doi: 10.1017/jpa.2019.75



# A new Ladinian (Middle Triassic) mysidacean shrimp (Crustacea, Lophogastrida) from northern Italy and southern Switzerland

Cristiano Larghi, <sup>1</sup> • Andrea Tintori, <sup>2,3</sup> Daniela Basso, <sup>4</sup> Gianluca Danini, <sup>5</sup> and Markus Felber<sup>6,7</sup>

Abstract.—Since the end of the nineteenth century, many paleontological studies have been developed on the Middle Triassic localities of the Monte San Giorgio area (Canton Ticino, Switzerland, and Lombardy, Italy). These localities were inscribed in 2003 and 2010 in the UNESCO World Heritage List due to their paleontological relevance. New crustaceans are here described from the Kalkschieferzone member of the upper Ladinian Meride Limestone, outcropping near Besnasca-Cà del Frate (Viggiù, Italy) and Meride (Mendrisio, Switzerland). Several hundred specimens of a new genus and new species of Lophogastrida, named here *Vicluvia lombardoae*, improve information on Triassic mysidaceans (sensu lato), a group of shrimp-like crustaceans presently including hundreds of species worldwide distributed in marine and freshwater environments. The paper discusses the relations between *Vicluvia* n. gen. and the other fossil genera belonging to the same family. *Vicluvia lombardoae* n. gen. n. sp. exhibits two dorsally vanishing transverse grooves with their branches regularly bending toward the posterior margin of the shield and a telson with a rounded and setose apex. It was probably a euryhaline species living in a transitional environment affected by frequent and ephemeral salinity variations. Middle Triassic taphonomic windows have preserved specimens of lophogastrids in shallow basins along the Tethys, from the present Alps to China as well as in the German Basin.

UUID: http://zoobank.org/1623e8f9-2ceb-4cd6-bcbe-4f05a873e1ff

# Introduction

The Middle Triassic localities of the Monte San Giorgio area in Lombardy (northern Italy) and Canton Ticino (southern Switzerland) are sites where marine deposits have been studied through mining and scientific excavations over a period of more than 170 years. They are among the most important locations providing a well-preserved record of Middle Triassic marine life. Because of great interest, the Swiss side of Monte San Giorgio was inscribed in the UNESCO World Heritage List in July 2003; in August 2010 it became a transboundary site after the extension to the Italian outcrops (Fig. 1).

Several excavations have been made in the past decades in Switzerland by the Università degli Studi di Milano and the Paleontological Institute and Museum of the University of Zürich, in cooperation with the Cantonal Museum of Natural History of Lugano, and in Italy by the Università degli Studi di Milano, in cooperation with the Museo Insubrico di Storia Naturale di Clivio and Induno Olona, and by the Museum of Natural History of Milan.

The discoveries from the 'Kalkschieferzone' (see Geological setting) include many well-preserved specimens of fish, reptiles, arthropods, and rare plants (Tintori and Renesto,

1983, 1990; Tintori, 1990a, b, c; Renesto, 1993; Lombardo, 1999, 2001; Tintori and Lombardo, 1999, 2007; Krzeminski and Lombardo, 2001; Renesto et al., 2003; Bechly and Stockar, 2011; Lombardo et al., 2012; Strada et al., 2014; Montagna et al., 2017). Part of the collected material is still waiting for preparation or is under study.

International consideration focused on the Monte San Giorgio fossiliferous levels during the nineteenth and twentieth centuries, and during the past 15 years several new Middle Triassic marine Lagerstätten were discovered outside Europe, mainly in southern China (Motani et al., 2008; Tintori et al., 2014). As in the Monte San Giorgio area, the discoveries include many fully articulated specimens of reptiles, fishes, and arthropods.

The Xingyi Fauna from the Zhugampo Member of the Falang Formation, outcropping in a large area encompassing Xingyi (Guizhou Province), Fuyuan, and Luoping (Yunnan Province), is probably the closest in age to the Kalkschieferzone in the Monte San Giorgio area (Jiang et al., 2009; Zou et al., 2015). A recent detailed excavation has been carried out near Nimaigu (Wusha, Xingyi) to settle the stratigraphic distribution of the several vertebrate taxa so far described (Ji et al., 2012; Tintori et al., 2012) from that fossiliferous level. Not all of the

<sup>&</sup>lt;sup>1</sup>Eni Spa – Exploration, 5th Office Building, Via Emilia 1, 20097, San Donato Milanese, Italy <cristiano.larghi@gmail.com>

<sup>&</sup>lt;sup>2</sup>Dipartimento di Scienze della Terra 'Ardito Desio,' Università degli Studi di Milano, via Mangiagalli 34, I-20133 Milano, Italy. A.T. <andrea.tintori@unimi.it>

<sup>&</sup>lt;sup>3</sup>Current address: TRIASSICA – Institute for Triassic Fossil Lagerstätten, 23828 Perledo (LC), Italy

<sup>&</sup>lt;sup>4</sup>Dipartimento di Scienze dell'Ambiente e della Terra, Università degli Studi di Milano-Bicocca, Piazza della Scienza 4, 20126 Milano, Italy <daniela.basso@unimib.it>

<sup>&</sup>lt;sup>5</sup>Civico Museo Insubrico di Storia Naturale di Clivio/Induno Olona <daniniluca.48@alice.it>

<sup>&</sup>lt;sup>6</sup>CGA SAGL, Casella Postale 124 6834-Morbio Inferiore, Switzerland <markus.felber@geoamb.ch>

<sup>&</sup>lt;sup>7</sup>MCSN, Lugano, Switzerland

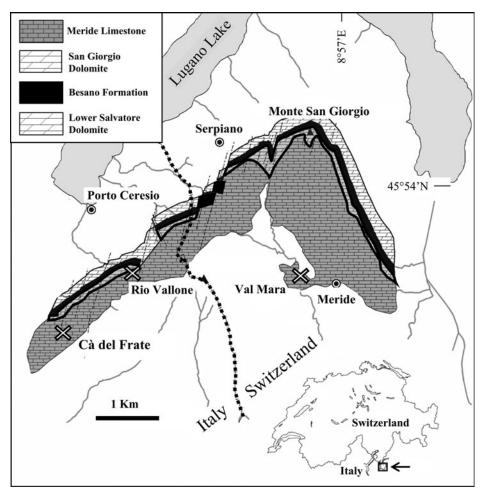


Figure 1. Map of the Monte San Giorgio area showing the Middle Triassic sequence with locations (X) of the sites Cà del Frate, Rio Vallone, and Val Mara (from Stockar, 2010, modified) and stratigraphic distribution of the insect fossils from Monte San Giorgio (right).

already known Xingyi Fauna taxa were collected during such an excavation, and for several reptile and fish taxa, the actual stratigraphic position is not yet ascertained in the series. However, two different assemblages can be recognized (Tintori et al., 2014), and the lower one yields also the lophogastrid mysidaceans described by Taylor, Schram, and Shen (2001) as Schimperella acanthocercus from a site near Dinxiao, about 30 km from Nimaigu. Following Wang et al. (2009), and as observed during the May 2017 excavations (personal observation, A.T., 2017), these lophogastrids are mostly on mass mortality surfaces (Wang et al., 2009, fig. 7). They are found in the Xingyi area together with the pachypleurosaur Keichousaurus (=Kweichousaurus in Wang et al., 2009), which characterizes the Lower Assemblage of the Xingyi fauna together with Habroichthys and Asialepidotus, fishes that are considered as marine (Tintori et al., 2013). Thus, this assemblage is clearly marine as it includes marine reptiles (Ji et al., 2012) and rare ammonoids (personal observation, A.T., 2017). By contrast, the fossiliferous level of the Zhuganpo Member is made of well-bedded limestone, marly limestone, and mudstone at the top of massive limestones deposited on a carbonate platform, and the upper part of the level itself is very rich in ammonoids, crinoids, and daonellids (Lu et al., 2018). The lower assemblage of the Xingyi Fauna has a few more taxa in common with the Kalkschieferzone fauna, such as the fishes *Peltopleurus* and *Saurichthys* and the sauropterygian *Lariosaurus*, all of them being quite widespread all along the Tethys during most of the Middle Triassic.

More recently, Feldmann et al. (2017) reported lophogastrid mysidaceans from the late Anisian Luoping Fauna (Member II of the Guanling Formation), Yunnan Province, where Fu et al. (2010) and Feldmann et al. (2012) previously described, respectively, Isopoda and Decapoda. Feldmann et al. (2017) described a new genus, *Yunnanocopia*, with two new species, *Y. grandis* and *Y. longicauda*, and a third possible new species was left in open nomenclature.

