

New findings reveal that the Middle Triassic ichthyosaur *Mixosaurus cornalianus* is the oldest amniote with a dorsal fin

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Two excellently preserved specimens of *Mixosaurus cornalianus* from the Anisian layers of the Middle Triassic Formazione di Besano, with soft parts associated with well-articulated skeletal elements, revealed the presence in this species of a dorsal fin and of a well-developed, triangular dorsal lobe of the caudal fin, both stiffened by an array of fibre bundles, as in Jurassic fast-swimming ichthyosaurs. This finding testifies that efficient swimming exaptations were already present in some Middle Triassic ichthyosaurs. *Mixosaurus* is then the oldest amniote so far known that developed a dorsal fin. The preservation of the fin shapes, scaleless skin, and three-dimensional dermal fibres is remarkable, allowing observation of their microstructure, and ruling out any artefactual interpretation. Stomach contents indicate that both specimens preyed upon cephalopods and small fishes. An internal organ, possibly a tract of the intestine, is also preserved in one specimen, which represents the first documented case in the ichthyosaurs of the Besano Formation, and a rarity in the fossil record of the clade.

Key words: Ichthyosauria, Mixosauridae, soft tissue preservation, functional morphology, Mesozoic, Italy.

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Introduction

Ichthyosaurs are among the most abundant fossil reptiles of the UNESCO World Heritage List (WHL) site of the Besano-Monte San Giorgio area (Lombardy, Italy; and Canton Ticino, Switzerland; Fig. 1), which is one of the richest sites of Middle Triassic palaeobiodiversity (e.g., Furrer 2003) even after the new discoveries in China (e.g., Benton et al. 2013). In fact, as in the present case, fossil preservation in some bituminous layers of the Besano Formation (= “Grenzbitumenzone” of Swiss literature) and of the Meride Limestone can reveal soft tissue preservation not found elsewhere in the world.

After the first reports (Curioni 1847), the Museo di Storia Naturale di Milano arranged several excavations in the surroundings of Besano, collecting a large number of fossils across the last two centuries. This historical collection was destroyed during the Second World War, so that, starting from 1975, the MSNM conducted new fieldwork.

The most productive and long-lasting locality (1985–2003) was the “Sasso Caldo” site (Fig. 1), where remarkable material was collected and published (e.g., Dal Sasso and Pinna 1996; Renesto and Avanzini 2002; Nosotti 2007; Renesto 2010; Renesto et al. 2014).

The specimens described herein were found on February 14th 1993, in the eastern corner of the quarry, within layer 63 of the referred series (Middle Besano Formation sensu Bindellini et al. 2019), which is datable as uppermost Anisian. During preparation, soft tissue anatomical structures with remarkable functional significance never seen before in mixosaurian-grade ichthyosaurs were exposed; their description and interpretation is the aim of the present contribution.

Institutional abbreviations.—BES SC, Besano Sasso Caldo locality, Museo di Storia Naturale di Milano, Milano, Italy; MSNM, Museo di Storia Naturale di Milano, Milano, Italy; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany.

Geological setting

The Middle Triassic carbonate succession of Monte San Giorgio consists of four different formations (Fig. 2) deposited in an intra-platform basin within a carbonate platform on the western margin of the Neo-Tethys (Furrer 1995; Röhl et al. 2001; Etter 2002; Stockar et al. 2012). Above the Anisian Salvatore Dolomite lies the 5–16 m thick Besano Formation (Anisian/Ladinian boundary), from which the greatest part of the well-known vertebrate fauna of Monte San Giorgio has been recovered (Bürgin et al. 1989; Furrer 2003). At the top of the Besano Formation is the San Giorgio Dolomite, which, in turn, grades into the well-bedded Ladinian Meride Limestone, that reaches a total thickness of 400–600 m (Furrer 1995). The Meride Limestone is divided in two parts (Wirz 1945), the Lower Meride Limestone, which is 90–150 m thick (Furrer 1995), and consists of finely laminated limestone with intercalated volcanic ash layers and contains three fossiliferous levels (Cava inferiore, Cava superior, and Cassina), each characterized by different vertebrate assemblages (Sander 1989; Bürgin et al. 1989). The overlying Upper Meride Limestone shows alternating well-bedded limestone and marlstone with an increasing clay content towards the top. Strong seasonal variations of salinity and water level are documented along with the influence of freshwater input from a nearby-emerged area. The uppermost part of the Meride Limestone comprises the so-called “Kalkschieferzone”, which is 120 m thick and represents the final phases of evolution of the intraplatform basin, then followed by the Carnian regressive phase (Pizzella Marls).

The Besano Formation consists of an alternation of laminated, bituminous dolomite and bituminous shale, and subordinate cineritic tuff that are dated as late Anisian–early Ladinian (Brack and Rieber 1986, 1993; Brack et al. 2005). Recent biozonation of the Sasso Caldo site, based on index-fossil invertebrates (ammonoids and the bivalve *Daonella*), indicate that the stratigraphic section cropping out therein is fairly consistent with the most recent biozonation reported by the Swiss authors (Brack et al. 2005) and allows confident correlation with the coeval Swiss localities (Bindellini et al. 2019). In particular, the two mixosaurs here described were collected below the two/three uppermost tuffitic layers and within the *N. secedensis* Zone (Middle Besano Formation), thus they are of late Anisian age.

The Besano Formation was deposited in a lagoonal basin whose estimated depth should have been around 30–100 m (Bernasconi 1991; Furrer 1995; Röhl et al. 2001; Etter 2002). The upper part of the water column was oxygenated, and a rich fauna, consisting mostly of cephalopods and vertebrates, thrived (Furrer 1995). At the bottom of the basin, water circulation was restricted, thus developing an anoxic environment; however, there is evidence of periodical settling of weak currents that generated dysaerobic conditions (Bernasconi 1994; Furrer 1995; Röhl et al. 2001).

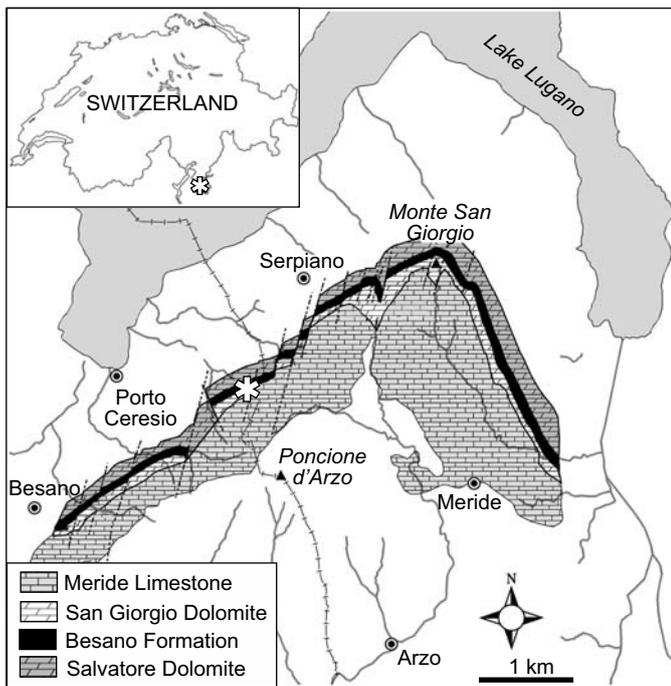


Fig. 1. General location and geological map of the Monte San Giorgio area. The asterisk indicates the position of the Sasso Caldo site.

