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# The research history of the Middle Triassic fishes of Monte San Giorgio: getting out of the shadow of aquatic reptiles

Toni Bürgin<sup>1\*</sup>

## Abstract

Around the middle of the nineteenth century, Italian palaeontologists began to investigate fossils of fishes and reptiles from the Middle Triassic outcrops in the vicinity of Monte San Giorgio (Canton Ticino, Switzerland). In 1924, researchers from the University of Zurich started their scientific excavations on the Swiss side. The many fish fossils found since then have often stood in the shadow of the more spectacular and mostly larger fossils of various aquatic reptiles. Beginning around 1980 the fish fossils in the collection of the Palaeontological Institute and Museum of Zurich University have subsequently been brought out of this shadow. The picture presently emerging is that of a species rich fish fauna located in six different fossiliferous beds of Anisian and Ladinian age with a few chondrichthyan, some coelacanth and a wealth of different actinopterygian taxa, many of them well preserved. The ongoing work not only results in taxonomic and systematic novelties, but gives also new insights into their palaeobiology, palaeoecology and palaeobiogeography.

**Keywords** Middle Triassic, Chondrichthyes, Actinopterygii, Sarcopterygii

## Introduction

Today, with about 37,000 species been described, fishes (e.g. Cyclostomata, Chondrichthyes and piscine Osteichthyes) represent more than half of all known extant vertebrates (Fricke et al., 2023). Their origin lies in the lower Cambrian (Shu et al., 2003). In the Ordovician and the Silurian, they radiated in a large number of different higher level taxa (Andreev et al., 2022; Friedman, 2022; Nelson et al., 2016; Zhou et al., 2022). The Devonian is often ascribed as the “age of fishes”, whereas the Mesozoic is informally called the “age of reptiles”. It is well known that during their life on earth, fishes represent the most important part of marine biotas. This holds also

for the Triassic. After the massive end-Permian extinction event, the recovery of the marine fish fauna seems to have been considerably faster than previously thought (Benton et al., 2013; Chen & Benton, 2012; Hu et al., 2010; Romano, 2021; Tintori et al., 2014). This is shown by newly discovered Early Triassic faunas from North America and China (Brayard et al., 2017; Dai et al., 2023).

The various Middle Triassic fossil sites on the Swiss side of Monte San Giorgio (village of Meride, today part of the community of Mendrisio, Canton Ticino), who have been exploited by researchers from the University of Zurich since 1924, got their worldwide fame largely due to the large number of often well preserved fossils of marine reptiles (Peyer, 1944). Taxa such as *Ceresiosaurus* or *Serpianosaurus* ven reflect their geographic origin. Until 1980, the fish fossils clearly stood in the shadow of these emblematic reptiles (Kuhn-Schnyder, 1974). This changed during the following decades. Today the Middle Triassic fish fossils from Monte San Giorgio have clearly shown their scientific importance (Etter, 2002;

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Felber, 2005; Felber et al., 1997; Rieppel, 2019). They have additionally stimulated ongoing research in the contemporaneous Prosanto Formation in Canton Graubünden, Eastern Switzerland (Bürgin et al., 1991; Furrer, 2019).

### Palaeoichthyological research before 1924

The Middle Triassic fossil bearing strata of Monte San Giorgio (Canton Ticino, Southern Switzerland) are exposed also on the Italian side of the border, near the village of Besano. The bituminous shales there have been exploited in open quarries and galleries since 1830, first to produce oil and gas for the city of Milano and later for pharmaceutical components and products (Saurolo). Italian palaeontologists were aware of the fossils there and have collected material as early as the middle of the nineteenth century (Bassani, 1886; Curioni, 1847, 1863). At the turn of the century, the industrial exploitation of the bituminous shales started on Swiss territory, too. The Società Anonima Miniere Scisti bituminosi di Meride e Besano began to work in 1907. The first mining site named Cava Tre Fontane is near Serpiano on the western slope of Monte San Giorgio. By 1917, a second site with the name of Val Porina was exploited (Furrer, 2023). Most of the fossil material found at these two sites was sent to the Museo Civico di Storia Naturale in Milano (Reposi, 1909). In his voluminous study, Giuglio de Alessandri (1869–1921), curator of geology and palaeontology at the Museo Civico di Storia Naturale in Milano, listed besides the Italian material six species originating from Cava Tre Fontane (de Alessandri, 1910). These include his *Belonorhynchus stoppanii* BASSANI 1886, *Colobodus? triasicus* BASSANI 1886, *Colobodus bassanii* DE ALESSANDRI 1910, *Ptycholepis barboi* BASSANI 1886, *Ophiopsis bellotti* BASSANI 1886, *Pholidophorus meridensis* DE ALESSANDRI 1910 and *Pholidopleurus typus* BRONN, 1858. An allied air raid in August 1943 damaged greater parts of the museum in Milano and almost all of de Alessandri's fish material was destroyed (Visconti, 1988) (Fig. 1).

Due to the initiative of Carl Johann Josef Ernst Wiman (1867–1944), the Geological Institute of the University of Uppsala achieved between 1908 and 1916 a small collection of vertebrate fossils from Cava Tre Fontane. The ichthyosaur material was described by Wiman himself (Wiman, 1912). In 1916, Erik Andersson (later known as Erik Helge Osvald Stensiö, 1891–1984) published a paper on the fossil fishes of this collection (Andersson, 1916). Within the introduction he writes: “Wenigstens in den Schiefen von der Cava Tre Fontane sind die Fossilien sehr häufig, und es scheint mir ein wenig rätselhaft, dass solch ein Fundort interessanter Triasvertebraten verhältnismässig so unbeachtet geblieben ist” (Andersson, 1916, p. 13). Additionally, to the species mentioned by de Alessandri

## 2. Über einige Trias-Fische aus der Cava Trefontane, Tessin.

Von

Erik Andersson.

(Hierzu Pl. I–III.)

### Einleitung.

In den letzten acht Jahren ist das geologische Institut Upsala in den Besitz einer schönen Sammlung fossiler Vertebraten aus der Triasformation Spitzbergs gekommen. Es ist sogar ein überraschender Reichtum an Arten von Ichthyosauriern, Stegocephalen und Fischen gefunden worden (12, 14, 17). Während des Studiums derselben haben sich beim Vergleich mit den Faunen anderer Triaslokalitäten unsere Interessen besonders an die norditalienischen Fundorte Perledo und Besano sowie an die schweizerische Schiefergrube Cava Trefontane in Tessin geknüpft. Durch die Initiative von Prof. C. WIMAN ist daher eine nicht unbedeutende Sammlung fossiler Vertebraten aus Besano, besonders aber aus der Cava Trefontane für das hiesige Institut zusammengebracht worden.

Die Mixosaurierreste sind von WIMAN schon 1912 beschrieben (13), und in seinem Aufsatz ist auch das geologische Vorkommen ausreichend behandelt. Betreffend den Erhaltungszustand des vorliegenden Materials kann dieser nur als günstig bezeichnet werden. Obgleich die knöchernen Überreste eines Individuums oft genug von einander getrennt und über die Steinplatte etwas zerstreut liegen, lässt sich doch die Zusammengehörigkeit der verschiedenen Elemente ohne Schwierigkeit erkennen. Ausserdem sind die Knochen verhältnismässig selten gebrochen oder zerdrückt, und der feine Schiefer hat das Erhalten feinerer Skulptur- und Strukturdetails ermöglicht. Wenigstens in den Schiefen von der Cava Trefontane sind die Fossilien sehr häufig, und es scheint mir ein wenig rätselhaft, dass solch ein Fundort interessanter Triasvertebraten verhältnismässig so unbeachtet geblieben ist.

**Fig. 1** Title paper of the publication by Erik Andersson (1916) on some Triassic fish remains from Monte San Giorgio

(1910), he added the coelacanth *Undina* sp. and the actinopterygians *Urolepis* sp., *Belonorhynchus robustus* BELLOTTI, *Heterolepidotus? Belotti* DE ALESSANDRI and *Peltopleurus splendens* KNER. For *Pholidophorus meridensis* BASSANI he coined the new genus *Meridensia* (Anderson, 1916).

The first fossils from Monte San Giorgio were purchased by the University of Zurich 1916 in connection with a dissertation on the geology of this region (Frauenfelder, 1916). This collection included some fish and reptile material, a total of eight specimens from Cava Tre Fontane. In 1919, inspired by the German palaeontologist Ferdinand Broili (1874–1946), Bernhard Peyer (1885–1963), then lecturer at the University of Zurich, visited the fabrication site Spinirolo near Meride during a meeting in Lugano. Here, on a pile of bituminous shales, he found some fossil fishes and the remains of an ichthyosaur paddle and recognized the great potential of the fossil sites on Swiss territory. But it was only in 1924, when he was able to start the first scientific digs there (Furrer, 2024).

### Palaeoichthyological research after 1924

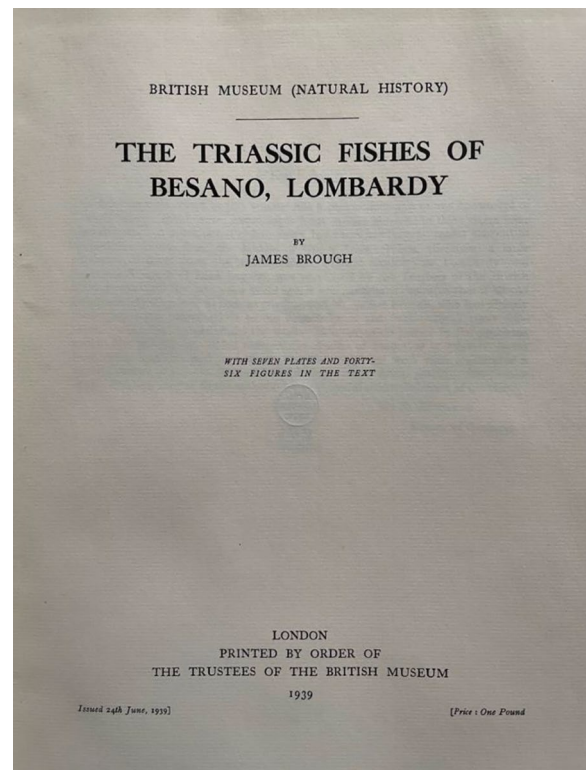
By the aid of a grant from the Georges and Antoine Claraz foundation, Bernhard Peyer and his team started the first scientific excavations in Cava Tre Fontane and in

Val Porina in spring 1924 (Peyer, 1925, 1934). They have been followed until 1938 with the new sites Acqua del Ghiffo (1927 & 1928), Val Serrata (1930), Cassina (1933 & 1937), Acqua Ferruginosa (1937) and Cassinello (1938).

In 1931, the German palaeontologist Hermann Aldinger (1902–1993) described some fragmentary material from the Grenzbitumenzone of Cava Tre Fontane, which he ascribed to the genus *Birgeria* STENSJÖ, 1916. Based on that material, he erected the new species *B. stensioei*, honouring the prolific work of Erik Stensjö (Aldinger, 1931).

