

SIDELINED SEASHELLS: REAPPRAISAL OF THE MIDDLE TRIASSIC AMMONOIDS OF SAMOBOR AND ŽUMBERAK MTS. (NORTH-WESTERN CROATIA) AND THEIR SYSTEMATICS AND BIOSTRATIGRAPHIC IMPLICATIONS

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Abstract. Basinal Middle Triassic successions of the Samobor and Žumberak Mts. (north-western Croatia) have historically produced fossils of ammonoids. These finds have, however, largely been neglected in the later literature. This paper describes and redescribes a large collection of ammonoids, most of which were collected by previous researchers throughout the 20th century. Aside from the detailed taxonomic descriptions and revisions, several taxa previously unknown from these localities were identified. Of the species whose holotypes were designated at the Gregurić Breg locality, some are found to be dubious, with validity of other remaining inconclusive and a single taxon, *Eoprotetrachyceras doraе* comb. nov., being treated as valid. Certain Middle Triassic ammonoid genera may also require future comprehensive revisions. A preliminary, modified ammonoid zonal/sub-zonal scheme for the Ladinian of the Tethyan province is proposed, to be inclusive of most of the data from the literature. The need for improvement of the subdivision of this stage is recognized. Based on ammonoids, condensed red nodular limestones of the Gregurić Breg locality (Samobor Mts.) most likely span the Avisianum subzone (upper Illyrian) – Longobardicum subzone (“middle” Longobardian), indicating that subsidence began in the earlier part of the Illyrian. At Mt. Žumberak, scant ammonoid remains indicate that the upper, limestone-rich portion of this succession spans at least the Avisianum subzone (upper Illyrian) – Longobardicum subzone (“middle” Longobardian), but additional data is needed for drawing more robust conclusions. Overall, the timing of basinal deposition is well correlated between Gregurić Breg and Žumberak localities (lower Illyrian – upper Longobardian).

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INTRODUCTION

The Samobor and Žumberak Mts., located in north-western Croatia, have been the subject of geological study since the late 19th century. Of particular interest are the successions of Middle Triassic basinal deposits, which have produced numerous fossils of ammonoids in certain localities. These deposits were first recognized by Gorjanović-Kramberger (1894), who also reported first ammonoid remains from Samobor Mts., at the now locally famous Gregurić Breg locality. This locality was more substantially sampled and studied by Salopek (1912, 1918, 1936), who described numerous cephalopods, bivalves, and provided a rudimentary description of the succession.

Although Gorjanović-Kramberger (1894) already mentioned similar deposits being present in the nearby Žumberak Mts., it was not until the latter half of the 20th century that the first scant ammonoid remains were reported (Šikić et al. 1979). In the early 90's, several additional adjacent localities in this area, yielding more substantial ammonoid remains, were briefly reported by Sakač (1994). Some of these localities, as well as the historical Gregurić Breg locality, were more recently investigated by Goričan et al. (2005), who focussed mostly on radiolarian and conodont biostratigraphy.

Despite well over a century of research, this area remains understudied. The major obstacles to researchers are the lack of outcrops due to the extensive soil coverage, the often significant tectonic disruption, and the lack of easily identifiable marker beds due to pronounced lateral variations within the studied basinal deposits. The ammonoids collected at these localities, which are widely considered some of the most biostratigraphically informative fossils of the Triassic, were not thoroughly investigated since the time of Salopek.

This paper presents a revision and redescription of the ammonoids collected in the area of interest, as well as the description of several species not previously known from these localities. A discussion on their taxonomy is also provided, with suggestions of possible revisions and synonymy of certain taxa. Based on the decades of research on the topic of high-resolution ammonoid biostratigraphy at well-studied sections across the western Tethyan province (Southern Alps, Balaton Highland, etc.), the ammonoids of Samobor and Žum-

berak Mts. are herein put into a revised stratigraphic framework. This, despite the challenges present by these localities and the lack of precise bed-by-bed sampling, provides valuable, precise data on the timing of the depositional events of this area and opens possibility for further research.

GEOLOGICAL SETTING

The Samobor and Žumberak Mts. (Fig. 1) belong to the transitional area between the External and Internal Dinarides. According to the tectonostratigraphic division of Schmid et al. (2020), this transitional area can be further subdivided into the East Bosnian-Durmitor and Pre Karst & Bosnian flysch units. These represent distal parts of the Adria margin (Velić et al. 2002; Vlahović et al. 2005) which are, in the Samobor-Žumberak Mts., characterized by Permian to Lower Triassic siliciclastics, Triassic to Lower Jurassic carbonates and a Jurassic to Cretaceous pelagic succession (Šikić et al. 1979).

Middle Triassic hemipelagic – pelagic deposits represent the result of a short-lived rifting event that affected large parts of the Northern Gondwana margin (van Hinsbergen et al. 2020). At the Gregurić Breg locality (Samobor Mts.), the rifting-related succession (Fig. 2a), overlaying late diagenetic dolostones, begins with thick-bedded shallow water limestones of probably late Pelsonian – late Illyrian age. They are followed by a lithologically varied hemipelagic succession consisting of cherts, volcanoclastics, and pelagic limestones, among which are the condensed grey and red nodular limestones from which the majority of the ammonoid fauna was collected. The latter limestones are the facies equivalent of the well-known Hallstatt facies of the Northern Alps and contain late Illyrian and Ladinian ammonoid species. The uppermost part of the succession consists of dark grey thinly bedded and silicified limestones with occurrences of *Daonella lommeli* (Wissmann in Wissmann & Münster, 1841) bivalves and intercalations of tuff and chert (Salopek 1936; Goričan et al. 2005; this paper).

Multiple adjacent localities (Kolići, Radilovec Jaruga, Vlašić Brdo, Bezjaki) in the southwestern part of Žumberak Mts. expose parts of an approximately 70 m thick basinal succession (Fig. 2b), which likewise overlays a thick dolostone interval. The lower part of the succession comprises an alternation

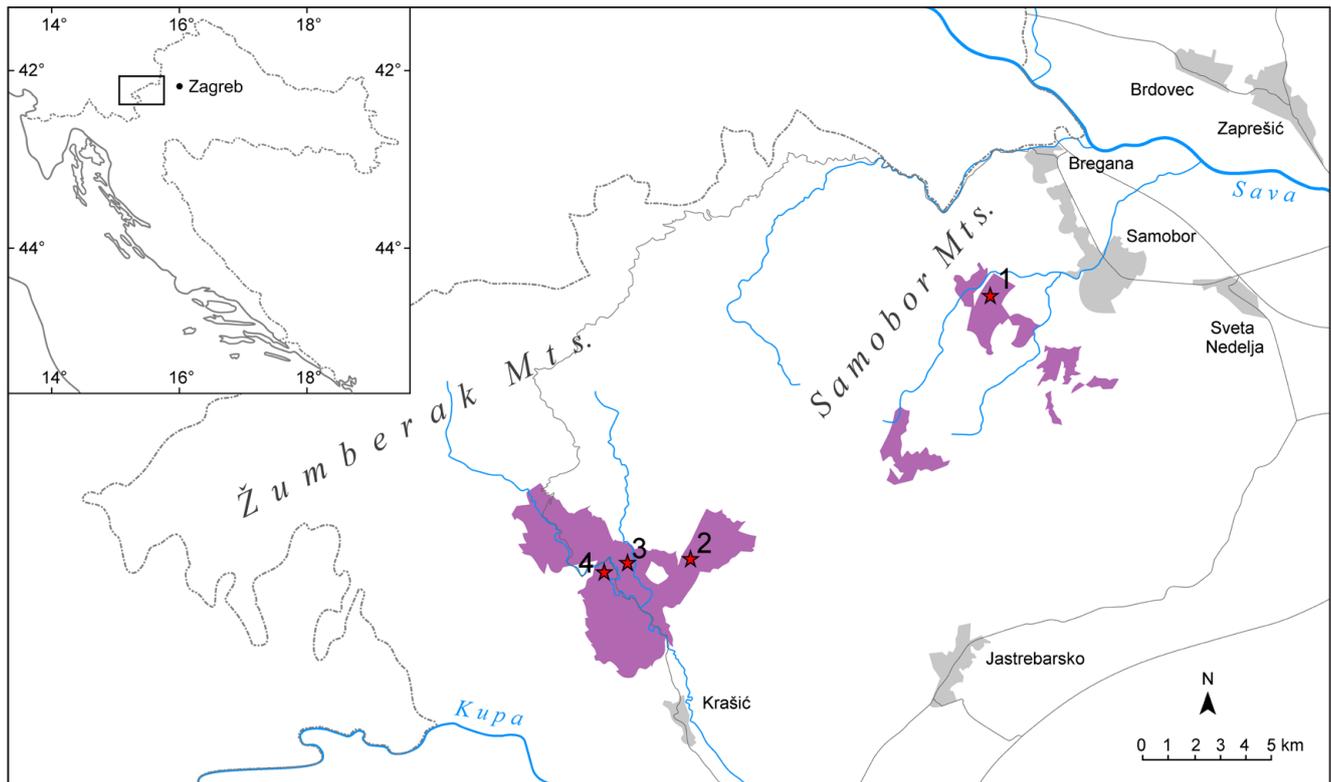


Fig. 1 - Topographic map of the Samobor and Žumberak Mts. area. Areas in purple mark the outcrops of Middle Triassic rocks, as per Pleničar et al. (1976) and Šikić et al. (1978). Red stars mark the localities of interest: 1 – Gregurić Breg, 2 – Radilovec Jaruga, 3 – Vlašić Brdo, 4 – Kolići.

of cherts, siltstones and volcanoclastics, while the upper part mostly comprises the hemipelagic limestones alternating with volcanoclastics. The lower portion was dated as Illyrian, due to the indicative radiolarians found at the Kolići and Bezjak localities (Goričan et al. 2005). The upper part of the section occasionally yields fossils of ammonoids. Shallow-water limestone boulders, most likely of displaced origin, also occur.

These and other contemporary basinal successions of the Internal Dinarides and Southern Alps were deposited on subsided blocks in graben and half-graben settings, at depths of no more than 300 meters (Goričan et al. 2005; Celarc et al. 2013). The red and grey nodular, condensed ammonoid bearing limestones were probably formed in well oxygenated conditions with reduced sedimentation rates, such as on current-swept deep structural highs or drowned platform slopes, with these low sedimentation rates also being facilitated by the absence of calcareous planktic microorganisms in the Triassic times (Wendt 1973; Tozer & Calon 1990; Blendinger 1991; Mandl 2000; Brack et al. 2007; Hornung et al. 2007;

Pomoni & Tselepidis 2013).

The progradation of carbonate platforms eventually infilled these basins, resulting in the deposition of shallow-water carbonates now preserved as late-diagenetic dolostone with little or no fossils (Grgasović 2007).

MATERIALS AND METHODS

The authors have examined over 200 ammonoid specimens stored in five public institutions: the Croatian Natural History Museum in Zagreb (HPM museum numbers), the Faculty of Science in Zagreb (Department of Geology, Division of Geology and Palaeontology; GPZ collection numbers), the Samobor Museum (SM museum numbers), The Museum of Krapina Neanderthals (MKN museum numbers), and the Faculty of Mining, Geology and Petroleum Engineering (RGNF collection numbers).

