

FIRST SKELETAL REMAINS OF *HELVETICOSAURUS* FROM THE MIDDLE TRIASSIC ITALIAN OUTCROPS OF THE SOUTHERN ALPS, WITH REMARKS ON AN ISOLATED TOOTH

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Abstract. The enigmatic marine reptile *Helveticosaurus zollingeri*, from the Middle Triassic Besano Formation of Monte San Giorgio, is known from three specimens found in Swiss territory. This paper describes the first skeletal remains of this taxon recovered from the corresponding Italian outcrops of Besano (Varese). An isolated tooth assigned to the same taxon and coming from the San Salvatore Dolomite, Rasa di Varese (Varese), is also redescribed herein. The skeletal remains have been CT scanned to inspect the preserved morphology of the bones hidden below the surface; CT data also allowed the identification of an associated ammonoid which has been crucial to determine the stratigraphic position of the studied material. The redescription of the tooth has been helped by a digital model of the specimen obtained through photogrammetry. With the additional new data obtained from the two specimens, the first skeletal reconstruction of *Helveticosaurus* is provided. This is followed by a phylogenetic test of the taxon, assessing its position among marine Triassic diapsids. Finally, in the light of recent studies we discuss the swimming mode and the possible ecological niche occupied by the animal: we suggest a distinction between the function of forelimbs and hindlimbs, and a distinction between different swimming styles likely performed by *Helveticosaurus*, depending on the speed of movements.

INTRODUCTION

Helveticosaurus zollingeri, to date, is known from three specimens housed in the Paläontologisches Institut und Museum der Universität Zürich. The holotype (PIMUZ T 4352) was collected in 1935 in the Galleria Arnaldo of Cava Tre Fontane (Monte San Giorgio, Canton Ticino, Switzerland); the preserved skeleton is 2.5 m long and has an estimated

full length of 3.6 m (Kuhn-Schwyder 1974). Earlier in 1933, a largely complete but disarticulated specimen (PIMUZ T 4353), and later in 1937, an isolated snout with 14 mesial teeth (PIMUZ T 4354), were recovered in the same locality (Rieppel 2019). So far, the only Italian record of *Helveticosaurus* is represented by a single tooth (ST166120) from the San Salvatore Dolomite [Dolomia della Rasa *sensu* Airaghi (1935), Rasa di Varese, Lombardy], tentatively attributed to this genus by Pieroni (2011) and Renesto & Pieroni (2013). All these specimens are dated to the late Anisian (Middle Triassic).

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The holotype and PIMUZ T 4353 are almost complete, although in both cases the skull is severely crushed, most of the tail is missing, and the sacral region is not well-preserved. *Helveticosaurus zollingeri* is a highly enigmatic animal. In fact, its morphology is distinct from all other known Triassic marine reptiles and its rare remains do not allow to place it in a satisfactory phylogenetic position among the Diapsida. Furthermore, for the same reasons its ecology is partly unexplored and not fully understood. The aims of this study are to describe a new specimen, recovered from the middle Besano Formation of Besano (Varese), found in 1952 and recently re-discovered in the collection of the Museo di Storia Naturale di Milano (MSNM V927 and V928); to redescribe the isolated tooth (ST166120) reported by Renesto & Pieroni (2013); to provide an updated skeletal reconstruction, and give a brief review of the swimming mode and the possible ecological role of *Helveticosaurus* in the seas where the Besano Formation deposited during the latest Anisian.

GEOLOGICAL AND STRATIGRAPHIC CONTEXT

The Middle Triassic carbonate succession of Monte San Giorgio consists of four formations that were deposited on a carbonate platform along the western margin of the Neo-Tethys (Furrer 1995; Röhl et al. 2001; Etter 2002; Stockar et al. 2012). Above the Anisian Lower San Salvatore Dolomite lies the 5- to 16-meters-thick Besano Formation (also known as Grenzbitumenzone), from which the greatest part of the well-known vertebrate fauna of Monte San Giorgio has been recovered (Bürgin et al. 1989; Furrer 2003). The Besano Formation was deposited in a shallow marine setting (30-130 m deep) and consists of an alternation of laminated dolomitic banks and bituminous shales with sparse cineritic tuffs (Bernasconi 1991; Bernasconi & Riva 1993, Bernasconi 1994; Furrer 1995; Röhl et al. 2001; Etter 2002), which are late Anisian-early Ladinian in age (Brack & Rieber 1986, 1993; Mundil et al. 1996; Brack et al. 2005; Wotzlaw et al. 2017). Recent biozonation of the Italian Sasso Caldo site (Besano, Varese) indicates that the stratigraphic section cropping out there is fairly consistent with the most recent biozonation reported from the Swiss sections (Brack et al.

2005) and allows confident correlation with the coeval Swiss localities and other Italian outcrops (Bindellini et al. 2019). The three slabs containing the bones here described come from the ammonoid-bearing layers of the Besano Formation (Fig. 1), since the profile of an ammonoid (with maximum diameter 71 mm) is clearly visible through computed tomography (CT) scans (Fig. 1C). This suggests that the fossil reptile is ascribed to the *N. secedensis* Zone or the upper *R. reitzi* Zone (Rieber 1973; Brack et al. 2005). The ammonoid shows a platicone evolute shell, with few (eight per half turn), slightly prorsiradiate, distant but clear ribs that terminate with a rounded and prominent marginal node each (Fig. 1). Smaller nodes can also be identified at the umbilical margin. Although this specimen is unprepared, the combination of characters visible in the CT scan and just described is diagnostic and enough to attribute the cephalopod to a species of the genus *Ticinites* Rieber, 1973. Species of this genus occur only in layer 58 of the Mirigioli section (Punkt 902) of the Besano Formation (Rieber 1973) and define the very base of the *N. secedensis* Zone (Brack & Rieber 1993; Brack et al. 2005). This layer was not excavated at the Sasso Caldo quarry (Bindellini et al. 2019), but evidently it was exploited in the Piodelle-Selva Bella mine (about 1.3 km S-W of the Sasso Caldo site). Thus, MSNM V927 and V928 belong to the lowermost portion of the middle part of the Besano Formation, which, following Röhl et al. (2001), coincides with the establishment of an intraplatform basin, from which a great number of ichthyosaurian remains and other pelagic vertebrates have been recovered (e.g., Dal Sasso & Pinna 1996; Brinkmann 1997; Maish & Matzke 1998; Renesto et al. 2020; Bindellini et al. 2021).

The isolated tooth crown (ST166120) from the Rasa di Varese (Varese) is preserved associated with a brachiopod referred to *Mentzelia* cf. *mentzeli* Dunker, 1851 (Renesto & Pieroni 2013). According to these authors, in the same level the species of the genus *Mentzelia* was found in association with the brachiopods *Punctospirella fragilis* Schlotheim, 1814 and *Coenothyris* cf. *vulgaris* Schlotheim, 1820, the gastropods *Kittlidiscus lottneri* Eck, 1865 and *Trachybembyx* sp. Kittl, 1894, the bivalvs *Macrodon-tella* cf. *lamellosa* Assmann, 1915 and ?*Aviculomyalina undulata* Zorn, 1971, as well as the ammonoids *Ticinites*, “*Celtites*” sp., and *Serpianites*. Therefore, the