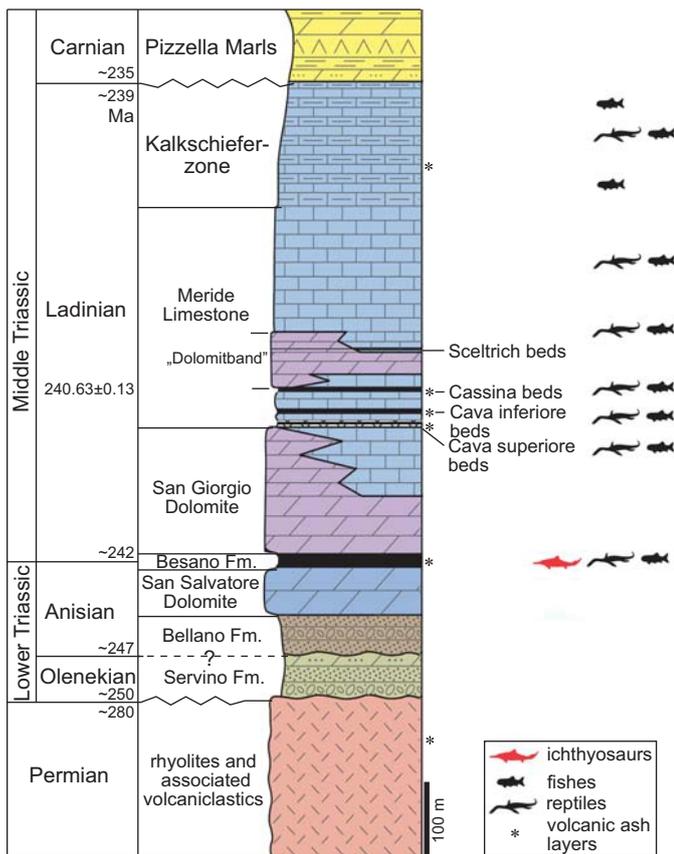


Fig. 2. Middle Triassic stratigraphic units of the Monte San Giorgio area. Stratigraphy modified from Commissione Scientifica Transnazionale Monte San Giorgio (2014; based on Furrer 1995); U-Pb ages after Mundil et al. (2010) and Stockar et al. (2012). The ichthyosaur outline indicates the Besano Formation, in which the specimens were collected.

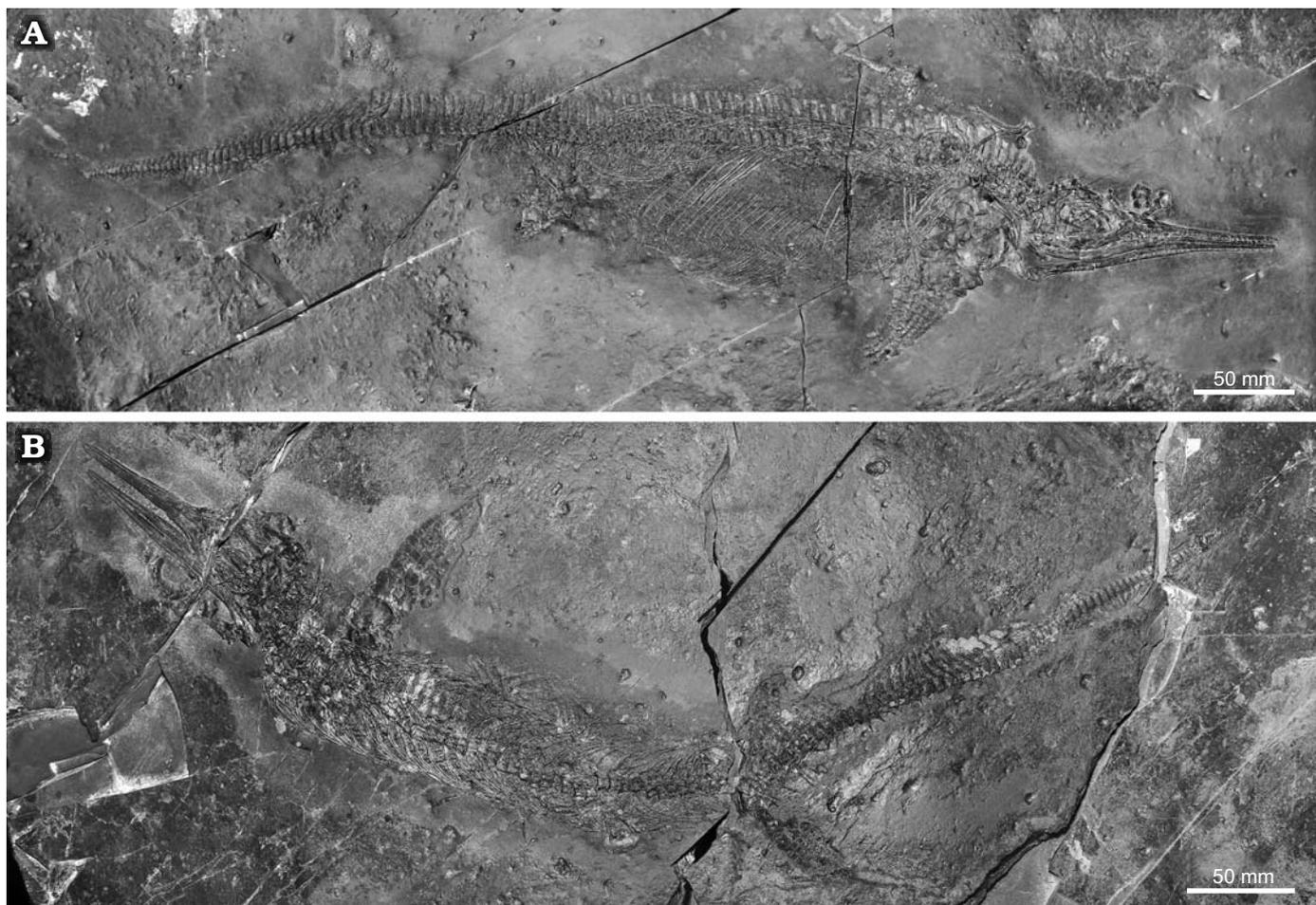


Fig. 3. Mixosaurid ichthyosaur *Mixosaurus cornalianus* Bassani, 1886, Sasso Caldo quarry, Besano, Italy, upper Anisian. **A.** BES SC 1000. **B.** BES SC 1001.

