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**Short Communication**

# Coelacanths from the Middle Triassic of Switzerland and the pace of actinistian evolution

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**Abstract -** Latimeria chalumnae (Actinistia) was regarded as the 'ancestor of the four-legged vertebrates' and rapidly became the iconic example of a 'living fossil'. Although its evolutionary position close to the origin of tetrapods is now dismissed, the question of its evolutionary pace is still a matter of debate. The UNESCOs' World Heritage Monte San Giorgio Triassic site, spanning the border between Italy and Switzerland in the Southern Alps, has yielded one of the major marine vertebrate assemblages of the Middle Triassic worldwide. This general overview of the Middle Triassic coelacanths from Switzerland heralds a project that will be conducted in the following years. The project consists firstly to prepare, describe and compare the coelacanth material from the Besano Formation housed in the collection of the University of Zurich.

**Keywords:** Sarcopterygii, Mesozoic, Europe, morphology, phylogeny

## 1. Introduction

The discovery of a living coelacanth in 1938 was regarded by some biologists as 'undoubtedly the most important zoological discovery of the 20th century' (Berra, 1997). *Latimeria chalumnae* (Actinistia) was regarded as the 'ancestor of the four-legged vertebrates' and rapidly became the iconic example of a 'living fossil'. Although its evolutionary position close to the origin of tetrapods is now dismissed, the question of its evolutionary pace is still a matter of debate. Recently, the slow evolutionary pace of actinistians was questioned by Casane and Laurenti (2013), who found no evidence of slowly evolving genome and morphology compared to other groups of vertebrates. The latter statement contradicts studies, which have shown that the rate of morphological evolution of the actinistians is comparatively slow (Schaeffer, 1952; Cloutier, 1991; Forey, 1998; Schultze, 2004; Friedman and Coates, 2006; Cavin and Guinot, 2014). Does this lineage evolve more slowly than others? Recent discoveries and unstudied material of coelacanths from two Middle Triassic localities in Switzerland, with a very unusual morphology compared to the general actinistian pattern, are opportunities to tackle this question.

## 2. Geological settings

The UNESCOs' World Heritage Monte San Giorgio Triassic site, spanning the border between Italy and Switzerland in the Southern Alps, has yielded one of the major marine vertebrate assemblages of the Middle Triassic worldwide. The Triassic succession ranges from the Late Anisian (Illyrian) to the Ladinian. The paleoenvironment correspond to the progressive transgression of a shallow epicontinental sea and an intraplatform basin, which opened in the Monte San Giorgio region. Most of the vertebrate taxa have been recovered in the Besano Formation, which is Late Anisian and Earliest Ladinian in age. The first discoveries of vertebrate fossils date back to the 19$^{th}$ century and were done in mines exploited for bituminous shales mostly near Besano, Italy (Fig. 1). The University of Zurich performed systematic excavations in the Besano Formation north of the village Meride, Switzerland, between 1924 and 1968. In the overlying Ladinian Meride Limestone, separated from the Besano Formation by the San Giorgio Dolomite, several levels have also yielded vertebrate assemblages during excavations conducted by the University of Zurich and by the Museo Cantonale di Storia Naturale of Lugano, Switzerland. On the Italian side of the Monte San Giorgio excavations were conducted by the Museo di Storia Naturale di Milano in the Besano Formation between 1975 and 2003 and by the University of Milano from 1990 to 1999 in the upper part of the Meride Limestone (Kalkschieferzone) (Tintori, this volume). The various vertebrate assemblages from the Besano Formation and Meride Limestone comprise various reptile groups (Furrer and Vandelli, 2014), mostly aquatic, and numerous actinopterygians, which still remain partly undescribed (López-Arbarello *et al*., 2016).

The Middle Triassic Prosanto Formation is formed

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by a 120 m thick sequence of dark limestones, shales and dolomites located in Eastern Switzerland. Excavations are conducted by the University of Zurich since 1989 in the Austroalpine Ducan region, near the town of Davos. The vertebrate assemblages of the Prosanto Formation show similarities with the assemblage of the Monte San Giorgio sites. More specifically, U/Pb zircon age dating of a volcanic ash layer in the most fossiliferous upper Prosanto Formation provided an age of 241 Ma, which corresponds to the fossiliferous levels of the lower Meride Limestone (Early Ladinian) at Monte San Giorgio (Furrer *et al*., 2008; Stockar *et al*. 2012).