In 1935 the Trustees of the British Museum of Natural History (today Natural History Museum) in London purchased a collection of 180 fossil fishes mainly from Besano from the German private collector and fossil dealer Karl Bender (1888–1940). They have been collected between 1929 and 1933. Most of these fossils have been studied by the British palaeontologist James Brough (?1904–1988). He published his studies in a book titled “The Triassic Fishes of Besano, Lombardy” (Brough, 1939). Among the material studied, there are some specimens originating from the Swiss side of Monte San Giorgio. These include *Meridensia meridensis* BMNH P. 19440 and P. 23808 from Valporina, *Peltopleurus lissocephalus* BMNH P. 19296 and *Luganoia lepidosteoides*, the holotype BMNH P. 19316 and P. 19327 (counterpart) labelled from Monte San Giorgio, Switzerland (Brough, 1939). In his introduction, Brough mentioned ongoing work by Bernhard Peyer on the genus *Colobodius*. Therefore, he omitted this species in his book, as well as the material of *Saurichthys* and some semionotiform fossils of minor quality (Brough, 1939). All these specimens are stored as “Bender collection” in the Department of Palaeontology and have been studied by in 1990 during my research on small- and medium-sized actinopterygians from Monte San Giorgio (Bürgin, 1991) (Fig. 2).

From 1950 to 1968 Peyer’s successor as professor of palaeontology and first director of the newly founded Palaeontological Institute and Museum, University of Zurich (PIMUZ), Emil Kuhn-Schnyder (1905–1994), opened the largest excavation at Point 902 near Mirigiolo (Kuhn-Schnyder, 1974). Another excavation followed from 1970 to 1975 at the Cassina site. In 1983 and 1984 Hans Rieber, the successor of Kuhn-Schnyder, exploited a site in Valle Stelle. From 1994 to 2004, further excavations at different localities were led by Heinz Furrer, curator at the PIMUZ. Between 1996 and 2003, on the invitation by Markus Felber—then curator at the Museo Cantonale di Storia Naturale in Lugano—a team of the University of Milano led by Andrea Tintori, investigated the Kalkschieferzone at Vecchi Mulini, close to Meride (Tintori, 2017; Tintori & Felber, 2015; Tintori et al., 1998). Since 2006, the Museo Cantonale di Storia Naturale in Lugano organized



**Fig. 2** Cover page of James Brough’s book on the Triassic fishes of Besano, 1939

yearly diggings under the lead of Rudolf Stockar at different sites, too (Furrer, 2024). Among the material collected there are many fish specimens that have been and need to be further studied (Bürgin, 1998).

### Chondrichthyan research

Presently, there are five genera and species of chondrichthyan fishes recognized from the Middle Triassic of Monte San Giorgio (Rieppel, 2019). The first shark remains, an isolated tooth of *Hybodus* cf. *plicatilis*, was found in 1924 during the first field season at Cava Tre Fontane. In 1944, Peyer mentioned further chondrichthyan material collected during his excavations at Monte San Giorgio. He ascribed it as belonging to the genera *Acrodus* and *Hybodus* (Peyer, 1944, p. 81). The first description of chondrichthyan fossils from the Swiss part of Monte San Giorgio was published by Emil Kuhn (Kuhn, 1946a). He ascribed the four specimens as belonging to the genus *Acrodus*. They had been collected between 1929 and 1933 from the Grenzbitumenzone in Val Porina and in Cava Tre Fontane/Valle Stelle. The material consisted of associated skull and skeletal remains with teeth and fin spine (Kuhn,

1946a: Fig. 1), a specimen with articulated teeth, an isolated fin spine and an unprepared specimen (Fig. 3).

Olivier Rieppel described the larger part of the chondrichthyan material anew and ascribed it to the genera *Hybodus*, *Acrodus*, *Asteracanthus* and *Palaeobates* (Rieppel, 1981). A year later, based on a small, nearly complete specimen, he erected the new genus and species *Acronemus tuberculatus* (Rieppel, 1981). In 1998, Raoul Mutter described the tooth variability in the dentition of *Acrodus* sp. (Mutter, 1997, 1998b) and described a new species, *Acrodus georgii* (Mutter, 1998a). *Acrodus georgii*, with a length between 2 and 3 m, was a large species. *Acronemus tuberculatus* was considerably smaller with a total length of 30 to 35 cm. The systematic position of the later is still debated (Maisey, 2011). The four other species are representatives of the family Hybodontiformes (Maisey, 1982). Further anatomical and taxonomic details can be found in the book of Olivier Rieppel on the fossils from Monte San Giorgio (Rieppel, 2019).

#### Osteichthyan research

Osteichthyan fishes are divided into the class Actinopterygii, the ray-finned fishes—and into the class Sarcopterygii, the lobe-finned fishes including tetrapods. Whereas the former taxon represents almost all of the

36,000 extant species, the lobe-finned fishes without the Tetrapodomorpha is represented by only 6 living species: 4 species of lungfishes and two coelacanths (Nelson et al., 2016).

#### Ray-finned fishes—Actinopterygians

Despite the wealth of material collected by Bernhard Peyer and Emil Kuhn-Schnyder, the ray-finned fishes did not receive any greater attention during their lifetimes. The dissertation of Sigmund Egil Guttormsen (1909–1999) was done under the supervision of Bernhard Peyer. He studied the jaws of some ganoid fishes and included material of the genus *Colobodius* from the Tessin collection (Guttormsen, 1937). In 1964, Kuhn-Schnyder published a list with the names of identified actinopterygians from Monte San Giorgio (Kuhn-Schnyder, 1964, p. 399) (Fig. 4).

The first profound investigation of actinopterygian material from the collection of the PIMUZ was done by Walter Schwarz (1941–2022) on the genus *Birgeria*. Schwarz worked mainly on a single, well preserved specimen, already mentioned by Kuhn (1946a, 1946b), which formed the basis for his detailed monograph (Schwarz, 1970). One reason for the restriction on a single specimen lay in the capacity of preparation work, which was during this time mainly used on the obviously more

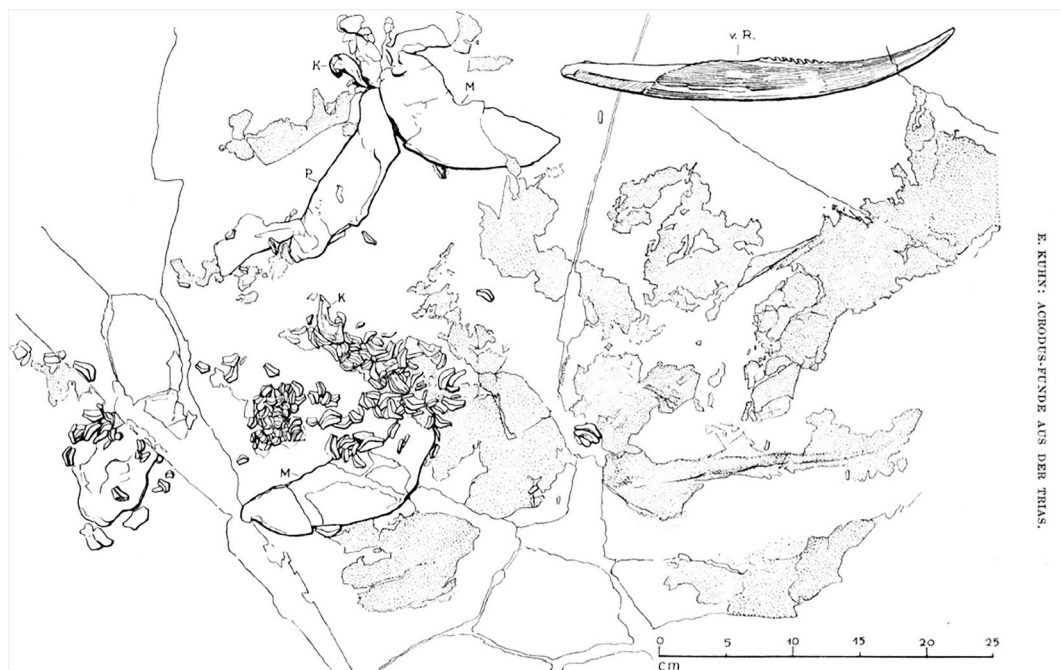


Fig. 1. *Acrodus* sp. Grenzbitumenhorizont der anisischen Stufe der Trias, Monte San Giorgio (Kt. Tessin). Exemplar a. K Kopfstachel, M Meckel'scher Knorpel, P Palatoquadratum, v. R. vorderer Rückenflössenstachel. Zoolog. Museum d. Universität Zürich. Vergr. 1 : 4.

**Fig. 3** Emil Kuhn's figure 1 from Kuhn (1946a), showing the large *Acrodus* fossil from Monte San Giorgio

Chondrostei	
Ordg. <i>Palaeoniscoidea</i>	
Fam. Birgeriidae	
<i>Birgeria</i>	
Ordg. Subholostei*)	
Fam. Perleidae (Colobodontidae)	
<i>Colobodus</i> *	
<i>Perleidus</i>	
<i>Meridensia</i> *	
Fam. Pholidopleuridae	
<i>Pholidopleurus</i>	
Fam. Saurichthyidae	
<i>Saurichthys</i> *; besonders zahlreich vertreten.	
Fam. Peltopleuridae	
<i>Peltopleurus</i> *	
<i>Placopleurus</i> *	
Fam. Luganoiidea	
<i>Luganoia</i> *	
<i>Besania</i> *	
Fam. Aetheodontidae	
<i>Aetheodontus</i> *	
Fam. Platsiagidae	
<i>Platsiagum</i>	
Fam. Cephaloxenidae	
<i>Cephaloxenus</i> *	
Holostei	
Ordg. Semionotidae	
Fam. Semionotidae	
<i>Semionotus</i> ?	
Fam. Eugnathidae (Furidae)	
<i>Eoeugnathus</i> ?	
<i>Ptycholepis</i>	
Crossopterygii	
Fam. Coelacanthidae: Die seltenen Reste eines Coelacanthiden sind noch nicht genauer untersucht.	