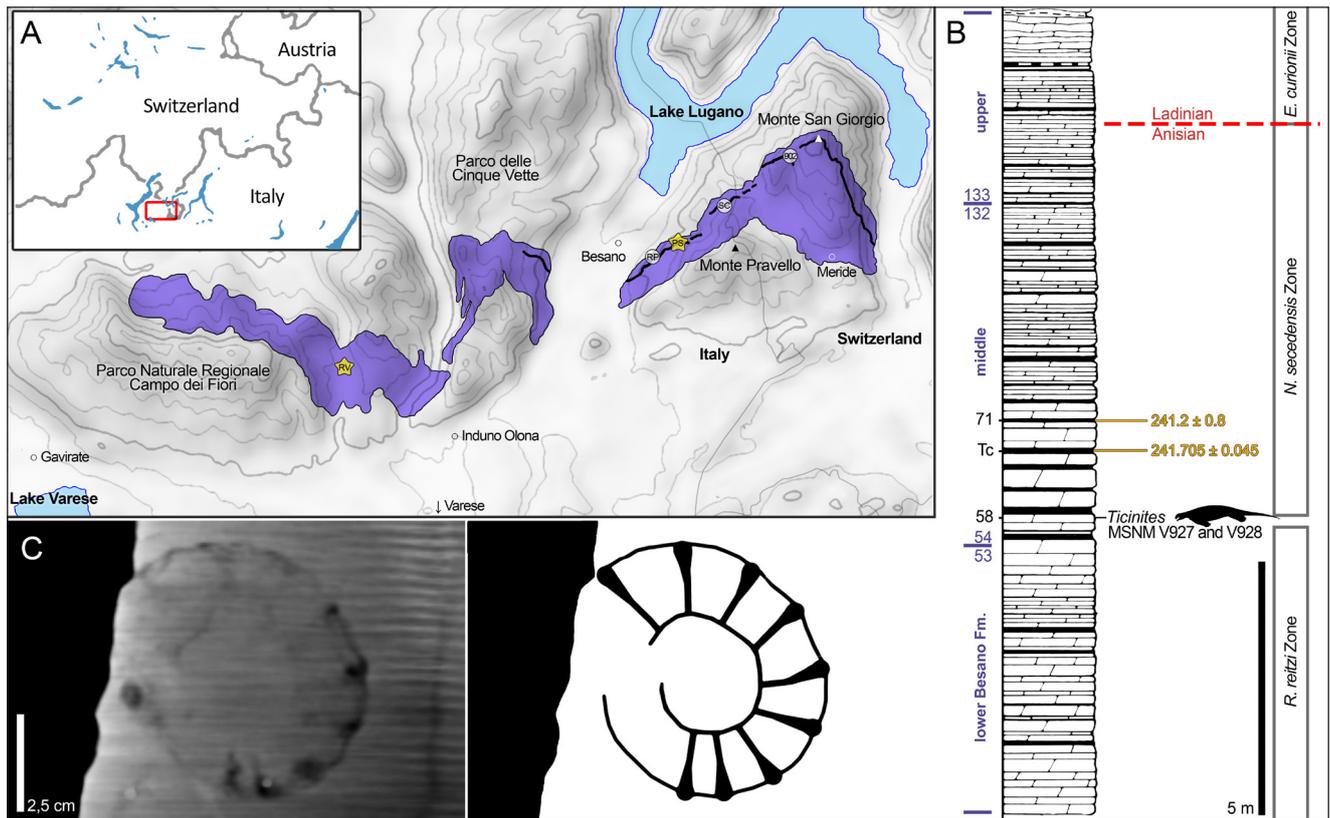


Fig. 1 - A) Map of the Varese Province with the Middle Triassic carbonate deposits (in purple) and the sites of origin of the specimens described in this paper (yellow stars). Localities abbreviations: 902, Punkt 902, Mirigioli; PS, Piodelle-Selva Bella mine; RP, Rio Ponticelli; RV, Rio Vallone; SC, Sasso Caldo. Outcrops of the Middle Triassic carbonate deposits modified from “Foglio 31 della Carta Geologica d’Italia (1:100.000) dell’Istituto Geografico Militare”. B) simplified stratigraphic log of the Besano Formation with the inferred stratigraphic position of the new specimen described (MSNM V927+V928); log modified from Brack et al. (2005); dating (in millions of years) of layer 71 from Mundil et al. (1996); dating of Tc Tuffs (layers 66–68) from Wotzlav et al. (2017). C) CT image and interpretative drawing of the *Ticinites* specimen associated with MSNM V927b.

specimen belongs to the layers of the Middle San Salvatore Dolomite from the *N. secedensis* Zone, uppermost Anisian (e.g., Brack et al. 2005), which was deposited at the same time as the middle part of the Besano Formation. The San Salvatore Dolomite at Rasa di Varese (Dolomia della Rasa *sensu* Airaghi, 1935) is constituted by thick dolomite layers deposited in a carbonate platform and in a reef environment (Zanin Buri 1965; Zorn 1971). During the latest Anisian, this platform sediments were deposited in eteropy with the sediments of the Besano Formation, directly above the Lower San Salvatore Dolomite, west of the Monte San Giorgio Basin (Zorn 1971; Stockar 2010).

Institutional abbreviations: PIMUZ, Paläontologisches Institut und Museum der Universität Zürich, Zürich, Switzerland; MSNM, Museo di Storia Naturale di Milano, Milan, Italy; SMF, Senckenberg Museum Frankfurt, Frankfurt, Germany; ST, Museo Scientifico-Naturalistico “Antonio Stoppani”, Seminario Pio XI, Venegono Inferiore (Varese), Italy.

MATERIAL

MSNM V927 and MSNM V928: Three slabs of laminated carbon-rich dolostone containing fossil bones were collected in 1952 from the waste material of the Piodelle-Selva Bella mine, near Besano (Varese), and deposited in the collections of the Museo di Storia Naturale di Milano with two different catalogue numbers (MSNM V927a,b and MSNM V928; Fig. 2 and Fig. 3). These specimens were never studied and remained indeterminate for decades. The bones pertain to the rib cage of a medium-large reptile and are included in a 12 cm-thick layer.

MSNM V927a and V927b are part and counterpart, and MSNM V928 also belongs to the same individual. In fact, although the skeletal portions comprised between the two remains are missing, the bottom layer thickness and lamination in MSNM V927 and MSNM V928 are identical, the axial elements are compatible in size, and all bones show left laterodorsal exposure, the same degree of articulation, fossilisation, and diagenetic compression.

The main slab (MSNM V927a) contains at least eight anterodorsal vertebrae exposed in dorsal view and nine ribs in lateral view, as well as the distal end of the left scapula and fragments of several gastralia scattered under the ribs. Its counterpart (MSNM V927b) hosts fragments of the same bones, in addition to their imprints, and six neural spines visible in the CT scan, perpendicularly entering the matrix. The third slab (MSNM V928) is smaller and includes at

least 10 smaller and shorter (i.e., posterodorsal) ribs in lateral view and at least nine fragmentary gastralia, tightly packed together. The preserved vertebrae are still aligned and in close contact with each other. All centra are deformed and dorsoventrally compressed to form a layer ~10 mm-thick. Nonetheless, the craniocaudal length of the centra is still preserved and their average length is ~34 mm. The neural arches and most of the neural spines are crushed over their centra and the zygapophyses are not recognisable.

ST166120: This specimen is a well-preserved isolated tooth, missing most of the root and the very tip of the crown apex (Fig. 4). It is partly embedded in the dolostone matrix which belongs to the San Salvatore Dolomite (Dolomia della Rasa *sensu* Airaghi 1935) and comes from Rasa di Varese (Varese). This outcrop is located 7 km southwest of Besano.

METHODS

X-ray computed tomography (CT) was performed on MSNM V927 and MSNM V928, with a Siemens Somatom Definition Dual Source CT Scanner, at the Radiology Department of the Fondazione IRCCS “Cà Granda” Ospedale Maggiore Policlinico di Milano. The best CT imaging was obtained with a bone algorithm on transverse (axial) slices, with scan parameters 140 kV, 180–270 mA, and slice thickness of 0.5 mm. Data were exported in DICOM format using eFilm (v. 1.5.3; Merge eFilm, Toronto, Canada). Analysis and post-processing were performed with RadiAnt, 3DViewer, and Synedra View Personal. Multiplanar reconstructions (MPR) and volume rendering reconstructions (VR) allowed us to inspect the bones hidden by other ones within the matrix, which were otherwise impossible to study without damaging the fossil.

We used photogrammetry to better study the isolated tooth ST166120 (File S1). A 3D model of the tooth was obtained with Meshroom by processing 85 shots, following Bindellini & Dal Sasso's (2021) method. Photos of all studied specimens were taken with a Nikon D7500 camera.

SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn, 1903

Helvetosauridae Peyer, 1955

Helvetosaurus Peyer, 1955

Emended diagnosis: *Helvetosaurus* is here re-diagnosed by the combination of the following characters: marine reptile at least 2 m long; high and deep snout; strong dentition of sub-thecodon implantation; caniniform mesial teeth with subtriangular cross-section; alternate tooth replacement with replacement waves passing from the front to the back of the jaws; at least 12 cervical vertebrae; at least 44 presacral vertebrae; transverse processes of dorsal vertebrae deeply striated, and well-spaced from each other; neurocentral suture persisting throughout the vertebral column; cervical ribs dicocephalous and with a free anterior process; dorsal ribs holocephalous; lateral surfaces of the ribs deeply striated; long scapular blade with a subrectangular dorsal margin; scapula lateral surface deeply striated; pubis with open obturator foramen; limb elements poorly ossified; at least two carpal ossifications; tarsal elements reduced to a single ossification; hyperphalangy in both manus and pes.

Helvetosaurus zollingeri Peyer, 1955

Holotype: PIMUZ T 4352, a nearly complete semi-articulated skeleton missing most of the tail.

Referred specimens: MSNM V927 (a and b: respectively the main slab, where the specimen is exposed dorsolaterally, and its counterpart, which includes a portion of the neural spines), anterodorsal portion of axial skeleton with distal end of scapula; MSNM V928, posterodorsal region of the same specimen including sacral ribs; ST166120, isolated tooth missing most of the root; PIMUZ T 4353, largely complete but disarticulated specimen; PIMUZ T 4354, isolated snout with 14 mesial teeth.

