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First biostratigraphic dating for a Cretaceous ichthyosaur from the Apennine Chain (Italy)

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ABSTRACT
We report a new fossil-bearing locality from the "Chaotic Complex" units in the Northern Apennine Chain of the Emilia-Romagna Region (northern Italy). The material collected includes an articulated series of nine caudal vertebrae referable to a large-bodied ichthyosaur. Based on the nannofossil assemblage sampled from the matrix encasing the vertebrae, we refer the specimen to the early Aptian:

this is the first accurate chronostratigraphic dating of a Cretaceous ichthyosaur from the Apennine Chain. The discovery of this new fossil-bearing locality is also significant because of the rather poor record of Aptian ichthyosaurs worldwide. Compared to the large majority of vertebrate remains from the "Chaotic Complex" units, usually represented by isolated or damaged skeletal elements, the specimen retains several vertebral elements in articulation and is associated to ichnological traces left by possibly saprophagous invertebrates, a taphonomic pattern which might indicate depositional conditions less destructive than those usually assumed for the genesis of the "Chaotic Complex" vertebrate fossils. The presence of both ichthyosaurs and thalattosuchians in the Aptian of Italy supports the persistence in the Western Tethys of the large-bodied pelagic reptile clades typical of the Middle and Late Jurassic along the first half of the Early Cretaceous.

KEY WORDS
Appennine Chain,
Aptian,
"Chaotic Complex" units,
Early Cretaceous,
Ichthyosauria,
Italy.

RÉSUMÉ

Première attribution biostratigraphique pour un ichtyosaure du Crétacé de la chaîne des Apennins (Italie).
Nous rapportons une nouvelle localité fossilifère des unités « complexe chaotique » dans la chaîne des Apennins du Nord de la région d'Émilie-Romagne (Nord de l'Italie). Le matériel qui y est collecté comprend une série articulée de neuf vertèbres caudales se rapportant à un ichtyosaure de grande taille. Sur la base de l'assemblage de nannofossiles prélevés dans la matrice entourant les vertèbres, nous rapportons le spécimen à l'Aptien primitif : il s'agit de la première datation chronostratigraphique précise d'un ichtyosaure crétacé de la chaîne des Apennins. Comparé à la grande majorité des restes de vertébrés des unités du « complexe chaotique », généralement représentés par des éléments squelettiques isolés ou endommagés, le spécimen conserve plusieurs éléments vertébraux en articulation et est associé à des traces ichnologiques laissées par un invertébré limnivore, un schéma taphonomique qui pourrait indiquer des conditions de dépôt moins énergétiques que celles habituellement supposées pour la genèse des vertébrés fossiles du « complexe Chaotique ». La présence à la fois d'ichtyosaures et de thalactosuchi dans l'Aptien d'Italie confirme la persistance dans la Téthys occidentale de reptiles pélagiques de grande taille typique du Jurassique moyen et supérieur le long de la première moitié du Crétacé inférieur.

MOTS CLÉS
Chaîne des Appennins,
Aptien,
unités du « complexe Chaotique »,
Crétacé précoce,
Ichthyosauria,
Italie.

INTRODUCTION

The Italian ichthyosaur fossil record

Ichthyosauria de Blainville, 1835 is a clade of marine reptiles that inhabited the oceans and the epicontinental seas during the Mesozoic (Maisch 2010; Bardet *et al.* 2014). The oldest ichthyosaur fossils are dated to the Early Triassic (Olenekian), and document the rapid ecomorphological diversification of the group in the aftermath of the end-Permian mass extinction (Maisch 2010; Motani *et al.* 2017). Compared to the Triassic radiation of the clade, the global record of the Jurassic and Cretaceous ichthyosaurs is relatively poorer in term of disparity, being mostly represented by the thunnosaurian clade (McGowan & Motani 2003; Fischer *et al.* 2011; Bardet *et al.* 2014). The second half of the Mesozoic was interpreted as a phase of decline for the ichthyosaurs, with only a single genus surviving an extinction event at the Jurassic-Cretaceous boundary (Bardet 1992; Benson *et al.* 2010; Fischer *et al.* 2016). However, recent re-evaluation of the Cretaceous ichthyosaurs has revealed an extensive survival of these reptiles in the Early Cretaceous and an unexpectedly rich diversity, in particular among the ophthalmosaurids (Fischer *et al.* 2012, 2014). The ichthyosaur diversity diminishes during the Aptian, with only a handful of diagnostic taxa recovered worldwide, then significantly increases in the Albian (Fischer *et al.* 2013a). The ichthyosaur extinction, dated to the Cenomanian-Turonian boundary, is suggested to be connected to the global environmental and climatic change that drove a significant biotic turnover in the marine realm during the first part of the Late Cretaceous (Benson *et al.* 2010; Fischer *et al.* 2016).

The fossil record of Ichthyosauria from Italy is relatively scarce, spanning from the Middle Triassic up to Cretaceous. The Monte San Giorgio site (Western Alps) has provided abundant and well-preserved ichthyosaur fossils of Triassic age (Repossi 1902; Dal Sasso & Pinna 1996; Brinkmann 1997). Additional ichthyosaur material is also reported in the Middle Triassic deposits from the Eastern Alps (Dalla Vecchia & Avanzini 2002; Dalla Vecchia 2009) and Sicily (Dal Sasso *et al.* 2014). Conversely, the documentation on post-Triassic ichthyosaurs from Italy is scarcer, and ranges in age between the Late Jurassic and the Early Cretaceous (Paparella *et al.* 2016; Serafini *et al.* 2020). The Jurassic record includes fragmentary bones and two partial specimens from the Rosso Ammonitico Veronese Formation (Upper Jurassic of Western Alps) (Serafini *et al.* 2020), and the holotype of *Gengasaurus nicosiai* Paparella, Maxwell, Cipriani, Roncacè & Caldwell, 2016 from the upper Kimmeridgian-lower Tithonian of the Central Apennines near Genga (Ancona Province) (Fastelli & Nicosia 1980; Paparella *et al.* 2016).

TABLE 1. — List and description of the ichthyosaur remains from Northern Italy with relative locality and geological units of discovery.

Taxon	Material	Accession number	Repository	Locality	Province	Unit	Reference
Ichthyosauria indet.	Articulated series of nine caudal centra	001-Pad	Storehouse authorized, Neviano degli Arduini Municipality, Parma	Paderna (Neviano degli Arduini)	Parma	Argille Varicolori della Val Samoggia	This work
"*Platypterygius* sp."	Anterior part of rostrum (premaxillae, dentaries). 34 teeth	251372	Museum "Augusta Redorici Roffi", Vignola	Gombola (Polinago)	Modena	Complesso di Rio Cargnone	Serafini *et al.* 2017
	Anterior part of rostrum (premaxillae, nasals, dentaries). 15 teeth	IPUM 30139	Paleontological Museum of Modena and Reggio Emilia University	Gombola (Polinago)	Modena	Complesso di Rio Cargnone	Fornaciari *et al.* 2017
	Anterior part of rostrum (premaxillae, nasals, dentaries). 21 teeth	IPUM 30140	Paleontological Museum of Modena and Reggio Emilia University	Gombola (Polinago)	Modena	Complesso di Rio Cargnone	Sirotti & Papazzoni 2002
	Distal part of a left humerus	IPUM 30141	Paleontological Museum of Modena and Reggio Emilia University	Gombola (Polinago)	Modena	Complesso di Rio Cargnone	Sirotti & Papazzoni 2002
	Two caudal centra	–	Museum "Augusta Redorici Roffi", Vignola	Prignano	Modena	Complesso di Rio Cargnone	Sirotti & Papazzoni 2002
Ichthyosauria indet.	Articulated series of nine caudal centra	11814	Paleontological Museum of Modena and Reggio Emilia University	Pavullo	Modena	Argille varicolori di Cassio	Serafini *et al.* 2019
"*Ichtyosaururus* sp."	Anterior part of rostrum (premaxillae, maxillae, nasals, lacrimal, vomera, palatines, pterygoids, dentary). 14 teeth	8845/IRE8	Geological Museum "Giovanni Cappellini", Bologna	Olmo (Porretta Terme)	Bologna	Argilliti variegate	Sirotti & Papazzoni 2002
"*Platypterygius* sp."	Premaxillae. One tooth	–	Museum "Augusta Redorici Roffi", Vignola	Monteveglio (Bazzano)	Bologna	Argille Varicolori della Val Samoggia	Sirotti & Papazzoni 2002
Ichthyosauria indet.	Anterior part of rostrum (premaxillae, nasals, vomera, dentary, splenial). 20 teeth	IGVR 94574	Geopaleontological Museum of Camposilvano, Velo Veronese, Verona	Tregnano	Verona	Maiolica	Fornaciari *et al.* 2017

