

A NEW SPECIES OF *SAURICHTHYS* (ACTINOPTERYGII: SAURICHTYDAE) FROM THE MIDDLE TRIASSIC OF MONTE SAN GIORGIO

SILVIO RENESTO¹, FABIO MAGNANI² & RUDOLF STOCKAR²

¹Dipartimento di Scienze Teoriche ed Applicate, Università degli Studi dell'Insubria, Via Dunant 3, I- 41100 Varese, Italy.
E-mail: silvio.renesto@uninsubria.it

²Repubblica e Cantone Ticino, Dipartimento del Territorio, Museo cantonale di storia naturale, Viale Carlo Cattaneo 4, CH-6900 Lugano, Switzerland.

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Abstract. A new species of the actinopterygian fish genus *Saurichthys* is described on the basis of several specimens from the Sceltrich beds (Meride Limestone Formation) of the UNESCO World Heritage area of Monte San Giorgio. The new species shows among other characters, unsegmented lepidotrichia in all fins and elongated and wide paired fins, suggesting a different adaptation for swimming and catching preys with respect to other *Saurichthys* species of Monte San Giorgio. Phylogenetic analysis suggests that the new species is closely related to the *Saurorhynchus* species group. The new finding adds further knowledge to the plasticity and functional adaptations of the genus *Saurichthys*, which was one of the most successful actinopterygians of the Triassic.

INTRODUCTION

Actinopterygians diversified extensively after the PT (Permian/Triassic) extinction event (Tintori et al. 2014; Kogan & Romano 2016a; Puttick et al. 2017). One of the most successful clades that radiated globally during the Triassic period is the paleopterygian family Saurichthyidae Owen, 1860. Ranging from the latest Permian to the Middle Jurassic (Romano et al. 2012; Tintori et al. 2014; Maxwell 2015), Saurichthyidae comprise nearly fif-

ty known species, of which the majority has been described from Early-Middle Triassic deposits (e.g. Romano et al. 2012; Kogan & Romano 2016a). Saurichthyids are characterized by an elongate rostrum and body, the arrangement of scales in longitudinal rather than transversal scale rows, the far posteriorly placed dorsal and anal fins and a symmetrical caudal fin. Based on their anatomy, saurichthyids are considered the earliest fast-start ambush predators among ray-finned fishes (Fletcher et al. 2014; Kogan et al. 2015). While their general body plan remained the same during all their evolutionary history, Saurichthyidae differentiated into several species, characterized by different body size, proportionally

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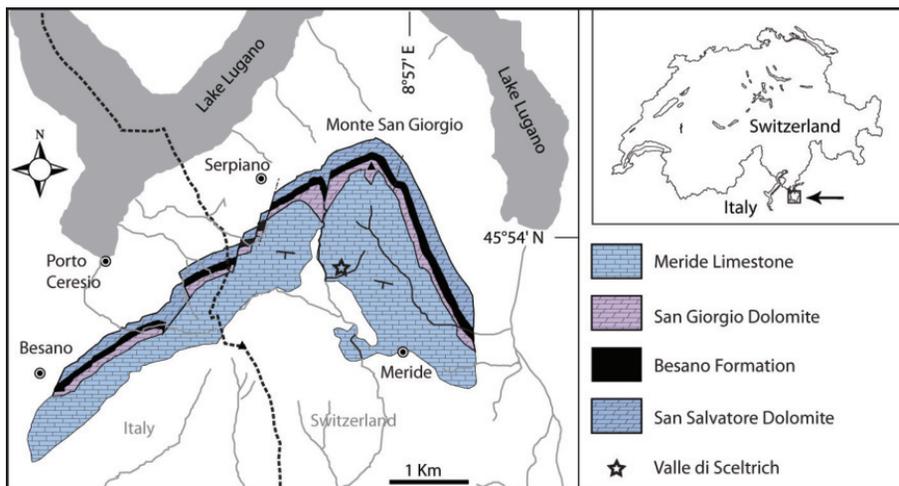


Fig. 1 - Map of the Monte San Giorgio area (Ticino, Southern Switzerland), showing the carbonate Anisian–Ladinian sequence together with the Valle di Sceltrich locality.

different jaw length, subopercular outline and size, extension of squamation, fin rays segmentation, and structure of the vertebral column (Rieppel 1985; Tintori 1990, 2013; Maxwell et al. 2015). Some of these differences have been interpreted both as evolutionary trends (Rieppel 1992; Mutter et al. 2008; Romano et al. 2012) and also as adaptations to different niches and feeding strategies (Hu et al. 2011; Tintori 2013; Tintori et al. 2014).

So far, six species of *Saurichthys* are known from the Middle Triassic (Anisian-Ladinian) Monte San Giorgio localities (Switzerland and Italy): *S. paucitrichus* Rieppel, 1992, *S. rieppeli* Maxwell, Romano, Wu & Furrer, 2015, and *S. breviabdominalis* Maxwell, Romano, Wu & Furrer, 2015 from the Besano Formation (also named Grenzbitumenzone by Swiss authors), *S. macrocephalus* (Deecke, 1889) and *S. curionii* (Bellotti, 1857) from the overlying Ladinian Meride Limestone, *S. costasquamosus* Rieppel, 1985 from both the Besano Formation and the Meride Limestone (Argyriou et al 2016a). In the present paper we describe a new species of *Saurichthys* from the Sceltrich beds (Meride Limestone) which adds further knowledge to the diversity and paleoecology of the genus *Saurichthys* from the Monte San Giorgio area.

GEOLOGICAL SETTING

The Middle Triassic carbonate succession of Monte San Giorgio (Switzerland-Italy; Figs. 1, 2), belonging to the western part of the Southern Alps, has been inscribed in the UNESCO World Heritage List (WHL) because of its unique paleontological value. It is, in particular, world-famous for

the exceptionally well-preserved fossil fishes and marine reptiles (e.g. Rieber 1973a; Kuhn-Schwyder 1974; Bürgin et al. 1989; Etter 2002; Rieppel 2019). In Middle Triassic times, the South-Alpine domain was situated at a northern intertropical latitude of about 15–18° (Muttoni et al. 2004) and was strongly influenced by monsoonal circulation (Preto et al. 2010). This passive continental margin open to the western Neo-Tethys was progressively submerged by a long-term transgression from the east. The marginal location of the Monte San Giorgio Basin resulted in a peculiar sedimentary succession and in temporarily dysoxic to anoxic bottom water conditions (e.g. Bernasconi 1994; Röhl et al. 2001; Etter 2002; Stockar 2010; Stockar et al. 2013). The Middle Triassic succession (Fig. 2) starts with fluvio-deltaic deposits (Bellano Formation, Illyrian; Sommaruga et al. 1997), unconformably overlying Lower Triassic transitional clastic deposits (Servino, Induan – Olenekian; Frauenfelder 1916; Sciunnach et al. 2015), in turn onlapping an erosional unconformity at the top of a Lower Permian volcanic basement. The following upper Anisian sediments indicate the progressive transgression of a shallow epicontinental sea and the related expansion of carbonate platforms (San Salvatore Dolomite; Zorn 1971) north of an emerged land area, which is nowadays covered by the Po Plain (Brusca et al. 1981; Picotti et al. 2007). During the latest Anisian and the Ladinian, although shallow-water sedimentation continued in the north, an intraplatform basin opened in the area of the Monte San Giorgio, which led to the deposition of the Besano Formation, the San Giorgio Dolomite, and the Meride Limestone (Rieber 1973a; Bernasconi 1994; Furrer 1995; Röhl et al. 2001). The Besano Formation (“Grenzbitu-

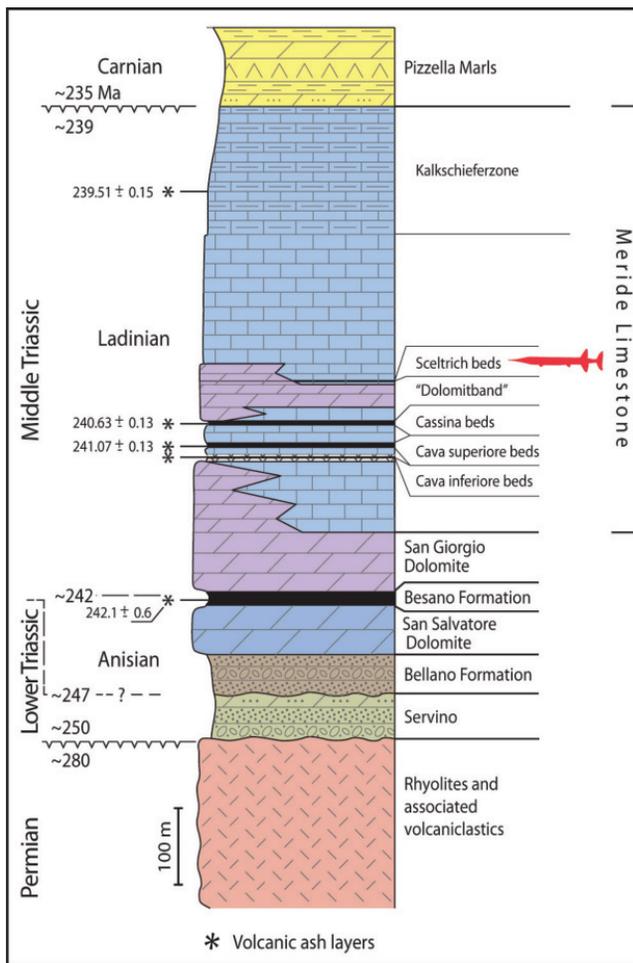


Fig. 2 - Stratigraphic column of the Monte San Giorgio area, *Saurichthys* shape indicates the level that yielded the new specimen.

menzone”; Frauenfelder 1916) directly overlies the Lower Salvatore Dolomite and is composed of a 16 m thick alternation of black shale and laminated dolostone. Its uppermost part includes the Anisian/Ladinian boundary (Brack & Rieber 1993; Brack et al. 2005). Most of the spectacular vertebrate fossils together with important index invertebrate fossils come from this formation (e.g. Rieber 1973a,b; Kuhn-Schnyder 1974; Bürgin et al. 1989; Etter 2002; Rieppel 2019). The Besano Formation grades upwards into the San Giorgio Dolomite and the Meride Limestone, together constituting a 614 m-thick sequence in total (Stockar et al. 2012). Recent studies (Stockar 2012; Stockar et al. 2013) showed that the San Giorgio Dolomite results from early and late diagenetic dolomitization, the latter cutting across stratification and affecting the original limestone in an irregular pattern up to a major volcanoclastic bed (“Val Serrata tuff”). The Lower Meride

Limestone consists of well-bedded micritic limestone, laminated limestone and volcanoclastic layers. Three fossiliferous intervals, informally known as “Cava inferiore beds”, “Cava superiore beds” and “Cassina beds”, mainly consist of finely laminated limestone and yielded different vertebrate fossil assemblages (e.g. Peyer 1931; Sander 1989; Furrer 1995; Stockar 2010; Stockar & Renesto 2011). The top of the Lower Meride Limestone is defined by a very discontinuous dolostone horizon (“Dolomitband”; Frauenfelder 1916) resulting from late diagenetic dolomitization cutting across the stratification of the Meride Limestone (Stockar 2012; Stockar et al. 2013). The overlying Upper Meride Limestone is a sequence of alternating well-bedded micritic limestone and marlstone. The uppermost part comprises the 120 m thick “Kalkschieferzone” (Senn 1924), made up of thinly-bedded, mostly laminated, limestone and marlstone with peculiar faunas of fishes, crustaceans and insects (e.g. Wirz 1945; Furrer 1995; Krzeminski & Lombardo 2001; Bechly & Stockar 2011; Lombardo et al. 2012; Montagna et al. 2018). Finally, the following Carnian regressive phase resulted in the formation of sabkha-type depositional environments and in the related sedimentation of evaporites (Pizzella Marls; Furrer 1995).

