A NEW COELACANTH SPECIMEN WITH ELONGATE RIBS FROM THE MIDDLE TRIASSIC (LADINIAN) KALKSCHIEFERZONE OF MONTE SAN GIORGIO (CANTON TICINO, SWITZERLAND)

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Abstract. A new finding of a coelacanth from the upper Ladinian upper Kalkschieferzone of the Meride Limestone Formation of Monte San Giorgio (UNESCO World Heritage area) is described. It represents the first known coelacanth from the Middle Triassic that undoubtedly bears elongate thin ribs. The incompleteness of the specimen prevents a reliable taxonomic assignment or the erection of a new species, however some characters, mainly scale morphology, are very similar to those of the holotype of *Heptanema paradoxum* Bellotti, 1857 from the roughly coeval Perledo Formation of Northern Italy. Elongate ribs are not reported in original descriptions of *H. paradoxum*, however small portion of ribs are visible among the scales of the holotype. Accordingly, the new specimen is tentatively ascribed to *Heptanema* as *Heptanema* cf *H. paradoxum*.

INTRODUCTION

Coelacanths (Actinistia) are a clade of sarcopterygian fishes known since the Early Devonian (Johanson et al. 2006). They reached highest diversity in the Early-Middle Triassic, being mostly known from Europe, North and South America (Cavin et al. 2013; Ferrante et al. 2017) and China (Tong et al. 2006; Wen et al. 2013). They declined in diversity during the Cretaceous and are absent from the Cenozoic fossil record, in fact coelacanths were considered extinct until 1938, when a living specimen of *Latimeria* was discovered (Smith 1939). Different coelacanth taxa are known in the Middle Triassic of Monte San Giorgio (UNESCO WH site), across the Italian Swiss boundary, with nearly complete specimens of *Ticinepomis peyeri* (Rieppel 1980), and fragments of a larger coelacanth tentatively referred to cf. *Holophagus* by Rieppel (1985), both from the upper Anisian - lower Ladinian Besano Formation. In addition, a complete specimen from the Sceltrich beds at the base of the upper Meride Limestone (Ladinian) has been recently described (Renesto & Stockar 2018) and ascribed to the genus *Heptanema* Bellotti, 1857. *Heptanema* was previously known only from a single species, *H. paradoxum* Bellotti, 1857, from the Ladinian of Perledo (east side of the Como Lake, Lombardy, Northern Italy).
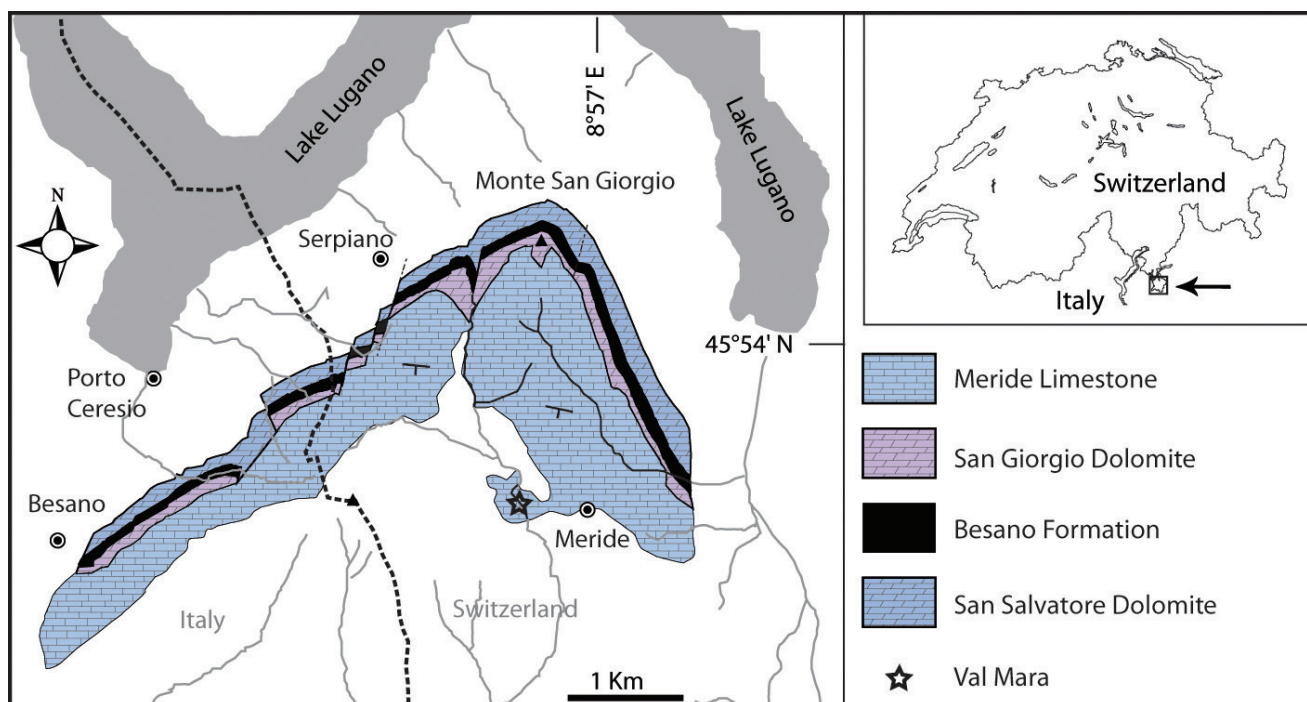
Fig. 1 - Location map of the Monte San Giorgio showing the Middle Triassic carbonate sequence and the location of the Gaggiolo valley ("Val Mara").

In the levels of the Prosanto Formation (Switzerland) coeval with the lower Meride Limestone, have been found large specimens of *Ticinepomis* cf *T. peyeri* (Cavin et al. 2013) and the highly derived *Foreya maxkuhni* (Cavin et al. 2017), while an undetermined coelacanth was collected from from Pelsonian (Anisian) beds of the Dolomites (Renesto & Kustatcher 2019).

