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Camunites, a new genus of Hungaritinae (Ammonoidea, Ceratitida) and its meaning for the Anisian (Middle Triassic) biostratigraphy

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ABSTRACT - Based on ammonoids collected in the uppermost part of the Prezzo Limestone (middle Illyrian, Anisian) in the Losine section (Camonica valley, Eastern Lombardy, Southern Alps), the new genus *Camunites* is described. *Camunites* gen. nov. comprises highly involute ceratitids characterized by a phragmocone with wedge-shaped whorl section, a distinct but rounded keel, a juvenile shell without nodes, and a smooth ventrolateral margin. The flanks show serried, weak, and scarcely elevated or barely visible ribs. The genus comprises *Ceratites inconstans* Reis, 1901, selected as the type species, and *Ceratites lenis* Hauer, 1896. We believe that the first appearance of *Camunites* (i.e. *C. inconstans,* here considered as the forerunner of the Subfamily Hungaritinae) can be used to define the base of the *Hungarites* Zone - *reitzi* Subzone (upper Anisian).

Keywords: Middle Triassic; Illyrian; NE Italy; Southern Alps; Lombardy; Ammonoids; biostratigraphy.

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1. INTRODUCTION

Reis (1901, 1907) described a Middle Triassic ammonoid fauna collected in isolated blocks attributable to the Wetterstein Limestone in various localities around the Zugspitz Massif (Bavarian Alps, Austria-Germany border). This fauna appears as a heterogeneous assemblage, both from a taxonomic and stratigraphic points of view. This 'old' collection is stored at the Bayerische Staatssammlung für Paläontologie und Historische Geologie of München.

The direct comparison between this 'old' collection and newly sampled specimens coming from stratigraphic units of the Southern Alps, collected bed by bed, allowed us to clarify the meaning of some of the taxa described by Reis. The comparison with specimens collected in the Anisian carbonate platforms (Illyrian, Dolomites) of the Latemar and Marmolada massifs (partly in Manfrin et al., 2005) allowed us to clarify and revise the taxonomy of multiple taxa:

a) the synonymy between *Ceratites bavaricus* Reis, 1901 (pl. 2, 19-23) and *Latemarites latemarensis* Brack and Rieber 1993. Later on, with the new combination as *Latemarites bavaricus*, the taxon was also reported in the Balaton Highland, Hungary (Vörös, 2018);

b) the synonymy between *Ceratites bavaricus* var. *crassulus* Reis, 1901 (pl. 2, 24) and *Latemarites bavaricus*;

c) the attribution of the specimens described by Reis (1907, pl. 2, 9, pl. 3: 1) as *Beyrichites Reuttensis* Beyr. to *Esinoceras tozer*i Fantini Sestini, 1996;

d) the attribution of *Beyrichites interplicatus* Reis, 1901 (pl. 6, 14-16) and *Norites plicatus* Reis, 1901 (pl. 4, 20-22) to the genus *Esinoceras*;

e) the identification of *Beyrichites Emmrichi* Mojs. (Reis, 1901, pl. 6, 19, pl. 7, 32) and *Beyrichites Emmrichi* var. *lateumbilicatus* Reis, 1907 as *Parasturia emmrichi* (Mojsisovics, 1882);

f) the attribution of *Ceratites spiculifer* Reis, 1907 (pl. 1, 19) to the genus *Reitziites*, even if in open nomenclature;

g) the attribution of *Ceratites Wettersteinensis* Reis, 1907 (pl. I, 17) to the genus *Parakellnerites*.

Another problematic species, *Ceratites inconstans* Reis, 1901 (pl. III, 4-6 only) had been identified in the Prezzo Limestone of the Losine section (Eastern Lombardy) and provisionally attributed with open nomenclature to the genus *Hungarites* (Mietto and Manfrin, 1995). Later on, the species was also reported, in the same stratigraphic position, in the Balaton Highland (Vörös et al., 1996, 2003, 2009; Vörös, 1998). Therefore, the revision of the Reis' collection made it possible to, at least, partly clarify the taxonomic value of some of the species described by him and to establish that the Zugspitz Massif ammonoid fauna refers to a precise Illyrian (upper Anisian) biostratigraphic interval, which includes (*sensu* Mietto and Manfrin, 1995) the *reitzi* Subzone ("*Hungarites*" *inconstans;*

Reitziites ? spiculifer), the *avisianum* Subzone (*Latemarites bavaricus*) and the *crassus* Subzone (*Esinoceras* spp., *Parasturia emmrichi*). In the present paper the taxonomic and stratigraphic meaning of *"Hungarites" inconstans* is clarified, a species that is particularly significant, in our opinion, due to its correlation potential. When the efforts of the Subcommission on Triassic Stratigraphy were focused on the redefinition of the Anisian/Ladinian boundary (Gaetani, 1993, 1994), the new Losine section in Camonica valley, Brescia Prealps (Lombardy, Southern Alps, Italy) was considered by the writers of great interest. This section, ca. 8 meters thick, encompasses the boundary between the Prezzo Limestone (*sensu* Gaetani, 1970) and the basal part of the so-called "transitional beds" (*sensu* Brack and Rieber, 1986), which lie below the Knollenkalk member of the Buchenstein Formation. The new Losine section yields abundant and well-preserved ammonoids, in a biostratigraphic interval between the uppermost part of the *trinodosus* Subzone and the lowermost part of the *reitzi* Subzone (Mietto and Manfrin, 1995), the middle Illyrian (late Anisian) in age. Indeed, the base of the *reitzi* Zone/Subzone has been proposed to define the GSSP of the Ladinian (Vörös, 1987, 1988, 1993a, 1993b, 1995, 2002; Gaetani and Brack, 1993; Vörös et al., 1991, 1996, 2003), before defining the GSSP of the Ladinian with the first occurrence of *Eoprotrachyceras curionii* at Bagolino (Brack et al., 2005). Among many collected samples, several ammonoid specimens, belonging to a single species in different growth stages, were collected from five distinct beds. These ammonoids, for their morphological features, resemble representatives of Hungaritinae, but cannot be attributed to any known genus so far described. With this paper, the new Losine section is described, and chiefly based on its abundant collected material, the new genus *Camunites* is introduced, with *Ceratites inconstans* as the type species.

2. AREA DESCRIPTION

A wide area of the Southern Alps (Italy) has been subject to basinal sedimentation and strong subsidence starting from the early Illyrian (late Anisian), resulting in the deposition of the Prezzo Limestone (*sensu* Gaetani, 1970), the "transitional beds" (*sensu* Brack and Rieber, 1986) and Buchenstein Formation (Richthofen, 1860) during the late Anisian. The outcrop area of the Prezzo Limestone is limited by the Grigne mountains to the West and by the Adanà and Chiese rivers to the East, including part of the Lombardian Prealps and of the Giudicarie area.

The Prezzo Limestone is well known for its fossiliferous content, especially for the frequent occurrence of ammonoids, which have been studied since the mid-1800s, and have been the object of continuous taxonomical, biostratigraphical and chronostratigraphical revisions (Benecke, 1866; Hauer, 1865; Lepsius, 1878; Varisco, 1881; Bittner, 1881, 1883; Mojsisovics, 1869, 1882; Tommasi, 1894, 1909, 1913a, 1913b; Arthaber, 1896b; Mariani, 1906; Salomon, 1908; Speyer, 1927; Cosijn, 1928; Völcker, 1931; Boni, 1943; Riedel, 1949; Sacchi Vialli and Vai, 1958; Assereto, 1963; Assereto and Casati, 1966; Speciale, 1967; Casati and Gnaccolini, 1967; Venzo and Pelosio, 1968; Gaetani, 1969, 1979; Brack and Rieber, 1986, 1991, 1993; Kovacs et al., 1990; Balini, 1991, 1992a, 1992b, 1993, 1998; Balini et al., 1993; Mietto and Manfrin, 1995; Mietto et al., 2003; Monnet et al., 2008; Balini et al., 2010; Balini and Renesto, 2012).

The Losine section (geographical coordinates WGS 84: N45°59'18.4"; E10°18'17") is a new important locality for the ammonoids of the Prezzo Limestone (Fig. 1). It is located on the right flank of the Camonica Valley and can be reached from the village of Losine along the mountain trail to the Concarena Massif. The outcrop is located on the left side of the trail, at an elevation of 804 m, close to a municipal waterworks station. It encompasses the uppermost Prezzo Limestone and the base of the "transitional beds" (Fig. 2). The Prezzo Limestone crops out on the trail and extends for ca. 4.30 m; it is made of an alternation of black marly limestones in 19-43 cm thick beds having mainly plane joints, alternating with 20-60 cm thick dark marls and silty limestone intervals, often made of amalgamated beds. An alternation of 67 cm of dark nodular lime mudstones, in dm-scale beds, and greenish tuffite follows the succession. This interval is here attributed to the "transitional beds" (*sensu* Brack and Rieber, 1986), and the tuffite at the top of the section most probably correspond to the Ta tuffs of Brack and Rieber (1993) and Brack et al. (2005). At the top of the section, about 3 m of nodular limestone with sparse chert nodules crop out.

A system of faults at the level of the trail marks the base of the sampled portion of the Losine section. At the footwall of these faults below the trail, a succession of 3.44 m of black limestones and dark marls crop out, which is attributed to the Prezzo Limestone. Only two fossiliferous horizons were found in this interval (CM x and CM y), which yielded a homogeneous ammonoid fauna (*Schreyerites* sp., *Longobardites* sp., *Monophyllites* sp.) that cannot be related to the one bearing *Camunites inconstans* illustrated by this work. The succession then continues downward, cut by a dacitic dike, but is barren of ammonoids. Identified taxa and the amounts of specimens through bed-by-bed sampling in the Losine section are reported in table 1.

3. METHODS AND MATERIAL STUDIED

Courtesy of A. Schairer†, at that time curator of the Bayerische Staatssammlung für Paläontologie und Historische Geologie of München, we had at our disposal a lot of perfect casts of some problematic species of the Reis' collection. The quoted casts are stored at the MGP-PD.