The localities of interest in the Samobor and Žumberak Mts. were visited. Outcrops, although limited, were examined and a fundamental understanding of the succession of strata was gained, allowing for construction of schematic stratigraphic columns (Fig. 2). Comparisons with previous literature and conversation with the locals allowed for the reidentification of locations where fossils were collected. This was especially useful for the Gregurić Breg locality. Several new fossils (mostly *Trematoceras* and *Proarcestes*) were collected at some of the localities, but the soil coverage prevented gain of more mean-

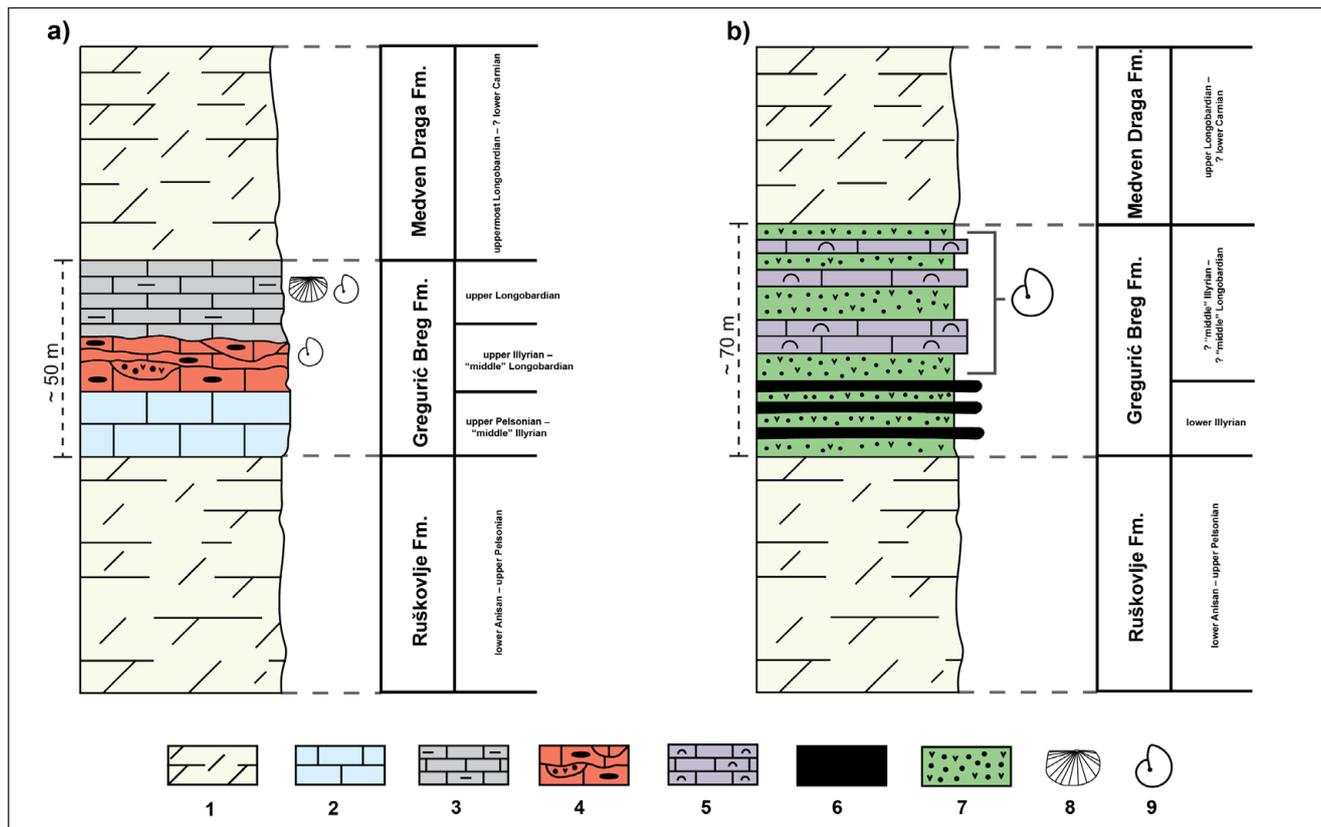


Fig. 2 - The schematic stratigraphic columns of the localities of interest; a) Gregurić Breg locality, Samobor Mts., b) generalization of the Žumberak Mts. localities. To see variation between Kolići and Bezjak sections (Žumberak Mts.), refer to Goričan et al. (2005). Legend: 1 – late diagenetic dolostone, 2 – shallower-water thick-bedded limestone, 3 – thinly bedded, marly limestones, with occasional occurrences of chert and pyroclastic rocks, 4 – grey to red nodular silicified limestone with lenses/layers of ammonitic limestone and pyroclastic rocks, 5 – bedded hemipelagic limestone with cephalopods and juvenile pelagic bivalves, 6 – radiolarian chert, 7 – pyroclastic rocks, 8 – occurrence of the bivalve *Daonella*, 9 – occurrence of ammonoids. The overall thickness of the basal deposits in each column is a rough estimate.

ingful results using currently available resources. Potential for bed-by-bed collecting is yet to be recognized but remains unlikely at the mostly exploited Gregurić Breg locality.

Some of the specimens were prepared using pneumatic tools and diluted (5%) hydrochloric acid. The photographs of the specimens were captured using cameras NIKON D3100 and CANON D6 (courtesy of Nives Borčić) and were edited in Adobe Photoshop. Drawings were illustrated in Adobe Illustrator.

When possible, the following measurements of specimens are given: conch diameter ($D = H + h + U$), the maximum whorl height in D (H), the minimum whorl height in D (h), the umbilical width (U), the whorl width in H (W), and the whorl width in h (w). All the measurements were taken in millimetres (mm). Additional parameters are also provided: W/H , U/D (both expressed in decimal), as well as the involution rate [SGR (%) = $(H-h)/h$]. Measurements marked with * are estimates.

The terminology used for the external morphology of the conch (e.g., coiling, ornamentation, ventral morphology) closely follows that of Arkell (1957) and Klug et al. (2015). The terminology of the suture line follows that of Wedekind (1916) and Kullmann & Wiedmann (1970), with additional modifications according to Korn et al. (2003). The terminology used for the shape of the whorl section is not standardized and is further clarified below. Note that ventral morphological features such as nodes, furrows, keels, etc. are not included in the shape of the whorl section:

Circular = with convex flanks passing uninterrupted into the rounded venter, about as high as wide; **sub-circular** is either more compressed or depressed.

Quadrate = with flat parallel to sub-parallel flanks, marked ventrolateral shoulders and a wide venter, as high as wide; **sub-quadrate** either has more convex flanks and/or less pronounced shoulders.

Rectangular = like quadrate but is either markedly compressed or depressed; **sub-rectangular** has more convex flanks and/or less pronounced shoulders.

Trapezoidal = with flat to feebly convex converging or diverging flanks, marked ventrolateral shoulders and a wide to moderately narrow venter, compressed to depressed; **sub-trapezoidal** is either more convex or has less pronounced shoulders.

Ovoid = a) with convex flanks uninterruptedly converging into a moderately wide to acute venter, widest below the mid-flank; or b) with convex flanks uninterruptedly converging into a wide venter, widest above the mid-flank, effectively reverse of a). Compression variable.

Triangular = with flat or very mildly convex flanks uninterruptedly converging into a relatively narrow to acute venter, widest relatively close to the umbilicus; **sub-triangular** has more convex flanks and is basically synonymous with **sub-ovoid**. Compression variable.

Elliptical = with convex flanks uninterruptedly converging into moderately wide to acute venter, widest approximately at the mid-flank, compressed.

Lanceolate (cf. Balini 1998; figured as a shape of the venter in Arkell 1957) = with flanks that are convex to flat in the middle part, and then converge concavely into a narrow to acute venter in the ventral part of the whorl, almost resembling a keel. Usually compressed.

RESULTS

Gregurić Breg Locality, Samobor Mts.

At the Gregurić Breg locality, 44 ammonoid taxa have been identified (Tab. 1; Pls. 1 – 9). A vast majority of the ammonoid fauna was collected from the red nodular limestone facies. Here, ammonoids mostly occur in several closely scattered lenticular bodies of uncertain origin, where they are extremely abundant and tightly packed (Salopek 1912; 1936). Along with ammonoids, the orthoceratid *Trematoceras* and the xiphoteuthidid *Atractites* are rather common macrofossils, often being found as fragments. The true nautilids are very rare, represented by a single specimen of *Syringonutilus subcarolinus* (Mojsisovics, 1882). Apart from cephalopods, these rocks also comprise bivalves identified as *Daonella* sp., *Bositra wengensis* (Wissmann in Wissmann & Münster, 1841), and *Mysidioptra kittlii* Bittner, 1895, as well as a single specimen of the gastropod *Loxonema croatica* Salopek, 1912. Very small, indeterminate crinoid ossicles are also present.

Thinly bedded limestones and marlstone containing *Daonella lommeli* that occur higher in the section also preserve a couple of small, fragmented ammonoid tests and impressions. They represent indeterminate ribbed, tuberculate forms. Salopek (1918) mentions an impression which he attributed to *Celtites epolensis* Mojsisovics, 1882, but this specimen was not identified during the subsequent research.

Although steinkerns are present, most examined ammonoids were, at least partially, preserved with shell. They are often covered by a somewhat thick ferro-manganese coating, which likely served to protect the shell from dissolution during diagenesis. The shell is recrystallized and in various states of preservation, but is often preserved rather well, although finer structures, such as growth lines, are seldom clearly visible. The body chambers (if preserved) and a few of the largest phragmacone chambers are usually infilled with red carbonate sediment, while the inner chambers of the phragmacone are filled with sparry calcite. Ammonoids

are often asymmetrically preserved, such that one side is eroded. This likely indicates formation of hardground surfaces during sedimentation, as well as erosion and possible reworking of fossils within the facies.

Mt. Žumberak Localities

Currently, the fossil record of ammonoids from Mt. Žumberak is much scarcer than that from the Gregurić Breg locality. Of the three nearby localities, the Vlašić Brdo locality has proven to be the most productive, although all ammonoids were collected in ex-situ boulders dug up during the building of the foundations of local houses (Sakač 1994; this paper). These specimens occur in yellowish-grey to reddish-grey, partially cherty bedded limestones, which are only slightly nodular. Along with ammonoids, orthoceratids and xiphoteuthids are also present, as are indeterminate crinoids, but also the remains of vertebrates (ribs, vertebrae), likely belonging to an ichthyosaur. Contrary to the statement of Sakač (1994) about ammonoids being “numerous and densely packed”, the observed specimens seem to be significantly rarer than those found at Gregurić Breg. Seventeen specimens belonging to nine taxa were identified (Tab. 2; Pls. 10, 11). Of these, *Falsanolcites recubariensis* (Mojsisovics, 1882), *Protrachyceras ladinum* (Mojsisovics, 1882), *Flexoptychites acutus* (Mojsisovics, 1882), and *Discoptychites* sp. are described in more detail. Some indeterminate, significantly damaged ammonoids are also stored in the collection of the HPM.

Sakač (1994) also reported scarce findings of ammonoids at the Radilovec Jaruga locality. Although the exact context of these findings, such as their host rock, is not clear from the report, the rough grainy texture of the fossils, mineral grains on their surface, and their reddish-white-green colour suggest they were found in tuffaceous rocks. Two ammonoids were identified (Tab. 2), a specimen of *Protrachyceras margaritosum* (Mojsisovics, 1882) and a specimen of *Monophyllites* sp.; only the first is described in more detail (Tab. 2; Pl. 10). A specimen of *Trematoceras* sp. has also been identified.

