by the root dentine) with a bright white-yellow backscattered light (Fig. 6G). No other teeth or cranial elements were found on the slab.

On the anterior end of the specimen, in the bottom left corner of the slab, a large bone surface can be seen (Fig. 8B). The combination of poor preservation and presence of concrete, together with the similar colour of the bone and the matrix, makes those elements very difficult to identify. The shapes and textures of these elements are hard to distinguish, and the entire structure seems merged and fused into one indistinct surface. Based on the anatomical position, we suppose that these could be appendicular elements, probably from the pectoral girdle. The UV analysis did not help to further identify these elements as under both UV-A and UV-C they appear as a continuous surface without recognizable anatomical features (Fig. 8C). Two elongated structures can be observed only under UV light under the v1 centrum: they appear flattened, grooved and segmented. Even if they are similar to the nearby ribs, their nature remains uncertain. Among the ribs of the left side of the ribcage, below the first anterior articulated vertebrae, two rounded elements are visible (Fig. 8D-E). They show a subtriangular shape and appear to lie beneath the ribs. The first one on the left seems more three-dimensional than the other but both are strongly eroded and probably compressed. Currently we are not able to identify these bones. According to their position and proportions, they could belong to the appendicular skeleton, possibly scapular fragments.

On the posterior end of the specimen, under the vertebral column next to the last ribs, a small structure can be seen almost exclusively under UV light. This flat element, with very low fluorescence, has a distal expansion on the left giving it a characteristic axe-head shape. Another small bone fragment is visible next to the distal end of the latter. On both fragments, the bone histology is difficult to distinguish. The size and shape of these bone elements is comparable to the medial portion of the ischiopubis of many ichthyosaur taxa (McGowan & Motani 2003; Delsett et al. 2017) but the position appears too anterior for a fragment of the pelvic girdle. We tentatively assign it to an ischiopubis fragment, possibly displaced anteriorly by taphonomic processes.

The general shape of the centra in frontal and lateral view, the proportions between vertebral and costal elements and the similar sizes of tuberculum and capitulum allow us to identify the portion of the vertebral column as the dorsal region, most likely from the anterior dorsal to mid-dorsal region.

The high fragmentation of single elements and the degree of compression and erosion prevent any morphometric consideration of most of the bones. The only region where accurate measurements can be taken is the posterior end of the specimen, on the last seven preserved centra (Table 1A). Unfortunately, even those three-dimensional elements show some degree of erosion, and from v24 to v26 the centra are dorso-ventrally incomplete. Centra from v20 to v23 are higher than long, with a CH/CL ratio value around 3. We cannot directly compare the height of the anterior and posterior centra because of differences in completeness along the column. The only anterior vertebra whose height can be reliably measured is v1, for which CH = 62 mm, notably smaller than the centra at the posterior end of the series. In contrast, we can confidently compare CL, which can be reliably measured throughout the column. The anterior dorsal centra are longer than the posterior ones.

Systematic affinities of V7101. The centrum height and length difference between the anterior and mid-dorsal regions found in V7101 is a common feature among ophthalmosaurids (Marsalek et al. 2006), where centra become higher and shorter towards the posterior dorsal region (Table 1A). This regionalization of the column reflects the biomechanical constraint of a lateral propulsion

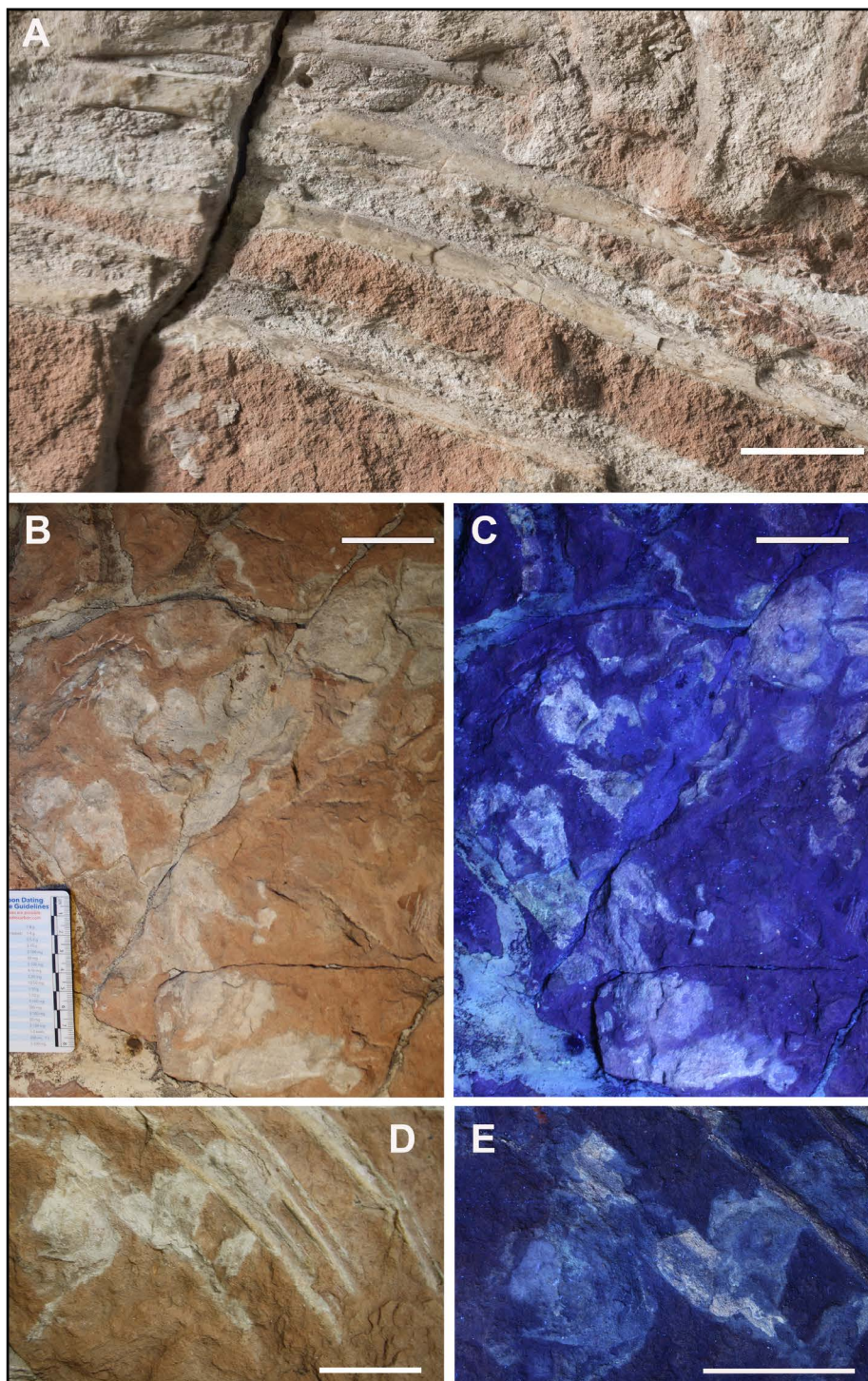


Fig 8 - V7101 details: Grooved ribs detail A). Unidentified pectoral elements under natural light (B) and UV-A light (C). Unidentified pectoral-appendicular elements under natural light (D) and UV-A light (E). Scale bars represent: 2 cm in (A) and 5 cm in (B–E).

swimming style, where the dorsal region must be more rigid than the flexible posterior caudal-flexural section (Buchholtz 2001). It is worth noting that the highest centrum in V7101 measures 80 mm (v20) with a CH/CL of 3, both values typical of the mid-dorsal region of *Ophthalmosaurus icenicus* (Appleby 1956; Massare et al. 2006; Moon & Kirton 2016), and of *Arthropterygius chrisorum* (Maxwell 2010). Consequently, the posterior dorsal region of V7101 may have presented centrum heights similar

to *O. icenicus*, indicating a similar degree of column regionalization. The degree of regionalization of the vertebral column is considered useful by some authors to distinguish already known species, such as *O. icenicus* and *O. natans* (Massare et al. 2006) but is not diagnostic above the specific level (Paparella et al. 2016). Column regionalization is a feature often subject to homoplasy, since high or low regionalization convergently evolved multiple times in different ichthyosaur lineages (Buchholtz 2001;

Tab. 1 - Measurements of vertebral elements (mm) in V7101 A) and V7102 B). Abbreviations: CH: centrum height; CW: centrum width; CL: centrum length; NaH: neural arch height; NaL: neural arch length; NsH: neural spine height; NsL: neural spine length.