The fossiliferous interval yielding the specimens described herein belongs to the lowermost part of the Upper Meride Limestone and was informally introduced as “Sceltrich beds” in Stockar (2012) and Stockar et al. (2013). Its age is assigned to the transition interval between the Gredleri and Archelaus Ammonoid Zones (sensu Brack & Rieber 1993) of the Ladinian Stage (Stockar et al. 2012). After a first exploration in 2010 yielding the first fossils from this horizon (Stockar 2012), two small bed-by-bed excavations on a surface of around 6 and 10 square meters respectively were started in 2012 by the Museo cantonale di storia naturale (MCSN, Lugano) under the direction of the last author. The site is located on the northern bank of a small creek (Valle di Sceltrich; Swiss National Coordinates: 716'910/84'370; WGS8 coordinates 8.4503/45.90084; Fig. 1), northwest of the village of Meride. The fossiliferous interval consists of a 30 cm thick sequence of prevailing organic-rich laminated limestone (up to 3.1 % TOC) intercalated between thick-bedded marly limestone. In the Valle di Sceltrich area, this fossiliferous horizon lies around 2.5 m above the “Dolomitband”. At plac-

es, the laminated limestone shows storm-generated concentrations of platform-derived skeletal grains and thin-shelled bivalve pavements (Stockar 2012; Stockar et al. 2013). Benthic microbial activity accounts for the microfibrils observed in the laminated limestone, including clotted-peloidal micrite and amorphous organic matter showing EPS (extracellular polymeric substance)-like structures as well as for the geochemical signature being characterized by high hydrogen indices and prevailing Type-II (Type I) kerogen (Stockar et al. 2013). Preservation of such a labile lipid-rich organic material requires anoxic/lower dysoxic bottom-water conditions (Stockar et al. 2013 and references therein). Lower dysoxic conditions were able to allow episodic seafloor colonization by thin-shelled opportunistic posidonioid bivalves (Stockar 2012; Stockar et al. 2013). On the other hand, both lower dysoxic and anoxic bottom-water conditions ruled out higher macrobenthos, including scavengers, and resulted in complete oxygen depletion within the sediment. Coupled with widespread oxygen depletion excluding benthic scavenger organisms, rapid coating of skeletons by benthic bacterial mats ('microbial shroud' effect; Gall 2001) played the key role in protecting the carcasses from decay and in holding skeletal elements together (see also Furrer 1995, 1999; Stockar 2010), thus accounting for the microfibrils observed in the laminated limestone and for the exquisite preservation of the vertebrate fossils (Stockar et al. 2013).

So far, the excavation carried out in the Sceltrich beds yielded a rich vertebrate fossil fauna mainly consisting of mostly articulated fish specimens (López-Arbarello et al. 2016, 2019; Renesto & Stockar 2018). Rare sauropterygian reptile bones and teeth, invertebrate fossils (mostly bivalves and crustaceans; Stockar & Garassino 2013) and terrestrial plant remains complete the fossil assemblage.

MATERIAL AND METHODS

Institutional abbreviations: MCSN – Museo Cantonale di Storia Naturale in Lugano; PIMUZ - Paläontologisches Institut und Museum, Universität Zürich.

The new *Saurichthys* species here described is based on eight preserved specimens, housed in the MCSN with the following catalogue numbers: MCSN 8318, 8347, 8428, 8429, 8449, 8450, 8480, 8481, 8485-8488, 8505, 8506, 8604-8607. The material has been collected from the Sceltrich beds of the Meride Limestone (Stockar et

al. 2013) in the locality Valle di Sceltrich (Monte San Giorgio, Canton Ticino, Switzerland; Fig. 1) during the 2012–2018 excavations carried out by the MCSN. The Sceltrich beds yielded four additional *Saurichthys* specimens (MCSN 8433, 8484, 8507, 8516) which may also belong to the new species but either lack diagnostic features (MCSN 8433, 8507, 8516) or represent juveniles (MCSN 8484). Five other *Saurichthys* specimens were collected from the same levels (MCSN 8447, 8517, 8518, 8519, 8608); these latter, on the basis of available evidences, may belong to *Saurichthys paucitrichus* Rieppel 1992, thus are not described in the present study. Open nomenclature is used in agreement with Bengtson (1988).

All specimens were mechanically prepared with vibrotools and sharp steel needles under a stereomicroscope by one of the authors (FM) and by the late S. Rampinelli. Several photos were taken using a Nikon D800 digital camera and Micro-Nikkor 105mm AFS lens and a SIGMA Sd Quattro H camera with a SIGMA 105mm f2.8 Macro OS lens.

The following specimens from Monte San Giorgio were analyzed as comparative material: PIMUZ T 4106 (*Saurichthys macrocephalus*), T 3913, T 3914, T 3915, T 3917, T 4154, T 4156 (*Saurichthys curionii*); MCSN 8014, 8023, 8295, 8559 (*S. curionii*).

The anatomical nomenclature used here follows that of previous works on *Saurichthys* (e.g. Rieppel 1985; Argyriou et al. 2016a; Kogan & Romano 2016a,b), but homology with similarly named bones of other vertebrates is not strictly implied. The dorsalmost bone in the operculogular series of *Saurichthys* has historically been interpreted as an expanded opercle (e.g. Stensiö 1925; Rieppel 1985), but recent reanalyses of the homologies of this element (Argyriou et al. 2016b) suggest that it is actually an expanded subopercle, since it contacts the ventral end of the hyomandibula. Thus the terminology used in the present study follows this interpretation. While describing the scales, "length" refers to their antero-posterior extension, "width" to the lateral dimension in mid-dorsal and mid-ventral scales, "depth" to the dorso-ventral extension of the mid-lateral and ventro-lateral scales. Measurements of body proportions and skeletal features follow Rieppel's (1985) scheme. Since ossified haemal arches are present along most of the vertebral column, the point of the transition from abdominal to caudal region of the axial skeleton is based on the appearance of haemal spines.

SYSTEMATIC PALAEONTOLOGY

Class OSTEICHTHYES Huxley, 1880

Subclass ACTINOPTERYGII Cope, 1887

Order **Saurichthyiformes** Aldinger, 1937

Family Saurichthyidae Owen, 1860

Genus *Saurichthys* Agassiz, 1834

Type species: *Saurichthys apicalis* Agassiz, 1834, from the Middle Triassic of Bavaria, Germany.

***Saurichthys sceltrichensis* sp. n.**

Figs 3-21

Holotype: MCSN 8505 (Fig. 3), a complete specimen with a total length of 430 mm, and a fork length of 385 mm. The skull and pectoral fins are seen in dorsal view; the axial skeleton in lateral view. The holotype is preserved on the same slab with two other specimens: one (MCSN 8480) lies above another specimen (MCSN

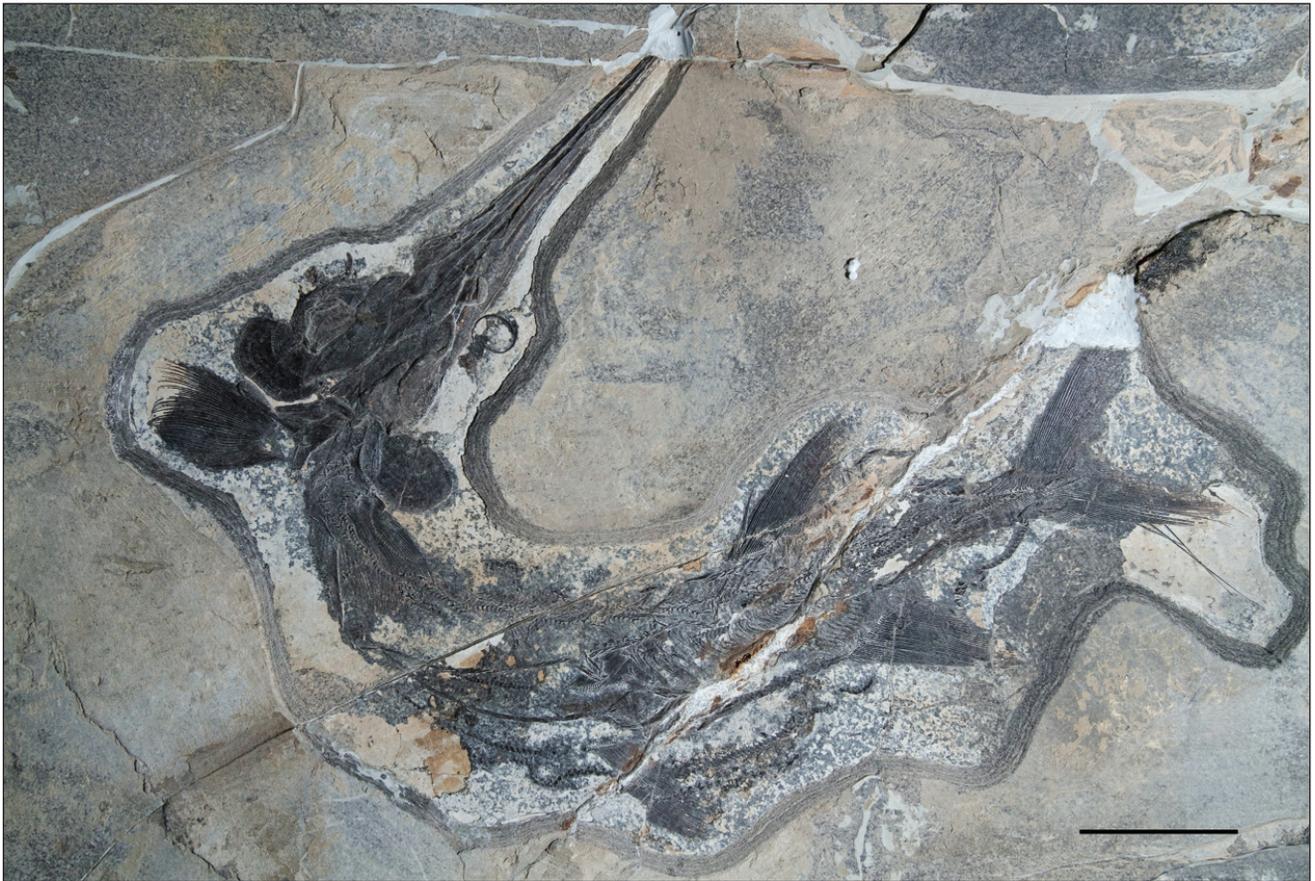


Fig. 3 - *Saurichthys sceltrichensis* sp. n. Specimen MCSN 8505, holotype. Scale bar equals 50 mm.