However, although in the past years following these new finds a major shift in the Triassic paleontological research from western to eastern Tethys has been recorded, not all the western Tethys fossils have been described yet. Apart from the new taxon herein described, it should be noted that Pelsonian (middle Anisian) specimens attributed to the lophogastrid *Schimperella* sp. have been recently found also in the Slovenian Alps (Križnar and Hitij, 2010), and early Ladinian crustaceans (Thylacocephala and Decapoda) have been recorded in the northern Grigna Mountain in Italy (Tintori, 2013).

### Geological setting

During the Middle Triassic, a thick sequence of up to 1,000 meters of limestones, dolomites, and organic shales was deposited in small basins along the western Tethys margin such as that at Monte San Giorgio (Fig. 2). There, several distinct stratigraphic units can be recognized, the most fossiliferous of which are the upper Anisian-lower Ladinian Besano Formation and the Ladinian Meride Limestone. During the late Anisian, there was also deposition of the widespread shallow-water carbonates of the Lower San Salvatore Dolomite (Zorn, 1971) that surrounded the Besano Formation lagoon. In the latest Anisian and Ladinian of the Monte San Giorgio area, the formation of an intraplatform basin with restricted circulation (Furrer, 1995) resulted in the alternate deposition of black shales and dolomites of the Besano Formation (once named Grenzbitumenzone by German researchers, e.g., Frauenfelder, 1916). Later, after the shallow-water San Giorgio Dolomite, the deposition of the well-bedded and/or laminated limestones and marly limestones of the Meride Limestone took place.

The lower Meride Limestone (Furrer, 1995) begins with finely laminated limestones and ends with a dolomitized level, whereas the overlying upper Meride Limestone is a sequence of alternating well-bedded limestones and marlstones with increasing clay content toward the top. The uppermost 120 meters of the unit were named Kalkschieferzone by Senn (1924) and yield, among others, most of the fossils described in this paper. The age of the Kalkschieferzone was stated as late Ladinian on the basis of its palynological content (Scheuring, 1978). Although no ammonoids or conodonts have been found, this age is supported by the fish assemblage (Tintori, 1998; Tintori and Lombardo, 1999), which is very similar to that found in the Perledo Member of the Perledo–Varenna Formation. Recently, Stockar et al. (2012) suggested a somewhat older age of the Kalkschieferzone, still in the late Ladinian but around its base.

This sequence records life in a tropical lagoon, sheltered and partially separated from the open sea, where water stratification periodically provided bottom anoxic conditions, allowing the preservation of organism remains and the accumulation of organic matter (Tintori, 1990a; Lombardo et al., 2012). Inferring by analysis of oil-source rock correlation, the Besano Formation and the Meride Limestone are the best oil-prone source rocks in the western Po Plain (Riva et al., 1985; Bernasconi and Riva, 1993).

These formations represent a regressive sequence with the filling of a lagoon, from true marine conditions to a probably unstable environment, with brackish or freshwater horizons, suggested in the uppermost part (the Kalkschiferzone) by the presence of clay, conchostracans, and insects (Tintori, 1990c; Strada et al., 2014).

The Kalkschieferzone provides about 20 fish species (Lombardo et al., 2012), the most common of which are very small actinopterygians such as *Prohalecites* (Tintori, 1990a). Others include *Peltopleurus* (Lombardo, 1999) and the nothosaurid *Lariosaurus* (Tintori and Renesto, 1990; Renesto et al., 2003). It also provides insects (Krzeminski and Lombardo, 2001; Bechly and Stockar, 2011; Strada et al., 2014; Montagna et al., 2017), the conchostracan *Laxitextella* (= *Palaeolimnadia* sp. in Tintori, 1990c) indicating the periodic influence of freshwater (Tintori, 1990c; Lombardo et al., 2012), and rare terrestrial

plants (Wirz, 1945; Stockar and Kustatscher, 2010; personal observation, A.T., 1996–2003). The biota of the Kalkschieferzone lived in a tropical climate subject to strong seasonal changes, with mainly marine conditions with possibly brackish and/or freshwater short periods (Lombardo et al., 2012).

The beds yielding the specimens of the type series (CMISN specimens) of the new genus and new species *Vicluvia lombar-doae*, here described, belong to the middle Kalkschieferzone outcropping in the Italian locality of Cà del Frate (village of Viggiù, Varese province; 45°53′01.43″N, 8°53′59.52″E).

The locality of Cà del Frate was already mentioned by De Alessandri (1910) in his monograph on Triassic fishes, but it is only since the beginning of the 1980s that systematic field work with bed-by-bed sampling has been conducted by a group of the Milano University supported by the local Museo Civico di Storia Naturale di Induno Olona (now Museo Insubrico di Storia Naturale di Clivio/Induno Olona).

The Cà del Frate fauna has been the subject of many studies; fishes, rare reptiles, and numerous crustaceans have been found. About 4,000 fishes, some specimens of the marine reptile *Lariosaurus*, and thousands of crustaceans belonging to the genera *Vicluvia* n. gen. and *Laxitextella*, mostly concentrated in mass mortality surfaces, have been collected during several field seasons in the years 1981–1997 (Tintori and Renesto, 1983, 1990; Tintori, 1990a, b, c; Renesto, 1993; Lombardo, 1999, 2001; Tintori and Lombardo, 1999; Renesto et al., 2003).

Other specimens of *Vicluvia lombardoae* n. gen. n. sp. (CMISN specimens) came from the excavation at site D in the lower Kalkschieferzone in Val Mara, near the village of Meride (Mendrisio, Canton Ticino, Switzerland; 45°53′33.90″N, 8° 56′47.04″E) (Lombardo et al., 2012). During the years 1997–2003, a joint project financed by the Cantonal Museum of Natural History in Lugano (MCSN) and operated by the Milano University allowed the collection of a few hundred fishes, several insects, and the same crustaceans as in Cà del Frate. The fossiliferous level of site D is placed between layer 102 of Scheuring (1978) and layer 60 of Wirz (1945).

Both the investigated sections consist of a few meters of thinbedded laminated limestones and marly limestones with minor marlstones and calcareous marlstones. Although most specimens have been collected during the detailed excavation, the oldest occurrence of the new species indicated by a single specimen, CMISN 1207, comes from just a few meters above the boundary between the San Giorgio Dolomite and the Meride Limestone, along the Rio Vallone near Porto Ceresio (Varese, Italy; 45°53′33.75″N; 8°54′40.29″E). This specimen is not included in the type series, being more ancient than the two main assemblages, and neither are the Swiss specimens that are somewhat older (uppermost part of the lower Kalkschieferzone) than the type series.

#### Materials and methods

Many hundreds of specimens were studied using a stereomicroscope equipped with a camera lucida drawing arm; measurements were taken with a caliper. To enhance details, some specimens were moistened with alcohol.

Repositories and institutional abbreviations.—The examined specimens are deposited in Civico Museo Insubrico di Storia

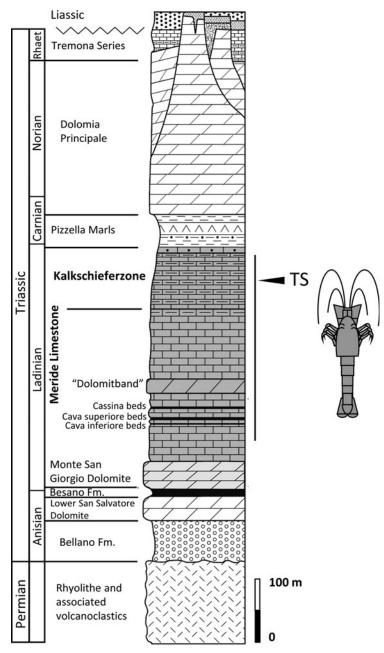


Figure 2. Stratigraphic column from Stockar (2010, modified) with distribution of Vicluvia (black bar). TS = type series.

Naturale, Clivio, Italy (CMISN; formerly Museo di Storia Naturale di Induno Olona, Induno Olona, Italy [MSNIO]) and in Museo Cantonale di Storia Naturale di Lugano, Switzerland (MCSN).