Here we describe a new finding of a coelacanth specimen from the Upper Kalkschieferzone of the upper Meride Limestone (late Ladinian). The specimen, despite its incompleteness, adds further knowledge to the diversity of the Actinistia in the Monte San Giorgio fossil Lagerstätte, and possibly to the anatomy of the poorly known species *Heptanema paradoxum* Bellotti, 1857.

GEOLOGICAL SETTING

The Middle Triassic carbonate succession of Monte San Giorgio (Switzerland-Italy; Figs. 1, 2), belonging to the western termination 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-preser-

ved fossil fishes and marine reptiles (e.g. Rieber 1973; Kuhn-Schnyder 1974; Bürgin et al. 1989; Etter 2002). In Middle Triassic times, the South-Alpine domain was progressively submerged by a long-term transgression from the east and the marginal location of the Monte San Giorgio basin resulted in a peculiar sedimentary succession and in at least 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 ba-
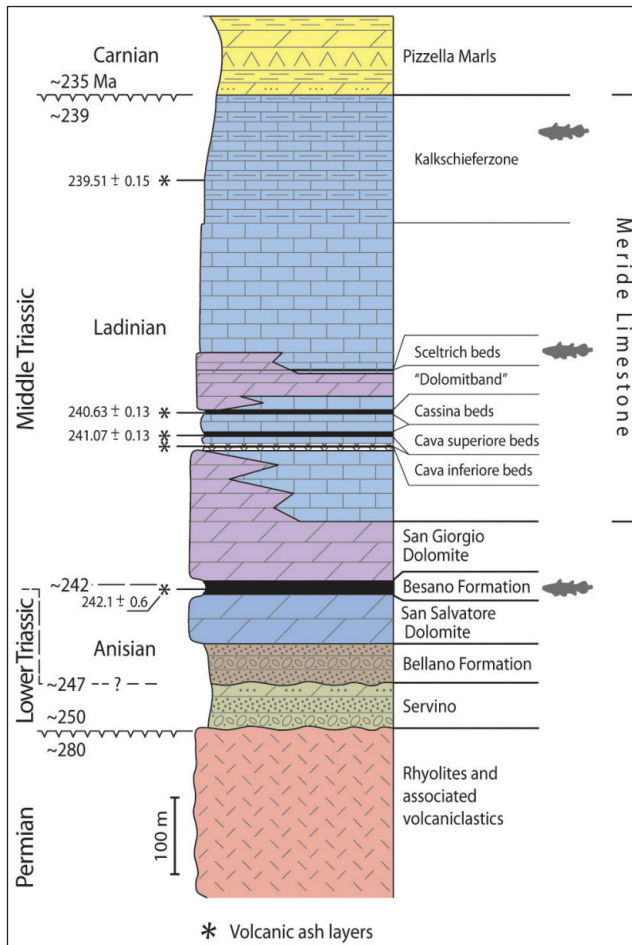
Fig. 2 - Middle Triassic stratigraphic units of the Monte San Giorgio area and occurrences of coelacanth fossil fishes. Stratigraphic column after Commissione scientifica transnazionale Monte San Giorgio 2014, modified. Single-zircon U-Pb ages of Meride Limestone after Stockar et al 2012.

sin 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 1973; Bernasconi 1994; Furrer 1995; Röhl et al. 2001). The Besano Formation ("Grenzbitumenzone"; 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. 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. 2013). The lower Meride Limestone consists of well-bedded

micritic limestone, laminated limestone and volcaniclastic 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). 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; its lowermost part contains a fossiliferous interval currently under study (Sceltrich beds; Renesto & Stockar 2018). The uppermost part of the upper Meride Limestone comprises the 120 m thick "Kalkschieferzone" (Senn 1924), made up of thinly-bedded, mostly laminated, limestone and marlstone with volcanic ash layers and bearing peculiar reptile and fish faunas, terrestrial plants, crustaceans and insects (e.g. Wirz 1945; Furrer 1995; Krzeminski & Lombardo 2001; Bechly & Stockar 2011; Lombardo et al. 2012, Montagna et al. 2018). Wirz (1945) divided the Kalkschieferzone into three subunits (Va, Vb and Vc), afterwards called lower, middle and upper Kalkschieferzone by Furrer (1995). The peculiar depositional environment of the Kalkschieferzone is regarded as a shallow lagoon recording strong seasonal variations of salinity and water level. During Ladinian times, the depositional environment was located at a northern intertropical latitude of about 15-18° (Muttoni et al. 2004) and was strongly influenced by monsoonal circulation (Preto et al. 2010). The resulting sedimentation is likely the product of alternating dry seasons, with low water level and high salinity, and wet seasons during which the hypersaline lagoon was flooded by lighter freshwater, resulting in density stratification with brackish surface water and oxygen-depleted bottom water (Furrer, 1995).