A							
VERTEBRA	CH	CW	CL	NaH	NaL	NsH	NsL
V1	62.1	53.5					
V2				28.9	25.0	48.8	24.6
V3				35.9	23.3	56.6	24.2
V4				35.5	21.2	66.7	24.4
V5				38.8	22.2	71.9	28.9
V6				39.3	28.4	72.3	28.8
V7			32.1	38.5	31.1	75.1	26.3
V8	41.7		32.1	35.9	37.5	81.0	29.4
V9	44.4		31.9	32.8	33.8	77.4	31.2
V10	43.7		38.1	33.6	33.6	63.9	24.5
V11			41.1	38.0	32.8	76.2	31.9
V12				37.0	32.4		33.6
V13							28.9
V14			36.9				
V15					35.3		
V16							
V17							
V18							
V19							
V20	80.4		26.8				
V21	78.0		27.5				
V22	80.2		30.0				
V23	81.0		28.0				
V24	78.0		34.8				
V25	74.0		35.7				
V26	75.0		36.5				
B							
VERTEBRA	CH	CL	NaH	NaL	NsH	NsL	
V1	70.0	76.8	54.4	48.2	61.3	27.3	
V2			39.8	27.5	76.2	33.6	
V3				26.7	66.8	35.2	
V4	61.3	38.3					
V5	47.6	39.5					
V6	59.3	39.8					
V7	51.2	36.0					
V8	52.8	40.6					
V9	45.2	44.5					
V10	46.3	34.5					
V11	48.4	27.0					
V12	39.4	39.4					
V13	45.8	38.8					
V14	29.6	34.2					
V15	24.7	31.7					

Massare et al. 2006; Fischer et al. 2011; Paparella et al. 2016). A comparison can be drawn with *Gengasaurus nicosiai* (Paparella et al. 2016), where anterior centra are longer and smaller than the posterior ones. However, *G. nicosiai* shows a CH/CL < 3 (2.8 at its maximum), a feature interpreted as indicative of a less regionalized vertebral column (Paparella et al. 2016). In V7101, it is difficult to determine the degree of regionalization due to the absence of the posterior dorsal and caudal region and the high fragmentation of the specimen; however, our data

suggest a condition closer to *O. icenicus*. The neural spines of V7101 resemble those from the mid-dorsal region of *Gengasaurus* in height and, using v1 CH as a reference for anterior centra, become higher than the centra by v4. Based on comparisons with *Ophthalmosaurus icenicus* (measurements and reconstruction from Buchholtz 2001, based on PMAG R 340), V7101 originates from an individual roughly 3–3.5 m in length, assuming a body shape similar to *O. icenicus*. While ontogenetic markers have been noted for the ichthyosaurian vertebral column

(Maxwell et al. 2016), the preservation of V7101 is insufficient to assess its maturity. Ribs in V7101 are bicapitate with marked longitudinal grooves, a character commonly found among Thunnosauria (Fischer et al. 2013). The strongly furrowed shape of costal elements in V7101 allows us to exclude some taxa: longitudinal costal grooves are much less developed in *Mollesaurus periallus* (Talevi & Fernández 2012) and *Ophthalmosaurus natans* (Massare et al. 2013), whereas they are pronounced in *O. icenicus* (Appleby 1956; McGowan & Motani 2003), among other taxa. Alleged appendicular elements in V7101 are damaged and fragmentary and therefore useless for taxonomic assignment.

The best inference we can currently make is to assign the specimen to the family Ophthalmosauridae: this open classification is based on the presence of different non-diagnostic characteristics (high CH/CL, costal grooves, tall dorsal neural spines) shared by V7101 and other taxa from the family such as *Ophthalmosaurus icenicus*, *Arthropterygius chrisorum* and *Gengasaurus nicosiai*. This attribution is consistent with the stratigraphic position of V7101 in the lower Kimmeridgian. Ophthalmosauridae is the only clade of ichthyosaurs so far recovered from Upper Jurassic rocks, undergoing a spectacular radiation starting in the Aalenian and continuing through the Early Cretaceous (Fischer et al. 2012, 2013, 2016). However, the presence of *Malawania anachronus*, a basal thunnosaurian, in the Lower Cretaceous of Iraq indicates that some other lineages have a ghost range spanning this interval (Fischer et al. 2013). The axial skeleton of *Malawania* differs from V7101, bearing trapezoidal neural spines and a less-regionalized vertebral column based on centrum length. We considered V7101 to be distinct from *Malawania* but, due to the fragmentary nature of V7101, we cannot definitely exclude an assignment to a family outside of Ophthalmosauridae.

Other fossils associated with V7101. The slab V7101 contains a diversified oryctocoenosis with the remains of other marine animals besides the ichthyosaur (Fig. 9A). The most abundant macrofossils on the slab are ammonite aptychi: around the skeleton we can recognize ten single valve portions of aptychi and several more fragments. Two ammonite aptychi morphotypes are represented on the slab: laevaptychi (seven) and lamellaptychi (three). The first are mostly found between ribs, some of them are quite large (up to 5 cm in length)

and slightly eroded, with a smooth surface still intact above the internal porous structure (Fig. 9B-C). Only this calcitic superficial layer is fluorescent under ultraviolet light and differs from the bone apatite in its pale-yellow colour and lower intensity. Lamellaptychi on V7101 are smaller and more fragmentary than the laevaptychi (Fig. 9D); they are recognized by their distinctive concentric laminar ornamentation and have been attributed to the Superfamily Haploceratoidea (Ammonitina) (Parent et al. 2014). Three rhyncholites were also found close to the ribcage: only one is complete and shows a longitudinally furrowed hood (arrowhead shape of the tip) typical of rhynchotheutids (ammonite calcified upper jaw) (Riegraf & Luterbacher 1989; Riegraf & Moosleitner 2010), possibly referable to *Gonatocheilus* (Fig. 9E).

The last category of macrofossils found on the slab is represented by two shark teeth. As mentioned above, the first (Fig. 9F-G) has been removed from the slab and housed separately with the same catalogue number, while the second, still in situ, was identified under UV light and then partially prepared (Fig. 9H). The two teeth are multicuspitate and very small (less than 1 cm) and both show the typical morphology of hexanchiform teeth. These specimens are described and identified below.

Class CHONDRICHTHYES Huxley, 1880
 Subclass ELASMOBRANCHII Bonaparte, 1838
 Superorder **Squalomorphii** Compagno, 1973
 Order **Hexanchiformes** Buen, 1926
 Family Hexanchidae Gray, 1851
 Genus *Notidanodon* Cappetta, 1975

Notidanodon sp.

Fig. 9F-H

Description. The tooth detached from the slab (herein informally labelled as “st1”) is rather small (8 mm in width) and poorly preserved, exhibiting most of the crown and only a small part of the root. The root is deeply affected by diagenetic dissolution and possibly by mechanical damage. The imprint is still visible on the counterpart but does not exhibit peculiar characters of the crown or the root. The root is also encrusted by the reddish matrix, while the crown is clean, with the enameloid preserved as a translucent layer and affected

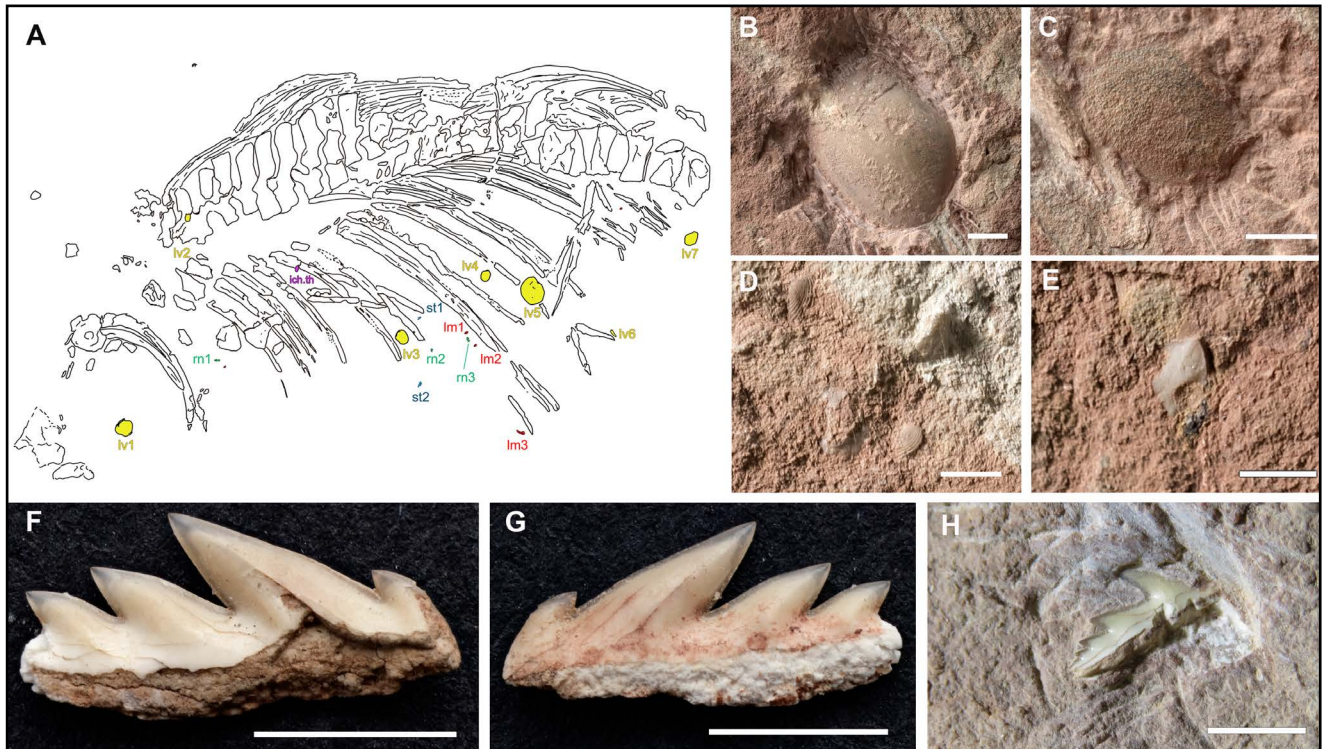


Fig. 9 - V7101 associated macrofauna: A) distribution of macrofossils around the skeleton. B, C) *Laevaptychus* detail. D) *Lamellaptychus* detail. E) rhyncholite detail. F–G) st1 hexanchiform tooth in labial (F) and lingual (G) face. H) st2 hexanchiform tooth, lingual face. Abbreviations: lv, *Laevaptychus*; lm, *Lamellaptychus*; rn, rhyncholites; st, shark tooth. Scale bars represent: 1 cm in (B–C), 5 mm in (D–E), 4 mm in (F–G) and 3 mm in (H).

by small fractures. The tooth has an overall labio-lingually compressed and mesio-distally elongated morphology. The cusps are slightly convex on the lingual face and slightly flattened on the labial face. The tooth preserves four pointed apicodistally oriented cusps: the main cusp (acrocone sensu Cappetta 1987) inclined ca. 39° , two cusplets preserved on the distal side and a smaller one preserved on the mesial side. The slant of the first distal cusplet is ca. 30° and ca. 23° in the second one preserved. Their size decreases distally. The mesial side is damaged; therefore, we cannot exclude the presence of other mesial accessory cusps. The mesial cusplet is medio-basal to and distinct from the main cusp and its size is not significantly smaller than the distal cusplets, though different and incomplete. The acrocone is ca. 2 mm high from its basal cutting edge. The mesial cutting edge of all cusps is slightly convex, the distal edge is straight.