Only two ammonoids in this area are tied to a stratigraphic column. These occur at the Kolići locality and were reported by Sakač (1994) and Goričan et al. (2005) but were not figured or described. They were found in weakly silicified limestones approximately 30 meters above the underlying

Order	Superfamily	Family	Subfamily	Species	Original identification (Salopek 1912; 1936)
Ceratiina	Sageceratoidea	Sageceratidae		<i>Sageceras walteri</i>	
	Ceratiotoidea	Hungaritidae		<i>Hungarites mojsisovicsi</i>	
		Ceratiitidae	Paraceratinae	<i>Hallilucites rusticus</i>	
				<i>Hallilucites</i> aff. <i>rusticus</i>	<i>Hallilucites zagoriensis</i> (nomen dubium)
				<i>Hallilucites</i> cf. <i>arietiformis</i>	
			Nevaditinae	<i>Nevadites</i> cf. <i>avenonensis</i>	
	Clydonitoidea	Trachyceratidae		" <i>Anolcites</i> " cf. <i>laczkói</i>	<i>Anolcites laczkói</i> var. <i>falcoidea</i>
			Arpaditinae	<i>Meginoceras</i> (?) sp.	<i>Anolcites</i> cf. <i>richthofeni</i>
			Anolcitinae	<i>Falsanolcites furcosus</i>	
				<i>Falsanolcites</i> cf. <i>rieberi</i>	<i>Anolcites laczkói</i>
				<i>Falsanolcites</i> cf. <i>gortanii</i>	<i>Anolcites arminiae</i> var. <i>angusta</i>
				<i>Falsanolcites</i> sp. Morphotype A	<i>Protrachyceras</i> aff. <i>vouki</i>
				<i>Falsanolcites</i> sp. Morphotype B	
			Protrachyceratinae	<i>Eoprotrachyceras</i> cf. <i>curionii</i>	
				<i>Eoprotrachyceras doraе</i>	
				<i>Eoprotrachyceras</i> sp. nov.	<i>Protrachyceras</i> cf. <i>pseudoarchelaus</i>
				<i>Protrachyceras margaritosum</i>	
				<i>Protrachyceras</i> cf. <i>pseudoarchelaus</i>	
				<i>Protrachyceras steinmanni</i>	
				<i>Protrachyceras longobardicum</i>	
				<i>Protrachyceras ladinum</i>	
				<i>Protrachyceras</i> sp.	<i>Protrachyceras</i> aff. <i>pseudoarchelaus</i>
	Ptychitoidae	Ptychitidae		<i>Flexoptychites</i> sp.	<i>Ptychites gretae</i> (nomen dubium)
				<i>Parasturia emmrichi</i>	<i>Ptychites</i> cf. <i>uhligi</i> ; <i>P.</i> cf. <i>angustoumbilicatus</i>
		Sturiidae		<i>Sturia sansovinii</i>	
				<i>Sturia semiarata</i>	
				<i>Sturia</i> sp.	
				<i>Discoptychites</i> sp.	
	Arcestoidae	Arcestidae		<i>Proarcestes</i> spp.	
		Joannitidae		<i>Joannites</i> sp.	<i>Joannites</i> (?) aff. <i>tridentinus</i>
		Cladiscitidae	Procladiscitinae	<i>Procladiscites</i> aff. <i>brancoi</i>	<i>Procladiscites</i> (<i>Hypocladiscites</i>) <i>brancoi</i>
				<i>Psilocladiscites molaris</i>	<i>Phyllocladiscites crassus</i>
	Pinacoceratoidea	Japonitidae		<i>Japonites raphaeliszoja</i>	
		Gymnitidae		<i>Gymnites bosnensis</i>	
				<i>Gymnites</i> cf. <i>incultus</i>	
				<i>Gymnites</i> (?) <i>uhligi</i>	
				<i>Gymnites</i> (?) " <i>bosnensis nodosa</i> "	
				<i>Epigymnites</i> cf. <i>ecki</i>	
				<i>Epigymnites credneri</i>	
				<i>Epigymnites</i> cf. <i>peciensis</i>	<i>Gymnites</i> cf. <i>obliquus</i>
				<i>Epigymnites</i> sp.	<i>Gymnites credneri</i>
				<i>Parapinacoceras aspidoides</i>	
				<i>Parapinacoceras</i> sp.	<i>Gymnites</i> (?) <i>intermedius</i> (nomen dubium)
		Pinacoceratidae		<i>Praepinacoceras damesi</i>	
Phylloceratina	Ussuritoidea	Ussuritidae		<i>Monophyllites wengensis</i>	

Tab. 1 - A list of examined Middle Triassic ammonoid taxa collected from the red nodular limestone facies of the Gregurić Breg locality. Note that the original identification is only specified when the new interpretation is significantly different; generic changes and changes in levels of certainty (cf., aff.) are not included.

Tab. 2 - A list of known Middle Triassic ammonoid taxa collected at multiple neighbouring localities in the Žumberak Mts.

Order	Superfamily	Family	Subfamily	Species	Locality
Ceratitina	Clydonitoidea	Trachyceratidae	Anolcitinae	<i>Falsanolocites recubariensis</i>	Vlašić Brdo
			Protrachyceratinae	<i>Protrachyceras margaritosum</i>	Radilovec Jaruga
				<i>Protrachyceras ladinum</i>	Vlašić Brdo
	Ptychitoidea	Ptychitidae		<i>Flexoptychites acutus</i>	Vlašić Brdo; Kolići
		Sturiidae		<i>Sturia</i> sp.	Vlašić Brdo
				<i>Discoptychites</i> sp.	Vlašić Brdo
	Arcestoidea	Arcestidae		<i>Proarcestes</i> sp.	Vlašić Brdo; Kolići
	Pinacoceratoidea	Japonitidae		<i>Japonites raphaeliszója</i>	Vlašić Brdo
		Gymnitidae		<i>Gymnites</i> cf. <i>incultus</i>	Vlašić Brdo
Phylloceratina	Ussuritoidea	Ussuritidae		<i>Monophyllites</i> sp.	Radilovec Jaruga; Vlašić Brdo

Anisian dolomite, indicating they occur in the lower half of the roughly 70 meters thick basinal succession present in this area (Goričan et al. 2005). One of them represents *Proarcestes* sp., while the other is a specimen of *Flexoptychites acutus* (Tab. 2; Pl. 10).

Ammonoids of the localities in the Žumberak Mts. are more poorly preserved than those found at the Gregurić Breg locality. The majority of them are preserved as steinkerns, while only a small proportion are covered by a poorly preserved shell that has recrystallized into sparry calcite, with no details being preserved (e.g., *Discoptychites* sp., *Japonites raphaeliszója*, a single *Proarcestes* sp.). Ferro-manganese crusts are not present on any specimens, which likely partially explains their poorly preserved or absent shells. Some ammonoids are asymmetrically preserved and partially eroded; this was observed in the field to be due to erosion at the bedding plane, likely indicating the formation of hardgrounds. The two ammonoids from the Radilovec Jaruga locality, likely collected from tuffaceous rocks, are some of the most poorly preserved, as they both lack tests, have poor steinkern surface preservation, and are deformed or fragmented.

DISCUSSION

Taxonomic Composition of the Gregurić Breg Ammonoid Assemblage

The present authors have examined 202 ammonoid specimens historically collected from the nodular limestones of this locality, not counting the numerous cross sections that can be seen in the rocks. By proportion (Fig. 3), members of closely related families Arcestidae and Joannitidae (combi-

ned for simplicity of classification; see Systematic Description) are by far the most numerous ammonoids in the collections (34%). The members of Trachyceratidae are significantly less numerous but are still very common (16%). *Monophyllites wengensis* (Klipstein, 1843), which makes up about 15% of the collections, is the most numerous ammonoid species. Members of Sturiidae, Gymnitidae and Ptychitidae are also somewhat common, while other families (Cladiscitidae, Ceratitidae, Pinacoceratidae, Japonitidae, Sageceratidae, Hungaritidae) appear significantly scarcer (< 5%). However, it must be noted that the abundance of ammonoids in the collections likely does not accurately reflect their true abundance in the assemblage, as they were sampled sporadically and selectively. This is very clearly shown by the abundance of small, often fragmentary discoidal ammonoids in these rocks, most likely belonging to *Sageceras walteri* (Mojsisovics, 1882) and *Praeepinacoceras damesi* (Mojsisovics, 1882). Hence, the members of Sageceratidae and Pinacoceratidae are likely much more common in this assemblage than what is suggested by the analysis of collected specimens. It is likely that juvenile ammonoids were similarly overlooked during sampling, which could alter the proportion of certain families.

Several specimens illustrated by Salopek (1912; 1936) could not be found in any of the studied collections and are therefore presently considered to be lost (Fig. 4). Some were not illustrated and thus had to be excluded from this research. However, two potentially important specimens were illustrated (Salopek 1936). Of these, the holotype of *Protrachyceras vouki* Salopek, 1936 is discussed in the Systematic Description section. The other specimen is the holotype of "*Kellnerites samoborensis*" Sa-

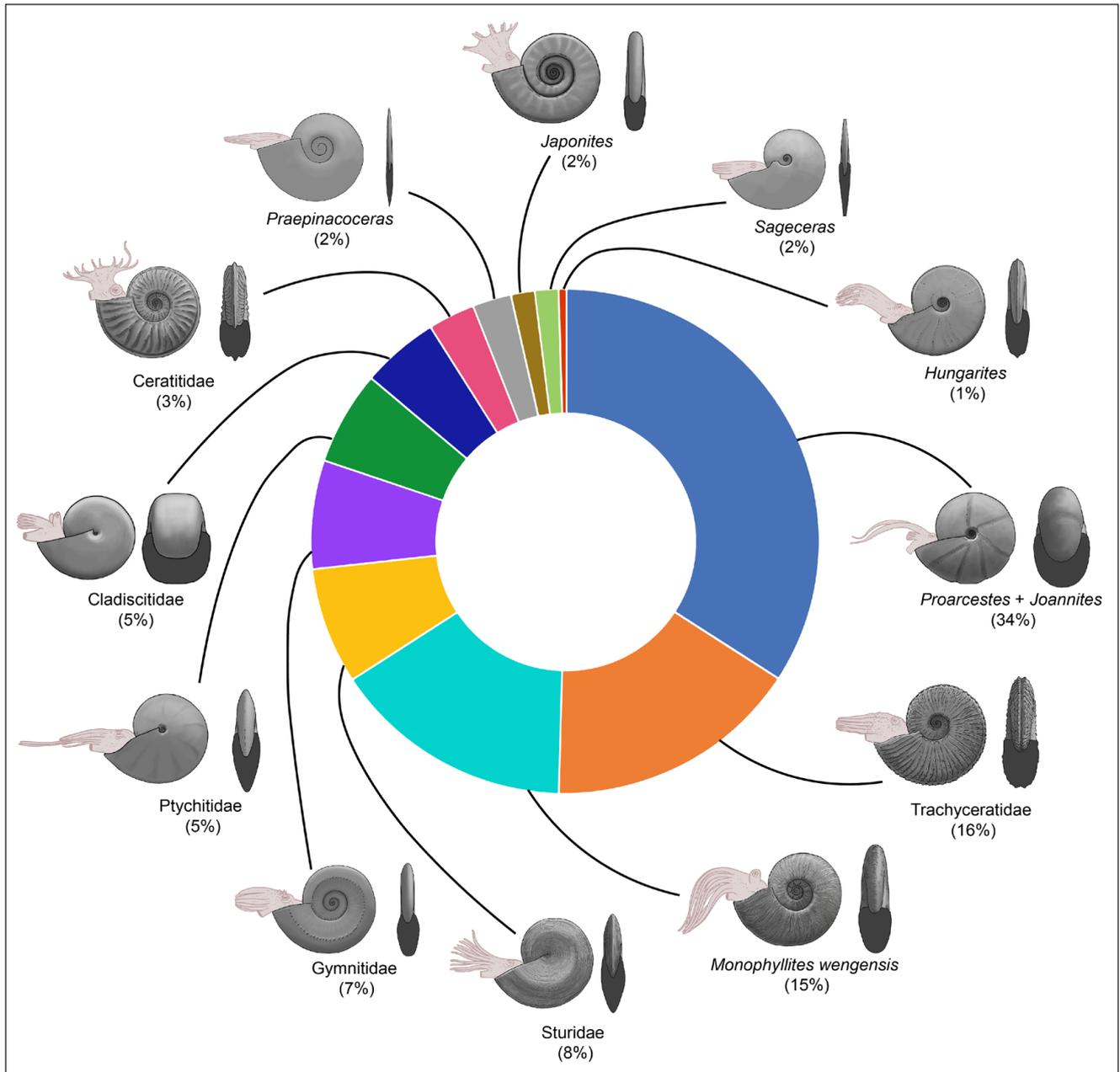


Fig. 3 - Proportion of the ammonoid taxa from the historic collections of the relevant institutions (HPM, GPZ, MKN, SM, RGNF). All specimens were collected at the Gregurić Breg locality (Samobor Mts.). Families Arcestidae and Joannitidae combined for ease of classification (see text). Ammonoid illustrations by Joshua Knüppe.