# Systematic paleontology

Class Malacostraca Latreille, 1802 Order Lophogastrida Boas, 1883 Family Eucopiidae Sars, 1885

Remarks.—Mysidaceans (s.l.) are shrimp-like malacostracans including more than 100 genera, with more than 1,000 species. Today they have a worldwide distribution. The

majority of species inhabit coastal and open seawater, whereas a few species are adapted to freshwater. Several taxa are also described from different groundwater habitats and marine and anchialine caves. Following the classification proposed by Taylor et al. (2001), mysidaceans include the extant Orders Mysida Haworth, 1825 and Lophogastrida Boas, 1883 and the extinct Pygocephalomorpha Beurlen, 1930.

The splitting of Mysidacea, together with the elevation of each former mysid suborder to order level, was previously proposed by Schram (1984, 1986) and by Brusca and Brusca (1990) and was later accepted by Martin and Davis (2001). Probably because of the poor sclerotization of the shield, the reports of some fossil mysidacean groups are rare. In addition, most mysidaceans are quite small and thus not easy to collect during

fieldwork, although, at least for the Triassic, they may occur in a great number.

Hessler (1969) reported for Mysida (s.l.) the genera *Schimperella* Bill, 1914 and *Francocaris* Broili, 1917, from the Upper Jurassic of Germany. Nevertheless, according to Schram (1986), *Francocaris grimmi* Broili, 1917, from the Jurassic Solnhofen limestones of Bavaria, is poorly understood, and this does not permit a clear assignment.

Of the two families of Lophogastrida, Lophogastridae Sars, 1857 and Eucopiidae, the family Lophogastridae is represented in the fossil record solely by the late Middle Jurassic form Lophogaster volutensis Secretan and Riou, 1986 from La Voulte-sur-Rhone in France. Other supposed lophogastrids, Dollocaris ingens Van Straelen, 1923 and Kilianicaris lerichei Van Straelen, 1923, have since been assigned to Thylacocephala Pinna et al., 1982 (Benton, 1993). Schram (1986) suggested a real lophogastridan affinity for Schimperella, assigning it to the family Eucopiidae together with Eucopia praecursor Secretan and Riou, 1986 of La Voulte-sur-Rhone.

Bill (1914) erected *Schimperella* to include two new species of mysidacean (s.l.), *S. beneckei* and *S. kessleri*, both from the lower Anisian (Middle Triassic) of Alsace (France). *Schimperella* was placed in Lophogastrida by Schram (1986) on the basis of the absence of a statocyst, the well-developed pleopods and pereiopods, the small abdominal pleurae, and the lophogastrid-like shield. Taylor et al. (2001) supported this lophogastridan affinity and proposed a new diagnosis for *Schimperella*.

Until now, the genus has included two valid species, *S. beneckei* (with *S. kessleri* as junior synonym following Benton, 1993) and *S. acanthocercus* Taylor, Schram, and Yan-Bin, 2001 from the late Ladinian Zhuganpo Member of the Falang Formation (Guizhou Province, southern China). The generic assignment of this last species should be now considered uncertain and in need of revision (see details in the discussion of the new species *V. lombardoae*).

Križna and Hitij (2010) reported *Schimperella* sp. also from the middle Anisian Strelovec Formation in Slovenia.

Feldmann et al. (2017) erected Yunnanocopia from the late Anisian Luoping Biota. Yunnanocopia includes two formally defined species, Y. grandis and Y. longicauda, and possibly a third left in open nomenclature. The specimens were recovered from two quarries in the middle part of Member II of the Guanling Formation, Luoping County, Yunnan Province (Feldmann et al., 2016). All the previous Triassic lophogastrids appear to be very common, with a vertical distribution varying from a few dozen centimeters for S. acanthocercus to several hundred meters for the new taxon herein described. In light of the direct collecting by one of us (A.T.) in both Monte San Gorgio (this paper) and the Xingyi areas, preservation and average size of the specimens can be very different from bed to bed. For a better definition of new species, a stratophenetic approach should be applied where possible to avoid misinterpretation of differences in the samples due only to taphonomic processes among specimens coming from different levels.

Feldmann et al. (2017) considered *Yunnanocopia* the oldest occurrence of mysidaceans; nevertheless, the assemblage with *Schimperella beneckei* from the 'Grès à Voltzia' Formation in France should be older. According to Gall and Grauvogel-

Stamm (2005), evidence of an early Anisian age for the Grès à Voltzia is given by conchostracans, foraminifers, and the occurrence of the bivalve *Myophoria vulgaris*. Recently, the Luoping Fauna has been dated to 242 Ma, thus toward the Anisian/Ladinian boundary (Tintori et al., 2016).

Feldmann et al. (2017) assigned *Yunnanocopia* to Eucopiidae, thus including in this family three fossil genera: *Eucopia* Dana, 1852; *Schimperella*, and *Yunnanocopia*. We agree with the considerations related to Eucopiidae reported by Feldmann et al. 2017 and, due to the similarities among *Vicluvia* and the other fossil genera included in the family, we tentatively assigned *Vicluvia* to the Eucopiidae with a sufficient degree of confidence.

#### Genus Vicluvia new genus

Type species.—Vicluvia lombardoae new genus new species.

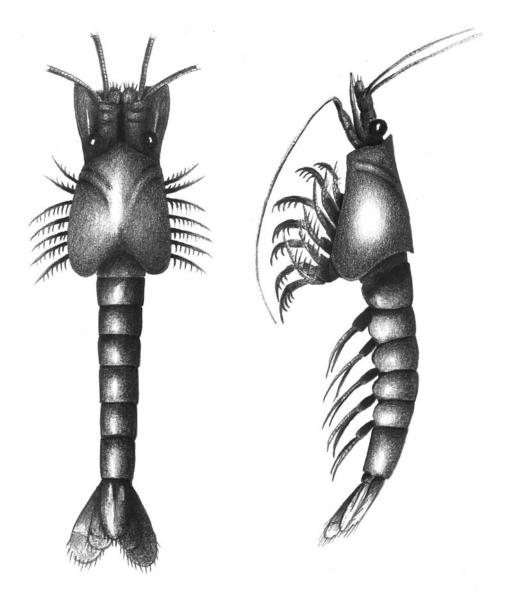
*Diagnosis.*—As for the type species by monotypy.

Occurrence.—In the type area, the Monte San Giorgio, the new taxon has been recorded in both Italy and Switzerland from the Meride Limestone (Ladinian), with the Kalkschieferzone (upper member) being by far the richest horizon. In the Kanton Graubünden, the lower Ladinian Prosanto Formation also yields rare specimens.

*Etymology.*—The name, here in feminine gender, derives from *Vicluvium*, an ancient Latin name of Viggiù, the village where the type locality of the type species is located.

Remarks.—Vicluvia differs from Schimperella mainly in the shape of the shield (Fig. 3), precervical and cervical grooves, antennal scale, and telson. Vicluvia exhibits a short shield, dorsally covering the first five thoracomeres; the two transverse grooves are dorsally vanishing and with their branches regularly arcing axially toward the posterior margin of the shield. In Schimperella, the shield does not cover dorsally all thoracic segments, and the transverse cervical groove is continuous and straight. In Vicluvia, the antennal scale is quite large but not like in Schimperella, where it is extremely large and obovate. Vicluvia exhibits a distally rounded telson whereas in Schimperella, the telson has a truncate distal margin.

Vicluvia differs from Yunnanocopia mainly in the shape of the precervical and cervical grooves (Fig. 4), in the size of the antennal scale, in the presence of antennular lamina (males), in the pleonal pleurae, and in the shape of telson. In Vicluvia, the branches of both the precervical and cervical grooves are parallel and regularly arcing axially toward the posterior margin of the shield; in Yunnanocopia, the two branches of the precervical groove are inclined posterolaterally and those of the cervical groove are concave forward. The antennal scales of Vicluvia are more than half the length of the shield, and the scales together are as wide as the shield; thus, they are larger than those of Yunnanocopia. Pleonal pleurae are moderately well developed in Vicluvia, whereas they are strongly reduced or absent in Yunnanocopia. Many specimens of Vicluvia, probably males, exhibit a setose lamina (appendix masculine?) in the last



 $\textbf{Figure 3.} \quad \text{Tentative reconstruction of } \textit{Vicluvia lombardoae} \text{ n. gen. n. sp.}$ 

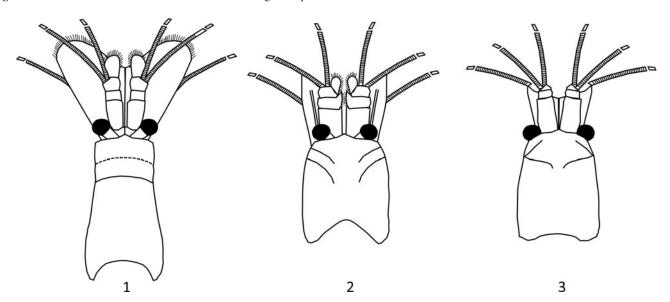


Figure 4. Reconstruction of the anterior body (dorsal view) in (1) Schimperella, (2) Vicluvia, and (3) Yunnannocopia.

peduncular segment of the antennule (basis), which is absent in *Yunnanocopia*. *Vicluvia* could have a diaeresis on the distally rounded telson, but this feature, hardly visible in a few specimens, could be an artefact due to bad preservation. In *Yunnanocopia*, uropods lack any indication of having been setose, although this could be due to bad preservation.