The following abbreviations and conventional labels are used in the systematic descriptions: MGP-PD=Museo di Geologia e Paleontologia dell'Università, Padova;

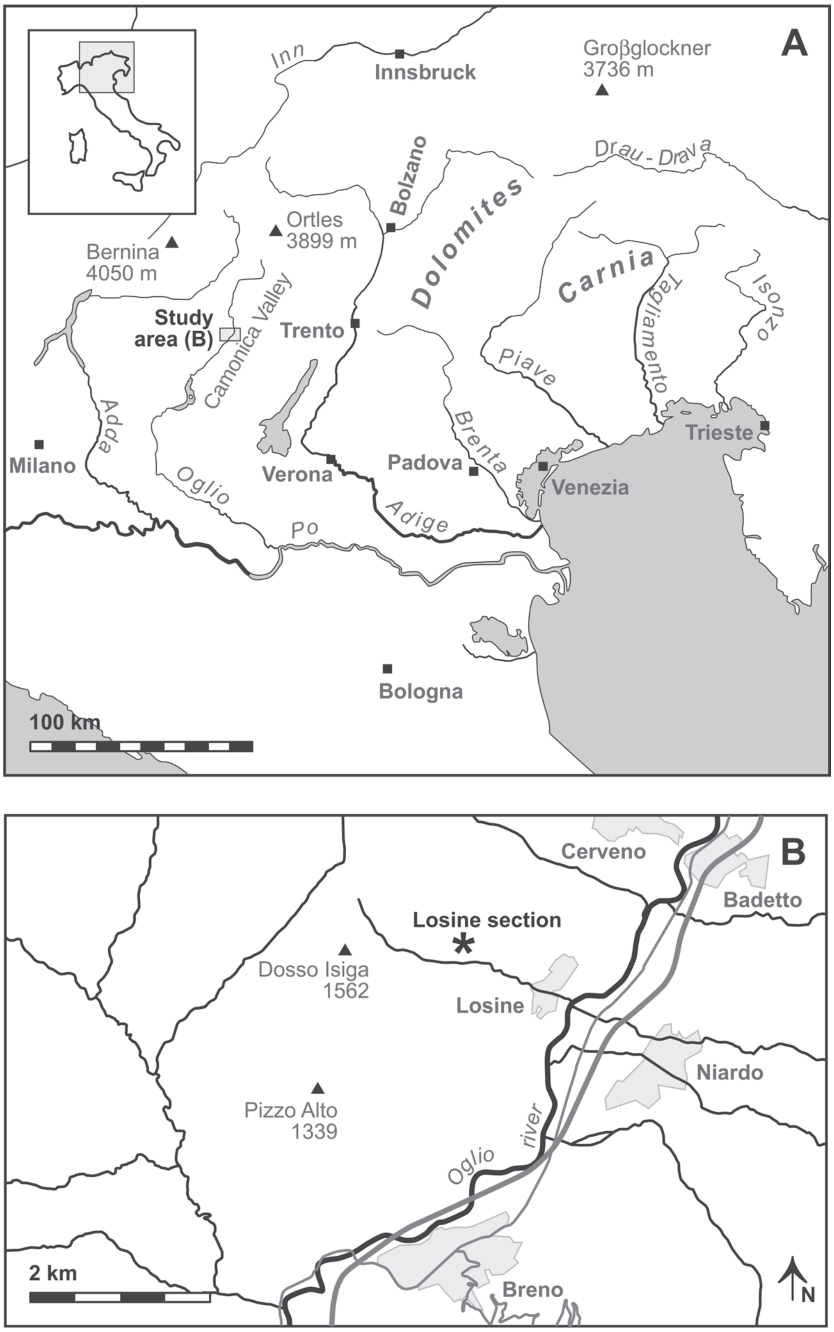

Fig. 1 - Location map of the Losine section in the Camonica Valley (Brescian Prealps).

BSPM = Bayerische Staatssammlung für Paläontologie und Historische Geologie of München.

Numbering of specimens. Every specimen directly collected by the writers (or our collaborators) and mentioned in the text is identified both by repository and by collecting numbers. Collecting numbers are composed by the acronym of the bed and the individual number of the specimen (i.e, CM 10.1=means 1^{st} specimen from the bed 10 of the Losine section). The designation "dt." refers to collections in debris. The repository number is in brackets. All the studied material is stored in the collection of the MGP-PD.

Morphological parameters (see chiefly Monnet et al., 2011, Klug et al., 2015). The measurements are given in millimeters: D1=conch diameter=H+h+U, D2=diameter measured half a whorl earlier, ah=D1-D2 (aperture height), H=max. whorl height in D1, h=min. whorl height in D1, U=umbilical width in D1, W=whorl width in H, w=whorl width in h, WSC=H/W (whorl shape compression), CWI=W/D1 (conch width index), WWI= W/H (whorl width index), UWI=U/D1 (umbilical width index), WER=$(D1/D2)^2$ (whorl expansion rate), WHER =$(H/h)^2$ (whorl height expansion rate), IZR=(H-ah)/H (imprint zone rate), H/D1=conch height index.

About the captions of the figures, the terms "right" or "left" refer to the life position of the specimens.

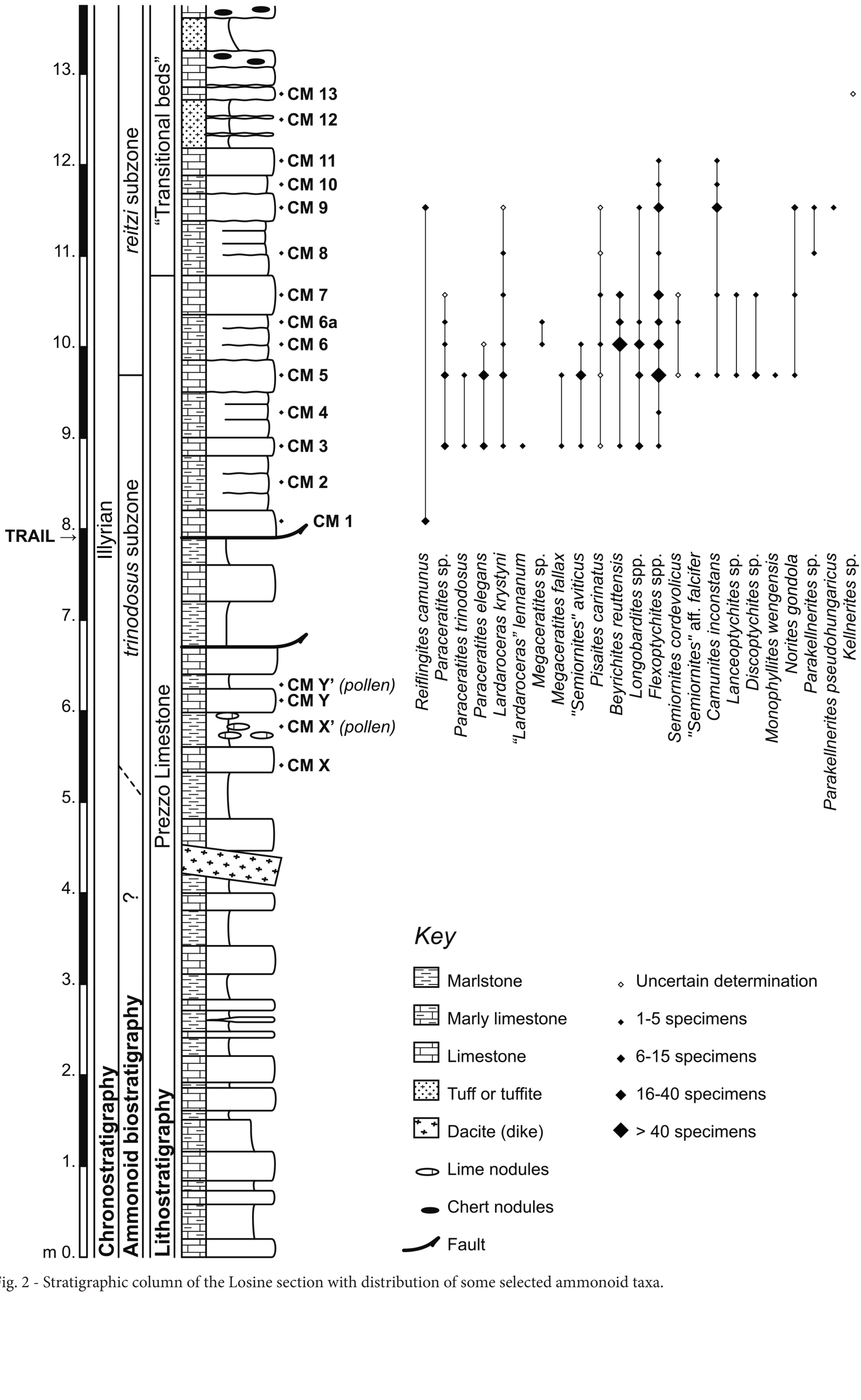

Fig. 2 - Stratigraphic column of the Losine section with distribution of some selected ammonoid taxa.

Tab. 1 - Distribution of the ammonoid fauna documented at Losine section with numbers of specimens for each species.