lopek, 1936. This species was considered by Vörös (2018) as potentially synonymous with *Reitziites reitzi* (Böckh, 1872). The present authors, however, consider this unlikely for two reasons. Firstly, Salopek (1936) describes *K. samoborensis* as having its first lateral row of nodes positioned above mid-flank on the body chamber; *R. reitzi* has its first lateral row of nodes positioned well below mid-flank. Secondly, the same author explicitly mentions that ribs of *K. samoborensis*, although very weak, pass onto the ven-

ter. This contrasts with *R. reitzi*, whose ribs often already disappear in the smooth band between the outer two rows of nodes, and the venter remains smooth. Although *R. reitzi* is a rather variable species (Vörös 2018), it is here hypothesized that *K. samoborensis* more likely represents a nevaditine, most likely *Paranevadites*, due to it being quadrituberculate. Whether this species is valid or not cannot be determined without a proper neotype, which is yet to be defined.

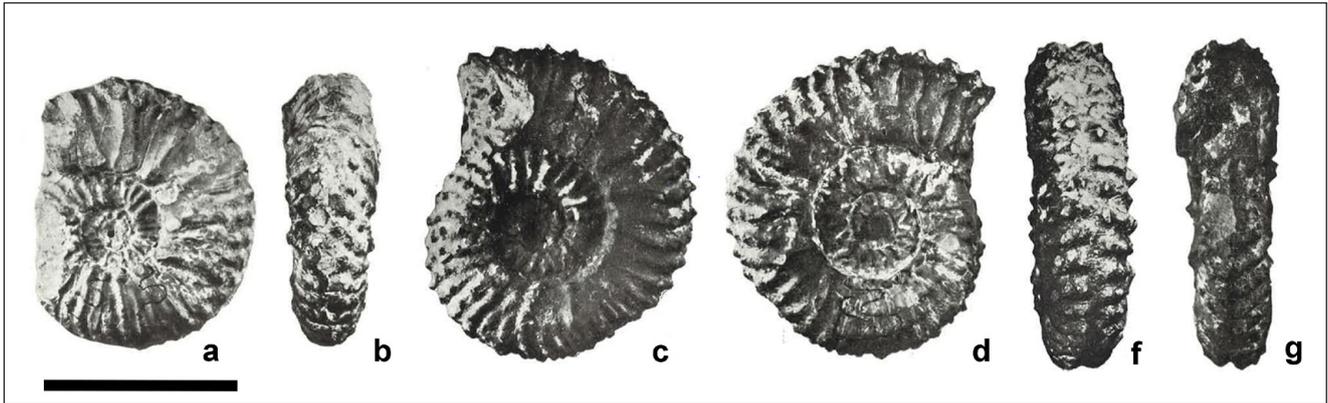


Fig. 4 - Lost holotype specimens from the Gregurić Breg locality (Samobor Mts.); a-b, HPM 3, holotype of *Kellnerites samoborensis* Salopek, 1936 (= *Paranevadites* sp.); a, left lateral view, b, ventral view; c-f, HPM 115, holotype of *Protrachyceras vouki* Salopek, 1936 (? = *Falsanolcites* sp. Morphotype A), c, right lateral view, d, left lateral view, e, ventral view, f, apertural view. Photographs adapted from Salopek (1936). Scale bar is 5 cm.

Ammonoid Biostratigraphy of the Tethyan Ladinian – an Overview

Although representing one of the two stages of the Middle Triassic, the subdivision of the Ladinian stage is still relatively poorly understood in the Tethyan province. Although its lower boundary has been decided on (Brack et al. 2005), the process and debate surrounding it has in turn produced a highly detailed ammonoid biostratigraphic scale of the preceding Illyrian substage, rivalling that of the upper Anisian of Nevada (Brack & Rieber 1986, 1993, Gaetani 1993; Mietto & Manfrin 1995a; Mietto et al. 2003; Manfrin et al. 2005; Vörös et al. 2003; Brack et al. 2003, 2005; Jenks et al. 2015). The uppermost Ladinian was also studied in detail during the investigation of the Ladinian – Carnian boundary in the Southern Alps (Broglio Loriga et al. 1999; Mietto & Manfrin 1995b, Mietto et al. 2008, 2012). The ammonoid faunas of these stratigraphic intervals are, as a result, well-known both taxonomically and biochronologically.

At the base of the Ladinian substage (Fassanian), most authors recognize at least one ammonoid zone, the Curionii zone (Brack & Rieber 1986, 1993; Fantini Sestini 1994; Brack et al. 2005; Vörös et al. 2008). The index taxon of this zone is *Eoprotrachyceras curionii*, the first occurrence (FO) of which also indicates the base of the Ladinian. However, some authors working in the Southern Alps recognized three horizons within this zone, each with slightly different fauna: the *Eoprotrachyceras curionii* horizon, the *Chieseiceras perticaense* horizon, and the *Falsanolcites recubariensis* horizon (Brack & Rieber 1986; Fantini Sestini 1994). The diversity of forms

present in these horizons is, however, relatively low. The latter two horizons were combined by Mietto & Manfrin (1995a) into a separate Recubariensis subzone; some authors accept such a subdivision (Mietto et al. 2018; Balini et al. 2010; Jenks et al. 2015), sometimes treating it as a subzone of the Curionii zone itself (Kozur 2003).

Although the lowermost parts of the Ladinian are currently less understood compared to the Illyrian substage (Anisan), the subdivision of this stage becomes particularly problematic in the levels above the horizon with *F. recubariensis*. This is in part due to the still undefined base of the Longobardian substage (i.e., upper Ladinian). Most recently, Jenks et al. (2015) suggested three possibilities. First of these is the FO of the genus *Protrachyceras*. This is potentially most practical for the western Tethyan province, as fossils of *Protrachyceras* and its predecessor *Eoprotrachyceras* are plentiful in this region (Fig. 8). However, their taxonomy suffers a problem in that the distinction between these taxa is based solely on the suture line. This feature is not well documented for some of the relevant species. The evolutionary transition from the ceratitic condition of *Eoprotrachyceras* and the sub-ammonitic to ammonitic condition of *Protrachyceras* also appears to be gradual.

The second option is drawing the Fassanian – Longobardian boundary at the uppermost ammonoid fauna of the Buchenstein Formation in the Southern Alps. However, this option raises potential problems, as it would mean that the lower part of the classic Archelaus zone (equivalent to the Longobardicum subzone), traditionally considered

to belong to the Longobardian, belongs instead to the underlying Fassanian substage (cf. Brack & Rieber 1993). The third option is to draw the boundary at the FO of several genera within the subfamily Arpaditinae, namely *Meginoceras* and *Silentoceras*. This option is appropriate for the localities in Canada, where these genera are common (Tozer 1994), as well as the eastern parts of the Tethyan province such as the Himalayas and potentially as west as Anatolia (Balini et al. 1998; Krystyn et al. 2004; Chen et al. 2016). Despite this, these two genera remain virtually unreported in the European western Tethys, to the point that the present authors have failed to identify any illustrations of these taxa in the literature, although some mention of their presence exists (e.g., *Silentoceras* on the stratigraphic column by Krystyn 1983; Mietto & Manfrin, pers. correspondence 2022).

The interval that follows the Recubariensis horizon has been a source of much uncertainty. Originally part of the over-encompassing Archelaus zone, Krystyn (1983) established the new Gredleri zone for this interval. This was based on the occurrence of *Protrachyceras* cf. *gredleri* in the condensed, but apparently well-bedded and not faunally mixed Hallstat-type limestones of Argolis, Greece. Unfortunately, no ammonoids were figured or described in that work. Despite the apparent rarity of the index taxon in the literature, the Gredleri zone was subsequently adopted as a name for the interval preceding the Archelaus zone. Some authors considered this interval as belonging to the Longobardian substage (Krystyn 1983; Mietto & Manfrin 1995a; Vörös 1998; Kozur 2003; Lucas 2010), while others considered it a part of the Fassanian (Brack & Rieber 1993; Brack et al. 2007; Balini et al. 2010; Chen et al. 2015; Jenks et al. 2015). The zone was also subdivided into the Margaritosum subzone and Gredleri subzone by Mietto & Manfrin (1995a), which some authors accepted (Lucas 2010; Balini et al. 2010; Jenks et al. 2015; Mietto et al. 2018). Recently, however, Mietto et al. (2018) concluded that the lectotype of *Protrachyceras gredleri* (Mojsisovics, 1882) was likely collected from much younger strata, equivalent to the upper Ladinian Neumayri subzone. Additionally, many of the apparent juvenile *P. gredleri* from the literature represent members of the genus *Falsanolcites* (cf. Rieber & Brack 2004), although this may not be true for all of them (see examples in Pisa 1966; Vörös 1998; Pálffy et al.

2003). As such, the taxonomy of this species is unstable, and its range is likely to be misinterpreted. Since this is a proposed index species, its taxonomic revision should become a priority.

As per Mietto et al. (2018), the interval between the Recubariensis horizon and the Archelaus zone would be better termed the Margaritosum zone. *P. margaritosum* appears above *F. recubariensis* in several stratigraphic sections in the Southern Alps (De Zanche & Mietto 1986; Brack & Rieber 1993; Fantini Sestini 1994; Mietto & Manfrin 1995a). Whether this interval belongs to the Fassanian or the Longobardian depends on the chosen definition of their boundary. Apart from the index taxon, the sequence of faunal elements of the Margaritosum zone remains poorly studied. Ammonoid occurrences in this interval appear to be somewhat rare in most well-studied stratigraphic sections where this zone is present (Brack & Rieber 1993).