# Vicluvia lombardoae new species Figures 5, 6

1991	Schimperella; Tintori and Brambilla, p. 65.
?1991	Coleoiden, Burgin et al., p. 102, fig. 2.
?1991	Schimperella beneckei Bill, 1914; Burgin et al.,
	p. 103, fig. 3.
1995	Schimperella beneckei; Furrer, p. 839, fig. 7b.
1999	Schimperella; Lombardo et al., p. 103.
2003	Schimperella n. sp.; Gozzi, Lombardo, and
	Larghi, p. 1.
2012	Schimperella; Lombardo, Tintori, and Tona, p. 2004.

*Holotype.*—CMISN 1179 (part and counterpart). Paratypes: CMISN 1180–1185, 1186 (part and counterpart), 1187 (part and counterpart), 1188 (part and counterpart), 1189–1191, 1192 (part and counterpart), 1193–1199, 1200 (part and counterpart), 1201 (part and counterpart), 1202–1206.

Diagnosis.—Shield short; two or three thoracic segments exposed dorsally; two transverse grooves laterally visible and dorsally vanishing with their branches arcing axially toward the posterior margin of the shield. Antennal scale large, ovate to lanceolate, and setose; a rounded setose lamina, at least in males, is present on the third antennular segment. Dactylus in the pereiopodal endopods long and narrow with a nail on its distal end and strong spines throughout the interior margin. Telson with rounded apex; telson and uropods setose.

Occurrence.—From early Ladinian to late Ladinian (Middle Triassic) on the base of the palynological content (Scheuring, 1978) and isotopic dating (Stockar et al., 2012). The type horizon is the middle Kalkschieferzone (upper member of the Meride Limestone) of late Ladinian age and the type locality is Besnasca/Cà del Frate (Viggiù, Varese, Italy).

Description.—Body medium in length, excluding antennae and antennulae, sometimes slightly exceeding 35 mm (30 mm in the holotype, CMISN 1179; 15 mm in CMISN 1185; 19 mm in CMISN 1203; 33 mm in CMISN 1192; 36 mm in CMISN 1186).

The cephalothorax (including the antennal scale) is less than half the total body length (nearly 45%) and the shield is less than one-third of the total body length. Dorsally (where it is shortest for its concave posterior margin) it covers approximately two-thirds of the cephalothorax length. The tail fan is less than one-sixth of the total body length. The cephalothorax, tubular in shape, is approximately 15–17 mm long in mature specimens (e.g., 15 in CMISN 1179, 16 mm in CMISN 1192).

The shield generally shows dorsally some thoracic sternites (e.g., dorsally preserved specimens CMISN 1179, 1191, 1195, 1203, 1204). The shield is concavely curved along its posterior

dorsal margin, and its lateral and posterior margins are free from the body. It was probably connected to the cephalothorax only in the anteriormost end. It is possibly produced in a short, wide, triangular rostrum, scarcely visible in only a few specimens (e.g., CMISN 1206, 1204). The shield anteriorly exhibits two transverse grooves. The most anterior one, the precervical groove, which is distinguishable in some specimens (e.g., CMISN 1186, 1179, 1203), is placed near the frontal margin (less than 1 mm from the frontal margin in the mature specimens). The second one, the cervical groove, is placed nearly 2 mm from the anterior margin in the mature specimens (e.g., 1.5 mm in CMISN 1203, 1.9 mm in CMISN 1179). Both these grooves are dorsally vanishing and their two branches are axially toward the posterior margin of the shield, becoming longitudinal in orientation (e.g., CMISN 1186, 1179, 1191, 1192, 1203). The shield is very short, dorsally covering not more than thoracomeres (thoracic somites; T) 1–5, whereas at least T6–T8 are dorsally visible (e.g., CMISN 1191, 1203, 1206).

The endophragmal skeleton is exceptionally well preserved in several ventrally oriented specimens (e.g., CMISN 1204) or in dorsally oriented specimens that are partially decorticated. The posteriormost margin of each thoracic sternite is visible in some specimens as a robust ridge (e.g., CMISN 1191). Small anteriorly directed projections are present on these ridges immediately adjacent to the median margin of coxal holes at the median point (e.g., CMISN 1191). Some specimens (e.g., CMISN 1204) show well-preserved coxal holes, having a slightly compressed circular shape.

The pleon reaches approximately 15–19 mm in some mature specimens (e.g., CMISN 1179, 1192), the width rarely exceeding 4 mm. Pleomeres (pleonal somites; A) 1–4 are of equal length; A5 and A6 become progressively longer such that A6 is almost double the length of A1. Pleurae are present on A1–A5, absent on A6. Pleurae of A1 are rounded and laterally oriented; pleurae of A2–A6 also rounded by becoming progressively more posteriorly directed toward tail end of animal (e.g., CMISN 1186, 1192). Some specimens show traces of the abdominal muscles and of the gut (mid- and hindgut, e.g., CMISN 1185, 1194, 1203).

The antennules are biflagellate, and the antennular peduncle is composed of three basal segments. The first segment is the longest, approximately three times the second one (e.g., CMISN 1182, 1185, 1196, 1203). The third segment, pentagonal in outline, exhibits on the inner-distal margin of some well-preserved specimens (e.g., CMISN 1187, 1189, 1199, 1203) a lamina, possibly a masculine appendix, with a rounded and setose margin. It also exhibits, in the external frontal margin, two very long flagella nearly as long as the total body length. The antennal peduncle is not well visible because of the superimposition and compression of the elements and the most common dorsal orientation of the specimens; it is possibly shorter than the antennular peduncle, but with a flagellum more robust than the antennular ones. The antennal scales are large and cover the antennal and antennular peduncles (in the dorsally and ventrally oriented specimens, respectively). The antennal scales are ovate to lanceolate, with the longest axis longitudinal to the body, with a longitudinal median carina and a possible transverse suture on the distal rounded frontal margin (e.g., CMISN 1187, 1195). The outer margin is naked and thickened,