The Cretaceous ichthyosaur record is almost uniquely limited to the Northern Apennines and is composed of several fragmentary and often isolated bones from chaotic deep-marine deposits (Table 1; Sirotti & Papazzoni 2002; Fornaciari *et al.* 2017; Serafini *et al.* 2017, 2019). The first specimens found were collected during the Nineteenth Century in the provinces of Modena and Bologna (Pantanelli 1889; Sirotti & Papazzoni 2002; Serafini *et al.* 2017, 2019). Three fragments of rostra, one humerus and a few isolated vertebrae have been recovered near Gombola, Pavullo and Prignano villages (Modena Province) (Sirotti & Papazzoni 2002; Serafini *et al.* 2017, 2019). One fragmentary rostrum and isolated teeth, largely embedded in a sandstone layer, were collected near Porretta Terme village (Bologna Province) (Sirotti & Papazzoni 2002). The anterior part of a rostrum was discovered near Monteveglio (Bologna Province) (Sirotti & Papazzoni 2002). More recently, a semi-articulated series of purported ichthyosaurian vertebrae was reported from the "Argille Varicolori" near Pavullo (Modena Province; Serafini *et al.* 2019). Although the ichthyosaur material from the Cretaceous of the Apennine chain so far mentioned was reported among the youngest records of the clade worldwide (Bardet 1992), the stratigraphic resolution of the specimens collected from the chaotic deep-marine deposits was not constrained accurately along the Aptian-Cenomanian interval (Sirotti & Papazzoni 2002).

Recently, a fragmentary ichthyosaur rostrum was collected from the Lessini Mountains (Veneto Region; Fornaciari *et al.* 2017). The specimen, which is referred to Platypterygiinae based on the dental morphology, is the first Cretaceous ichthyosaur from Italy which has been accurately dated biostratigraphycally: on the basis of the associated microfossils, the reptile is referred to the basal part of the upper Albian (Fornaciari *et al.* 2017).

During the last decades, an increasing number of ichthyosaur, mosasaur and plesiosaur remains has been recovered in Cretaceous deposits from the Northern Apennine chain (Italy) (Renesto 1993; Sirotti & Papazzoni 2002; Fanti *et al.* 2014; Serafini *et al.* 2019). The ichthyosaur fossils consist of fragmentary rostra, teeth and vertebrae, variably dated along a *c.* 35 Myr long interval ranging between the Aptian and the Cenomanian (Sirotti & Papazzoni 2002). In this study, we describe an associated series of large-sized ichthyosaur vertebrae collected from the Emilian Apennine chain. The aim of this study is the description of the fossil, its systematic interpretation and biostratigraphic dating of the specimen based on the analysis of the associated calcareous nannoplankton.

The discovery of ichthyosaurian material here presented took place during the field surveys of "Inter Amnes: archeology between Enza, Parma and Baganza rivers" Project as part of S.F.E.R.A. Programme, provided by DUSIC - Department

University of Parma for the archeological studies in Emilia Romagna region. The project aims to analyze, for the first time in an extensive way, the ancient settlement patterns in the Apennines context by acquiring new data from survey campaigns (Morigi *et al.* 2020). In the study area the project has developed five survey campaigns (2016-2020). The project's multidisciplinary approach has led to the recovery of a number of Ichthyosaurs vertebrae, surfaced during ploughing works in summer 2020 on the western bank of a minor river called Termina, near the village of Paderna (Neviano degli Arduini, Province of Parma).

The material is guarded for now, as all Inter Amnes's exhibits, in the Project's storehouse authorized by local offices of Ministry of Culture, located in Neviano degli Arduini Municipality (Parma) under the accession number 001-Pad.

In this framework, data output from the fossil material found have been acquired and managed on project GIS platform to provide a reference model for further interpretation, under a diachronic point of view, using geo-archeological and landscape archeology methods.

GEOLOGICAL SETTING

The Apennines is an orogenetic chain characterized by the tectonic stacking of several geological units which derived from different paleogeographic domains (Fig. 1A; i.e., the Tuscan-Umbrian, Subligurian and Ligurian domains, the latter divided into Internal and External units; Elter *et al.* 2003; Remitti *et al.* 2011; Conti *et al.* 2020). The area of study is placed into the External Ligurian domain in the western part of Northern Apennines (Fig. 1B; Cerrina Ferroni *et al.* 2002). The Ligurian units are the remnants of a submarine accretionary prism developed during the subduction of the Western Tethys oceanic crust (known as Ligure-Piemontese Ocean) and its sedimentary cover during the Late Cretaceous to Early-Middle Eocene interval (the "Ligurian phase"; Carmignani *et al.* 2001). From the Oligocene, the collision between African and European continental plates caused overthrusting of the frontal part of the Ligurian accretionary prism onto the eastern African margin (known as "Adria foreland") (Carmignani *et al.* 2001). This second phase is recorded in the Epiligurian stratigraphic succession above the Ligurian units (Fig. 1B; Piazza *et al.* 2016).

Placed at the base of the Ligurid succession, the "Chaotic Complex" unit (also called "*Complessi di Base*" or "*Argille scagliose*"; Cowan & Pini 2001; Vannucchi & Bettelli 2010) is formed by thick chaotic units which represent a polygenetic product of the Early Cretaceous to Oligocene orogenetic evolution (Cowan & Pini 2001). At mesoscopic scale, these rocks show a scaliness and chaotic assemblage of blocky components (mainly limestone and sandstone) embedded within the matrix (Bettelli *et al.* 2002; Cerrina Ferroni *et al.* 2002; Vannucchi & Bettelli 2010; Festa *et al.* 2020). Above the "Chaotic Complex" units, the pelagic succession is formed by thick deposits of siliceous-carbonate turbidites (Fig. 1B; "*Flysch di Monte Caio*" and "*Flysch di Monte Cassio*" Formations of the Upper Cretaceous) and a marly-carbonate succession of Paleocene-Eocene age (Fig. 1B; "*Marne Rosate di Bersatico*" Formation; Cerrina Ferroni *et al.* 2002).

All Northern Apennines ichthyosaur specimens were found in the "Chaotic Complex", in particular into the varicoloured shales called "*Argille varicolori di Cassio*" (AVV),"*Argille varicolori della Val Samoggia*" (AVS) and "*Argille variegate*" Formations (Botti *et al.* 2002; Cerrina Ferroni *et al.* 2002; Papani *et al.* 2002; Sirotti & Papazzoni 2002; Bettelli *et al.* 2002). In the area of study, the AVS appears in the tectonic window below the Ligurian units along unclear contacts with other sedimentary successions of the Cretaceous-Paleocene age (Catanzariti *et al.* 2002). The fossil described here was recovered in the AVS Formation (Fig. 1B; De Nardo & Fornaciari 1992; De Nardo 1994). Other chaotic shale deposits exposed in the studied locality are the "*Argille di Lupazzano*" (ALU) and "*Argille di Signano*" (SIG) (Fig. 1B).