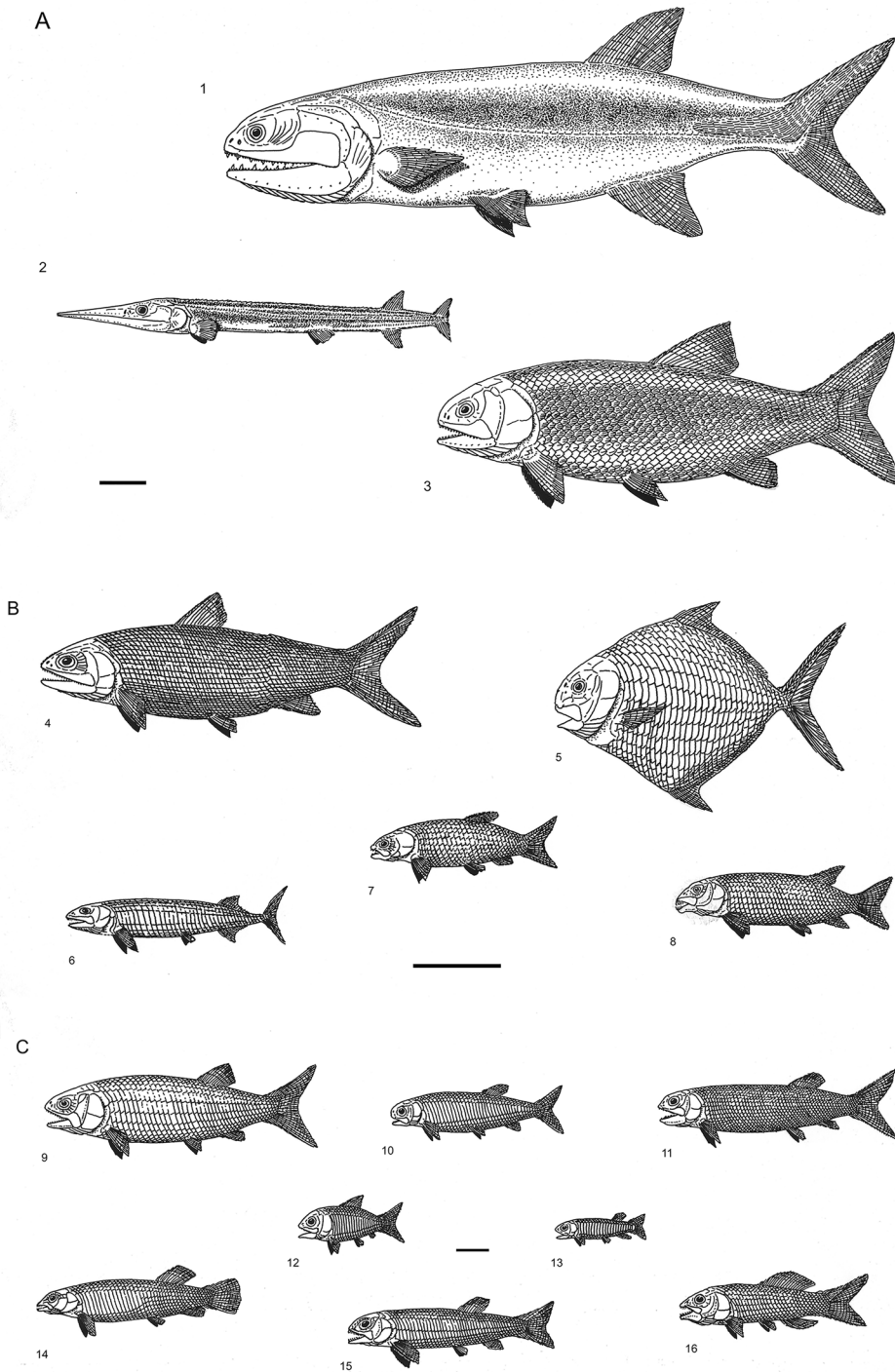
**Fig. 4** List of actinopterygian fishes from Monte San Giorgio compiled by Emil Kuhn-Schnyder (1964)

spectacular aquatic reptiles. The remaining material (67 specimens) was much later studied by Carlo Romano in a Ph. D. thesis and helped to clarify some important details in the anatomy of this large-sized predatory fish (Romano, 2007; Romano & Brinkmann, 2009).

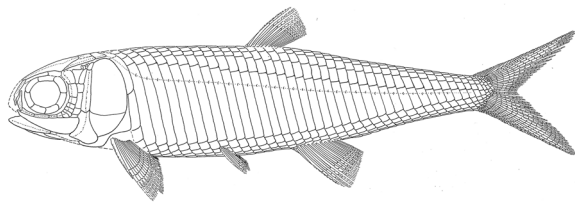
In 1980, John Griffith (?1933–?2003), then at the Department of Zoology at Westfield College, University of London, started to study some of the small actinopterygians from Monte San Giorgio in the Tessin collection of the PIMUZ. His focus was mainly on the perleidiform, peltopleuriform and luganoiiform material. Previously he had studied a Carnian marine fish fauna from Polzberg, Austria, and discussed the interrelationships of several actinopterygian taxa found there (Griffith, 1977). During his stay in Zurich, he studied and reclassified the actinopterygian fish material from Monte San Giorgio in the PIMUZ collection and prepared a comparative list with his and the identification by Kuhn-Schnyder from 1964 set aside. In April 1980, he loaned 73 specimens, mainly from the excavation Point 902 (Grenzbitumenzone). Later in August 1981, he loaned six additional specimens. He started to prepare a preliminary description of a new peltopleuriform species, but due to a change in position and health problems, he did not finish his manuscript. All the specimens he loaned, have been given back in September 1987. In June 1989, he handed over to me some of the original drawings and photographs of his new species.

The next actinopterygian taxa studied in detail was the genus *Saurichthys*, a medium- to large-sized predatory fish with a pointed, elongated snout. Olivier Rieppel studied 17 specimens from the Tessin collection of the PIMUZ (Rieppel, 1985a) and described the following species: *Saurichthys curionii* (BELLOTTI, 1857), *S. macrocephalus* (DEECKE 1886) and his new species *S. costasquamosus*. In this study he recognized some peculiar anal fin structures, as well as a cone-shaped, presumably intromittent organ. He, for the first time speculated on the possibility of viviparity in this genus (Bürgin, 1990; Maxwell et al., 2018; Rieppel, 1985a). Additional, smaller specimens of *Saurichthys* from the Tessin collection were described in a subsequent paper (Rieppel, 1992). Besides the description of some juvenile specimens of *Saurichthys curionii* and *S. costasquamosus*, he erected the new species *S. paucitrichus*. Furthermore, he presented a phylogenetic analysis of the genus *Saurichthys* and discussed its ecology. In 2015, Erin Maxwell, Carlo Romano, Feixiang Wu and Heinz Furrer described two new species auf *Saurichthys* from the Middle Triassic Besano Formation of Monte San Giorgio: *S. breviabdominalis* and *S. rieppeli* (Maxwell et al., 2015). Sue Beardmore and Heinz Furrer studied the interesting taphonomy of these frequent fossils (Beardmore & Furrer, 2015, 2019). In 2021 Silvio Renesto, Fabio Magnani and Rudolf Stocker described the new species *S. sceltrichensis* from the Sceltrich beds (Meride Limestone) (Renesto et al., 2021). Additional studies on morphology, biology, systematics, taphonomy and palaeogeography of the genus *Saurichthys* complemented the picture of this taxon (Argyriou et al., 2018; Beardmore & Furrer, 2015; Maxwell et al., 2013, 2021; Renesto & Stockar, 2009, 2015; Romano et al., 2012; Scheyer et al., 2014; Schmid & Sanchez-Villagra, 2010; Tintori, 2019).

From October 1987 to May 1990 I, with the support of a Swiss National Fund project (No. 3.535.0.86.), studied the small- and medium-sized actinopterygians in the Tessin collection of the PIMUZ. I was able to use some of the previous work done by John Griffith (see above). During this project a total of 730 specimens have been carefully measured and studied in detail. The result of this project was a publication entitled “Basal Ray-finned Fishes from the Middle Triassic of Monte San Giorgio”, which listed 18 different genera, 3 of them new, and 30 species, 16 of them new (Bürgin, 1992). The species described in detail are *Gyrolepis* sp., *Ptycholepis barboi* BASSANI 1886, *P. priscus* BÜRGIN 1992, *P. schaefferi* BÜRGIN 1992, *P. magnus* BÜRGIN 1992, *Bobasatrania cersiensis* BÜRGIN 1992, *Pholidopleurus ticinensis* BÜRGIN 1992, *Gracilignathichthys microlepis* BÜRGIN 1992, *Platsiagum minus* EGERTON 1872, *Perleidus* sp., *Meridensia meridensis* ANDERSSON (= STENSJÖ)1916, *Aetheodontus besanensis* BROUGH 1939, *Ctenognathichthys bellottii*



**Fig. 5** Various actinopterygian fishes from Monte San Giorgio, **A**, large-sized fishes (30–100 cm), **B** medium-sized fishes (10–29 cm), **C** small sized fishes (2–9 cm); reconstructions by the author. 1—*Birgeria stensiöi*, 2—*Saurichthys curionii*, 3—*Colobodus bassanii*, 4—*Ptycholepis barboi*, 5—*Bobasatrania ceresiensis*, 6—*Pholidopleurus ticinensis*, 7—*Ticinolepis crassidens*, 8—*Ctenognathichthys bellotti*, 9—*Meridensia meridensis*, 10—*Peltopleurus lissocephalus*, 11—*Aetheodontus besanensis*, 12—*Placopleurus minus*, 13—*Habroichthys minimus*, 14—*Luganoia lepidosteoides*, 15—*Peltoperleidus macrodontus*, 16—*Ophiopsidae* indet. Scale bars **A** and **B**=10 cm, **C**=1 cm



**Fig. 6** *Placopleurus besanensis* BROUGH 1939, reconstruction by the author based mainly on PIMUZ T 1234

(BÜRGIN 1992), *Peltopterleius bellipinnis* BÜRGIN 1992, *P. elonginathus* BÜRGIN 1992, *P. macrodontus* BÜRGIN 1992, *P. triserius* BÜRGIN 1992, *Dipteronotus ornatus* BÜRGIN 1992, *Luganoia lepidosteiformes* BROUGH 1939, *Peltopterleius lissocephalus* BROUGH 1939, *P. rugosus* BROUGH 1939, *P. nothocephalus* BÜRGIN 1992, *Peltopterleius* sp., *Nannolepis* sp., *Peripeltopterleius vexillipinnis* BÜRGIN 1992, *P. besanensis* BÜRGIN 1992, *P. hypsisomus* BÜRGIN 1992, *Cephaloxenus macropterus* BROUGH 1939, *C. squamiserratus* BÜRGIN 1992, *Habroichthys minimus* BROUGH 1939, *H. griffithi* BÜRGIN 1992 and *Habroichthys* sp. (Fig. 5).

The neopterygian genera and species identified during the studies of 1987 to 1990 have been listed in an overview of Middle Triassic marine fish faunas from Switzerland (Bürgin, 1999a, Appendix 1). However, due to a change of job and occupation, the neopterygian material has only partly been published. The unpublished material will be used in subsequent and collaborative work.

One of the is the genus *Placopleurus* Brough 1939. There are 98 specimens being studied by myself. These include *Placopleurus primus* BROUGH, 1939 and *P. besanensis* BROUGH, 1939, as well as two probably new species. The genus itself shows close anatomical similarities to the Chinese genus *Venusichthys* (Xu & Zhao, 2016) (Fig. 6).

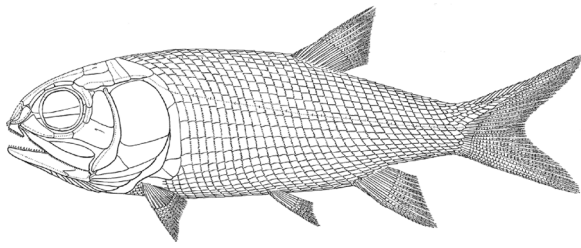
The genus *Colobodus*, due to its larger size, was not included in my studies, as well as the specimens of the genera *Saurichthys* (studied by Olivier Rieppel, see above) and *Birgeria* (studied by Carlo Romano, see above). From 1998 to 2002, Raoul Mutter in his Ph.D. thesis studied the complete material of the genus *Colobodus* in the collection of the PIMUZ (Mutter, 2001a, b, 2002, 2004). He revised the family Colobodontidae sensu Andersson 1916 and discriminated on anatomical and meristic characters several taxa, some of them probably new. Unfortunately, due to a change of occupation, all the proposed new species have not yet been published (Mutter, 2002). The valid species recognized in his thesis are: *Crenilepis sandbergeri* DAMES 1888, *Colobodus bassanii* DE ALESSANDRI 1910, *C. maximus* (QUENSTEDT, 1867) and *C. koenigi* STOLLEY 1920. Due to the absence of a holotype, he designated a neotype for *C. bassanii* (Mutter, 2003).