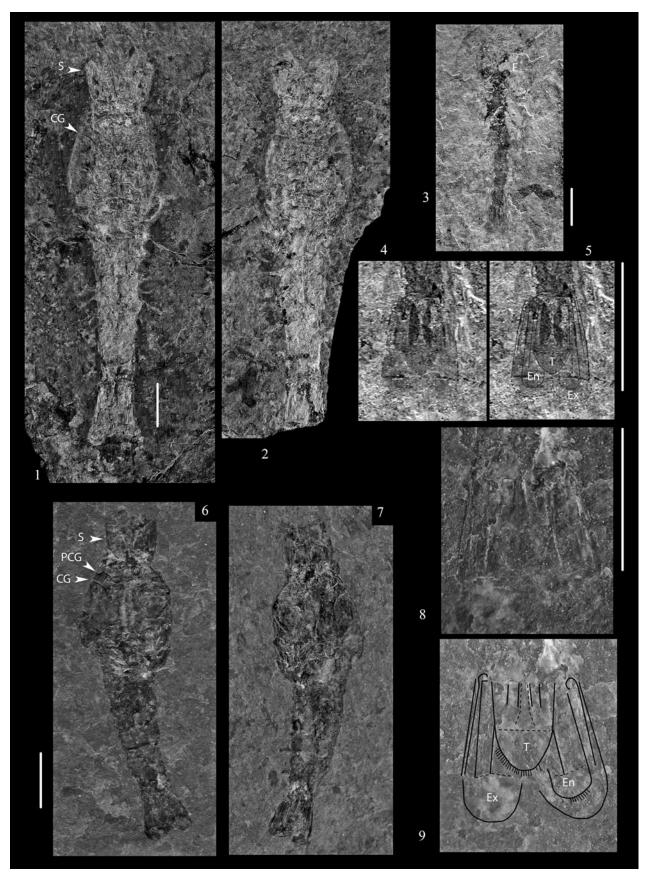
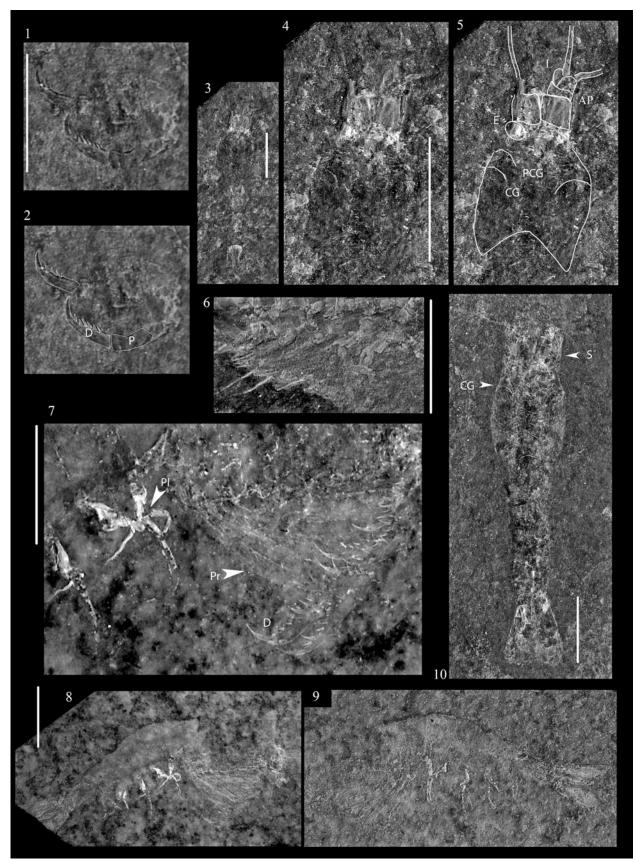


Figure 5. Vicluvia lombardoae n. gen. n. sp. from the Meride Limestone, Ladinian, Besnasca/Cà del Frate, Viggiù, Italy. (1, 2) Paratype CMISN 1192: (1) part; (2) counterpart. (3–5) Paratype CMISN 1206: (3) general view; (4) details of tail fan; (5) explanations. (6–9) Holotype CMISN 1179: (6) part; (7) counterpart; (8) details of tail fan; (9) explanations. CG = cervical groove; E = eye; En = endopod; Ex = exopod; PCG = precervical groove; S = antennal scale; T = telson. Scale bars = 5 mm.



**Figure 6.** *Vicluvia lombardoae* n. gen. n. sp. from the Meride Limestone, Ladinian, Besnasca/Cà del Frate, Viggiù, Italy. (1, 2) Paratype CMISN 1193: (1) details of pereiopods; (2) explanations. (3–5) Paratype CMISN 1203: (3) general view; (4) details of shield; (5) explanations. (6) Paratype CMISN 1180, details of the pleopods. (7–9) Paratype CMISN 1207: (7) details of the appendices; (8) general view; (9) counterpart. (10) Paratype CMISN 1195, general view. AP = antennular peduncle; CG = cervical groove; D = dactylus; E = eye; L = lamina; P = propodus; PCG = precervical groove; Pl = pleopods; Pr = pereiopods; S = antennal scale. Scale bars = 5 mm.

the internal one setose (e.g., CMISN 1187). The eyes are bulbous and relatively large compared to the size of the whole body.

The distal segments of the pereiopodal endopods are often well preserved (e.g., CMISN 1193, 1197, 1200, 1207). They exhibit a long, narrow, and pointed dactylus with a furrow in the middle, strong spines throughout the interior margin (~9– 12 on the mature specimen CMISN 1207) with the strongest on its distal end. The propodus is subrectangular (distally wider, nearly as long as the dactylus) while the carpus, hardly visible, is short (possibly half the length of the propodus). Merus, ischium, and preischium poorly visible. The pereiopodal exopods, hardly distinguishable on few specimens, possibly exhibit a single elongate flagellum. The pleopods, not always visible, are made up of a rectangular segment and two narrow, annulate rami, the anteriormost being more robust and longer than the other (e.g., CMISN 1180, 1181, 1192). They reach almost 3.5 mm in length in adults (e.g., CMISN 1192), and the posterior ones are slightly shorter than those near the anterior end of the pleon.

The tail fan is made up of the telson and a pair of biramous uropods. The exopods are elongate and triangular, exhibit a diaeresis, and are highly setose distally (e.g., CMISN 1185). The lobate endopods, highly setose distally, are slightly shorter than the exopods but are longer than the telson. Because of the superimposition and compression of the elements in the examined specimens, it is not clear whether the endopods have a diaeresis. The telson, distinctly visible in two exceptionally well-preserved specimens (CMISN 1179, 1206), is subrectangular and elongate with a rounded and highly setose distal end. The telson is also ornamented by a pair of curved longitudinal grooves, concave side facing laterally; in the holotype it reaches a maximum size of 2.5 mm in length and 1.3 mm in width at its base.

The body proportions change during growth (allometric growth), and most of the ontogenetic variations are related to enlargement of the shield and elongation of the pleon compared to the tail fan. The ratio of the shield to the tail fan is less than 1.4 in juvenile specimens (smaller individuals, less than 20 mm in size) and more than 1.6 in adult specimens (larger individuals, more than 30 mm in size).

*Etymology*.—The name honors Cristina Lombardo (Dipartimento di Scienze della Terra 'A. Desio,' Università degli Studi di Milano) for her work on the Kalkschieferzone fauna.

Materials.—Specimen CMISN 1207 from the Rio Vallone near Porto Ceresio and many hundred topotypes reposed in the same CMISN (without catalog number) from Besnasca/Cà del Frate (Viggiù, Varese, Italy). Hundreds of specimens from site D in the lower Kalkschieferzone in Val Mara, near the village of Meride (Mendrisio, Canton Ticino, Switzerland) and deposited in the MCSN were also examined. A few of the Val Mara specimens (from bed A and collected in 1996) were considered particularly informative, so they were given repository numbers (MCSN 3173–3184).

State of preservation.—In these laminate limestones, the decay of crustacean skeletons is reduced, so even delicate structures such as pleopods and antennae are usually well preserved. As pointed out by Montagna et al. (2017), the very nice

preservation of arthropods was probably due to the presence of microbial films at the bottom, quickly sealing the dead organism and allowing also quite common phosphatization of soft tissues in arthropods. However, as beds rich in *Vicluvia lombardoae* n. gen. n. sp. are recorded from a thick stratigraphic interval, size can vary from bed to bed, as for the overall preservation quality. Furthermore, the specimens are preserved in a variety of orientations, and this has a substantial impact on the outline and proportions of specimens.

Orientations vary from lateral to dorsoventral, with every intermediate; some specimens are twisted, with the main body regions seen in different orientations. This confirms that the animals were rather delicate and the exoskeleton was poorly sclerotized and susceptible to postmortem distortion.

Remarks.—Benton (1993) stated the synonymy for the two species erected by Bill (1914) in the genus Schimperella: S. beneckei and S. kessleri. Gall (1971) had previously hinted at this suggestion, noting that the differences between the two species, in terms of the degree of cephalothorax cover provided by the shield, may be explained by taphonomical deformations. The uncertain status of S. kessleri was discussed also by Schram (1986) and Taylor et al. (2001); the correct status of this species could only be definitively defined by examination of the original materials, but it seems to be missing (fide Taylor et al., 2001). In agreement with Feldmann et al. (2016), the original illustrations of S. kessleri (Bill, 1914, pl. 16, figs. 3, 4) suggest that this species may be the female counterpart of S. beneckei. Regardless, there are few similarities between Vicluvia lombardoae n. gen. n. sp. and Schimperella beneckei. In addition to the characters of generic rank, Vicluvia lombardoae differs from Schimperella in the dactylus, which is longer, sharp, and armed with strong spines in Vicluvia.

The specimens figured and identified by Bürgin et al. (1991) as coleoidean arms (p. 102, fig. 2) and *S. beneckei* (p. 103, fig. 3) belong to *Vicluvia lombardoae* because they show the diagnostic characters of the armed dactylus and rounded telson.

