

RESEARCH ARTICLE

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Middle Triassic Nautilida from the Besano Formation of Monte San Giorgio, Switzerland

Vittorio Pieroni*

Abstract

For the first time, nautilids from the Besano Formation (Anisian/Ladinian boundary) are documented. The extremely rare material was collected from two different outcrops at Monte San Giorgio (Southern Alps, Ticino, Switzerland). This material is represented by only five specimens described here. The three best specimens belong to the taxa *Enoploceras rieberi* sp. nov., *Germanonautilus* aff. *ellipticus* and *Syringonautilus* sp. indet., documenting the presence of the families Tainoceratidae and Syringonautilidae in the middle Besano Formation. Another nautilid specimen is described in open nomenclature, representing an additional taxon. The new species *Enoploceras rieberi* n. sp. is currently the only occurrence of the genus *Enoploceras* in the Middle Triassic. Nautilida are poorly known from the Middle Triassic Tethyan region, mostly from sediments deposited in pelagic environments. This is the first record of these nautilids from an usually anoxic depositional paleoenvironment of an intra-platform basin, where the sediments of the Besano Formation were laid down.

Keywords: Nautilida, Middle Triassic, Besano Formation, Southern Alps, Switzerland

Introduction

The fossil record of Triassic coiled nautilids in the north-western Tethys Realm is very scarce. Many species are based on very few poorly preserved specimens. Therefore, the range of intrapopulation variability and the evolutionary trends of many Tethyan Triassic nautiloid genera are poorly known (Dzik, 1984).

After the few historical works documenting nautilids from the Middle Triassic carbonate platform formations cropping out in the Southern Alps of Lombardy (Airaghi, 1902; Mariani, 1914; Mojsisovics, 1882; Rossi-Ronchetti, 1960; Stoppani, 1860; Tommasi, 1885), some other occurrences have been described from this area recently. In particular, from the San Salvatore Dolomite of Rasa di Varese (Varese) in the informal unit “Rasa dolomite” (see Airaghi, 1935), the new species *Mojsvaroceras gianii* was introduced by Pieroni and Prinoth (2021), while from the

Esino Limestone of Val Parina (Val Brembana, Bergamo), well preserved specimens were described by Pieroni (2020).

In relatively deep, pelagic intra-platform basins known from the Southern Alps of Lombardy, a few poorly preserved nautilids from the Prezzo Limestone of Val Brembana (Mojsisovics, 1880; Tommasi, 1894; Venzo & Pelosio, 1968) and from the Varenna Limestone of Varenna (*Pleuronautilus taramellii* Tommasi, 1894) have been recognized so far.

The Middle Triassic Besano Formation (formerly called “Grenzbitumenzone” in most publications) is exposed in the Monte San Giorgio area, which was registered in 2003 as a UNESCO World Heritage Site because of its important vertebrate fauna from the Middle Triassic. This important fossiliferous formation crops out across the border between Southern Switzerland (Canton Ticino) and Northern Italy (Province Varese). Invertebrate fossils are also relatively common in the Besano Formation and some of the main clades of marine molluscs such as ammonoids, orthoceratoids and bivalves (especially the genus *Daonella*) have been documented, notably by

Editorial handling: Christian Klug

*Correspondence: info@marianopieroni.it

Museo di Storia Naturale “A. Stoppani”, Seminario Arcivescovile “Pio XI”, Via Papa Pio XI, 32, 21040 Venegono Inferiore, Varese, Italy



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Airaghi (1912a, 1912b), Rieber (1965, 1968, 1969, 1970, 1973a, 1973b, 1974a, 1974b) and Schatz (2005a, 2005b), as well as some rare coleoids (Rieber, 1970, 1974a). They represent nekctic cephalopods or bivalves adapted to an environment characterized by anoxic condition in bottom waters of an intra-platform basin (Bernasconi, 1991; Schatz, 2005a). Recently, Pieroni and Furrer (2020) documented also findings of gastropods. Benthic molluscs are abundant in carbonate platform formations, while they are scarce in the Besano Formation, especially due to the taphonomy of shells, which are usually dissolved and the specimens are mostly preserved as internal or external molds.

Nautilids are very rare in the Besano Formation. From Monte San Giorgio (Punkt 902/ Mirigioli, Meride, Ticino, bed nr. 45, 47, 49, 58, 61), only Rieber (1973a, 1973b: Tab. 12) described some specimens of orthoceratoids classified as *Michelinoceras campanile* (Mojsisovics, 1869) from the Late Anisian (Illyrian) “Polymorphus Zone”. Based on unpublished material in the PIMUZ collection (personal information by Alexander Pohle, 29/09/2022), orthoceratoids occur more or less regularly between beds nr. 41–104 (more than 35 specimens).

Here I document, for the first time, nautilids from the Besano Formation (Anisian/Ladinian boundary) of Monte San Giorgio. The illustrated material comes from the most important collection of Besano Formation fossils in the Paläontologisches Museum der Universität Zürich (PIMUZ). To my knowledge, no other specimens of nautilids are present in the other main collections of the Besano Formation in museums of Switzerland and Italy. The specimen PIMUZ 37902 is described as a new species.

Locations and age

The Besano Formation at Mirigioli is composed of a 16-m-thick alternation of black shale and laminated dolostone. Its uppermost part includes the Anisian/Ladinian boundary (Brack & Rieber, 1993; Brack et al., 2005).

After the revision of the stratigraphy for the collection inventory (Furrer and Rieber 2011, unpublished), beds 2–53 were informally named as “Lower Besano Formation”, and beds 54–132 as “Middle Besano Formation”, with the limit of the Reitzi and Secedensis Zones (Illyrian) placed between beds 57 and 58. The “Upper Besano Formation” corresponds to the beds 133–186, with the limit of the Anisian/Ladinian boundary placed between beds 149 and 150 (see López-Arbarello et al., 2016: Fig. 3).