The bed yielding the Coelacanth specimen described here belongs to the Upper Kalkschieferzone, Late Ladinian in age (Stockar et al. 2013), where a small excavation on a surface of around 2 square meters was carried out in Summer 2020 by the Cantonal Museum of Natural
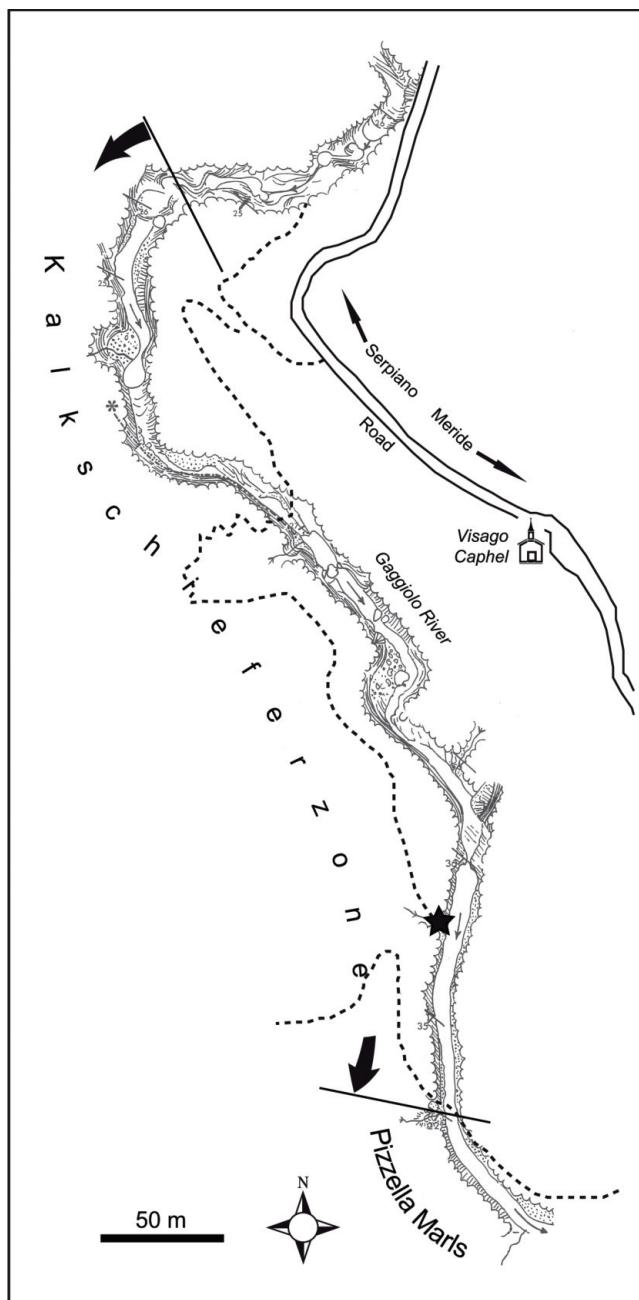
Fig. 3 - Map of the Gaggiolo valley ("Val Mara"; after Scheuring, 1978, modified) and location of the excavation site (star).

History (MCSN). The site is located in the valley of the Gaggiolo River, also known as "Val Mara", west of Meride village (Fig. 3). The investigated section consists of an alternation of thin-bedded laminated limestones and marly limestones with subordinated marlstones and calcareous marlstones. The only other fossil occurrences from this bed are two small actinopterygian fish specimens, which are ascribed to *Peltopleurus* sp. and to *Prohalecites porroi*.

Systematic Paleontology

Sarcopterygii Romer, 1955
Actinistia Cope, 1872
Heptanema Bellotti, 1857

Type species: *H. paradoxum* Bellotti, 1857

Heptanema cf. *H. paradoxum* Bellotti, 1857

Material: Specimen MCSN 8610, an incomplete specimen exposed in lateral (left) view.
Locality: Val Mara, Monte San Giorgio, Cantone Ticino, Switzerland.
Horizon: upper Kalkschieferzone, upper Meride Limestone, (Middle Triassic, late Ladinian).

Measurements (in mm): Length of the preserved portion of the specimen: 105; anteroposterior length of the basal plate of second dorsal fin: 12.0; anteroposterior length of the basal plate of the anal fin: 9.0; height of a neural arch of the mid-abdominal region: 3.7; height of its neural spine: 7.0; height of neural arch of mid-caudal region: 4.5; height of its neural spine: 10.0; height of the opposed haemal arch: 4.5; height of its haemal spine: 9.7; height of a mid-caudal radial, dorsal lobe: 11.3; ventral lobe: 10.5.

Description

The specimen (Fig. 4) is mostly articulated but incomplete: only the abdominal region, posterior to the first dorsal fin and the entire caudal region are preserved. The basal plates of the second dorsal and of the anal fins are preserved along with the dorsal and ventral lobes of the caudal fin; however most lepidotrichia and some radials of the caudal fin are disarticulated.

Axial skeleton. 35 neural arches are preserved, plus two fragments of the anteriormost preserved neural spines (Fig. 4). Considering that the anterior portion of the body is missing beyond the insertion of the first dorsal fin, it can be hypothesized that the actual number of neural arches should have reached at least 45.