The taxonomic assignment of the most recent species attributed to Schimperella, S. acanthocercus Taylor, Schram, and Yan-Bin, 2001, based on specimens from the Ladinian Falang Formation (southwestern China), will be revised (personal communication, A. Tintori, 2019) in light of new, betterpreserved specimens recently collected from the same unit in both the type locality and the Nimaigu (Wusha of Xingyi) excavation site (personal observation, A.T., 2016–2017). The specimens studied by Taylor et al. (2001) seem not preserved enough for a confident generic assignment considering the diagnostic relevance of the shield shape and precervical and cervical grooves in Schimperella, Yunnannocopia, and Vicluvia. There are only a few resemblances between Vicluvia lombardoae n. gen. n. sp. and Schimperella acanthocercus. The antennular peduncle of S. acanthocercus is simpler than that of Vicluvia lombardoae and does not exhibit the masculine process on the third peduncular segment.

In addition to the characters of the more generic rank, *Vicluvia lombardoae* differs from *Yunnanocopia grandis* Feldmann et al., 2017 and *Y. longicauda* Feldmann et al., 2017 in the longer dactylus, which is sharp and armed with strong spines.

#### **Discussion**

Crustaceans are among the least-known invertebrates from the Middle Triassic rocks of the studied area. The first crustacean reported from the Besano Formation of Monte San Giorgio was the penaeid *Antrimpos mirigiolensis* Etter, 1994. The same unit, outcropping at Sasso Caldo near Besano (Italy), provided thylacocephalans (Affer and Teruzzi, 1999).

A new macruran decapod, *Meridecaris ladinica* Stockar and Garassino, 2013, was described from the lowermost part of the upper Meride Limestone, from an interval informally introduced as 'Sceltrich beds' by Stockar et al. (2013). In the same paper, Stockar and Garassino (2013) reported the presence of two further specimens of natant decapods from the Besano Formation at Sasso Caldo site; they are still undescribed.

In the youngest fossiliferous unit of the Monte San Giorgio, the Kalkschieferzone, besides ostracods and the conchostracan *Laxitextella* (Tintori and Brambilla, 1991; i.e., *Palaeolimnadia* sp. in Tintori, 1990c), only the mysidacean (s.l.) *Vicluvia lombardoae* n. gen. n. sp. is a common crustacean (Figs. 4–6).

Until now, only one specimen of decapod was reported from the Kalkschieferzone and tentatively assigned by Larghi and Tintori (2007) to the 'wastebasket genus' *Antrimpos* Münster, 1839.

The accumulation of layers of mass mortality of Vicluvia lombardoae n. gen. n. sp. could reflect normal population dynamics, corresponding to seasonal variations in physical factors and/or in reproductive cycles. It is important to keep in mind that these surfaces are usually devoid of any other organic remains, no fishes or conchostracans having been recorded (personal observation, A.T., 1996–2003). Fluctuations in environmental factors such as temperature, salinity, oxygen, and phytoplankton biomass influence the seasonal patterns of variation in populations of many modern crustaceans. Mysidaceans living in estuarine transitional environments show temporal variations in population structure, which have a salinity-related reproductive significance (Greenwood et al., 1989; Azeiteiro et al., 1999, 2001). Although reproduction seems continuous throughout the year in many species, some observations show peaks in connection with variations of salinity (Azeiteiro et al., 1999, 2001). Sudden seasonal increase in freshwater supply decreases salinity, whereas high temperatures in the dry months increase it; during these seasonal changes, mature mysids disappear from the population as their progeny develop (Azeiteiro et al., 1999).

#### Acknowledgments

We thank C. Lombardo, who was for many years field director in the fossil localities of Cà del Frate and Val Mara and responsible for collecting the large number of specimens here examined. The MSNIO (now CMISN) and the MCSN in Lugano supported the excavation in the Cà del Frate and Val Mara sites, respectively. G. Teruzzi allowed comparison with the material stored in the Museo Civico di Storia Naturale di Milano. We thank the referees C. Schweitzer and J. Haug for careful reading of the manuscript and for their valuable comments. We thank J. Jin, T. Wappler, and J. Kastigar for the editorial and stylistic revision of the manuscript and E. Barnes for the English

revision. We also acknowledge all the people who helped during the fieldwork.

#### References

- Affer, D., and Teruzzi, G., 1999, Thylacocephalan crustaceans from the Besano Formation, Middle Triassic, N. Italy: Rivista del Museo civico 'E. Caffi' di Bergamo, v. 20, p. 5–8.
- Azeiteiro, U.M.M., Jesus, L., and Marques, J.C., 1999, Distribution, population dynamics and production of the suprabenthic mysid *Mesopodopsis slabberi* Van Beneden in the Mondego estuary (Western coast of Portugal): Journal of Crustacean Biology, v. 19, p. 498–509.
- Azeiteiro, U.M., Fonseca, J., and Marques, J.C.S., 2001, Biometry, estimates of production and seasonal variation in the biochemical composition of *Mesopodopsis slabberi* (Van Beneden, 1861) (Crustacea: Mysidacea): Boletín Instituto Español de Oceanografía, v. 17, p. 15–25.
- Bechly, G., and Stockar, R., 2011, The first Mesozoic record of the extinct apterygote insect genus Dasyleptus (Insecta: Archaeognatha: Monura: Dasyleptidae) from the Triassic of Monte San Giorgio (Switzerland): Palaeodiversity, v. 4, p. 23–37.
- Benton, M.J., 1993, The Fossil Record 2: London, Chapman and Hall, 845 p. Bernasconi, S., and Riva, A., 1993, Organic geochemistry and depositional environment of a hydrocarbon source rock: The Middle Triassic Grenzbitumnzone Formation, southern Alps, Italy/Switzerland, in Spencer, A.M., ed., Generation, Accumulation and Production of Europe's Hydrocarbons III: Berlin, Springer-Verlag, 380 p.
- Beurlen, K., 1930, Vergleichende Stammgeschichte Grundlagen Methoden. Probleme unter besondere Berucksichtigung der hoheren Krebse: Forschung der Geologie und Paleontologie, v. 8, p. 317–586.
- Bill, P.C., 1914, Über Crustaceen aus dem Voltziensandstein des Elsasses: Mitteilungen der Geologischen Landesanstalt Elsass-Lothringen, v. 8, p. 289–338.
- Boas, J.E.V., 1883, Studien uber die Verwandtschaftsbeziehungen der Malakostraken: Morphologisches Jahrbuch, v. 8, p. 485–579.
- Broili, F., 1917, Eine neue Crustaceen Form aus dem lithographischen Schiefer des oberen Jura von Franken: Zentralblatt für Mineralogie, Geologie und Paläontologie Jahrbuch, v. 1917, p. 426–429.
- Brusca, R.C., and Brusca, G.J., 1990, İnvertebrates: Sunderland, Massachusetts,
  Sinauer Associates, 922 p.
  Bürgin, T., Eichenberger, U., Furrer, H., and Schanz, T.K., 1991, Die Prosanto-
- Bürgin, T., Eichenberger, U., Furrer, H., and Schanz, T.K., 1991, Die Prosanto-Formation eine fischreiche Fossil-Lagerstätte in der Mitteltrias der Silvretta-Decke (Kanton Graubünden, Schweiz): Eclogae Geologicae Helvetiae, v. 84, no. 3, p. 921–990.
- Dana, J.D., 1852, Crustacea, part I, *in* United States Exploring Expedition, During the Years 1838, 1839, 1840, 1841, 1842, under the Command of Charles Wilkes, U.S.N, Vol. 13: Philadelphia, C. Sherman, 692 p.
- De Alessandri, G., 1910, Studii sui pesci triasici della Lombardia: Memorie della Società Italiana di Science Naturali, v. 7, p. 1–147.
- Etter, W., 1994, A new penaeid shrimp (Antrimpos mirigiolensis n. sp., Crustacea, Decapoda) from the Middle Triassic of the Monte San Giorgio (Ticino, Switzerland): Neues Jahrbuch fur Geologie und Palaontologie Monatshefte, v. 4, p. 223–230.
- Feldmann, R.M., Schweitzer, C.E., Hu, S., Zhang, Q., Zhou, C., Xie, T., Huang, J., and Wen, W., 2012, Macrurous Decapoda from the Luoping Biota (Middle Triassic) of China: Journal of Paleontology, v. 86, p. 425–441.
- Feldmann, R.M., Schweitzer, C.E., Hu, S., Huang, J., Zhou, C., Zhang, Q., Wen, W., Xie, T., and Maguire, E., 2016, Spatial distribution of Crustacea and associated organisms in the Luoping biota (Anisian, Middle Triassic), Yunnan Province, China: Evidence of periodic mass kills: Journal of Paleontology, doi:10.1017/jpa.2015.60.
- Feldmann, R.M., Schweitzer, C.E., Hu, S., Huang, J., Zhou, C., Zhang, Q., Wen, W., Xie, T., Schram, F.R., and Jones, W.T., 2017, Earliest occurrence of lophogastrid mysidacean arthropods (Crustacea, Eucopiidae) from the Anisian Luoping Biota, Yunnan Province, China: Journal of Paleontology, v. 91, p. 100–115.
- Frauenfelder, A., 1916, Beiträge zur Geologie der Tessiner Kalkalpen: Eclogae geologicae Helvetiae, v. 14, p. 247–367.
- Fu, W.L., Wilson, G.D.F., Jiang, D.Y., Sun, Y.L., Hao, W.C., and Sun, Z.Y., 2010, A new species of *Protamphisopus* Nicholls (Crustacea, Isopoda, Phreatoicidea) from Middle Triassic Luoping Fauna of Yunnan Province: China: Journal of Paleontology, v. 84, p. 1003–1013.
- Furrer, H., 1995, The Kalkschieferzone (Upper Meride Limestone; Ladinian) near Meride (Canton Ticino, southern Switzerland) and the evolution of a Middle Triassic intraplatform basin: Eclogae geologicae Helvetiae, v. 88, p. 827–852.
- Gall, J.C., 1971, Faunes et paysages du Grès à Voltzia du Nord des Vosges: Essai paléoécologique sur le buntsandstein supérieur, Université de Strasbourg, Service de la carte géologique d'Alsace et de Lorraine, Mémoires, v. 34, p. 1–318.