SEDIMENTOLOGICAL AND STRATIGRAPHIC FEATURES

The "*Argille varicolori della Val Samoggia*" Formation (AVS) consists of strongly deformed rocks which resulted from intense disruption of the original stratigraphic and sedimentological features (De Nardo & Fornaciari 1992; De Nardo 1994; Panini *et al.* 2001; Cerrina Ferroni *et al.* 2002). At mesoscale observation, the AVS represents a composite unit derived mainly from tectonic processes with the local contribution of sedimentary processes (Panini *et al.* 2001; Cerrina Ferroni *et al.* 2002). These rocks are mainly formed by red, gray, green and blackish shales. In certain portions of the horizons, the structural fabrics appear to be pervasively filled by pluridecimetric-scale "boudins" of fine-grained sandstones (De Nardo & Fornaciari 1992; De Nardo 1994). It is supposed that the AVS originated from coherent well-bedded stratigraphic successions made of varicolored clay and marl, alternating with limestone, sandstone and siltstone in decimeter-thick beds (Panini *et al.* 2001), which is interpreted as representing a hemipelagic paleoenvironment affected by limited terrigenous sedimentation inputs (Panini *et al.* 2001, 2002). Inside the AVS, a pelitic-arenaceous lithofacies made up of blackish and gray clays interspersed with micritic and arenaceous limestone layers is recognised (AVSa, "*Argille a palombini*" in De Nardo & Fornaciari 1992; Cerrina Ferroni *et al.* 2002; Papani *et al.* 2002). Biostratigraphic data support an age ranging between the Hauterivian and the Cenomanian for the AVS (De Nardo 1994; Cerrina Ferroni *et al.* 2002; Catanzariti *et al.* 2002; Papani *et al.* 2002).

MATERIAL AND METHODS

The vertebral centra were measured following Kolb & Sander (2009). The main morphometric ratios were compared with other ichthyosaurs. Anatomical terminology follows Fischer *et al.* (2011).

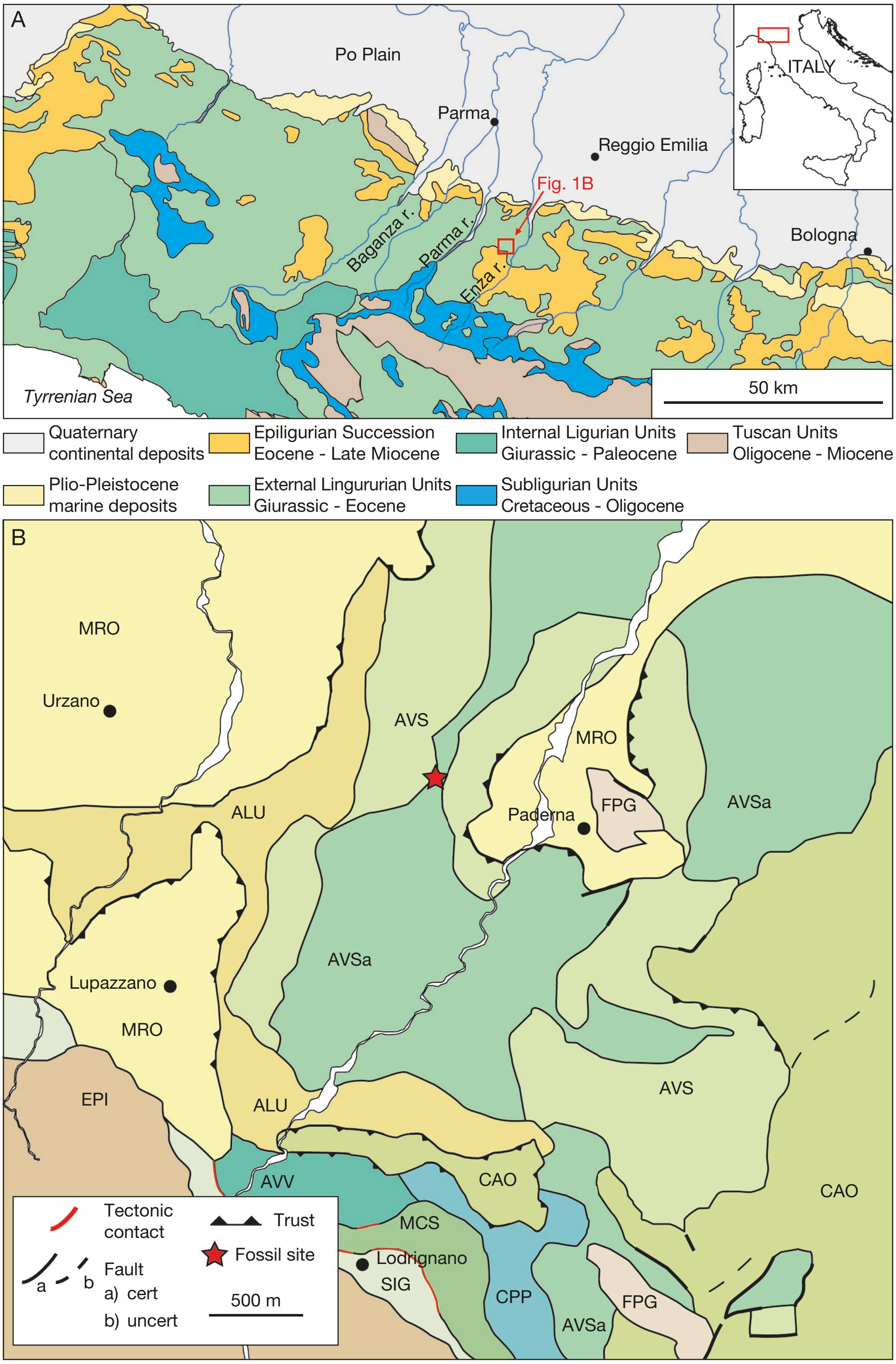

FIG. 1. — **A**, Schematic geological map of the Northern Apennines; **B**, simplified geological map of the study area; Samoggia Tectonic Unit: **ALU**, *"Argille di Lupazzano"* Formation; **AVS**,*"Argille Varicolori della Val Samoggia"* Formation; **AVSa**, "*Argille Varicolori della Val Samoggia*" pelitic-arenaceous lithofacies; **FPG**, *"Poggio"* Formation; *"Groppallo"* Unit: *"Pietra Parcellara"* Complex; *"Cassio"* Tectonic Unit: **AVV**, *"Argille Varicolori di Cassio"* Formation; **MCS**, *"Flysch di Monte Cassio"* Formation; **SIG**, *"Argille di Signano"* Formation; *"Caio"* Tectonic Unit: **CAO**, *"Flysch di Monte Caio"* Formation; **MRO**, *"Marne Rosate di Tizzano"* Formations: MRO; **EPI**, Epiligurian Succession. Credits: A, map modified after Remitti *et al.* 2011 and Piazza *et al.* 2016; B, modified after Cerrina Feroni *et al.* 2002 and Papani *et al.* 2002

We collected 11 rock samples that were tested for calcareous nannofossil analyses in order to provide a reliable age for the ichthyosaur vertebrae and the relative deposit. The sampling was carried out along an exposed sedimentary interval collocated a few meters from the fossil. Due to the complex chaotic frame of the varicolored shales, it was not possible to deduce the real thickness of the section which presumably appears to be about ten meters. The deposits are mainly formed by gray-green scaliness shales with decimetric levels of red or black shales (De Nardo 1994; De Nardo & Fornaciari 1992). The end of the sequence was placed at a calcareous level presumably belonging to a metric block immersed in the chaotic shale matrix.

Abbreviations

Institution

PAD	Paderna collection, Neviano degli Arduini Municipality Archive, Neviano degli Arduini, Parma Province.