Relatively poor representation of faunal elements in otherwise well-studied sections is also a problem plaguing the following interval: the Archelaus zone. This classic zone has been subdivided into two separate intervals by Mietto & Manfrin (1995a): the lower Longobardicum and the upper Neumayri subzones. This subdivision has been accepted by multiple subsequent authors (Broglia Loriga et al. 1999; Lucas 2010; Balini et al. 2010; Mietto et al. 2012, Chen et al. 2015; 2016). Other authors, however, opted to continue using the undivided Archelaus zone (Vörös 1998; Brack et al. 1999; Kozur 2003; Pálffy et al. 2003; Brack et al. 2005, 2007; Brack & Rieber 2019). In several works, both options are considered (Balini et al. 2000, 2006; Jenks et al. 2015). In well studied stratigraphic sections, the exact boundary of the Margaritosum and the Longobardicum subzone is currently still unclear, and their superposition is rarely preserved (Brack & Rieber 1993; Mietto & Manfrin 1995a; Fantini Sestini 1994). The exceptions to the latter problem are the Bagolino section (Brack & Rieber 1986, 1993) and the Esino limestones of Val Parina (Fantini Sestini 1994). There, the index taxon *Protrachyceras longobardicum* occurs above *P. margaritosum*. The superimposition of the Neumayri subzone by the uppermost Ladinian Regoledanus zone, as well as its subsequent superimposition by the lowermost Carnian strata, is well documented and studied in the Southern Alps (Mietto & Manfrin 1995a, b; Broglia Loriga et al. 1999; Mietto et al. 2012). The

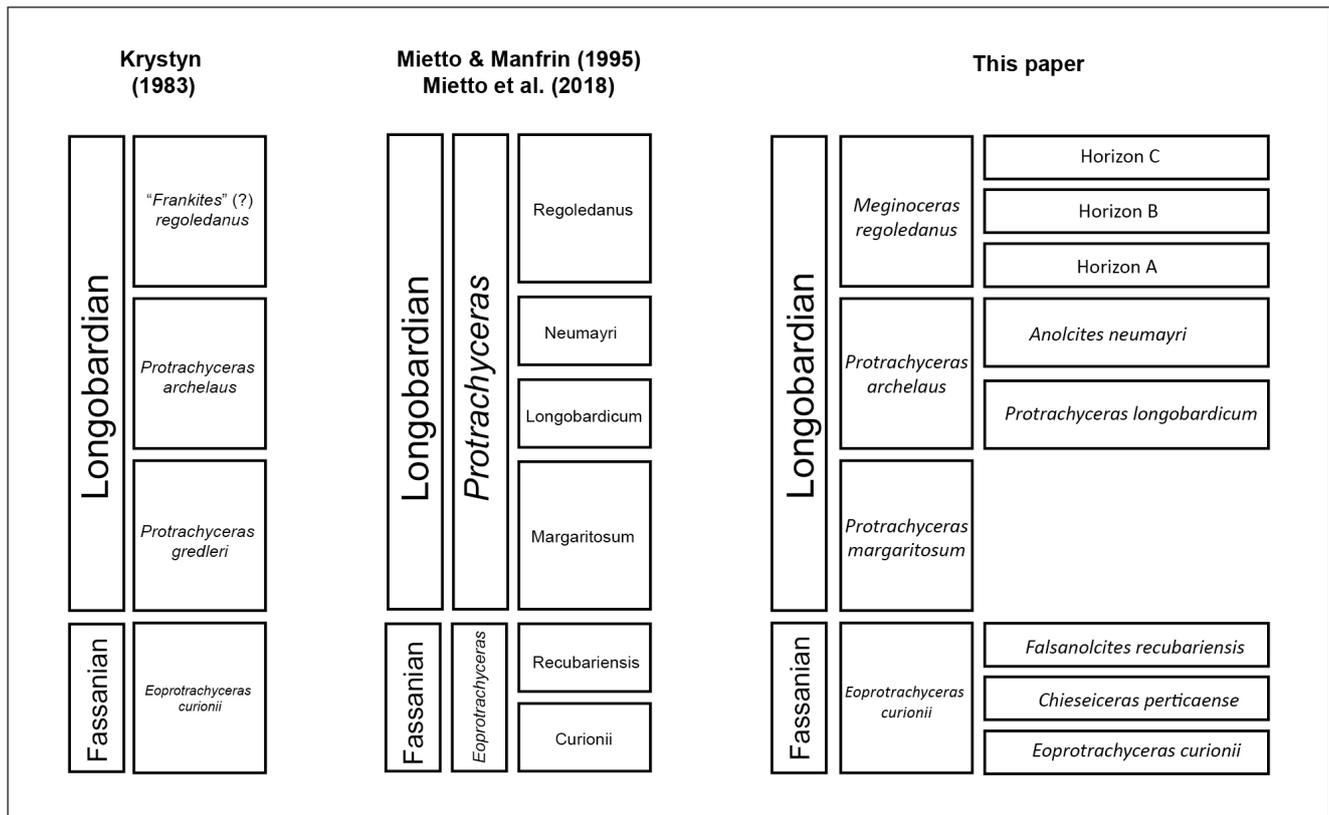


Fig. 5 - Comparison of the commonly used Ladinian ammonoid zonal/sub-zonal schemes of the Tethyan province with the scheme proposed in this paper.

contact between the Neumayri subzone and the lower Longobardicum subzone is, however, mostly implied in condensed facies or is unclear in uncondensed sections (Mietto & Manfrin 1995a).

A modified preliminary subdivision of the Tethyan Ladinian

This paper's ammonoid zonal scheme of the Tethyan Ladinian (Fig. 5) is primarily based on the proposal of Krystyn (1983) and works which use the same subdivision (e.g., Brack & Rieber 1993, 2019; Brack et al. 1995, 2005). Several modifications and additions are nevertheless proposed. As per the proposal of Mietto et al. (2018), the Gredleri zone is replaced by the more well-supported Margaritosum zone, as discussed in the previous chapter. These intervals are, however, largely considered equivalent. The Fassanian–Longobardian boundary is drawn only tentatively at the base of this zone.

Furthermore, the zonal scheme (Fig. 5) is augmented with the addition of subzones and horizons, to try and compile most of the previously collected biostratigraphic data from the literature. Firstly, the

Curionii zone is subdivided into the Curionii, Perticaense and Recubariensis horizons, or, alternatively, subzones. The latter two subdivisions are the equivalents of the Recubariensis subzone of Mietto & Manfrin (1995a), but are tentatively considered separate. Overlap between the index taxa *Chiseiceras perticaense* and *Falsanolcites recubariensis* exists and it is evident at the Pèrtica section in Lombardy (Brack & Rieber 1986), but the vertical distribution of taxa at localities like Bagolino (Brack & Rieber 1993; Gaetani 1993; Brack et al. 2005) and Val Parina (Fantini Sestini 1994) suggest this overlap might be minimal. The Archelaus zone (cf. Krystyn 1983) is tentatively kept but is subdivided into the Longobardicum and Neumayri subzones of Mietto & Manfrin (1995a), since they are the equivalents of this interval. However, their boundary is marked as uncertain due to the lack of published evidence of their direct superposition. Lastly, the Regoledanus zone is provisionally subdivided into three unnamed horizons, based on the extensive work of various authors that considers the topic of the Ladinian – Carnian boundary (charts in: Mietto & Manfrin 1995b; Broglio Loriga et al. 1999).

All of the elements of the proposed subdivision should, at least in theory judging by the available data, represent interval zones bound by the first appearances of index taxa. The genus-based zonal subdivision first proposed by Mietto & Manfrin (1995a) is not used here due to two key factors. Firstly, the problem of using the first occurrence of genera as zonal markers, especially regarding the phylogenetically connected genera that occur in a certain sequence, is that the exact taxonomic boundary between one such genus and another can be difficult to objectively establish. This is due to the existence of transitional forms (see Systematic Description section for Protrachyceratinae). The second problem is the possibility of future discoveries of the members of the same genus that occur earlier than those currently known. To this one could also add possible revisions of the genus that may exclude some members. For these reasons, zones based on species are considered more stable.

This scheme (Fig. 5) is only tentative and mostly based on literature, but the present authors believe it is inclusive of most of the published data. There is the possibility for the further improvement of the Ladinian ammonoid zonal schemes in the western Tethyan province. Ideally such improvements should be made in stratigraphic sections without significant condensation. Condensed Hallstatt-type limestone can also provide useful data if the condensation has not reached the level of mixed fauna (e.g., Krystyn 1983; Vörös 1998). The crucial factor, however, is the careful taxonomic treatment and, if necessary, revision of certain taxa; some of the ammonoid collections mentioned in the various cited works are yet to be properly figured and described in detail. For this endeavour, basinal deposits in north-western Croatia should also be further prospected for ammonoid remains. Nevertheless, the current knowledge of the western Tethyan Ladinian biostratigraphy is quite adequate for drawing meaningful conclusions about the stratigraphy of the studied localities.

Implications for the stratigraphy of the studied area

At the Gregurić Breg locality, the vast majority of ammonoid specimens were collected from the condensed nodular, Hallstatt-type limestone facies (Fig. 2a). As can be discerned from the descriptions of Salopek (1912; 1936) and the subsequent fieldwork at the locality, almost all ammonoids were col-

lected from multiple neighbouring lenticular bodies within a small area, spanning less than 30 m. Precise geometry of these sedimentary bodies is not clear due to them being mostly exploited or covered by recent soil, so their origin (as neptunic dykes, fracture fillings, etc.) was not presently determined. Such local accumulations of cephalopod fossils are, however, a distinct feature of Hallstatt-type limestones, and can occur either as stratiform accumulations or as fillings of various fractures and cavities (Krystyn et al. 1968; Schlager 1969; Wendt 1973; Hornung et al. 2007). The number of beds and their continuity (e.g., intercalations of different lithologies, such as chert or volcanoclastics) is also not precisely known, but the nodular limestone horizon of this locality is evidently rather thin. Despite a lack of more precise bed-by-bed information, these factors, combined with interpretations of Hallstatt-type and similar limestones as products of reduced sedimentation rates (Wendt 1973; Schlager 1974; Wendt & Aigner 1985; Tozer & Calon 1990; Blendinger 1991; Mandl 2000; Pomoni & Tselepidis 2013), allow for the treatment of this horizon as a “pseudo-discontinuity” between strata that over- and underlie it. Hence, the ammonoids found here, although not collected bed-by-bed, can still help reveal the timing of the significantly reduced sedimentation and constrain the upper and lower boundaries of other basinal deposits of this locality.

The oldest ammonoids found at the Gregurić Breg locality are dated to the late Illyrian (Fig. 6). This stratigraphic interval is well studied in the western Tethyan province, and the ranges of a significant portion of the ammonoids which occur in this interval are known to a precise degree. This work utilizes the most recently established ammonoid zonal/sub-zonal scheme established at the Balaton Highland, which also correlates well with the Alpine localities (Vörös 2018). However, contrary to the decision of Vörös (2018), the horizon with *Chiesoceras chiesense* (Mojsisovics, 1882) is also included in the stratigraphic chart. Despite being confined to a single bed or a couple of beds in otherwise uncondensed sections, it must be noted that this horizon might correspond to a maximum flooding surface and could therefore itself be significantly condensed and thus represent a significant amount of time (De Zanche et al. 1993; Gianolla et al. 1998; Mietto et al. 2003). Not everybody agrees with this interpretation, however (e.g., Brack & Rieber 2003).