- Gall, J.C., and Grauvogel-Stamm, L., 2005, The early Middle Triassic 'Grès à Voltzia' Formation of eastern France: A model of environmental refugium: Comptes Rendus Palevol, v. 4, p. 637–652.
- Gozzi, E., Lombardo, C., and, Larghi, C., 2003, Exceptional fossil preservation in the Besano-Monte San Giorgio Area: The case of the arthropods: Abstract and Poster, EPA Workshop 2003, Exceptional Preservation, Teruel, Spain, 24–27 September, p. 59–61.
- Greenwood, J.G., Jones, M.B., and Greenwood, J., 1989, Salinity effects on brood maturation of the mysid crustacean *Mesopodopsis slabberi*: Marine Biological Association (United Kingdom) Journal, v. 69, p. 683–694.
- Haworth, A.H., 1825, A new binary arrangement of the macrurous Crustacea: Philosophical Magazine and Journal of Natural Philosophy, Chemistry and Arts, v. 65, p. 183–184.
- Hessler, R.R., 1969, Peracarida, in Moore, R.C., ed., Treatise on Invertebrate Paleontology, Part R, Arthropoda 4, Volume 1: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America and University of Kansas Press, p. R360–R393.
- Ji, C., Sang, W.L., Diao, G.W., Motani, R., and Tintori, A., 2012, Biodiversity and stratigraphic distribution of the first late Ladinian (Middle Triassic) marine vertebrate fauna (Xingyi Fauna) from South China: Journal of Vertebrate Paleontology, v. 32, 131 p.
- Jiang, D., Motani, R., Hao, W., Rieppel, O., Sun, Y., Tintori, A., Sun, Z., and Schmitz, L., 2009, Biodiversity and sequence of the Middle Triassic Panxian marine reptile fauna, Guizhou Province, China: Acta Geologica Sinica, v. 83, p. 451–459.
- Križnar, M., and Hitij, T., 2010, Nevretenčarji (Invertebrates) Strelovške formacij: Scopolia Supplementum. v. 5, p. 91–107.
- Krzeminski, W., and Lombardo, C., 2001, New fossil Ephemeroptera and Coleoptera from the Ladinian (Middle Triassic) of Canton Ticino (Switzerland): Rivista Italiana di Paleontologia e Stratigrafia, v. 107, p. 69–78.
- Larghi, C., and Tintori, A., 2007, First record of a decapod from the Meride Limestone: New data from one of the best Ladinian (Middle Triassic) taphonomic windows of a transitional environment: Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano, v. 35, p. 68–69.
- Latreille, P.A., 1802, Histoire naturelle générale et particulière des Crustacés et des insectes. Tome 3, Familles naturelles des genres: Paris, F. Dufart, 479 p.
- Lombardo, C., 1999, Sexual dimorphism in a new species of the actinopterygian Peltopleurus from the Triassic of northern Italy. Palaeontology, v. 42, p. 741–760.
- Lombardo, C., 2001, Actynopterigians from the Middle Triassic of northern Italy and Canton Ticino (Switzerland): Anatomical descriptions and nomenclatural problems: Rivista Italiana di Paleontologia e Stratigrafia, v. 107, p. 345–369.
- Lombardo, C., Tintori, A., Felber, M., Danini, G., Moratto, D., Pacor, G., and Tentor, M., 1999, Faunal assemblages in the Kalschieferzone (Meride Limestone, Upper Ladinian) of Meride (Canton Ticino, Switzerland): Rivista del Museo Civico di Scienze Naturali 'Enrico Caffi,' v. 20 (supplement), p. 101–104.
- Lombardo, C., Tintori, A., and Tona, D., 2012, A new species of Sangior-gioichthys (Actinopterygii, Semionotiformes) from the Kalkschieferzone of Monte San Giorgio (Middle Triassic; Meride, Canton Ticino, Switzerland):
   Bollettino della Società Paleontologica Italiana, v. 51, no. 3, p. 203–212.
   Lu, H., Jiang, D.Y., Motani, R., Ni, P.G., Sun, Z.Y., Tintori, A., Xiao, S.Z.,
- Lu, H., Jiang, D.Y., Motani, R., Ni, P.G., Sun, Z.Y., Tintori, A., Xiao, S.Z., Zhou, M., Ji, C., and Fu, W.L., 2018, Middle Triassic Xingyi fauna: Showing turnover of marine reptiles from coastal to oceanic environments: Palaeoworld, v. 27, p. 17–116.
- Martin, J.W., and Davis, G.E., 2001, An Updated Classification of the Recent Crustacea: Los Angeles, Natural History Museum of Los Angeles County, 124 p.
- Montagna, M., Haug, J.T., Strada, L., Haug, C., Felber, M., and Tintori, A. 2017, Central nervous system and muscular bundles preserved in a 240 million year old giant bristletail (Archaeognatha, Machilidae): Science Reports, v. 7, 46016, doi:10.1038/srep46016.
- Motani, R., Jiang, D.Y., Tintori, A., Sun, Y.L., Hao, W.C., Boyd, A., Hinic-Frlog, S., Schmitz, L., Shin, J.Y., and Sun, Z.Y., 2008, Horizons and assemblages of Middle Triassic marine reptiles from Panxian, Guizhou, China: Journal of Vertebrate Paleontology, v. 28, p. 900–903.
- Münster, Von G., 1839, Decapoda Macroura. Abbildung und Beschreibung der fossilen langschwänzigen Krebse in den Kalkschiefern von Bayern: Beitrage Petrefactenkde, v. 2, p. 1–88.
- Pinna, G., Arduini, P., Pesarini, C., and Teruzzi, G., 1982, Thylacocephala: una nuova classe di crostacei fossili: Atti della Società Italiana di Scienze Naturali e del Museo civico di Storia Naturale di Milano, v. 123, p. 469–482.
- Renesto, S., 1993, A juvenile *Lariosaurus* (Reptilia, Sauropterygia) from the Kalkschieferzone (Uppermost Ladinian) near Viggiù (Varese, northern Italy): Rivista Italiana di Paleontologia e Stratigrafia, v. 92, p. 199–212.
- Renesto, S., Lombardo, C., Tintori, A., and Danini, G., 2003, Nothosaurid embryos from the Middle Triassic of northern Italy: An insight into the