Beds	*Reiflingites camunus (Assereto)*	*Paraceratites sp.*	*Paraceratites trinodosus (Mojsisovics)*	*Paraceratites elegans (Mojsisovics)*	*Paraceratites cf. elegans (Mojsisovics)*	*cf. Paraceratites sp.*	*Lardaroceras sp.*	*Lardaroceras krystyni Balini*	*Lardaroceras cf. krystyni Balini*	*cf. Lardaroceras sp.*	*Megaceratites fallax Balini*	*"Seniornutes" aviticus (Mojsisovics)*	*Semiornites sp.*	*Beyrichites reuttensis (Beyrich)*	*Ceratitoids indet.*	*Longobardites sp.*	*Longobardites zsigmondyi (Böckh)*	*Longobardites brembanus Assereto & Casati*	*Longobardites cf. zsigmondyi (Böckh)*	*"Lardaroceras" lennanum (Mojsisovics)*	*Flexoptychites sp.*	*Flexoptychites flexuosus (Mojsisovics)*	*Pisaites sp.*	*Pisaites cf. carinatus Balini*	*Paraceratites cf. trinodosus (Mojsisovics)*	*"Semiornites" cf. aviticus (Mojsisovics)*	*cf. Semiornites sp.*	*Semiornites cf. cordevolicus (Mojsisovics)*	*"Semiornites" aff. falcifer (Hauer)*	*Camunites inconstans (Reis)*	*Flexoptychites cf. flexuosus (Mojsisovics)*	*Lanceoptychites sp.*	*Discoptychites sp.*	*Discoptychites suttneri (Mojsisovics)*	*Norites gondola (Mojsisovics)*	*cf. Proarcestes sp.*	*Monophyllites wengensis (Klipstein)*	*Pisaites carinatus Balini*	*Megaceratites sp.*	*Beyrichites sp.*	*Beyrichites cf. reuttensis (Beyrich)*	*Semiornites cordevolicus (Mojsisovics)*	*cf. Discoptychites sp.*	*Praepinacoceras sp.*	*Parakellnerites sp.*	*cf. Parakellnerites sp.*	*Parakellnerites pseudohungaricus (Balini)*	*Flexoptychites acutus (Mojsisovics)*	*Norites sp.*	*cf. Kellnerites sp.*	*TOTAL*	*SUBZONES*
CM 13																																																		1	1	
CM 11															1						1									1																					3	
CM 10															3							2								1																					6	
CM 9	1						1		1	1					5	2					9	24		2						28					6										1		2	2	2		87	
CM 8							1	1	1	1											1			1																					1	1					8	*reitzi*
CM 7						1	1	1					4	6	14						4	23		3				1		1		1	1		1			1					1	1							65	
CM 6A		1					1			1			1	11	4	5						7					1												4	1		1									38	
CM 6		1			3		5	3	1	2		2	3	42	6	19	11				3	16	1															1	4	1	2										126	
CM 5/6													1																																						1	
CM 5		9	1	29	11	10	6	10	27	10	1	17	3		14	5	6				1	63		2	1	5	2	1	1	1	1	1	2	5	1	1	1														248	
CM 4																					1	4																													5	
CM 3- CM 3L		6	2	14	5	2	1	5	3	1	1	1	1	3	1	1	5	3	2	2	2	2	2																												65	
CM 1	7																																																		7	*trinodosus*
	8	17	3	43	19	13	16	20	33	16	2	20	13	62	48	32	22	3	2	2	22	141	3	8	1	5	3	2	1	32	1	2	3	5	8	1	1	2	8	2	2	1	1	1	2	1	2	2	2	1	660	

3.1. SYSTEMATIC PALEONTOLOGY

Subclass Ammonoidea Zittel, 1884
Order Ceratitida Hyatt, 1884
Superfamily Ceratitoidea Mojsisovics, 1879a
Family Ceratitidae Mojsisovics, 1879a
Subfamily Hungaritinae Waagen, 1895, amended

Description: the quoted Subfamily included those genera that lack the classic bi-trinodose flank nodes formula. The occurrence of roughly arranged, barely visible nodes, or frilled swellings in the ventrolateral position quickly disappears in the phragmocone during phylogeny. These features are replaced by smooth ventrolateral shoulders. Whorl section wedged-shaped or subrectangular. Venter more or less distinctly carinate. The presence of spaced lateral and ventrolateral nodes is occasional, as a rule in mature body chambers, and associated with scarcely ornamented flanks. At the umbilical rim, radial swellings could be present. When present, ribs or plicae could be fairly visible, but also indistinct and roughly organized. Otherwise, ribs are well marked, distinct, well elevated, and rounded in section. Several specimens collected in the Losine section, exhibit growth stages characterized by a subtrigonal, wedge-shaped whorl section and a rounded but distinct ventral keel, that becomes more marked in the body chamber of gerontic specimens. Moreover, the ventrolateral margin, smooth up to a diameter of about 3 cm, develops tiny ventrolateral nodes sometimes becoming true spines in gerontic stages. These specimens are here referred to as the new genus *Camunites*. The occurrence of a distinct ventral keel associated with a wedge-shaped whorl section and a smooth ventrolateral margin in juvenile growth stages represent innovative characters well documented in representatives of the genus *Hungarites*, where these morphological features occur in the phragmocone during all ontogenetic stages. Owing to the close morphology of Hungaritidae with the Subfamily Paraceratitinae (e.g. the occurrence of a row of lateral and ventrolateral nodes), there is a necessity to amend the Family Hungaritidae in the Subfamily Hungaritinae, and to revise its composition, considering *Camunites* the forerunner of the quoted subfamily.

Included genera: *Hungarites* Mojsisovics, 1879a (=*Bullatihungarites* Vörös, 2018); *Iberites* Hyatt, 1900; *Halilucites* Diener, 1905; ?*Perrinoceras* Johnston, 1941; *Nodihungarites* Vörös, 2018; *Camunites* gen. nov.

Remarks: Vörös (2018) introduced in its monograph of upper Anisian ammonoids of the Balaton Highland, two new genera referred to the subfamily Hungaritinae: *Bullatihungarites* and *Nodihungarites*. *Nodihungarites* can be accepted by the presence of nodes in the ventrolateral position only in the body chamber of mature exemplars. This character permits to discriminate this genus from *Israelites* Parnes, 1962, in which ventrolateral nodes often occur also in the phragmocone. Moreover, *Israelites* bear marked lateral nodes, at least from intermediate growth stages, for these features cannot be included in the quoted Subfamily. Contrary to Tozer's (1981) statement, due to the occurrence of flattened venter in the inner whorls and the lack of ventrolateral shoulders in the outer part of the coiling, the genus *Negebites* Parnes, 1962 cannot be included in the Hungaritinae. *Bullatihungarites* has been defined by the presence or absence of bullae in a periumbilical position. However, based on our experience, such a character typically falls within the intrageneric variability of the genus *Hungarites*. This assertion is based on the observations of a lot of specimens referred to *Hungarites* (e.g. *H. mojsisovicsi*) in which more or less marked umbilical bullae may be present or not. All other morphological features of *Bullatihungarites* perfectly fit with the former genus to which it is here synonymized. In agreement with Parnes (1975, 1977, 1986), *Paraceratitoides* Parnes, *Gevanites* Parnes and *Andalusites* Parnes are not considered as representatives of Hungaritidae (Hungaritinae) as it was instead suggested by Tozer (1981). Despite the occurrence of a distinct ventral keel, also present in the Hungaritinae, these genera show, from early growth stages, ribbed and knotted shells involving also the ventrolateral margin, associated with a more or less inflated subtrapezoidal whorl section such as *Repossia* Rieber, 1973, *Rieppelites* Monnet and Bucher, 2005, *Parakellnerites* Rieber, 1973 or *Silberlingitoides* Monnet and Bucher, 2006, that belong to Paraceratitinae. Contrary to the statement of Fantini Sestini (1994), the morphological characters of the type species on *Rossiceras* (i.e. *R. gervasutti* Fantini Sestini, 1994), differ from those of the other representatives of the quoted genus and are not typical of the Hungaritinae.

Among the *Hungarites* species, *H. costosus* Mojsisovics, 1882 shows more evolute coiling and marked ribs, that become sigmoid swellings towards the ventrolateral margin as in *Halilucites* Diener. Nevertheless, *H. costosus* lacks the diagnostic grooves bordering the ventral keel of *Halilucites* Diener, 1905. In large specimens of the latter genus, these grooves become shallower. The ventral keel is triangular in *H. costosus* but slender, subquadrate in shape in *Halilucites*. As suggested in Manfrin et al. (2005, p. 498) we believe that *H. costosus* is an intermediate form between the genus *Hungarites* and the genus *Halilucites*. For this reason, also *Halilucites* is included in the Hungaritinae.

Occurrence and Age: in the Tethys realm, representatives of the Subfamily Hungaritinae make their first appearance at the base of the *reitzi* Subzone (*sensu* Mietto and Manfrin, 1995) of the middle Illyrian. The last representatives of the subfamily are *"Hungarites" inermis* Tozer (Tozer, 1994; Waller and Stanley, 2005) from the upper Longobardian (upper Ladinian) of North America and dubitatively the enigmatic genus *Perrinoceras* Johnston, 1941 from the basal Carnian of Nevada.

Genus ***Camunites*** Mietto and Manfrin gen. nov.

Origin of the name: from Val Camonica (Brescia) where the new genus is best documented.

Type species: *Ceratites inconstans* Reis, 1901, p. 79-80, pl. III, figs. 4-6, ? 7-8.

Diagnosis: hungaritid characterized by a juvenile shell without nodes on the flank and smooth ventrolateral margin. During growth, the latter is characterized by serried, weak, tiny pointed, sometimes coarsely arranged nodes or swellings. During ontogeny, the venter shows a rounded keel. The phragmocone shows a wedge-shaped whorl section that becomes subrectangular in the body chamber of large specimens. From early ontogenetic stages, the flanks bear numerous weak, often bundled, sigmoid ribs, barely visible or absent in large specimens.

Included species: *Ceratites lenis* Hauer, 1896; *Ceratites inconstans* Reis, 1901.

Description: very involute and compressed shell, with the phragmocone rapidly increasing in height during ontogeny. The phragmocone shows a subtrigonal, wedge-shaped whorl section with the largest width at the inner third of the flank. The body chamber of mature specimens is subrectangular in section showing a distinct umbilical egression. The venter is characterized by a distinct but rounded keel in the phragmocone. In the body chamber of large specimens, the venter is low-arched in shape or maintains an evident keel. The ventrolateral margin shows a distinct marginal edge. Ornamentation consists of ribs and nodes. On the phragmocone, ribs are serried, scarcely elevated, generally variable in size, and attenuated or indistinct along the flank, often originating in bundles from weak umbilical swellings. During ontogeny, the ribs gradually fade and then disappear so that only growth lines generally occur. When present, the swellings at the umbilical rim slightly protrude towards the umbilicus. Juvenile shells exhibit a smooth ventrolateral margin. During growth, the latter is characterized by quite numerous, tiny, often indistinct nodes or swellings, more or less obliquely elongated. In large specimens, sharp-spaced nodes can be present in the ventrolateral position. The lateral nodes, when present, are small, spaced, and rounded, which only appear at intermediate or late growth stages.

The suture line is ceratitic, consisting of four complete saddles between the ventrolateral and the umbilical rims. The first two saddles are well-elongated, and the other two are brachyphyllic in shape.