Preservation degree

G	good;
M	moderate;
P	poor;
VG	very good.

Abundance

A	abundant;
B	barren;
C	common;
F	few;
R	rare;
V	very abundant.

Others

ALU	"*Argille di Lupazzano*";
AVS	"*Argille varicolori della Val Samoggia*" Formation;
CH	centrum height;
CL	centrum length;
CW	centrum width;
HO	highest occurrence;
LO	lower occurrence;
SIG	"*Argille di Signano*'".

CALCAREOUS NANNOFOSSIL BIOSTRATIGRAPHIC ANALYSES

Semi-quantitative analysis of 12 samples, derived from the stratigraphic section and the sedimentary matrix encrusting the vertebrate material (PAD 10) was performed for calcareous nannofossil determination (Figs 2; 3). Smear slides were prepared from unprocessed sediments according to the standard techniques (Backman & Shackleton 1983; Rio *et al.* 1990). The distribution pattern of selected calcareous nannofossil taxa was obtained from light microscope analysis under crossed polarizers, transmitted light, and phase contrast light at 1250× magnification.

In order to characterize the calcareous nannofossil record, we adopted four preservation and six abundance classes for each species (Tables 2; 3). Preservation degree: very good (VG) – no evidence of dissolution and/or overgrowth, no alteration of the primary morphological characteristics, the specimens appearing diaphanous; the specimens are identifiable to the species level; good (G) – little or no evidence of dissolution and/or overgrowth, the primary morphological characteristics are only slightly altered; the specimens are identifiable to the species level; moderate (M) – the specimens exhibiting some etching and/or overgrowth, the primary morphological characteristics are sometimes altered; however, most specimens are identifiable to the species level; poor (P) – the specimens are severely etched or exhibiting overgrowth, the primary morphological characteristics are largely destroyed, fragmentation had occurred; the specimens cannot be identified at the species and/or generic level. Abundance: very abundant (V) – 11 to 100 specimens for field of view; abundant (A) – 1 to 10 specimens for field of view; common (C) – 1 specimen for 2-10 fields of view; few (F) – 1 specimen for 11-100 fields of view; rare (R) –1 specimen for 101-1000 fields of view; barren (B) = no specimens detected.

Calcareous nannofossil species considered in this paper are listed in the range chart, where they are arranged alphabetically by generic epithet. Bibliographic references for these taxa can be found in Perch-Nielsen (1985) and Bown (1998) and Nannotax web site (https://www.mikrotax.org/Nannotax3/).

SYSTEMATIC PALEONTOLOGY

Order ICHTHYOSAURIA de Blainville, 1835

Ichthyosauria gen. et sp. indet.
(Fig. 4)

Material. — 001-Pad1, 001-Pad2, 001-Pad3, 001-Pad4, 001-Pad5: nine articulated anterior caudal centra and an isolated centrum fragment.

Locality and horizon. — Paderna (Neviano degli Arduini municipality, Parma Province), Termina valley; "*Argille Varicolori della Val Samoggia*" Formation (AVS); lower Aptian (this study).

Description

The specimen is represented by a series of vertebral centra ranging 32-38 mm in length and 91-97 mm in both width and height (Fig. 4). No neural arches or ribs were found in association with the centra. The centra are very closely spaced (i.e., only a relatively thin fine-sediment matrix fills the intervertebral space) and aligned along their anteroposterior axes, a pattern which likely represents their original anatomical connection. The centra are divided into two blocks. The largest block (30 cm long) contains six centra and is crossed by a fracture. The first centrum is the most fragmentary, preserving only the right dorsal part of the bone, while the others are almost complete. The second block (15 cm long) is composed of three centra, one of which is missing its left ventral part. A single incomplete centrum was found in the same area but isolated from the two blocks. All centra appear slightly tilted to one side and

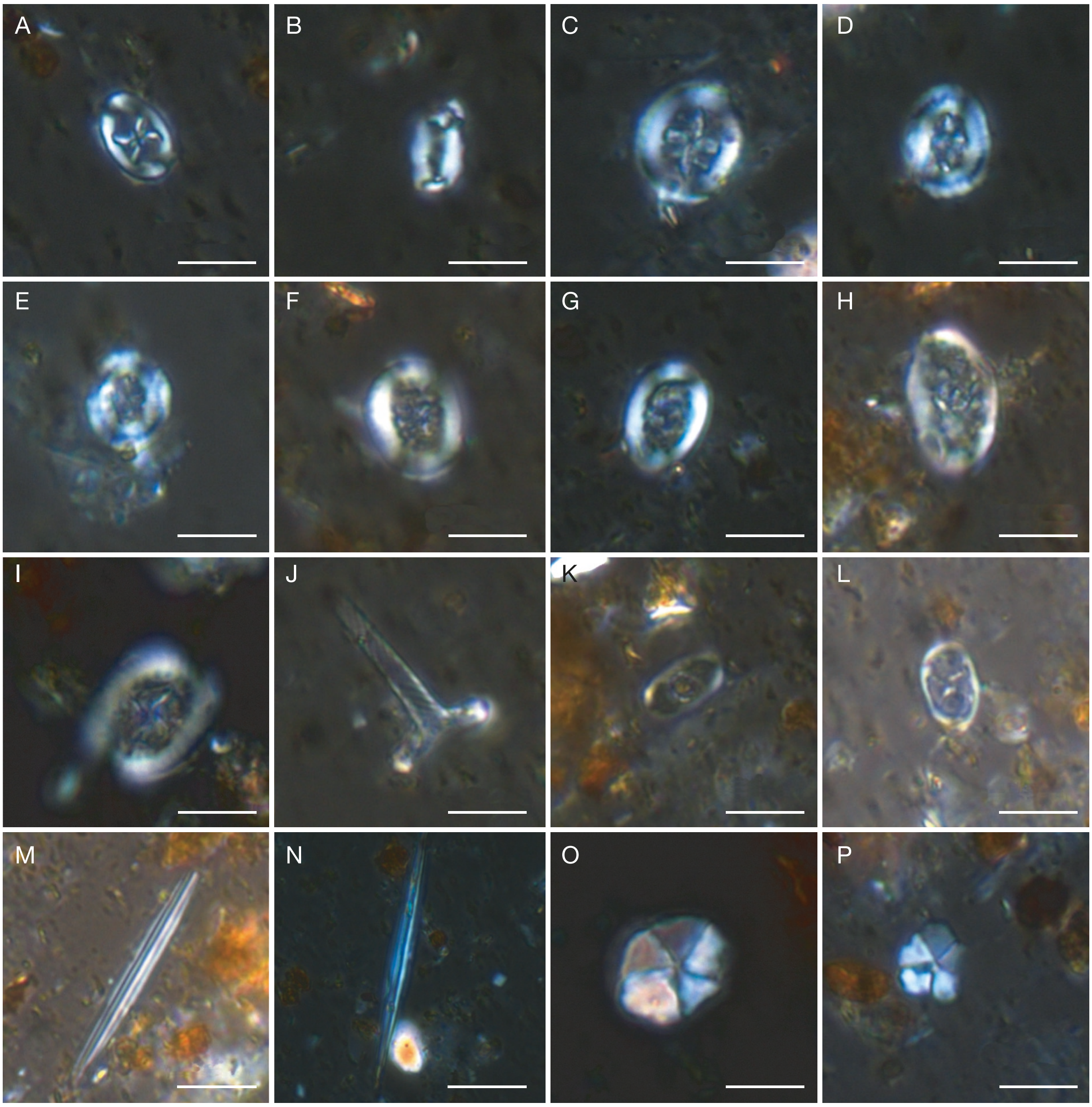

FIG. 2. — Photomicrographs of selected calcareous nannofossil taxa from the vertebrae sample; the photos are at crossed nicols and at 1250× magnification: **A**, *Eiffellithus striatus* (Black, 1971) Applegate & Bergen, 1988; **B**, *Rhagodiscus angustus* (Stradner, 1963) Reinhardt, 1971; **C**-**E**, *Helenea chiastia* Worsley, 1971; **F**-**H**, *Cretarhabdus conicus* Bramlette & Martini, 1964; **I**, **J**, *Rhagodiscus splendens* (Deflandre, 1953) Verbeek, 1977; **K**, *Zeugrhabdotus noeliae* Rood, Hay & Barnard 1971; **L**, *Chiastozygus tenuis* Black, 1971; **M**, **N**, *Lithraphidites carniolensis* Deflandre, 1963; **O**, *Micrantholithus imbricatus* (Manivit, 1966) Varol & Bowman, 2019; **P**, *Braarudosphaera regularis* Black, 1973. Scale bars: 5 µm.