Material and methods

The detailed osteological description is available as SOM (Supplementary Online Material available at http://app.pan.pl/SOM/app65-Renesto_etal_SOM.pdf) and it is only briefly summarized here to testify that the two specimens show a typical combination of skeletal features allowing their assignment to *Mixosaurus cornalianus* Bassani, 1886 as diagnosed by Maisch and Matzke (1997, 2000), Jiang et al. (2006), and Ji et al. (2016).

Scanning electron microscopy (SEM) images and elemental peaks were obtained by analysing microsamples, taken from carefully selected areas of the specimen, with a Jeol JSM 5610 LV (IXRF Systems Inc.) equipped with an EDS 500 spectrometer.

Systematic palaeontology

Ichthyopterygia Owen, 1840

Ichthyosauria Blainville, 1835

Mixosauridae Baur, 1887

Genus *Mixosaurus* Baur, 1887

Type species: *Mixosaurus cornalianus* Bassani, 1886; Besano Formation (Triassic), Monte San Giorgio locality, Italy-Switzerland.

Mixosaurus cornalianus Bassani, 1886

Figs. 3–8.

Material.—Two nearly complete and articulated specimens: BES SC 1000 in right lateral view (Fig. 3A), BES SC 1001 in dorsal view (Fig. 3B). Coded as 20.S288-2.3 and 20.S288-2.4, respectively, in the Inventario Patrimoniale dello Stato (State Heritage Database). From Sasso Caldo site (45°54'03.7" N 8°55'10.6" E, elev. 650 m), Besano, Varese Province, NW Lombardy, N. Italy; Middle Besano Formation (sensu Bindellini et al. 2019), Uppermost Anisian, *Nevadites secedensis* Zone (sensu Brack et al. 2005), Middle Triassic.

Description.—The premaxilla is caudally pointed, only forming the rostral margin of the external naris; the maxilla shows a high and wide postnarial process contacting the prefrontal, and excluding the lacrimal from the external naris; the latter is very small and slit-like; a long sagittal crest is present on the skull roof, along with a large rostral terrace of the upper temporal fenestra, both reaching the na-

sals; the nasals are short, not extending caudally beyond the rostral margin of the orbit; the prefrontal and postfrontal are large, each forming about one half of the dorsal margin of the orbit; the upper temporal fenestra is small and slit-like, formed by supratemporal and parietal only; the cheek region is made up of a large supratemporal and a large squamosal. The dentition is subthecodont and isodont; the posterior maxillary and dentary teeth are slender, pointed, and widely spaced; there are 17 maxillary teeth (in BES SC 1000); the maxillary tooth row extends backwards beyond the caudal margin of the postnarial process; the pubis is more than twice the size of the ischium, the neural spines are high and narrow, approximately three times higher than the centra except for the last caudals; the caudal peak occurs at the level of the caudal vertebrae 17–18; the mid caudal vertebrae are larger than the preceding ones; the length of the hindfins is less than two thirds that of the forefins; in the forefins, five metacarpals are present with constricted shafts.

The body size, proportions, and degree of ossification of the two skeletons, compared with a larger mixosaurid sample (Brinkmann 1996, 1997, 2004), indicate they had almost reached a fully adult age.

Soft tissues: Preservation of vertebrate soft tissues has been reported for several specimens from the Grenzbitumenzone/Besano Formation and the Meride Limestone Formation, such as the tanystropheids *Macrocnemus* (Peyer 1937; Renesto and Avanzini 2002) and *Tanystropheus* (Renesto 2005; Renesto and Saller 2018), the sauropterygian *Neusticosaurus* (Sander 1989), and the fish *Saurichthys* (Renesto and Stockar 2009; Maxwell et al. 2013; Argyriou et al. 2016). Preservation of soft parts is likely due to authigenic mineralization induced by bacterial activity in oxygen-depleted environments, often in fully reducing conditions (Martill et al. 1992), in the presence of organic matter that may also represent the source of the mineralizing phosphates. Microbial activity creates microenvironments within the decaying carcass (Noto 2009; Sagemann et al. 1999). Depending on the microbial activity, phosphatization of soft parts may be limited only to some areas of the carcass, according to local variations of the pH (Briggs and Wilby 1996) which may (or may not) allow precipitation of phosphates that replace integ-

Table 1. Selected measurements (in mm) of the soft tissues of the specimens studied herein. Brackets indicate incomplete elements.

		BES SC 1000	BES SC 1001
Dorsal fin	length of leading edge	(68)	–
Caudal fin	length of leading edge	66	–
	dorsoventral height	(43)	–
	base length	51	–
Dorsal and caudal fin	diameter of a single collagen fibre (in μm)	60–70	–
Intestine	preserved length along U-shaped arrangement	–	(35)
	transverse diameter of preserved portion	–	9–11

umentary structures or even internal organs (e.g., Dal Sasso and Maganuco 2011).

In both specimens here described, patches of skin are preserved over the body, along with remains of other soft tissue (probably belonging to the stomach) lying inside the rib cage. In BES SC 1000, the upper lobe of the caudal fin is also preserved, along with the trailing edge of the dorsal fin (Fig. 4). In BES SC 1001, a possible tract of intestine is exposed (Fig. 5), and traces of the dorsal lobe of the caudal fin are also present. It is the first time that the presence of these structures is reported for *Mixosaurus*, and their preservation is good enough to allow a description of their internal microstructure.

Dorsal and caudal fins: In BES SC 1000, a well-delimited, straight, elongate, and apparently stiff structure made by tightly packed fibrous elements is positioned above the longest presacral neural spines, together with its basal portions (Fig. 4B). Given its specific identity, shape, position, and size (68 mm from base to its well-preserved apex), we exclude from being a loose flap of decaying tissue, as seen in rarely preserved cutaneous and subcutaneous tissues of *Stenopterygius*, which have a clearly wavy, not stiffened aspect (CDS personal observation on SMNS 54051, SMNS 81958). Therefore, the structure seen in BES SC 1000 most likely represents the leading edge of the dorsal fin. It lies above dorsal vertebrae 15–23 and at the level of the trailing edge of the forefins, thus it is placed more cranially than in most of the tentative depictions published so far (e.g., Kuhn-Schnyder 1974; Motani et al. 1996). At a closer look, an array of collagen fibres (sensu Lingham-Soliar and Plodowski 2007; that is, each visible fibre may represent a bundle of packed collagen microfibrils) densely packed together is clearly visible under binocular microscope (Fig. 4D). These fibres extend parallel to each other, and are inclined at an angle of approximately 26° with respect to the body axis. All fibrous structures are in relief, giving a near three-dimensional appearance; their nature and microstructure is confirmed by SEM analysis (see below).