Locality and horizon: MSNM V927 and MSNM V928 come from the Piodelle-Selva Bella mine, Besano, Varese (Italy); Besano Formation, *N. secedensis* Zone, level/stratum correspondent to layer 58 of the Mirigioli section, latest Anisian. ST166120 comes from Rasa di Varese (Italy); San Salvatore Dolomite (Dolomia della Rasa *sensu* Airaghi 1935), *N. secedensis* Zone, associated with *Serpianites serpianensis* (V. Pieroni, pers. comm. 2021), latest Anisian (Renesto & Pieroni 2013). PIMUZ T 4352, PIMUZ T 4353, and PIMUZ T 4354 were collected respectively in 1935, 1933, and 1937 in Cava Tre Fontane (Monte San Giorgio, Canton Ticino, Switzerland).

Diagnosis: Same as for genus.

Description

Scapula. The preserved portion of the scapula is represented only by the dorsalmost (i.e. distal) lateromedially flattened portion of the scapular blade (Fig. 2). The dorsal margin has a sub-squared profile, the posterior margin is concave and the exposed surface of the bone is feebly convex. This, together with its orientation and because it overlaps the rib cage, indicates that is a left scapula exposed in lateral view. Mediolaterally it is very thin (from 4 to 2 mm). The sub-squared morphology of the distal end of this scapular blade is very similar to the holotype of *Helvetosaurus* (Peyer 1955; Rieppel 1989; pers. obs. 2020 on PIMUZ T 4352). The preserved length of the scapular blade is 54 mm, and the maximum dorsal expansion reaches a width of 72 mm, circa 1.3 times the value of the homologous measurement in PIMUZ T 4352 (56 mm). The seemingly larger size of the MSNM specimen can be the consequence of a significant taphonomical compression, testified also by the shortened dorsoventral height of the vertebral centra and neural spines. Considering that the centra of MSNM V927 are 34.2 mm long on average (Tab. 1) and that the proximal ends of the ribs measure 22.4 mm on average (lengths close to those of PIMUZ T 4352 and 4353), the *in vivo* dimensions of the MSNM specimen might have been rather similar to that of PIMUZ T 4352, i.e., about 2 m of presacral length (3.6 m total body length estimated by Kuhn-Schnyder 1974). The quadran-

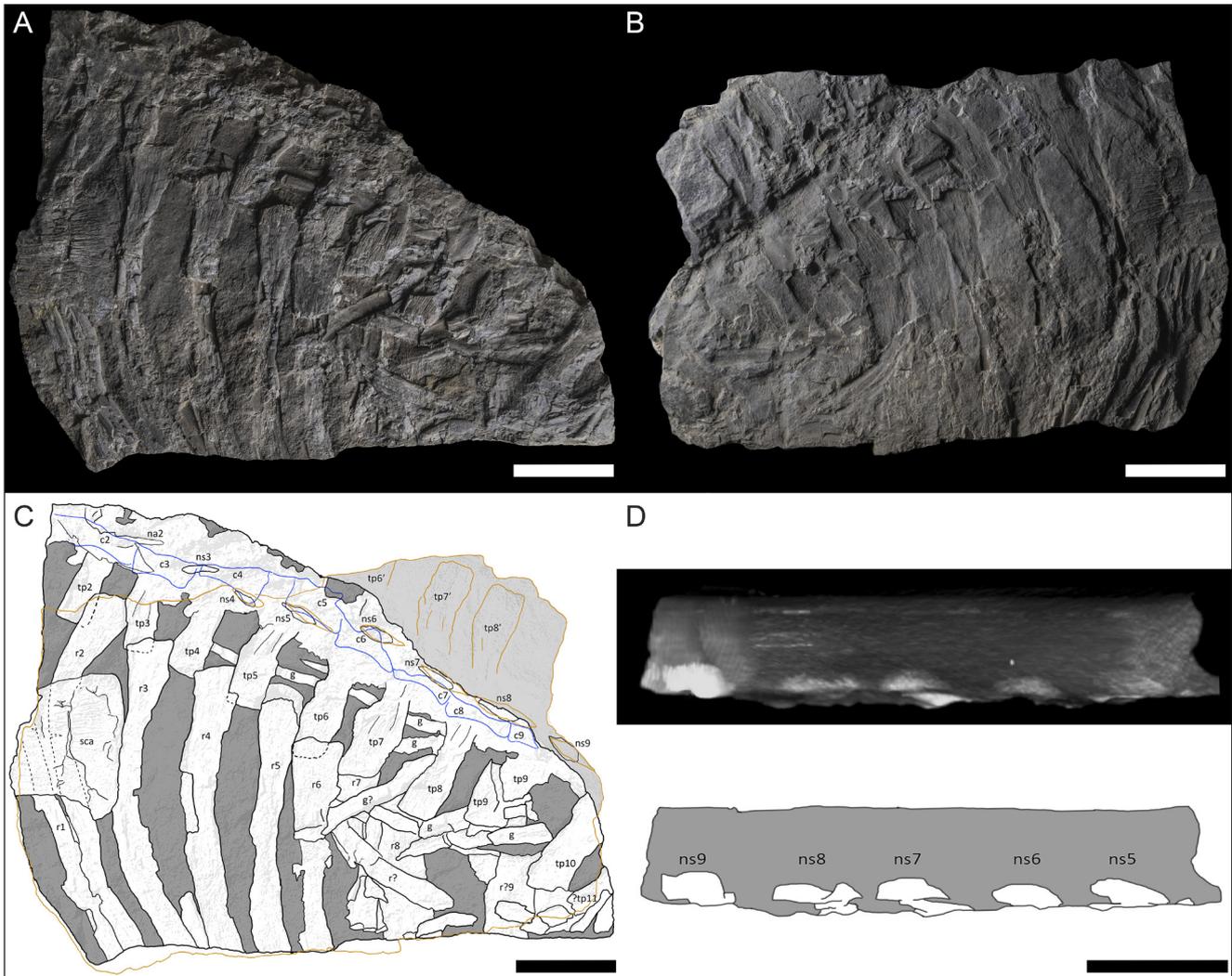


Fig. 2 - *Helveticosaurus zollingeri*, specimen MSNM V927. A) part MSNM V927a embedding most of the anterodorsal axial elements in left laterodorsal view; B) counterpart MSNM V927b with an additional area embedding right transverse processes and neural spines; C) interpretative drawing of the bones preserved in A and B; D) CT image of the neural spines embedded in MSNM V927b as seen in cross-section (top), and their interpretative drawing (bottom). Abbreviations: c, vertebral centrum; g, gastralgium; ns, neural spine; r, rib; sca, scapula; tp, transverse process. Scale bars equal 50 mm.

gular profile of the dorsal portion of the scapula is very different from *Placodus* (SMF R1035), but more similar to *Paraplacodus* (PIMUZ T 4775), although the latter is much smaller in absolute size.

The scapula of MSNM V927 shows several deep narrow longitudinal striations that cover the entire surface of the bone and are not the result of taphonomical processes. These are also clear in the holotype of *Helveticosaurus*, and to a minor extent in *Paraplacodus* (PIMUZ T 4775).

Dorsal vertebrae. At least eight fully articulated centra are preserved in dorsal view in MSNM V927, 11 transverse processes can be numbered in cranio-caudal sequence, and six neural spines are visible

still aligned in the CT scan of MSNM V927b (Fig. 2). No vertebrae are visible in MSNM V928. The dorsal centra do not show a parapophysis, and each diapophysis articulates with a single-headed rib. The centra are amphicoelous, slightly longer than wide, and lateromedially constricted in the middle; their height is not measurable due to diagenetic compression. The neural canal is never exposed except in the fifth vertebra, where it is 6.5 mm wide; this width is constant for all its length. Only one neural arch is visible on the surface of MSNM V927a (above the cranialmost centrum): its dorsal roof seems to be somewhat shaped as a triangle.

The transverse processes are distinctly elongate (up to 60 mm) and their distal extremities host

Position	Centra		Transverse processes		Neural canal	Neural spines		Ribs
	max. mediolateral diameter (estim.)	max. proximodistal length	mediolateral length	distal end craniocaudal width	mediolateral width	dorsoventral height	max. mediolateral length	craniocaudal width of the head
1	n.p.	n.p.	n.p.	n.p.	n.p.	n.p.	n.p.	n.p.
2	29.6	36	38	16.7	8.6	n.p.	n.p.	21.8
3	26.7	35.6	45.5	16.6	n.p.	n.p.	19.5	19.5
4	27.4	36.3	43.3	16.8	n.p.	16.1	24.5	24.3
5	28	34	51.5	17.2	6.5	13.3	34.9	22
6	27.8	32.4	58.3	18	n.p.	16.2	29.9	24.5
7	n.p.	32.1	59.5	18	n.p.	12.5	27.3	n.p.
8	n.p.	33.2	60.4	15.7	n.p.	11.4	29.3	n.p.
9	n.p.	n.p.	40.3	15.6	n.p.	n.p.	25	n.p.
10	n.p.	n.p.	44.4	18	n.p.	n.p.	n.p.	n.p.
M	27.90	34.23	49.02	16.96	7.55	13.90	27.20	22.42

Tab. 1 - Selected measurements (in mm) of the bones preserved in MSNM V927, a referred specimen of *Helveticosaurus zollingeri* from the Middle Triassic of Besano. N.B. "Position" does not refer to the anatomical position of the elements along the axial skeleton, but is used only to number them in this specimen, from the cranialmost to the caudalmost. Abbreviations: M, mean value; n.p., not possible.