The specimens described herein were collected in the Middle Besano Formation of Monte San Giorgio and

have a latest Anisian age (Illyrian, Secedensis Zone; see Fig. 1). The specimen PIMUZ 29942 was collected in 1927 in the old mine Valle Stelle above Tre Fontane (Meride, today part of the community Mendrisio, Canton Ticino), located 1300 m WSW of Monte San Giorgio. Four specimens (PIMUZ 31220, 37902, 37903, 38668) come from the site referred to as Point 902 or Mirigioli (Meride), located 800 m WSW of Monte San Giorgio. They were excavated during the largest paleontological excavation in the Besano Formation, which was carried out under the direction of Emil Kuhn-Schnyder from the University of Zürich from 1950 to 1968.

Material and methods

Four specimens were collected from laminated dolomites (PIMUZ 29942, 31220, 37902, 38668) and one from a light grey dolomite bed (PIMUZ 37903) of the Besano Formation. With the exception of the very poorly preserved specimen PIMUZ 31220 (imprint assigned to Nautilida with some reservation, insufficient for taxonomic identification), all specimens are preserved as more or less deformed internal molds (Steinkern) and are only partially covered with recrystallized shell. Specimen PIMUZ 37903 is preserved as internal mold and partially as external mold and a silicon rubber cast was produced. From specimen PIMUZ 29942, partially included in the matrix, a plaster cast replica was produced to allow a more complete illustration of the ventral view and a reconstruction of the whorl section. Simplified drawings were made for the specimens PIMUZ 37902 and PIMUZ 29942, showing the shell characters. These two specimens are on display at the Paläontologisches Museum (future Naturhistorisches Museum, University of Zurich) in Zurich, whereas PIMUZ 29942 is on long-term loan in the Museo dei fossili del Monte San Giorgio, Meride (Canton Ticino).

Abbreviations: The dimensions are always given in mm: dm = measured diameter; wh = maximum whorl height at given diameter; ww = maximum width at given diameter; uw = width of umbilicus at given diameter.

Systematic paleontology

For the systematic descriptions, the works of Kummel (1953, 1964), Mundlos et al. (1984), Dzik (1984) and Perez-Valera et al. (2017) have been used.

Class Cephalopoda Cuvier, 1797

Subclass Nautiloidea Agassiz, 1847

Suborder Tainoceratina Shimansky, 1957.

Family Tainoceratidae Hyatt, 1883

Genus *Enoploceras* Hyatt in Zittel, 1900.