## 3. The coelacanth material

In 1980, Rieppel described from Monte San Giorgio a new coelacanth found in the upper part of the Besano Formation (Anisian/Ladinian boundary) (Fig. 1). *Ticinepomis peyeri*, known by a subcomplete specimen, is characterized, among other characters, by a massive pectoral girdle and an ornamentation of tubercles on some dermal bones. The phylogenetic position of this taxon was regarded as uncertain by Forey (1998), but most recent studies place it within the latimeriids (Dutel *et al*., 2012; Cavin *et al*., 2013). Rieppel (1985) then recorded from the middle part of the Besano Formation (latest Anisian), fragments of coelacanths that he referred to cf. *Holophagus picenus* (*Undina picena* according to Forey, 1998). Rieppel referred these elements to actinistians on the basis of the structure of the scales, but he admitted that the dermal bone pattern is peculiar in several respects. Rieppel didn't use for the description of this strange coelacanth the large collection of unprepared coelacanth specimens collected during the excavation conducted in the 50s and 60s in the Besano Formation (Fig. 2). This material consists of 80, mostly fragmentary and unprepared specimens of a very unusual coelacanth taxon. One feature of this taxon is the ornamentation of the dermal bones, which was superficially studied by Ørvig (1977) in the frame of a broader survey of 'odontodes' in fishes. However, the general morphology of this coelacanth and its systematic affinities have never been addressed. More histological studies have been done by Mutter (2002) for comparison with the actinopterygian family Colobodontidae.

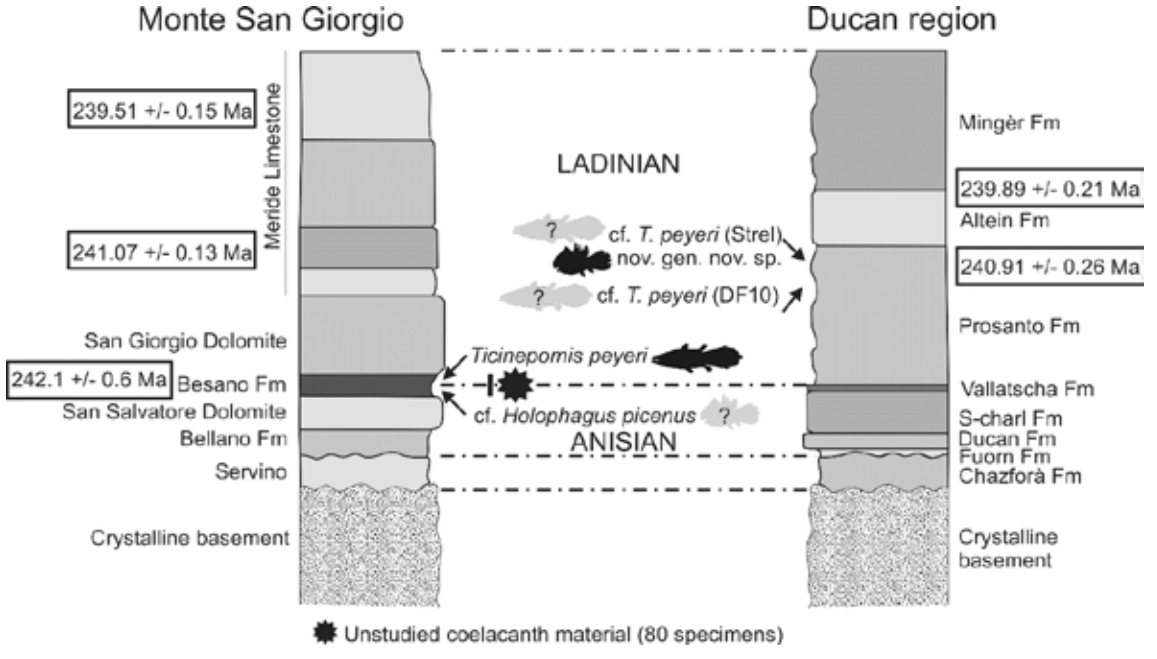


**Figure 1.** Simplified and schematic stratigraphic columns (not to scale) showing Middle Triassic successions at Monte San Giorgio (Ticino), and of the Ducan region (Graubünden), with the coelacanths discoveries. Radiometric dates are framed. Modified from López-Arbarello *et al*. (2016) for Monte San Giorgio and Cavin *et al*. (2013) for the Ducan region.