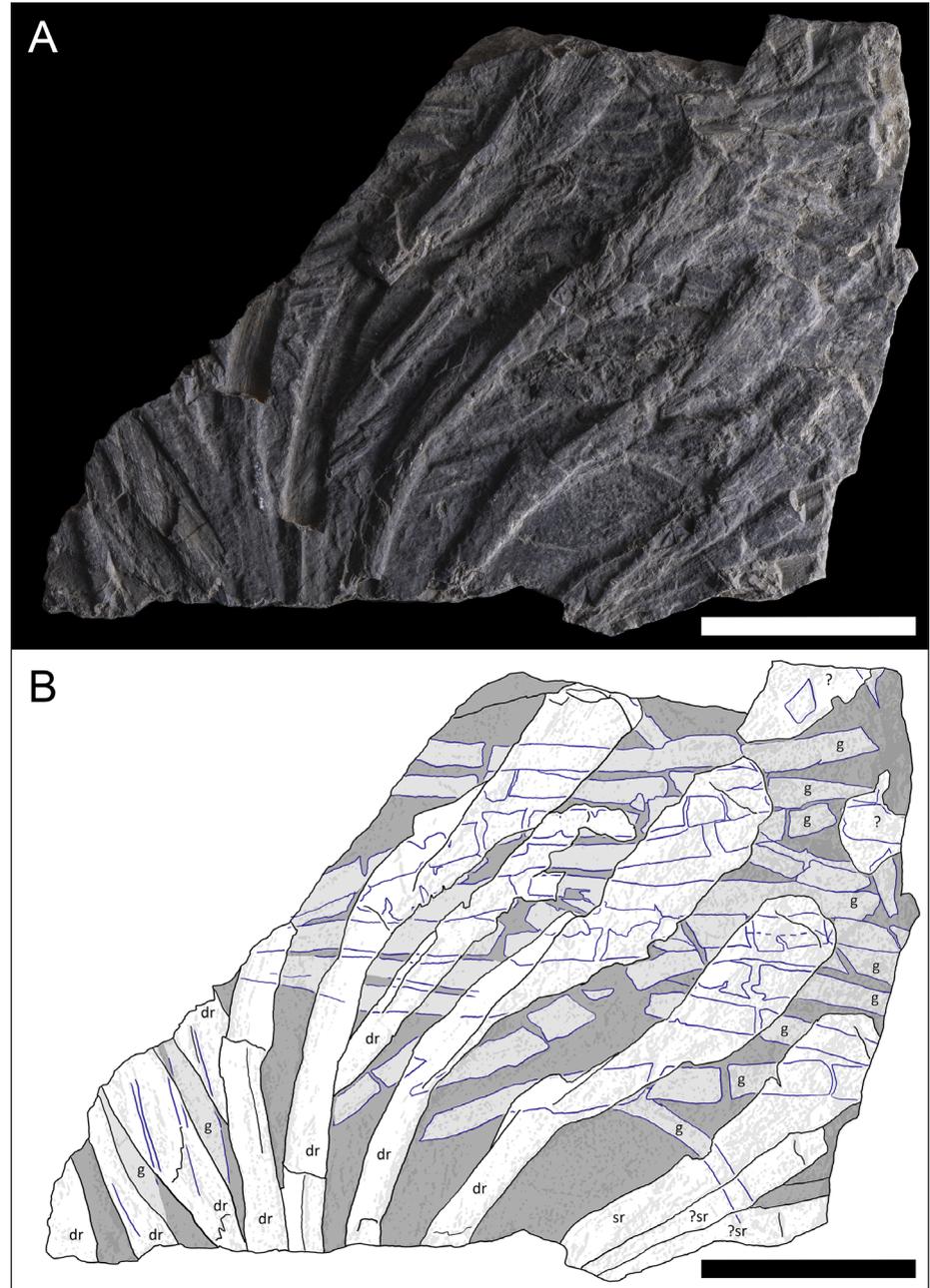
the articulation surfaces (diapophyses) for unicipitate ribs. Transverse processes are proportionally much shorter than in *Eusauropsargis* (Nosotti & Rieppel 2003; Scheyer et al. 2017), but more similar in length to *Sauropsargis* (Huene, 1936) and placodonts. Each transverse process is constricted proximally, approaching the neural arch, and slightly expanded distally in craniocaudal direction. Like the ribs and the scapula, the surface of the bone is characterised by deep striations. The distal extremity of the transverse process has an average width of 17 mm (~20 mm in PIMUZ T 4352). This width looks also larger than what can be observed in *Nothosaurus giganteus*. The ventral surface of each transverse process is characterised by the presence of an anterior and a posterior diapophyseal lamina (visible in CT data of MSNM V927a; Fig. S1), which distally run parallel to the caudal and cranial margins of the process, then diverge towards the vertebral centrum, delimiting a median fossa that in ventral view appears V-shaped. This peculiar anatomy is shared by MSNM V927 with the holotype of *Helveticosaurus zollingeri* (PIMUZ T 4352), as well as with the referred specimen PIMUZ T 4353 (Peyer 1955; Rieppel 1989). The dorsal surface of the transverse process symmetrically hosts similar laminae, although much less pronounced.

As for the zygapophyses, these are not visible in their entirety, being probably hidden by the compressed (and variably crushed) fragments of the neural arches. Above the smashed structures, at least six neural spines are preserved. Their broken bases are exposed on the surface of slab MSNM V

927a: they are compressed laterally and the cross-section on the dorsal plan is fusiform in outline, with a thicker central portion and tapered cranial and caudal margins. The five caudalmost neural spines are completely embedded in the matrix and visible only in the CT data of MSNM V927b (Fig. 2D). They are not as tall as observed in PIMUZ T 4352, although – like in the centra – some diagenetic compression has occurred. Moving from the most proximal to the most caudal, the spines become gradually taller. As it occurs in the anterodorsal vertebrae of PIMUZ T 4352 and 4353, the craniocaudal length of the spines is shorter at their base, whereas it becomes longer approaching the dorsal margin. The dorsal termination of the spines is almost straight and has a quadrangular aspect if observed from the lateral side. All the spines visible in MSNM V927b are caudally inclined. Above the neural spines, no dorsal *Placodus*-like osteoderms are visible.

Dorsal ribs. In MSNM V927 at least nine anterodorsal ribs are preserved (Fig. 2). These ribs are mildly recurved before reaching their midlength and are much thicker in craniocaudal direction than mediolaterally; the first two proximal ribs appear thinner than the other ones. Each rib possesses a slightly expanded unicipital head that articulates with the vertebral diapophysis located at the distal end of each transverse process. A groove extends proximodistally along the midline on the lateral side of the rib; this element is a biological feature and not the consequence of compression. As described

Fig. 3 - *Helveticosaurus zollingeri*, specimen MSNM V928. A) slab embedding the axial posterodorsal (and partly sacral) elements in left laterodorsal view; B) interpretative drawing of the bones preserved in A. Abbreviations: dr, dorsal rib; g, gastralia; sr, sacral rib. Scale bars equal 50 mm.



for the scapula and for the transverse processes, the surface of the ribs is strongly striated, a characteristic that is typical of *Helveticosaurus*. The posterodorsal ribs, preserved in MSNM V928, are similar to the anterodorsal ribs just described, but are distinguished by a clear bend that separates the straight proximal region of the head from the curved mediiodistal portion of the rib; consequently they are much thinner and more recurved than the shaft of the anterodorsal ribs. In addition, in the head region the lateral side of the rib shows a longitudinal concavity that is absent in the anterodorsal elements; a midline groove is present in the rest of the rib shaft. The distal ends of the caudalmost dorsal ribs seem

to converge towards the supposed position of the pelvis, as preserved in PIMUZ T 4352 (Peyer 1955). None of the ribs shows an unciniate process, which is present in *Paraplagodus* (Rieppel 2000) and is also reported in *Eusaurosphargis* (Scheyer et al. 2017).