Type species. *Nautilus wulfeni* Mojsisovics, 1873

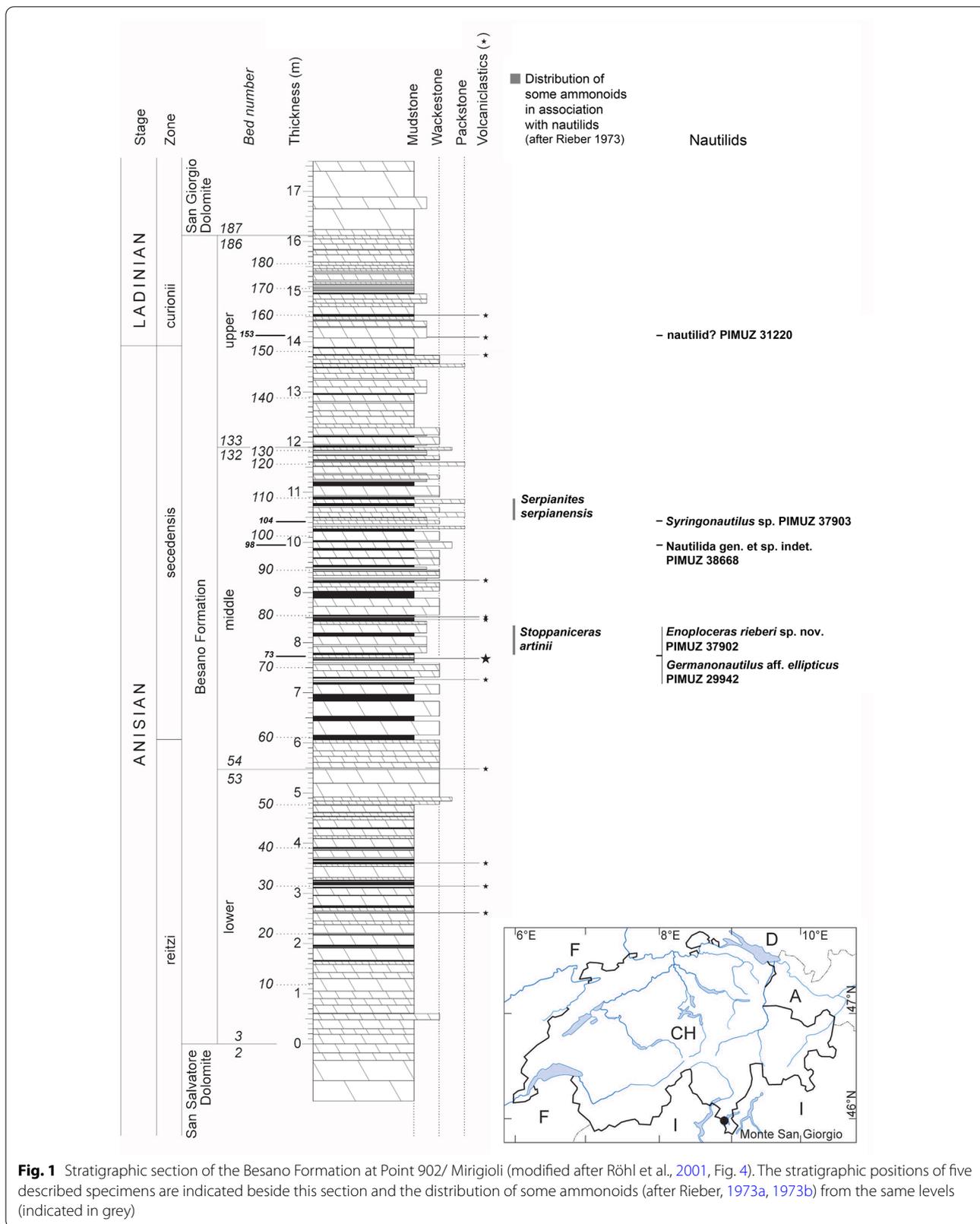


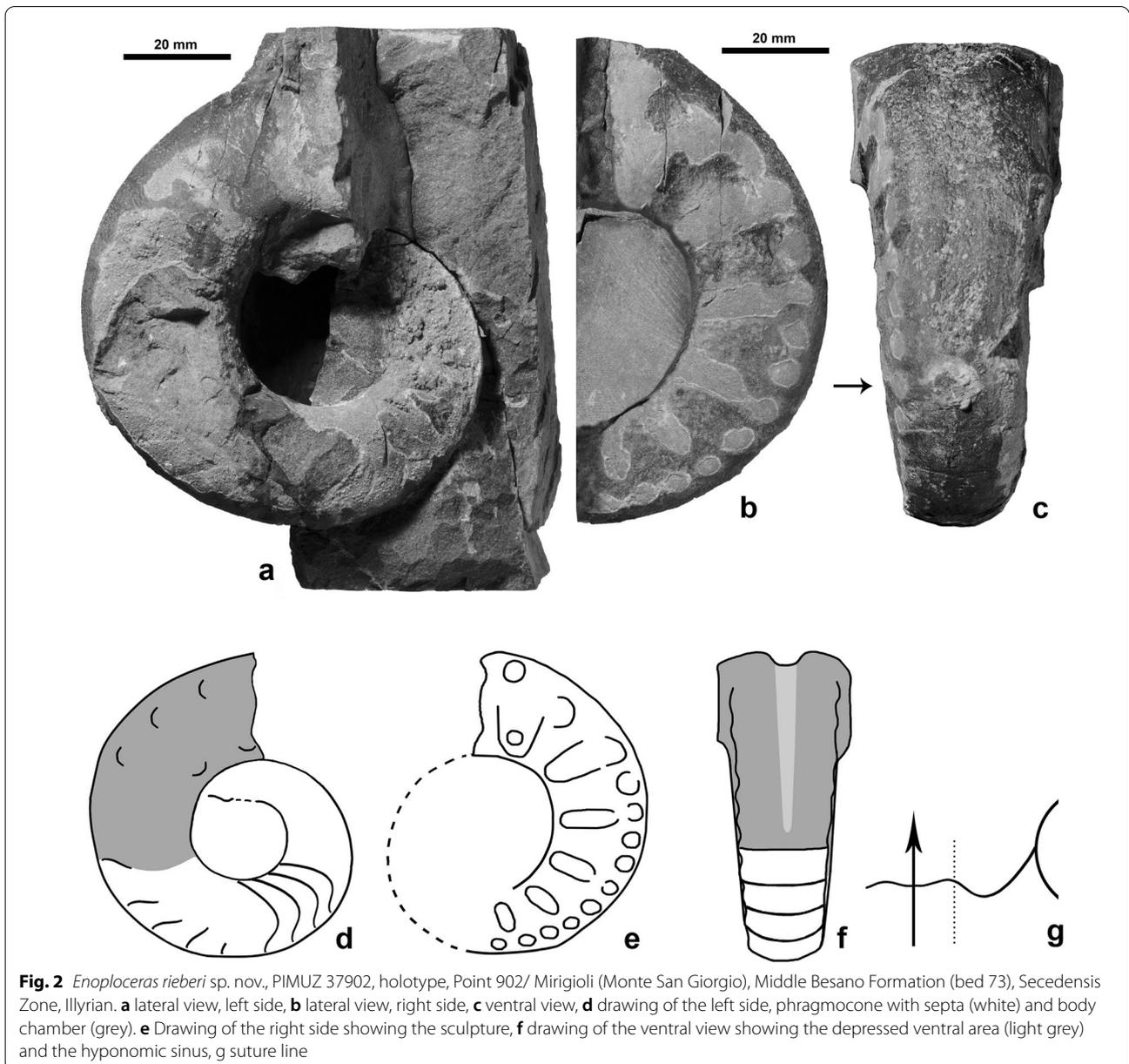
Fig. 1 Stratigraphic section of the Besano Formation at Point 902/ Mirigioli (modified after Röhl et al., 2001, Fig. 4). The stratigraphic positions of five described specimens are indicated beside this section and the distribution of some ammonoids (after Rieber, 1973a, 1973b) from the same levels (indicated in grey)

Systematic position: *Enoploceras* was previously considered as subgenus of *Pleuromutilus* Mojsisovics, 1882 by Kummel (1953), later as a genus by Kummel (1964). Dzik discussed the phylogeny of *Pleuromutilus* and the possibility that it is a polyphyletic taxon composed of several evolutionary lineages that branched independently. In his phylogenetic reconstruction (Dzik, 1984, p. 162, Fig. 62), the type species *Enoploceras wulfeni* (no. 77) evolved from *Metacoceras* Hyatt, 1883, without direct relationship with *Pleuromutilus*, while in his proposed systematics (Dzik, 1984, p. 173), he considers *Enoploceras* a junior synonym of *Metacoceras*.

Enoploceras rieberi sp. nov. ZooBank LSID: urn:lsid:zoo bank.org:act:AFE292E-55CF-4E36-8BB1-05AF39386182, Fig. 2 a–g.

Derivatio nominis Honoring the paleontologist Hans Rieber (PIMUZ), who has contributed so much to the knowledge of fossils from Monte San Giorgio.

Holotype Specimen PIMUZ 37902, preserved as internal mold (Steinkern), partially covered by shell (right side) and partially included in the matrix.



Locus typicus Point 902/ Mirigioli, Meride, Ticino, Switzerland.

Stratum typicum Middle Besano Formation, Illyrian, Secedensis Zone (laminated dolostone, bed 73).

Diagnosis *Enoploceras* with evolute to advolute conch with a very low whorl overlap and subquadrate whorl section; umbilicus wide and shallow; umbilical walls subvertical; flanks flat, irregularly sculptured. Umbilical nodes fused with the consecutive massive ribs. Number of marginal nodes twice as many as the umbilical nodes. Venter arched, with shallow central furrow at mature stage. Suture simple, with broadly arched lateral lobe, almost straight on the venter.

Measurements $dm = 88.5$ mm ($dm_2 = 57.9$ mm), $wh = 31.5$ mm, $uw = 34.5$ mm, $ww = 37$ mm.