The second tooth (herein labelled as “st2”) is still on the slab and is located near the 10th rib of the ichthyosaur skeleton (Fig. 9H), exposing the lingual face based on the convex cusp surface. Its size (ca. 6 mm wide in the exposed portion) and its overall aspect are similar to st1. Five cusps are

recognizable, three on the distal side and one on the mesial side, accidentally broken during preparation (though the crown base is still visible). There is an alleged fourth distal cusplet, though the distal side is damaged. The three distal accessory cusps gradually decrease in size distally, while the acrocone is larger, higher and more upright than the one from st1. The slant of the main cusp is ca. 53° . The first distal cusplet is inclined 39° distally.

Discussion. Both teeth show a remarkable labio-lingual compression and mesio-distal elongation, a common feature in extinct and extant hexanchiforms, with the exception of very plesiomorphic genera such as *Welcommia*, *Pseudonotidanus* and *Crassonotidanus* (Cappetta 1990; Underwood & Ward 2004; Kriwet & Klug 2011). Both teeth can be referred to Hexanchidae based on the distally decreasing distal cusplets, together with the well-marked mesial cusplets (Cappetta 2012; Szabó 2020). The hexanchid sharks include a dozen genera extant, some represented also by fossils: *Heptranchias*, *Hexanchus* and *Notorynchus*. Seven genera are only represented by fossil species and include *Notidanodon*, *Notidanoides*, *Pachyhexanchus*, *Pseudonotidanus*, *Welcommia*, *Weltonia*,

and *Gladioserratus* (see Cappetta & Grant-Mackie 2018). The mesial cusplet is not attributable to a serrated mesial edge as in the genera *Notorynchus* and *Gladioserratus*. The teeth are referred herein to the genus *Notidanodon* (Hexanchidae) on the basis of the following dental characters (Cappetta 1975; Hovestadt et al. 1983; Thies 1987; Long et al. 1993; Cappetta & Mackie 2018; Szabó 2020): (i) numerous well-developed and acute distal and mesial cusplets are present (in contrast to other hexanchids, in which the mesial cusplets are absent or present as serrations on the mesial edge); (ii) anterolateral files of the genus display an apically or apicodistally directed principal cusp and distal cusplets; (iii) mesial cusplets are usually almost as large as the distal cusplets and are mesiobasal to and distinct from the main cusp. Moreover, the teeth resemble those of *Notidanodon* sp. described by Szabó (2020), who briefly revised Mesozoic hexanchids (for further discussion and comparison of differential characters see Szabó (2020) and references therein). We retain open nomenclature for the shark teeth associated with V7101, since the two teeth are too incomplete to be confidently ascribed to any known species, pending further revision of hexanchid taxa.

Furthermore, the genus *Notidanodon* is not homogeneous and needs revision (Cappetta & Grant-Mackie 2018). Tooth st1 is identified as a lower lateral tooth, due to the strong distal inclination of the acrocone, while st2, with its more upright acrocone, strong distal notch (sensu Cappetta & Grant-Mackie 2018) and three distal cusplets is here interpreted as a lower anterior tooth.

The *Notidanodon* teeth described herein are particularly significant because they extend the oldest record of *Notidanodon* to the lower Kimmeridgian, corroborating previous attributions from the Kimmeridgian/Tithonian boundary of Hungary (see Cappetta & Grant-Mackie 2018; Szabó 2020 for the stratigraphical distribution of the genus and the discussion above regarding the integrated biostratigraphy). Other hexanchid teeth associated with the ichthyosaur *Gengasaurus nicosiai* from Italy were recently described and figured by Paparella et al. (2016) as ?Crassonotidae gen. et sp. indet. The name Crassonotidae has been recently replaced by Crassodontidanidae by Kriwet and Klug (2016) (see also Szabó 2020) and includes the genera *Notidanooides* and *Pachyhexanchus* (Kriwet & Klug 2014). However, the teeth associated with *G. nicosiai* cannot be

referred to one of these genera but exhibit the same characters as those associated with V7101. For this reason, the shark teeth reported by Paparella et al. (2016) are referred herein to *Notidanodon* sp. Previous records of Jurassic hexanchiforms from Italy are reported by Seguenza (1887) and D’Erasmus (1922). Seguenza (1887) reported the new species “*Notidanus*” *insignis* from the Oxfordian of Capo S. Andrea near Taormina (Sicily). Unfortunately, the species is neither described nor figured, and is consequently a *nomen dubium*. D’Erasmus (1922: 24, pl. 4, fig. 20) described and figured another Jurassic hexanchiform from Veneto region with a similar dental morphology, the species “*Notidanus*” cf. *hügeliae* (*Notidanooides muensteri*) from the Middle Jurassic “*Posidonomya alpina* beds” of Acque Fredde (Garda Lake, Verona; see also Sirna et al. 1994). The only other hexanchiform taxon reported from northeastern Italy is the orthacodontid *Sphenodus* (see D’Erasmus 1922; Sirna et al. 1994).

SPECIMEN V7102

Order **Ichthyosauria** Blainville, 1835

Family indet.

Fig. 10–12

Description. The specimen V7102 consists of a small portion of vertebral column (55 cm in length) with a few ribs merged together and partially fused above the centra forming a continuous surface (Fig. 10A–B). Despite the semi-articulated nature of the specimen, the poor preservation does not allow individual vertebral elements to be distinguished. Centra overlap one to another in what appears to be a ‘stacked coins’ organization, very common among ichthyosaur remains, but vertebral elements are broken and fused together, making the column appear almost as a continuous surface (Fig. 11A). The entire structure is partially flattened, but the 3D depth map shows a minor elevation gain towards the centra (Supplementary Fig. S1). Centra are fragmentary and the ventral part is often missing. The amphicoelic structure of the vertebrae is only recognizable under UV light (Fig. 12A–B) in the central part of the preserved column, where a relatively undamaged concavity can be seen. Fifteen vertebral elements can be recognized under UV-A light, and four neural spines are present (Fig. 11B), three (v1–3) on the right end (of which one is the

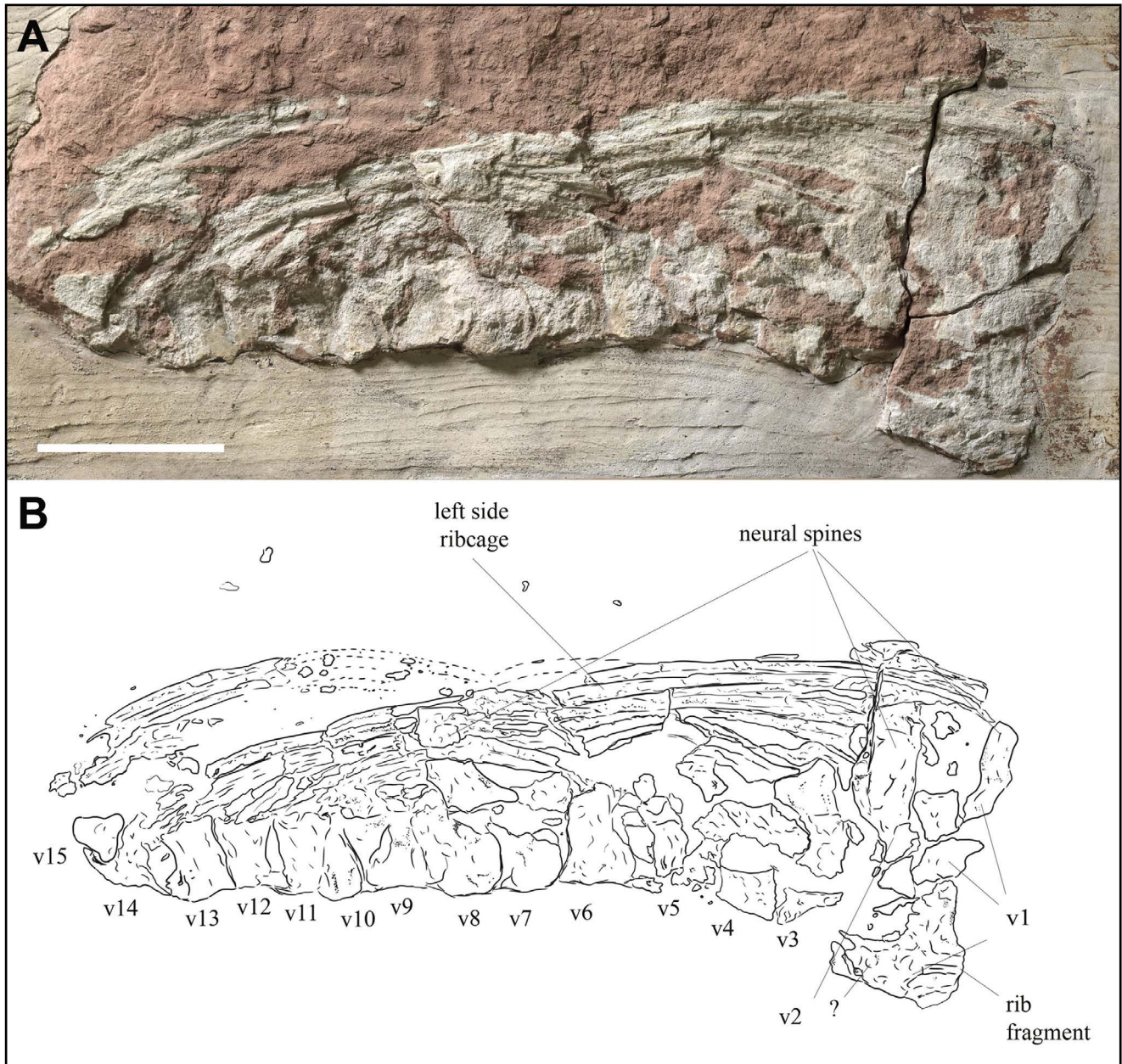


Fig. 10 - Overview of V7102 under natural light A) with interpretive line drawing B). Vertebrae are numbered from the right. Abbreviations: v, vertebra. Scale bar represents 10 cm.

very first element from the upper right corner) and one in the mid-part (v7). Given the disposition of the neural spines, the column can be oriented with anterior to the right. Consequently, the ribcage is visible from the left-hand side. Individual ribs are not distinguishable (Fig. 11C) but a crack running near the distal end across the specimen allows one rib to be viewed in cross section and the characteristic “8” shape can be recognized (Fig. 11D). An odd structure can be seen in the bottom right corner, with a shape resembling an “L”. This element is still enigmatic: the most conservative hypothesis

is that it could be the result of two centrum fragments merged together by taphonomic processes. At the base of this complex, a small tubular structure can be seen, possibly a rib fragment from the right portion of the ribcage. The most common visible bone tissue is the cancellous one, but some shreds of compact bone can be seen under natural and UV light ventrally to the centrum fragments and towards the ribs.