shifted relative to each other. The left surfaces of the centra are better preserved than their right counterparts, a preservation artifact which might indicate that the vertebrae were partially exposed and suffered some degree of erosion prior to their discovery. As a consequence, only the left apophyses are preserved. The centra are anteroposteriorly short, displaying a distinct amphicoelous appearance. A synapophysis is present and placed in the lateroventral surface. Most centra show a distinct suture for the neurocentral pedicels on their dorsal surface, crossed longitudinally by the floor of the neural canal. The neurocentral pedicel facets appear narrower and longer in the anterior vertebrae and become more oval in the posterior ones. No subcentral foramina or haemal arch facets are present. The centrum height (CH), centrum length (CL) and centrum width (CW) of the vertebrae decrease moderately along the anteroposterior direction of the articulated series (Fig. 4; Table 3). The general shape of the articular surfaces is subcircular with the height to width ratio (CH/CW) around *c.* 0.9 in all centra. The vertebrae are much shorter in length than dorsoventrally tall, with a CH/CL ratio ranging between 2.6 and 2.9.

We report three small elongate and sub-cylindrical elements, about 5 mm in diameter each, found inside the sedimentary matrix infilling the intervertebral space between two consecutive

Table 2. — Nannofossil vertical distribution along the measured section. Abbreviations: CaCO3 concentration: **h**, high; **s**, scarce; **a**, absent; abundance of nannofossils: **A**, abundant, 1 to 10 specimens per field of view; **C**, common, 1 specimen per 2-10 fields of view; **F**, few, 1 specimen per 11–100 fields of view; **R**, rare, 1 specimen per 101–1000 fields of view; preservation degree: **G**, good; **M**, moderate; **P**, poor (see the text for further clarification).

sample	m	preservation	[CaCO3]	*Assipetra terebrodentarius*	*Braarudosphaera regularis*	*Chiastozygus tenuis*	*Cretarhabdus conicus*	*Cyclagelosphaera margerelii*	*Eiffellithus striatus*	*Helenea chiastia*	*Lithraphidites carniolensis*	*Micrantholithus hoschulzii*	*Micrantholithus imbricatus*	*Micrantholithus obtusus*	*Nannoconus kamptneri*	*Nannoconus pseudoseptentrionalis*	*Nannoconus sp.*	*Nannoconus steinmannii*	*Retecapsa angustiforata*	*Rhagodiscus angustus*	*Rhagodiscus asper*	*Rhagodiscus splendens*	*Staurolithites mutterlosei*	*Watznaueria barnesiae*	*Watznaueria britannica*	*Zeugrhabdotus diplogrammus*	*Zeugrhabdotus embergeri*	*Zeugrhabdotus noeliae*	*Zeugrhabdotus scutula*
PAD11	9.4	G	h	F	–	–	–	C	–	R	F	C	–	R	C	C	C	C	F	R	F	F	R	A	R	C	F	F	–
PAD09	8.5	P	a	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
PAD08	7.3	P	a	–	–	–	–	–	–	–	F	–	–	–	–	–	–	–	–	–	R	–	–	C	F	–	–	–	–
PAD07	6.35	P	a	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
PAD06	5.15	P	a	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
PAD05	4.7	P	a	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
PAD04	3.85	P	a	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
PAD10 VERTEBRAE	3.5	M	s	F	R	R	R	–	F	F	F	F	F	F	F	–	F	R	R	F	F	–	F	A	C	C	F	–	R
PAD03	2.8	P	a	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
PAD02	2.45	P	a	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
PAD01	2.05	P	a	–	–	–	–	–	R	R	–	–	–	–	–	–	–	–	–	–	R	–	–	R	R	–	–	–	–
PAD00	1.1	P	a	–	–	–	–	–	–	–	–	–	–	R	–	–	–	–	–	–	–	–	–	C	R	–	R	–	–

Table 3. — Measurements of vertebral elements (mm) of the Paderna specimen. Abbreviations: **CH**, centrum height; **CL**, centrum length; **CW**, centrum width.

Specimen	Number	Vertebrae	CH (mm)	CL (mm)	CW (mm)	CH/CL	CH/CW
PAD1	V01*	47?	–	38.47	–	–	–
PAD2	V02	48?	97.48	37.63	97.11	2.59	1.00
PAD2	V03	49?	94.08	32.11	96.99	2.93	0.97
PAD2	V04*	50?	96.87	36.74	96.94	2.64	0.99
PAD3	V05	52?	93.14	35.57	96.70	2.88	0.96
PAD3	V06	53?	92.36	32.03	96.73	2.88	0.96
PAD4	V07	54?	–	–	–	–	–
PAD5	V08	55?	91.57	32.26	93.12	2.84	0.98
PAD5	V09	56?	90.69	33.29	91.99	2.72	0.99
PAD5	V10*	57?	85.00	29.32	93.32	2.90	0.91

vertebral centra (Fig. 5). These structures are oriented radially relative to the center of the adjacent intervertebral facet (Fig. 5A), and distally they reach the rim of the intercentral facet. Internally, each structure appears as a sedimentary infilling (Fig. 5B). We suggest that these elements are biological in origin, and interpret them as ichnological traces left by a limnivorous/saprophagous invertebrate.

RESULTS

Biostratigraphic analysis

The calcareous nannofossils biostratigraphic analyses carried out on 11 samples showed a scarcity of calcium carbonate content and consequently of calcareous nannofossils (). Only four of the studied samples were found to be Figs 2; 3; Table 2 fossiliferous or scarcely fossiliferous. Among them, the sample PAD 10 (i.e., the one sampled from the vertebrae) contains a paleontological assemblage that can be traced back precisely to the Aptian stage (126-113 Ma).

A possible correspondence of the calcareous nannofossils assemblage taken from the PAD 10 sample (which includes the vertebrae) and the PAD 11 sample would suggest a provenance of the studied ichthyosaur fossil from the calcareous level. Nevertheless, the absence in the other rock samples of some biostratigraphic markers does not allow us to confidently confirm such correspondence. Given the lack of direct stratigraphic correlation, even if there is some biostratigraphic compatibility, we proceeded to evaluate the relative age only on the sediment directly sampled from the vertebrae (PAD 10). The micropaleontological assemblage found includes 21 species mainly distributed in the Lower