The dorsal lobe of the caudal fin of BES SC 1000 (Fig. 4C) lies at the level of the peak of the caudal vertebrae, just above caudal vertebrae 14–22, it is almost complete and shows a triangular outline. The preserved portion of the fin is 43 mm high (Table 1), the cranial margin is 66 mm long, and the ventral margin (i.e., the base) measures 51 mm. The concave ventral margin mirrors exactly the outline of the caudal peak of the vertebral column, showing the original in vivo position of the fin lobe. In fact, the fin has been set off dorsally and slightly rotated counterclockwise, with post-mortem shifting of a few centimetres. The fossilised skin surface that covers most of the fin seems to retain few details, but in areas where the skin is missing, the underlying array of fibres becomes visible (Fig. 4E, F). As in the dorsal fin, these fibrous structures are in relief. At the cranioventral corner of the base of the fin, fibres can be observed diagonally oriented at an angle of approximately 32° with the body axis. Other almost straight, feebly waved

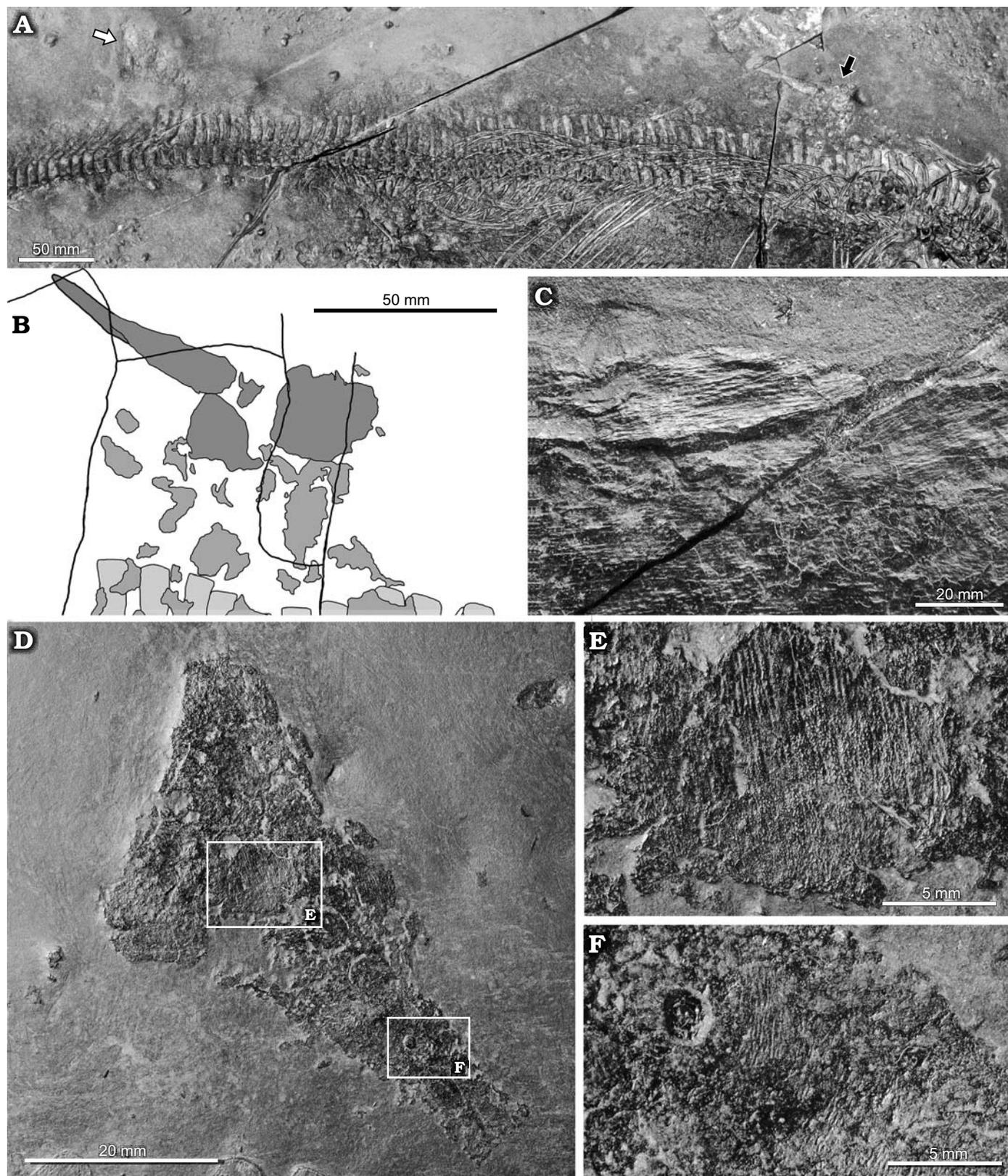


Fig. 4. Mixosaurid ichthyosaur *Mixosaurus cornalianus* Bassani, 1886 (BES SC 1000), Sasso Caldo quarry, Besano, Italy, upper Anisian. **A.** General view of the specimen showing the position of the dorsal fin (black arrow) and of the dorsal lobe of the caudal fin (white arrow). **B.** Explanatory drawing showing the position of the dorsal fin (dark grey), skin remains (grey), and neural spines (light grey). **C.** Close up of the shaft of the dorsal fin showing parallel fibres. **D.** Dorsal lobe of the caudal fin. **E, F.** Close ups of the areas of the dorsal lobe of the caudal fin where other fibres and skin remains are exposed.