Systematic affinities of V7102. Preservation of V7102 is insufficient for estimation of axial regionalization, body size or maturity (Table 1B).

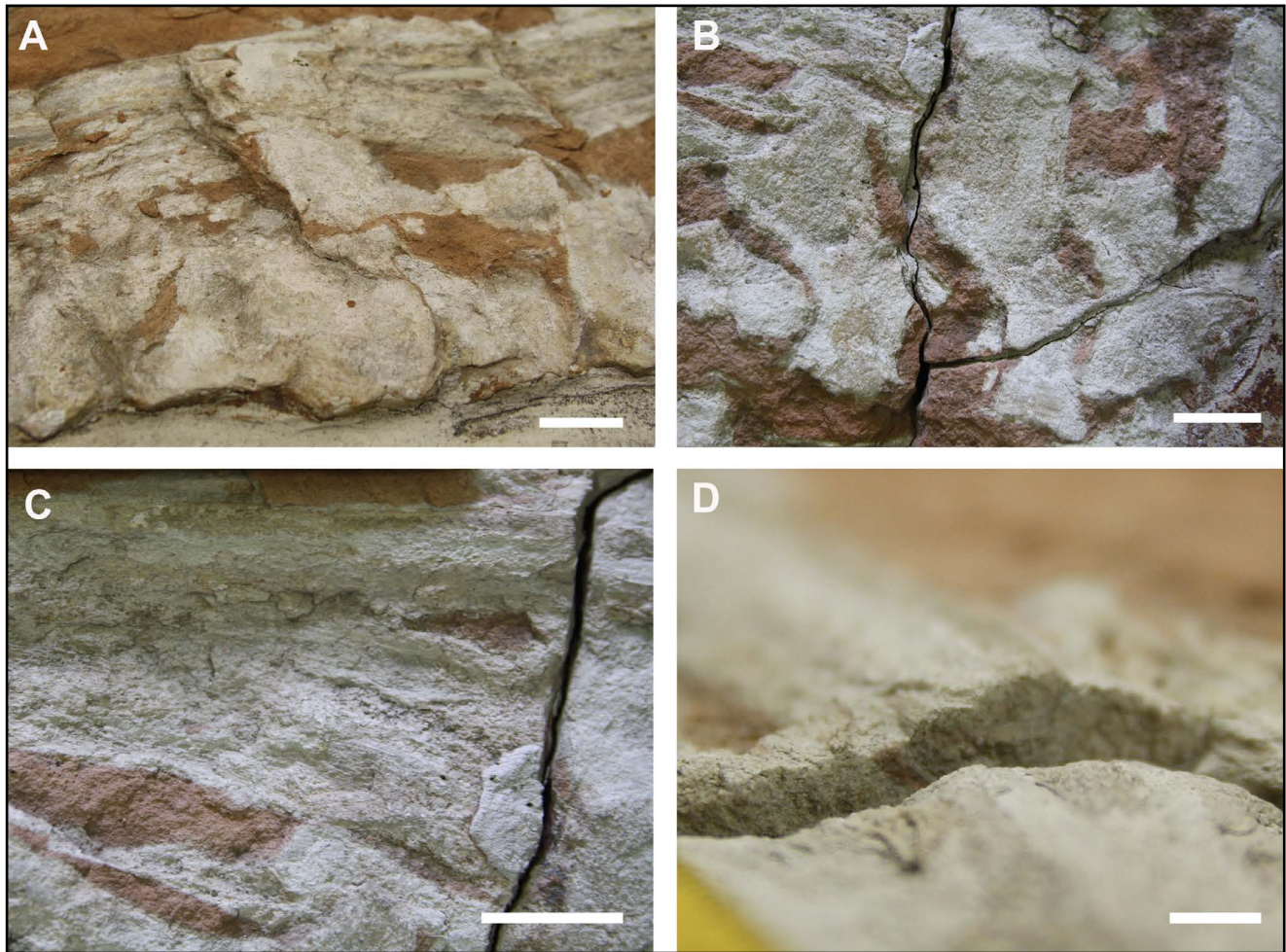


Fig. 11 - Details of V7102. A), partially overlapping and damaged centra; B) neural arches and spines; C) merged ribs surface; D) “8” shaped cross section of a rib through a crack. Scale bars represent: 2 cm in (A-C) and 1 cm in (D).

The tall rectangular neural spines, a very badly preserved amphicoelic centrum and the longitudinally grooved ribs are the only features in V7102 that allow its identification as an ichthyosaur. V7102 can most likely be assigned to *Thunnosauria* based on the presence of deeply grooved ribs, though the character is considered typical but non-diagnostic of this clade (Motani, 1999; Fischer et al. 2013; Moon 2017). Due to the fragmentary and generally poor preservation of this specimen, we prefer to ascribe it to the order *Ichthyosauria* without further taxonomic specification.

TAPHONOMY OF MONTE INTERROTTO'S ICHTHYOSAUR DEADFALLS

Large marine vertebrate deadfalls have gained attention in the last decade due to the remarkable ecosystems they build; different or-

ganisms thrive on soft tissues and bones as the carcass provides different nutrients during the various stages of decomposition (Smith et al. 2015). Most studies focus on extant whales, but similar ecological successions were found on fossil cetaceans (e.g., Danise & Dominici 2014), chondrichthyans (Amalfitano et al. 2019) and Mesozoic marine reptiles (Danise et al. 2014; Danise & Higgs 2015; Dick 2015), both in deep and shallow waters. Analysis of fossil deadfalls provides information on biostratigraphic processes, allowing a better understanding of palaeoecology and reconstruction of palaeoenvironmental conditions in the depositional basin.

V7101 offers interesting information about the taphonomic history of the ichthyosaur. The poor preservation of the skeleton can be attributed to long exposure of the carcass on the sea floor. The worst preservation affects the anterior half of the fossil, probably less protected by the sediment

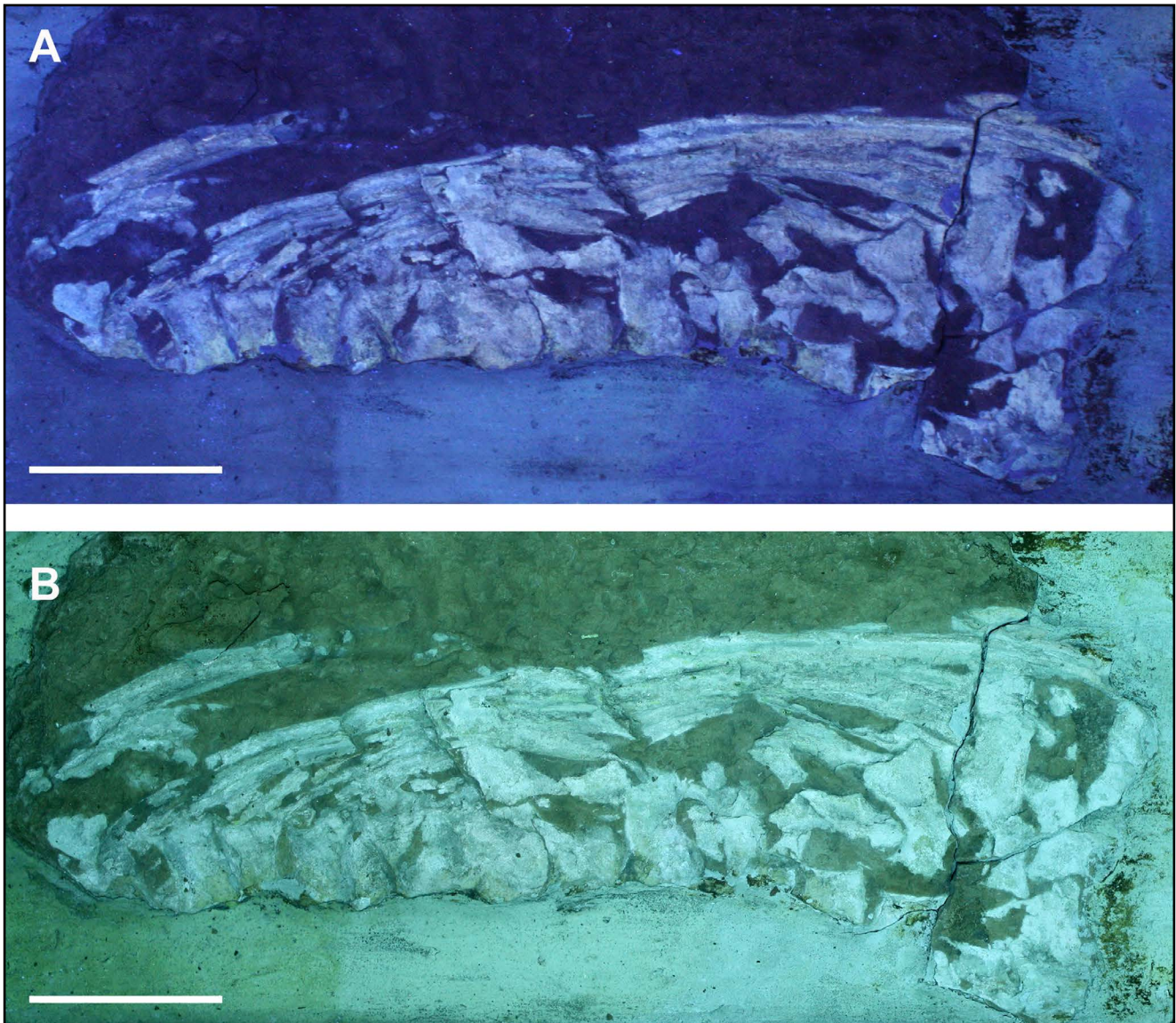


Fig. 12 - V7102 under UV-A light A) and under UV-C and UV-A light B). Scale bars represent 10 cm.