Description Evolute to advolute conch, with the last whorl only slightly embracing the former volution and a whorl expansion rate of about 2.3. The preserved conch comprises slightly more than the last whorl. The umbilicus is moderately wide ($uw/dm = 0.39$) and shallow. The whorl section, wider than high, is subquadrate to subrectangular, with the maximum width at the umbilical shoulders. The ventral area is convex, arched, with rounded but distinct ventrolateral shoulders. On the body chamber, from the diameter of 77 mm, the ventral area bears a longitudinal shallow depression. This depression corresponds to a rounded and shallow hyponomic sinus at the aperture. The flanks are slightly convex, subparallel. The umbilical shoulders are angular and rounded. The umbilical wall is subvertical. The ribs on the flanks are simple, straight, massive and scarcely elevated. These ribs start from the umbilical shoulder with a small swelling, fading before reaching the ventrolateral margin, where they meet a row of rounded nodes. In the last half-whorl, there are 6 irregularly spaced ribs, whereas the marginal nodes are 13. The nodes increase in size through ontogeny, but only the last marginal node and the last two ribs are well marked and bear true umbilical nodes. The growth lines as well as the siphuncle are not preserved. The suture line shows a shallow rounded lobe on the flank, while it is almost straight on the venter. The body chamber corresponds to 100° of volution. The recrystallized shell has a coarse surface.

Discussion The new species, based on a single specimen, shows similarities with some other species documented in the literature, which belong to the Triassic genus *Enoploceras*. According to Kummel (1953), the whorl cross section of *Enoploceras* is slightly wider than

high, subquadratic, with ventral and umbilical shoulders sharply rounded, with flattened venter, flanks and umbilical walls at maturity. The present specimen is probably closely related to the type species of *Enoploceras*, *Nautilus wulfeni* Mojsisovics, 1873, from the Carnian of Hallstatt (Austria). The type species, however, is slightly more involute ($uw/dm = 0.27$) with a more steeply inclined umbilical wall and with a lower number of marginal nodes connected to the umbilical nodes by feeble radial ribs.

Enoploceras rieberi sp. nov. resembles *Pleuromutilus semseyi* Frech, 1911 (Carnian, Hungary), assigned by Kummel (1953) to *Enoploceras*, which has a similar umbilical width ($uw/dm = 0.38$) and bears massive irregular ribs. However, this species has a higher number of ribs per whorl, without marginal nodes separated from the ribs, a wider whorl section and less rounded lateral lobe. This species was previously described by Diener (1901) as "*Pleuromutilus cf. tommasii*" (Parona, 1889). The specimen described by Diener (1901: pl. 1, Fig. 2a, b) shows sigmoidal ribs and the venter joins the convex flank at a longitudinal keel. In the original specimen described by Parona (1889: pl. 1, Fig. 2; Carnian, Lombardy, Italy) as "*Nautilus (Trematodiscus) Tommasii*", the umbilical nodes are connected by ribs to the corresponding marginal nodes. The specimen figured by Diener (1901) is probably related to forms such as *Nautilus rectangularis* Hauer, 1855 (= *Trematodiscus rectangularis* in Mojsisovics, 1882 = *Thuringionutilus rectangularis* in Mojsisovics, 1902 = *Aulametacoceras rectangulare* in Kummel, 1953).

Other species, similar to the present one, assigned to *Enoploceras* by Kummel (1953) are considered here. *Nautilus planilateratus* Hauer, 1860, *Nautilus fischeri* Mojsisovics, 1873, *Pleuromutilus gaudryi* Mojsisovics, 1902 (see also Jurkovšek et al., 2002, Carnian, Slovenia), *Pleuromutilus lepsiusi* Mojsisovics, 1902, *P. (Enoploceras) ausseanus* Diener, 1919, and *P. (Enoploceras) lepsiusiformis* Diener, 1919 have been described from the Carnian of Hallstatt. These species are characterized by more involute conchs, three or four rows of nodes, and keels on the venter in some species. *Pleuromutilus tibeticus* Mojsisovics, 1896 from the Carnian of the Himalayas, is more involute, with an octagonal whorl section and a venter area defined by two low keels. *Pleuromutilus kossmati* Diener, 1901 from the Carnian of Hungary, has a higher number of ribs, four rows of nodes on the ribs and a marginal keel. From the Upper Triassic of Timor, some species were described by Kieslinger (1924): *Pleuromutilus (Enoploceras) molengraaffi* Kieslinger, 1924; *P. (Enoploceras) lepsiusi* Mojsisovics, 1902; *P. (Enoploceras) malayicus* Welter, 1914; *P. (Enoploceras) wulfeniformis* Kieslinger, 1924; *P. (Enoploceras) pseudoplanilateratus*

Kieslinger, 1924; *P. nov. sp. ex aff. wulfeni* (Mojsisovics) Kieslinger, 1924; *P. (Enoploceras) pseudowulfeni* Kieslinger, 1924. These species differ notably from the present one in their peculiar sculpture on the flanks, which consists of sigmoid ribs or three rows of strong nodes, while some other species are quite smooth.

Pleuromutilus (Enoploceras) newelli Kummel, 1953 from the Lower Triassic (Olenekian) of Idaho, U.S.A., has a much wider whorl section, is more rapidly expanding and has no ribs. It represents the only Lower Triassic species belonging to *Enoploceras*, while the other documented species come from the Upper Triassic.

There are three additional species sharing some character states quite with the new species, which are, however, not considered to belong to *Enoploceras* by the authors. *Pleuromutilus rollieri* Arthaber, 1896 from the Anisian of Tiefengraben (Austria) has a higher number of ribs, which are always connected to the small marginal nodes, and has a deeper lateral lobe. *Anoploceras qinghaiense* He, 1986 from the Anisian (Aegean) of China (Mt. Burhan Budai, Central Qinghai) has a trapezoidal whorl section, a higher number of ribs, and an almost smooth mature conch. The specimen figured by Gliwa et al., 2020 (fig. 17b, Lower Julfa Formation, Upper Permian, Iran) classified as *Pleuromutilus sp.* (specimen MB.C.29347) shows a quite similar overall shape. However, not all characters are visible on that incomplete specimen.