- viviparity of Nothosaurs: Journal Vertebrate Paleontology, v. 23, p. 958–961.
- Riva, A., Salvatori, T., Cavaliere, R., Ricchiuto, T., and Novelli, L., 1985, Origin of oils in Po Basin, northern Italy: Organic Geochemistry, v. 10, p. 391–400.
- Sars, G.O., 1885, Report on the Schizopoda collected by the HMS Challenger during the years 1873–1876, in Nartes, G.S., ed., Report on the Scientific Results of the Voyage of the H.M.S. Challenger during the Years 1873– 1876: London, Longmans & Co., p. 1–228, pls. 1–38.
- Sars, M., 1857, Om 3 nye norske Krebsdyr: Forhandlimgar vid det Skandinaviska Naturforskaremotet, v. 7, p. 160–175.
- Scheuring, B.W., 1978, Mikrofloren aus den Meridenkalken des M.te San Giorgio (Kanton Tessin): Schweizerische Paläontologische Abhandlungen, v. 100, p. 1–100.
- Schram, F.R., 1984, Relationships within eumalacostracan crustaceans: Transactions of the San Diego Society of Natural History, v. 20, p. 301–312.
- Schram, F.R., 1986, Crustacea: New York, Oxford University Press, 606 p.
- Secretan, S., and Riou, B., 1986, Les Mysidaces (Crustacea, Peracarida) du Callovien de la Voulte-sur-Rhone: Annales de Paleontologie, v. 72, p. 295–323.
- Senn, A., 1924, Beiträge zur Geologie des Alpensüdrandes zwischen Mendrisio und Varese: Eclogae Geologicae Helvetiae, v. 18, p. 550–632.
- Stockar, R., 2010, Facies, depositional environment, and palaeoecology of the Middle Triassic Cassina beds (Meride Limestone, Monte San Giorgio, Switzerland): Swiss Journal of Geosciences, v. 103, p. 101–119.
- Stockar, R., and Garassino, A., 2013, Meridecaris ladinica n. gen. n. sp. (Crustacea, Decapoda, Clytiopsidae) from the Middle Triassic (Ladinian) of Monte San Giorgio (Canton Ticino, Switzerland): Neues Jahrbuch für Geologie und Palaontologie-Abhandlungen, v. 270, p. 347–356.
- Stockar, R., and Kustatscher, E., 2010, The Ladinian flora from the Cassina beds (Meride limestone, Monte San Giorgio, Switzerland): Preliminary results: Rivista Italiana di Paleontologia e Stratigrafia, v. 116, p. 173–188.
- Stockar, R., Baumgartner, P.O., and Condon, D., 2012, Integrated Ladinian biochronostratigraphy and geochrononology of the Monte San Giorgio, (southern Alps, Switzerland): Swiss Journal of Geosciences, v. 105, p. 85–108.
- Stockar, R., Adatte, T., Baumgartner, P.O., and Föllmi, K.B., 2013, Palaeo-environmental significance of organic facies and stable isotope signatures: The Ladinian San Giorgio Dolomite and Meride Limestone of Monte San Giorgio (Switzerland, WHL UNESCO): Sedimentology, v. 60, p. 239–269.
- Strada, L., Montagna, M., and Tintori, A., 2014, A new genus and species of the family Trachypachidae (Coleoptera, Adephaga) from the upper Ladinian (Middle Triassic) of Monte San Giorgio: Rivista Italiana di Paleontologia e Stratigrafia, v. 120, p. 183–190.
- Taylor, R.S., Schram, F.R., and Yan-Bin, S., 2001, A new upper Middle Triassic shrimp (Crustacea: Lophogastrida) from Guizhou, China, with discussion regarding other fossil 'mysidaceans': Journal of Paleontology, v. 75, p. 310–318.
- Tintori, A., 1990a, The actinopterygian fish *Prohalecites* from the Triassic of northern Italy: Palaeontology, v. 33, p. 155–174.
- Tintori, A., 1990b, *Dipteronotus olgiatii* n. sp. (actynopterigii, Perleidiformes) from the Kalkschieferzone of Cà del Frate (N. Italy): Atti Ticinensi di Scienze della Terra, v. 33, p. 191–197.
- Tintori, A., 1990c, Estherids from the Kalkschieferzone (Triassic) of Lombardy (N. Italy), in Robba, E., ed., Atti del Quarto Simposio di Ecologia e Paleoecologia delle Comunità Bentoniche: Torino, Museo regionale di Scienze Naturali di Torino, p. 95–105.
- Tintori, A., 1998, Fish biodiversity in the marine Norian (Late Triassic) of northern Italy: The first Neopterygian radiation: Italian Journal of Zoology, v. 65, p. 193–198.
- 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, v. 119, p. 287–302.
- Tintori, A., and Brambilla, E., 1991, Sexual dimorphism in a conchostracan population from late Ladinian of southern Calcareous Alps (N. Italy): Contributions from the Palaontological Museum, University of Oslo, v. 364, p. 65–66.
- Tintori, A., and Lombardo, C., 1999, Late Ladinian fish faunas from Lombardy (N-Italy): Stratigraphy and paleobiology, in Arratia, G., and Schultze, H.P., eds., Mesozoic Fishes 2: Systematics and Fossil Record, München, Verlag Pfeil, p. 495–504.
- Tintori, A., and Lombardo, C., 2007, A 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, v. 113, p. 369–381.
- Tintori, A., and Renesto, S., 1983, The Macrosemiidae (Pisces, Actinopterygii) from the Upper Triassic of Lombardy: Rivista Italiana di Paleontologia e Stratigrafia, v. 89, p. 209–222.
- Tintori, A., and Renesto, S., 1990, A new *Lariosaurus* from the Kalkschieferzone (Uppermost Ladinian) of Valceresio (Varese, N. Italy): Bollettino della Società Paleontologica Italiana, v. 29, p. 309–319.

- Tintori, A., Sun, Z.Y., Lombardo, C., Jiang, D.Y., Ji, C., and Motani, R., 2012, A new 'Flying' fish from the late Ladinian (Middle Triassic) of Wusha (Guizhou Province, southern China): Gortania, v. 33, p. 39–50.
- Tintori, A., Jiang, D.Y., Motani, R., Sun, Z.Y., Ji, C., Zou, X.D., and Ma, L.T., 2013, Faunal sequence of Middle Triassic Xingyi Fauna: Evidence from the excavation at Nimaigu of Wusha District, Xingyi City, Guizhou Province: Abstract Book of the 2nd International Symposium on Triassic and Later Marine Vertebrate Faunas, September 10–15, 2013, Xingyi, China, p. 63–65.
- Tintori, A., Hitij, T., Jiang, D.Y., Lombardo, C., and Sun, Z.Y., 2014, Triassic actinopterygian fishes: The recovery after the end-Permian crisis: Integrative Zoology, v. 9, p. 394–411.
- Tintori, A., Lombardo, C., and Kustatscher, E., 2016, The Pelsonian (Anisian, Middle Triassic) fish assemblage from Monte Prà della Vacca/Kühwiesenkopf (Braies Dolomites, Italy): Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, v. 282, p. 181–200.
- Van Straelen, V., 1923, Les mysidaces du Callovian de la Boulte-sur- Rhone: Bulletin de la Societé Geologique de France, v. 23, p. 432–439.

- Wang, X.F., Chen, X.H., Wang, C.S., and Cheng, L., 2009, The Triassic Guanling fossil group: A key GeoPark from a barren mountain, Guizhou Province, China, in Lipps, J.H., and Granier, B.R.C., eds., PaleoParks: The protection and conservation of fossil sites worldwide: Notebooks on Geology, v. 3, p. 11–28.
- Wirz, A., 1945, Die Triasfauna der Tessiner Kalkalpen. XV Beiträge zur Kenntnis des Ladinikums in Gebiete des Monte San Giorgio: Schweizerische Paläontologische Abhandlungen, v. 65, p. 1–84.
- Zorn, H., 1971, Paläontologische, stratigraphische und sedimentologische Untersuchungen des Salvatoredolomits (Mitteltrias) der Tessiner Kalkalpen: Schweizerische Paläontologische Abhandlungen, v. 91, p. 1–90.
- Zou, X.D., Balini, M., Jiang, D.Y., Tintori, A., Sun, Z.Y., and Sun, Y.L., 2015, The ammonoids from the Zhuganpo Member at Nimaigu and their bearing for dating the Xingyi Fossilägerstatte (Middle Triassic, Guizhou, China): Rivista Italiana di Paleontologia e Stratigrafia, v. 121, p. 135–161.

Accepted: 11 September 2019