for a longer time than the posterior portion, and more exposed to biotic and abiotic degradation. This hypothesis matches with the very low sedimentation rate hypothesized for the RAV Fm., possibly combined with well-oxygenated waters (Martire et al. 2006). Bones are strongly eroded, possibly due to dissolution combined with biotic degradation and scavenging activities (e.g., Hedges 2002; Trueman et al. 2003). The right portion of the ribcage shows better preservation of the compact bone than the left one: as indicated by the elements merged together above the column, the right side of the ribcage was displaced upward relative to the column by the weight of the carcass as it lay on its right-hand side during necrolysis. Thus, the right side of the rib cage was protected by the

left side of the body for some time, preventing degradation of the bones to the degree seen on the left ribcage. Additional taphonomic information can be inferred by the preservation and disposition of the bones. Five different landing types of the carcass on the seafloor can be deduced in marine reptiles based on the degree of articulation of the skeleton (Martill 1993; Stinnesbeck et al. 2014; Delsett et al. 2015): anterior, posterior, lateral, dorsal and ventral landing. The posterior one, though, has never been identified in ichthyosaurs, probably due to their anteriorly shifted centre of mass (Delsett et al. 2015). A ventral landing can be excluded for V7101, since in this model all four limbs of the carcass are usually preserved while the vertebral column disarticulates as the intervertebral

ligaments decay. Instead, an articulated vertebral column is commonly associated with a dorsal, lateral or anterior landing. In a lateral landing, the elements below are usually better preserved, in the anterior type the rostrum is the first structure to impact on the sea floor, resulting in bone damage or even in the piling of the snout into the sediment (Wetzel & Reisdorf 2007). All these three landing types are consistent with the condition of V7101. It could have sunk, possibly after a floating period, and eventually shifted on to the right side of the carcass. The skull and cervical region are not preserved in V7101, even if there is some empty space on the slab to the left of the most proximal vertebra, suggesting detachment of this region before the final burial of the skeleton. Delsett et al. (2015) used modern cetaceans as taphonomic models for marine reptiles. The authors pointed out that in modern dolphins, the head is usually the last element to detach from the rest of the body during necrolysis; the trachea is resistant to decay processes because of its cartilage rings, so it usually keeps the head connected to the body for a long time (Schäfer 1972). In odontocetes, the trachea is structurally thick, a feature interpreted as a diving adaptation in marine mammals (Cozzi et al. 2005). Since ichthyosaurs and cetaceans share an almost identical ecology and body plan, it is reasonable to infer that the trachea in ichthyosaurs could have been similarly thickened. Therefore, the missing skull in V7101 could be the result of active processes, possibly connected to scavenging or current activity, especially if the carcass landed anteriorly. In this case, the head might have remained anchored in the sediment and the body could have detached during necrolysis and drifted away. We consider the two *Notidanodon* teeth associated with V7101 (Fig. 9A, F-H) as evidence of scavenging. Hexanchids are known to scavenge on large marine vertebrate deadfalls, with examples in extant and extinct taxa (Compagno et al. 2005; Eastman 2013). Extant genera such as *Hexanchus* are known to feed on fish and marine mammal carcasses on continental shelves as well as on abyssal plains (Compagno et al. 2005; McNeil et al. 2016), and teeth of *Notidanodon dentatus* have been found associated with a plesiosaur skeleton from the Upper Cretaceous of Seymour Island (Antarctica) and Argentina (Eastman 2013: 31; Bogan et al. 2016). Hexanchid teeth were also found in association with the Upper Jurassic Italian ichthyosaur *Gengasaurus*

(Paparella et al. 2016). No bite marks were found on V7101, possibly due to the heavy erosion on the skeletal elements.

The presence of the ichthyosaur tooth stuck on the ninth rib (Fig. 5B, 6E-G; Supplementary Fig. S2) is quite odd. The tooth is very small and firmly anchored in the cancellous bone. We advance three hypotheses to explain its presence:

1) The tooth belongs to the same specimen. It was swallowed or moved back during necrolysis, displaced into contact with the rib and was then cemented with the bone. This explanation is not completely satisfactory because the tooth is on the outer side of the ribcage: even taking displacement into account, it would probably have remained on the inner side, coming from the internal part of the carcass. Moreover, no other cranial elements were found displaced on the skeleton.

2) The tooth belongs to another ichthyosaur and is a result of predation on the living animal or aggressive courtship by a conspecific. This scenario is also unlikely, since it seems difficult for a small-toothed, narrow-snouted predator to bite the lateral side of a rounded and thick-bodied animal, through muscle and probably a thick fat layer (Lindgren et al. 2018) to end up embedded in the rib.

3) The tooth belongs to another ichthyosaur and is related to scavenging. This hypothesis seems much more plausible, especially if the rib was already partially exposed during decomposition on the sea floor or while the carcass was floating.

This last scenario is very interesting because it would be the first record of scavenging activity between two ichthyosaurs. In fact, while traces of trauma inflicted by conspecifics are commonly found throughout the Jurassic and Cretaceous (Pardo-Pérez et al. 2018; Zammit & Kear 2011) and predation between genera is known from a few specimens (Böttcher 1989), necrophagy between ichthyosaurs is never mentioned in the literature. If correctly interpreted, this could indicate a previously undocumented trophic interaction in the group. Unfortunately, the tooth is too fragmentary to determine to which feeding guild (*sensu* Fischer et al. 2016) it belonged.

Both the shark and ichthyosaur teeth can be assigned to the first stage of large vertebrate deadfall successions, the “mobile scavenger stage” (Smith et al. 2015). This stage is well known in modern and fossil cetaceans as well as in ichthyosaurs (Danise et al. 2014).

Finally, the ammonite aptychi and rhyncholites could also be a part of the ichthyosaur deadfall community. Dick (2015) describes a rich nektonic fall community on a *Stenopterygius quadriscissus* carcass from the Posidonienschiefer Fm. (Toarcian, Lower Jurassic), identifying ammonite remains as evidence for an “enrichment opportunistic stage.” In this decomposition stage, the bacterial breakdown of the carcass attracts smaller benthic and epibenthic saprotrophic organisms. Ammonite aptychi were also found in Dick’s study; it is unclear if the ones found on V7101 are in fact related to the deadfall ecology or if their presence is just casual. Nevertheless, ammonite aptychi are common in the middle member of the RAV Fm.

It is worth noting that the macrofauna associated with V7101 is remarkably similar to the one found on the holotype of *Gengasaurus nicosiai*: laevaptychi, rhyncholites and hexanchid teeth are in fact also reported by Paparella et al. (2016). The *Saccocoma* acme observed in the matrix of *Gengasaurus* could be also compared to the one observed for the specimens of Monte Interrotto, even if the ages are significantly different (late Kimmeridgian–early Tithonian for the former, early Kimmeridgian for the latter), possibly indicating a similar palaeoenvironment.

V7102 shares the same eroded and corroded appearance with V7101, indicative of a similar extended period on the sea floor prior to the burial. No scavenging traces could be found on this specimen. The only other taphonomic information we could glean is the strong lateral compression shown by the crushed centra and fused ribs, indicative of a diagenetic regime similar to the one imposed on V7101.

CONCLUSIONS

The description of the new specimens from Monte Interrotto reveals the presence of parvipelvic ichthyosaurs from the undersampled lower Kimmeridgian of the western Tethyan Ocean, representing an important addition to the record of post-Triassic ichthyosaurs from Italy. Unfortunately, most ichthyosaurs from the Oxfordian–lower Kimmeridgian of Europe are very fragmentary and taxonomically problematic, and V7101 and V7102 are no exception. The skeletons are frag-

mentary and strongly eroded, likely due to the very slow sedimentation typical of the RAV depositional setting, resulting in prolonged exposure of carcasses on the sea floor and consequently dissolution phenomena (Martire et al. 2006). Despite the poor preservation and their poorly documented recovery, the two specimens from Monte Interrotto offered many interesting results, especially from the larger and more complete one, here interpreted as a lower Kimmeridgian ophthalmosaurid. The skeleton is mostly represented by the axial component, which is strongly eroded to the cancellous bone. Anatomical details and complete bones are visible only under UV–A or UV–C radiation. Posterior centra show a high ratio between centrum height and centrum length, indicating a strongly regionalized vertebral column as seen in some ophthalmosaurids such as *Ophthalmosaurus icenicus* (see Massare et al. 2006).

A rich fossil fauna is associated with V7101, including aptychi, rhyncholites and two hexanchiform shark teeth, possibly remains of scavengers. We ascribe these two teeth to the genus *Notidanodon*, representing the oldest reported occurrence of this genus. An ichthyosaur tooth embedded on a rib of the skeleton is interpreted as a possible evidence of scavenging between two ichthyosaurs, a biological interaction not previously reported in this order.