The neural arches are high (at least two times higher than wide) bearing high neural spines. The neural spines of the abdominal region are thin and distally tapering, their height increases at the level of the 18th preserved element. At the transition from the abdominal to the caudal region, the neu-
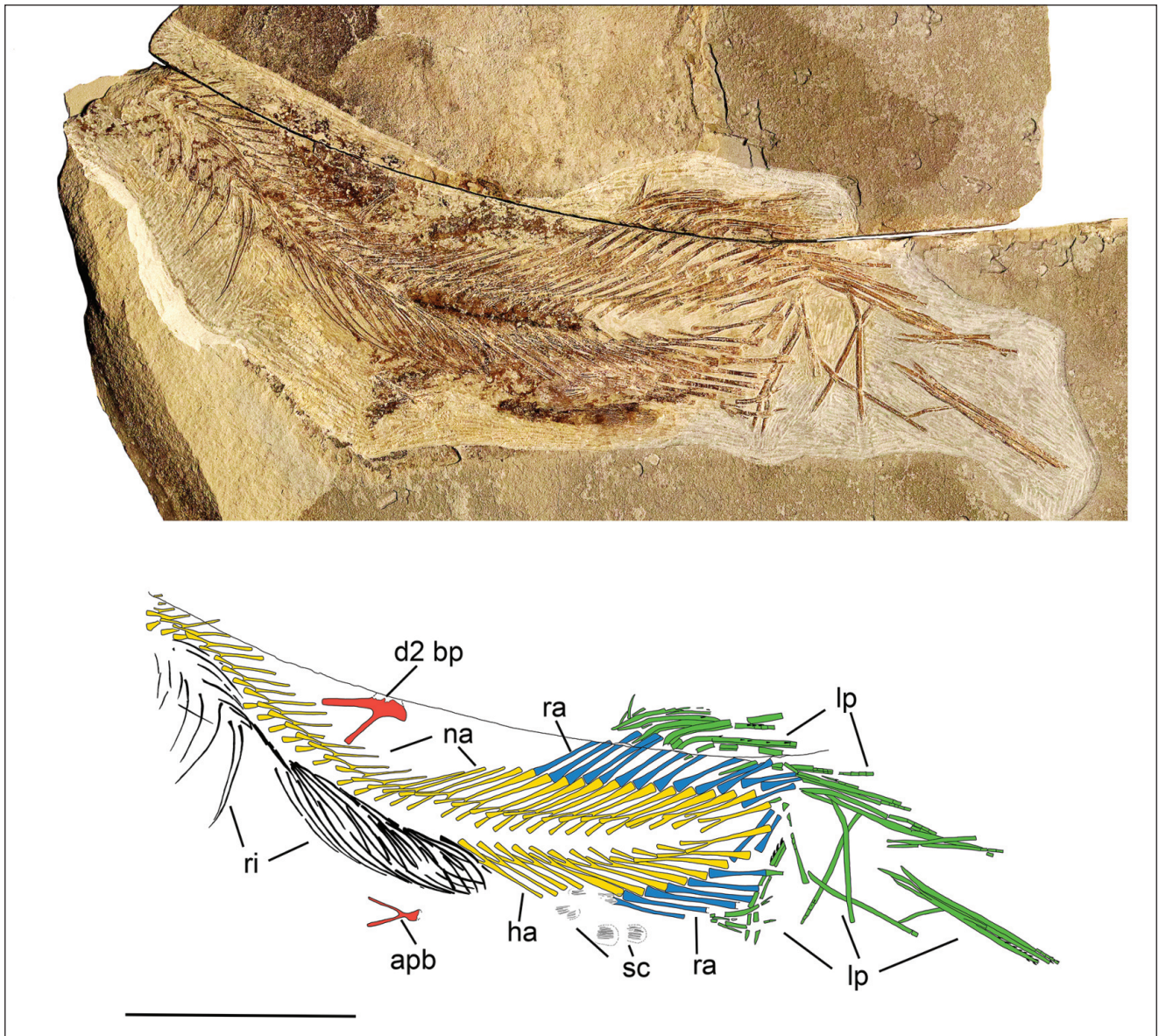
Fig. 4 - Specimen MCSN 8610. A) the specimen as preserved; B) interpretative drawing. Abbreviations are: apb, basal plate of the anal fin; d2bp, basal plate of the second dorsal fin; ha, haemal arches; lp, lepidotrichia; na, neural arches; ra, radials; ri, ribs, sc, scales. Scale bar equals 50 mm.

ral spines start to widen anteroposteriorly at their top becoming more robust and expanded meeting each other at their dorsal end.

12 haemal arches are preserved, bearing tall haemal spines, the first four haemal spines are narrower than the following eight, which are distinctly expanded distally, their shape mirroring that of the corresponding neural spines.

At least 33 long and thin ribs are preserved (Fig. 4-5), belonging both to the left and right sides of the body.

Median fins. The first dorsal fin is missing, only the basal plate of the second dorsal fin is preserved (Fig. 6A), it has a wide and rounded

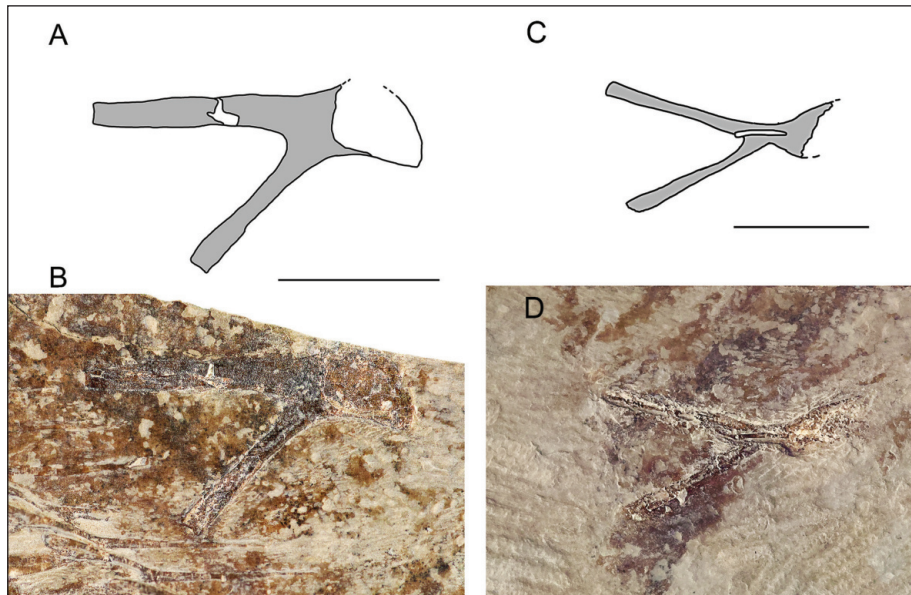Fig. 5 - Specimen MCSN 8610. Detail of the ribs. Scale bar equals 5 mm.

Fig. 6 - Specimen MCSN 8610. A) sketched outline and B) photo of the basal plate of the second dorsal fin, C) sketched outline and D) photo of the basal plate of the anal fin. In both drawings the portion of the bone actually preserved is shaded in grey, the empty space surrounded by the black line is the portion preserved only as impression. Scale bars equal 5 mm.

posterior plate, which is incompletely preserved, however most its outline can be inferred from the impression left in the matrix. Anteriorly the plate is bifurcated, with a robust sub-horizontal process and a more slender anteroventral one forming an angle of about 46°.

The basal plate of the anal fin (Fig. 6C-D) is similar to that of the second dorsal fin, but smaller and with more slender anterodorsal and anteroventral processes, that are nearly equal in length.