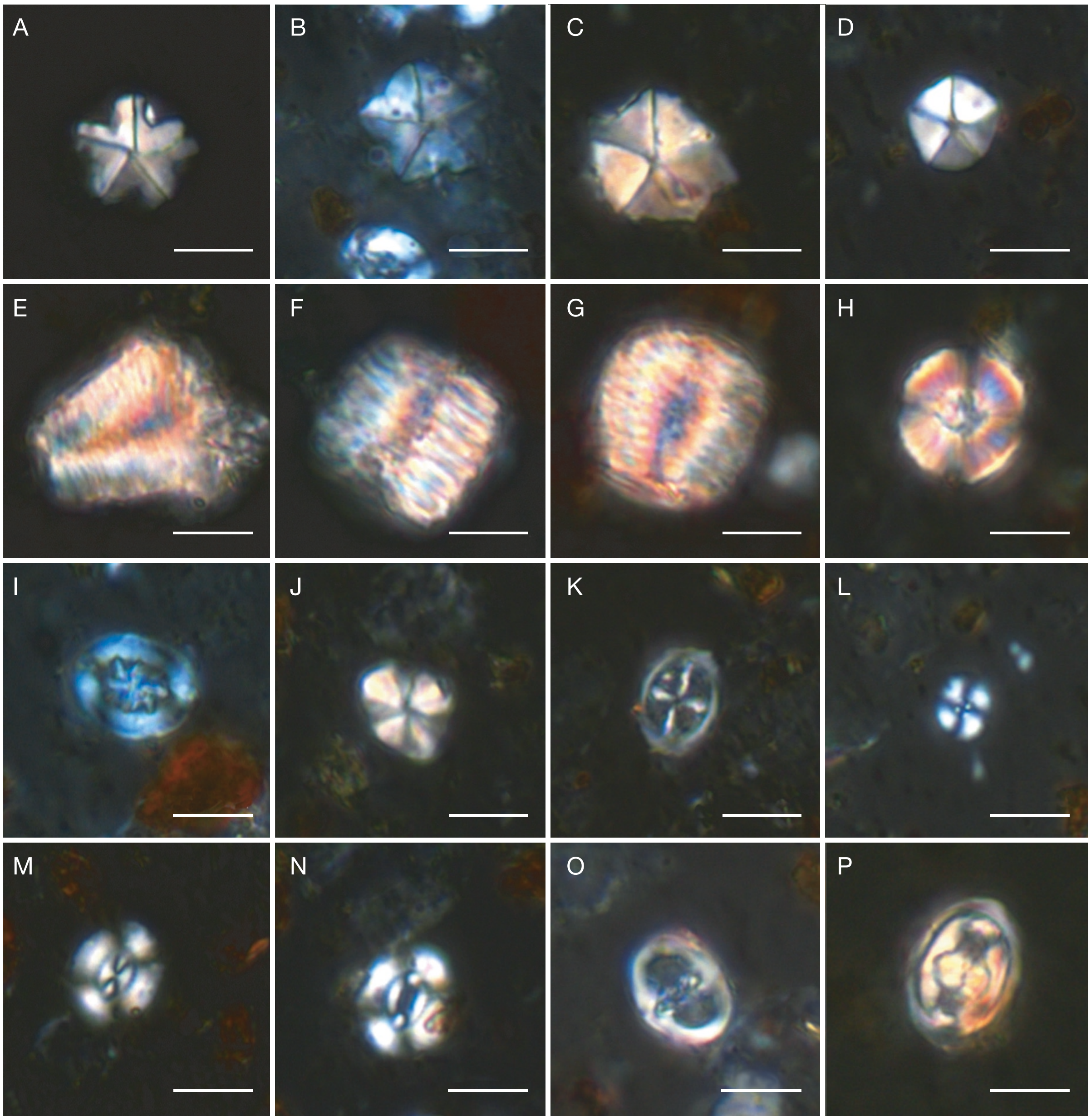

Fig. 3. — Photomicrographs of selected calcareous nannofossil taxa from the samples; the photos are at crossed nicols and at 1250x magnification: **A**, **B**, *Micrantholithus obtusus* Stradner, 1963, sample vertebrae; **C**, **D**, *Micrantholithus hoschulzii* (Reinhardt, 1966) Thierstein, 1971, sample vertebrae; **E**, *Nannoconus kamptneri* Brönnimann, 1955, sample vertebrae; **F**, **G**, *Nannoconus truittii* Brönnimann, 1955, sample vertebrae; **H**, *Nannoconus* sp., sample vertebrae; **I**, *Retecapsa angustiforata* Black, 1971, sample vertebrae; **J**, *Assipetra terebrodentarius* (= *Rucinolithus terebrodentarius*) Applegate, Bralower, Covington & Wise *in* Covington & Wise, 1987, sample vertebrae; **K**, *Staurolithites mutterlosei* Crux, 1989, sample vertebrae; **L**, *Cyclagelosphaera margerelii* Noël, 1965, PAD11 sample; **M**, *Watznaueria barnesiae* (Black *in* Black & Barnes, 1959) Perch-Nielsen, 1968, sample vertebrae; **N**, *Watznaueria britannica* (Stradner, 1963) Reinhardt, 1964, sample vertebrae; **O**, *Zeugrhabdotus diplogrammus* Deflandre *in* Deflandre & Fert, 1954, sample vertebrae; **P**, *Zeugrhabdotus embergeri* (Noël, 1959) Perch-Nielsen, 1984, sample vertebrae. Scale bars: 5μm.

Cretaceous. Among these, *Braarudosphaera regularis* Black, 1973, *Rhagodiscus angustus* (Stradner, 1963) Reinhardt, 1971, and *Rhagodiscus splendens* (Deflandre, 1953) Verbeek, 1977, have a lower occurrence (LO) at the base of the Aptian, and thus demarcate the maximum age of the studied fossil. All the other species listed have a distribution range compatible, albeit not limited, with the Aptian. In particular, two species, *Micrantholithus hoschultzii* (Reinhardt, 1966) Thierstein, 1971 and *M. obtusus* Stradner, 1963, have a limited distribution range with highest occurrence (HO) at, respectively, the end of the Aptian, and the lower Aptian. This last limit further constrains the age of the ichthyosaur fossil from Paderna between 126 and 122 Ma.

Discussion

The material is unambiguously interpreted as a series of ichthyosaur caudal vertebrae based on the combination of strongly anteroposteriorly compressed centra with distinct amphicoelous articular facets, and presence of a synapophysis projected lateroventrally (McGowan & Motani 2003; Kolb &