V7101 also shows remarkable similarities with the Italian ophthalmosaurid *Gengasaurus nicosiai*: the two specimens share similar body proportions, though with a different degree of axial regionalization. In absence of other diagnostic features, this difference in regionalization suggests they might represent separate taxa, which has implications for Late Jurassic ichthyosaur diversity in the western Tethys. Moreover, the two specimens share similar taphonomic features, such as the presence of hexanchiform teeth associated with scavenging activities. V7101 represents the second most complete post-Triassic ichthyosaur from Italy to date.

Acknowledgements: The authors deeply thank Roberto Zorzini and †Anna Vaccari (Museo Civico di Storia Naturale di Verona) for useful information and permission to examine the specimens in their care. Thanks are also due to Stefano Castelli (Department of Geosciences of University of Padova) for his valuable help with photographs. We thank the reviewers, Ilaria Paparella (University of Alberta) and the editor for helpful comments and suggestions.

Research funded by ex 60% (DOR) fundings of Università di Padova (Luca Giusberti and Jacopo Amalfitano) and by MIUR grant FFABR to Cesare A. Papazzoni.

REFERENCES

- Amalfitano J., Giusberti L., Fornaciari E., Dalla Vecchia F.M., Luciani V., Kriwet J., & Carnevale G. (2019) - Large deadfalls of the "ginsu" shark *Cretoxyrhina mantelli* (Agassiz, 1835) (Neoselachii, Lamniformes) from the Upper Cretaceous of northeastern Italy. *Cretaceous Research*, 98: 250–275.
- Appleby R.M. (1956) - The osteology and taxonomy of the fossil reptile *Ophthalmosaurus*. *Proceeding of the Zoological Society of London*, 16: 403–47.
- Arkhangelsky M.S., Zverkov N.G., Spasskaya O.S. & Evgrafov A.V. (2018) - On the first reliable record of the ichthyosaur *Ophthalmosaurus icenicus* Seeley in the Oxfordian–Kimmeridgian beds of European Russia. *Paleontological Journal*, 52: 49–57.
- Barbieri G. & Grandesso P. (2007) - Carta Geologica d'Italia alla scala 1:50.000, Foglio 082 Asiago, Note Illustrative, 135 pp.
- Bardet N., Falconnet J., Fischer V., Houssaye A., Jouve S., Pereda Suberbiola X., Pérez-García A., Rage J.-C. & Vincent P. (2014) - Mesozoic marine reptile palaeobiogeography in response to drifting plates. *Gondwana Research*, 26: 869–887.
- Bartolini A., Pittet B., Mattioli E. & Hunziker J.C. (2003) - Shallow-platform palaeoenvironmental conditions recorded in deep-shelf sediments: C and O stable isotopes in Upper Jurassic sections of southern Germany (Oxfordian–Kimmeridgian). *Sedimentary Geology*, 160: 107–130.
- Benson R.B.J., Butler R.J., Lindgren J. & Smith A.S. (2010) - Mesozoic marine tetrapod diversity: mass extinctions and temporal heterogeneity in geological megabiases affecting vertebrates. *Proceeding of the Royal Society B* (2010), 277: 829–834.
- Benton M.J. (2015) - Vertebrate Paleontology. Fourth Edition. Wiley Blackwell, 468 pp.
- Benzaggagh M., Homberg C., Schnyder J. & Ben Abdesselam-Mahdaoui S. (2015) - Description et biozonation des sections de crinoïdes saccocomidés du Jurassique supérieur (Oxfordien–Tithonien) du domaine téthysien occidental. *Annales de Paléontologie*, 101: 95–117.
- Bizzarini F. (1996) - Sui resti di coccodrillo del Rosso Ammonitico Veronese di Sasso di Asiago (Altopiano dei Sette Comuni, Prealpi Venete). *Annali dei Musei Civici di Rovereto, Sezione Archeologia, Storia, Scienze Naturali*, 11: 339–348.
- Bizzarini F. (2003) - L'ittiosauro del Museo Civico della Laguna Sud. Chioggia. *Rivista di Studi e Ricerche, Chioggia*, 23: 117–124.
- Bogan S., Agnolin F. & Novas F. (2016) - New selachian records from the Upper Cretaceous of southern Patagonia: paleobiogeographical implications and the description of a new taxon. *Journal of Vertebrate Paleontology*, e1105235. doi.org/10.1080/02724634.2016.1105235.
- Bosellini A. & Dal Cin R. (1969) - Il Giurassico medio–superiore di Fonzaso (Feltrino occidentale). *Annali dell'Università di Ferrara. Sezione IX, Scienze geologiche e paleontologiche*, 4: 235–247.
- Böttcher R. (1989) - Über die Nahrung eines *Leptopterygius* (Ichthyosauria, Reptilia) aus dem süddeutschen Posidonien-schiefer (Unterer Jura) mit Bemerkungen über den Magen der Ichthyosaurier. *Stuttgarter Beiträge zur Naturkunde* (B), 155: 1–19.
- Bown P.R. & Young J.R. (1998) - Techniques. In: Bown P.R. (Ed.) - Calcareous nannofossil biostratigraphy. British Micropaleontological Society Publications Series: 16–28. Kluwer Academic Publishers, London.
- Brinkmann W. (1997) - Die Ichthyosaurier (Reptilia) aus der Grenzbitumenzone (Mitteltrias) des Monte San Giorgio (Tessin, Schweiz)-der aktuelle Forschungsstand. *Vierteljahrsschrift der Naturforschenden Gesellschaft in Zürich*, 142(4): 165–177.
- Buchholtz E.A. (2001) - Swimming styles in Jurassic ichthyosaurs. *Journal of Vertebrate Paleontology*, 21: 61–73.
- Buffetaut E. & Thierry J. (1977) - Les crocodyliens fossiles du Jurassique moyen et supérieur de Bourgogne. *Geobios*, 10: 151–193.
- Cappetta H. (1975) - Sélaciens et Holocéphale du Gargasien de la région de Gargas (Vaucluse). *Géologie méditerranéenne*, 2: 115–134.
- Cappetta H. (1987) - Mesozoic and Cenozoic Elasmobranchii, Chondrichthyes II. In: Schultze H.-P. (Ed.) - Handbook of Paleichthyology, 3B. Gustav Fischer Verlag, Stuttgart, New York, 193 pp.
- Cappetta H. (1990) - Hexanchiforme nouveau (Neoselachii) du Crétacé inférieur du Sud de la France. *Palaeovertebrata*, 20: 33–54.
- Cappetta H. (2012) - Chondrichthyes (Mesozoic and Cenozoic Elasmobranchii: teeth). In: Schultze H.-P. (Ed.) - Handbook of Paleichthyology. 3E. Verlag Dr. Friedrich Pfeil, München, 512 pp.
- Cappetta H. & Grant-Mackie J. (2018) - Discovery of the most ancient *Notidanodon* tooth (Neoselachii: Hexanchiformes) in the Late Jurassic of New Zealand. New considerations on the systematics and range of the genus. *Palaeovertebrata*, 42: 1–8.
- Casellato C.E. (2010) - Calcareous nannofossil biostratigraphy of upper Callovian–lower Berriasian successions from the Southern Alps, North Italy. *Rivista Italiana di Paleontologia e Stratigrafia*, 116: 357–404.
- Cau A. (2014) - The affinities of '*Steneosaurus baretton?*' (Crocodylomorpha, Thalattosuchia), from the Jurassic of Northern Italy, and implications for cranial evolution among geosaurine metriorhynchids. *Historical Biology*, 26: 433–440.
- Cau A. (2019) - A revision of the diagnosis and affinities of the metriorhynchoids (Crocodylomorpha, Thalattosuchia) from the Rosso Ammonitico Veronese Formation (Jurassic of Italy) using specimen-level analyses. *PeerJ*, 7: e7364. doi.org/10.7717/peerj.7364
- Cau A. & Fanti F. (2014) - A Pliosaurid Plesiosaurian from the Rosso Ammonitico Veronese Formation of Italy. *Acta Palaeontologica Polonica*, 59: 617–634.
- Cau A. & Fanti F. (2016) - High evolutionary rates and the origin of the Rosso Ammonitico Veronese Formation (Middle–Upper Jurassic of Italy) reptiles. *Historical Biol-*