Caudal fin. Fourteen radials of the dorsal lobe are preserved and eight-nine of the ventral lobe (Fig. 4). The great difference in the number of radials between the dorsal and ventral lobes of the caudal fin may be due to preservational bias than reflecting an actual asymmetry of the fin but a slight asymmetry cannot be excluded. Both radials of the dorsal and ventral lobe are stout and expanded both at their proximal and distal end. The radials of the dorsal lobe extend along the leading edge of the lepidotrichia when the latter are preserved in their original position. Most lepidotrichia, especially those of the ventral lobe of the fin, however are incomplete, fragmented or disarticulated, thus preventing from assessing an exact count. The better preserved ones show that they are segmented only in their distal third. Some lepidotrichia of both the dorsal and ventral lobe bear rows of stout spines (Fig. 7). The first lepidotrichia of the dorsal lobe are much shorter than the following ones and unsegmented. The supplementary lobe of the tail is not preserved.

Scales. Few scales are preserved in the ventral portion of the caudal region (Fig. 8), just anterior to the first radials of the ventral lobe of the caudal fin. These scales are subcircular in shape (Fig. 9) and their entire surface is visible, including the much larger and smooth portion usually embedded in the skin that is at least two times longer than the exposed portion, the latter being ornamented by a series of 15-16 longitudinal ridges; in some scales one to three of the central ridges are stouter and more prominent.

Discussion

The lack of the entire skull, pectoral girdle and anteriormost portion of the body renders very difficult to give a taxonomic assignment for specimen MCSN 8610, however a comparative analysis of available characters has been attempted in order to suggest possible relationships.

Specimen MCSN 8610 differs from most well-known Triassic coelacanths for the presence of elongate ribs (Forey 1998), indeed, it is the first Middle Triassic coelacanth in which this feature is undoubtedly present. According to Forey (1998) the presence of denticles on caudal fin, is a feature of the members of the clade Latimerioidei, and within Latimerioidei, the presence of elongate thin ribs is considered by some authors (e.g. Forey 1998) a character shared by the Mawsoniidae (but more recently the validity of this assumption has been questioned, as further detailed below), a clade that comprises the Late Triassic/Lower Jurassic genus *Diplurus* New-
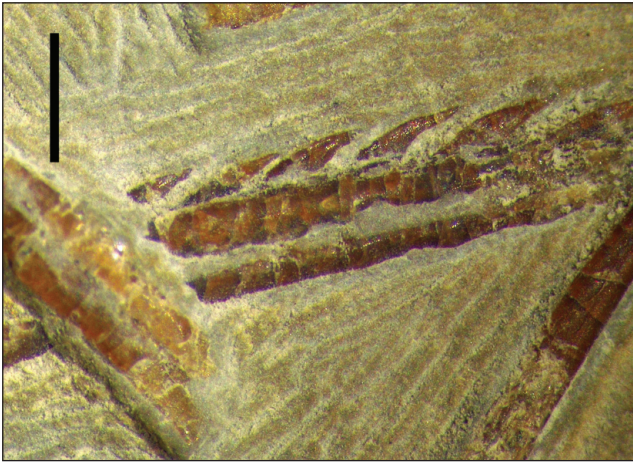
Fig. 7 - Specimen MCSN 8610. Detail of a lepidotrichium of the ventral lobe of the caudal fin showing robust spines. Scale bar equals 2 mm.

berry, 1878, the Late Triassic *Chinlea* Schaeffer, 1967 and the Jurassic and Cretaceous genera *Mawsonia* Woodward, 1907 (in Mawson & Woodward 1907); *Axelrodichthys* Maisey, 1986; *Parnaibaia* Yabumoto, 2008. Other less know taxa of uncertain affinities, or erected on poorly preserved specimens have also been ascribed to the Mawsoniidae (see Miguel et al. 2013 for a reappraisal).

As specified above, the only known coelacanth taxa showing elongate ribs are the Late Triassic (Carnian) to Early Jurassic (Sinemurian) *Diplurus* (Schaeffer 1948, 1952) the Late Triassic (Carnian) *Chinlea* (Schaeffer 1967), the Late Jurassic-early Cretaceous (Tithonian-Berrasian) *Parnaibaia* (Yabumoto 2008), the Cretaceous (Aptian-Campanian) *Axelrodichthys* (Maisey 1986) and, possibly, the Late Permian *Changxingia aspratilis* (Wang & Liu 1981).

Apart for the much younger age*, Parnaibaia* and *Axelrodichthys* can be excluded for the size and scale ornamentation: in *Parnaibaia* scales bear about 40 narrow and closely spaced ridges plus a very prominent median ridge (Yabumoto 2008) not present in specimen MCSN 8610, while *Axelrodichthys* scales are ornamented by many short irregular ridges (Forey 1998) and there is a distinct "bulge", a ventral projection on basal plate of D2 (Fragoso et al. 2018). *Changxingia* is much older than MCSN 8610, and its scales are ornamented by more numerous and narrower ridges, in addition *Changxingia* has 22 haemal spines (12 in MCSN 8610).

Among less known Middle Triassic taxa sometimes included in the Mawsoniidae (Miguel et al. 2013), *Alcoveria brevis* Beltan, 1972 from the late Ladinian of Montral Alcover (Spain) has a much deeper body shape and apparently lacks of the ribs (Beltan 1972, 1975, 1984; Forey 1998).

The postcranial skeleton of *Garnbergia ommata* Martin & Wenz, 1984, from the Ladinian of Kunzelsau Baden Wurttenberg (Germany), is poorly known, however the preserved scales are ornamented by many (at least 40) thin subparallel ridges, while MCSN 8610 scales have fewer and coarser ridges.

Coelacanthus lunzensis Teller, 1891 form the Carnian of Lunz Sandstone of Austria, is also known from a single fragmentary specimen (Reis 1900) that however, shows the same ornamentation of the scales present in *Garnbergia ommata* (Martin & Wenz, 1984).

Chinlea is Late Triassic (Norian) in age and shows scales ornamented by 40 thin parallel ridges, thus different from those of MCSN 8610.