Remarks: *Camunites* gen nov. shows morphological similarities with *Hungarites* Mojsisovics, 1879a, *Parakellnerites* Rieber, 1973, *Pisaites* Balini, 1992b and *Lardaroceras* Balini, 1992a. *Hungarites* is easily recognizable by the lack of any trace of nodes on the ventrolateral margin and a more distinct and marked keel at least on the phragmocone. *Parakellnerites* bears generally keeled whorls but the flanks, at least on the phragmocone, show well-marked ribs and regularly spaced nodes in lateral and ventrolateral positions which already occur in early ontogenetic stages. *Pisaites* show a subrectangular whorl section from early growth stages and, as in *Parakellnerites,* lateral and ventrolateral nodes regularly occur. *Lardaroceras* has a subtrigonal whorl section as in *Camunites*, but its flanks always show regularly arranged ribs and ventrolateral nodes, at least on the phragmocone. *Camunites* clearly shows morphologies typical of Paraceratitinae (e.g., nodate ventrolateral margins), together with innovative characters, as a discrete keel associated with a wedge-shaped whorl section, a generally weak or indistinct ornamentation as in the genus *Hungarites* and early growth stages with smooth ventrolateral margin, suggesting that *Camunites* is the forerunner of the subfamily Hungaritinae. Both in the Bagolino section in Southern Alps (Brack and Rieber, 1993) and the Felsöörs section in the Balaton Highlands (Vörös, 1998) the genus *Hungarites* appears later than *Camunites*.

Occurrence and Age: *Camunites* gen. nov. appears in the middle Illyrian, at the base of the *reitzi* Subzone-*Hungarites* Zone (*sensu* Mietto and Manfrin, 1995), as documented in the Prezzo Limestone of the Losine section in bed CM5 (Val Camonica, Brescia). As shown in the Bagolino section (Brack et al., 2005), *Camunites* disappears below the appearance of the genus *Hungarites* and *Hyparpadites bagolinensis* (Brack and Rieber, 1993).

As *Hungarites leni*s and *H.* cf. *lenis*, the genus is also documented at Bagolino in the Brescian Prealps (Brack and Rieber, 1993), at Haliluci in Bosnia Herzegovina (Hauer, 1896: *Ceratites lenis*, pl. 6, figs. 1-2, 7 only), in the Wettersteinkalke (Reis, 1901, 1907: *Ceratites inconstans*) of the Wettersteingebirge (Northern Calcareous Alps) and probably in the Balaton Highland (Vörös et al., 1996, 2003; Vörös, 1998, *"Hungarites" inconstans*). As "*Ceratites* nov. f. indet.", it is also documented at Reutte in Northern Calcareous Alps (Mojsisovics, 1882).

Camunites inconstans (Reis, 1901)
(Figs. 3-5)

Lectotype: specimen illustrated by Reis, 1901, pl. III, figs. 4-6, stored in the Bayerische Staatssammlung für Paläontologie und Historische Geologie of München, BSPM 1901 II 552).

Synonymy list:

	?	1882	*Ceratites* nov. f. indet. - Mojsisovics, 1882, p. 35, pl. 8, figs 2a-c.
v		*1901	*Ceratites inconstans* nov. spec. Reis, p. 79-80, pl. 3, figs 4-6, ?7-8, non 9; pl. 7, figs 8, ?9.

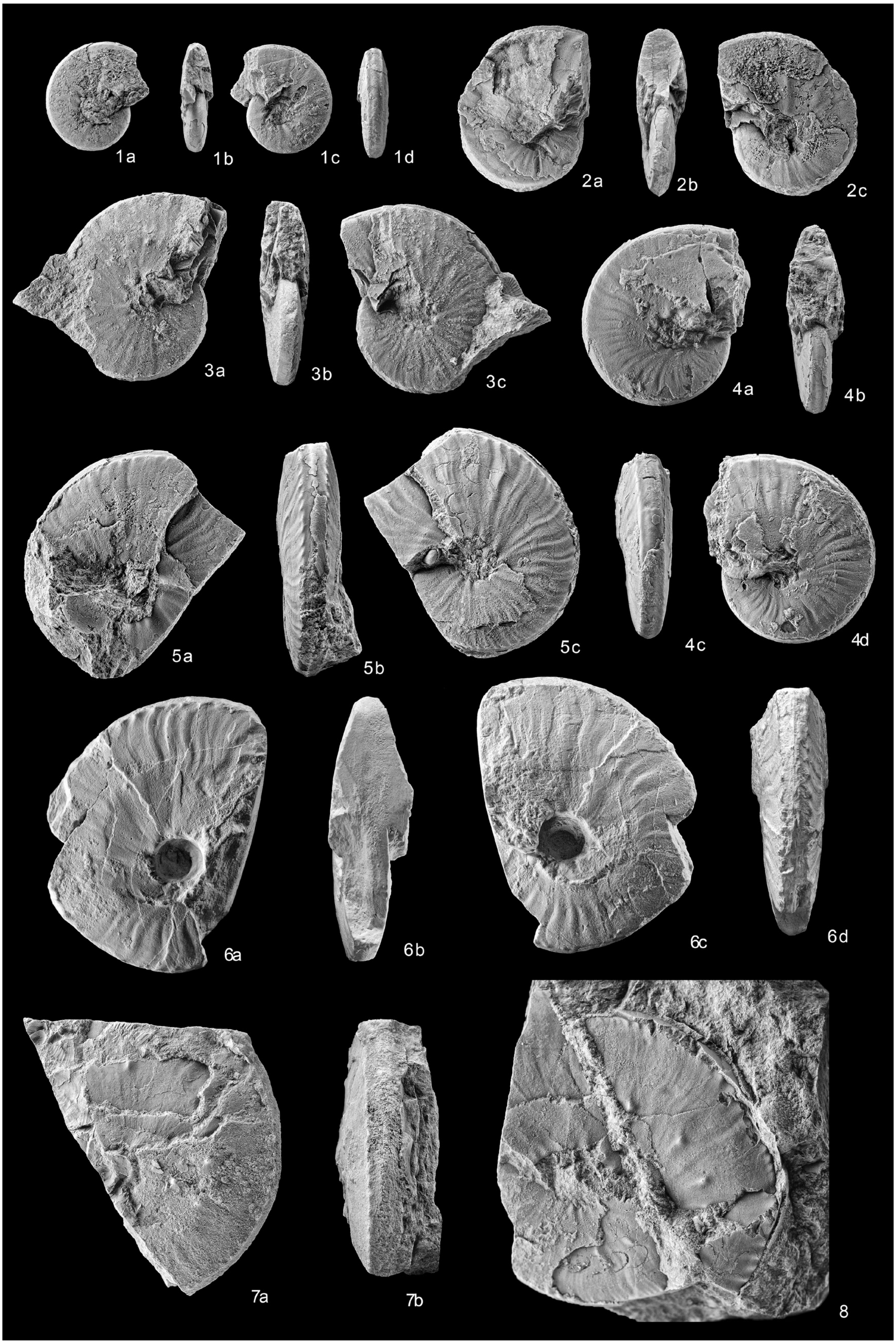

Fig. 3 - *Camunites inconstans* (Reis, 1901). 1: specimen CM 9.23 (MGP-PD 31906), 1a. left view, 1b. oral view, 1c. right view, 1d. ventral view; 2: specimen CM 5.7 (MGP-PD 31887), 2a. left view, 2b. oral view, 2c. right view; 3: specimen CM 9.18 (MGP-PD 31901), 3a. left view, 3b. oral view, 3c. right view; 4: specimen CM 9.24 (MGP-PD 31907), 4a. left view; 4b. oral view, 4c. ventral view, 4d. right view; 5: specimen CM 9.14 (MGP-PD 31897), 5a. left view, 5b. ventral view, 5c. right view; 6: cast of the specimen selected as lectotype (BSPM 1901 II 552) EA 22, 6a. left view, 6b. oral view, 6c. right view, 6d. ventral view; 7: specimen CM 10.1 (MGP-PD 31917), 7a. right view, 7b. ventral view; 8: specimen CM 9.11 (MGP-PD 31894), right view.