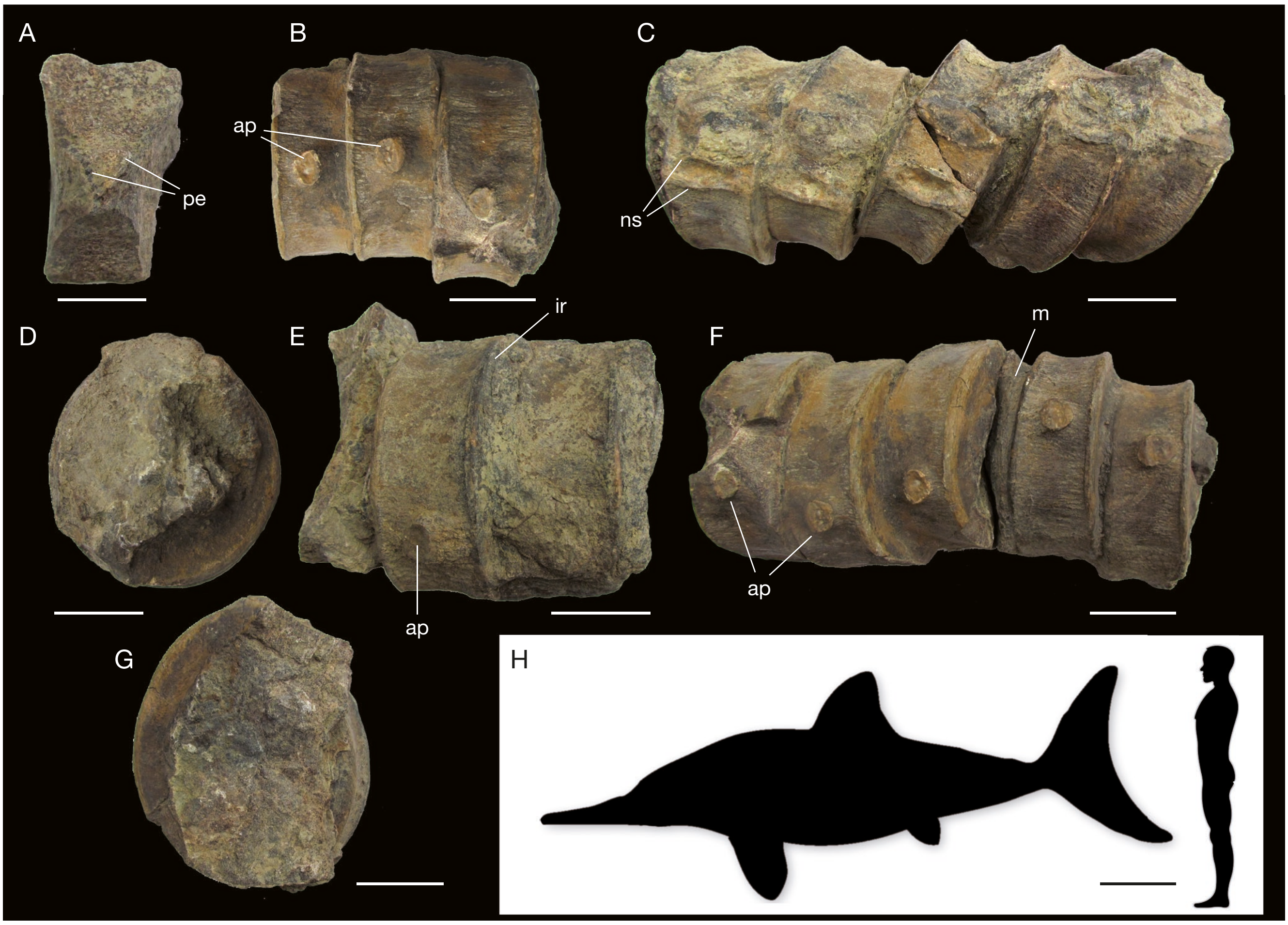

Fig. 4. — Caudal vertebrae 001-Pad2, 3 and 5 and hypothetical total body size of the Paderna ichthyosaur: **A**, the internal section of one of the centra showing the typical distinct amphicoelous appearance; **B**, **E**, 001-Pad5, the block containing most posterior three centra, in left lateral view (**B**) and dorsal view (**E**); **C**, **F**, 001-Pad2-3, the longest and proximal block containing five centra in anatomical connection in left lateral view (**C**) and in dorsal view (**F**), crossed by a fracture; **D**, **G**, anterior (**D**) and posterior (**G**) views of the centra; **H**, generalized thunnosaurian body silhouette showing the approximate body size of the animal compatible with the Paderna vertebrae (see McGowan & Motani 2003: fig. 68G). Abbreviations: **ap**, apophysis; **ir**, intercentral facet rim; **m**, sediment matrix; **ns**, neuroapophysis pedicel facet scar; **pe**, eroded margin of periosteum. Scale bars: A-G, 5 cm; H, 50 cm.

Sander 2009). Although the very limited amount of material makes any accurate placement of the described vertebrae along the caudal series tentative, the width to height ratio of the centra consistently close to one and the very moderate variation of the centrum length along the preserved series might indicate a position in the preflexural part of the tail, in agreement to other Upper Jurassic and Early Cretaceous ichthyosaurs (e.g. Paparella *et al.* 2016). The vertebrae from Paderna are in overall size larger than two ichthyosaur caudal centra from Cretaceous strata in Prignano (Modena Province, Sirotti & Papazzoni 2002). Yet, such size and proportional differences are likely affected by the ontogenetic status of the specimens (which is currently unknown) and by the position of the centra along the tail, and thus cannot be considered as taxonomically significant.

Due to the very limited phylogenetic informativeness of the preflexural caudal centra among the ichthyosaurs, only a very cursory comparison between the Paderna specimen and Late Jurassic to Early Cretaceous ichthyosaur taxa is possible. Both in size and in overall proportions, the caudal centra from Paderna are broadly similar to those of most thunnosaurians (e.g. Massare *et al.* 2006; Kolb & Sander 2009; Druckenmiller & Maxwell 2010; Maxwell & Kear 2010; Zammit *et al.* 2010; Fischer *et al.* 2011, 2012, 2013b, 2014, 2016; Delsett *et al.* 2017).

In conclusion, although both size and overall proportions of the Paderna material closely resemble those of penecontemporary ophthalmosauridth taxa, the lack of synapomorphies in the preserved vertebrae prevents the unambiguous referral of the new specimen to any clade less inclusive than Ichthyosauria.

The Paderna material is particularly significant as it provides the first accurate biostratigraphic placement for a Cretaceous ichthyosaur from the Apennine Chain (e.g. Bardet 1992; Sirotti & Papazzoni 2002; Fischer *et al.* 2011, 2012, 2016). Previous studies assumed a Cenomanian age for the ichthyosaur remains from the Northern Apennine (e.g. Bardet 1992; and references therein), and thus included the material from Emilia among the youngest records of this clade worldwide. A more conservative, but poorly constrained, Albian-Turonian

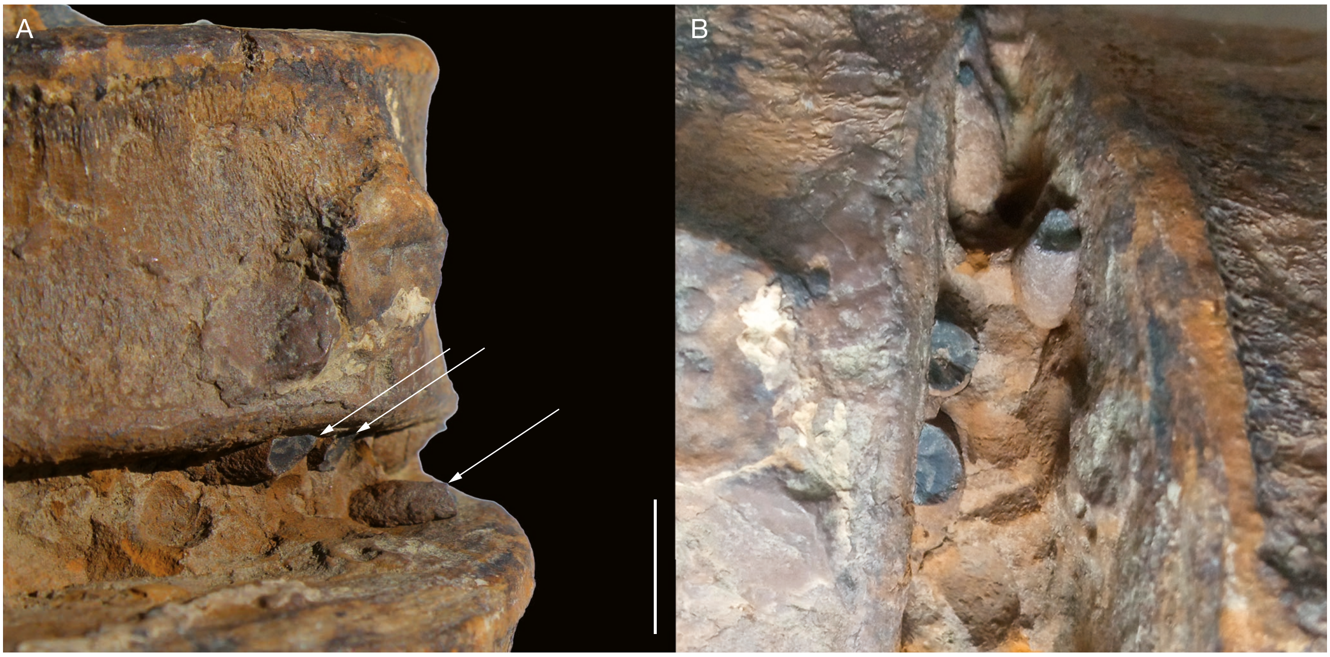

Fig. 5. — Small elongate and sub-cylindrical elements found inside the sedimentary matrix infilling the intervertebral space. **Arrows** indicate eroded tip of three elements. Scale bar: 20 mm.

age range was suggested by Sirotti & Papazzoni (2002) which was based merely on the age of the lithological units: these authors remarked the absence of any fossil index associated with the ichthyosaur material from Bologna and Modena provinces. The early Aptian age inferred for the Paderna material is significantly older than any age previously suggested for the Cretaceous ichthyosaurs from Italy and is about 15-20 Myr older than the ichthyosaur rostrum from the Lessini Mountains (Fornaciari *et al.* 2017).