- ogy, 28: 952–962.
- Chiari M., Cobianchi M. & Picotti V. (2007) - Integrated stratigraphy (radiolarians and calcareous nannofossils) of the Middle to Upper Jurassic Alpine radiolarites (Lombardian Basin, Italy): constraints to their genetic interpretation. *Palaeogeography Palaeoclimatology Palaeoecology*, 249: 233–270.
- Citton P., Fabbi S., Cipriani A., Jansen M. & Romano M. (2019) - Hybodont dentition from the Upper Jurassic of Monte Nerone Pelagic Carbonate Platform (Umbria-Marche Apennines, Italy) and its ecological implications. *Geological Journal*, 54 (1): 278–290.
- Clari P.A., Marini P., Pastorini M. & Pavia G. (1984) - Il Rosso Ammonitico Inferiore (Baioiciano–Calloviano) nei Monti Lessini settentrionali (Verona). *Rivista Italiana di Paleontologia e Stratigrafia*, 90: 15–86.
- Cobianchi M. (2002) - I nannofossili calcarei del Giurassico medio e superiore del bacino di Belluno (Alpi Calcarea Meridionali). *Atti Ticinesi di Scienze della Terra*, 43: 3–24.
- Compagno L., Dando M. & Fowler S. (2005) - Sharks of the World. Princeton University Press, Princeton, New Jersey, 496 pp.
- Cozzi B., Bagnoli P., Acocella F. & Costantino M.L. (2005) - Structure and Biomechanical Properties of the Trachea of the Striped Dolphin *Stenella coeruleoalba*: Evidence for Evolutionary Adaptations to Diving. *The Anatomical Record, Part A*, 284A: 500–510.
- Dal Sasso C. & Pinna G. (1996) - *Besanosaurus leptorhynchus* n. gen. n. sp., a new shastasaurid ichthyosaur from the Middle Triassic of Besano (Lombardy, N. Italy). *Paleontologia Lombarda, Nuova serie*, 4: 1–23.
- Danise S. & Dominici S. (2014) - A record of fossil shallow-water whale falls from Italy. *Lethaia*, 47: 229–243.
- Danise S. & Higgs N.D. (2015) - Bone-eating *Osedax* worms lived on Mesozoic marine reptile deadfalls. *Biology Letters*, 11: 20150072. doi.org/10.1098/rsbl.2015.007.
- Danise S., Twitchett R.J. & Matts K. (2014) - Ecological succession of a Jurassic shallow-water ichthyosaur fall. *Nature Communications*, 5: 4789.
- Della Bruna G. & Martire L. (1985) - La successione giurassica (Pliensbachiano–Kimmeridgiano) delle Alpi Feltrine (Belluno). *Rivista Italiana di Paleontologia e Stratigrafia*, 91: 15–62.
- Delsett L.L., Novis L., Roberts A.J., Koevoets M., Hammer O., Druckenmiller P.S. & Hurum H.J. (2015) - The Slotsmøya marine reptile *Lagerstätte*: Depositional environments, taphonomy and diagenesis. *Geological Society of London, Special Publications*, 434: 165–188.
- Delsett L.L., Roberts A.J., Druckenmiller P.S. & Hurum H.J. (2017) - A new ophthalmosaurid (Ichthyosauria) from Svalbard, Norway, and evolution of the ichthyopterygian pelvic girdle. *PLoS ONE*, 12: e0169971. doi.org/10.1371/journal.pone.0169971.
- De Marinis G. & Nicosia U. (2000) - L'Ittiosauro di Genga. Cassa di Risparmio di Fabriano e Cupramontana Edizioni, Castelferretti, Ancona, 220 pp.
- D'Erasmus G. (1922) - Catalogo dei pesci fossili delle Tre Venezie. *Memorie dell'Istituto Geologico della R. Università di Padova*, 6: 1–181.
- De Stefani S. (1883) - Sui primi resti fossili di un ittiosauro e di un cheloniano scoperti nella provincia veronese. *Memorie dell'Accademia di agricoltura arti e commercio di Verona* (serie 3), 60: 95–105.
- De Zigno A. (1883) - Sui Vertebrati fossili dei terreni mesozoici delle Alpi venete. *Nuovi Saggi della Regia Accademia di Scienze, Lettere ed Arti in Padova*, 9. Tipografia G. B. Randi, Padova (offprint), 11 pp.
- Dick D.G. (2015) - An ichthyosaur carcass-fall community from the *Posidonia* Shale (Toarcian) of Germany. *Palaios*, 30: 353–361.
- Dick D.G. & Maxwell E.E. (2015) - The evolution and extinction of the ichthyosaurs from the perspective of quantitative ecospace modelling. *Biological Letters*, 11: 20150339.
- Eastman J.T. (2013) - Antarctic fish biology: evolution in a unique environment. Academic Press, 322 pp.
- Edmund A.G. (1969) - Dentition. In: Gans C. Bellairs A. D'A. & Parsons T.S. (Eds) - Biology of the Reptilia. Volume 1. Morphology A: 117–200. Academic Press, London and New York.
- Fastelli C. & Nicosia U. (1980) - L'Ittiosauro di Genga (Ancona). In: Parisi G. (Ed.) - I vertebrati fossili italiani. Verona: Catalogo della Mostra: 95–101. Tipografia La Grafica, Vago, Verona.
- Fischer V., Appleby R.M., Naish D., Liston J., Riding J.B., Brindley S. & Godefroit P. (2013) - A basal thunnosaurian from Iraq reveals disparate phylogenetic origins for Cretaceous ichthyosaurs. *Biological Letters*, 9: 20130021.
- Fischer V., Bardet N., Benson R., Arkhangelsky M.S. & Friedman M. (2016) - Extinction of fish-shaped marine reptiles associated with reduced evolutionary rates and global environmental volatility. *Nature Communications*, 7: 10825.
- Fischer V., Clément A., Guiomar M. & Godefroit P. (2011) - The first definite record of a Valanginian ichthyosaur and its implications on the evolution of post-Liassic Ichthyosauria. *Cretaceous Research*, 32: 155–163.
- Fischer V., Maisch M.W., Naish D., Kosma R., Liston J., Joger U., Krüger F.J., Pardo-Pérez J., Tainsch J. & Appleby R.M. (2012) - New Ophthalmosaurid Ichthyosaurs from the European Lower Cretaceous Demonstrate Extensive Ichthyosaur Survival across the Jurassic–Cretaceous Boundary. *PLoS ONE*, 7: e29234. doi.org/10.1371/journal.pone.0029234.
- Fornaciari B., Maxwell E.E., Fornaciari E., Papazzoni C.A. & Zorzini R. (2017) - A new platypterygiine ichthyosaur rostrum from the Lower Cretaceous of the Lessini Mountains (Northern Italy). *Cretaceous Research*, 71: 137–144.
- Hedges R.E.M. (2002) - Bone diagenesis: an overview of processes. *Archaeometry* 44: 319–328.
- Hess H. (2002) - Remains of saccocomids (Crinoidea: Echinodermata) from the Upper Jurassic of southern Germany. *Stuttgarter Beiträge zur Naturkunde Serie B (Geologie und Paläontologie)*, 329: 57 pp.
- Hovestadt M., Hovestadt D. & Smith R. (1983) - A contribution to the fish fauna of the Belgian Palaeocene: a

- review of *Notidanodon loozii* (Vincent 1876). *Tertiary Research*, 5: 71–79.
- Ji C., Jiang D.-Y., Motani R., Rieppel O., Hao W. & Sun Z.-Y. (2016) - Phylogeny of the Ichthyopterygia incorporating recent discoveries from South China. *Journal of Vertebrate Paleontology*, 36: e1025956. doi.org/10.1080/02724634.2015.1025956.
- Kriwet J. & Klug S. (2011) - A new Jurassic cow shark (Chondrichthyes, Hexanchiformes) with comments on Jurassic hexanchiform systematics. *Swiss Journal of Geosciences*, 104: 107–114.
- Kriwet J. & Klug S. (2014) - Dental patterns of the stem-group hexanchoid shark, *Notidanooides muensteri* (Elasmobranchii, Hexanchiformes). *Journal of Vertebrate Paleontology*, 34(6): 1292–1306.
- Kriwet J. & Klug S. (2016) - Crassodontidanidae, a replacement name for Crassonotidae Kriwet and Klug 2011 (Chondrichthyes, Hexanchiformes). *Journal of Vertebrate Paleontology*, 3: e1119698.
- Laub C. (1994) - The Radiolarit-Rhyncholithen-Kalke of the Rosso Ammonitico in the Central Southern Alps (Middle/Upper Jurassic, North Italy). *Palaeontographica*, A, 234: 89–166.
- Lindgren J., Sjövall P., Thiel V., Zheng W., Ito S., Wakamatsu K., Hauff R., Kear B., Engdahl A., Alwmark C., Eriksson M., Jarenmark M., Sachs S., Ahlberg P., Marone F., Kuriyama T., Gustafsson O., Malmberg P., Thomen A. & Schweitzer M. (2018) - Soft-tissue evidence for homeothermy and crypsis in a Jurassic ichthyosaur. *Nature*, 564: 359–365.
- Long D.J., Murphy M.A. & Rodda P.U. (1993) - A new world occurrence of *Notidanodon lanceolatus* (Chondrichthyes, Hexanchidae) and comments on hexanchid shark evolution. *Journal of Paleontology*, 67: 655–659.
- Maisch M.W. (2010) - Phylogeny, systematics, and origin of the Ichthyosauria – the state of the art. *Palaeodiversity*, 3: 151–214.
- Martill D.M. (1993) - Soupy substrates: a medium for the exceptional preservation of ichthyosaurs of the *Posidonia* Shale (Lower Jurassic) of Germany. *Kaupia: Darmstädter Beiträge zur Naturgeschichte*, 2: 77–97.
- Martire L. (1996) - Stratigraphy, facies and synsedimentary tectonics in the Jurassic Rosso Ammonitico Veronese (Altopiano di Asiago, NE Italy). *Facies*, 35: 209–236.
- Martire L., Clari P.A., Lodi P. & Pignatti P. (2006) - The Rosso Ammonitico Veronese (Middle–Upper Jurassic of the Trento Plateau): a proposal of lithostratigraphic ordering and formalization. *Rivista Italiana di Paleontologia e Stratigrafia*, 112: 227–250.
- Massare J.A., Buchholtz E.A., Kenney J.M. & Chromat A.M. (2006) - Vertebral morphology of *Ophthalmosaurus natans* (Reptilia: Ichthyosauria) from the Jurassic Sundance Formation of Wyoming. *Paludicola*, 5: 242–54.
- Massare J.A., Wahl W.R., Ross M. & Connely M.V. (2013) - Palaeoecology of the marine reptiles of the Redwater Shale Member of the Sundance Formation (Jurassic) of central Wyoming, USA. *Geological Magazine*, 151: 167–182.
- Massari F. & Westphal H. (2011) - Microbialites in the Middle–Upper Jurassic Ammonitico Rosso of the Southern Alps (Italy). In: Tewari V. & Seckbach J. (Eds) - Stromatolites: Interaction of Microbes with Sediments. Cellular Origin. Life in Extreme Habitats and Astrobiology, 18: 223–250.
- Maxwell E.E. (2010) - Generic reassignment of an ichthyosaur from the Queen Elizabeth Islands, Northwest Territories, Canada. *Journal of Vertebrate Paleontology*, 30: 403–415.
- Maxwell E.E., Dick D., Padilla S. & Parra L.M. (2016) - A new ophthalmosaurid ichthyosaur from the Early Cretaceous of Colombia. *Papers in Palaeontology*, 2: 59–70.
- McGowan C. & Motani R. (2003) - Ichthyopterygia. In: Sues H.-D. (Ed.) - Handbook of Paleoheterology, Part 8. Verlag Dr. Friedrich Pfeil, München, 175 pp.
- McNeil B., Lowry D., Larson S. & Griffing D. (2016) - Feeding behavior of subadult sixgill sharks (*Hexanchus griseus*) at a bait station. *PLoS ONE*, 11: e0156730. doi.org/10.1371/journal.pone.0156730.
- Moon B.C. (2017) - A new phylogeny of ichthyosaurs (Reptilia: Diapsida). *Journal of Systematic Palaeontology*, 17: 129–155.
- Moon B.C. & Kirton A.M. (2016) - Ichthyosaurs of the British Middle and Upper Jurassic. Part 1, *Ophthalmosaurus*. *Monographs of the Palaeontographical Society, London*, 170, 647: 1–84.
- Moon B.C. & Kirton A.M. (2018) - Ichthyosaurs of the British Middle and Upper Jurassic. Part 2, *Brachypterygius, Nanopterygius, Macropterygius* and Taxa invalida. *Monographs of the Palaeontographical Society, London*, 172 (issue 650): 85–177.
- Motani R. (1999) - Phylogeny of the Ichthyopterygia. *Journal of Vertebrate Paleontology*, 19: 472–495.
- Motani R. (2009) - The evolution of marine reptiles. *Evolution: Education and Outreach*, 2: 224–235.
- Motani R., Jiang D.Y., Chen G., Tintori A., Rieppel O., Ji C. & Huang J.D. (2015) - A basal ichthyosauriform with a short snout from the Lower Triassic of China. *Nature*, 517: 485–488.
- Ogg J. (1981) - Middle and Upper Jurassic sedimentation history of the Trento Plateau (Northern Italy). In: Farinacci A. & Elmi S. (Eds) - Rosso Ammonitico Symposium Proceedings, Technoprint, Roma: 479–503.
- Omboni G. (1890) - Il cocodrillo fossile (*Steneosaurus baretoni*, Zigno) di Treschè, nei Sette Comuni. *Atti del R. Istituto veneto di Scienze, Lettere ed Arti*, 8: 987–1006.
- Paparella I., Maxwell E., Cipriani A., Roncà S. & Caldwell M.W. (2016) - The first ophthalmosaurid ichthyosaur from the Upper Jurassic of the Umbrian–Marchean Apennines (Marche, Central Italy). *Geological Magazine*, 154: 837–858.
- Pardo-Pérez J., Kear B., Mallison H., Gómez M., Moroni M. & Maxwell E.E. (2018) - Pathological survey on *Temnodontosaurus* from the Early Jurassic of southern Germany. *PLoS ONE*, 13: e0204951. doi.org/10.1371/journal.pone.0204951.
- Parent H., Westermann G.E.G. & Chamberlain J.A. Jr. (2014) - Ammonite aptychi: Functions and role in propulsion. *Geobios*, 47: 45–55.