In 1995, I described new material of actinopterygian fishes from the middle Kalkschieferzone (uppermost Ladinian), excavated by the team of Heinz Furrer (PIMUZ) in the Val Mara near the village of Meride (Bürgin, 1995; Furrer, 1995a). The taxa described therein are *Gyrolepis* sp., *Perleius altolepis* (DECKE, 1889), two probably new species of *Peltopterleius*, *Archaeosemionotus* sp., *Ophiopsis* cf. *lepturus* and *Prohalecites porroi* (BELLOTTI, 1857). The later species was described in detail by Andrea Tintori based on abundant material from the Italian locality Ca'del Frate (Tintori, 1990a). Because of the small sample size and the lack of distinct discriminating characters I refrained from the designation of two new species of *Peltopterleius*. *Archaeosemionotus* sp. was later transferred into the new genus *Ticinolepis* (see López-Arbarello et al., 2016).

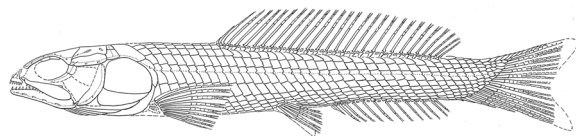
In 2002, Cristina Lombardo described the new genus *Caelaticthys*, with the new species *C. nitens* from late Ladinian Kalkschieferzone of Ca' del Frate in Northern Italy, and the new species *C. meridensis* from the Kalkschieferzone near Meride in Canton Ticino (Lombardo, 2002). The genus shows a mixture of primitive and advanced characters. She placed it tentatively as a palaeoniscid grade actinopterygian. Andrew Neuman und Raoul Mutter grouped both species in the family Platysiagidae (Neuman & Mutter, 2005).

In 2003, Annette Herzog, as a result of her thesis on the Middle Triassic actinopterygians from the Prosanto Formation in Graubünden, published a new description of *Eoeugnathus megalepis* BROUGH 1939 (Herzog, 2003b). This species was originally established by James Brough in his study on the Triassic fishes of Besano (Brough, 1939). The species is well represented in the fish fauna of Monte San Giorgio, too, where 46 specimens are in the collection of the PIMUZ. They have been studied in detail by myself and recently by Adriana López-Arbarello (pers. com.) The species shows close anatomical similarities to the ionoscopiform genus *Subortichthys* from the Middle Triassic of Yunnan, China (Ma & Xu, 2017). Contrary, Zuoyu Sun and co-authors placed *Eoeugnathus* in their newly erected order Panxianichthyiformes, the basal sister-group to the Ionoscopiformes (Sun et al., 2016) (Fig. 7).

The genus *Eosemionotus* STOLLEY, 1920 was subject of a further study by myself. I described the new species *Eosemionotus ceresiensis* based on well preserved material from the upper Besano Formation (Bürgin, 2004). Additional material from the Meride Limestone (Cava inferiore, Cava superiore, Cassina and Sceltrich beds) resulted in a taxonomic and systematic revision of the genus *Eosemionotus* by Adriana López-Arbarello, Heinz Furrer, Rudolf Stockar and myself. Described have been three new species: *Eosemionotus diskosomus*, *E. sceltrichensis*, and *E. minutus* (López-Arbarello et al.,



**Fig. 7** *Eoegnathus megalepis* BROUGH 1939, composite reconstruction by the author based mainly on PIMUZT 1356



**Fig. 8** *Besania* sp., reconstruction by the author based mainly on PIMUZT 3927

2019). The cladistic analysis retrieved *Eosemionotus* as the oldest member of the family Macrosemiidae within the order Semionotiformes (Ginglymodi).

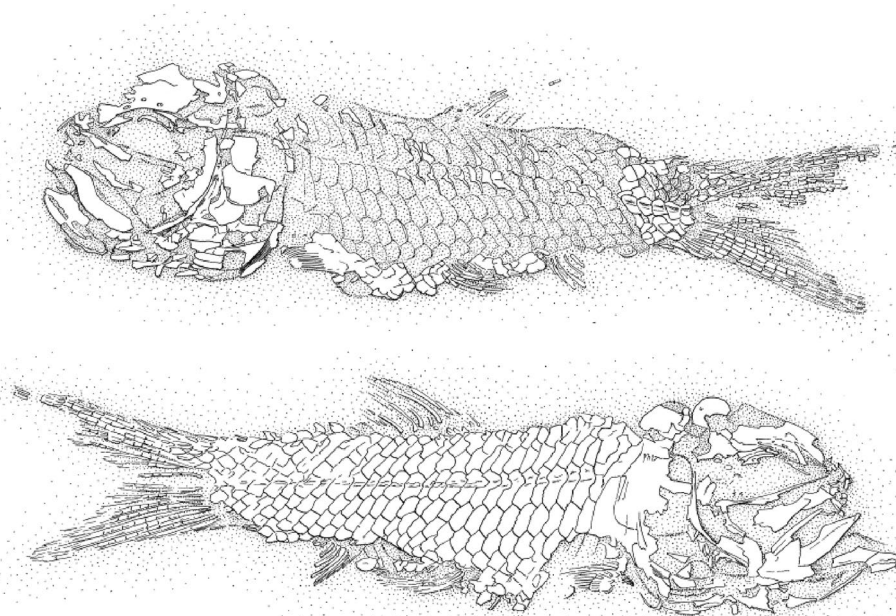
In 2005, Annette Herzog and myself described well preserved material of the genus *Besania* BROUGH 1939 from the contemporaneous Prosanto Formation in Graubünden. Brough (1939) proposed a close relationship with the genus *Luganoia*. We could show however,

that both genera are distinctly different from each other and *Besania* to be close to the basal Halecostomi (Herzog & Bärgin, 2005). The genus *Besania* is well represented in the Middle Triassic of Monte San Giorgio, too (Fig. 8).

In 2007, Andrea Tintori and Cristina Lombardo described the new semionotiform genus and species *Sangiorgioichthys aldae* from the lower Kalkschieferzone (upper Meride Limestone, uppermost Ladinian) of Val Mara (near Meride) and Ca' del Frate (Viggiu, Italy) (Tintori & Lombardo, 2007). Five years later, a second species, *Sangiorgioichthys valmarensis*, was described from the same locality by Cristina Lombardo, Andrea Tintori and Daniele Tona (Lombardo et al., 2012). The genus was also shown to be present in the Middle Anisian Luoping fauna of China (López-Arbarello et al., 2011).

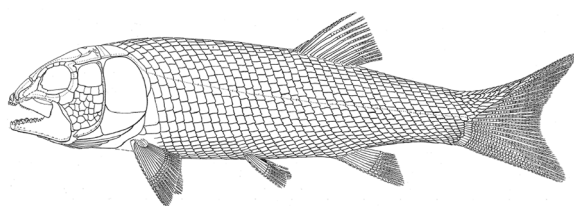
In 2007, Gloria Arratia and Annette Herzog described a new halecomorph fish from the Middle Triassic Prosanto Formation of Graubünden (Arratia & Herzog, 2007). Initially listed as Teleostei indet. (Herzog, 2003a, 2003b), the new genus and species *Prosantichthys buergini*, seems closer to the halecostome family Parasemionotidae. The same species is present at Monte San Giorgio too, where it was tentatively ascribed to the family Pholidophoridae (Bärgin, 1999a, 1999b) (Fig. 9).

In 2013, Cristina Lombardo published a paper on an enigmatic basal actinopterygian fish from the Late Ladinian Kalkschieferzone of Monte San Giorgio. The single specimen shows anatomical characters, which are



**Fig. 9** *Prosantichthys* (=Pholidophoridae gen. et sp. indet. by Bärgin, 1999a, 1999b), plate and counterplate, PIMUZT 3928





**Fig. 10** *Ticinolepis crassidens*, reconstruction by the author based mainly on PIMUZ T 273

representative for fishes of the family Redfieldiiformes (Lombardo, 2013). This family was previously known from freshwater deposits of North America, Africa and Australia (Schaeffer, 1984). The presence of abundant freshwater crustaceans in the Kalkschieferzone indicates a temporary influx of freshwater. A similar species, referred as Redfieldiiformes indet., is described in a fish fauna of the Erfurt-Formation of the German Lettenkeuper (Böttcher, 2015).

In 2014, Adriana López-Arbarello, Rudolf Stockar and myself clarified the difficult phylogenetic relationships of the genus *Archaeosemionotus* DEECKE, 1889 from Perledo (López-Arbarello et al., 2014) and described subsequently together with Heinz Furrer the new genus *Ticinolepis* with its two new species *T. crassidens* and *T. longaeva* from the Middle Triassic of Monte San Giorgio (López-Arbarello et al., 2016) (Fig. 10).

Since many years Gloria Arratia studies basal Teleostomorpha (e.g. Arratia, 1997a, 1997b, 2000a, 2000b, 2001, 2004, 2013, 2015; Arratia & Schultze, 2024). In 2022, she published a paper on the outstanding small suction-feeder *Marcopoloichthys furreri* from the Middle Triassic Prosanto Formation of Graubünden (Arratia, 2022). The genus itself was erected by Italian and Chinese scientists (Tintori et al., 2007) on fossils from the Early Ladinian of the Cunardo Formation (Lombardy, Northern Italy) and the Middle Anisian of the Guanling Formation (Yunnan Province, South China). The same genus is present at Monte San Giorgio, too. It was listed as Neopterygii incertae sedis in the list of Bürgin (1999a, 1999b: Appendix 1). Meanwhile it is described as a new species of genus *Marcopoloichthys* (Arratia et al., subm.). It shows the same unique feeding apparatus.

#### Lobe-finned fishes—Sarcopterygians

The first remains of lobe-finned fishes (Sarcopterygii) on the Swiss side of Monte San Giorgio have been found at Cava Tre Fontane (Andersson, 1916). They have been assigned to the actinistian genus *Undina*. Some material collected by the teams of Bernhard Peyer and Emil Kuhn-Schnyder at Monte San Giorgio was first studied in detail by Olivier Rieppel (Rieppel, 1980). Based on that material

he erected the new genus and species *Ticinopomis peyeri*. It is a small species of about 12 cm total length. Fragmentary remains have been attributed to cf. *Undina picenus* (Rieppel, 1985b).

In 2013, Lionel Cavin, Heinz Furrer and Christian Obrist described new coelacanth material from the Middle Triassic Prosanto Formation in Graubünden (Cavin et al., 2013). They restudied the material of *Ticinopomis peyeri* RIEPPEL 1980 and emended the diagnosis of this genus and species.

In 2017, Christophe Ferrante, Rossana Martini, Heinz Furrer and Lionel Cavin published a paper on the Middle Triassic coelacanths from Switzerland (Ferrante et al., 2017). Therein they mentioned an unknown species from the middle Besano Formation of Monte San Giorgio. It was described in a subsequent paper as *Rieppelia heinzfurreri* (Ferrante & Cavin, 2023). Like *Foreyia maxkuhnii* from the Prosanto Formation of Graubünden, it shows a highly derived anatomy, with a relatively large head and a short and compact body (Ferrante & Cavin, 2023, Fig. 4).

In 2018, Silvio Renesto and Rudolf Stockar described a new, small coelacanth specimen from the Cassina beds, Lower Meride Limestone (Renesto & Stockar, 2018). Based on its anatomy they classified it as *Heptanema* sp., with close affinities to the poorly known *Heptanema paradoxum* BELLOTTI, 1857 from the Ladinian Perledo Formation of Northern Italy.