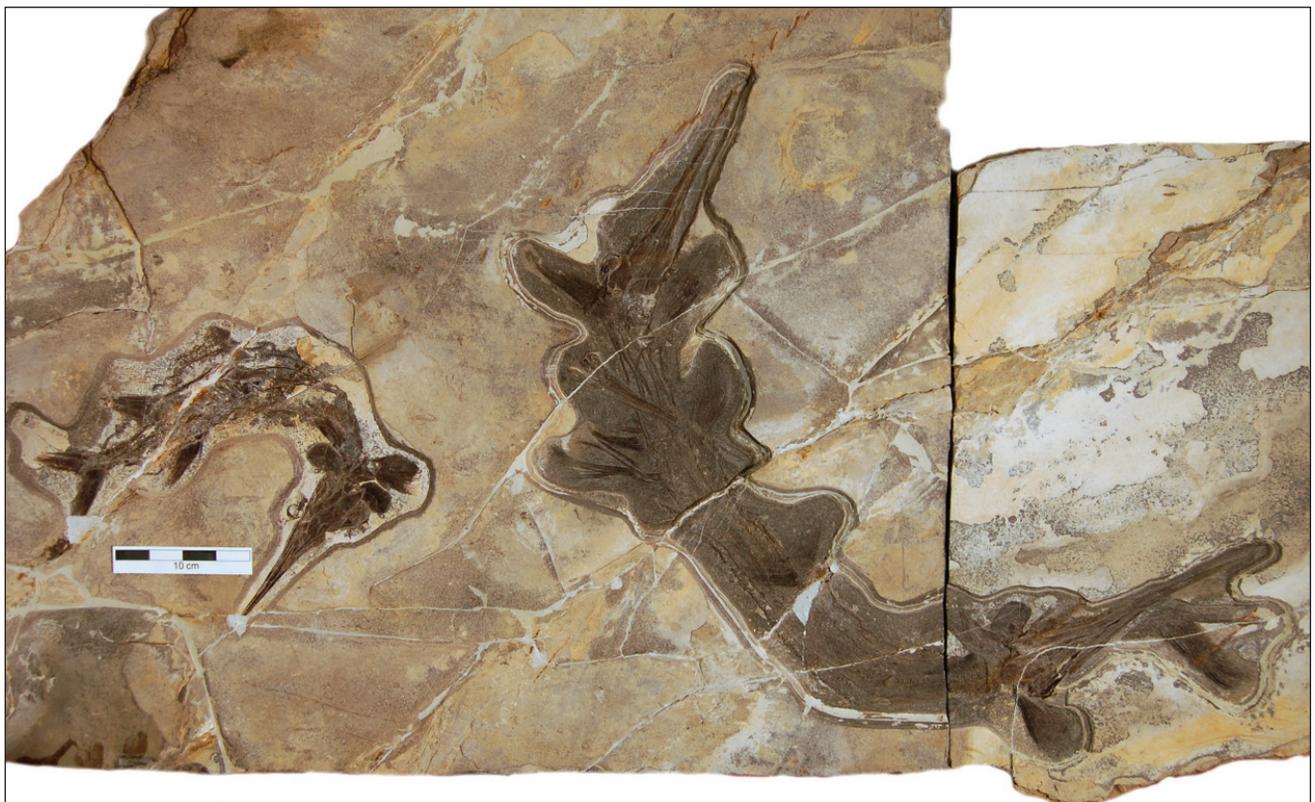


Fig. 4 - *Saurichthys sceltrichensis* sp. n. The entire slab containing the holotype MCSN 8505 and other two specimens (MCSN 8480 and 8506) plus the rostrum of a fourth one (MCSN 8507). Scale bar equals 100 mm.



Fig. 5 - *Saurichthys sceltrichensis* sp. n. Skulls of A) specimen MCSN 8505 (holotype), B) MCSN 8428, C) MCSN 8506, D) MCSN 8429. Scale bars equal 50 mm.

8506), and is also pierced by a saurichthyid rostrum fragment (MCSN 8507) just behind its dorsal fin (Fig. 4).

Derivatio nominis: From the type locality (Valle di Sceltrich) because this is the most abundant species of *Saurichthys* in this locality and horizon, and the fish is furthermore exclusively known from there.

Paratypes: MCSN 8428, 8429, 8480, 8481, 8607.

Referred specimens: MCSN 8318, 8347, 8449, 8450, 8485-8488, 8506, 8604-8606.

Diagnosis: *Saurichthys sceltrichensis* sp. n. is diagnosed by the unique combination of the following characters: subopercle 1.4–1.5 times higher than long; presence of well-ossified haemal arches in the

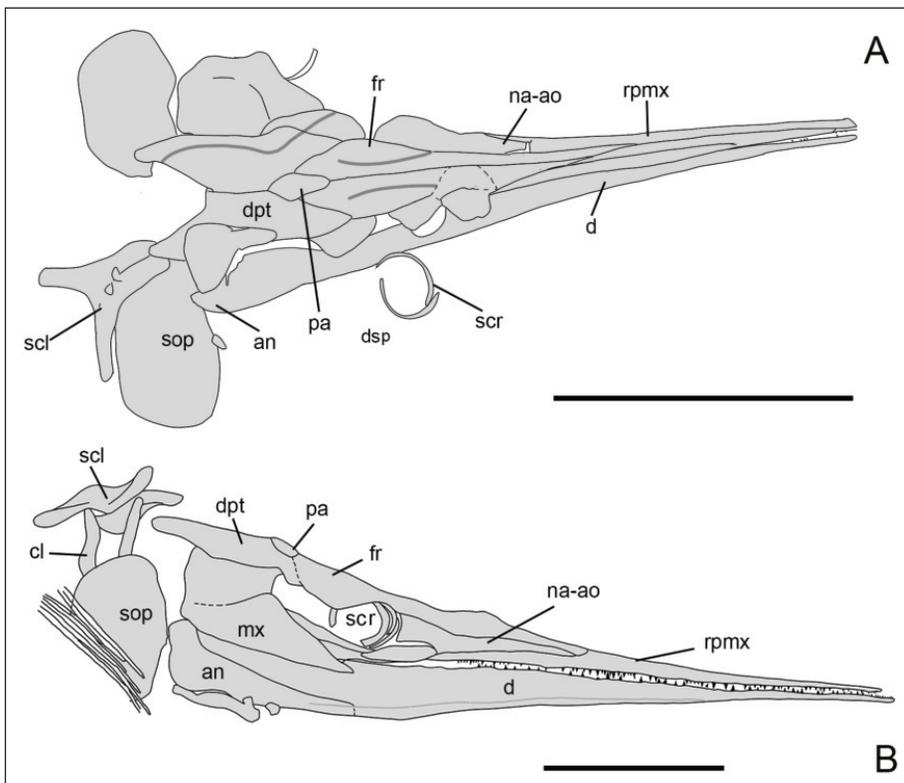


Fig. 6 - *Saurichthys sceltrichensis* sp. n. Interpretative drawings of A) the skull of the holotype, (MCSN 8505) and B) of specimen MCSN 8428. Abbreviations are: an, angular; cl, chleithrum; d, dentary; dsp, dermosphenotic; dpt, dermopterotic; fr, frontal; mx, maxilla; na-ao, nasalo-antorbital; pa, parietal; rpmx, rostromaxilla; scl, supracleithrum; scr, sclerotic ring bones; sop, subopercle. Dark grey lines represent the path of sensory canals. Scale bars equal 50 mm.

Specimen (MCSN)	TL	FL	SL	PL	DL	MD	SOL	SOD
8318	305	290	105	192	240	25	13	18
8347	-	-	127	262	325	-	16	21
8428	-	-	183	385	513	-	25	37
8429	-	-	215	-	-	-	31	44
8449	-	432	-	250	336	35	-	-
8450	-	-	75*	-	-	-	10	13
8480	670	625	190	370	495	50	24	35
8481	255	237	73	150	190	180	11	15
8485	-	-	-	-	-	-	12	16
8487	(95)	(10)	-	57	75	7	-	-
8505	430	385	120	250	288	30	19	27
8506	(670)	(620)	-	-	-	-	-	-
8604	410	400	145	246	310	40	-	-
8606	305	280	114	175	220	20	12	18

Tab.1 - Measurements (in mm) taken on *Saurichthys sceltrichensis* sp. n. Abbreviations: TL, total length (from the apex of the rostrum to the end of the caudal fin); FL, fork length (from the apex of the rostrum to the apex of the caudal peduncle); SL, skull length; PL, pelvic insertion length (from the apex of the rostrum to the first ray of the pelvic fin); DL, dorsal insertion length (from the apex of the rostrum to the first ray of the dorsal fin); MD, maximum depth of the body; SOL, subopercle length; SOD, subopercle depth. The asterisk (*) in the SL of MCSN 8450 indicates that the measurements were taken from the mandible (from the apex of the dentary to the end of the angular). Measures in brackets indicate that the measurement is an estimation due to disarticulation of the skull (MCSN 8487) or superimposition of another specimen (MCSN 8506).

posterior portion of the abdominal region; parietal anteriorly narrow; all fins with unsegmented, distally branched lepidotrichia; paired fins expanded; mid-lateral scales diamond-shaped.

Type locality: Valle di Sceltrich (cf. Stockar et al. 2013), on the southwestern slope of Monte San Giorgio (Canton Ticino, Switzerland).

Type stratum: From the Ladinian (late Middle Triassic) 'Sceltrich beds', Meride Limestone (cf. Stockar et al. 2013).

Measurements Measurements of the best preserved specimens are given in Tab.1

Description

Skull. (Fig. 5-7) The rostrum shows the elongate and anteriorly pointed outline which is typical for *Saurichthys*. The unpaired rostromaxillary bone forms the main portion of the rostrum, it is followed posteriorly by paired nasaloantorbitals and frontals. The maxilla has the typical subtriangular, anteriorly pointed shape with a postorbital plate height to length ratio of approximately 0,7 (in the specimens with the skull exposed in lateral view and the maxilla well visible). The frontal is elongated caudally and is constricted in the orbit area, so that orbit opens both laterally and dorsally; its suture with the dermopterotic lies posterior to the orbit. The parietal is a single, median bone, without any sign of a suture along its midline. The anterior margin of the parietal, which contacts the frontals, is deeply convex, whereas the posterior border is angled and wedged between the dermopterotics, so that the bone has an arrow-head outline (Fig. 7). Two paired sensory canals are visible on the dermal skull roof, corresponding to the supraorbital canal and the postorbital canal, respectively. The supraorbital canal runs from the nasaloantorbital to the part above the orbit, whereas the postorbital canal is visible crossing the dermopterotics in antero-posterior direction (Fig. 6A).

The sclerotic ring consists of two thin crescent-shaped bones (Fig. 5-6).

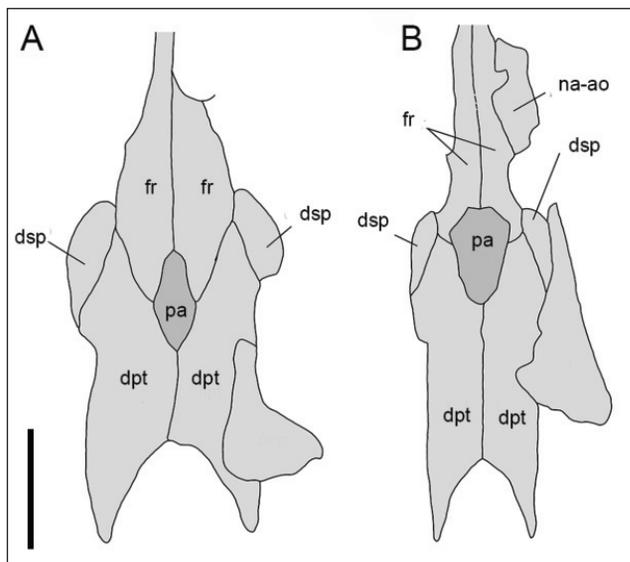


Fig. 7 - *Saurichthys sceltrichensis* sp. n. Comparison between the skull roof of the holotype (MCSN 8505) (A) and of *S. curionii* specimen MCSN 8559 (B). Abbreviations are: dsp, dermosphenotic; dpt, dermopterotic; fr, frontal; na-ao, nasaloantorbital; pa, parietal. Scale bars equal 10 mm.