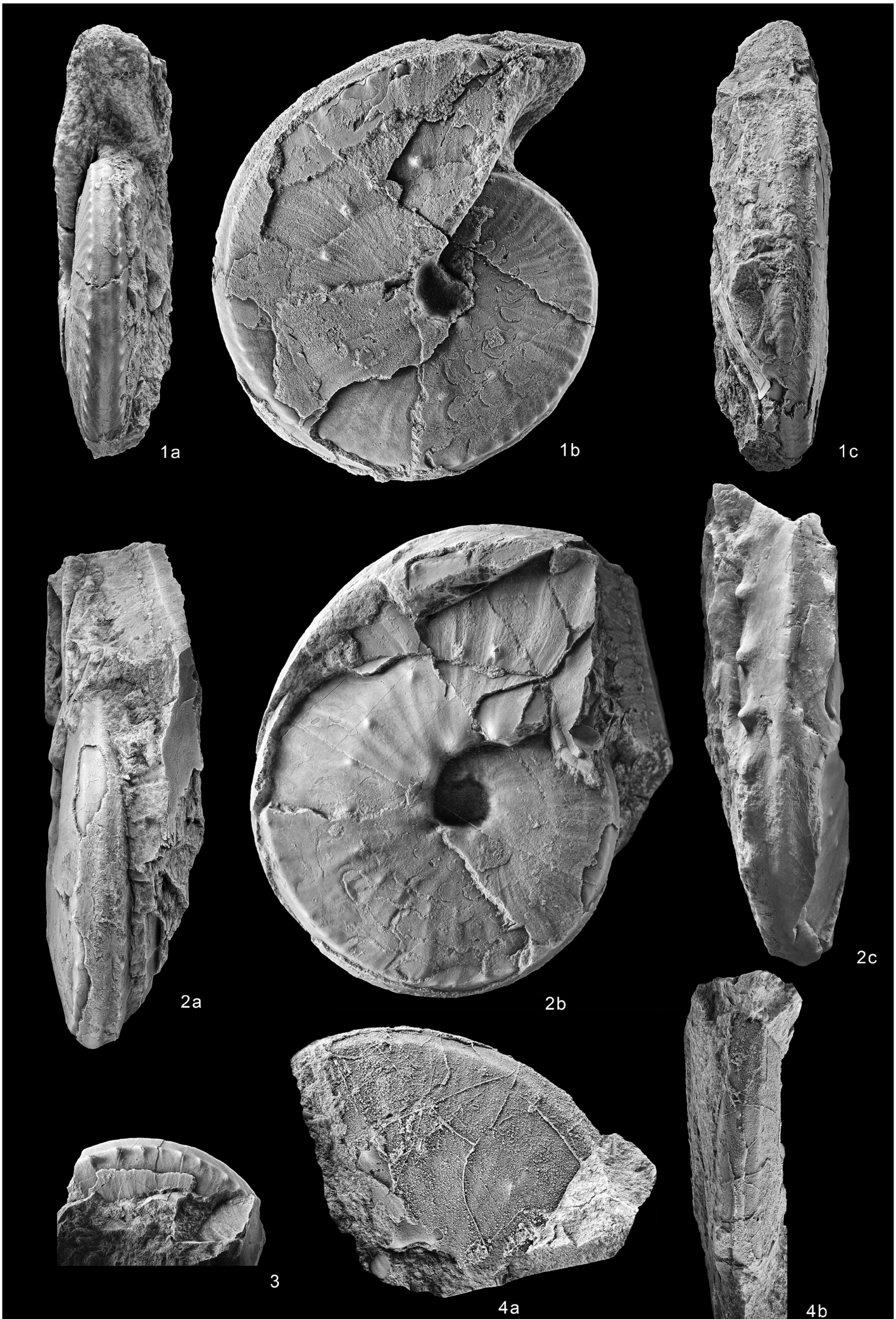

Fig. 4 - *Camunites inconstans* (Reis, 1901). 1: specimen CM 9.26 (MGP-PD 26759), 1a. oral view, 1b. left view, 1c. ventral view; 2: specimen CM 9.3 (MGP-PD 31890), 2a. oral view; 2b. left view; 2c. ventral view; 3: specimen CM 9.25 (MGP-PD 31908), 3a. right view, 3b. ventral view. All figures are in natural size.

1907 *Ceratites inconstans* Reis - Reis, p. 125-126.
? 1993 *"Hungarites"* cf. *lenis* (Hauer, 1896) - Brack and Rieber, 1993, p. 464, pl. 5, figs 1-2.
v 1995 *"Hungarites" inconstans* (Reis, 1900) - Mietto and Manfrin, pl. 2, figs 4-6, 11-12.

Type horizon and type locality: Wetterstein Limestone of Wetterschroffenhalde (Zugspitz Massif, Bavarian Alps, Germany.

Measurements: the measurements (in mm) of the examined specimens are reported in table 2 and figure 6.

Other material: Zugspitz Massif: EA 22 (cast MGP-PD 31969 of the original specimen of *Ceratites inconstans* Reis, 1901, pl. III, figs. 4-6, here selected as lectotype; Losine section: CM 5.7 (MGP-PD 31887); CM 7.12 (-31888); CM 9.2 (-31889), -.3 (-31890), -.4 (-31891), -5 (-31892) and 6 (-31893), -.11 (-31894), -.12 (-31895), -.13 (-31896), -.14 (- 31897), -.15 (-31898), -.16 (-31899), -.17 (-31900), -.18 (-31901), -.19 (-31902), -.20 (-31903), -.21 (-31904), -.22 (-31905), -.23 (-31906), -.24 (-31907), -.25 (-31908), -.26 (-26759), -.27 (-31909), -.39 (-31910), -.40 (-31911), -.41 (-31912), -.42 (-31913), -.43 (-31914), -.44 (-31915); CM 10.1 (-31917); CM 11.1 (-31918).

Description: the lectotype, which is here re-illustrated (Fig. 3.6) and coming from Wetterschroffenhalde

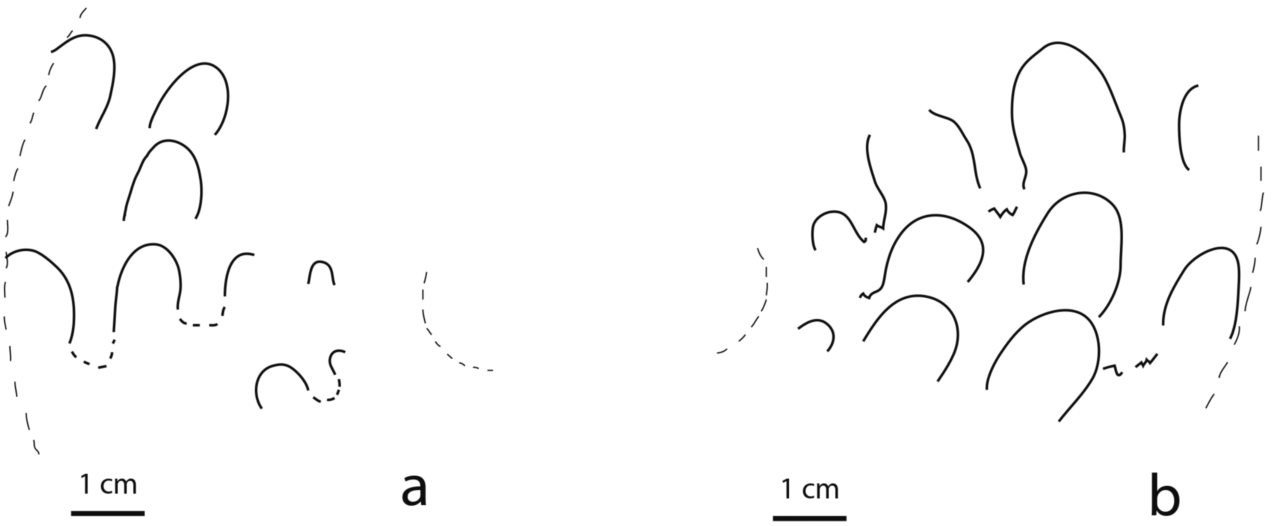

Fig. 5 - Suture lines of *Camunites inconstans* (Reis, 1901): a. specimen CM 9.3 (MGP-PD 31890), b. specimen CM 9.14 (MGP-PD 31897).

Tab. 2 - Measurements (in mm) and morphological parameters of *Camunites inconstans* (Reis, 1901); * estimated value.

morphological parameters	D1	D2	ah	H	h	U	W	w	WSC	CWI	WWI	UWI	WER	WHER	IZR	H/D1
CM9.23 (pl.1, fig. 1)	21.0	13.5	7.5	9.9	5.9	5.2	6.1	4.4	1.62	0.29	0.61.	0.25	2.42	2.81	0.24	0.47
CM 5.7 (pl. 1, fig. 2)	29.2	19.3	9.9	15.1	9.4	4.7	8.9	5.1	1.70	0.30	0.59	0.16	2.29	2.58	0.34	0.52
CM 9.18 (pl.1, fig. 3)	33.2	21.9	11.3	15.5	10.8	6.9	9.2	6.5	1.68	0.28	0.59	0.21	2.30	2.06	0.27	0.47
CM9.24 (pl.1 fig. 4)	34.9	22.3	12.4	17.4	11.4	6.1	9.8	6.0	1.77	0.28	0.56	0.17	2.90	2.45	0.29	0.50
CM 9.14 (pl. 1 fiog. 5)	41.0	26.0	15.0	20.1	13.4	7.5	10.6	–	1.90	0.26	0.53	0.18	2.49	2.25	0.25	0.49
EA 22 (Pl. 1, fig. 6)	50.3	32.4	17.8	26.0	16.2	8.1	12.5	9.8	2.08	0.25	0.48	0.16	2.41	2.57	0.31	0.52
CM 9.11 (pl. 1, fig. 8)	53.5*	31.1*	19.4*	28.3*	17.1*	8.1*	–	–	–	–	–	0.15*	2.46*	2.74*	0.31*	0.53*
CM 10.1 (pl. 1, fig. 7)	–	–	–	30.0	–	–	13.6*	–	2.20*	–	0.45*	–	–	–	–	–
CM 9.26 (pl. 2, fig. 1)	73.8	51.6	22.2	35.3	25.8	12.7	–	14.1	–	–	–	0.17	2.05	1.87	0.37	0.48
CM 9.3 (pl. 2, fig. 2)	91.4	64.4	27.0	39.8	32.4	19.2	–	14.3*	–	–	–	0.21	2.01	1.51	0.32	0.43
CM 9.25 (pl.2, fig. 3)	–	–	–	40.3	–	–	14.3*	–	2.82*	–	0.35*	–	–	–	–	–

* estimated value

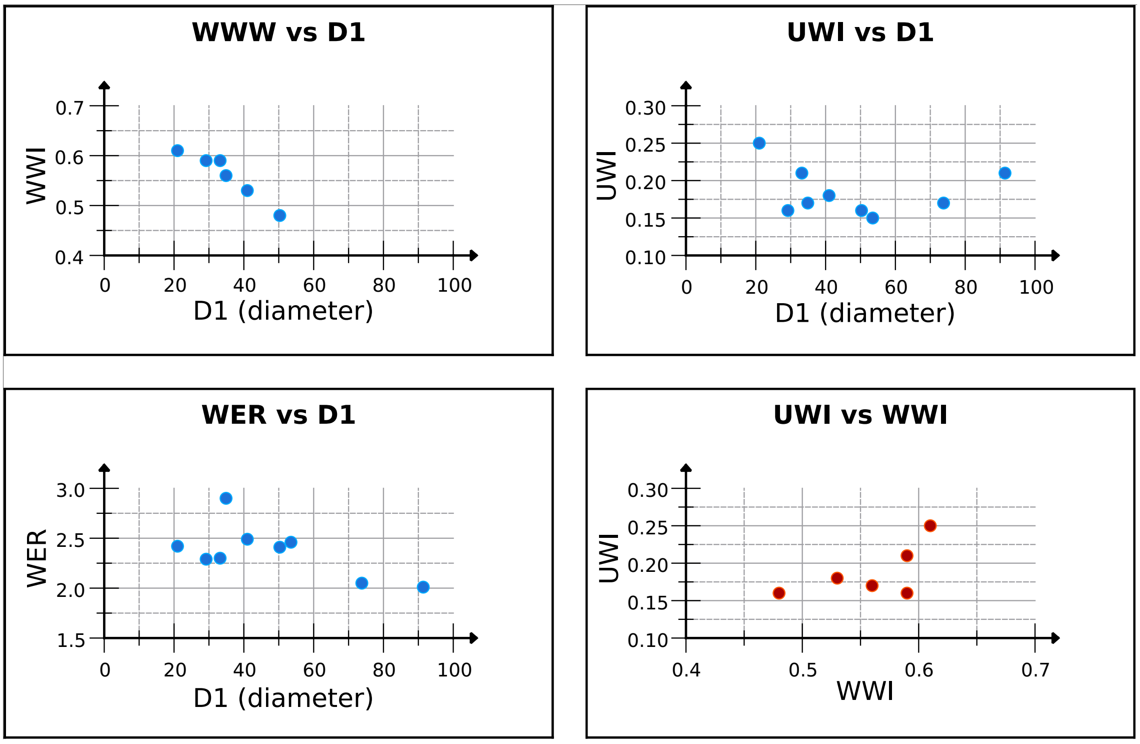

Fig. 6 - Morphological parameters of the studied specimens of *Camunites inconstans* (Reis, 1901), represented as cross plots to highlight some typical dependencies. The represented parameters are D1=conch diameter; WWI=whorl width index, UWI umbilical width index and WER=whorl expansion rate. See methods for a more complete definition of these parameters.