Diplurus shares with MCSN 8610 the presence of thin elongate ribs that nearly reach the midventral line, a slender body and the presence of stout denticles on the leading edges of the lepidotrichians; in *D. newarki* the scales are ornamented by 13-15 ridges (Schaeffer 1948, 1952), as in MCSN 8610, while *D. longicaudatus* scales bear about 40 thin and closely spaced ridges.

Some authors (Forey 1998; Schultze 2004; Miguel et al. 2013) nested also the genus *Heptanema* within Mawsoniidae, at least tentatively. The holotype and only specimen of *Heptanema paradoxum* Bellotti,1857 (Fig. 10) has a body shape very similar to that of *Diplurus* (Forey 1998; Renesto & Stockar 2018) and of specimen MCSN 8610. The presence of elongate ribs is not reported for *Heptanema* (De Alessandri 1910), however Renesto & Stockar (2018 fig. 12A) noted the presence of parallel bony rods anteroposteriorly inclined that are visible beneath the scales in the posterior third of the abdominal region of *H. paradoxum* holotype (Fig.11B), and interpreted them as fragments of short ribs. The poor preservation of the anterior abdominal region and the scale covering on *H. paradoxum* holotype does not allow to establish their true shape, but there is the possibility that the ribs may have been instead as elongate as in MCSN 8610 (and in *Diplurus*). In this case the correction of Forey's (1998) scoring of the character of the rib (from presence to absence), by Renesto & Stockar (2018) is indeed wrong and the original scoring by Forey (1998) is right.
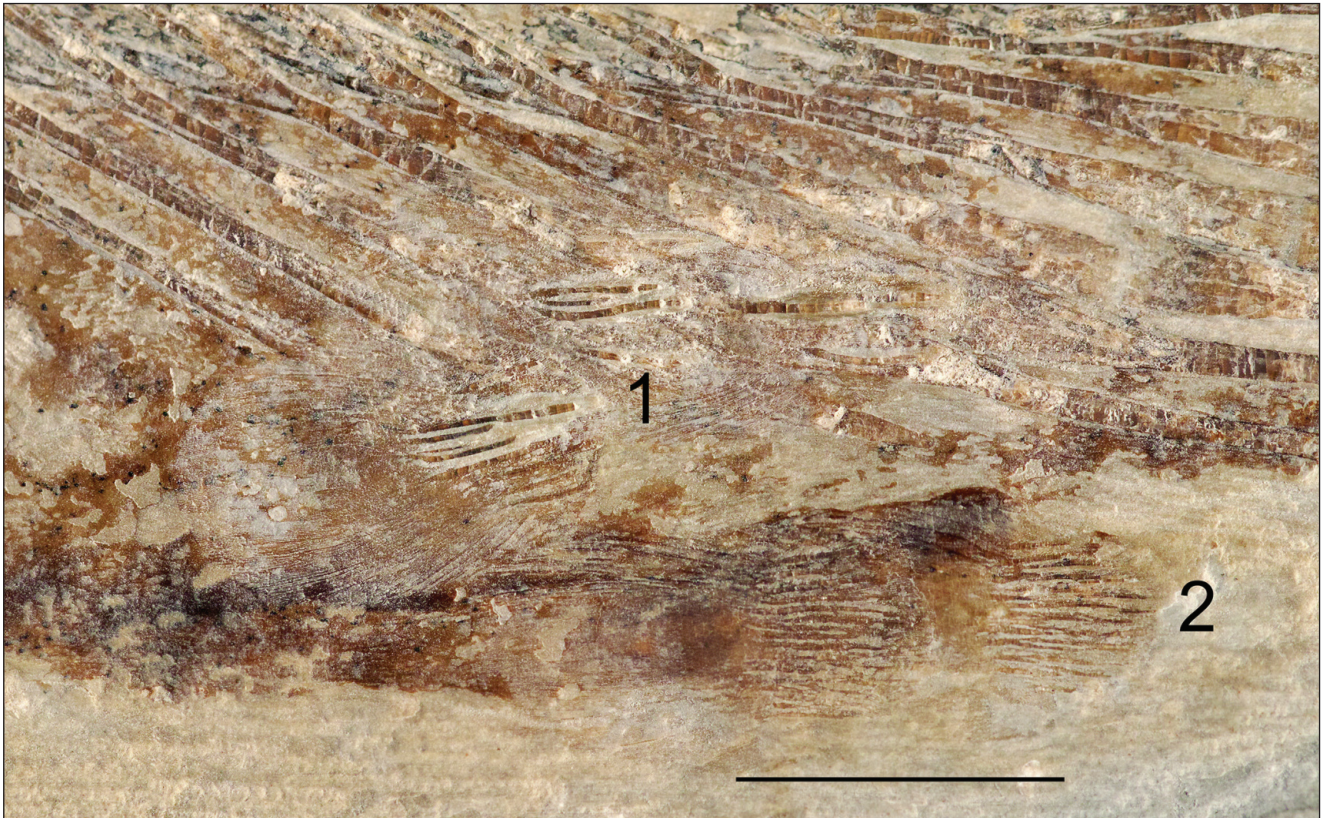
Fig. 8 - Specimen MCSN 8610. Patch of scales preserved in the posteroventral region of the body showing two different morphologies: 1, scales with few stout ridges, 2, scales with several more slender ridges. Scale bar equals 5 mm.

In addition, the scales of the posterodorsal and posteroventral region of the holotype of *H. paradoxum* (Fig. 11B-C) are very similar to those preserved in the ventral region of specimen MCSN 8610, while the scales of the lateral regions of the body of *H. paradoxum* bear a single very prominent ridge (Fig. 11 B).