In 2023 Christophe Ferrante, Heinz Furrer, Rossana Martini and Lionel Cavin revised the material of *Ticinopomis* RIEPPEL 1980 and erected the new species *Ticinopomis ducanensis*, which is present both in the Besano Formation of Monte San Giorgio as well as in the Prosanto Formation of Graubünden (Ferrante et al., 2023). Additionally, they included some palaeobiological and palaeoecological considerations on the known coelacanths from the Middle Triassic of Switzerland.

#### Discussion and conclusion

One hundred years after the start of the scientific investigations by Bernhard Peyer from the University of Zurich, the research on Middle Triassic fishes from the numerous sites of Monte San Giorgio no longer stands in the shadow of the aquatic reptiles. Especially the last four decades have shown a wealth of new investigations and many taxa new to science. The restart of fish investigations in the years around 1980 has shown the great potential of the previously collected material by the PIMUZ, as well as new material collected from the Kalkschieferzone by researchers of the PIMUZ, the University of Milano and the Museo Cantonale di Storia Naturale in Lugano. Since 2012, a nice selection of fishes is also exposed in the

Museum of Fossils from Monte San Giorgio in Meride ([www.museodeifossili.ch](http://www.museodeifossili.ch)).

My SNF project on small- and medium-sized actinopterygians initiated systematic excavations in the contemporaneous Prosanto Formation (Canton Graubünden, Eastern Switzerland), which resulted in another great number of often exquisitely preserved fish fossils (Bürgin et al., 1991; Bürgin & Herzog, 2002; Cavin et al., 2017; Furrer, 1995b, 2019; Herzog, 2003a, 2003b; Mutter & Herzog, 2004; Herzog & Bürgin, 2005). One of them is the remarkable stem teleostean *Marcopoloichthys furreri*, a very small species with suction feeding abilities (Arratia, 2022).

The Middle Triassic fishes of Monte San Giorgio already known come from six different fossil bearing beds. The oldest is the Besano Formation at the Anisian–Ladinian boundary (Furrer, 2003, 2024). It is the most species-rich horizon. Somewhat younger (Early Ladinian) are the Cava inferiore, the Cava superiore and the Cassina beds of the Lower Meride Limestone (Early Ladinian). At the base of the Upper Meride Limestone lie the Sceltrich beds, which has been studied between 2010 and 2021. The youngest horizon is the Kalkschieferzone (Late Ladinian). All these beds show a clearly reduced taxic diversity.

The fossil fishes from the Middle Triassic of Monte San Giorgio offer a stimulating reference to other contemporaneous fish faunas worldwide. These include the research on the Italian side by Andrea Tintori, Cristina Lombardo and co-workers from the University of Milano (Lombardo, 1999; Lombardo & Tintori, 2004; Tintori, 2013, 1990b, 1990c; Tintori et al., 2007), the Middle Triassic sites of the Kamnik-Savinja Alps in Slovenia (Hitji et al., 2010; Miklavc et al., 2016), the Muschelkalk in Germany (Arratia & Schultze, 2024; Schultze & Kriwet, 2021; Schultze & Möller, 1986) and the Netherlands (Haarhuis & Diependaal, 2019; Oosterink, 1986), the Muschelkalk of Spain (Beltan, 1972, 1984, 2019; Cartanya, 1999; Cartanya et al., 2015) and especially the prolific outcrops in the Middle Triassic of China, with the Luoping and the Panxian fauna (Lin et al., 2011; Lombardo et al., 2011; Ren & Xu, 2011; Sun et al., 2008, 2009, 2012; Tintori et al., 2010a, 2010b; Wu et al., 2018; Xu, 2019) and the Xingyi fauna (Tintori et al., 2011, 2015).

Most of the work up to now has been focused primarily on the alpha-level taxonomy. There are still many open questions concerning the higher-level systematics of most of the actinopterygian taxa being studied. Nevertheless, all the present studies open new research opportunities on global dispersal, evolution, faunal composition and ecology of early Mesozoic chondrichthyan and osteichthyan fishes. Although the main goal of the present paper is to present the research history of the

fossil fishes from Monte San Giorgio, it is to hope, that it will stimulate new studies and further cooperation in the field.

#### Abbreviations

BMNH P.	British Museum (Natural History), palaeontological collection
MCSN:	Museo cantonale di storia naturale, Lugano
PIMUZ:	Paläontologisches Institut, Universität Zürich
T	Tessin collection of the PIMUZ

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#### Author contributions

T.B. wrote the text and prepared all reconstructions.

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#### Competing interests

The author declares no competing interests.

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#### References

- Aldinger, H. (1931). Über Reste von *Birgeria* (Pisces, Palaeoniscidae) aus der alpinen Trias. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie. Beilage-Band (b)*, 66, 167–181.
- Andersson, E. (1916). Über einige Trias-Fische aus der Cava Tre Fontane, Tessin. *Bulletin of the Geological Institutions of the University of Uppsala*, XV, 13–34.
- Argyriou, T., Clauss, M., Maxwell, E. E., Furrer, H., & Sanchez-Villagra, M. (2015). Exceptional preservation reveals gastrointestinal anatomy and evolution in early actinopterygian fishes. *Scientific Reports*, 6, 18758. <https://doi.org/10.1038/resp18758>
- Argyriou, T., Giles, S., Friedman, M., Romano, C., Kogan, I., & Sánchez-Villagra, M. R. (2018). Internal cranial anatomy of Early Triassic species of †*Saurichthys* (Actinopterygii: †Saurichthyiformes): Implications for the phylogenetic placement of †Saurichthyiformes. *BMC Evolutionary Biology*, 18(161), 1–43. <https://doi.org/10.1186/s12862-018-1264-4>
- Arratia, G. (1997a). Basal teleosts and teleostean phylogeny. *Palaeo Ichthyologica*, 7, 1–168.