(Austria), is characterized by a fairly well-preserved, intermediate growth stage shell which is quite involute, discoidal in shape, and characterized by a wedge-shaped whorl section. The venter is narrow, roundly keeled, and bordered by serried, tiny, obliquely elongated nodes. The umbilicus is deep and bordered by a steep umbilical wall. On the flank, slightly sigmoid, weak, sometimes barely visible ribs occur. The suture line is not visible on the lectotype.

Although from a different location of the type locality of the lectotype, the newly found specimens referable to *C. inconstans* allow the description of the ontogeny of the species and some morphological features not ever recognizable in the lectotype. From the Losine section, 33 specimens representing various growth stages were examined. Only the specimens best preserved were used for the description and are illustrated in figures 3 and 4. On the phragmocone, the shell is very compressed, characterized by a slender, highly involute subtrigonal whorl section, somewhat increasing in height during ontogeny (WWI=0.61-0.48; UWI=0.52-0.48; WER= 2.42-2.01; IZR 0.24-0.32, see below). The venter is narrow, with a discrete but rounded keel and is bordered by a distinct ventrolateral edge. The body chamber of mature specimens (CM 9.26: Fig. 4.1; CM 9.3: Fig. 4.2) is subrectangular in section and less involute with respect to the phragmocone, due to the egression of the umbilicus and, consequently, the slower increase in height of the whorl. From early growth stages, the flanks are characterized by dense, thin, attenuated, sometimes flattened, bundled, proverse, or slightly sigmoid ribs of variable size. The ribs on the body chamber of large specimens are barely visible or absent. Initially, at the umbilical rim, weak swellings protruding towards the umbilicus are present. During ontogeny, the umbilical swellings generally tend to disappear. Until 2.5-3 cm in diameter, the ventrolateral margin is smooth as in the genus *Hungarites* but, during growth, tiny, serried, often obliquely elongated nodes occur. Later on, the ventrolateral nodes can be irregularly arranged, barely visible, spaced, or absent in the last part of the phragmocone and part of the body chamber. In the last portion of the body chamber of mature specimens, marked and somewhat spaced spiny nodes can be present. In the midflank of specimens at intermediate-late growth stages, a row of spaced, small rounded nodes occurs, involving most if not all of the body chamber. The body chamber is distinctly keeled. Measurements in mm and morphological parameters are displayed in Table 2 and Figure 6.

The suture line is ceratitic, with four entire saddles on the flank (Fig. 5). The first two are well elongated, while the other two are brachyphyllic in shape. The first and second lateral lobes are finely denticulated. Moreover, the first lateral lobe is nearly twice deeper nearly twice than the second. The second lateral saddle is slightly higher with respect to the first lateral one.

Remarks: *Camunites inconstans* differs from *C. lenis* (Hauer, 1896, pl. 6, figs. 1, 2, 7 only) by the occurrence of rows of spaced nodes in the mid flank of the last part of the phragmocone and on the body chamber, which maintains an evident keel. Moreover, on the ventrolateral margin of the last part of the body chamber, pointed or spiny nodes can be present. *C. lenis* occupies a younger stratigraphical position than *C. inconstans*, showing an intermediate morphological framework between the latter species and representatives of the genus *Hungarites*. *C. lenis* lacks the lateral row of nodes. Moreover, with reference of the ventrolateral (marginal) nodes and the ribs morphology of the inner whorls, Brack and Rieber (1993, p. 463) report that "At a diameter larger than 4 cm the ribbing becomes weak and indistinct and marginal tubercles are transformed to low, densely arranged, marginal swellings" i.e. at a lesser diameter respect *C. inconstans*. Despite the statement of Vörös (2018, p. 100), we agree with Brack and Rieber (1993) in considering the specimen illustrated in plate 2, figs. 6-7 a juvenile representative of *C. lenis*. From an ontogenetic approach, the morphology of its last part of the flank and that of the ventrolateral margin perfectly fits with the onset of the morphology of the last whorl of the largest specimen (Brack and Rieber, 1993, pl. 2, fig. 5). Moreover, with reference to the illustrations of Brack and Rieber (1993), the specimen of their plate 2, figs. 6-7, that Vörös (2018) refers to his new species *Parahungarites solyensis*, was found together with the largest species of plate 2, fig. 5 in the same layer at 54.25 m of the Bagolino section, associated with representatives of the genus *Kellnerites* which characterized the lower part of the *reitzi* Zone/Subzone. On the contrary, the occurrence of *P. solyensis* is restricted to the following a*visianum* Zone/Subzone.

"Hungarites" cf. *lenis* illustrated by Brack and Rieber (1993, pl. 5, figs. 1-2) from Bagolino and found about 50 cm below *C. lenis* is probably conspecific with *C. inconstans*, because of the occurrence of a lateral row of nodes at large growth stages. Unfortunately, in this specimen, the outer part of the body chamber is crushed and so poorly preserved, so that the occurrence of ventrolateral nodes cannot be observed.

In the description of *Lardaroceras krystyni*, Balini (1992a) compares this taxon with other morphologically similar species, including *Ceratites lenis* and *C. inconstans*, suggesting possible phyletic or taxonomical relationships between these taxa. With reference to *C. lenis* the general shell morphology and the whorl section are very similar but the flank ornamentation becomes different from early ontogenetic stages (see Brack and Rieber, 1993, pl. 2, figs. 6-7) in which the ribbing becomes weak and indistinct and the marginal tubercles appear as frilled, tiny, obliquely elongated swellings. As expressed below in the synonymy list, we agree with Balini (1992a) in considering different the morphology of the smaller specimens initially referred to *C. inconstans* by Reis (1901, pl. 3, figs. 7-9) with respect to the Reis' bigger specimen (pl. 3, figs. 4-6). The larger specimen illustrated by Reis, is herein elevated to lectotype of *C. inconstans*. The differences with *L. krystyni*, about at the same diameter, essentially concern the ribs framework and the morphology of the ventrolateral nodes. With reference to the present description of *C. inconstans*, *L. krystyni* shows on the phragmocone, instead, a homogeneous morphology of the ribs. These are slightly rounded in section and regularly spaced. On the ventrolateral margin, tiny roundly pointed nodes regularly occur.

Occurrence and Age: *Camunites inconstans* marks the base of the *reitzi* subzone and thus of the *Hungarites* zone (*sensu* Mietto and Manfrin, 1995) of the middle Illyrian (upper Anisian). This species is also present in the Wettersteingebirge (Reis, 1901, 1907). It probably also occurs in the Bagolino section of the Brescian Prealps (cf. Brack and Rieber, 1993) and at Reutte in Northern Calcareous Alps (Mojsisovics, 1882). The occurrences in the Balaton area, more precisely in the Vörösberény, Felsöörs and Szentantalfa sections (cf. Vörös et al., 1996, 2003, 2009; Vörös, 1998), are however no more reported in Vörös (2018).

4. DISCUSSION

4.1. AMMONOID TAXA CO-OCCURRING WITH *CAMUNITES INCONSTANS*

As reported in figure 2 and table 1, in which the bed-by-bed distribution of sampled ammonoids of Losine section is reported, *Camunites inconstans* occurs with some significant ammonoids species at Losine, which taxonomic status requires a revision. Here, the taxonomic positions of *Reiflingites camunus* (Assereto, 1963) and *Parakellnerites pseudohungaricus* (Balini, 1992a) are discussed.

4.1.1. About *Reiflingites camunus* (Assereto, 1963)

According to the statement of Balini (1992b, p. 182), the genus *Asseretoceras* Balini, 1992b differs from genus *Reiflingites* Arthaber, 1896a "… in the details of the external last quarter of the lateral side, the shape of the venter and the suture line.". The ventrolateral spiny nodes in *Asseretoceras* are similar, however, to those of the internal moulds of some *Reiflingites*. For example, *Ceratites altecostatus* Arthaber, 1896a that we consider, due to the rib framework and subexagonal whorl section, a representative of *Reiflingites*, as referred by Tatzreiter and Vörös (1991, p. 250-251, pl. 3, fig. 1) and suggested by Arthaber (1896a, p. 60), Assereto (1963, p. 66-68, 71) and Tatzreiter (2001, p. 152, 157). Since this character is fairly recognized in the species originally referred to the quoted genus (see Arthaber 1896a: *Reiflingites eugeniae*, *R. torosus* and *R. rota*), the writers believe that this morphological feature can have specific, not generic taxonomical significance.

Balini (1992b) observed that internal moulds of *Asseretoceras* have a slightly bicarinate-sulcate venter. From the examination of 28 specimens of *Reiflingites camunus*, coming from the Prezzo Limestone cropping out at the Losine section, Cividate Camuno (ex coll.