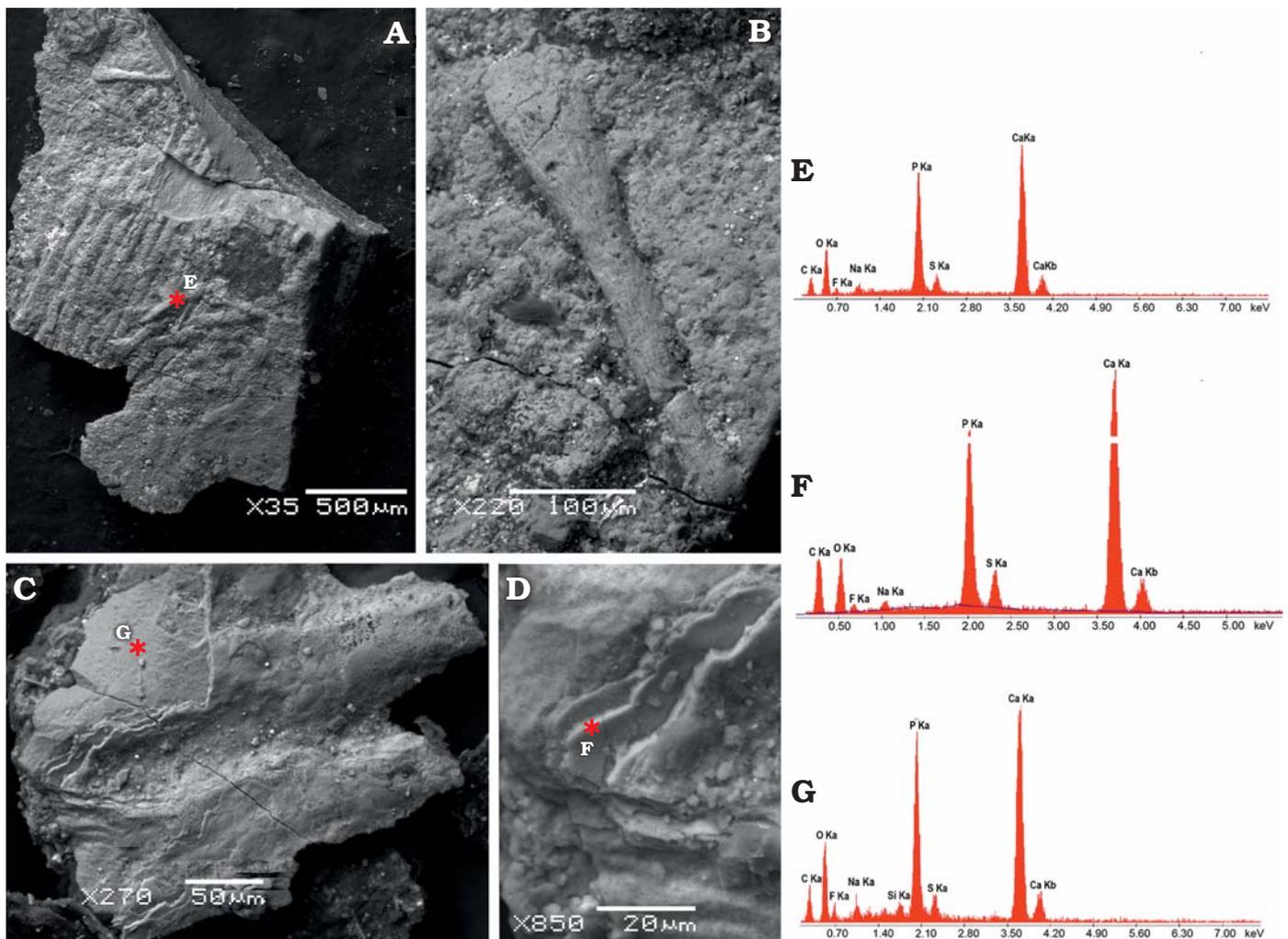


Fig. 5. SEM images of microsampled soft tissues of mixosaurid ichthyosaur *Mixosaurus cornalianus* Bassani, 1886 (BES SC 1000), Sasso Caldo quarry, Besano, Italy, upper Anisian. **A.** Collagen fibres packed in parallel bundles from the leading edge of the dorsal fin. **B.** Close-up of a single fibre showing very fine striations, interpreted as collagen fibrils. **C.** A pair of collagen fibres from the base of the caudal fin, still covered by a patch of multi-layered scaleless skin. **D.** Close-up of the skin layers seen in C. Asterisks indicate locations of the back-scattered electron element microanalysis performed on dorsal fin fibres (**E**), caudal fin fibres (**F**), and caudal fin skin (**G**). The peaks illustrate the relative abundance of each element, with higher intensities indicating greater abundance. Note the enrichment of calcium and phosphorus in the fossilised soft tissue, with some variation in secondary minerals.