The worldwide record of Ichthyosauria in the Aptian is rather poor, probably because of sampling bias, with only a handful of diagnostic ichthyosaurs recovered from that stage (Fischer *et al.* 2013a, 2014). The discovery of new material - and the identification of any novel fossil-bearing locality – dated to the Aptian is thus particularly significant for improving the knowledge of this phase of the icththyosaurian history. From a regional (i.e., Ligurian/western Tethys) perspective, it is noteworthy that the Paderna reptile is penecontemporary to the thalattosuchian crocodylomorph material from western Sicily recently found (Chiarenza *et al.* 2015), being both dated to the NC6 zone of the early Aptian according to the associated nannoplancton assemblages. The occurrence of large-bodied ichthyosaurs (this study) and metriorhynchids (Chiarenza *et al.* 2015) in the early Aptian supports the persistence in the Western Tethys of the pelagic reptile clades "typical" of the Late Jurassic (Fischer *et al.* 2021; and references therein) up to the middle of the Early Cretaceous (see Chiarenza *et al.* 2015).

Compared to the other fossil reptiles from the Northern Apennine, the preservation of the Paderna specimen is unusual and might indicate peculiar taphonomic conditions. The large majority of the vertebrate material found in the Cretaceous levels from Emilia-Romagna and south-western Lombardy is represented by isolated material (i.e., vertebral centra; e.g. Sirotti & Papazzoni 2002; appendicular elements; e.g. Renesto 1993; Sirotti & Papazzoni 2002), or incomplete segments of the snout including both upper and lower jaw elements tightly connected (e.g. Sirotti 1990; Sirotti & Papazzoni 2002; Fanti *et al.* 2014). All these specimens have been interpreted as remains of intensely disarticulated skeletons which were subjected to high-energy depositional and tectonical conditions. A notable exception is the specimen from Pavullo, recently described by Serafini *et al.* (2019), which shows a preservational pattern comparable to the Paderna material here described: both specimens differ from all other mentioned records since they include a series of several vertebrae still aligned in their original anatomical connection. Furthermore, the Paderna specimen is the first from the Apennine Chain which includes invertebrate traces directly associated to reptile remains. From a taphonomic perspective, the preservation of the Paderna and Pavullo ichthyosaurs might have required a low-energy depositional and post-depositional pattern (tectonic processes with the local contribution of sedimentary and diapiric processes; see Festa *et al.* 2020) relatively less disruptive than those traditionally suggested for the genesis of the "Chaotic Complex" fossils (e.g. Sirotti & Papazzoni 2002). The majority of the marine reptile finds from these units were not (or could not be) analysed from a taphonomic perspective (i.e., they are surface finds often not associated to any depositional/taphonomic investigation; see review in Sirotti & Papazzoni 2002). This problem is further exacerbated by the perplexing genesis of the different "Chaotic Complex" deposits (Cowan & Pini 2001; Vannucchi & Bettelli 2010).

Thus, for most of these elements it is currently not possible to discriminate between isolated elements due to pre-depositional dissociation from a floating carcass and isolated elements due to post-depositional erosion of previously embedded remains. The "high energy scenario" for the disarticulation of the "Chaotic Complex" reptiles has been usually based on sedimentological and geomorphological analyses at the whole units, and not from a strictly taphonomic investigation of the collected fossils (e.g. Sirotti & Papazzoni 2002). From this perspective, the discovery of an articulated vertebral series (which is also the first being stratigraphically constrained) associated to invertebrate ichnofossils represents a promising step toward a more comprehensive analysis of the genesis of the "Chaotic Complex" fossil record.

CONCLUSIONS

We report ichthyosaur remains from a new fossil locality in the Northern Apennine chain. The material is the northernmost occurrence of this clade in the Apennine orogenetic system. Although based on a limited set of caudal centra which prevents an accurate taxonomic identification of the material, this new specimen is taphonomically and stratigraphically significant. In particular, it indicates that the environmental and depositional conditions at the genesis of the "*Argille Varicolori*" units were more heterogeneous than previously depicted, did not necessarily involve high-energy dynamics at the mesoscale, and might include relatively low-energy settings which allowed the preservation of skeletal remains moderately complete and articulated. The direct association of a complex of index microfossils with the vertebrate material has provided the first unambiguous age determination for a Cretaceous ichthyosaur from Italy and its correlation with the global history of the clade. The early Aptian stage constrained for the Paderna fossils significantly predates any age previously suggested for the ichthyosaurs from the Northern Apennine and the Lessini Mountains. The presence of both ichthyosaurs and thalattosuchians in the early Aptian of Italy supports the persistence of the "Late Jurassic community" of large-bodied pelagic reptiles in the Western Tethys for most of the Early Cretaceous.

Since this paper went to press, Serafini *et al.* (2022) provided the biostratigraphic zonation for an ichthyosaur rostrum from the Northern Appenine chain. The material has been dated to the Albian-Cenomanian interval.

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Authors' contribution

AF, SC and AM conceived and designed the research. AM, FG and FF developed the field surveys and locality mapping. SC, AF, FF and FG collected the geological samples. DP performed the biostratigraphic analyses. SC, AF, DP and AC analyzed the fossil material. AF, SC and DP photographed the material. SC, DP and AC prepared the figures. All authors contributed to the manuscript.

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APPENDIX

Appendix 1. — Calcareous nannofossil appendix.

Assipetra terebrodentarius (Applegate, Bralower, Covington & Wise *in* Covington & Wise, 1987) Rutledge & Bergen *in* Bergen, 1994
Braarudosphaera regularis Black, 1973.
Chiastozygus tenuis Black, 1971.
Cretarhabdus conicus Bramlette & Martini, 1964.
Cyclagelosphaera margerelii Noël, 1965.
Eiffellithus striatus (Black, 1971) Applegate & Bergen, 1988.
Heleneachiastia Worsley, 1971.
Lithraphidite scarniolensis Deflandre, 1963.
Micrantholithus hoschulzii (Reinhardt, 1966) Thierstein, 1971.
Micrantholithus imbricatus (Manivit, 1966) Varol & Bowman, 2019.
Micrantholithus obtusus Stradner, 1963.
Nannoconus kamptneri Brönnimann, 1955.
Nannoconus pseudoseptentrionalis Rutledge & Bown, 1996.
Nannoconus sp.
Nannoconus steinmannii Kamptner, 1931.
Retecapsa angustiforata Black, 1971.
Rhagodiscus angustus (Stradner, 1963) Reinhardt, 1971.
Rhagodiscus asper (Stradner, 1963) Reinhardt, 1967.
Rhagodiscus splendens (Deflandre, 1953) Verbeek, 1977.
Staurolithites mutterlosei Crux, 1989.
Watznaueria barnesiae (Black *in* Black & Barnes, 1959) Perch-Nielsen, 1968.
Watznaueria britannica (Stradner, 1963) Reinhardt, 1964.
Zeugrhabdotus diplogrammus Deflandre *in* Deflandre & Fert, 1954.
Zeugrhabdotus embergeri (Noël, 1959) Perch-Nielsen, 1984.
Zeugrhabdotus noeliae Rood , Hay & Barnard, 1971.
Zeugrhabdotus scutula (Bergen, 1994) Rutledge & Bown, 1996.