Riedel, 1949) and from the unpublished Valzurio locality (Oltressenda Alta, Seriana Valley, Bergamasc Prealps; WGS 84: N45°55'27"; E 09°57'58"; 1005 m a.s.l.), we believe that this hypothesis is questionable. As displayed in Table 3 and illustrated in Figure 7, internal moulds of the juvenile forms show a venter, which is, either rounded or slightly rounded venter, or rounded then flattened. On the contrary, the internal moulds of the adult specimens show either a faintly depressed (2 specimens), or a faintly depressed to flattened (2 specimens), or a flattened venter (3 specimens) (Fig. 7 and Tab. 3). On the whole, the venter of *Asseretoceras camunum* (*sensu* Balini, 1992b) is well comparable with that of *Reiflingites*.

Most of the species referred to as the genus *Reiflingites* as illustrated by Arthaber (1896a, pl. 7, figs. 3, 5-6) have their first lateral saddle situated between the ventrolateral shoulder and is followed by other two saddles along the flank. These suture lines are identical to those illustrated by Balini (1992b, p. 182) for the genus *Asseretoceras*. Moreover, the similarity of diagnostic characters of *Asseretoceras* and *Reiflingites*, such as the ribbing (i.e., primary and intercalatory ribs regularly alternated on the flank or regularly bifurcated near the umbilical rim) and the whorl section, the degree of the shell involution and the incised ventrolateral rib interspaces, is impressive. Consequently, we synonymize *Asseretoceras* to *Reiflingites*.

4.1.2. About *Parakellnerites pseudohungaricus* (Balini, 1992a)

The species referred to *Lardaroceras pseudohungaricum* Balini, 1992a shows some morphological features quite different from *Lardaroceras krystyni* Balini, 1992a, type species of the genus *Lardaroceras* Balini, 1992a. *L. pseudohungaricum* exhibits a subtrapezoidal whorl section, particularly marked during ontogeny due to the occurrence of three rows of nodes at umbilical, lateral and ventrolateral positions (Balini, 1992a, pl. 2, fig. 1). Moreover, *L. pseudohungaricum* shows a fastigated or roundly keeled venter also on the body chamber. The

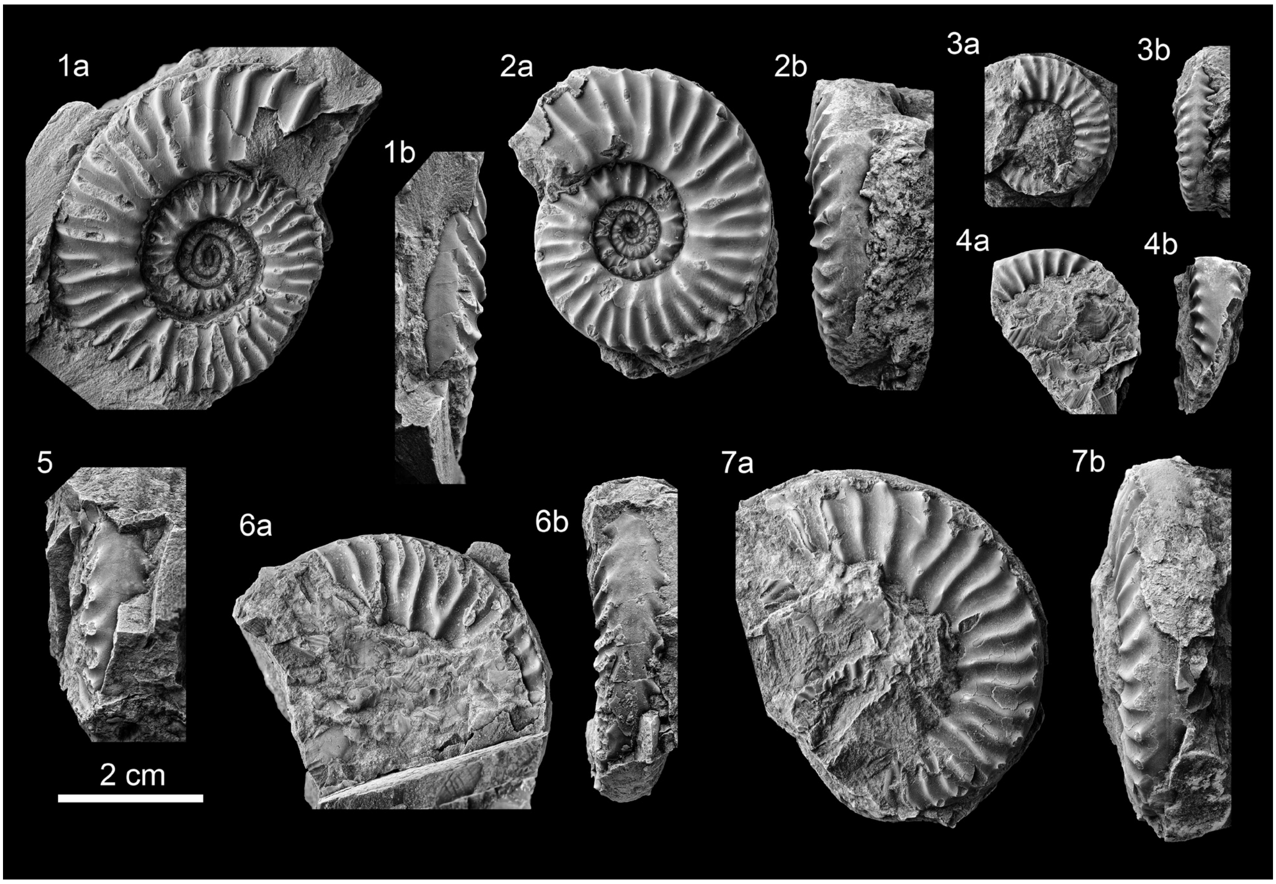

Fig. 7 - *Reiflingites camunus* (Assereto, 1963). 1: specimen CM1.1 (MGP-PD 29618), Losine section (Brescia), *trinodosus* Subzone, 1a. left view, 1b. ventral view, venter fairly depressed; 2: specimen CM 1.5 (MGP-PD 29622), Losine section (Brescia), *trinodosus* Subzone, 2a. right view, 2b, ventral view, venter flattened; 3: specimen CM 9.34 (MGP-PD 32410), Losine section (Brescia), *reitzi* Subzone, 3a. right view, 3b, ventral view, venter slightly rounded; 4: specimen VZA.13 (MGP-PD 32411), Valzurio (Bergamo), *trinodosus* Subzone, 4a. left view, 4b, ventral view, venter slightly rounded; 5: specimen VZA.14 (MGP-PD 32412), Valzurio (Bergamo), *trinodosus* Subzone, ventral view, venter slightly rounded; 6: specimen VZA.17 (MGP-PD 32413), Valzurio (Bergamo), *trinodosus* Subzone, 6a. right view, 6b, ventral view, venter flattened; 7: specimen VZA.5 (MGP-PD 32414), Valzurio (Bergamo), *trinodosus* Subzone, 7a. right view, 7b, ventral view, venter flattened.

Tab. 3 - Venter morphology (internal mould) relative to diverse ontogenetic growth stages of *Reiflingites camunus* (Assereto, 1963).

Inventory	Taxonomy	Growth stage	Venter (internal mould)	Locality	Repository MGP-PD
CM 1.1	Reiflingites camunus	Adult	faintly depressed	Losine section	29618
CM 1.2	Reiflingites camunus	Juvenile	slightly rounded	Losine section	29619
CM 1.3a	Reiflingites camunus	Juvenile	not checked	Losine section	29620a
CM 1.3b	Reiflingites camunus	Juvenile	not checked	Losine section	29620b
CM 1.4	Reiflingites camunus	Adult	flattened	Losine section	29621
CM 1.5	Reiflingites camunus	Juvenile	flattened	Losine section	29622
CM 1.6a	Reiflingites camunus	Juvenile	rounded to flattened	Losine section	32353a
CM 1.6b	Reiflingites camunus	Juvenile	not checked	Losine section	32353b
CM9.34	Reiflingites camunus	Juvenile	slightly rounded	Losine section	32354
CIV.2	Reiflingites camunus	Juvenile	rounded	Cividate Camuno	32355
VZ dt.1	Reiflingites camunus	Juvenile	slightly rounded	Valzurio	32356
VZ dt.10a	Reiflingites camunus	Adult	faintly depressed	Valzurio	32357
VZA.1	Reiflingites camunus	Adult	not checked	Valzurio	32358
VZA.2	Reiflingites camunus	Juvenile	not checked	Valzurio	32359
VZA.3	Reiflingites camunus	Juvenile	not checked	Valzurio	32360
VZA.5	Reiflingites camunus	Adult	flattened	Valzurio	32361
VZA.7	Reiflingites camunus	Juvenile	rounded	Valzurio	32362
VZA.9	Reiflingites camunus	Juvenile	not checked	Valzurio	32363
VZA.11	Reiflingites camunus	Juvenile	not checked	Valzurio	32364
VZA.12	Reiflingites camunus	Juvenile	rounded	Valzurio	32365
VZA.13	Reiflingites camunus	Juvenile	slightly rounded	Valzurio	32366
VZA.14	Reiflingites camunus	intermediate	slightly rounded	Valzurio	32367
VZA.15	Reiflingites camunus	Juvenile	rounded	Valzurio	32368
VZA.16	Reiflingites camunus	Juvenile	rounded	Valzurio	32369
VZA.17	Reiflingites camunus	Adult	flattened	Valzurio	32370
VZA.18	Reiflingites camunus	Juvenile	rounded	Valzurio	32371
VZA.19	Reiflingites camunus	Adult	faintly depressed to flattened	Valzurio	32372
VZA.20	Reiflingites camunus	Adult	faintly depressed to flattened	Valzurio	32373

suture line of *L. pseudohungaricum* is simpler than *L. krystyni*, due to the occurrence, in the former species, of nearly entire saddles particularly in their tips. All these morphological characters do not occur in *L. krystyni*. Instead, *L. pseudohungaricum* shows the general morphological features typical of *Parakellnerites* Rieber, 1973. The supposed diagnostic relevance of the absence of an evident periumbilical margin in *Parakellnerites* (Balini, 1992a, p. 11) is more apparent than real. This assertion is referred to the type specimens coming from the Grenzbitumenzone of Canton Ticino (Switzerland), described and illustrated by Rieber (1973). The comparison between the schematic pictures of the section of *Parakellerites* illustrated by Rieber (1973, figs. 6, 7, 10) and the photos of the equivalent specimens (Plates 1-6) shows strong incongruences about the morphology of the umbilical wall. More recently, better-preserved specimens of *Parakellnerites* from Punta Zonia and Latemar localities were described by Brack and Rieber (1993). For example, in the diagnosis of *Parakellnerites zoniaensis*, Brack and Rieber (1993, p. 466) report a "… perpendicular to slightly overhanging umbilical wall." The same authors, describe *Parakellnerites rothpletzi* (Mojsisovics, 1882) (p. 467) as having "… a wall perpendicular on the inner whorls to slightly overhanging on the outer ones". These statements emended the original diagnosis of *Parakellnerites* and imply that a steep umbilical wall is not a distinctive character of *Lardaroceras*. Based on the whorl section, the ornamentation, and possibly the suture line, we thus believe that *Lardaroceras pseudohungaricum* Balini, 1992a must be attributed to the genus *Parakellnerites* Rieber, 1973.