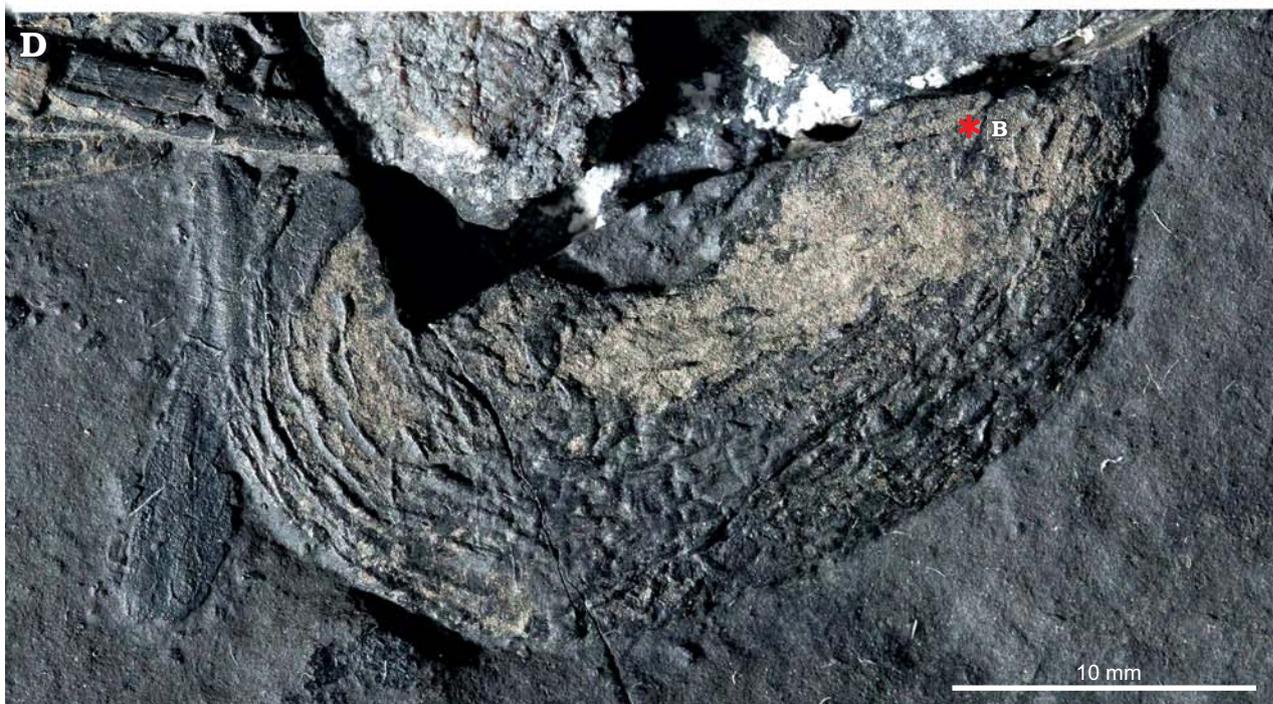
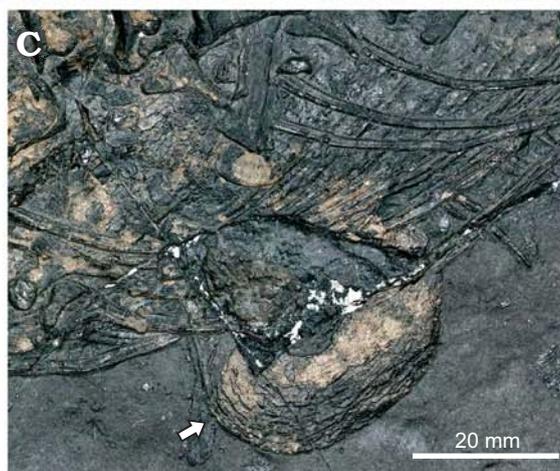
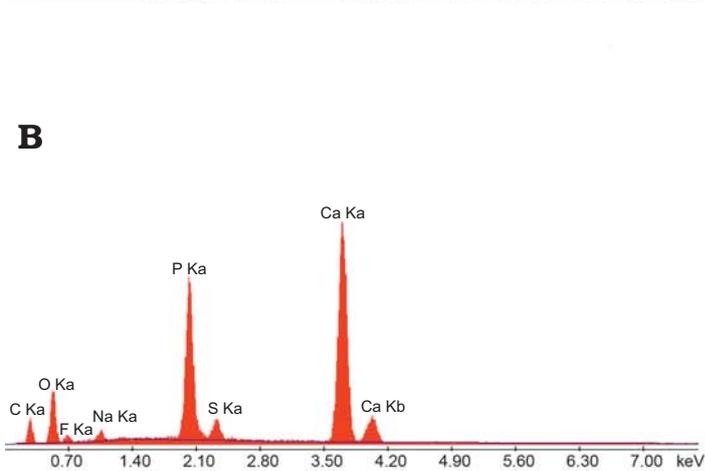
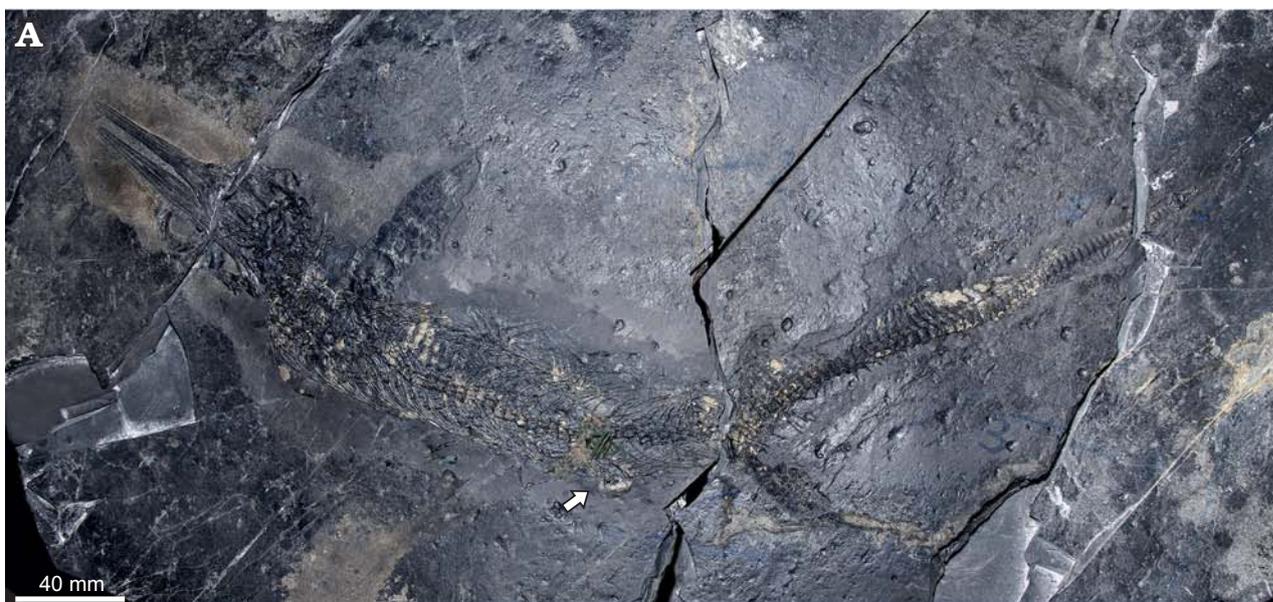
arrays of fibres are visible in the central portion and cranial margin of the fin, with an inclination of 58–53°. A small portion of the dorsal lobe of the caudal fin is present also in BES SC 1001, at the level of caudal vertebrae 19–22, but only few patches of skin are preserved.

Under SEM observation of a tissue microsample from the base of the caudal fin of BES SC 1000, each array consists of parallel fibres with a diameter of 60–70 μm each, which are part of the innermost dermal layer. The lack of transverse segmentation and the size range of the fibres are consistent with the collagen microstructure (e.g., Laurent 2018), unlike somatic muscular myofibres, which are striated and have larger diameters (e.g., Muhl et al. 1976).

Apparently homologous and better-preserved fibres, sampled from the trailing edge of the dorsal fin of BES SC 1000, are composed of very fine striations, likely corresponding to collagen fibrils (Fig. 5A–C).

SEM analysis of the microsample from the base of the caudal fin also recovered remnants of skin with an excellent degree of preservation, fossilised through replication in authigenic calcium phosphate (Fig. 5G). No scales or scutes are evident, and the external surface is smooth, as in *Stenopterygius* (Lindgren et al. 2018). Moreover, the skin of *Mixosaurus* shows a multi-layered subsurface architecture (Fig. 5D), corresponding to the laminated epidermis and dermis of modern tetrapods, which is also seen

Fig. 6. Mixosaurid ichthyosaur *Mixosaurus cornalianus* Bassani, 1886 (BES SC 1001), Sasso Caldo quarry, Besano, Italy, upper Anisian. **A.** General view → of the specimen. **B.** Back-scattered SEM element microanalysis of the possible intestine. **C.** Close up of the abdominal area with the protruding portion of the organ. **D.** Close up of the possible intestine, showing the longitudinal folds of the organ (left) and the internal granulosity (right). Arrows (in A, C) point to the organ position; asterisk indicates location of the back-scattered electron element microanalysis of the tissue.



in *Stenopterygius* (Lindgren et al. 2018). In our sample the first layer is smooth and continuous, whereas the second layer appears vacuolar or fine-grained. Theoretically there should be a layer of fibrous connective tissue between the right and left dermal layers, and internal to a thin fat layer (Erin Maxwell, personal communication 2020), which our surficial non-invasive sampling did not penetrate.

In any case, our SEM images and elemental microanalyses clearly demonstrate that the fibres of BES SC 1000 are fossilised anatomical structures, well in relief within the ichthyosaur skin tissue, and not sedimentary cracks or tool marks, as it was questioned recently for similar finds in Jurassic ichthyosaurs (Smithwick et al. 2017).