Sacral ribs. Seemingly, the anterior margins of the caudalmost ribs preserved in MSNM V928 (Fig. 3) straighten and become slightly concave, a character that can be observed in the sacral region of Thalattosauria and Sauropterygia (e.g., Müller 2005; Rieppel 2000). Thus, the first straight rib in MSNM V928 is here interpreted as a sacral rib. Unfortunately, due to the fragmentary nature of our specimen,

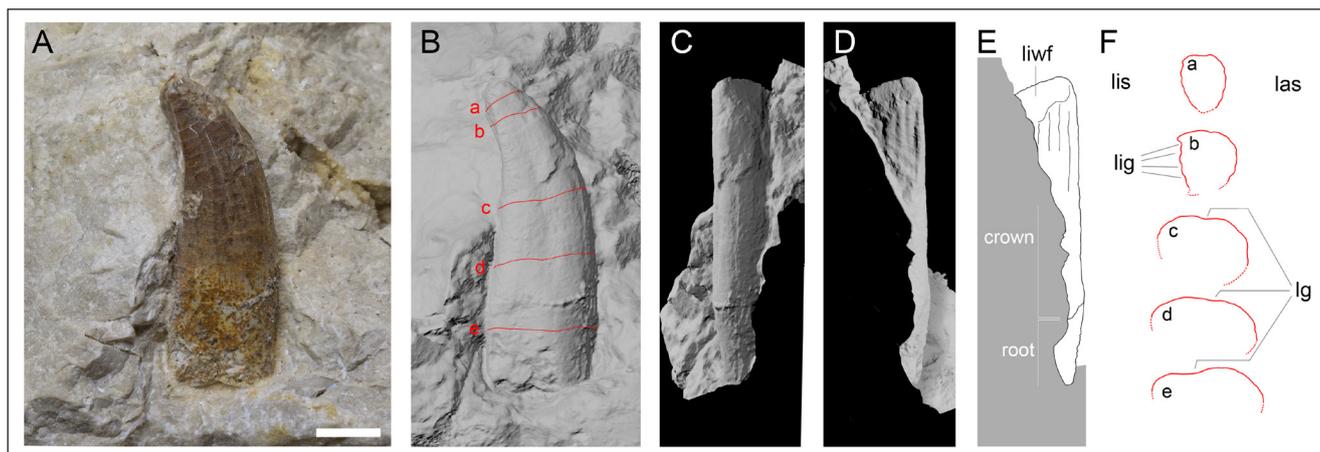


Fig. 4 - *Helveticosaurus zollingeri*, specimen ST166120. A) photo in distal or mesial view; B), C) e D) 3D model obtained through photogrammetry in lateral, labial and lingual view respectively; E) interpretative drawing of D; F) transverse sections of the tooth as indicated in B. Abbreviations: las, labial surface; lg, lateral groove; lig, lingual groove; lis, lingual surface; liwf, lingual wear facet. Scale bar equals 5 mm.

it is impossible to state how many sacral ribs it possessed. The distal ends of these ribs are also not preserved. Nevertheless, given the reduced spacing of the caudalmost ribs on the surface of the slab and the fact that they seem to converge distally, we suspect that specimen MSNM V928 possessed at least three sacral ribs. This hypothesis is consistent with the preserved portion of the sacral region of the *Helveticosaurus* holotype, PIMUZ T 4352 (pers. obs. 2019). In this specimen, the last preserved dorsal rib possesses a concavity similar to the dorsal ribs preceding it, does not show particular signs of sacralization (*sensu* Rieppel 1994), and is followed by three straight and shorter (although poorly preserved) ribs, which we suspect to be sacrals. These three ribs do not show a clear anteroposterior thickening in comparison to the posterior dorsal ribs. Moreover, the iliac blade of PIMUZ T 4352 shows morphology and proportions more similar to *Placodus* (SMF R1035, three sacrals) than to *Eusauropsphargis* (PIMUZ A/III 4380, two sacrals).

Gastralia. At least five disarticulated gastralia can be numbered in MSNM V927 (Fig. 2), and 14 in MSNM V928 (Fig. 3). In the posterodorsal region, the gastralia are densely packed together, possibly still preserving their *in vivo* distribution. How many elements composed each gastral row is unclear, but since all visible elements are straight, long, and do not show any pointed end they likely represent medioventral elements. The only exception is represented by the recurved element that in

MSNM V928 is partly covered by the sacral rib(s). The preserved gastralia are thinner than the ribs, dorsoventrally flattened and crossed by a median groove that extends for all of their length, both on the dorsal and on the ventral side, representing a biological feature.

The tooth. Specimen ST166120 (Fig. 4) is an isolated tooth lacking most of the root. It has already been briefly presented and figured by Pieroni (2011) and Renesto & Pieroni (2013). This tooth is 26 mm in height and has a maximum labiolingual width of 9 mm (Tab. 2). The tooth crown is slightly recurved lingually. The upper half of the crown is mesiodistally longer than labiolingually wide; on the other hand, the lower half of the crown and the root become more expanded labiolingually and mesiodistally compressed (Fig. 4F). Such variations in the shape of the cross-section, from the base to the apex of the crown, are seen also in *Paraplacodus*, despite in this taxon the teeth are proportionally longer and rounder, showing no lateral cutting edges (PIMUZ T 4773). The root of ST166120 shows a suboval section, slightly constricted in the middle by a groove on both sides. This groove extends apicobasally, becomes less pronounced on the crown surface, and disappears towards the tip. At the base of the crown, the transverse section is suboval as well; it becomes triangular above the mid-height of the crown. Here, its narrowest side, i.e., the lingual side of the tooth, is delimited laterally by two sharp edges, whereas the lateral sides converge in

Crown length	23 mm
Crown apex m-d Ø	4.2 mm
Crown apex la-li Ø	2.9 mm
Crown base m-d Ø	-
Crown base la-li Ø	8.1 mm
Root preserved base m-d Ø	-
Root preserved base la-li Ø	7.6 mm

Tab. 2 - Selected measurements of ST 166120, a referred tooth of *Helveticosaurus zollingeri* from the Middle Triassic of Dolomia della Rasa (Varese). Abbreviations: la-li, labiolingual; m-d, mesiodistal, Ø, diameter.

a rounded labial surface. At the crown tip, the apicalmost surface preserves an irregular wear surface, inclined by 45° towards one of the two sides. At the apex, the lingual surface also shows five faint striations or grooves that extend apicobasally but do not significantly affect the profile of the cross-section. These grooves delimit five visible narrow bulges that run in apicobasal direction, with the lateralmost higher than the central ones and defining one of the two lateral sharp edges of the crown.

The triangular cross-section, associated with two sharp cutting edges (or carinae) that run in apicobasal direction for more than half the length of the crown, suggests that this tooth belonged to a carnivorous generalist and was used to pierce and cut its prey (Massare 1987).

DISCUSSION

Taxonomic identification

The most diagnostic character in the postcranial elements of MSNM V927 is the presence of straight, well-developed (~50 mm long) transverse processes, departing from amphicoelous vertebral centra at a right angle. These are similar to *Saurosphargis voltzi*, although in this taxon they are closer to each other (Huene, 1936: plate 13). In MSNM V927, the neural spines are short (~15–20 mm tall) and slightly reclined towards the tail, and all bones, including the scapula, are textured with strong striations (T. Scheyer, pers. com. 2020). All elements are comparable in size to those of the holotype of *Helveticosaurus zollingeri* (PIMUZ T 4352).

Above the neural spines, no dorsal osteoderms, typical of species of *Placodus*, are visible in the CT scan. The dorsal spines are also shorter than in species of *Nothosaurus*. The anterodorsal ribs are

holocephalous and there is no trace of an uncinat process as seen in *Paraplocodus broilii*; the lateral surface of the ribs and the transverse process is deeply striated, similarly to what has been observed in *Helveticosaurus zollingeri* holotype. *Saurosphargis voltzi* shares similar striations on the lateral surface of the ribs, but the ribs of this taxon show a round and slightly prominent uncinat process (Huene 1936: plate 13) that is absent in *Helveticosaurus*. On the other hand, in *Eusaurosphargis dalsassoii* the dorsal ribs are proportionally much shorter than in *Helveticosaurus* and possess uncinat processes as well (Scheyer et al. 2017)

The dorsal portion of the scapula shows a quadrangular profile, which is very different from *Placodus* (SMF R1035), where it is anteroposteriorly longer and rounded. Nevertheless, this shape recalls the morphology of *Paraplocodus* (PIMUZ T 4775), although the absolute size of this taxon is much smaller. Moreover, the scapula of MSNM V927 shows several deep narrow longitudinal striations (Fig. 2) covering the lateral surface of the bone; these striations are similar to those of *Helveticosaurus* holotype, and to a minor extent to those of *Paraplocodus* (PIMUZ T 4775).

The general morphology of the tooth described (ST166120) recalls the mesial teeth of placodonts. The profile of its transverse section is triangular, mesiodistally flattened, and delimited by sharp edges; this makes this tooth different from placodonts: *Placodus* has shorter and sturdier mesial teeth, *Paraplocodus* mesial teeth show two lateral grooves and a major medial bulge on the lingual side (e.g., Peyer 1935; Rieppel 2000), that are absent in ST166120. In sum, the caniniform morphology of this specimen is consistent with the mesialmost maxillary teeth of *Helveticosaurus zollingeri* (Peyer 1955: taf. 91).