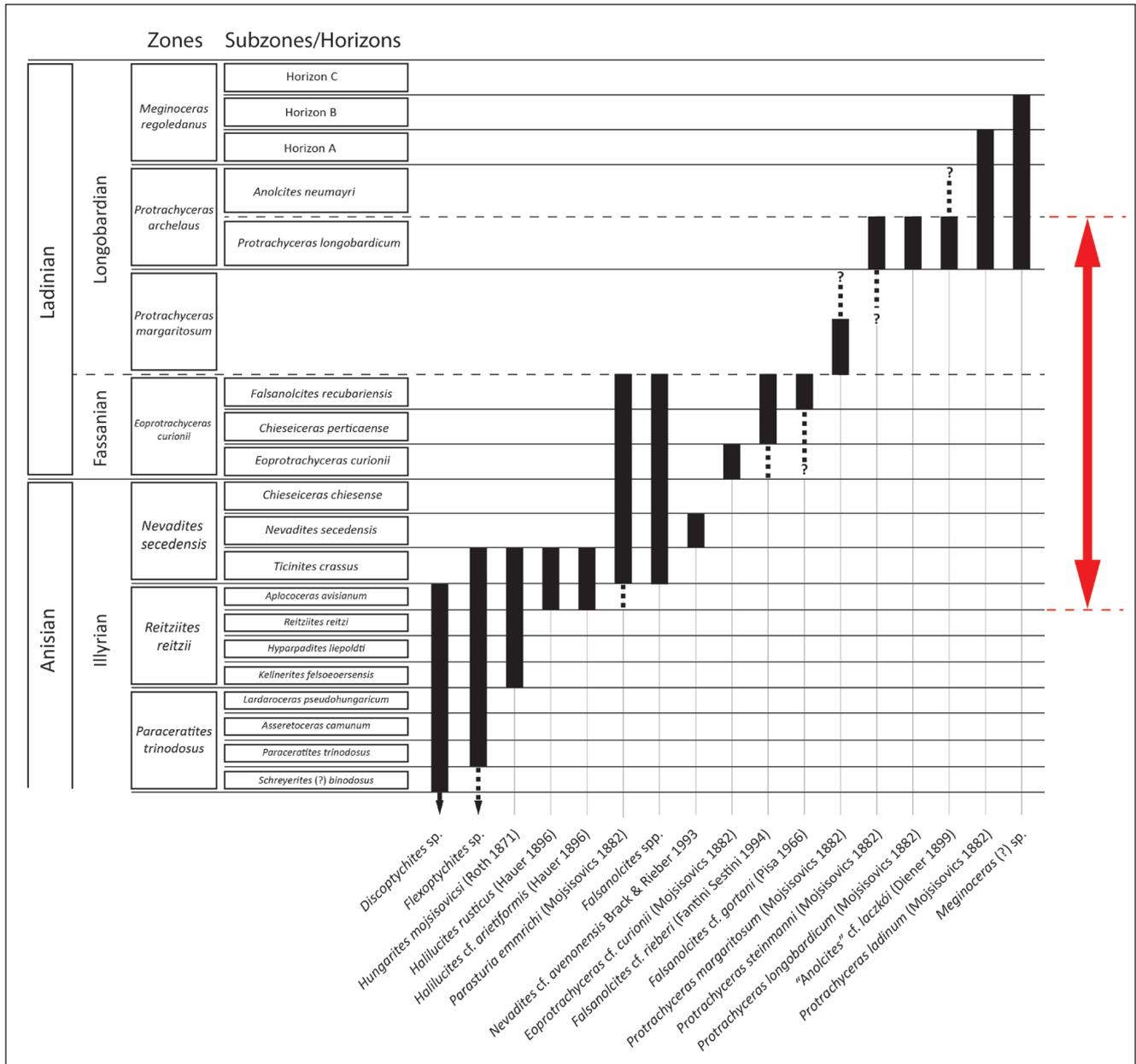


Fig. 6 - Ammonoid range chart for the red nodular limestones of the Gregurić Breg locality. Red arrow indicates the most likely span of deposition of these rocks. The ammonoid zonal/subzonal scheme used is discussed in the main text. Ammonoid ranges based on: Brack & Rieber (1986, 1993, 2019), Fantini Sestini (1994, 1996), Mietto & Manfrin (1995a, b), Broglio Loriga et al. (1999), Mietto et al. (2003, 2012, 2018), Rieber & Brack (2004), Brack et al. (2005), Manfrin et al. (2005), Vörös et al. (2008), and Vörös (1998, 2014, 2018).

Ammonoids of this locality which are undoubtedly restricted to the Illyrian (Fig. 6) are *Hungarites mojsisovicsi* (Böckh, 1872), *Halilucites* spp., *Nevadites* cf. *avenonensis*, *Discoptychites* sp. and *Flexoptychites* sp., while *Parasturia emmrichi* (Mojsisovics, 1882) and possibly some of the species of *Falsanolites* range from the uppermost Illyrian to lower Ladinian (Brack & Rieber 1986, 1993, 2019; Brack et al. 2005; Fantini Sestini 1996; Mietto & Manfrin 1995a; Mietto et al. 2003; Manfrin et al. 2005; Vörös 2014, 2018). Based on the FO of these taxa, it is

here suggested that the condensed nodular limestone horizon is not older than the Avisianum subzone of the Reitzi zone. Of the mentioned taxa, only *H. mojsisovicsi*, *Discoptychites* sp. and *Flexoptychites* sp. also occur in strata older than the Avisianum subzone. *Nevadites* cf. *avenonensis* is an element of the younger Secedensis subzone. The identification of the now lost holotype of "*Kellnerites samoborensis*" Salopek 1936 as a potential specimen of *Reitziites reitzi* by Vörös (2018), an ammonoid which would indicate the Reitzi subzone, is discussed in the previous

chapter and deemed unlikely. This age constraint implies that the strata underlying these beds, such as other basinal deposits and massive shallow-water limestones, have likely been deposited in earlier parts of the Illyrian, or even during the Pelsonian.

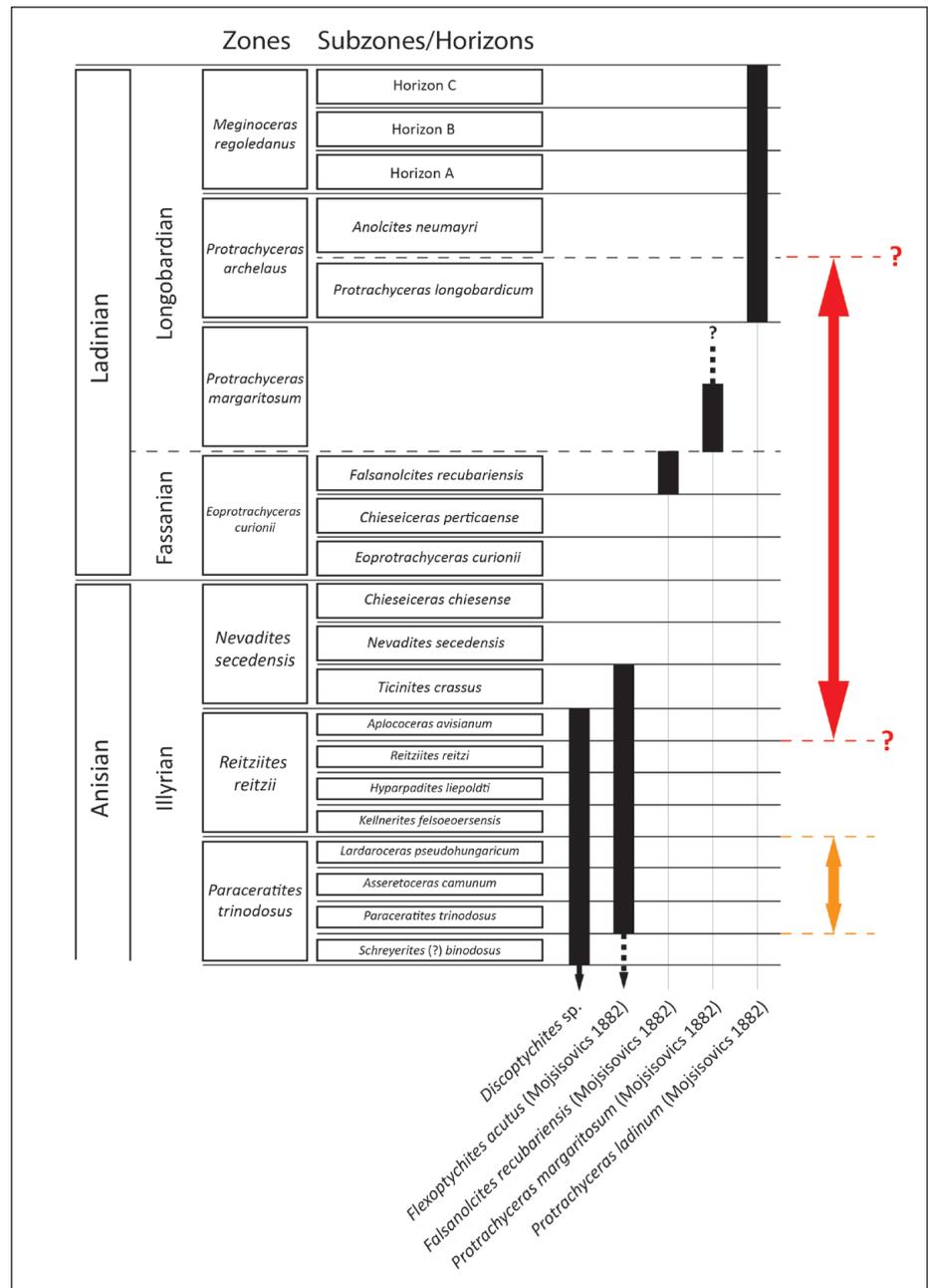
Deposition of the nodular limestones during the subsequent Fassanian substage (Early Ladinian) is clearly indicated by the presence of *Eoprotrachyceras* spp. and *Falsanolcites* spp., with the latter being particularly numerous (Brack & Rieber 1986; Rieber & Brack 2004; Brack et al. 2005; Vörös et al. 2008). Interestingly, the latest Illyrian – early Ladinian genus *Chieseiveras* has not been identified. This suggests that some horizons, such as those with *C. chiesense* or *C. perticaense*, may be missing or were not sampled. The lower Longobardian Margaritosum zone (cf. Mietto et al. 2018) is also preserved in this horizon, as proven by the presence of its index taxon, *Protrachyceras margaritosum*. The Longobardicum zone is indicated by the presence of *Protrachyceras longobardicum* (Mojsisovics, 1882), *P. steinmanni* (Mojsisovics, 1882), *P. ladinum* (Mojsisovics, 1882), *P. aff. pseudoarchelaus*, and possibly *Megjnoceras* (?) sp. and “*Anolcites*” cf. *laczkoii* Diener, 1899. No faunal elements exclusively restricted to the Neumayri or Regoledanus zones have been identified (see Mietto & Manfrin 1995a, b; Broglio Loriga et al. 1999; Mietto et al. 2012); the range of *Protrachyceras ladinum* is discussed in the Systematic Descriptions. As such, the upper limit of the age of the nodular limestone horizon is most likely the Longobardicum zone (Fig. 6). This is further supported by the fossil content of the overlying strata, which feature *Daonella lommeli*, a bivalve traditionally thought to be indicative of the uppermost Ladinian (Neumayri subzone and Regoledanus zone in the scheme used), but for which data from the Himalayas also indicates an occurrence in the lowermost Carnian Canadensis ammonoid zone (Balini et al. 1998; Krystyn et al. 2004).

In summary (Fig. 6), the nodular limestone horizon of the Gregurić Breg locality was likely deposited in the interval between the Anisian Avisianum subzone of the uppermost Reitzi zone (uppermost Illyrian) and the Ladinian Longobardicum (lower Archelaus) zone (“middle” Longobardian). This, taken together with the reduced thickness of this horizon, indicates that these limestones are significantly condensed. Although the use of ammonoids offers a better resolution, these results agree with the micropaleontological analysis of Goričan et al. (2005).