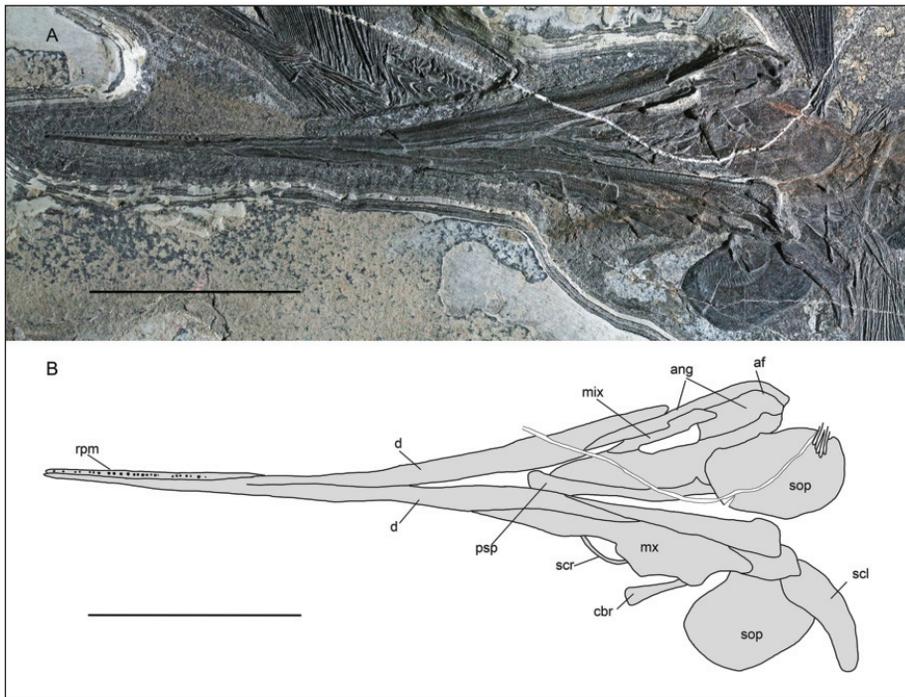


Fig. 8 - *Saurichthys sceltrichensis* sp. n. A) Specimen MCSN 8480, skull in ventral view B) line drawing of A. Abbreviations: af, articular fossa; ang, angular; cbr, ceratobranchial; d, dentary; mix, mixocoronoid; mx, maxilla; psp, parasphenoid; rpm, rostromaxilla; sop, subopercle; scl, supraclithrum; scr, sclerotic ring. Scale bars equals 50 mm.

The elongate anterior portion of the parasphenoid is visible in specimen MCSN 8480, exposed in ventral view; it is characterized by a crest running along the longitudinal axis of the bone. Posterior to the orbit, the median area of the parasphenoid bears several small teeth.

Lower jaw. The dentary (Fig. 6, 8) is elongate and slender. It forms most of the lower jaw. Its external surface is ornamented with subvertical striae in its lateral portion, and with tubercles in the ventral region, extending to almost the entire length of the bone. The angular is subtriangular, located in

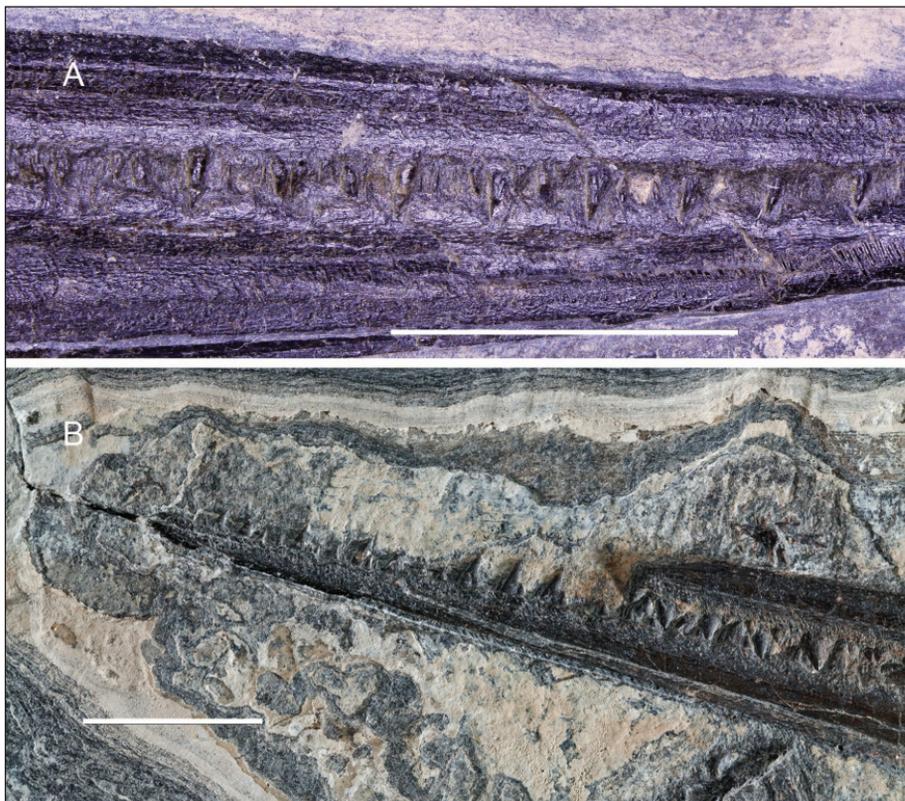
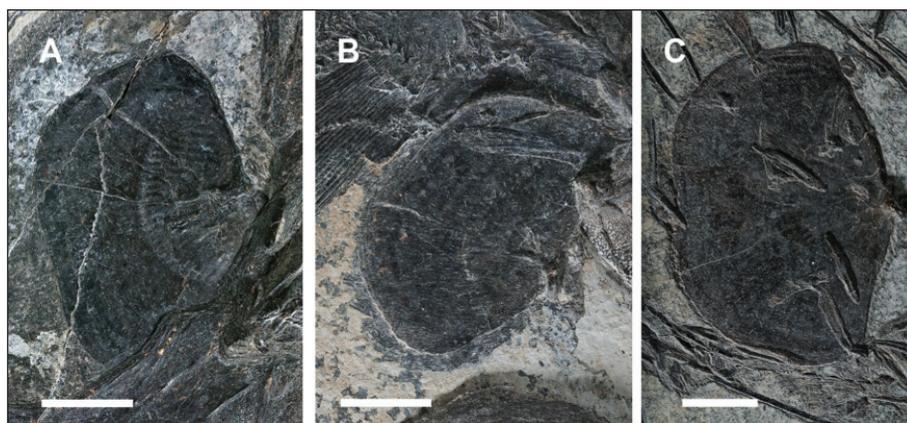


Fig. 9 - *Saurichthys sceltrichensis* sp. n. detail of the dentition of specimen MCSN 8428 (A) and MCSN 8429 (B). Scale bars equals 10 mm.

Fig. 10 - *Saurichthys sceltrichensis* sp. n. subopercle of specimen MCSN 8480 (A), MCSN 8505, holotype (B) and MCSN 8429 (C), medial view. Scale bars equal 10 mm.



the postero-ventral part of the mandible. The angular is ornamented with tubercles, which occasionally may be fused to form striae. The left mandibular branch of specimen MCSN 8480 shows the internal side, bearing the mixicoronoid, the insertion area of the abductor muscle of the maxilla, and the articular fossa of the jaw joint (Fig. 8). The abductor fossa is an elliptical depression extending from halfway the length of the angular anteriorly, to the posterior margin of this bone. The articular fossa is a concavity running near the posterior vertical edge of the angular.

Dentition. The jaws of *S. sceltrichensis* sp. n. bear teeth of three different size classes (Fig. 9). On the labial edge of both jaws, large teeth (up to 2.25 mm high) are intercalated with several smaller ones (up to 0.4 mm high). Near the external edge of the jaws, some denticles are present (up to 0.25 mm high). Teeth are conical, they are ornamented with vertical striae running from the tooth base to a smooth acrodin cap that covers the tooth apex. The jaw margins have incisions on their labial edge, each corresponding to a crypt for the teeth of the opposite jaw. Specimen MCSN 8429 shows a lower jaw that is distinctly longer than the upper jaw (Fig. 9B). The anterior tip of the rostromaxillae in this specimen shows tiny tubercles, indicating that the upper jaw is complete and the length disparity is not an artefact. In this specimen even the anteriormost portion of the dentary bears several robust teeth.

Subopercle. The subopercle (Fig. 10) has a subelliptical outline with an almost straight anterior margin. The external surface is ornamented by concentric striae, some tubercles are present near the dorsal and ventral edges of the bone. The internal surface is smooth except for a circular recess posterior to the articular process between the subopercle

and the jaws. In smaller specimens (e.g. MCSN 8450, 8481), the subopercle has a more circular shape. The depth/length ratio increases during growth, so that in adult specimens (e.g. MCSN 8505, 8480) the subopercle becomes 1.4–1.5 times deeper than long.

Cleithrum. The cleithrum shows the inverted T-shape which is typical of most *Saurichthys* species, showing a dorsal, an antero-ventral, and a posterior branch. The external surface of the bone is ornamented by rows of tubercles running parallel to the outline of the bone. The antero-ventral process of the cleithrum is bilobate at its anterior end, probably for articulation with the clavicle (Rieppel 1985). The posterior process is broad and rounded, and the dorsal process is elongate and slender.

The endoskeletal pectoral girdle is not preserved in the examined material.

Axial skeleton. The axial skeleton is made by paired neural and haemal elements encircling the notochord. There are 80 abdominal and 64 caudal neural arch elements, for a total of 144 neural arches (corresponding to 72 vertebrae). The hemi-neural arches meet their antimere along the midline. The neural arches are expanded at their ventral margin, they bear anteroposteriorly elongate prezygapophyses, and well-developed postzygapophyses (Fig. 11, 13) that overlap part of the adjacent neural arches, thus stiffening the trunk. The high paired neural spines are postero-dorsally inclined and widen towards their distal end up to the caudal peduncle, where the neural spine disappear and the neural arches assume a “T”-shaped outline in lateral view, which is retained in the entire caudal portion of the axial skeleton. In some specimens such as MCSN 8480, 8607 (Fig. 11, 13) and the holotype, the anteriormost hemi-neural arches are disassociated so

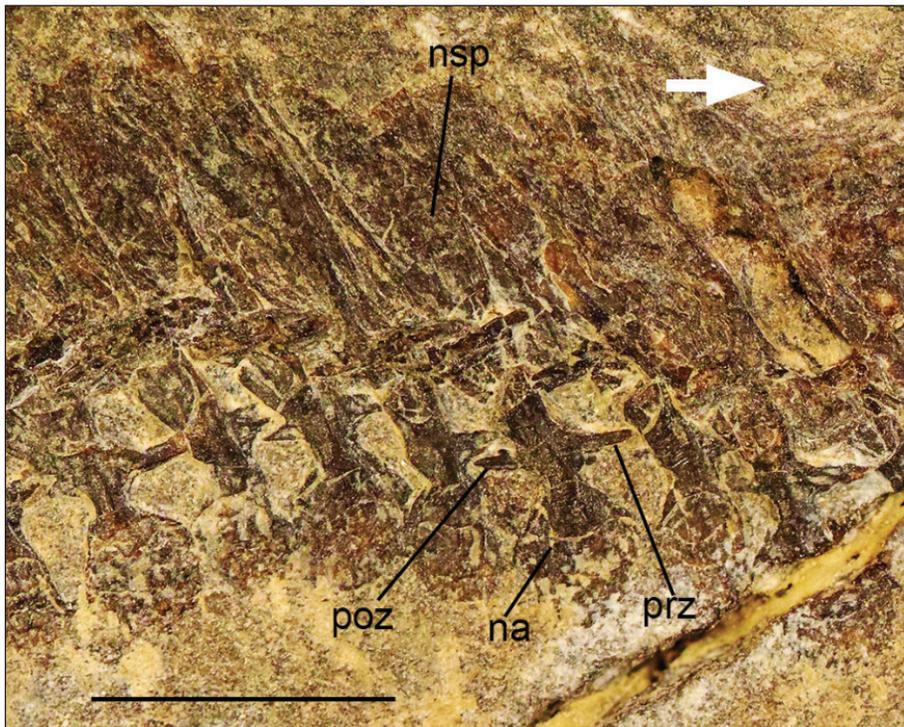


Fig. 11 - *Saurichthys sceltrichensis* sp. n. Neural arches and spines of the anterior region of specimen MCSN 8607, showing the presence of well developed, interlocking pre- and postzygapophyses. Abbreviations are: na, neural arches; nsp, neural spines; poz, postzygapophyses; prz, prezygapophyses. The white arrow indicates anterior (cranial) side. Scale bar equals 5 mm.

that the left and right hemi-neural arches are shifted reciprocally so that both are visible.