Taken together, the proportions of the transverse processes, the fully striated scapula and ribs, the absence of uncinat processes, the shape of the scapular blade, the relevant size of the bones, and the morphology of the tooth render the specimens cited herein more similar to *Helveticosaurus zollingeri* than to any other taxon.

Testing the phylogenetic position

To perform the phylogenetic analysis reported below we used PAUP* 4.0 and modified Scheyer et al.'s (2017) data matrix [in turn modified from Neenan

et al. (2013) - but see also Klein & Scheyer (2014)]. A heuristic search was used as search option; this was run with 100 trees set as the number of maximum trees in memory (automatically increased by 100 if this limit was hit), 10000 random replicates, and the Tree Bisection Reconnection (TBR) mode activated. A revision of the matrix used by Scheyer et al. (2017) led us to rescore a few characters for *Helveticosaurus*: namely, character 11 from “?” to “2” and character 67 from “1” to “0”, according to our interpretation of the skull; character 90 has been rescored from “?” to “0” according to our interpretation of the sacral ribs. Following our interpretation and description, specimen MSNM V928 might have possessed at least three sacral ribs; to test this hypothesis, in *Helveticosaurus* line, we modified Scheyer et al.’s (2017) character 88 from “?” to “1&2”: “1” describes the condition of possessing three ribs, whereas “2” stands for four or more. Such scoring does not describe a case of polymorphism but was chosen to take into account our new observation of more than two sacral ribs (i.e., excluding state ‘0’), while taking into account the uncertainty of the exact number of ribs (i.e. states 1 or 2). In addition, this allows to assess the reconstructed ancestral state of this character following a parsimony criterium. This single character matters since, among the taxa closest to *Helveticosaurus*, Thalattosauria and *Eusauropsphargis* possess two sacral ribs, whereas basal sauropterygians have three sacral ribs (e.g., Neenan et al. 2013).

The new line of *Helveticosaurus* now reads as follow: ?000100???2?00???1?????????01?????????????0?????????????1??1?0000000?000?00?010?1?10(1 2)?0010110000100?10010000111?11021010?012112?1?11000??.

Our analysis resulted in 8 MPTs of score 571 (Fig. S2). None of these trees recovered the clade “Helveticosauridae” *sensu* Nosotti & Rieppel (2003); also, *Helveticosaurus* never clustered as sister taxon of *Eusauropsphargis*, as reported by Li et al. (2014). On the other hand, in trees 1, 3, 4, and 7, *Helveticosaurus* was recovered as sister taxon of the clade Placodontia; in trees 2, 5, 6, and 8, *Helveticosaurus* was recovered as sister taxon to the group *Eusauropsphargis*+Sauropterygia, as also seen in Scheyer et al.’s (2018: fig 12b) analysis 8. The strict consensus tree is reported in Fig. 5. Given the topology of the 8 trees described above, in this tree a polytomy is found between *Helveticosaurus*, *Eusauropsphargis*, and Sauropterygia.

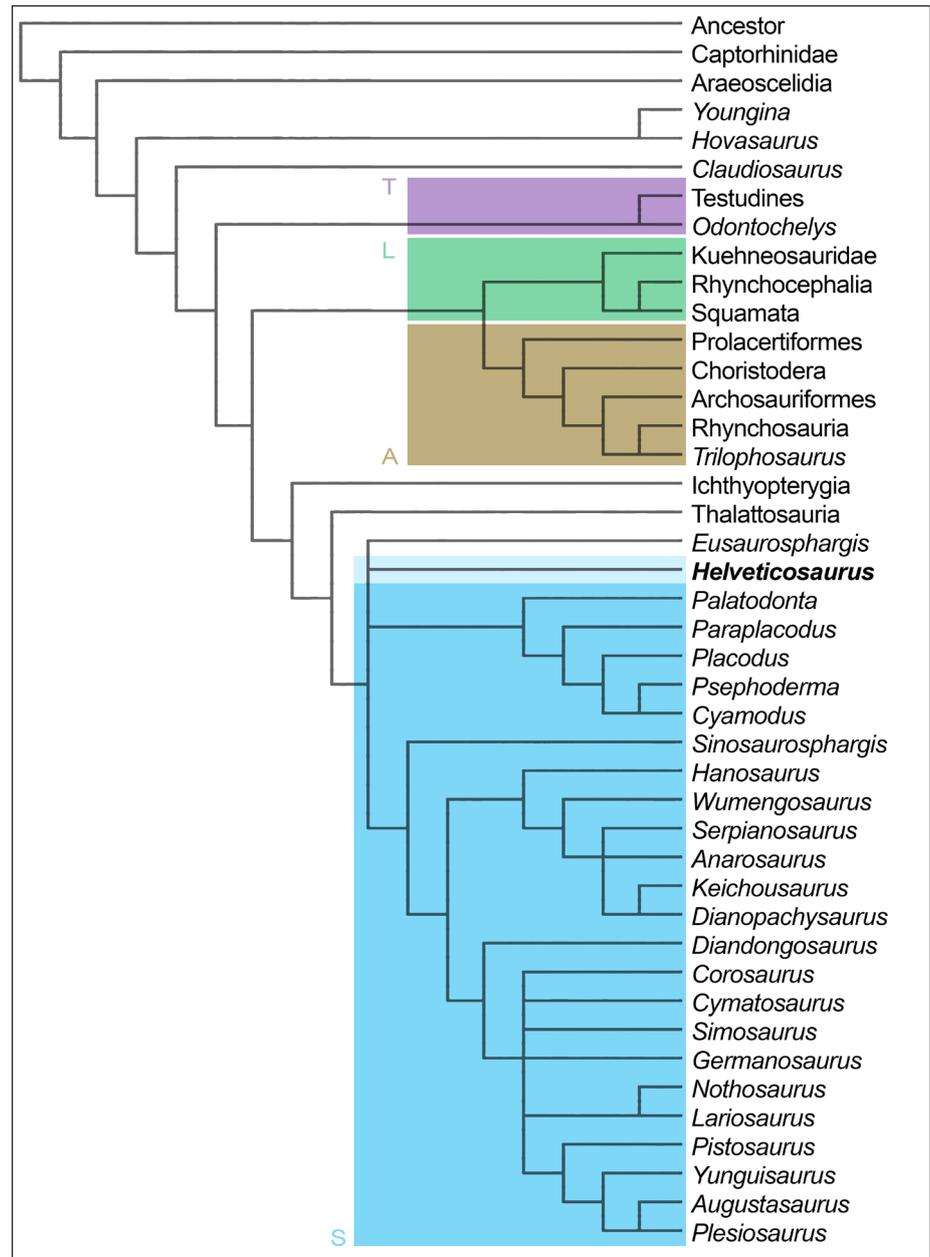
The PAUP* character reconstruction tool, when applied to the strict consensus tree, both with ACCTRAN (accelerated transformation) and DELTRAN (delayed transformation) character optimization, at the base of the polytomy *Eusauropsphargis*+*Helveticosaurus*+Sauropterygia predicts an ancestral state of “1” for character 88, which supports the hypothesis that *Helveticosaurus* had three sacral ribs.

Aquatic adaptations and swimming capabilities

The presence of *Helveticosaurus zollingeri* in Italy was reported for the first time by Renesto & Pieroni (2013) thanks to the isolated tooth from the Dolomia della Rasa (San Salvatore Dolomite). The occurrence of a species of *Helveticosaurus* in both the San Salvatore Dolomite and the Besano Formation suggests that its habitat might have been related to those environments, i.e., more proximal to the shoreline than to the open sea. This hypothesis is consistent with what is known about the anatomy of *Helveticosaurus*, which will be briefly reviewed in the following paragraph.