The different basinal succession preserved at the various Žumberak Mts. localities cannot, unfortunately, be dated as precisely. Of the stratigraphically informative taxa (Fig. 7), only the longer ranging taxa *Flexoptychites acutus* and *Discoptychites* sp. are confined to the Illyrian, with *Discoptychites* likely not reaching past the Avisianum subzone of the Reitzi zone (Manfrin et al. 2005; Vörös 2014, 2018); shorter ranging Anisian taxa are yet to be found. The short ranging Ladinian taxa are few but present; *Falsanolcites recubariensis* indicates the Recubariensis horizon of the Curionii zone (Fassanian), the lower Longobardian Margaritosum zone is indicated by the presence of *Protrachyceras margaritosum*, and *Protrachyceras ladinum* indicates the upper parts of the Longobardian but is present in multiple zones (Fantini Sestini 1994; Mietto & Manfrin 1995a, b; Vörös 1998; Mietto et al. 2018). The minimum age range provided by these fossils spans the Avisianum subzone of the Reitzi zone (upper Anisian) to the Longobardicum subzone of the Archelaus zone of the Ladinian (Fig. 7), but this may be expanded by future discoveries.

Unlike the nodular limestones of Gregurić Breg (Fig. 2a), this zonal range has a different implication due to several uncertainties. Most of the faunal elements were not collected at well exposed or well-studied sections, apart from two specimens of long ranging taxa *Flexoptychites acutus* and *Proarvestes* sp. collected at the Kolići locality (Sakač 1994; Goričan et al. 2005). While this may seem comparable to the collection methods practiced at the Gregurić Breg locality (Salopek 1912; 1936), it is important to note that specimens of the Mt. Žumberak localities occur in both limestones and volcanoclastics. This strongly suggests that these specimens do not all occur in the same general “horizon”, as is the case at the Gregurić Breg locality. Since *Flexoptychites acutus*, a species restricted to the Anisian and likely not occurring in strata younger than the Crassus subzone of the Secedensis zone (Illyrian), occurs some ~30-35 meters above the base of the basinal succession recorded at the Kolići section, it is reasonable to presume that the younger, Ladinian taxa occur further up the likely ~70 meter thick succession (Goričan et al. 2005). This, and the lithologies of their host rocks, would restrict them to the upper part of the local succession, where limestones alternate with volcanoclastics (Fig. 2b). The chert beds in the lower part of the succession were successfully

Fig. 7 - Ammonoid range chart for the upper limestone-rich part of the Žumberak Mts. basinal succession. Red arrow indicates the most likely span of deposition for these rocks, while the orange arrow indicates the correlated span given by radiolarians in the lower chert-rich part of the succession (Goričan et al. 2005). The ammonoid zonal/subzonal scheme used is discussed in the main text. Ammonoid ranges based on: Brack & Rieber (1986, 1993), Fantini Sestini (1994, 1996), Mietto & Manfrin (1995a, b), Vörös (1998, 2014, 2018), Manfrin et al. (2005), Mietto et al. (2018).



dated as Illyrian using radiolarians (Goričan et al. 2005), with one of the samples (Bezjak locality) being narrowed down to the *Tiborella florida* and the lower part of the *Spongosilicarmiger transitus* radiolarian zones (cf. Kozur 2003). With corrections according to the most recently proposed Illyrian ammonoid zonal scheme (Vörös 2018), these intervals correlate well with the Trinodosus ammonoid zone (Fig. 7). Therefore, current ammonoid finds at these localities, although mostly poorly documented, are likely restricted to the upper, limestone-rich part of the basinal succession, but the deposition of the succession likely began in the earlier parts of the Illyrian compared to what can be established using

ammonoids only (Fig. 7). Therefore, although indicative in that they show basal conditions persisted well into the Longobardian, more ammonoid specimens with better collection data are needed to draw further conclusions.

The likely uppermost ages of the basinal successions preserved at the Mt. Žumberak and Samobor Mts. localities also provide important information about the age of the deposits which overlie them. These are represented by massive, late diagenetic dolostones (Fig. 2) of the Medven Draga Formation (Šikić et al. 1979; Grgasović 1997, 2007). Since they preserved little to no fossils, their age is based on superposition alone, and was previously

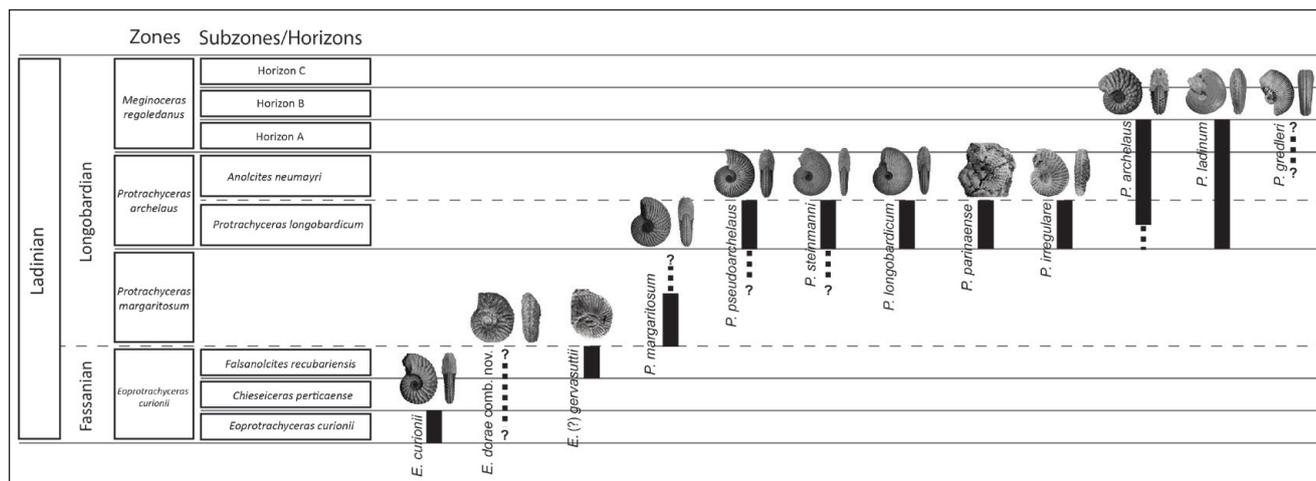


Fig. 8 - Known and likely biostratigraphic ranges of the named species of *Eoprotrachyceras* and *Protrachyceras* from the western Tethyan province. The species *E. gervasuttii* might alternatively be classified as *Falsanolites* (Rieber & Brack 2005; Mietto & Manfrin 2018). Eastern Tethyan species (e.g., *Protrachyceras spitiense* Diener 1908) are excluded, even though some similar unnamed taxa might be present (cf. Mietto & Manfrin 1995a). Images of ammonoids adapted from Mojsisovics (1882), Jadoul et al. (1993), Fantini Sestini (1994), and Urlichs (2017). Ranges of taxa adapted from Brack & Rieber (1993), Fantini Sestini (1994), Mietto & Manfrin (1995a, b), Vörös (1998), Brack et al. (2005), Vörös et al. (2008), and Mietto & Manfrin (2018). Zonal scheme is proposed in this paper.

assumed to be late Longobardian. The youngest examined ammonoids from the basinal successions (Figs. 6, 7) currently support this conclusion, but some caution is necessary. Specifically, the bivalve *Daonella lommeli* which occurs in thinly bedded limestones of the Gregurić Breg locality is now known to not only occur in the upper Ladinian, but also in the lowermost Carnian (Balini et al. 1998; Krystyn et al. 2004). From the same beds, Salopek (1918) reported impressions of the ammonoid *Celtites epolensis*; this could potentially restrict these beds to the uppermost Ladinian (cf. Broglio Loriga et al. 1999), but this specimen was not originally figured, nor was it identified in the present study. More ammonoid remains from equivalent strata were mentioned by Salopek (1936), and a few indeterminate fragments were identified by the present authors, suggesting a possibility of future discoveries that could indicate the age of these deposits more precisely. Nevertheless, even now it seems likely that the overlying Medven Draga dolomites are not only late Ladinian, but more precisely latest Longobardian or potentially even partially early Carnian in age. Although the dolostones of the Slapnica Formation, which overlies the Medven Draga Fm., have also been identified as Carnian based on microfossils, these are not restricted to any part of the stage and do not exclude the possibility of the early Carnian age of at least the part of the Medven Draga dolomites

(Grgasović 1997). As such, it is herein proposed that the Medven Draga formation should tentatively be regarded as uppermost Ladinian –? lower Carnian.

There is also a possibility that the somewhat deeper water conditions locally persisted across the Ladinian – Carnian boundary. The so-called “Lipovec limestone” exposed in the Samobor Mts. is an alternation of dark-coloured decimetre thick limestone beds with centimetre thick dark beds of marlstones, which is directly overlain by dolostones. Originally thought to represent Paleozoic strata (e.g., Šikić et al. 1979), it was later established as a Triassic succession, and somewhat unhelpfully classified as “marine sublittoral” (Babić et al. 1979). Despite their depositional environment not being thoroughly described and unlikely to be hemipelagic or pelagic, these rocks were likely deposited at substantially greater water depths than the dolomites capping them. The fossil record features simple trace fossils, fragments of bivalves and echinoderms, sponge spicules, ostracods, benthic foraminifera, *Tubiphytes*-like forms, and fragmentary calcareous algae (Babić et al. 1979). The dark colour and limonitized pyrite nodules also imply low oxygen conditions. Among rare macrofossils, several fragmentary ammonoids were referred to *Brotteotrachyceras brotheus* (Münster, 1834), *Trachyceras* sp., *Clionitites* sp., and *Lecanites glaucus* (Münster, 1834), clearly indicating that these deposits at least partially belong to

the lower Carnian (Babić et al. 1979). The contact of the “Lipovec limestones” with the underlying strata is currently unknown. As such, two possible origins of these strata exist and should be explored in future research: they may represent a separate Carnian subsidence event, or a local persistence of deeper marine conditions present in the broader area during the late Anisian and the Ladinian.

SYSTEMATIC DESCRIPTIONS

The classification scheme adopted in this work follows that of Tozer (1981) and is mostly updated following Tozer (1994) and Mietto et al. (2008). Families Ptychitidae and Sturiidae are separated from Pinacoceratoidea into Ptychitoidea, following the opinion of Tozer (1994). The family Japonitidae is kept separate from Gymnitidae, as per Tozer (1981) and Vörös (2018).

In the list of synonyms for each taxon, the present authors have decided only to list works where the species in question is at least partially figured, as to avoid potentially erroneous species assignments. The exceptions to this are the works of Salopek (1912; 1914; 1918; 1936), as they describe specimens which were mostly personally examined by the authors.

In the Systematic Descriptions section, preference is given to those taxa which are stratigraphically important. Aside from index fossils, this includes short ranging, as well as longer ranging taxa which are limited to certain stages or substages (e.g., *Flexoptychites*, *Discoptychites*). Other taxa (Pl. 9) described in detail include those in need of nomenclatural revision. Some species are well known and do not require further descriptions (e.g., *Monophyllites wengensis*, *Parapinacoceras aspidoides*, *Praepinacoceras damesi*, *Sageceras walteri*, etc.), and were correctly reported, identified, and described (Salopek 1912; 1936).

Order **Ceratitida** Hyatt, 1884

Superfamily Ceratitoidea Mojsisovics, 1879

Family Hungaritidae Waagen, 1895

Genus *Hungarites* Mojsisovics, 1879

Type species: *Ceratites mojsisovicsi* (Roth, 1887)

Hungarites mojsisovicsi (Roth, 1871)

Pl. 1, fig. 5.