Ossified haemal elements are present along most of the vertebral column. In the abdominal region they are box-like (Figs. 12-13). In the abdominal region, where the haemal arches are well visible, there is a 1:2 ratio between the haemal and neural arches (each haemal arch corresponds to two neural arches), whereas in the caudal region the haemal arches show a 1:1 ratio with the neural arches throughout the vertebral column. Posterior to the insertion of the pelvic fins, the haemal arches bear elongate, ventrocaudally directed haemal spines.

Paired fins. Pectoral fins (Fig. 14 A, B) are long and distally wide, assuming a subtriangular fan-like

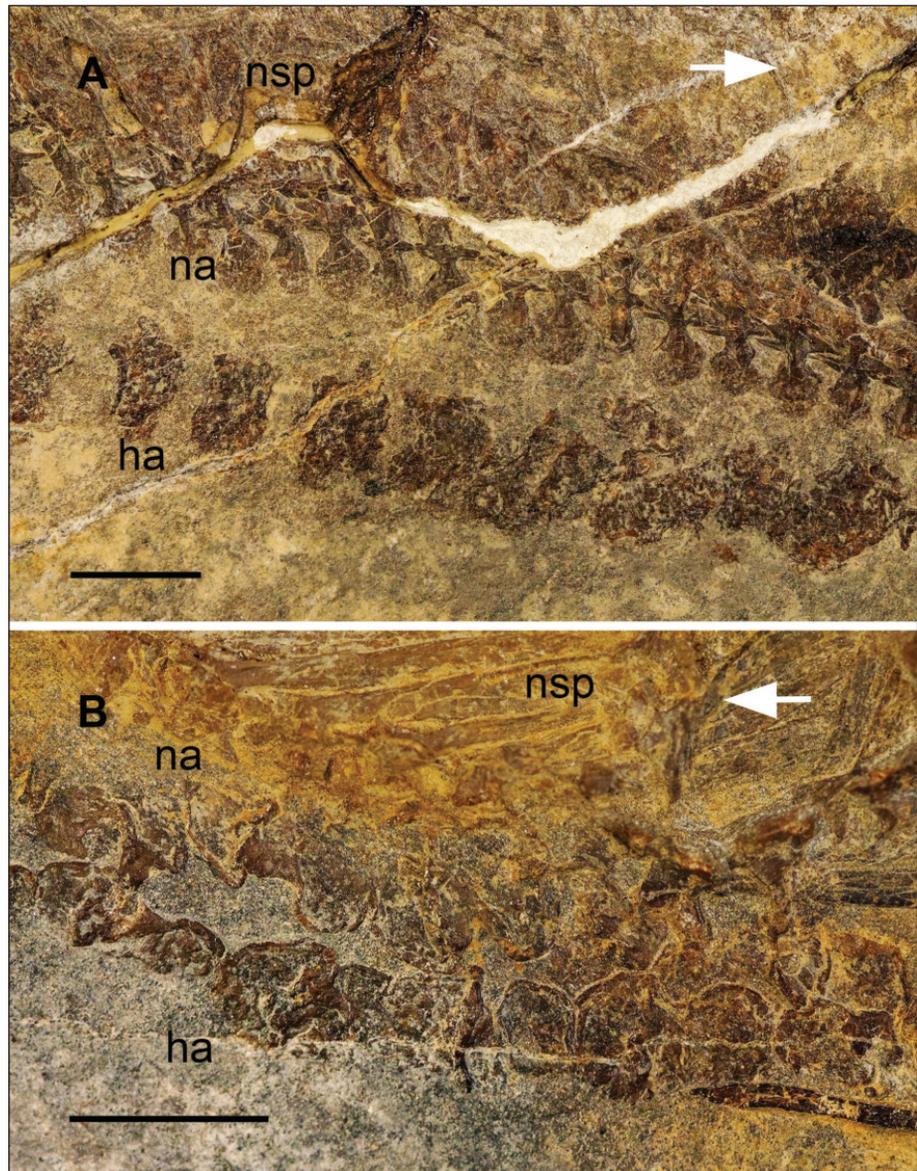
shape; in the holotype the pectoral fins consist of up to 50 (Tab. 2) unsegmented lepidotrichia. All lepidotrichia are distally branched at least once (twice in the longest lepidotrichia). Some lepidotrichia of the left pectoral fin of specimen MCSN 8480 show nodular thickenings probably due to the formation of callus, which we interpret as healed fractures. The radials of the pectoral fin are not preserved in any specimen.

The pelvic fins (Fig. 14 C, D) are also proportionally elongate, they lie posterior to the middle of the trunk (measured from occiput to the caudal end of the axial skeleton). In the holotype, each pelvic fin consists of 40 unsegmented, distally branched lepidotrichia. The pelvic plate and the radials are

Specimen (MCSN)	Pectoral fins	Pelvic fins	Dorsal fin	Anal fin	Caudal fin
8318	-/-	28	64	47	48/30
8347	31	27	-/-	-/-	-
8428	40	35	-/-	-/-	-
8449	-/-	-/40	65	63	48/41
8450	-/-	29/-	51	-	43/36
8480	37/18	36/40	68	53	36/42
8481	-/31	-/35	66	54	44/42+14
8485	-/22	24/27	46	29	-
8487	-/-	-/26	39	35	30/33+10
8488	-/-	-/-	-	40	-
8505	41/30	37/37	65	66	48/44
8506	-/-	-/-	-	-	-/45
8604	-/28	37/37	53	40	42/41
8605	-/38	-/45	60	55	45/50+8
8606	23/25	50/34	62	50	40/40

Tab. 2 - Number of preserved fin rays in specimen of *Saurichthys sceltrichensis* sp. n. For paired fins the first number refers to the right fin, the second, when present, to the left fin. For the caudal fin the count is epichordal lobe/hypocordal lobe + terminal lobe (when preserved).

Fig. 12 - *Saurichthys sceltrichensis* sp. n. Details of the vertebral column in the abdominal region of specimen MCSN 8607 showing ossified, box-like haemal arches: A) area immediately posterior to the skull, B) area anterior to the pelvic fins. Abbreviations are: ha, haemal arches; na, neural arches; nsp, neural spines. The white arrows indicate anterior (cranial) side. Scale bars equal 5 mm.

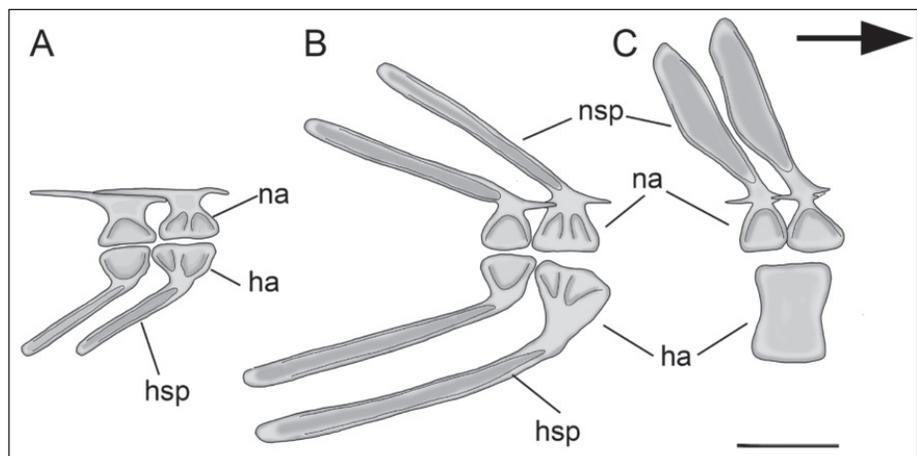


not visible in the studied specimens.

Median fins. The number of lepidotrichia in the dorsal fin in the examined specimens ranges from 50 to 73. Lepidotrichia are elongate and unsegmented

and are all distally branched once (Fig. 15 A-B). The dorsal fin is supported by a single series of pterygiophores in the anterior part, and two series in the posterior part. There are 16 axonosts (proximal

Fig. 13 - Interpretative drawings of vertebral elements from different regions of vertebral column in *Saurichthys sceltrichensis* sp. n.: A) caudal peduncle, B) caudal region and C) abdominal region. Abbreviations are: ha, haemal arches; na, neural arches; hsp, haemal spines, nsp, neural spines. The black arrow indicates anterior (cranial) side. Scale bar equals 10 mm.



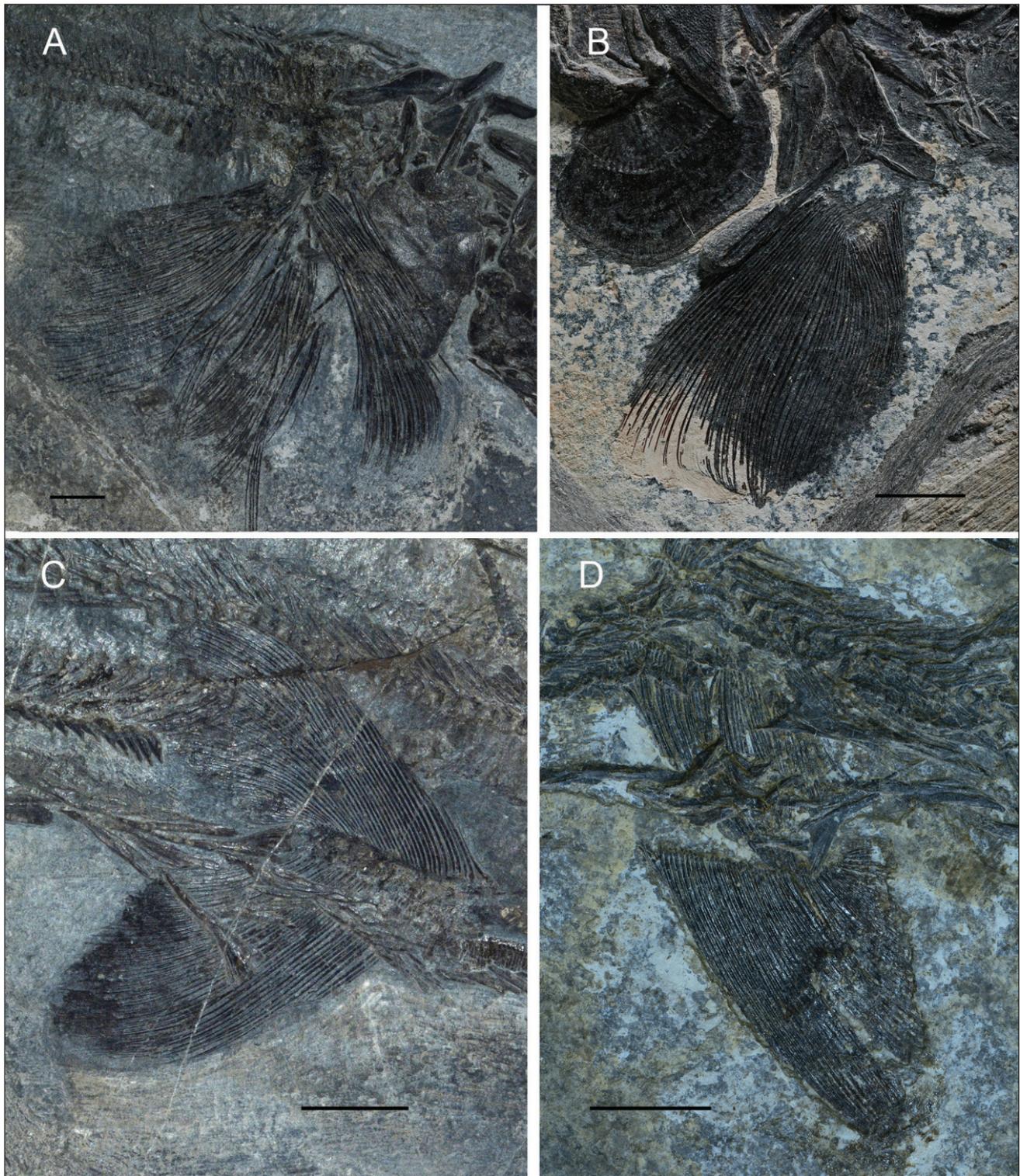


Fig. 14 - *Saurichthys sceltrichensis* sp. n. Pectoral fins of specimen MCSN 8428 (A) and MCSN 8505 (B); pelvic fins of specimen MCSN 8428 (C) and MCSN 8449 (D). Scale bars equal 10 mm in A, B and D, 20 mm in C.

pterygiophores) in total. The length of the axonosts decreases caudally, but the proximal pterygiophores show the same morphology throughout the fin base. Only the first axonost is distinctly wider than the others. The baseosts (distal pterygiophores) are detectable only in the incomplete dorsal fin of speci-

men MCSN 8428 (Fig. 16). The baseost series starts at the level of the 19th lepidotrichium. In MCSN 8428, four baseosts are in situ and an additional, disarticulated baseost is located just anterior to the dorsal fin. The baseosts are box-shaped and in two of them a foramen is clearly visible.