Enoploceras rieberi sp. nov. is characterized by its unusual lateral sculpture: there are twice as many marginal nodes as umbilical nodes; these umbilical nodes are fused with the consecutive massive ribs, which fade before they reach the marginal nodes. This particular feature is not present in other species of *Enoploceras* documented in the literature and discussed here. The present new species appears to be the only Middle Triassic representative of the genus *Enoploceras*.

Genus *Germanonutilus* Mojsisovics, 1902 (rev. Mundlos et al., 1984).

Type species. *Nautilus bidorsatus* Schlotheim, 1832.

Systematic position: following Dzik (1984), this genus might have evolved from *Domatoceras* Hyatt, 1891 (family Grypoceratidae Hyatt in Zittel, 1900) rather than *Metacoceras* Hyatt, 1883 (family Tainoceratidae), such as traditionally assumed in literature. However, Mundlos et al. (1984) and Perez-Valera et al., (2017: p. 176) include *Germanonutilus* again in the family Tainoceratidae and define its characters. Following these last authors, *Germanonutilus* differs from *Metacoceras* and from *Mojsvaroceras* in the reduced sculpture pattern, which is either absent or limited to shallow growth lines and ventrolateral nodes, and also in the subtrapezoidal whorl

section with tabular or slightly concave and wide venter, as well as a greater rate of whorl overlap.

Germanonutilus aff. ellipticus Parnes, 1986 Fig. 3 a–f.

Material Specimen PIMUZ 29942, a poorly preserved natural mold of the living chamber, filled by carbonate sediment; with slightly deformed coiling, partially included in the matrix. The original shell is dissolved, with its morphology preserved on the ventral area.

Measurements At maximum dm (deformed) of 95 mm other dimensions are: wh=40 mm, uw=33 mm, ww=75 mm; at dm of 70 mm other dimensions are: wh=34 mm, uw=24 mm, ww=69 mm.

Locality and age Valle Stelle (Meride, Canton Ticino). Middle Besano Formation, Illyrian, Secedensis Zone (recovered from a laminated bituminous dolostone in a gallery of the former mine; correlating to bed 73). In association with an imprint of an ammonoid (Fig. 4) classified here as *Stoppaniceras cf. artinii* (Airaghi, 1912a, 1912b).

Description Evolute shell (uw/dm=0.34), consisting of about the last whorl. The umbilicus is broad, without any preserved structure. Siphuncle and suture line are not visible. The whorl section, wider than high, is subelliptical, with the maximum width at the umbilical shoulders. The ventral area is convex, widely arched, with more or less rounded distinct ventrolateral shoulders. The flanks are rounded and convex. The umbilical shoulder passes to the inclined umbilical wall forming a continuous curve. The growth lines are observable only on the ventral area and form a wide and deep hyponomic sinus.

Discussion The genus *Germanonutilus* is usually characterized by a narrow umbilicus and trapezoidal whorl sections, with more or less flattened or depressed venter. The specimen described here shows similarities in particular with *Germanonutilus ellipticus* Parnes, 1986. This species was described by Parnes (1986) from the Middle Triassic of Israel (Negev, Saharonim Formation, Lower Ladinian). It has a relatively wide umbilicus, a well-rounded elliptical whorl section, which is wider than high, and a regularly arched convex venter. The present specimen is more evolute (uw/dm=0.34 at dm=70 mm) than *Germanonutilus ellipticus* (uw/dm=0.24 at dm=80 mm, Parnes 1986 showing a wider umbilicus