Rieppel (1989) discussed in detail the locomotion (aquatic and terrestrial) of *Helveticosaurus*. Hyperphalangy and paedomorphosis of several skeletal elements (e.g., mostly an unossified carpus and tarsus) clearly suggest a specialisation of the limbs for underwater locomotion. The author highlighted the presence of a humerus with a well-developed entepicondyle, where the flexor tendons of the hand and digits were attached, and therefore suggested that *Helveticosaurus* had occasional excursions on land. Rieppel (1989) also noted that paedomorphosis affected the hindlimb and the pelvic girdle more than the forelimb and the pectoral girdle, thus suggesting greater functional demand imposed on the forelimbs. After comparing rowing vs subaqueous flight (Robinson 1975; Godfrey 1984), the author hypothesised the mode of aquatic propulsion of *Helveticosaurus* as an intermediate form of the two and referred to the “otariid model” (*sensu* Godfrey 1984) as the most suitable to describe the swimming mode of the animal. Showing no particular specializations related either to rowing or to subaqueous flight, Rieppel (1989) suggested that the main propulsive thrust while swimming would have been provided by lateral undulation of the tail (estimated to be ~1.5 m long in the holotype) and of the posterior portion of the trunk, whereas the rowing of the forelimbs in an otariid-like cycle would have

Fig. 5 - Strict consensus tree of 8 MPITs, obtained from Scheyer et al. (2017) modified “third matrix” (see text). In four of the MPITs, *Helveticosaurus* was recovered as sister taxon of the clade Placodontia, whereas in the remaining four it was recovered as sister taxon to the group *Eusaurosphargis* + Sauropterygia. Turtle lineage highlighted in lilac, Lepidosauromorpha in green, Arcosauromorpha in light brown, and Sauropterygia in light blue.



greatly supported the underwater locomotion. A well-developed pectoral girdle and the inferred presence of powerful muscles could have provided these requirements. These could also have allowed the animal’s locomotion during its occasional excursion on land, and strong development of the transversospinalis system should have granted the possibility to lift the anterior portion of the trunk, the neck, and the head off the ground (Rieppel 1989).

Helveticosaurus undoubtedly had an aquatic or semiaquatic lifestyle, approaching the land only for basking, nidifying, grooming, or resting. This lifestyle is consistent with the finding of fossil specimens, such as ST166120, in a platform environment. MSNM V927 and 928 were recovered at the base

of the *N. secedensis* zone, which chronologically coincides with the beginning of the establishment of the intraplatform basin that characterizes the middle portion of the Besano Formation (Röhl et al. 2001): likely, the carcass of the animal has been transported from the shallow sea of the platform and sunk not far from its margin, in deeper sea.

Several adaptations to a semiaquatic lifestyle can be observed in *Helveticosaurus* (PIMUZ T 4352 and 4353); these are listed below, along with a new skeletal reconstruction of the animal (Fig. 6):

- elongate body shape (PIMUZ T 4352);
- laterally compressed, dorsoventrally tall tail (reported also by Peyer, 1955; PIMUZ T 4353);

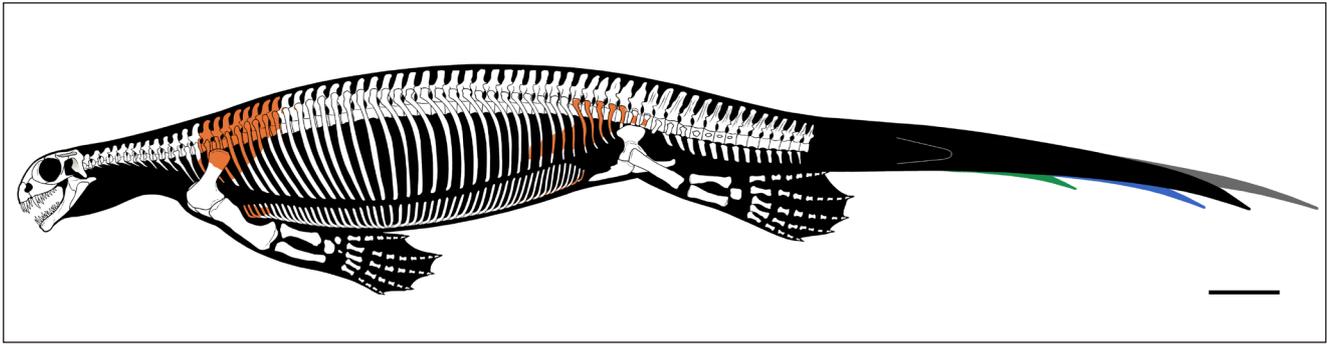


Fig. 6 - Skeletal reconstruction of *Helveticosaurus zollingeri*, based on all specimens known to date (Peyer 1955; Kuhn-Schnyder 1974; Rieppel 1989; Renesto & Pieroni 2013; this paper - bones highlighted in orange). To estimate the length of the tail, here we propose different options: in black, the original estimate of Kuhn-Schnyder (1974); the white outline is based on the body proportions of *Eusaurosphargis* (PIMUZ A/III 4380); the blue tail is based on *Placodus* (cast exposed in PIMUZ and SMF R1035); the grey tail is based on *Askeptosaurus* (Muller 2005); the green tail represents a conservative estimate based on the mean value between the white and the blue estimate. Line drawing by Marco Auditore. Scale bar equals 20 cm.

- skeletal paedomorphosis (e.g., carpus and tarsus mostly unossified in PIMUZ T 4352);
- hindlimbs length reduction (humerus longer than femur both in PIMUZ T 4352 and PIMUZ T 4353);
- broadened hand and foot, possibly webbed (oar-like *sensu* Massare 1994; PIMUZ T 4352);
- polyphalangy and elongated digits (PIMUZ T 4352);
- well-spaced phalanges (i.e., large amount of articular cartilage; PIMUZ T 4352).

Similar adaptations, typically acquired by convergent evolution, are variably present among vertebrates with a semiaquatic lifestyle, especially in transitional forms that secondarily moved back to water (e.g., *Ambulocetus*, *Spinosaurus*, *Thalassocnus*). In *Helveticosaurus*, carpus and tarsus are greatly unossified; their reconstruction in Fig. 6 is based on Rieppel's (1989: p.139-143) considerations. The distance among the phalanges is estimated on the basis of what is still observable in the holotype, since some digits appear less disarticulated than the rest of the limbs (in digit IV and V of left manus and left pes, some phalanges are still in line). Phalanges are partly unossified as well, missing most of the epiphyses. To reconstruct the tail, since most of it is missing, in Fig. 6 we propose various options to estimate its length. The presence of a middle caudal vertebra with a tall (although incomplete) neural spine and no transverse processes, preserved in PIMUZ T 4353, suggests that, in any case, the tail was dorsoventrally tall and laterally compressed at its base, a morphology that potentially grants to this appendage a valuable role in generating thrust while undulating laterally (e.g., Fish et al. 2021).

According to the categories defined by Motani & Vermeij (2021), given the discussion above and the anatomy of the animal, *Helveticosaurus* should fall in the M4 category, along with sea otters and most pinnipeds; among extinct vertebrates, the M4 category also includes all those sauropterygians that possess a humerus longer than the femur (including, e.g., Placodontia) and likely Saurosphargidae (sister clade to Sauropterygia according to some authors, e.g., Li et al. 2014). In step “M4 vertebrates”, terrestrial locomotion is limited only to exceptional cases and, if this attribution is confirmed, these animals evolved a fully marine diet and perhaps maintained water balance without terrestrial freshwater. Among sauropterygians, *Placodus gigas* (Drevermann, 1933) shares the most similar body proportions to *Helveticosaurus*, despite the latter possesses a slenderer silhouette and proportionally longer forelimbs. Carpus and tarsus are also greatly unossified in Nothosauria, although to a lesser degree than in *Helveticosaurus* (Rieppel, 1989). Taxa belonging to this clade, along with Pachypleurosauridae, possessing a humerus shorter than the femur, have been classified by Motani & Vermeij (2021) in M2-3 categories, so one step back in marine adaptations relative to Placodontia. Going further into this discussion, below we evaluate different swimming models to better define the swimming style of *Helveticosaurus*.

The otariid model, as described by Williams (2018), requires that the propulsive forces are generated almost entirely by the pectoral appendages, with the hind flippers occasionally being used for steering, as also seen in penguins and sea turtles. In this model, Feldkamp (1987) recognised three distinct

stroke phases: (1) a power phase, (2) a paddle phase (during which the majority of thrust is produced), and (3) a recovery phase. Following the hypotheses of Massare (1994), the oar-like non-hydrofoil limbs of *Helveticosaurus* might have been suitable more for subaqueous rowing than for subaqueous flight. In turn, the hindlimb of *Helveticosaurus* may have had a role in creating drag and therefore steering. Actually, the otariid model describes an already highly specialised swimming style that involves the loss of the tail and does not include any kind of body undulation, which is very likely present in a secondarily aquatic reptile like *Helveticosaurus*. According to Rieppel's (1989) observations and following Massare's (1994) bauplan II, the major thrust should have been produced by lateral undulation of the trunk and the tail. Therefore, the otariid model may not be entirely appropriate to describe the swimming style of *Helveticosaurus*. An array of tightly packed gastralia, as well as wide laterally projecting transverse processes, along with large ribs, might have limited to some degree the ability to undulate the trunk. Nonetheless, although massive, ribs and transverse processes are well-spaced (more than in some placodonts such as *Paraplacodus*), leaving room for some lateral movement of the axial skeleton in the trunk region. Consequently, some degree of lateral undulations of the trunk, at least of the posterior part (as suggested by Rieppel 1989), should be taken into account. With respect to the gastralia, tightly packed gastralia are also found in ichthyosaurs from the Middle Triassic with an inferred anguilliform swimming style (e.g., *Cymbospondylus* and *Besanosaurus*; Merriam 1908; Dal Sasso & Pinna 1996).