Intestine: A finely corrugated structure of apparent soft tissue nature protrudes off the ventral margin of the abdominal region on the right side of BES SC 1001, approximately at the level of the presacral vertebra 40, i.e., cranial to the pelvic girdle (Fig. 6). It shows surficial corrugations and has a U-shaped tubular structure, it measures 31 mm along its long axis, 17 mm perpendicular to it and 9–11 mm in transverse diameter. Secondary ridges, perpendicular to the longitudinal ones, are visible under grazing light and seem to define millimetric internal subdivisions, or contents.

In our opinion, this structure may represent a tract of the *Mixosaurus* guts, namely a lithified intestinal segment, filled by remains of ingested prey. Some of the granularities glimpsed within the organ look subrectangular in shape and would be compatible in size with the small vertebrae contained in the stomach region; the transverse diameter of the organ is also consistent with the dimensional range of the intestinal tube in a 0.9–1.0 m long reptile (Vitt and Caldwell 2009).

The main corrugations would represent the longitudinal folds of the original external layer of muscular tissue, which might have become fossilised thanks to a prolapse outside the abdominal cavity, under direct contact with the sediment undergoing diagenesis. This event might explain why there is no apparent continuity of gut remains cranial and caudal to this section of the organ, within the abdomen of BES SC 1001, where different chemical conditions likely made the decay of soft tissues prevalent.

Fluorescence induced by UV light did not show similar soft tissue remnants nearby; a microsample of the organ, taken along its broken section and analysed under SEM, did not recover any diagnostic anatomical microstructure. Contrary to the skin and collagen fibres, this organ is extensively colonised by a number of pyrite crystals, and in cross-section it appears amorphous. Fossil preservation, in this case, does not reach the cellular level and is limited to replication of the external morphology. Nevertheless, the organic origin of this structure is confirmed by SEM element microanalysis (Fig. 6B), which gives a chemical signal very similar to skin and collagen of BES SC 1000 (Fig. 6E, G), and also to the visceral tissue fossilised in the theropod dinosaur *Scipionyx* (Dal Sasso and Maganuco 2011: fig. 143).

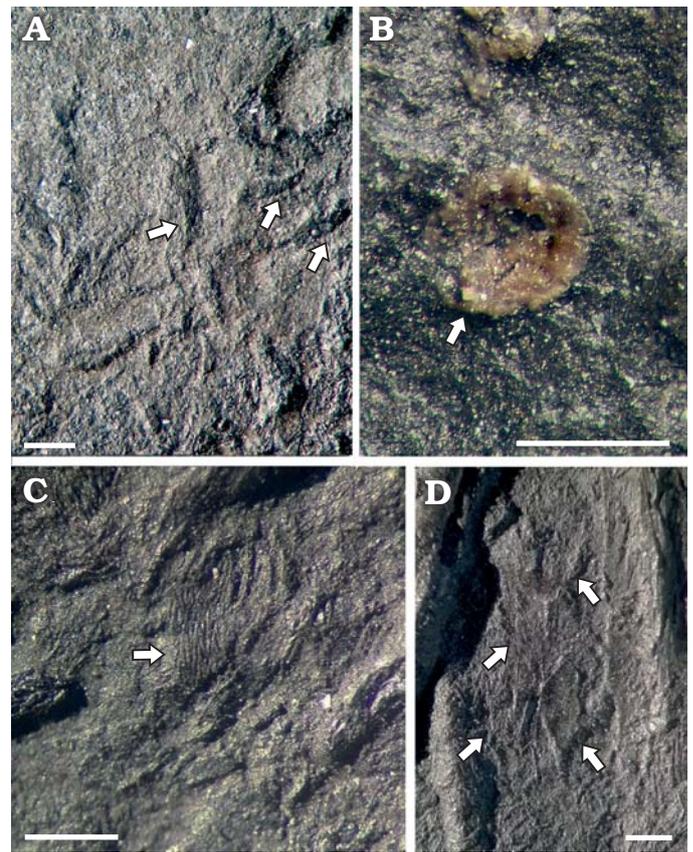


Fig. 7. Stomach contents of mixosaurid ichthyosaur *Mixosaurus cornalianus* Bassani, 1886 (A, B, BES SC 1000; C, D, BES SC 1001), Sasso Caldo quarry, Besano, Italy, upper Anisian. **A.** Cephalopod hooklets (arrowed). **B.** Enigmatic (neoselachian?) vertebral centrum (arrowed) embedded in the dark material of the decayed stomach. **C.** Isolated actinistian scale (arrowed). **D.** Semi-articulated actinopterygian scales (arrowed) embedded in the stomach area. Scale bars 1 mm.

If our interpretation is correct, this find confirms, after indirect hypotheses based on coprolites (e.g., Pollard 1968) that, in ichthyosaurs, the ingested bones could pass through the intestines. Bones are much harder than scales, and more difficult to process throughout the guts. Not all reptiles are able to do that, as the pyloric valve at the end of the stomach can be too narrow to allow transit of solid material (for a complete account see Dal Sasso and Maganuco 2011). In this respect, BES SC 1001 might represent an important addition to our knowledge of digestive physiology in the Ichthyosauria.

Stomach contents: In the thoracic region of BES SC 1000, several hooklets of cephalopods are detectable (Fig. 7A), as is frequent in *Mixosaurus* specimens; in addition, a finely rough area of dark material, 100 mm long and 40 mm wide, overlies the left ribs and contains a number of tiny, ebony-brownish polygonal to cylindrical elements, whose diameter varies from 0.1 to 0.8 mm. These elements represent vertebral centra (Fig. 7B), often grouped in clusters and embedded in the rough material, whereas the sediment surrounding the *Mixosaurus* skeleton is devoid of them; thus it is feasible that this area would represent stomach remains and contents. The attribution of these centra is difficult because

they differ significantly from the C-shaped or ring-shaped vertebral centra of Triassic actinopterygians, and are also too small and different from vertebral centra of marine reptiles, while there is some resemblance to some Triassic neoselachian vertebrae (Mears et al. 2016: fig. 8). Neoselachian remains are known since the Lower Triassic (Koot et al. 2015), but in the Besano Formation only hybodont sharks have been found so far, thus the attribution to neoselachians must be considered as tentative.

In BES SC 1001, isolated or partially articulated scales (Fig. 7C, D) are preserved in the stomach area. They show a pattern of ridges that suggest they belonged to some actinistian, a group that is well represented in the Besano Formation (Rieppel 1980, 1985; Cavin et al. 2013; Ferrante et al. 2017; Renesto and Stockar 2018).

Given that all other reported gastric contents of mixosaurids from Monte San Giorgio consist exclusively of cephalopod hooklets (Rieber 1970; Brinkmann 1997), the two new specimens testify that adult *Mixosaurus* also preyed on small fishes, as medium-large ichthyosaurs did (e.g., Pollard 1968; Druckenmiller et al. 2014; Dick et al. 2016).