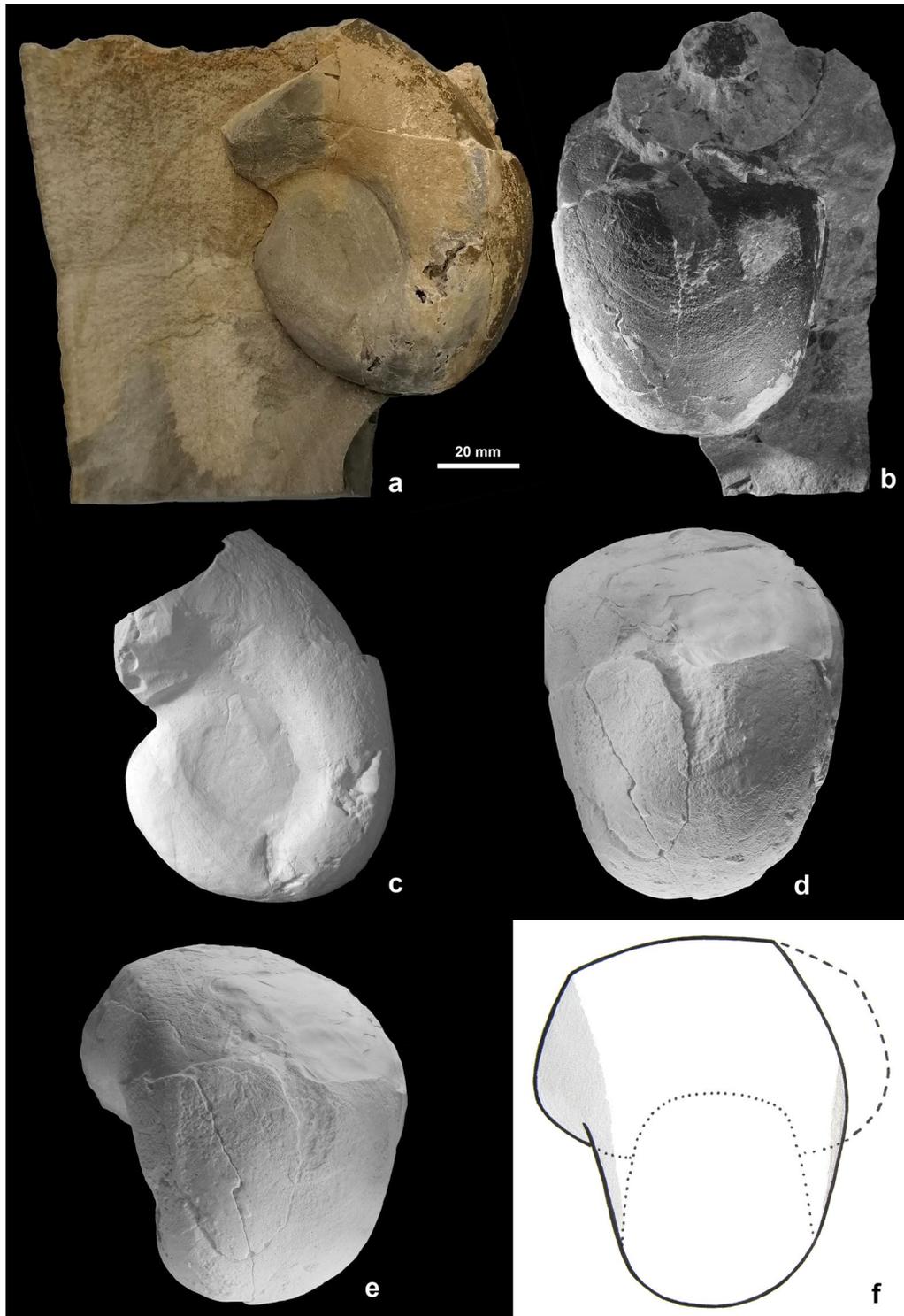


Fig. 3 *Germanonautilus* aff. *ellipticus* Parnes, 1986, PIMUZ 29942, Valle Stelle/Tre Fontane (Monte San Giorgio), Middle Besano Formation (bed 73), Secedensis Zone, Illyrian: **a** original specimen partially included in the matrix, lateral view, **b** ventral view, associated with an external mold of *Stoppaniceras* cf. *artinii*, **c** plaster cast replica of the same specimen, lateral view, **d** plaster cast replica of the same specimen, ventral view, **e** plaster cast replica of the same specimen, ventrolateral view, **f** drawing of the ventral view showing the hypothetical whorl section (in grey the flank areas)



Fig. 4 *Stoppaniceras cf. artinii* (Airaghi, 1912a, 1912b) associated with PIMUZ 29942. Image obtained producing positive silicon cast from negative external mold

and a last whorl only slightly embracing the former volution. Up to now, forms similar to *G. ellipticus* were not documented in Southern Alps. *Germanonautilus brooksi*

Smith, 1927 from Alaska (Carnian) described by Kummel (1953), shows a well-rounded elliptical whorl section and a wide umbilicus. Following Kummel (1953, p. 29). the specimens described originally by Smith are small conchs probably corresponding to immature growth stages, with deeply embracing whorls and more distinct umbilical shoulders.

Family Syringonautilidae Mojsisovics, 1902

Genus *Syringonautilus* Mojsisovics, 1902

Type species. *Nautilus lilianus* Mojsisovics, 1882

Syringonautilus sp. Figure 5 a–c.

Material Specimen PIMUZ 37903, partially preserved as internal mold (about the last half-whorl, fractured and slightly deformed), partially as external mold from which a silicon cast was produced.

Measurements At maximum dm (deformed) of 44.5 mm other dimensions are: wh = 23.5 mm, uw = 10 mm, ww = 25 mm.

Locality and age Point 902/ Mirigioli (Meride, Canton Ticino). Middle Besano Formation, Illyrian, Secedensis Zone (bed 104, light grey dolomite).

Description The specimen consists of about the last whorl, lacking its inner whorls. It shows a rapidly expanding smooth conch, with whorls deeply embracing. The whorl section is more or less elliptical. The anterior whorl section is higher than wide, well rounded and with the maximum width at the umbilical shoulders.

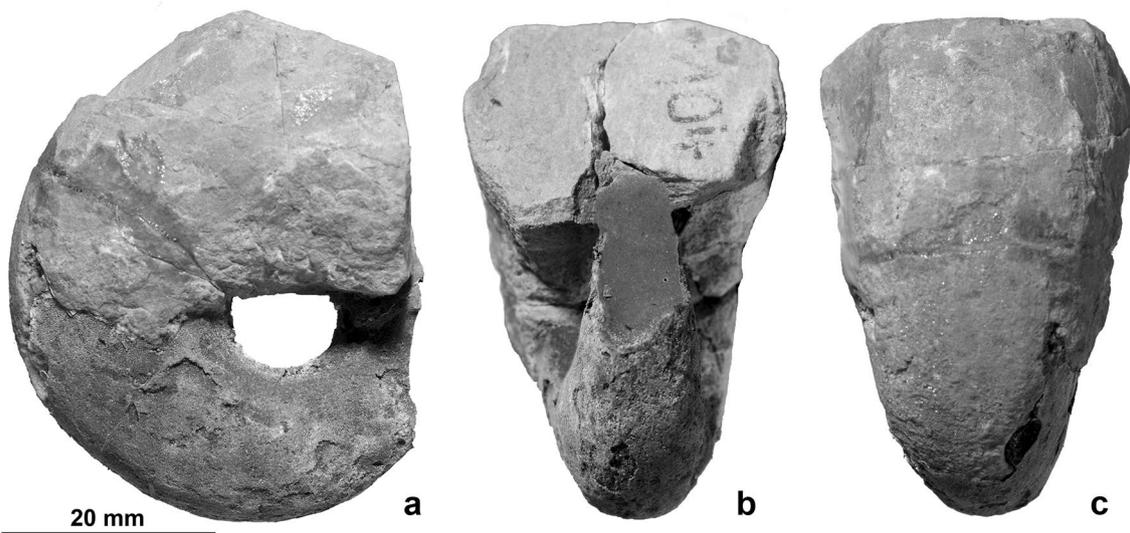


Fig. 5 *Syringonautilus sp.*, PIMUZ 37903, P. 902/Mirigioli (Monte San Giorgio), Middle Besano Formation (bed 104), uppermost Anisian: **a** lateral view, left side, **b** oral view, **c** ventral view

The umbilical shoulder passes to the inclined umbilical wall forming a continuous curve. The flanks are convex, but slightly flattened, converging externally. In the last half-whorl, the ventrolateral shoulder becomes angularly rounded and corresponds to the maximum width of whorl. The venter is convex and rounded, slightly flattened. The other characters are not observable.