- Arratia, G. (1997b). The monophyly of Teleostei and stem-group teleosts. In G. Arratia & H.-P. Schultze (Eds.), *Mesozoic fishes 2—Systematics and fossil record* (pp. 265–334). Pfeil.
- Arratia, G. (2000a). New teleostean fishes from the Jurassic of southern Germany and the systematic problems concerning the “pholidophoriforms”. *Paläontologische Zeitschrift*, *74*(1/2), 113–143.
- Arratia, G. (2000b). Phylogenetic relationships of Teleostei. Past and Present. *Estudios Oceanológicos*, *19*, 19–51.
- Arratia, G. (2001). The sister-group of Teleostei: Consensus and disagreements. *Journal of Vertebrate Paleontology*, *21*(4), 767–773.
- Arratia, G. (2004). Mesozoic halecostomes and the early radiation of teleosts. In G. Arratia & A. Tintori (Eds.), *Mesozoic fishes 3 systematics, paleoenvironments and biodiversity* (pp. 279–315). Pfeil.
- Arratia, G. (2013). Anatomy, taxonomy, and phylogeny of Triassic pholidophorid fishes (Actinopterygii, Teleostei). *Journal of Vertebrate Paleontology*, *33*(supplement 1), 1–138.
- Arratia, G. (2015). Complexities of Early Teleostei and the Evolution of Particular Morphological Structures through Time. *Copeia*, *103*(4), 999–1025.
- Arratia, G. (2022). The outstanding suction-feeder *Marcopoloichthys furreri* new species (Actinopterygian) from the Middle Triassic Thetys Realm of Europe and its implications for early evolution of neopterygian fishes. *Fossil Record*, *25*(2), 231–261.
- Arratia, G., Bärgin, T. & Furrer, H. (subm.). A new suction feeder and miniature teleostemorph, *Marcopoloichthys mirigoliensis*, from the lower Besano Formation (late Anisian) of Monte San Giorgio. *Swiss Journal of Palaeontology*.
- Arratia, G., & Herzog, A. (2007). A new halecostome fish from the Middle Triassic of Switzerland and its systematic implications. *Journal of Vertebrate Paleontology*, *27*(4), 838–849.
- Arratia, G., & Schultze, H.-P. (2024). The oldest teleosts (Teleostemorphia): Their early taxonomic, phenotypic, and ecological diversification during the Triassic. *Fossil Record*, *27*(1), 29–53.
- Bassani, F. (1886). Sui fossili e sull’eta degli schist bituminosi triasici di Besano in Lombardia. *Atti Societa Italiana Di Scienze Naturali*, *29*, 15–72.
- Beardmore, S. R., & Furrer, H. (2015). Taphonomic analysis of *Saurichthys* from two stratigraphic horizons in the Middle Triassic of Monte San Giorgio, Switzerland. *Swiss Journal of Geosciences*, *109*, 1–16. <https://doi.org/10.1007/s00015-015-0194-z>
- Beardmore, S. R., & Furrer, H. (2019). Taphonomic variation within a Middle Triassic fossil lagerstätte (Cassina beds, Meride Limestone) at Monte San Giorgio. *Paläontologische Zeitschrift*, *93*, 49–67. <https://doi.org/10.1007/s12542-018-0415-7>
- Bellotti, C. (1857). Descrizione di alcune nuove specie di pesci fossili di Perledo e di altri località Lombarde. In: A. Stoppani (ed.) *Studii Geologici e Paleontologici sulla Lombardia* (pp. 419–438). Turati, Milano.
- Beltan, L. (1972). La faune ichthyologique du Muschelkalk de la Catalogne Espagnole. *Memorias De La Real Academia Ciencias y Artes De Barcelona*, *41*, 281–325.
- Belton, L. (1984). Quelques poissons du Muschelkalk superieur d’Espagne. *Acta Geologica Hispanica*, *19*(2), 117–127.
- Benton, M. J., Zhang, Q., Hu, S., Chen, Z.-Q., Wen, W., Liu, J., Huang, J., Zhou, C., Xie, T., Tong, J., & Choo, B. (2013). Exceptional vertebrate biotas from the Triassic of China, and the expansion of marine ecosystems after the Permo-Triassic mass extinction. *Earth-Science Reviews*, *125*, 199–243. <https://doi.org/10.1016/j.earscirev.2013.05.014>
- Böttcher, R. (2015). 8. Fische des Lettenkeupers. In: H. Hagdorn, R. Schoch & G. Schweigert (Eds.), *Der Lettenkeuper—Ein Fenster in die Zeit vor den Dinosauriern. Palaeodiversity, Sonderband*, pp. 141–202.
- Brayard, A., Krumenacker, L. J., Bottling, J. P., Jenks, J. F., Bylund, K. G., Fara, E., Venin, E., Olivier, N., Goudemand, N., Saucède, T., Charbonnier, S., Romano, C., Doguzhaeva, L., Thuy, B., Hautmann, M., Stephen, D. A., Thomazo, C., & Escarguel, G. (2017). Unexpected Early Triassic marine ecosystem and the rise of the Modern evolutionary fauna. *Science Advances*, *3*, e1602159. <https://doi.org/10.1126/sciv.1602159>
- Bronn, H. G. (1858). Beiträge zur triassischen Fauna und Flora der bituminösen Schiefer von Raibl. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde*, 1–63.
- Brough, J. (1939). *The Triassic Fishes of Besano, Lombardy* (p. 117). British Museum Natural History.
- Bärgin, T. (1990). Reproduction in Middle Triassic actinopterygians; complex fin structures and evidence of viviparity in fossil fishes. *Zoological Journal of the Linnean Society*, *100*(4), 379–391.
- Bärgin, T. (1991). La storia dei pesci fossili di Besano. *Paleocronache*, *1*(1), 42–49.
- Bärgin, T. (1992). Basal ray-finned fishes (Osteichthyes; Actinopterygii) from the middle-Triassic of Monte San Giorgio (Canton Tessin, Switzerland): Systematic palaeontology with notes on functional morphology and palaeoecology. *Schweizerische Paläontologische Abhandlungen*, *114*, 1–164.
- Bärgin, T. (1995). Actinopterygian fishes (Osteichthyes; Actinopterygii) from the Kalkschieferzone (Uppermost Ladinian) near Meride (Canton Ticino, Southern Switzerland). *Eclogae Geologicae Helvetiae*, *88*(3), 803–826.
- Bärgin, T. (1998). Pesci fossili del Triassico del Monte San Giorgio (Svizzera meridionale) e della zona di Besano (Italia settentrionale). *Geologica Insubrica*, *3*(1), 1–9.
- Bärgin, T. (1999a). Middle Triassic marine fish faunas from Switzerland. In G. Arratia & H.-P. Schultze (Eds.), *Mesozoic fishes 2—Systematics and fossil record* (pp. 481–494). Pfeil.
- Bärgin, T. (1999b). New actinopterygian fishes (Osteichthyes) from the Lower Meride limestones (Lower Ladinian) of Aqua del Ghiffo (Monte San Giorgio, Southern Switzerland). *Rivista Museo Civico Scientifico e. “caffi” Bergamo*, *20*, 57–62.
- Bärgin, T. (2004). *Eosemionotus ceresiensis* sp. nov., a new semionotiform fish (Actinopterygii, Halecostomi) from the Middle Triassic of Monte San Giorgio (Southern Switzerland). In G. Arratia & A. Tintori (Eds.), *Mesozoic fishes 3—Systematics, paleoenvironments and biodiversity* (pp. 239–251). Pfeil.
- Bärgin, T., Eichenberger, U., Furrer, H., & Tschanz, K. (1991). Die Prosanto-Formation - eine fischreiche Fossil-Lagerstätte in der Mitteltrias der Silvretta-Decke (Kanton Graubünden, Schweiz). *Eclogae Geologicae Helvetiae*, *84*, 921–990.
- Bärgin, T., & Herzog, A. (2002). Die Gattung *Ctenognathichthys* (Actinopterygii; Perleidiformes) aus der Prosanto-Formation (Ladin, Mitteltrias) Garubündens (Schweiz), mit der Beschreibung einer neuen Art, *C. hattichi* sp. nov. *Eclogae Geologicae Helvetiae*, *95*, 461–469.
- Cartanya, J. (1999). An overview of the Middle Triassic actinopterygians from Alcover, Montral and El Pinetell (Catalonia, Spain). In G. Arratia & H.-P. Schultze (Eds.), *Mesozoic fishes, 2—Systematics and Fossil record* (pp. 535–551). Pfeil.
- Cartanya, J., Fortuny, J., Bolet, AT., & Garcia-Artigas, R. (2019). *Moradebrichthys vilaseca* gen et sp. nov., a new perleiidid (Actinopterygii: Osteichthyes) from the Upper Muschelkalk facies of Catalonia (NE Iberian Peninsula). *Neues Jahrbuch Geologisch Paläontologische Abhandlungen*, *292*(2), 171–190.
- Cartanya, J., Fortuny, J., Bolet, AT., & Mutter, R. J. (2015). *Colobodog giganteus* BELTAN, 1972) comb. Nov. from the Upper Muschelkalk facies of Catalonia (NE Iberian Peninsula). *Neues Jahrbuch Geologisch Paläontologische Abhandlungen*, *278*(3), 323–333.
- Cavin, L., Furrer, H., & Obrist, C. (2013). New coelacanth material from the Middle Triassic of eastern Switzerland, and comments on the taxic diversity of actinistians. *Swiss Journal of Geosciences*, *106*, 161–177.
- Cavin, L., Menecart, B., Obrist, C., Costeur, L., & Furrer, H. (2017). Heterochron evolution explains novel body shape in a Triassic coelacanth from Switzerland. *Scientific Reports*, *7*, 13695. <https://doi.org/10.1038/s41598-017-13796-0>
- Chen, Z.-Q., & Benton, M. (2012). The timing and pattern of biotic recovery following the end-permian mass extinction. *Nature Geosciences, Review Article*. <https://doi.org/10.1038/NNGEO1475>
- Curioni, G. (1847). Cenni sopra un nuovo Saurio fossile dei monti di Perledo sul Lario e sul terreno che lo rachiude. *Giornale dell’ I.R. Istituto Lombardo di scienze, lettere ed arti*, *8*, 166–167.
- Curioni, G. (1863). Sui giacimenti metalliferi e bituminosi nei terreni triasici di Besano. *Memorie Istituto Lombardia Di Scienze e Lettere*, *9*, 241–268.
- Dai, X., Davies, J. H. F. L., Yuan, Z., Brayard, A., Ovtcharova, M., Xu, G., Liu, X., Smith, C. P. A., Schweitzer, C. E., Li, M., Perrot, M. G., Jiang, S., Miao, L., Cao, Y., Bai, R., Wang, F., Guo, W., Song, H., Tian, L., ... Song, H. (2023). A Mesozoic fossil lagerstätte from 250.8 million years ago shows a modern-type marine ecosystem. *Science*, *379*, 567–572.
- Dames, W. (1888). Die Ganoiden des deutschen Muschelkalks. *Paläontologische Abhandlungen*, *4*(2), 133–179.

- De Alessandri, G. (1910). Studii sui pesci triassici della Lombardia. *Memorie Societa Italiana Scienza Naturale Milano*, VII(Fasc 1), 1–147.
- Deecke, W. (1889). Über Fische aus verschiedenen Horizonten der Trias. *Palaeontographica*, 35, 97–138.
- Egerton, M. G. (1872). Palaeichthyological Notes N. 6. On a fossil fish from the Upper beds of the New Red Sandstone at Bromsgrove. *Annals and Magazine of Natural History*, 2(13), 1–10.
- Etter, W. (2002). Monte San Giorgio: Remarkable Triassic marine vertebrates. In D. J. Bottjer, W. Etter, J. W. Hagadorn, & C. M. Tang (Eds.), *Exceptional fossil preservation: A unique view on the evolution of marine life*. Columbia University Press.
- Felber, M. (2005). *Il Monte San Giorgio*. Casagrande.
- Felber, M., Furrer, H., & Tintori, A. (1997). I pesci fossili del Ticino. In L. Locatelli (Ed.), *La pesca nel cantone Ticino* (pp. 267–286). Armando Dadò.
- Ferrante, C., & Cavin, L. (2023). Early Mesozoic burst of morphological disparity in the slow-evolving coelacanth fish lineage. *Scientific Reports*, 13(1), 11356. <https://doi.org/10.1038/s41598-023-37849-9>
- Ferrante, C., Furrer, H., Martini, R., & Cavin, L. (2023). Revision of the Middle Triassic coelacanth *Ticinepomis* Rieppel 1980 (Actinistia, Latimeriidae) with paleobiological and paleoecological considerations. *Swiss Journal of Palaeontology*, 142, 18. <https://doi.org/10.1186/s13358-023-00276-4>
- Ferrante, C., Martini, R., Furrer, H., & Cavin, L. (2017). Coelacanths from the Middle Triassic of Switzerland and the pace of actinistian evolution. *Research & Knowledge*, 3(2), 59–62.
- Frauenfelder, A. (1916). Beiträge zur Geologie der Tessiner Kalkalpen. Inaugural-Dissertation von Albert Frauenfelder. *Eclogae Geologicae Helveticae*, 14(2), 247–371.
- Fricke, R., Eschmeyer, W. N. & Van der Laan, R. (Eds.) 2023. Eschmeyer's catalog of fishes: Genera, species, references. Retrieved January 7, 2024, from <http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp>.
- Friedman, M. (2022). The macroevolutionary history of bony fishes: a paleontological view. *Annual Review of Ecology, Evolution, and Systematics*, 53, 353–377.
- Furrer, H. (1995a). The Kalkschieferzone (Upper Meride Limestone, Ladinian) near Meride (Canton Ticino, Southern Switzerland) and the evolution of a Middle Triassic intraplatform basin. *Eclogae Geologicae Helveticae*, 88(3), 827–852.
- Furrer, H. (1995b). The Prosanto Formation, a marine Middle Triassic Fossil-Lagerstätte near Davos (Canton Graubünden, Eastern Swiss Alps). *Eclogae Geologicae Helveticae*, 88(3), 681–683.
- Furrer, H. (2003). Der Monte San Giorgio im Südtessin-vom Berg der Saurier zur Fossil-Lagerstätte internationaler Bedeutung. *Neujahrsblatt Der Naturforschenden Gesellschaft Zürich*, 206, 64.
- Furrer, H. (2015). *Saurichthys—Versteinerte Jäger der Triasmeere*. Paläontologisches Institut und Museum der Universität Zürich, p. 16.
- Furrer, H. (2019). Fische und Saurier aus dem Hochgebirge—Fossilien aus der mittleren Trias bei Davos. *Neujahrsblatt Der Naturforschenden Gesellschaft in Zürich*, 221, 1–112.
- Furrer, H. (2023). *Geschichte des Bergwerks Miniera Tre Fontane in Meride*. Fondazione del Monte San Giorgio, p. 64.
- Furrer, H. (2024). Palaeontological research and excavations at Monte San Giorgio. *Swiss Journal of Palaeontology*. <https://doi.org/10.1186/s13358-024-00314-9>
- Griffith, J. (1977). The Upper Triassic fishes from Polzberg bei Lunz, Austria. *Zoological Journal of the Linnean Society*, 60, 1–93.
- Guttormsen, S. E. (1937). Beiträge zur Kenntnis des Ganoidengebisses, insbesondere des Gebisses von *Colobodus*. *Abhandlungen Der Schweizerischen Paläontologischen Gesellschaft*, 56, 1–41.
- Haarhuis, A. & Diependaal, H. J. (2019). The fish fauna of the Winterswijk Vossenfeld Formation. *Grondboor & Hammer*, 73(5/6), Editie. *Staringia*, 16, 198–207.
- Herzog, A. (2003a). *Die Knochenfische der Prosanto-Formation (Mitteltrias, GR)—Systematik, Funktionsmorphologie und Paläoökologie*. Unpublished PhD. Thesis, Universität Zürich.
- Herzog, A. (2003b). Eine Neubeschreibung der Gattung *Eoegnathus* BROUGH 1939 (Actinopterygii; Halecomorphi) aus der alpinen Mitteltrias Graubündens (Schweiz). *Paläontologische Zeitschrift*, 77(1), 223–240.
- Herzog, A. & Bürgin, T. (2005). A new species of *Besania* BROUGH 1939 from the Middle Triassic of Canton Grisons (Switzerland) with a phylogenetic status of the taxon. *Eclogae geologicae Helveticae*, 98, 113–122.
- Hitij, T., Zaloher, J., Celarc, B., Kriznar, M., Renesto, S., & Tintori, A. (2010). *Kraljestvo Tethys—Okamneli svet triasnih vretencajev Kamnisko-Savinjskih Alp—The Kingdom of Tethys—The Fossilized World of Triassic Vertebrates from the Kamnisko-Savinjske Alps*. *SCOPOLIA Revija Prirodoslovnega Muzeja Slovenije*, 5, 1–197.
- Hu, S.-X., Zhang, Q.-Y., Chen, Z.-Q., Zhou, C.-Y., Lü, T., Wen, W., Huang, J.-Y., & Benton, M. (2010). The Luoping biota: Exceptional preservation, and new evidence on the Triassic recovery from end-Permian mass extinction. *Proceedings of the Royal Society, B*. <https://doi.org/10.1089/rspb.2010.2235>
- Kuhn, E. (1946a). Über *Acrodus*-Funde aus dem Grenzbitumenhorizont der anisichen Stufe der Trias des Monte San Giorgio (Kanton Tessin). *Eclogae Geologicae Helveticae*, 3(2), 662–673.
- Kuhn, E. (1946b). Über einen Fund von *Birgeria* aus der Trias des Monte San Giorgio (Kanton Tessin). *Eclogae Geologicae Helveticae*, 39, 363–364.
- Kuhn-Schnyder, E. (1964). Die Wirbeltierfauna der Trias der Tessiner Kalkalpen. *Geologische Rundschau*, 53(1), 393–412.
- Kuhn-Schnyder, E. (1974). Triasfauna der Tessiner Kalkalpen. *Neujahrsblatt Der Naturforschenden Gesellschaft Zürich*, 176, 1–119.
- Lin, H. Q., Sun, Z. Y., Tintori, A., Lombardo, C., Jiang, D. Y., & Hao, W. C. (2011). A new species of *Habroichthys* BROUGH, 1939 (Actinopterygii; Peltoleporiformes) from the Pelsonian (Anisian, Middle Triassic) of Yunann Province, South China. *Neues Jahrbuch Geologische Und Paläontologische Abhandlungen*, 262(1), 79–89.
- Lombardo, C. (1999). Sexual dimorphism in a new species of the Actinopterygian *Peltopleurus* from the Triassic of Northern Italy. *Palaeontology*, 43(4), 741–760.
- Lombardo, C. (2002). *Caelatichthys* gen. n.: a new palaeonisciform from the Middle Triassic of Northern Italy and Canton Ticino (Switzerland). *Rivista Italiana Di Paleontologia e Stratigrafia*, 108(3), 399–414.
- Lombardo, C. (2013). A new basal actinopterygian fish from the Late Ladinian of Monte San Giorgio (Canton Ticino, Switzerland). *Swiss Journal of Geosciences*, 106(2), 219–230.
- Lombardo, C., Sun, Z.-Y., Tintori, A., Jiang, D.-J., & Hao, W.-C. (2011). A new species of the genus *Perleidus* (Actinopterygii: Perleidiformes) from the Middle Triassic of Southern China. *Bollettino Della Società Paleontologica Italiana*, 50(2), 75–83.
- Lombardo, C., & Tintori, A. (2004). New perleidiforms from the Triassic of the Southern Alps and the revision of *Serolepis* from the Triassic of Württemberg (Germany). In G. Arratia & A. Tintori (Eds.), *Mesozoic fishes 3 systematics, paleoenvironments and biodiversity* (pp. 179–196). Pfeil.
- Lombardo, C., Tintori, A., & Tona, D. (2012). A new species of Sangiorgioichthys (Actinopterygii, Semionotiformes) from the Kalkschieferzone of Monte San Giorgio (Middle Triassic; Meride, Canton Ticino, Switzerland). *Bollettino Della Società Paleontologica Italiana*, 51(3), 203–212.
- López-Arbarello, A., Bürgin, T., Furrer, H., & Stockar, R. (2016). New holostean fishes (Actinopterygii: Neopterygii) from the Middle Triassic of the Monte San Giorgio (Canton Ticino, Switzerland). *PeerJ*, 4, e2234. <https://doi.org/10.7717/peerj.2234>
- López-Arbarello, A., Bürgin, T., Furrer, H., & Stockar, R. (2019). Taxonomy and phylogeny of *Eosemionotus* Stolley, 1920 (Neopterygii: Ginglymodi) from the Middle Triassic of Europe. *Palaeontologia Electronica*, 22(1), 1–64.
- López-Arbarello, A., Stockar, R., & Bürgin, T. (2014). Phylogenetic relationships of the triassic *Archaeosemionotus* Deecke (Halecomorphi, Ionoscopiformes) from the 'Perledo Fauna. *PLoS ONE*, 9(10), e108665. <https://doi.org/10.1371/journal.pone.018665>
- Ma, X.-Y., & Xu, G.-H. (2017). A new ionoscopiform fish (Holostei: Halecomorphi) from the Middle Triassic (Anisian) of Yunann, China. *Vertebrata Palasiatica*, 55(2), 92–106.
- Maisey, J. G. (1982). The anatomy and interrelationships of Mesozoic hybodontiform sharks. *American Museum Novitates*, 2724, 1–48.
- Maisey, J. G. (2011). The braincase of the Middle Triassic shark *Acronemus tuberculatus* (Bassani, 1866). *Palaeontology*, 5, 417–428.
- Maxwell, E. E., Argyriou, T., Stockar, R., & Furrer, H. (2018). Re-evaluation of the ontogeny and reproductive biology of the Triassic fish *Saurichthys* (Actinopterygii: Saurichthyidae). *Palaeontology*. <https://doi.org/10.1111/pala.12355>
- Maxwell, E. E., Furrer, H., & Sánchez-Villagra, M. R. (2013). Exceptional preservation demonstrates a new mode of axial skeleton elongation in early