The Prosanto Formation near Davos (Graubünden, Switzerland) has yielded two specimens of actinistians, an isolated caudal skeleton and a subcomplete specimen preserved in ventral view that have been referred to cf. *Ticinepomis peyeri* (Cavin *et al*., 2013). Recently, two new specimens have been unearthed in the Prosanto Formation by Christian Obrist, who conducts annual excavations together with the team of the Zurich University. These specimens, currently under study, belong to a new highly derived coelacanth taxon. Among several bizarre features, this taxon share with *Ticinepomis peyeri* a massive pectoral girdle, but in a much more developed manner than in the later. Another unusual character is the skull roof bones arrangement, which is very different from the typical coelacanth pattern, and the strong ornamentation of tubercles on dermal bones. These features are reminiscent of the coelacanth from Monte San Giorgio referred to cf. *Holophagus picenus* by Rieppel (1985), and we hypostatize here that they belong to the same, or to a closely related taxon.

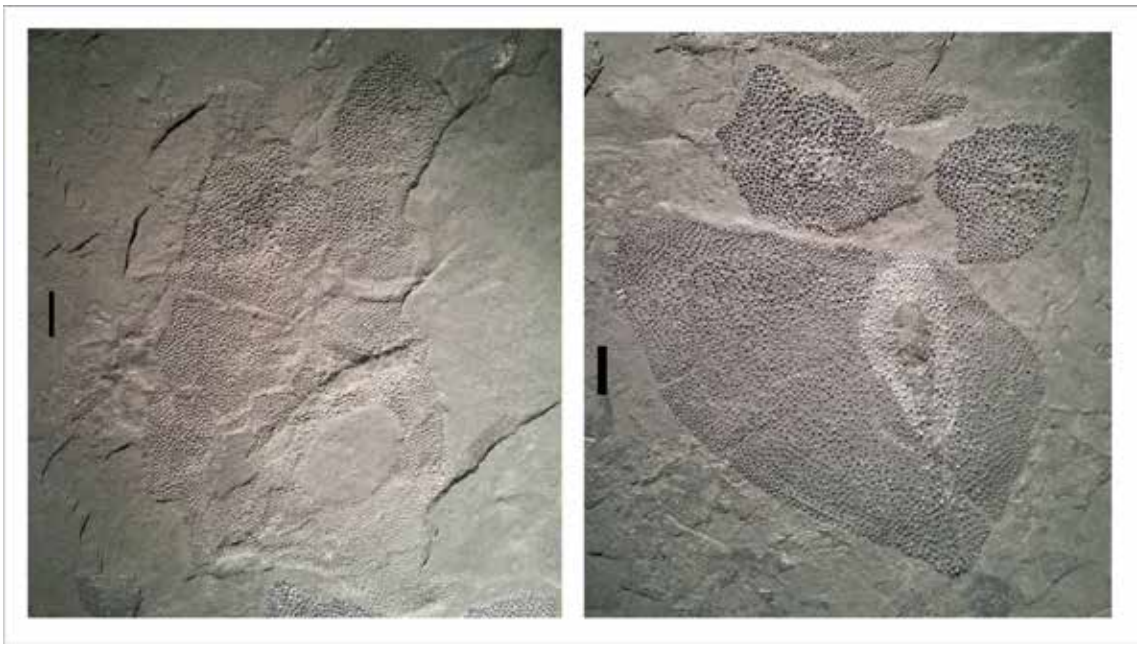

**Figure 2.** PIMUZ T 31. Unprepared specimen of a coelacanth from the middle Besano Formation, Middle Triassic (latest Anisian) of Ticino, Switzerland. The specimen likely belongs to a new taxon characterized by very unusual characters. Scale bars: 10 mm.

## 4. Perspectives and conclusion

This general overview of the Middle Triassic coelacanths from Switzerland heralds a project that will be conducted in the following years. The project consists firstly to prepare, describe and compare the coelacanth material from the Besano Formation housed in the collection of the University of Zurich.

Other coelacanths have been described from the Alpine Middle and Upper Triassic of Central and Southern Europe, such as "*Coelacanthus*" (Teller, 1891) from Lunz in Austria, *Graphiurichthys* (Kner, 1866) from Raibl, *Heptanema* (Bellotti, 1857; Alessandri, 1910) from Perledo and "*Holophagus*" from Giffoni (Costa, 1862; Bassani, 1895) in Italy. These taxa are poorly known and represented by few specimens only and their osteological and systematic revision is also planned in the project.

In a second step, we will conduct cladistic analyses in order to resolve the phylogenetic position of the new and "abnormal" taxon, especially in relation to the contemporaneous *Ticinepomis* but also within the Actinistia in general. We will then perform morphometric and phylogenetic diversity analyses by taking into account the whole data record of actinistians, from the Devonian to the present. Eventually, we will compare some trends of the evolutionary history of coelacanths with other fish clades by confronting these traits with variations of biotic and abiotic parameters.

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