4.2. *CAMUNITES GEN*. NOV. AS A MARKER IN MIDDLE TRIASSIC TETHYAN AMMONOID BIOSTRATIGRAPHY

Mietto and Manfrin (1995), based on the major event's concept introduced by Krystyn (1978) and Tozer (1978, 1984), proposed a new ammonoid interval biochronozone for the middle Illyrian, the *Hungarites* Zone (see synthesis in Jenks et al., 2015). The base of this zone in the new Losine section is marked by the first occurrence, in bed CM5, of *Camunites* gen. nov. (Fig. 2). This taxon was indicated in Mietto and Manfrin (1995, p. 550) as n. gen. B, and used to define the base of the *Hungarites* Zone because it was considered the ancestor of the subfamily Hungaritinae. In the original definition, this biozone comprises the *reitzi* and the *avisianum* subzones. Bed CM5 is correlated with layers BT5 of La Baita and AD110 of Adanà, two coeval sections from the Val Camonica and the Giudicarie area respectively, described by Balini (1992a).

There is a long-standing debate about the biostratigraphic significance of the ammonoid *Reitziites reitzi* (Böckh, 1872). Initially, the so-called "Niveaux des *Ceratites reitzi*" were identified by Böckh (1874). Later, these levels were renamed as "Horizon", and then "Zone", by Mojsisovics (1874, 1879b, 1882). Mojsisovics et al. (1895) abandoned this biostratigraphic unit in favor of the *Protrachyceras curionii* Zone, as referred by Brack and Rieber (1994). It was considered that the *curionii* zone was more useful for the correlations between the Southern Alps and Balaton Highlands. Mojsisovics himself was probably doubtful about the correct attribution of the samples from the Southern Alps that he examined and classified as *Ceratites reitzi*. An exact stratigraphic position for the beds bearing *Reitziites reitzi* was only recently established (e.g., Brack and Rieber, 1993; Brack et al., 2005; Vörös, 1993a, 1993b). As the GSSP for the base of the Ladinian was in discussion, a proposal arose of defining the Ladinian with the base of the *reitzi* Zone at bed 105 of the Felsöörs section (Balaton Highlands, Hungary), with the first occurrence of *R. reitzi* (Vörös et al., 2003).

This proposal was extensively discussed (e.g., Manfrin and Mietto, 1995; Mietto et al., 2003; Brack and Rieber, 2003) but discarded in favor of the younger first occurrence of *Eoprotrachyceras curionii* at Bagolino in the Brescia Prealps (Brack et al., 2005). At Bagolino, now the stratotype of the Ladinian, the base of the *reitzi* Zone (*sensu* Brack et al., 2005) is marked by the occurrence of the genus *Kellnerites*, while *R. reitzi* only appears some 3-4 m above. A finer biostratigraphic subdivision for this interval was proposed based on data from Felsöörs in Hungary (Vörös et al., 1996, 2003; Vörös, 2018) and from the Giudicarie area and Val Camonica in Italy (Balini, 1992a). In Hungary, between the first occurrence of *Reiflingites* (formerly *Asseretoceras*; see above) *camunus* and the first occurrence of *R. reitzi*, four subzones are described (Vörös, 2018, *R. camunus*, *Parakellnerites* (formerly *Lardaroceras*: see above) *pseudohungaricus*, *Kellnerites felsoeoersensis* (Stürzenbaum, 1876) and *Hyparpadites liepoldti* (Mojsisovics, 1882). These four subzones (Fig. 8) were initially identified by the same authors as biohorizons or beds, and are, according to Vörös et al. (2003), part of the upper *Paraceratites trinodosus* Zone and part of the *reitzi* Zone (Vörös, 2018).

As revealed by the Losine section (Fig. 2), *Camunites inconstans* first occurs after appearance of the genus *Lardaroceras*, i.e., within the *P. pseudohungaricus* subzone of Vörös et al. (1996, 2003). This interval coincides, in the Brescia Prealps, with the informal "*Lardaroceras* beds" biostratigraphic unit of Balini (1992a, 1993), within the Prezzo Limestone.

Interestingly, bed 99c at Felsöörs shows a faunal association given by *Asseretoceras* sp. (=*Reiflingites* sp.), *"Hungarites" (=Camunites) inconstans* and *Lardaroceras* (=*Parakellnerites*) *pseudohungaricum* (Vörös et al., 1996, 2003, 2009; Vörös, 1998), which is identical to the fauna of bed CM9 at Losine (Tab. 1), thus suggesting a reliable tool of correlation. However, in Vörös (2018) *"Hungarites" inconstans* do not appear in the quoted bed 99c of Felsöörs section.

Numerous events were used to build a finely resolved ammonoid biozonation of this stratigraphic interval. Mietto and Manfrin (1995) define the base of the *reitzi* Subzone with the appearance of subfamily Hungaritinae, while Brack et al. (2005) used the appearance of *Kellnerites* to mark the base of their *R. reitzi* Zone. Also due to its historical meaning, Vörös et al. (2003) define the base of the *reitzi* zone with the first occurrence of *Reitziites reitzi*. Interestingly, Hungaritinae, *Kellnerites* and *Reitziites* are documented outside the Mediterranean area, as in Japan (Bando, 1964). *Halilucites*, *Kellnerites* and *Reitziites* were recently recognized in the Himalayas (Krystyn et al., 2004). Moreover, representatives of Hungaritinae were also documented in eastern Panthalassa from the Late Ladinian (i.e. *"Hungarites" inermis* Tozer, 1994) of British Columbia (Tozer, 1994) and Nevada (Waller and Stanley, 2005). This wide geographical distribution corroborates the significance of the subfamily Hungaritinae for correlation purposes. In the writers' opinion, based on the major event's concept and a wide period and paleogeographic distribution, the appearance of Subfamily Hungaritinae, which coincides with the first occurrence of *Camunites inconstans*, should be preferred with respect to other taxa for the definition of the base of the *reitzi* Subzone.

4. CONCLUSIONS

Camunites gen. nov., and its type species C. *inconstans* (Reis, 1901), here described mark the earliest appearance of subfamily Hungaritinae, which is considered a major evolutionary event for ammonoids in this interval (Mietto and Manfrin, 1995). From the abundant material (Tab. 1) of the middle Illyrian (upper Anisian) Losine section several specimens bear characteristic features of the Hungaritinae subfamily, such as a juvenile shell

<table>
<tr><th></th><th></th><th colspan="2">Mietto and Manfrin, 1995
mod. Manfrin et al., 2005</th><th colspan="2">Vörös, 2018</th></tr>
<tr><th>Stage</th><th>substage</th><th>zone</th><th>subzone</th><th>zone</th><th>subzone</th></tr>
<tr><td>LADINIAN</td><td>FASSANIAN</td><td>Eoprotrachyceras</td><td>E. curionii</td><td>Eoprotrachyceras curionii</td><td>Eoprotrachyceras curionii</td></tr>
<tr><td rowspan="11">ANISIAN</td><td rowspan="9">ILLYRIAN</td><td rowspan="3">Nevadites</td><td>Chieseiceras chiesense</td><td rowspan="3">Nevadites secedensis</td><td rowspan="2">Nevadites secedensis</td></tr>
<tr><td>“Nevadites” secedensis</td></tr>
<tr><td>Ticinites crassus</td><td>Ticinites crassus</td></tr>
<tr><td rowspan="5">Hungarites</td><td>Aplococeras avisianum</td><td rowspan="4">Reitziites reitzi</td><td>Aplococeras avisianum</td></tr>
<tr><td rowspan="4">Reitziites reitzi</td><td>Reitziites reitzi</td></tr>
<tr><td>Hyparpadites liepoldti</td></tr>
<tr><td>Kellnerites felsoroersensis</td></tr>
<tr><td rowspan="4">Paraceratites trinodosus</td><td>Lardaroceras pseudohungaricum</td></tr>
<tr><td rowspan="2">Paraceratites</td><td>Paraceratites trinodosus</td><td>Asseretoceras camunum</td></tr>
<tr><td>Schreyerites abichi</td><td>Paraceratites trinodosus</td></tr>
<tr><td rowspan="2">PELSONIAN</td><td rowspan="2">Balatonites</td><td>Schreyerites binodosus</td><td>Schreyerites? binodosus</td></tr>
<tr><td>Balatonites balatonicus</td><td>Balatonites balatonicus</td><td>Bulogites zoldianus</td></tr>
</table>

Fig. 8 - Comparison of biozonal schemes for the Illyrian Subtage of the Tethys. The first scheme was proposed by Mietto and Manfrin 1995 (partly modified in Manfrin et al., 2005). The second one is definitively adopted for the Balaton Highland (Hungary) by Vörös, 2018.

characterized by a keeled venter associated by a smooth ventrolateral margin, faint flank ornamentation and the lack of lateral nodes. However, during ontogeny, *C. inconstans* maintains morphologies typical of the subfamily Paraceratitinae, such as the occurrence of lateral and ventrolateral nodes. Based on geographical distribution and applying the major events philosophy (Krystyn, 1978), we believe that the first occurrence of *Camunites inconstans* (i.e. first appearance of the Hungaritinae Subfamily, is the best event for defining the base of the *reitzi* Subzone.

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