Stratigraphy gives further support to the assignment of specimen MCSN 8610 to *Heptanema paradoxum* rather than to *Diplurus newarki*: *H. paradoxum* has been found in the Perledo Member of the Perledo-Varenna Formation (Renesto & Stockar 2018) that is late Ladinian in age (Gaetani et al. 1992), thus correlable with the Kalkschieferzone that yielded MCSN 8610, while *D. newarki* is Carnian in age. The outcrops of the Kalkschieferzone and of the Perledo Member are about 35 km away from each other (Tintori 1998) and they were deposited in the same sedimentary basin, but under different environmental conditions (Bernasconi 1991; Bernasconi & Riva 1993; Lombardo 1997).

The assignment of MCSN 8610 to *Heptanema* may add knowledge about the anatomy of this po-orly known genus and may also suggest that *Heptanema* belongs to the Mawsoniidae. According to Forey (1998), the presence of a parietonasal proportionally elongated in relation to the postparietal shield. present in the holotype of *H. paradoxum* and in *Heptanema* sp. from the Meride Limestone (Renesto & Stockar 2018), is a character of the Latimeroidei and the presence of thin elongate ribs in specimen MCSN 8610 could be diagnostic for the Mawsoniidae (Forey 1998).

On the other hand, the validity of the presence of elongate thin abdominal ribs as a synapomorphy of the Mawsoniidae has been questioned. In recent years it has been reported that many mawsoniid genera show short pleural ribs associated with a calcified lung (Brito et al. 2010; Cupello et al. 2018 and references therein) while the presence of elongate ribs with no calcified lung is a character shared by few permo-triassic taxa like *Diplurus*, *Changxingia*, probably *Chinlea*, and eventually *Heptanema,* and may represent a plesiomorphic feature, in fact Toriño et al. (2021) in their revised phylogeny of the Actinistia nested *Diplurus* within the Latimeriidae.

Fig. 9 - Specimen MCSN 8610. Close up of a scale fully exposed, showing the finely striated portion usually embedded below other scales. A) Black and white photo, with digitally increased texture to enhance the visibility of the texture; B) the scale as preserved. Scale bar equals 2 mm
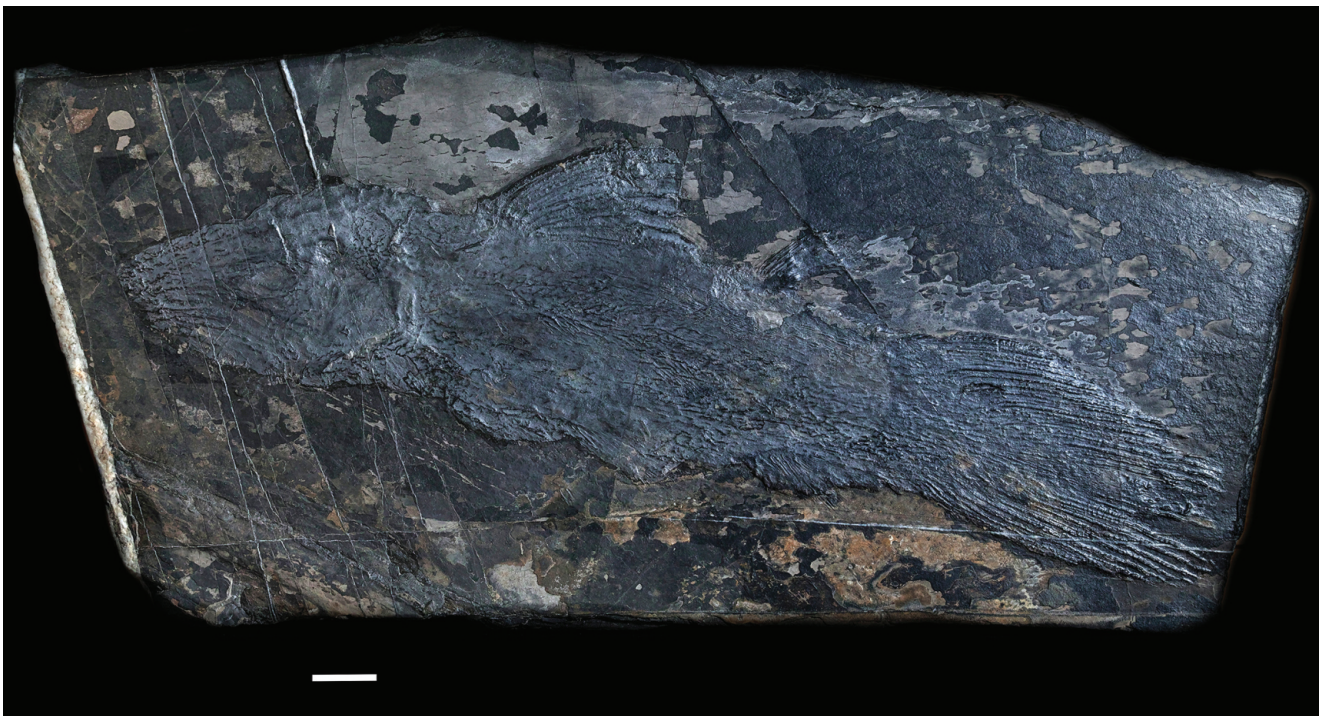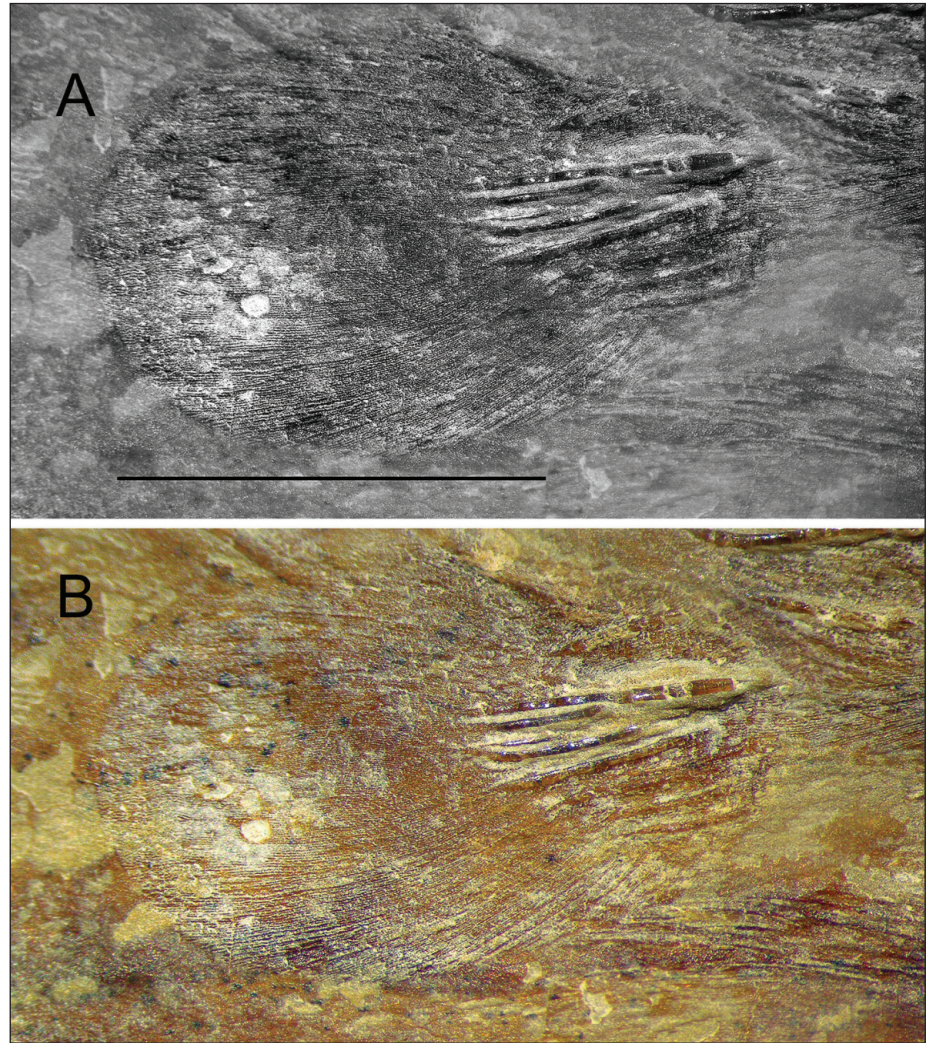