Discussion

A large number of fossils of *Mixosaurus cornalianus* is known (Brinkmann 1998, 2004; Motani 1999; Maisch and Matzke 2000), but the two specimens described here represent the first evidence that this ichthyosaur had both a dorsal fin and a well-developed dorsal lobe of the caudal fin. So far, *Mixosaurus cornalianus* has been reconstructed either with or without dorsal fins, and the shape and position of the dorsal fin has been conjectural. The specimens described here not only testify that a dorsal fin and a lobate, incipiently semilunate caudal fin were undoubtedly present, but also allow reconstruction of the shape of the fin with remarkable precision (Fig. 8). More importantly, the preservation of the internal structure of the fins, although incomplete, allows us to propose hypotheses about the swimming efficiency of *Mixosaurus cornalianus* (and possibly other *Mixosaurus* species).

The fibres preserved in the dorsal and caudal fins of BES SC 1000 (Fig. 5) show striking macroscopic and microscopic similarities to those found in Jurassic ichthyosaurs, including thunniform taxa such as *Stenopterygius* (Lingham-Soliar and Plodowski 2007). According to these authors, the collagen fibre architecture of *Stenopterygius* was nearly identical to that of large lamniform sharks like *Carcharodon carcharias* (Lingham-Soliar 2005a, b) and provided adequate stiffness to allow stability and efficient propulsion during high speed swimming. The dorsal fin in *C. carcharias* acts as a dynamic stabilizer: during fast swimming the dermal fibres go under tension playing a fundamental role in stiffening the fin against yaw and roll, while during slow swimming the fibres lose tension allowing more flexibility (Lingham-Soliar 2005a, b). In the dorsal and caudal fins of Jurassic ichthy-

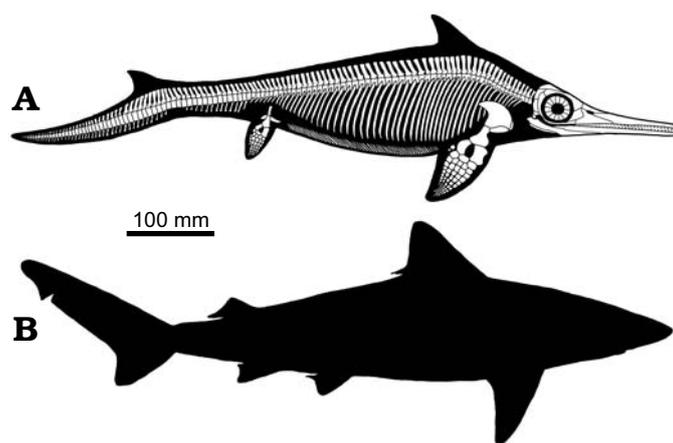


Fig. 8. Reconstruction of the skeleton and body outline of mixosaurid ichthyosaur *Mixosaurus cornalianus* with the dorsal fin and the dorsal lobe of the caudal fin, as preserved in BES SC 1000 (A) compared to the body outline of the small tail shark *Carcharinus porosus* (B), which average length is similar to that of *Mixosaurus*.

saur, bending stresses on the vertical plane are compensated by a mesh of lefthand and righthand bundles of fibres, while bending stresses on the lateral plane are contrasted by fibres that run parallel, or at an acute angle, with respect to the long axis of the ichthyosaur body (Clark and Cowey 1958; Wainwright et al. 1976; Lingham-Soliar 2005a; Lingham-Soliar and Plodowski 2007), and are mainly present at the base and at the tip of the dorsal fin where major torsional stresses are applied.

In BES SC 1000 the preserved portion of the dorsal fin shows a large number of dermal fibre bundles that are tightly grouped together; in the dorsal lobe of the caudal fin, arrays of fibres oriented parallel to the body axis are clearly detectable and follow the pattern described for Jurassic ichthyosaurs, whereas the presence of right/left hand oriented fibres cannot be ascertained. However, the fibres parallel to the body axis of BES SC 1000 are straight as in *Stenopterygius*, a feature that was considered indicative of a high degree of fibre tension and fin stiffness (Lingham-Soliar and Plodowski 2007). A stiff dorsal fin is essential to stabilize the body during swimming, reducing yaw and roll, and a lobed caudal fin contributes to increase propulsive thrust and fast start acceleration. In extant fast swimming sharks, the main component of stiffness of the control surfaces of the fins is represented by bundles of straight collagen fibres (Lingham-Soliar 2005a, b) and, since straight collagen fibres have a very small stretch when under tension, they represent the main anatomical structure giving stiffness to the fins. *Mixosaurus cornalianus* shows a dermal architecture similar to Early Jurassic taxa, indicating that this exaptation evolved earlier in the ichthyosaur lineage than high-speed pelagic swimming.

Mixosaurus cornalianus shares some of the characters listed by Webb (1984) as typical of BCF (body/caudal fin) periodic swimmers, that are able to perform sustained swimming, such as a relatively stiff and streamlined anterior body and a large anterior depth and mass, a narrow caudal body

region, and fins relatively small with respect to body size. The position of the dorsal fin in *Mixosaurus* (Fig. 8A) is intriguing since it is placed more cranially than in Jurassic ichthyosaurs and most odontocete cetaceans, somewhat similar to some carchariform sharks (e.g., the small tail shark, *Carcharinus porosus*, Fig. 8B). The fin is placed over the base of the pectoral fins, in correspondence to the deepest point of the body, as it occurs, albeit not exclusively, in “sustained swimmers” (Fletcher et al. 2014). On the other hand, *Mixosaurus* lacked both a lunate tail of high aspect ratio maximising thrust, and a narrow caudal peduncle providing quick oscillation and allowing locally large amplitude displacements, and control of the attack angle. These features that characterize thunniform swimmers appear in Jurassic ichthyosaurs; thus the swimming speed of *Mixosaurus* was certainly lower. Nevertheless, the stiff dorsal fin acting as a stabilizer might have improved the swimming abilities of *Mixosaurus*, allowing it to approach those of some carchariform sharks with a deeply heterocercal tail.

Conclusions

The evidence that *Mixosaurus cornalianus* possessed a dorsal and a caudal fin (Fig. 8), both anatomically well-defined and mechanically efficient, compels a re-examination of evolutionary trends in mixosaurian-grade ichthyosaurs, as well as a reconsideration of their swimming capabilities, as recent research on the matter (e.g., Gutarra et al. 2019) has often used a model that now must be considered definitely obsolete. The dietary preferences of the two specimens examined in this paper also support the idea that *M. cornalianus* was an efficient open water swimmer, exploiting BCF (body/caudal fin) periodic propulsion (sensu Webb 1984).

The fossilization of portions of the viscera is also remarkable. Traces of fossilised internal organs have been described almost exclusively in Early Jurassic specimens from Holzmaden (Keller 1976; Böttcher 1989, 1990; Lindgren et al. 2018). Pending a definitive organ characterization, BES SC 1001 is certainly the first documented case in the ichthyosaurs of the Besano Formation.

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