- ray-finned fishes. *Nature Communications*, 4, 2570. <https://doi.org/10.1038/ncomms3570>
- Maxwell, E. E., Romano, C., & Wu, F.-X. (2021). Regional disparity in the axial skeleton of Saurichthyidae and implications for the axial regionalization in non-teleostean actinopterygians. *Journal of Zoology*. <https://doi.org/10.1111/jzo.12878>, 1–13
- Maxwell, E. E., Romano, C., Wu, F., & Furrer, H. (2015). Two new species of *Saurichthys* (Actinopterygii: Saurichthyidae) from the Middle Triassic of Monte San Giorgio, Switzerland, with implications for character evolution in the genus. *Zoological Journal of the Linnean Society*, 173, 887–912. <https://doi.org/10.1111/zoj.12224>
- Miklavc, P., Celarc, B., & Šmuc, A. (2016). Anisian Strelovec Formation in the Robanov kot, Savinja Alps (Northern Slovenia). *Geologija*, 59, 23–34.
- Mutter, R.J. (1997). *Kieferbezeichnung und systematische Stellung eines Selachier-Restes (Acrodus) aus der Grenzbitumenzone (Mitteltrias) des Monte San Giorgio (Kanton Tessin, Schweiz)*. Unpublished master thesis, Universität Zürich, p. 102.
- Mutter, R. J. (1998a). Zur systematischen Stellung einiger Bezeichnungreste von *Acrodus georgii* sp. nov. (Selachii, Hybodontoida) aus der Grenzbitumenzone (Mittlere Trias) des Monte San Giorgio (Kanton Tessin Schweiz). *Eclogae Geologicae Helveticae*, 91, 513–519.
- Mutter, R. J. (1998b). Tooth variability and reconstruction of dentition in *Acrodus* sp. (Chondrichthyes, Selachii, Hybodontoida) from the Grenzbitumenzone (Middle Triassic) of Monte San Giorgio (Ticino, Switzerland). *Geologica Insubrica*, 3(1), 23–31.
- Mutter, R. J. (2001a). The skull of Colobodontidae sensu ANDERSON 1916 (emended) (Actinopterygii: Perleidiformes). *Geologia Insubrica*, 6(1), 65–78.
- Mutter, R. J. (2001b). *Colobodus*, ein Potpurri grösserer Fische aus der europäischen Trias. *Vierteljahrsschrift Der Naturforschenden Gesellschaft Zürich*, 146(1), 7–14.
- Mutter, R.J. (2002). *Revision of the Triassic Family Colobodontidae sensu Andersson 1916 (emended) with a Tentative Assessment of Perleidiform Interrelationships (Actinopterygii: Perleidiformes)*. Unpublished dissertation Universität Zürich, p. 355.
- Mutter, R. J. (2003). *Colobodus Agassiz, 1844 (Osteichthyes, Perleidiformes): Proposed designation of C. bassanii de Alessandri, 1910 as the type species, with designation of a neotype*. *Bulletin of Zoological Nomenclature*, 60(2), 135–137.
- Mutter, R. J. (2004). The “perleidiform” family Colobodontidae: A review. In G. Arratia & A. Tintori (Eds.), *Mesozoic fishes 3—Systematics, paleoenvironments and biodiversity* (pp. 197–208). Pfeil.
- Mutter, R. J., & Herzog, A. (2004). A new genus of Triassic actinopterygian with an evaluation of deepened flank scales in fusiform fossil fishes. *Journal of Vertebrate Paleontology*, 24(4), 794–801.
- Nelson, J. S., Grande, T. C., & Wilson, M. V. H. (2016). *Fishes of the world* (5th ed.). Wiley.
- Neuman, A. G., & Mutter, R. J. (2005). *Helmolepis cyphognathus*, sp. nov., a new platysgiagid actinopterygian from the Lower Triassic Sulphur Mountain Formation (British Columbia, Canada). *Canadian Journal of Earth Sciences*, 42, 25–36.
- Oosterink, H. W. (1986). Winterswijk, Geologie deel II. De Trias-periode (geologie, mineralien en fossielen). *Wetenschappelijke Mededelingen k. N.n.v.*, 178, 1–120.
- Peyer, B. (1925). Vorläufige Mitteilungen über Trias-Fossilien aus Meride (Tessin). *Verhandlungen der Schweizerischen Naturforschenden Gesellschaft*, Aarau 1925, 2. Teil, 146.
- Peyer, B. (1934). Zehn Jahre Tessiner Fossiliengrabungen des Zoologischen Museums der Universität Zürich. *Verhandlungen Der Schweizerischen Naturforschenden Gesellschaft, Zürich, 1934*, 257–261.
- Peyer, B. (1944). Die Reptilien vom Monte San Giorgio. *Neujahrsblatt Der Naturforschenden Gesellschaft Zürich*, 146, 1–95.
- Quenstedt, F. A. (1867). *Handbuch der Petrefaktenkunde* (2nd ed.). Kaupp'sche Buchhandlung, Tübingen.
- Ren, Y., & Xu, G.-H. (2011). A new species of *Pteronisculus* from the Middle Triassic (Anisian) of Luoping, China, and phylogenetic relationships of early actinopterygian fishes. *Vertebrata Palasiatica*, 59(3), 169–199.
- Renesto, S., Magnani, F., & Stockar, R. (2021). A new species of *Saurichthys* (Actinopterygii: Saurichthyidae) from the Middle Triassic of Monte San Giorgio. *Rivista Italiana Di Paleontologia e Stratigrafia*, 127(1), 49–71.
- Renesto, S., & Stockar, R. (2009). Exceptional preservation of embryos in the actinopterygian *Saurichthys* from the Middle Triassic of Monte San Giorgio, Switzerland. *Swiss Journal of Geosciences*, 102(2), 323–330. <https://doi.org/10.1007/s00015-009-1323-3>
- Renesto, S., & Stockar, R. (2015). Prey content in a *Saurichthys* reveals the presence of advanced halecomorph fishes in the Middle Triassic of Monte San Giorgio. *Neues Jahrbuch Geologische Und Paläontologische Abhandlungen*, 278(1), 95–107.
- Renesto, S., & Stockar, R. (2018). First record of a coelacanth fish from the Middle Triassic Merid limestone of Monte San Giorgio (Canton Ticino, Switzerland). *Rivista Italiana Di Paleontologia e Stratigrafia*, 124(3), 639–653.
- Reposi, E. (1909). Gli scisti bituminosi di Meride e Besano a la loro industria. Traversa, Lugano.
- Rieppel, O. (1980). A new coelacanth from the Middle Triassic of Monte San Giorgio, Switzerland. *Eclogae Geologicae Helveticae*, 73(3), 921–939.
- Rieppel, O. (1981). The hybodontiform sharks from the Middle Triassic of Monte San Giorgio, Switzerland. *Neues Jahrbuch Geologische Paläontologische Abhandlungen*, 161(3), 324–353.
- Rieppel, O. (1985a). Die Triasfauna der Tessiner Kalkalpen XXV. Die Gattung *Saurichthys* (Pisces, Actinopterygii) from the Middle Triassic of Monte San Giorgio, (Switzerland), with comments on the phylogenetic interrelationships of the genus. *Palaeontographica A*, 221, 63–94.
- Rieppel, O. (1985b). A second actinistian from the Middle Triassic of Monte San Giorgio, Switzerland. *Eclogae Geologicae Helveticae*, 78(3), 707–713.
- Rieppel, O. (1992). A new species of the genus *Saurichthys* (Pisces, Actinopterygii) aus der mittleren Trias des Monte San Giorgio, Kanton Tessin. *Schweizerische Paläontologische Abhandlungen*, 108, 1–103.
- Rieppel, O. (2019). *Mesozoic sea dragons: Triassic marine life from the ancient tropical lagoon of Monte San Giorgio*. Indiana University Press.
- Romano, C. (2007). *A redescription and a new reconstruction of Birgeria stensioei ALDINGER 1931 (Birgeriidae, Actinopterygii) from the Middle Triassic of Monte San Giorgio (Canton Ticino, Switzerland) with comments on its ontogeny and the interrelationships of the genus Birgeria STENSIÖ 1919*. Unpublished thesis, Paläontologisches Institut und Museum, Universität Zürich.
- Romano, C. (2021). A hiatus obscures the early evolution of modern lineages of bony fishes. *Frontiers in Earth Sciences*, 8(6), 1–13.
- Romano, C., & Brinkmann, W. (2009). Reappraisal of the lower actinopterygian *Birgeria stensioei* ALDINGER, 1931 (Osteichthyes; Birgeriidae) from the Middle Triassic of Monte San Giorgio (Switzerland) and Besano (Italy). *Neues Jahrbuch Für Geologie Und Paläontologie, Abhandlungen*, 252(1), 17–31.
- Romano, C., Kogan, I., Jenks, J., Jerjen, I., & Brinkmann, W. (2012). *Saurichthys* and other fossil fishes from the late Smithian (Early Triassic) of Bear Lake County (Idaho, USA), with a discussion of saurichthyid palaeogeography and evolution. *Bulletin of Geosciences*, 87(3), 543–570.
- Schaeffer, B. (1984). On the relationships of the Triassic and Liassic Redfieldiiform fishes. *American Museum Novitates*, 1737, 1–18.
- Scheyer, T. M., Schmid, L., Furrer, H., & Sánchez-Villagra, M. R. (2014). An assessment of age determination in fossil fish: The case of the opercula in the Mesozoic actinopterygian *Saurichthys*. *Swiss Journal of Palaeontology*, 133(2), 243–257. <https://doi.org/10.1007/s13358-014-0068-4>
- Schmid, L., & Sanchez-Villagra, M. R. (2010). Potential genetic bases of morphological evolution in the Triassic fish *Saurichthys*. *Journal of Experimental Zoology, Part B Molecular and Developmental Evolution*, 314B, 1–8.
- Schultze, H. P., & Kriwet, J. (2021). Fische der germanischen Trias. In N. Hauschke, M. Franz, & Bachmann (Eds.), *Trias Aufbruch in das Erdmittelalter, Bd. 1* (pp. 317–323). Pfeil.
- Schultze, H.-P., & Möller, H. (1986). Wirbeltierreste aus dem Mittleren Muschelkalk (Trias) von Göttingen, West-Deutschland. *Paläontologische Zeitschrift*, 60, 109–129.
- Schwarz, W. (1970). *Birgeria stensioei* Aldinger. In E. Kuhn-Schneyder & B. Peyer (Eds.), *Die Triasfauna der Tessiner Kalkalpen. Schweizerische Paläontologische Abhandlungen* (vol. 89, pp. 1–93).
- Stolley, E. (1920). Beiträge zur Kenntnis der Ganoiden des deutschen Muschelkalks. *Palaeontographica, Abteilung A*, 63, 25–96.
- Sun, Z.-Y., Lombardo, C., Tintori, A., Jiang, D.-Y., Hao, W. C., & Sun, Y. I. (2012). *Fuyuanperleidus dengi* GENG et al. 2012 (Osteichthyes, Actinopterygii)