Fig. 10 - *Heptanema paradoxum* Bellotti 1857, holotype, specimen SMF P1242 of the Vertebrate Palaeontological collection of the Senckenberg Forschungsinstitut und Naturmuseum in Frankfurt, Germany. Scale bar equals 10 mm.
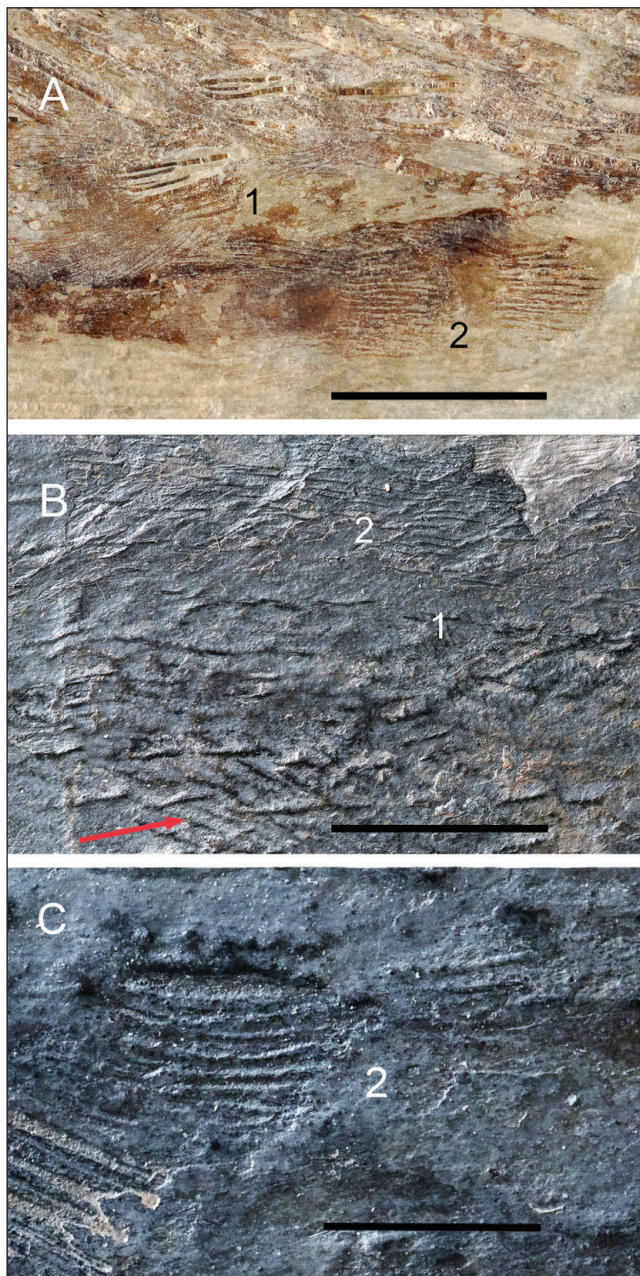
Fig. 11 - Comparison between the scales of MCSN 6810 (A) and the dorsal scales (B) and posteroventral scales (C) of the holotype of *H. paradoxum*. Number refers to scale morphology: 1, scales with few stout ridges, 2, scales with many and more slender ridges; the arrow in (B) points to the portion of ribs lying underneath. Scale bars equal 2 mm (A-B) and 1 mm (C).

However, any consideration about the phylogenetic relationships of coelacanths is well beyond the aim of this paper, where only a taxonomic assignment of MCSN 8610 can be attempted. In conclusion, while the possibility that specimen MCSN 8610 represents a new species cannot be dismissed, on the basis of the available evidence it is preferred here to ascribe it to *Heptanema* cf *H. paradoxum*.

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