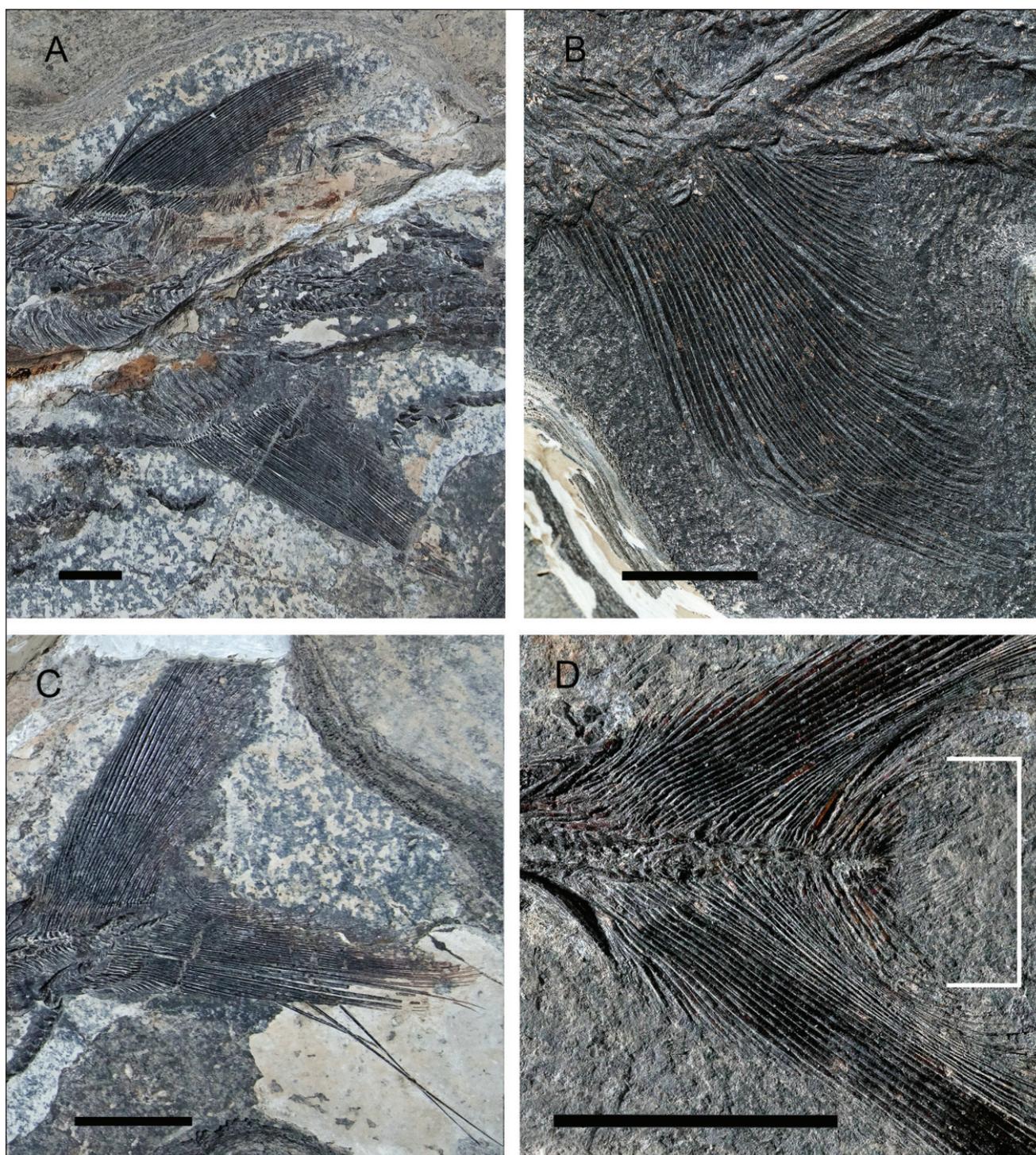


Fig. 15 - *Saurichthys sceltrichensis* sp. n. A) Dorsal and anal fins of the holotype (MCSN 8505), B) anal fin of specimen MCSN 8480. Scale bars equal 10 mm. *Saurichthys sceltrichensis* sp. n. Caudal fin of the holotype (C) and of specimen MCSN 8481 (D); in (D) the white bracket indicates the caudal “tuft”. Scale bars equal 10 mm.

The shape and size of the anal fin is similar to that of the dorsal fin (Fig. 15 A-B): it consists of up to 66 unsegmented fin rays in the holotype which bifurcate once distally.

The caudal fin (Fig. 15 C-D) is symmetrical (abbreviate-diphycercal, Brough 1936) and deeply forked as is typical in *Saurichthys*. Each lobe is

composed of up to 48 unsegmented fin rays that become distally branched. In MCSN 8481, a juvenile specimen, a ‘tuft’ composed of 14 or 15 small lepidotrichia (Fig. 15 D) is present between the epichordal and the hypochordal lobe (= ‘terminal lobe’; Rieppel 1985:30).

Fringing fulcra are absent in all fins.

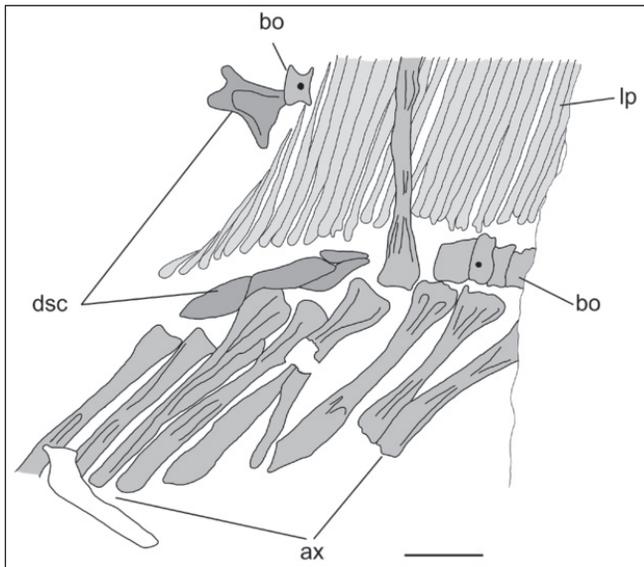


Fig. 16 - *Saurichthys sceltrichensis* sp. n. Drawing of the endoskeleton of the dorsal fin of specimen MCSN 8428. Abbreviations: ax, axonosts; bo, baseosts; dsc, scales of the dorsal row; lp, lepidotrichia. Scale bar equals 5 mm.

Squamation. *Saurichthys sceltrichensis* sp. n. bears six scale rows (Fig. 17): one mid-dorsal, one mid-ventral, two mid-lateral, and two ventro-lateral rows.

The mid-dorsal scales (Fig. 17A) are elongate and narrow. The exposed portion is ornamented with strongly-developed tubercles in adult specimens (e.g. MCSN 8429). Two small, unpaired ba-

sal fulcra are present at the base of the dorsal fin. The mid-dorsal scales posterior to the dorsal fin are broader than preceding ones and gradually increase their width caudally so that the last scale at the base of the caudal fin is the widest one.

The mid-ventral scale row starts about midway between the pectoral fins and pelvic fins and runs backwards until the caudal fin, with an interruption in correspondence of the anal fin. The mid-ventral scales (Fig. 17B) are elongate, narrow and ornamented with strongly developed tubercles in large specimens (e.g. MCSN 8429). At the level of the pelvic fins, the mid-ventral scale row divides into two rows forming the anal loop which is made up of six scales on each side (Fig. 18). The anal loop scales are small and leaf-like in the anterior part, whereas the two most posterior pairs are much larger. The last anal loop scale is a long and narrow paired structure. The unpaired mid-ventral scales between the anal loop and the anal fin are again shorter and similar in morphology to the mid-ventral scales anterior to the anal loop. In the caudal peduncle, the five or six mid-ventral scales anterior to the caudal fin are modified in a similar manner as the opposing mid-dorsal scales: they are broadened and flattened and their size increases posteriorly.

In smaller (juvenile) specimens (e.g. MCSN 8450, 8481) the mid-dorsal and mid-ventral scale rows have the same shape of the adult specimens, but they have weakly-developed tubercles. The

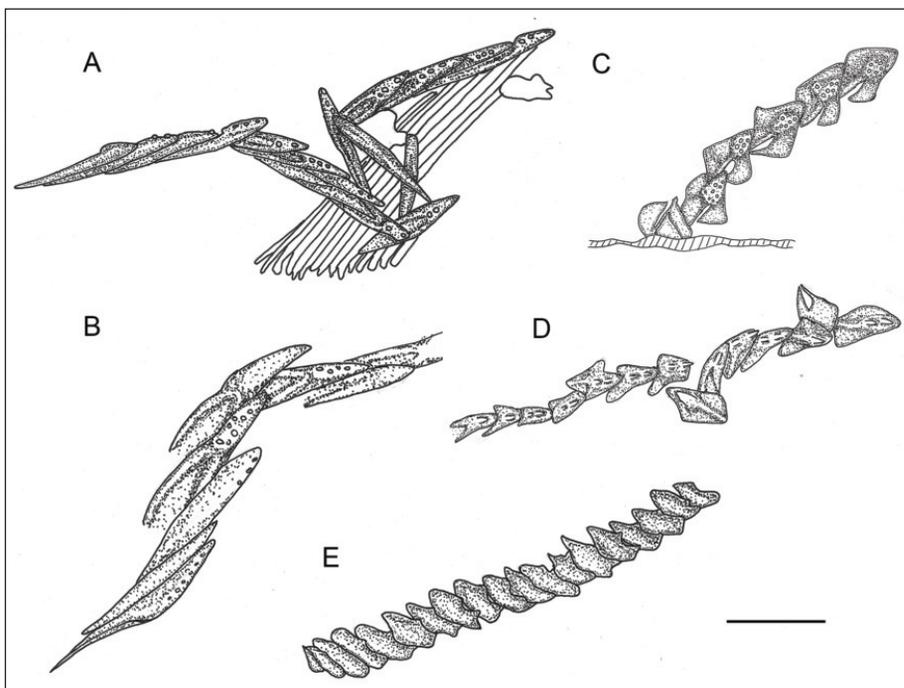


Fig. 17 - *Saurichthys sceltrichensis* sp. n. Squamation. A) scales of the mid-dorsal row of the holotype MCSN 8505, B) scales of the mid-ventral row of specimen MCSN 8480, C) scales of the mid-lateral row of specimen MCSN 8480, D-E) scales of the ventro-lateral row of specimen MCSN 8480, and 8505, respectively. Scale bar equals 5 mm.