Discussion This poorly preserved specimen shows similarities with species of *Syringonautilus* (e.g., Mojsisovics, 1882; Pieroni, 2020) from the Middle Triassic of the Alps. Following Kummel (1953, p. 60), *Syringonautilus* can be distinguished from *Syringoceras* only by the position of its siphuncle: while in *Syringonautilus* it is subcentral, in *Syringoceras* it is nearly marginal. However, this character is still unknown in many species, and it is not visible in the present specimen. The whorl section of *Syringoceras* is usually slightly compressed (Kummel, 1953, p. 61) and more expanded in *Syringonautilus* as in the present specimen. Among the species belonging to *Syringonautilus* documented in literature, *Syringonautilus bosnensis* (Hauer, 1892, p. 6 [254], pl. 1, Fig. 3a–c; Trinodosus Zone of Han Bulog, Bosnia) shares the shape of whorl section and the umbilical width with the specimen here described. The whorls of *Syringonautilus lilianus*

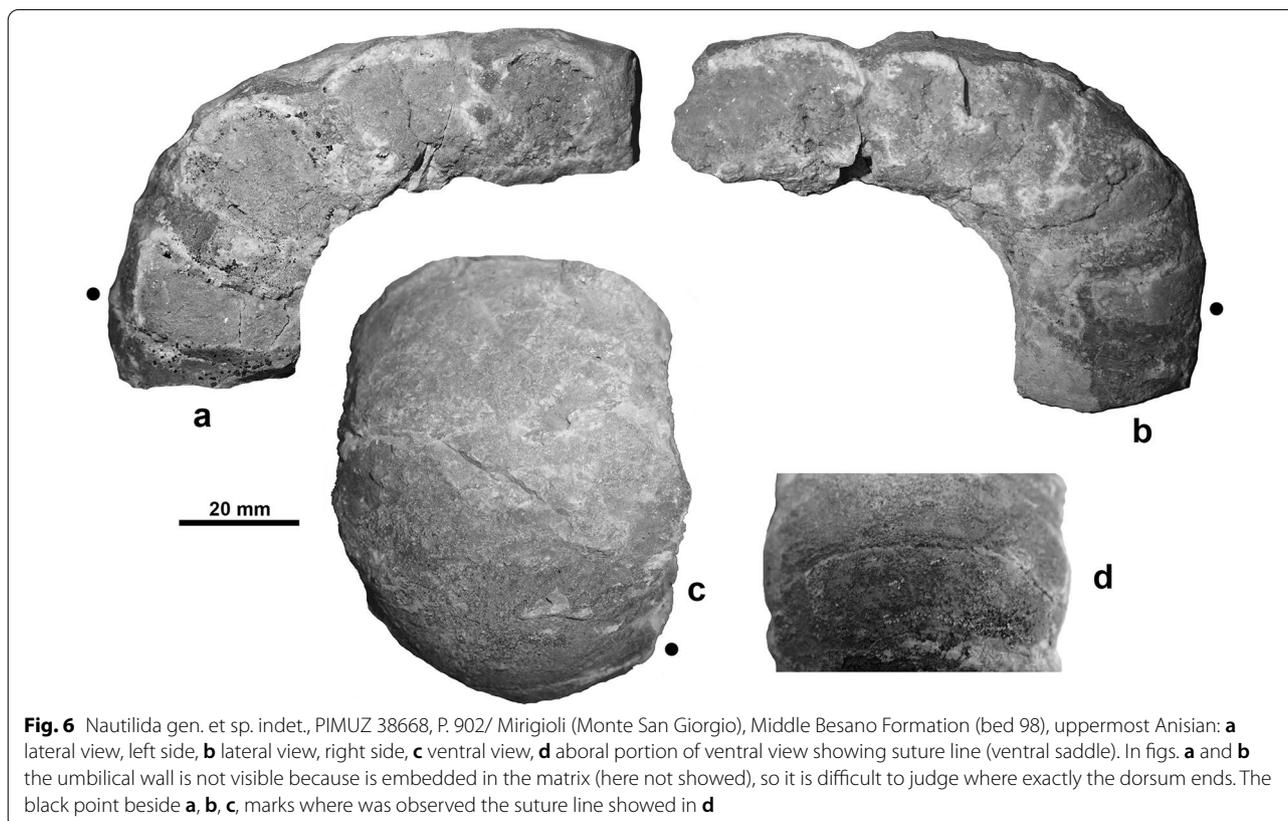
(Mojsisovics, 1882) are less rapidly expanding and the conch has a wider umbilicus and circular to subquadrate whorl sections. *Syringonautilus* cf. *lilianus* (Mojsisovics, 1882) from Rasa di Varese (Varese, Lombardy, Rasa Dolomite, San Salvatore Dolomite, Reitzi Zone sup.) was described by Pieroni (2011, p. 57, pl. 2 cefalopodi, Fig. 3). It shows a more subquadrate whorl section and is more evolute.

Nautilida gen. et sp. indet. Figure 6 a–d.

Material Specimen PIMUZ 38668, internal and external mold of a poorly preserved phragmocone (about half a whorl, fractured and deformed), with some recrystallized shell remains.

Measurements Deformed preserved portion with maximum dm of 105 mm, estimate dm (at this position) = 125, estimate wh = 29 mm aperturally, estimate wh = 23 mm apically, ww = 58 mm aperturally, ww = 51 mm apically.

Locality and age Point 902/ Mirigioli (Meride, Canton Ticino). Middle Besano Formation, Illyrian, Secedensis Zone (bed 98, laminated bituminous dolostone).



Description The specimen consists of about half-whorl, lacking inner whorls and umbilical wall not visible (included in the matrix?). It has rather rapidly expanding whorls, with strongly depressed whorl sections (estimate $w/w_h = 2$). Some blunt ribs are visible on the flank. The suture line shows a shallow rounded lobe on the flank, while it forms a shallow arched ventral saddle.