- Picotti V. & Cobianchi M. (2017) - Jurassic stratigraphy of the Belluno Basin and Friuli Platform: a perspective on far-field compression in the Adria passive margin. *Swiss Journal of Geosciences*, 110: 833–850.
- Pittet B. & Mattioli E. (2002) - The carbonate signal and calcareous nannofossil distribution in an Upper Jurassic section (Balingen-Tieringen, Late Oxfordian, southern Germany). *Palaeogeography Palaeoclimatology Palaeoecology*, 179: 71–96.
- Reposi D.E. (1902) - Il Mixosauro degli strati Triassici di Besano in Lombardia. *Atti della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano*, 41: 361–372.
- Riegraf W. & Luterbacher H. (1989) - Jurassic and Cretaceous rhyncholites (Cephalopod jaws) from the North Atlantic Ocean (Deep Sea Drilling Project Leg 1–79) and their European counterparts. Evidence for the uniformity of the Western Tethys. *Geologische Rundschau*, 78: 1141–1163.
- Riegraf W. & Moosleitner G. (2010) - Barremian rhyncholites (Lower Cretaceous Ammonoidea: calcified upper jaws) from the Serre de Bleyton (Département Drôme, SE France). *Annalen des Naturhistorischen Museums in Wien. Serie A für Mineralogie und Petrographie, Geologie und Paläontologie, Anthropologie und Prähistorie*, 112: 627–658.
- Roth P.H. (1981) - Mid-Cretaceous calcareous nannoplankton from the central Pacific: Implications for paleoceanography: 471–489. In: Thiede J., Valuer T.L. et al. - *Initial Reports of the Deep Sea Drilling Project*, 62. U.S. Government Printing Office, Washington. doi:10.2973/dsdp.proc.62.113.1981
- Roth P.H. (1984) - Preservation of calcareous nannofossils and fine-grained carbonate particles in mid-Cretaceous sediments from the southern Angola Basin, Site 530: 651–655. In: Hay W.W., Sibuet J.-C. et al. - *Initial Reports of the Deep Sea Drilling Project*, 75. U.S. Government Printing Office, Washington. doi:10.2973/dsdp.proc.75.112.1984
- Sander P.M. (2000) - Ichthyosauria: their diversity, distribution, and phylogeny. *Paläontologische Zeitschrift*, 74: 1–35.
- Sarti C. (1993) - Il Kimmeridgiano delle Prealpi Veneto-Trentine: Fauna e Biostratigrafia. *Memorie del Museo Civico di Storia Naturale di Verona* (serie 2), 5: 1–154.
- Savary B., Cecca F. & Bartolini A. (2003) - Étude stratigraphique du Rosso Ammonitico du Monte Inici (domaine Trapanais, Sicile occidentale): événements biosédimentaires au Jurassique moyen–Crétacé inférieur. *Geodiversitas*, 25(2): 217–235.
- Schäfer W. (1972) - Ecology and Paleocology of Marine Environments. Oliver & Boyd, Edinburgh, 568 pp.
- Seguenza G. (1887) - Brevissimi cenni intorno la geologia del Capo Sant'Andrea presso Taormina. *Rendiconto della Reale Accademia di Scienze Fisiche e Matematiche di Napoli*, 5: 78–88 (offprint).
- Serafini G., Fornaciari B. & Papazzoni C.A. (2017) - Risultati preliminari sul nuovo rostro di ittiosauro trovato a Gombola (MO). *Atti della Società dei Naturalisti e Matematici di Modena*, 148: 145–160.
- Serafini G., Rondelli R., Fornaciari B. & Papazzoni C.A. (2019) - Segnalazione di un nuovo ittiosauro dal Cretaceo dell'Appennino modenese (Pavullo nel Frignano). *Atti della Società dei Naturalisti e Matematici di Modena*, 150: 111–120.
- Sirna G., Dalla Vecchia F.M., Muscio G. & Piccoli G. (1994) - Catalogue of Paleozoic and Mesozoic vertebrates and vertebrate localities of the Tre Venezie area (north eastern Italy). *Memorie di Scienze Geologiche, Padova*, 46: 255–281.
- Sirotti A. & Papazzoni C.A. (2002) - On the Cretaceous ichthyosaur remains from the Northern Apennines (Italy). *Bollettino della Società Paleontologica Italiana*, 41: 237–248.
- Smith C.R., Glover A.G., Treude T., Higgs N.D. & Amon D.J. (2015) - Whale-fall ecosystems: recent insights into ecology, paleoecology, and evolution. *Annual Review of Marine Science*, 7: 571–596.
- Stinnesbeck W., Frey E., Rivas L., Pardo-Pérez J., Leppe M., Salazar C. & Zambrano Lobos P. (2014) - A Lower Cretaceous ichthyosaur graveyard in deep marine slope channel deposits at Torres del Paine National Park, Southern Chile. *Geological Society of America Bulletin*, 126: 1317–1339.
- Szabó M. (2020) - A Late Jurassic (Kimmeridgian–early Tithonian) fish fauna of the Eperkés-hegy (Olaszfalu, Bakony Mts., Hungary): the oldest record of *Notidanodon* Capetta, 1975 and a short revision of Mesozoic Hexanchidae. *Palaeobiodiversity and Palaeoenvironments*, 100: 151–170.
- Talevi M. & Fernández M.S. (2012) - Unexpected skeletal histology of an ichthyosaur from the Middle Jurassic of Patagonia: implications for evolution of bone microstructure among secondary aquatic tetrapods. *Naturwissenschaften*, 99: 241–244.
- Thies D. (1987) - Palaeoecology of Lower Cretaceous cow sharks (Neoselachii, Hexanchiformes). *Paläontologische Zeitschrift*, 61: 133–140.
- Trueman C.N., Benton M.J. & Palmer M.R. (2003) - Geochemical taphonomy of shallow marine vertebrate assemblages. *Palaeogeography Palaeoclimatology Palaeoecology*, 197: 151–169.
- Tyborowski D., Skrzycki P. & Dec M. (2018) - Internal structure of ichthyosaur rostrum from the Upper Jurassic of Poland with comments on ecomorphological adaptations of ophthalmosaurid skull. *Historical Biology*, doi.org/10.1080/08912963.2018.1559308.
- Underwood C.J. & Ward D.J. (2004) - Neoselachian sharks and rays from the British Bathonian (Middle Jurassic). *Palaeontology*, 47: 447–501.
- Wetzel A. & Reisdorf A.G. (2007) - Ichnofabrics elucidate the accumulation history of a condensed interval containing a vertically emplaced ichthyosaur skull. In: Bromley R.G., Buatois L.A., Mángano G., Genise J.F. & Melchor R.N. (Eds) - Sediment–Organism Interactions: Multifaceted Ichnology. *SEPM Special Publication*, 88: 241–251.
- Zammit M. & Kear B.P. (2011) - Healed bite marks on a Cretaceous ichthyosaur. *Acta Palaeontologica Polonica*, 56: 859–863.