Fig. 18 - *Saurichthys sceltrichensis* sp. n., anal loop of mid-ventral scale row in the holotype (MCSN 8505). Scale bar equals 10 mm.



mid-lateral scale rows start posterior to the skull and reach the caudal fin and show a 1:1 ratio between the neural arches and with the mid-dorsal scale row. The mid-lateral scales (Fig. 17C) are diamond-shaped and their surface is convex, they are covered with tubercles on top of the raised surface. In the caudal peduncle, the mid-lateral scales become smaller and triangular-shaped. The internal surface of the mid-lateral scales shows an incision in the anterior scale margin, indicating the passage of the lateral line sensory canal.

The paired ventro-lateral scale rows begin anteriorly almost at the same level as the mid-ventral scale row. In the abdominal region, they are small and triangular and ornamented with small, caudally-directed spines along their midline. Caudally to the pelvic fins, the ventro-lateral scales develop an elliptical outline, becoming dorsoventrally elongate with a smooth surface, while caudally to the anal fin they are again triangular-shaped and smaller, with a smooth but raised surface (Fig. 17D-E).

Prey evidences and gastrointestinal tract preservation

In the anterior portion of the abdominal cavity of MCSN 8481, just posterior to the head, three complete specimens belonging to Peltopleuriformes (cf. *Habroichthys*) are preserved (Fig. 19A-B); two of them are well visible, the third one lies below the other two and only a portion of the skull roof is visible; also in MCSN 8428 a peltopleuriform specimen is visible in the region of the abdominal cavity, just anterior to the pelvic fins (Fig.

19C-D), the perfect preservation suggests it may be a taphonomic artifact, that is, the peltopleuriform might have been deposited above the carcass of MCSN 8428 rather than being ingested however the overlapping of some mid ventral scales support the interpretation as a prey item. In MCSN 8318, the internal cast of part of the gastrointestinal tract is visible, the cololite (*sensu* Agassiz 1833-1843 and Argyriou 2016a) runs parallel to the notochord close to the ventral margin of the abdominal cavity and ends slightly posteriorly to the pelvic fins as if prolaxed somewhat after death. In MCSN 8450, the final tract of the intestine is visible (Fig. 19E) where the cololite tapers off before reaching the cloaca, individuated by the anal loop; in this specimen the characteristic constrictions of the spiral valve turns cannot be seen clearly.

Discussion

The skeletal correlates of the examined specimens allow their assignment to the genus *Saurichthys* with confidence (see Stensiö 1925; Rieppel 1985; Mutter et al. 2008; Kogan & Romano 2016a). Up to now, six species of *Saurichthys* are known from the Middle Triassic of Monte San Giorgio: *S. curionii* (Bellotti 1857), *S. macrocephalus* (Deecke 1889), *S. costasquamosus* Rieppel 1985, *S. paucitrichus* Rieppel 1992, *S. rieppeli* Maxwell et al. 2015, and *S. breviabdominalis* Maxwell et al., 2015. These species have different but overlapping stratigraphic ranges. The newly described specimens show a unique combination of characters which, while present separately also in other *Saurichthys* species, never

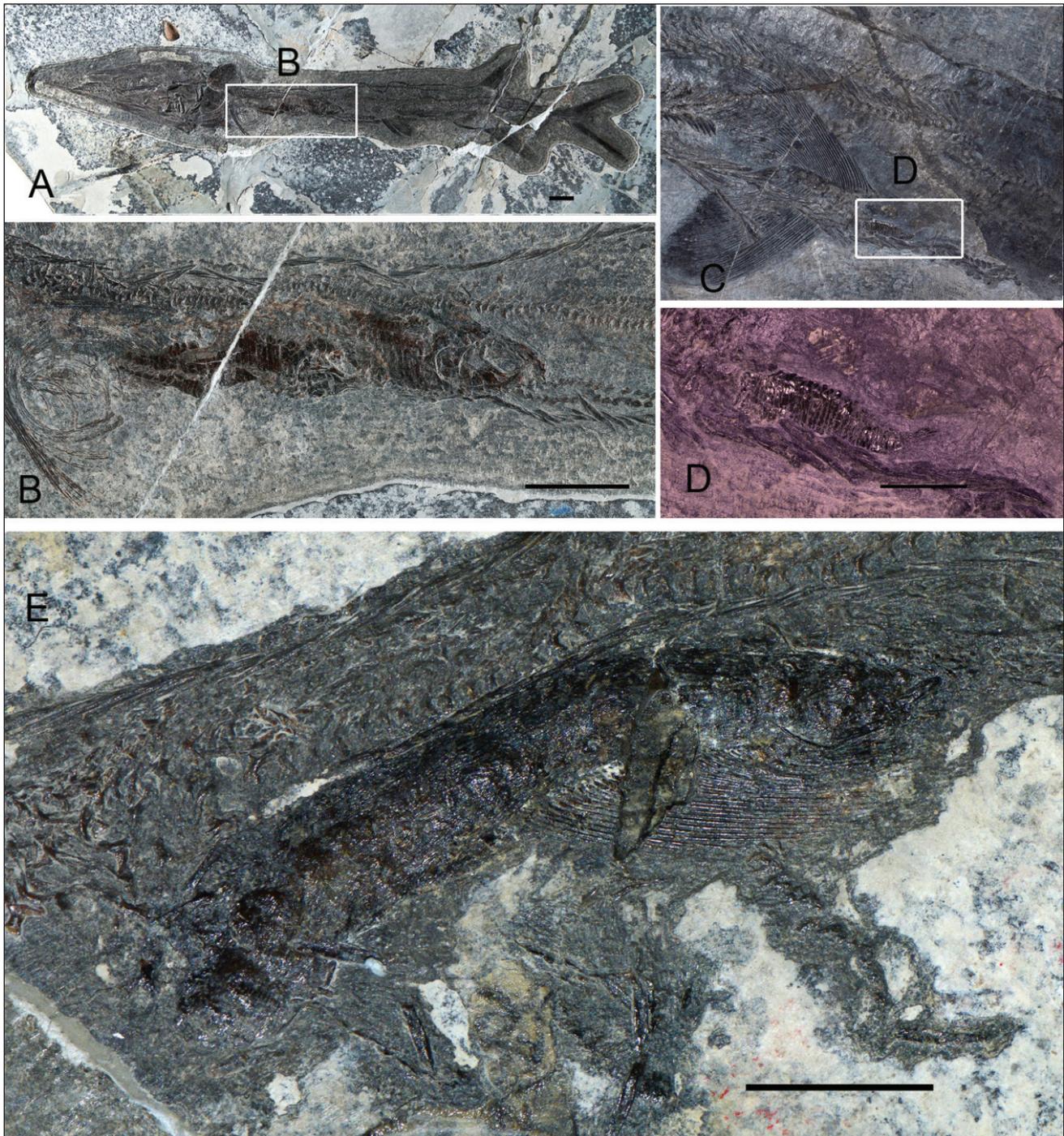


Fig. 19 - *Saurichthys sceltrichensis* sp. n. A-B) peltopleuriform specimens preserved in the abdominal region of specimen MCSN 8481, C-D) peltopleuriform specimen preserved close to the pelvic fins of specimen MCSN 8428, E) cololite preserved in the abdominal region of specimen MCSN 8450. Scale bars equal 10 mm.

occur together. The characters are: subopercle 1.4–1.5 times higher than long; presence of well-ossified haemal arches in the posterior portion of the abdominal region; parietal anteriorly narrow; all fins with unsegmented, distally branched lepidotrichia; paired fins expanded, mid-lateral scales diamond-shaped.

Specimens attributed to *Saurichthys sceltrichensis* sp. n. differ from those belonging to other known *Saurichthys* species from Monte San Giorgio in several characters, the main differences are listed here: they differ from *S. costasquamosus* and *S. macrocephalus* in the more slender skull with smaller teeth, from *S. paucitrichus* in the larger adult size and the higher num-

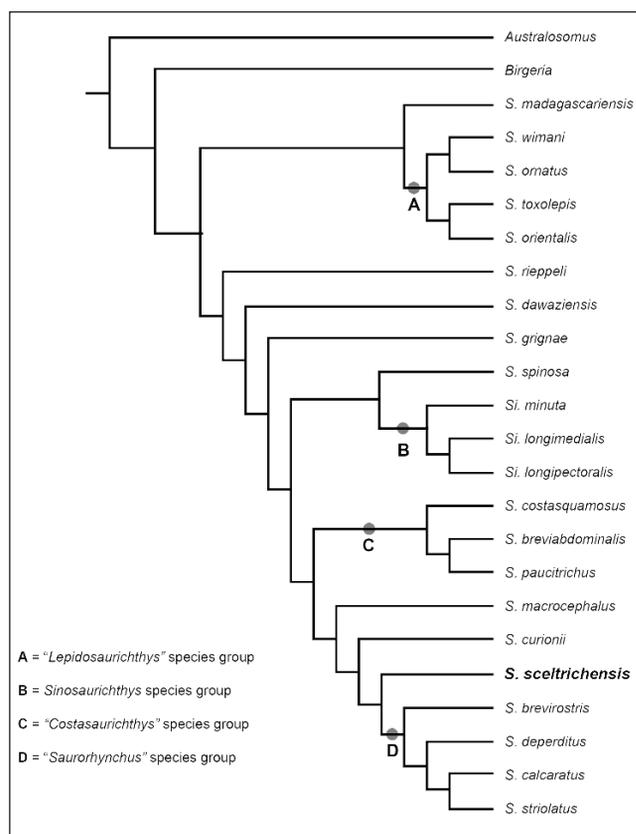


Fig. 20 - 50% majority rule consensus tree of two most parsimonious trees, showing the phylogenetic relationships of *Saurichthys sceltrichensis* sp. n.

ber of lepidotrichia; from *S. costasquamosus*, *S. paucitrichus* and *S. breviabdominalis* in the lack of rib-like elongate lateral scales, from *S. breviabdominalis* also in the number of vertebral segments; from *S. curionii* in the narrower parietal, the subopercle which is distinctly higher than long, in the relative size and number of lepidotrichia of the pectoral and anal fin, in the broader mid-dorsal and mid-ventral scales in the caudal peduncle, and in the diamond-shaped mid-lateral scales; from *S. rieppeli* in the lack of rectangular haemal arches in the anterior region. Finally, the Sceltrich specimens differ from all *Saurichthys* species of the Monte San Giorgio for the presence of unsegmented fin rays in all fins (*S. curionii* has unsegmented rays in the paired fins, whereas median fins are segmented) and for the presence of distinctive postzygapophyses that, according to Kogan et al. (2020, p.479) so far are known only from *S. ornatus*, *S. elongatus* (Stensio 1925), *S. dawaziensis*, *S. yangjiuanensis* and in the *Sinosaurichthys* group; Tintori (2013) reports the possible presence of very short postzygapophyses also in *S. grignae*. The reciprocal overlapping of pre- and postzygapophyses helps to stiffen the body.

In *S. sceltrichensis* sp. n. the number of lepidotrichia in the pectoral fin is much higher than in *S. curionii* (Rieppel 1985), being comparable only with that of *S. grignae* Tintori, 2013.

The rays of the median fins of *S. sceltrichensis* sp. n. are unsegmented, while all other saurichthyids from Monte San Giorgio (Rieppel 1985; Rieppel 1992; Maxwell et al. 2015), as well as *S. grignae* (Tintori 2013), have segmented median fin rays.

The presence of unsegmented fin rays in all fins is known from several *Saurichthys* species, namely the Early Triassic *S. toxolepis* Mutter et al., 2008, and *S. dayi* Raymond, 1925, the Middle Triassic (Anisian) *S. minimableri* Werneburg et al., 2014 and *S. spinosa* Wu et al., 2018, and the Upper Triassic (Carnian) *S. striolatus* (Bronn 1858; Kogan et al. 2020), and *S. calcaratus* (Griffith 1977; Kogan et al. 2020). *S. sceltrichensis* is the first Ladinian (Middle Triassic) saurichthyid with unsegmented fin rays in all fins.