Looking among less specialised (but still semiaquatic) vertebrates, to understand how *Helveticosaurus* could have swum, a model worth to be evaluated is the otter model. Otters can use several combinations of their appendages to paddle and generate thrust; most importantly, otters can simultaneously make use of undulatory propulsion using their elongate, flexible bodies and tails (Fish 1994). According to Thewissen & Fish (1997), lutrines are the best extant functional models for early cetacean locomotion: the locomotor dynamic of *Ambulocetus* may have been most similar to that of *Lutra* or, to a lesser degree, to *Pteronura*. Williams (2018) describes the stroke cycle of sea otters (*Enhydra lutris*) as made of two phases: (1) a power phase (when thrust is produced), and (2) a recovery phase (when the limb

is repositioned for the next stroke). While swimming slowly and close to the surface, sea otters alternate strokes of the hindlimbs to generate thrust: since this drag-based mode of swimming is inefficient, in order to move quickly underwater otters can switch to an undulatory mode of swimming involving dorsoventral body flexion and simultaneous movements of the paired hindlimbs. In contrast to sea otters, giant river otters (*Pteronura brasiliensis*) have four webbed broad limbs and a paddle-like tail, dorsoventrally compressed (Beichman 2019); the trunk and tail undulations and the simultaneous paddling maximise thrust production while fast swimming (Fish 1994).

Among reptiles, short and broad limbs were cited by Massare (1994) as characteristics of smaller early mosasaurs, such as *Clidastes*. Among these, in contrast to crocodylians and bigger mosasaurs, the undulation of the entire body was likely the main propulsive action (with the amplitude increasing towards the tail; Lingham-Soliar 1991), the limbs were probably kept close to the sides of the body while swimming and used for extra thrust only during lunges. On the contrary, among sauropterygians, large *Notbosaurus* species (such as *N. giganteus* and *N. mirabilis*) likely provided the power stroke while swimming with paired movement of the forelimbs in an underwater flight cycle or an otariid-like stroke cycle, showing biomechanical adaptations convergently evolved later in Pistosauria (Krahl et al. 2013; Zhang et al. 2014). On the other hand, Placodontia shows a plethora of different swimming styles (e.g., Scheyer & Klein 2021): for example, it has been hypothesized that an anguilliform swimming mode for *Psephoderma* is very unlikely due to its rigid trunk and a sedentary lifestyle at the bottom of shallow waters (Renesto & Tintori 1995; Klein et al. 2015); *Cyamodus*, still being heavily armoured, thanks to a long and massive humerus would have more likely relied on powerful stroke cycles of row-like forelimbs (Klein et al. 2015); in both *Cyamodus* and *Psephoderma* some propulsion should have been granted also by lateral undulation of the hindlimbs, thanks to the sacral gap in the dorsal armour (Renesto & Tintori 1995; Klein et al. 2015); eventually *Placodus*, that possesses only a single row of osteoderms along the axial skeleton and among Placodontia shares the most similar bauplan with *Helveticosaurus*, has been classified as a subcarangiform swimmer (Braun & Reif 1985), an hypothesis supported by a laterally

compressed long tail (Drevermann 1933) and bone histology (Klein et al. 2015).

Once the necessary distinctions are made, especially in the bauplan of the vertebral column of a reptile, we can postulate that the swimming style of *Helveticosaurus* might have been a unique intermediate between the otariid and the otter model. In the latter, a flattened tail assumes a major role in generating thrust, as postulated by Rieppel (1989) for *Helveticosaurus*. In any case, the swimming style of *Helveticosaurus* must have been associated with lateral undulations of the tail (of which the length is still unknown) primarily, and the trunk secondarily, as in early mosasaurs, at least for its posterior portion. Unlike early mosasaurs, the limbs of *Helveticosaurus* might have had a more important role in generating thrust, especially the forelimbs, given the robust anatomy of the humerus (Rieppel 1989), as proposed for some nothosaurs and placodonts. Namely, while swimming at slow speed, the forelimbs could have generated thrust in a forelimb-otariid-like stroke cycle; nonetheless, the efficiency of such movements was limited by the non-hydrofoil, oar-like appendages, making a true subaqueous flight (as seen in large *Nothosaurus* species and later in pistosaurs) impossible in *Helveticosaurus*. The lateral undulations of the tail would still have had an important role, whereas the hindlimbs (less robust and less ossified than the forelimbs) might have been kept close to the body or had a minor role in producing thrust in a hindlimb-otter-like stroke cycle. While swimming at high speed, lateral undulations of the body, especially of the tail, would have generated most of the thrust, as also hypothesized for *Placodus* (Braun & Reif 1985; Klein et al. 2015); the limbs, kept close to the body, should have helped to minimize the drag produced during locomotion; the broad distal portion of the limbs could have also maximized the propulsion while undulating in concert with the body (as seen in giant river otters) and/or used for extra thrust during lunges (as postulated for early mosasaurs; Massare 1994). The true role of the hindlimbs in generating thrust, especially at high speed, depends on the tail length, estimated to be ~1.5 m in the holotype, for a total body length of ~3.5 m (Kuhn-Schnyder 1974), but still unknown. Their function might have been at least similar to that of rudder blades: being broad and possibly webbed, they could have generated a con-

siderable drag that could have been used to steer effectively and enhance maneuverability. Having four limbs to serve with this purpose could have granted great maneuverability, especially useful in shoreline environments.

The swimming style was of course strictly related to the hunting strategies and the diet of *Helveticosaurus*. Like smaller mosasaurs (Massare 1994), *Helveticosaurus* might have been capable of rapid acceleration, typical of ambush predators. Dentition and cranial anatomy suggest that this animal should have been a generalist predator. This is strengthened by the triangular cross-section, associated with two sharp cutting edges, observed in the tooth here described. Namely, the front teeth in particular were likely used to pierce and cut soft and/or bony prey, such as cephalopods, but also small and medium-sized vertebrates (Massare 1987).

CONCLUSIONS

The MSNM specimens, in spite of their fragmentary condition, represent an important addition to the rare fossil occurrence of *Helveticosaurus zollingeri*. Besides being the first record of skeletal remains and the second of the taxon in Italy, the specimen from Besano preserves a portion of the axial skeleton that is missing in the *Helveticosaurus zollingeri* holotype, shedding some light on the anatomy of its sacral region. In particular, MSNM V928 possibly hosts a portion of three sacral ribs: due to the fragmentary remains of *Helveticosaurus*, these bones were never reported before and are described here for the first time. Among the taxa closest to *Helveticosaurus*, Thalattosauria and *Eusaurosphargis* possess two sacral ribs, whereas basal Sauropterygia have three sacral ribs. To test the presence of three or more sacral ribs in *Helveticosaurus*, we updated the phylogenetic analysis of Scheyer et al. (2017). The PAUP analysis predicted the presence of three sacral ribs in *Helveticosaurus*, supporting our claim. Furthermore, in half of the MPITs, *Helveticosaurus* was recovered as sister taxon of the clade Placodontia, whereas in the rest of the MPITs, *Helveticosaurus* was recovered as sister taxon to the group Eusaurosphargis+Sauropterygia. The results also show that a loss of resolution appears at the base of the clade comprising (*Helveticosaurus*

(*Eusauropsphargis* (Sauropterygia))), suggesting that, pending further material, the position of *Helveticosaurus* still needs to be fully resolved.

The redescription of ST166120, aided by a digital model of the specimen, helped to better understand the morphology of the *Helveticosaurus* dentition and to better define the niche occupied by this animal in the Middle Triassic coastal ecosystems: our results strengthen the idea that *Helveticosaurus* might have been a dweller of the carbonate platform, with an amphibious lifestyle strictly associated to the shoreline environments and a carnivorous generalistic diet.

A reappraisal of the swimming style of *Helveticosaurus* leads us to suspect that this bizarre reptile might have been a unique intermediate between the otariid and the otter model: with the lateral undulation of tail generating the main propulsive thrust, the animal while swimming at slow speed could have also generated thrust with the forelimbs in a forelimb-otariid-like (or a hindlimb-otter-like) stroke cycle, whereas while swimming at higher speeds the limbs, kept close to the body, should have helped to minimize the drag, maximized the propulsion while undulating in concert with the body, and/or used for extra thrust during lunges.

This new finding is a consequence and part of the revision of the Besano fauna of the MSNM collections. The rediscovery of this unique specimen further encourages a reanalysis of the Besano-Monte San Giorgio fossils that are housed in the historical collections of natural history museums.

SUPPLEMENTARY FILE: 3D model obtained with photogrammetry of specimen ST166120.

Download the 3D pdf file here: <https://drive.google.com/file/d/1wDyfCPmFUeYjMdv1mEKZ0awZ0QaQxy0y/view?usp=sharing>

N.B. Open it with the latest updated version of Adobe Acrobat

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