- from the Middle Triassic of Yunann Province, South China. *Rivista Italiana Di Paleontologia e Stratigrafia*, 118(3), 359–373. <https://doi.org/10.13130/2039-4942/6011>
- Sun, Z.-Y., Tintori, A., Jiang, D.-Y., Lombardo, C., Rusconi, M., Hao, W. C., & Sun, Y.-L. (2009). A New Perleidiform (Osteichthyes, Actinopterygii) from the Middle Anisian (Middle Triassic) of Yunnan, South China. *Acta Geologica Sinica*, 83(3), 460–470.
- Sun, Z.-Y., Tintori, A., Lombardo, C. R. S., Jiang, D.-Y., Hao, W. C., Sun, Y.-L., Wu, F.-X., & Rusconi, M. (2008). A new species of the genus *Colobodus* AGASSIZ, 1844 (Osteichthyes, Actinopterygii) from the Pelsonian (Anisian, Middle Triassic) of Guizhou, South China. *Rivista Italiana Di Paleontologia e Stratigrafia*, 114(3), 359–373.
- Sun, Z., Tintori, A., Xu, Y., Lombardo, C., Peigang, N., & Dayong, J. (2016). A new non-parasemionotiform order of the Halecomorphi (Neopterygii, Actinopterygii) from the Middle Triassic of Tethys. *Journal of Systematic Palaeontology*, 2016, 359–373.
- Tintori, A. (1990a). The actinopterygian fish *Prohalecites* from the Triassic of northern Italy. *Palaeontology*, 33, 155–174.
- Tintori, A. (1990b). Ca' del Frate (Varese). In A. Tintori, G. Muscio, & F. Bizzarini (Eds.), *Pesci fossili italiani: scoperte e riscoperte—mostra paleontologica*. New Interlitho.
- Tintori, A. (1990c). *Dipteronotus olgiatii* n. sp. (Actinopterygii, Perleidiformes) from the Kalkschieferzone of Ca' del Frate (N. Italy). *Atti Ticinesi Di Scienze Della Terra*, 33, 191–197.
- Tintori, A. (2013). A new species of *Saurichthys* (Actinopterygii) from the Middle Triassic (Early Ladinian) of the Northern Grigna mountain (Lombardy, Italy). *Rivista Italiana Di Paleontologia e Stratigrafia*, 119(3), 287–302.
- Tintori, A. (2017). 40 years of field work in the Triassic marine vertebrate sites. *Research & Knowledge*, 3(2), 9–12.
- Tintori, A. (2019). Predators and preys: A case history for *Saurichthys* (*Costasaurichthys*) *costasquamosus* Rieppel, 1985 from the Ladinian of Lombardy (Italy). *Rivista Italiana Di Paleontologia e Stratigrafia*, 125(1), 271–282.
- Tintori, A., & Felber, M. (2015). I vertebrati marini del Triassico Medio nel XXI secolo: Dal Monte San Giorgio alla Cina. *Geologia Insubrica*, 11, 63–80.
- Tintori, A., Hitij, T., Jiang, D., Lombardo, C., & Sun, Z. (2014). Triassic actinopterygian fishes: The recovery after the end-Permian crisis. *Integrative Zoology*, 9(4), 394–411.
- Tintori, A., & Lombardo, C. (2007). New early Semionotidae (Semionotiformes, Actinopterygii) from the upper Ladinian of Monte San Giorgio area (Southern Switzerland and northern Italy). *Rivista Italiana Di Paleontologia e Stratigrafia*, 113(3), 369–381.
- Tintori, A., Lombardo, C., Danini, G. L., Felber, M., Marazzi, B., & Vendico, M. (1998). Scavi paleontologici nella Kalkschieferzone di Meride (Canton Ticino, Svizzera): Risultati preliminari della campagna 1997. *Geologia Insubrica*, 3(1), 11–16.
- Tintori, A., Lombardo, C., & Renesto, S. (2010). *I vertebrati triassici della Lombardia 150 anni dopo Stoppani. Una Nuova Geologia per la Lombardia. Istituto Lombardo-Accademia di Scienze e Lettere, Convegno in onore di MB Cita*. pp. 89–114.
- Tintori, A., Sun, Z.-Y., Lombardo, C., Jiang, D.-Y., Sun, Y.-L., & Hao, W.-C. (2010). A new basal neopterygian from the Middle Triassic of Luoping County (South China). *Rivista Italiana Di Paleontologia e Stratigrafia*, 116(2), 161–172.
- Tintori, A., Sun, Z.-Y., Lombardo, C., Jiang, D.-Y., Sun, Y.-L., Rusconi, M., & Hao, W.-C. (2007). New specialized basal Neopterygians (Actinopterygii) from Triassic of the Tethys realm. *Geologica Insubrica*, 10(2), 13–20.
- Tintori, A., Zuoyu, S., Peigang, N., Lombardo, C., Dayong, J., & Motani, R. (2015). Oldest stem teleostei from the Late Ladinian (Middle Triassic) of Southern China. *Rivista Italiana Di Paleontologia e Stratigrafia*, 121(3), 285–296.
- Visconti, A. (1988). *I 150 anni del Museo Civico di Storia Naturale di Milano* (1838–1988). Museo Civico di Storia Naturale, Milano.
- Wiman, C. (1912). Ueber *Mixosaurus Cornalianus* Bass. sp. *Bulletin of the Geological Institutions of the University of Uppsala*, XI, 230–241.
- Wu, F.-X., Sun, Y.-L., & Fang, G.-Y. (2018). A new species of *Saurichthys* from the Middle Triassic (Anisian) of southwestern China. *Vertebrate Palaeoasiatica*, 56(4), 273–294.
- Xu, G.-H. (2019). Osteology and phylogeny of *Robustichthys luopingensis*, the largest holostean fish in the Middle Triassic. *PeerJ*, 7, e7184. <https://doi.org/10.7717/peerj.7184>
- Xu, G.-H., & Zhao, L.-J. (2016). A Middle Triassic stem-neopterygian fish from China shows remarkable secondary sexual characteristics. *Science Bulletin*. <https://doi.org/10.1007/s11434-016-1007-0>

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