S. sceltrichensis sp. n. differs from other species with unsegmented fins for the morphology of the scales. In addition, *S. toxolepis* has a subopercle with a posterior border bearing a short, rounded projection (Mutter et al. 2008), *S. minimableri* has a quadripartite parietal complex with bones of unusual shape and a maximum body length of about 10 cm (Werneburg et al. 2014), *S. spinosa* has abdominal vertebrae lacking neural spines and alternately bearing laterally-stretching paraneural plates (Wu et al. 2018), *S. striolatus* and *S. calcaratus* have only four scale rows (Bronn 1958; Griffith 1959, 1977).

In conclusion the combination of characters possessed by the specimens here described is not present in any known saurichthyid taxon, thus the erection of a new species is justified.

PHYLOGENY

In order to establish the relationships of *S. sceltrichensis* sp. n. with other Saurichthyidae, a character set for *S. sceltrichensis* sp. n. has been added to a slightly modified version of matrix by Maxwell et al. (2015. Appendix 1 in supplementary material). The changes in character coding with respect to the original data set by Maxwell et al. (2015) are detailed in Appendix 1. In addition, scoring for *S. wimani* (Woodward 1912), based on Woodward (1912), Stensio (1925) and Kogan & Romano (2016b), and *S. spinosa* Wu et al. 2018 have been added (see Ap-

pendix 2). Parsimony analysis has been conducted by TNT (Goloboff et al. 2008), in particular we used parsimony ratchet (Nixon 1999). Two equally parsimonious trees have been obtained after 675,073 total rearrangements, with a best score of 211. In all trees, *S. sceltrichensis* sp. n. nested as a sister taxon of the *Saurorhynchus* species group of Maxwell et al. (2015), which includes (*Saurorhynchus* (*S. brevirostris*, *S. deperditus*, *S. striolatus*, and *S. calcaratus*)). *S. curionii* falls one node behind, resulting as the sister taxon of the clade comprising *S. sceltrichensis* sp. n. plus the *Saurorhynchus* species group.

The consensus tree (Fig. 20) (50% Majority rule, Consistency index 0.403, Retention index 0.581), recovered the topology of Maxwell et al. (2015) for what concerns the western Tethyan saurichthyids, with *S. spinosa* (Wu et al. 2018) as sister group of the *Sinosaurichthys* species group (sensu Tintori 2013); the “*Costasaurichthys*” species group which, according to Tintori’s (2013) informal definition (for this reason the group name is cited within quotation marks), comprises the *Saurichthys* species from the Besano Formation bearing rib-like mid-lateral scales, and the *Saurorhynchus* species group.

In contrast with Maxwell et al. 2015, however, our analysis also supported the validity of the “*Lepidosaurichthys* species group”, sensu Tintori (2013), which was unsupported by the results in Maxwell et al.’s (2015) analysis. Tintori (2013) informally included in this group a clade of Early Triassic taxa comprising *S. wimani*, *S. ornatus*, *S. elongatus* and *S. toxoloepis*. According to our analysis, the Middle Triassic *S. orientalis* Sytchevskaya, 1999 from freshwater deposits of Central Asia can be added to the “*Lepidosaurichthys* species group” (*S. elongatus* was not included in the analysis). An affinity of *S. orientalis* to Early Triassic species has been proposed by Romano et al. (2012), who considered it a survivor of the “early saurichthyid morphotype”. Additionally, *S. madagascariensis* represents the earliest divergence within the group only in one tree, while it is nested as the sister taxon of the “*Lepidosaurichthys*” species group sensu Tintori (2013) in the other tree. In the consensus tree, it falls in an unresolved trichotomy at the base of the *Saurichthys* tree. Since the Early Triassic saurichthyids plus *S. orientalis* show as sister to saurichthyids from the Middle and Late Triassic (*S. rieppeli* and others), this suggests that two radiations occurred within the group, an Early and a Middle Triassic one.

FUNCTIONAL ANALYSIS

The overall body architecture of *Saurichthys* with a very long and narrow, pointed skull, and a long, slender body characterized by an elongate antorbital region and posterior displacement of the unpaired fins is similar to that extant genera *Belone* (garfish) and *Lepisosteus* (gar/garpike) that are ambush predators. These fishes attack preys by a sudden, fast strike, starting either from a resting position or after a slow approach towards the prey (see Kogan et al. 2015 for a detailed analysis).

Among different *Saurichthys* species, the overall morphology and body proportions of *S. sceltrichensis* sp. n. are very similar to those of *S. curionii*, but with some significant anatomical differences, especially in the structure of the fins, that suggest different swimming adaptations in these two taxa.

As previously described, *S. sceltrichensis* sp. n. differs from *S. curionii* in having unsegmented lepidotrichia in all fins and proportionally much longer and wider paired fins, with a higher number of lepidotrichia (Fig. 21).

Some authors consider the switching change from segmented towards unsegmented lepidotrichia as an evolutionary trend within Saurichthyidae (e.g. Rieppel 1985, 1992; Schmid & Sánchez-Villagra 2010; Romano et al. 2012). Based on our phylogenetic conclusions as well as those of Maxwell et al. (2015), we support the hypothesis that unsegmented fins, like other functionally related features, such as the grid-like structure in the vertebral column (see Kogan et al. 2020 and references therein) were acquired independently in several species. This supports the hypothesis that the presence or absence of segmentation has a functional explanation other than being a possible phylogenetic signal.

Segmented lepidotrichia render the fins more flexible, allowing higher manoeuvrability and a more efficient swimming (e.g. *S. madagascariensis* and *S. wimani*). In addition, segmented lepidotrichia in the caudal fin allow for “cupping” (Lauder et al. 2015; Flammang et al. 2015) of the fin, that increases global speed in cruisers.

Unsegmented lepidotrichia in the caudal fin as in *S. sceltrichensis* sp. n. allow instead increasing the speed during the starting phase, though the global speed during swimming becomes lower by comparison to more flexible fins of identical outline. An increased starting speed may be useful if

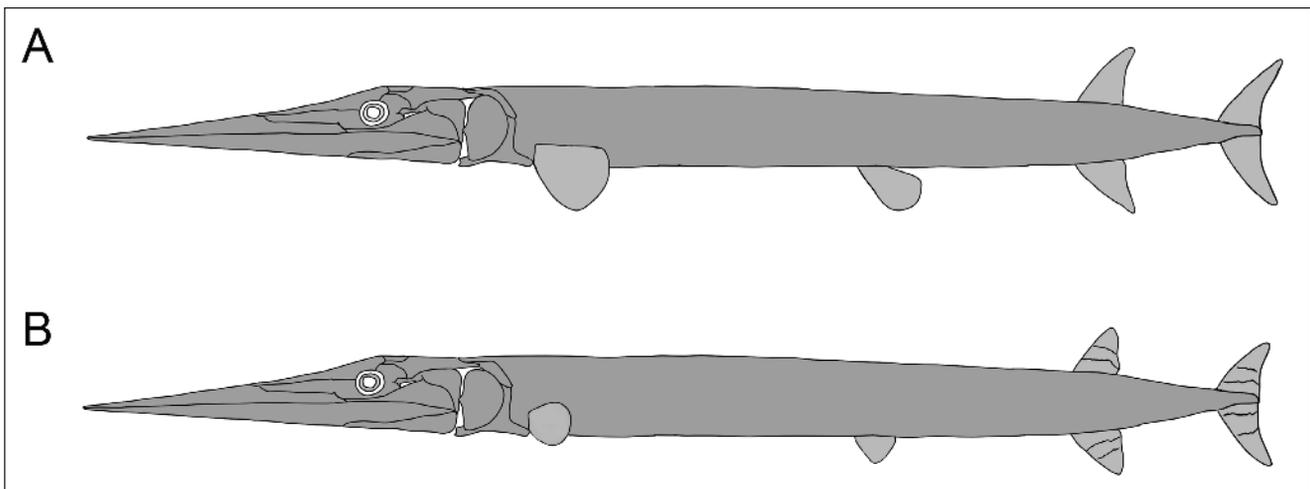


Fig. 21 - Shape comparison between *Saurichthys sceltrichensis* sp. n. (A) and *S. curionii* (B).

the predator can get very close to preys by swimming slowly, remaining unnoticed by exploiting the narrow, anteriorly pointed head profile to minimize water disturbance that could be detected by the lateral line system of the preys. The “abbreviate-diphycercal” (Brough 1936; Kogan et al. 2015) caudal fin of *Saurichthys*, consisting of symmetrical epaxial and hypaxial lobes, coupled with the symmetrical dorsal and anal fins, placed close to the caudal fin, forms the so-called “double-tail configuration” (Kogan et al. 2015) which allows for powerful strikes. According to Weihs (1989) a “double tail configuration” in which the “front tail” (sensu Weihs 1989, i. e. the functional unit formed by the symmetrical dorsal and anal fins) lies at a distance of about 0.4 times the body length from the true tail, is indicative of an adaptation to fast sustained swimming with “high tail beat frequencies” like in mackerels and tunas (Weihs 1989, p. 158) while the posterior migration of the “front tail” close to the tail fin as occurring in exocids increases the thrust for rapid acceleration. With this “double tail configuration”, the lack of segmentation in the dorsal and anal fin of *S. sceltrichensis* sp. n. may have the same function as in the caudal fin, enabling the fish to perform short high-speed thrusts to catch preys. A similar behaviour can be observed in extant ambush predator fishes like gar-pike (*Lepisosteus*), that after getting close to preys, attack suddenly with a short but very fast thrust.

The difference in relative size and the higher number of lepidotrichia in the paired fins of *S. sceltrichensis* sp. n. with respect to *S. curionii* also indicates a different functional adaptation.

Pectoral fins with unsegmented lepidotrichia do not allow for a propulsion based on lift by undulation, but rather only for movements based on drag (Geerlink & Videler 1987), which is useful for slow rowing movements, with an active propulsive phase and a passive recovery phase. However, unsegmented pectoral fins are more efficient than segmented fins when used as brakes or, if properly oriented, as stiff hydrofoils creating some lift if the fin is large enough. In extant belonids the propulsive phase is very short, and is followed by a phase in which the fishes reach the prey by inertia, with the pectoral and pelvic fins acting as stabilizers. However in belonids the pectoral fins are inserted higher on the body and taper distally, while the pectoral fins of *S. sceltrichensis* sp. n. are inserted more ventrally, and are wider and rounded distally, like in the gar-pike (*Lepisosteus*) that uses the pectoral fins mostly for slow swimming and braking. Also the large, unsegmented pelvic fins of *S. sceltrichensis* sp. n. probably had a similar function as in the pike (*Esox lucius*) and in the garpike, where they counteract the upward drift of the body caused by the pectoral fins during braking (Harris 1938), and have also a stabilizing and, at a lesser extent, locomotor function. Standen (2008) and Osburn (1906) reported that both the pike and the garpike can move their pelvic fins slowly, in coordination with the pectoral fins, to control the fish asset when lying still in water or when swimming slowly for instance to close the distance from the prey, until the latter falls within reach (Branson 1966).

Large paired fins may also be useful in complex habitats with a complex topology. In the ex-

tant pikes (*Esox*), for instance, good manoeuvring performance by median and paired fins propulsion (MPF propulsion, Domenici & Blake 1997) is ensured by the presence of large median paired fins that can be used for hovering and backwards swimming. The same function may be applied to the wide paired fins of *S. sceltrichensis* sp. n., while its robust and deep posterior body portion of the body, provided with the “functionally double caudal fin”, assured a fast acceleration as previously stated.

In conclusion, the differences in the fin structure, size and segmentation pattern between *S. sceltrichensis* sp. n. and *S. curionii* suggest different feeding strategies and perhaps micro-environments. *S. sceltrichensis* sp. n. may have been a faster striker than *S. curionii* and better at MPF propulsion (manoeuvring), specialized for stalking preys from a nearly immobile position, or slow approach in a more complex habitat. *S. curionii* may have lived instead in a more open environment.

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