Discussion This specimen represents an additional taxon, although it is too poorly preserved for identification even on family level. Among the Middle Triassic Nautilida from the Tethys, strongly depressed whorl section with blunt lateral ribs and rapidly expanding whorls occur in some species of *Mojsvaroceras* Hyatt, 1883 (see *M. gianii* Pieroni & Prinoth, 2021). The ventral saddle is a character known from the family Syringonautilidae. Their conchs are usually without ribs (in this family, only *Weitschatinautilus* Engeser, 1995 bears ribs in the mature stage), and in the genus *Holconautilus* Mojsisovics, 1902 (Tainoceratidae), the whorls are usually expanding more slowly.

Discussion

Among the five nautilid specimens described herein from the Besano Formation of Ticino, the three best preserved specimens belong to three genera of Triassic nautilids, which are geographically widespread in the Tethyan region. *Germanonautilus* and *Syringonautilus* are well known from the Middle Triassic of the north-western Tethys and of the Sephardic Paleobioprovince (e.g., Parnes 1986). The new species *Enoploceras rieberi* n. sp. is the first occurrence of the genus *Enoploceras* in the Middle Triassic. *Pleuromautilus* (*Enoploceras*) *newelli* Kummel, 1953 from the Olenekian of Idaho, U.S.A., represents the single North American species and the only one from the Lower Triassic belonging to the genus *Enoploceras*, which is better documented in the Upper Triassic (see Kummel, 1953, p. 41). This new species from the Besano Formation thus fills a big stratigraphic gap.

The Besano Formation cephalopod fauna (e.g., Airaghi, 1912a, 1912b; Rieber, 1973a, 1973b) is characterized by species, which are absent or rare in other reported assemblages from the Middle Triassic of the Southern Alps. They represent species apparently adapted to a special environment in a restricted intra-platform basin, characterized by anoxic conditions (Bernasconi, 1991; Furrer, 1995; Röhl et al., 2001; Schatz, 2005a). During the Late Anisian, the Germanic Basin was connected to the Tethys via the East Carpathian gate, the Silesian Moravian gate and the Burgundian gate (late Anisian to early Ladinian; Bachmann et al., 2010), while the Sephardic Realm was rather open to the Tethys (Escudero-Mozo et al., 2015; Pieroni & Prinoth, 2021). Species closely related to forms from the Sephardic province were found in the

time equivalent shallow water carbonates of the middle San Salvatore Dolomite at Rasa di Varese, East of Monte San Giorgio (*Mojsvaroceras gianii* Pieroni & Prinoth, 2021). The occurrence of species such as *Germanonautilus* aff. *ellipticus* Parnes, 1986 in the Besano Formation might confirm a faunal exchange with the Tethys and the Sephardic Paleobioprovince because this species looks similar to taxa documented only from Israel. Moreover, migrations and links between Sephardic nautilid faunas and Tethyan communities were documented by Pieroni (2020) from the Esino Limestone of Val Brembana (see also Klug et al., 2005).

The nautilid taxa from Monte San Giorgio likely derived from taxa documented in these diverse paleobioprovinces. However, up to now, none of the species described here was documented in the other north-western Tethyan Middle Triassic formations of the Southern Alps. *Germanonautilus* aff. *ellipticus* Parnes, 1986 can be considered only with some reservation as similar to the Sephardic species erected by Parnes (1986 and references in his paper). Presuming that the specimens here described did not drift far from their habitat as empty conchs (Yacobucci, 2018), it can be assumed that these species were adapted to the special environment of the Besano-Monte San Giorgio basin.

Among living *Nautilus*, populations are relatively isolated from one another (Sinclair et al., 2007, 2011; Vandepas et al., 2016). Extant nautilids are largely nektobenthic/demersal (do not swim far above the sea floor) and have rarely been observed in mid-water (Vandepas et al., 2016). The paleogeographic context and the lifestyle of nautilids are plausible explanations for the extreme rarity and biodiversity of the fauna portrayed herein.

Conclusions

The fauna described here differs from other Tethyan faunas and might be endemic of the Besano-Monte San Giorgio basin. Despite the extreme scarcity of nautilids in the Besano Formation with only five specimens from a century of fieldwork, they are surprisingly diverse, with all specimens belonging to different genera. The small fauna from Monte San Giorgio represents an important contribution to the taxonomy and stratigraphic and biogeographic distribution of the relatively poorly studied Triassic Nautilida.

The new species *Enoploceras rieberi* n. sp. is described. It currently represents the only occurrence of the genus *Enoploceras* in the Middle Triassic and thus provides crucial new information about the evolutionary continuity in this genus between the oldest Lower Triassic species (Olenekian, Idaho, U.S.A. with only one occurrence) and the better known and diversified Upper Triassic species. In conclusion, biodiversity, migrations and phylogeny

of Tethyan Middle Triassic nautilids, in particular from the Southern Alps, are still poorly known and every new occurrence has a great potential to improve our understanding of their paleobiology.

Acknowledgements

The author is indebted to Heinz Furrer and Christian Klug (Zürich) as well as to Luca Zulliger (Museo dei Fossili del Monte San Giorgio, Meride) for the permission to study the specimens described here. Rosi Roth (Zürich) is thanked for some photographs (specimens: PIMUZ 37902, PIMUZ 37903). Heinz Furrer helped with stratigraphic information and read a first version of the manuscript. I would like to thank Dieter Korn (Museum für Naturkunde Berlin) and Alexander Pohle (Zürich) for their helpful reviews. Christian Klug worked through the revised manuscript and improved the English. Alexander Pohle is also thanked for information and photos of the specimens PIMUZ 31220 and PIMUZ 38668.

Author contributions

VP designed and wrote the study, produced the figures, and identified all the material described herein. VP photographed the specimen PIMUZ 29942 classified as *Germanonutilus* aff. *ellipticus* Parnes. The author read and approved the final manuscript.

Funding

Not applicable.

Availability of data and materials

The material described and illustrated here comes from the collection of Besano Formation fossils in the Paläontologisches Museum der Universität Zürich (PIMUZ). Specimens PIMUZ 29942 and PIMUZ 37903 are on display in this museum, whereas PIMUZ 29942 is exhibited on long-term loan in the Museo dei fossili del Monte San Giorgio, Meride (Canton Ticino).

Declarations

Competing interests

The author declares that he has no competing interests.

Received: 12 September 2022 Accepted: 28 November 2022

Published online: 23 December 2022

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