- * 1871 *Ceratites mojsisovicsi* Böckh M. S. — Roth, p. 213.
- 1872 *Ceratites Zalaensis* n. sp. — Böckh, p. 145, pl. VII, figs 1, 2.
- 1873 *Ceratites Zalaensis* n. sp. — Böckh, p. 155, pl. VII, figs 1, 2.
- 1882 *Hungarites mojsisovicsi* (Boeckh) E. v. M. — Mojsisovics, p. 222, pl. VII, fig. 6, pl. VIII, fig. 3.
- non 1903 *Hungarites mojsisovicsi* Roth sp. — Frech, p. 10, pl. III, figs. 2, 3.
- non 1910 *Hungarites mojsisovicsi* Roth (*Judicrites*) — Renz, p. 33, pl. I, fig. 5.
- v 1912 *Hungarites* sp. ind. ex aff. *Mojsisovicsi* (Boeckh) Roth. — Salopek, p. 15., pl. V, fig. 2
- 1989 *Hungarites mojsisovicsi* (Roth, 1871) — Vörös & Pálffy, p. 19., pl. I, fig. 4, pl. II, fig. 2.
- 1989 *Hungarites* cf. *lenis* (Hauer, 1896) — Vörös & Pálffy, p. 19., pl. I, fig. 6.
- pars? 1993 *Hungarites zalaensis* (Böckh, 1872) — Brack & Rieber, p. 461, pl. 1, only figs. 3, 7, 8.
- 1993 *Hungarites mojsisovicsi* — Gaetani (ed.), p. 117, pl. 13, fig. 3.
- ? 1995a *Hungarites zalaensis* (Böckh, 1872) — Mietto & Manfrin, p. 551 (partim), pl. III, only fig. 6, non fig. 7.
- non 1995 *Hungarites zalaensis* (Böckh, 1872) — De Zanche et al., pl. II, fig. 7.
- 1998 *Hungarites mojsisovicsi* (Roth, 1871) — Vörös, p. 21, 38, 42, pl. IV, figs. 4, 5 (non fig. 6), pl. VI, fig. 1.
- 2002 *Hungarites mojsisovicsi* (Roth) — Vörös, p. 486, pl. 1, figs. 1, 2.
- ? 2005 *Hungarites zalaensis* (Böckh, 1872) — Manfrin et al., p. 481, figs. 9/24–27, non fig. 28.
- 2018 *Hungarites mojsisovicsi* (Roth, 1871) — Vörös, p. 116–119, text figs. 64 – 69, pl. XXX, figs. 4–6, pl. XXXI, figs. 1–5, pl. XXXII, figs. 1–4, pl. XXXIII, fig. 1,2, pl. XXXIV, figs. 1–3.

Material: a single partially and somewhat poorly preserved steinkern (HPM 109), with some parts possibly covered by fragments of the shell. It was previously very briefly described by Salopek (1912) but was not figured, except for the suture line. Collected at the Gregurić Breg locality.

Dimensions:

	D	H	h	U	W	W	W/H	U/D	SGR
HPM 109	-	34.1	-	-	15	-	0.44	-	-

Description. A moderate-sized *Hungarites*. The whorl section is very high oval, with the whorls being widest in the inner fourth of the flank. The flanks are very feebly convex, almost flat, and pass into rounded but distinct ventrolateral shoulders. The venter has a narrow and tall medial keel, laterally surrounded by flat and smooth bands which are angled towards the shoulders. The umbilical edge is rounded, while the umbilical wall is subvertical. There is no perceivable ornamentation on the flanks.

The external suture line, although poorly visible, is ceratitic to sub-ammonitic, as saddles are also weakly wrinkled. Four larger serrated lobes make up the external suture (E, A, U₂, U₃), with additional very small inner umbilical elements also being present in the region of the umbilical edge. The A lobe is the deepest, most developed one.

Remarks. Although Salopek (1912) originally designated this form as only being related to *H. mojsisovicsi*, attribution to this species is very probable considering the recent thorough revision of the genus (Vörös 2018). Very weak ornamentation is typical for this taxon and separates it from other species of *Hungarites*, while the almost sub-ammonitic suture also sometimes occurs (Vörös 2018).

Occurrence. *H. mojsisovicsi* has been recognized in the Southern Alps, the Balaton Highland and in the Dinarides. According to the data from the Balaton Highland (Vörös 2018), it ranges from the Felsoeoersensis subzone to the Crassus subzone, making it indicative of the Reitzii and early Secedensis zones of the Illyrian substage.

Family Ceratitidae Mojsisovics, 1879
Subfamily Paraceratitinae Silberling, 1962
Genus *Halilucites* Diener, 1905

Type species: *Ceratites* (*Hungarites*?) *rusticus* Hauer, 1896

Halilucites rusticus (Hauer, 1896)

Pl. 1, figs. 2, 3.

- * 1896 *Ceratites* (*Hungarites*) *rusticus* n. sp. — Hauer, p. 259, pl. IX, figs 1–4.
- ? 1896. *Ceratites* (*Hungarites*?) *planilateratus* Hauer — Hauer, pp. 261–262, pl. 11, Figs 1–3.
- v 1912 *Halilucites* cf. *rusticus* Hau. — Salopek, pp. 14–15, pl. I, fig. 2.
- ? 1913 *Ceratites* (*Halilucites*) aff. *rusticus* v. Hauer spec. — Toulou, p. 655, pl. XXIII, fig. 7.
- 1995 *Halilucites rusticus* (Hauer, 1896) — De Zanche et al., p. 148, pl. III, fig. 4.
- 1998 *Halilucites rusticus* (Hauer, 1896) — Vörös, p. 31, pl. VII, fig. 2.
- 2002 *Halilucites rusticus* (Hauer) — Vörös, p. 488, pl. 2, fig. 1.
- 2003 *Halilucites rusticus* (Hauer, 1896) — Mietto et al., p. 459, pl. 1, fig. 14, pl. 2, fig. 6.
- 2005 *Halilucites rusticus* (Hauer, 1896) — Manfrin et al., p. 496, figs 11/16, 17, 19, 20.
- ? 2007 *Halilucites rusticus* (Hauer, 1896) — Brack et al., p. 334, fig. 5/10.
- 2018 *Halilucites rusticus* (Hauer, 1896) — Vörös, pp. 100, 101; text fig. 58; pl. XXIV, figs. 13, 14; pl. XXV, fig. 1.
- 2019 *Halilucites rusticus* (Hauer, 1896) — Brack & Rieber, fig. 3, pl. 8.

Material: two partially preserved steinkerns (HPM 108.1, HPM 108.2), only one of which was figured by Salopek (1912). The second fragment was not figured but corresponds well with the first one and could have once conceivably belonged to the same individual. Collected at the Gregurić Breg locality.

Dimensions:

	D	H	h	U	W	w	W/H	U/D	SGR
HPM 108.1	-	25.1	-	-	18.6	-	0.73	-	-
HPM 108.2	60.7	20.5*	16.2	24*	-	-	-	0.40	27%*

Description. A moderate sized sub-evolute *Halilucites*. The whorl section is subquadrate, with its greatest width approximately at the mid-flank. Flanks are slightly convex. The venter is wide and tricarinate, with a blunt medial keel bordered by pronounced lateral furrows, which are in turn bordered by ventrolateral shoulders. Where well preserved, the medial keel is higher than the ventrolateral shoulders. The umbilical edge is rounded, while the umbilical wall is subvertical but not very high. Such variability is, however, quite common and explained by the Buckman's First Rule of Covariation (Westermann 1966; Monnet et al. 2015).

Flanks are ornamented by radial ribs and spiral rows of nodes. The ribbing is strong, coarse, and relatively irregular. It is mostly made up of slightly sigmoid and ventrally projected acute ribs that are narrower than the interspaces. The ribs appear as primaries, bifurcated ribs (bifurcating at various heights) and as intercalatory ribs of varying lengths. Individual ribs can vary in strength. The umbilical nodes are relatively weak but perceptible and appear irregularly, while blunt lateral nodes also appear somewhat irregularly at the bifurcation points of the ribs. Marginal nodes are either absent or very weak.

The suture is ceratitic with denticulate lobes and rounded saddles. There are likely four main lobes on the flank (A, E, U₂, U₃), with additional smaller umbilical lobes being present in the region of the umbilicus. Lobe A is the deepest and the most developed one.

Remarks. This specimen was originally assigned to *H. rusticus* with some uncertainty, but comparison with the more recent literature indicates that its morphology, including the presence of lateral nodes and the relatively irregular ribbing, fits well with this taxon. Despite this, some variation appears to be present among various figured specimens (e.g., compare Manfrin et al. 2005 with Vörös 2018), but it is here considered to be comparatively minor. That said, it should be noted that the specimens redescribed and figured here are relatively more evolute, more coarsely ornamented, and less compressed.

Among the species of *Halilucites* named by Hauer (1896), *H. rusticus* is characterized by well-developed lateral nodes, and variably dense, irregular ribbing with intercalated and split ribs. Its involution seems somewhat variable, as does the compression of its whorls. *H. arietitiformis* has more regu-

lar, mostly primary ribbing, sub-rectangular whorls with flat sides, and is somewhat more evolute. *Halilucites obliquus* (Hauer, 1896) and very similar *Halilucites intermedius* (Hauer, 1896) are more involute, have higher and more compressed whorls, exhibit well developed umbilical nodes but lack the lateral ones, and have very dense, relatively regular ribs. *Halilucites planilateratus* (Hauer, 1896) was considered by Manfrin et al. (2005) to belong to *H. rusticus*, while Vörös (2018) regarded it to be a specimen of *H. arietitiformis*; here, it is listed in the synonymy for both species, with query. The relationship of these species is described below, under *Halilucites* aff. *rusticus*.

Occurrence. Specimens of *H. rusticus* were described and figured from localities in the Dinarides, the Balaton Highland and the Southern Alps. It is characteristic for the Crassus subzone of the Secedensis zone, but also occurs stratigraphically lower, in the Avisianum subzone of the Reitzii zone. Both zones belong to the upper Illyrian stage of the Anisian.

***Halilucites* aff. *rusticus* (Hauer, 1896)**

Pl. 1, fig. 1.

v 1912 *Halilucites zagoriensis* n. sp. — Salopek, p. 14, pl. I, fig. 1.

Material: a single specimen (HPM 107) preserved as a steinkern, serving as a holotype of *Halilucites zagoriensis* Salopek, 1912. Preservation is somewhat poor and unequal on the left and right side. Collected at the Gregurić Breg locality.

Dimensions:

	D	H	h	U	W	W	W/H	U/D	SGR
HPM 107	73.4	25.7	20.5	27.2	14	-	0.54	0.37	25%

Description. A moderate sized, sub-evolute *Halilucites*. The whorl section is high subtrapezoidal, being widest in the inner third of the whorl height. Flanks are feebly convex. The venter is relatively narrow for the genus and is tri-carinate, with a rather high blunt medial keel bordered by lateral furrows, which are themselves flanked by carinate ventrolateral shoulders. The medial keel is significantly higher than the lateral shoulders. The umbilical edge is rounded, while the umbilical wall is vertical, but not very high.

The flanks are ornamented by radial ribs and spiral rows of nodes. The ribbing is very dense and relatively weak, generally sigmoid and projected ven-

trally and as wide as the interspaces. As far as can be seen, ribs are mainly primary or intercalated, but also sometimes bifurcated. Only well-developed umbilical nodes, rounded in cross section and present on almost every primary rib, can clearly be observed. Marginal nodes are clearly absent, while the lateral nodes are apparently absent on the body chamber but possibly present in the inner third of the height of the inner whorls.

The suture line, very poorly visible, is ceratitic, with denticulate lobes and mostly rounded saddles, sometimes very slightly wrinkled. The illustration of the suture by Salopek (1912, pl. I, fig. 1c) somewhat exaggerates the level of denticulation on the saddles. Five lobes are present on the flank, with lobe A being the deepest and most developed one.

Remarks. The somewhat poor preservation of the specimen obscures some of its crucial morphological features, such as the presence or absence of lateral nodes. It is therefore difficult to ascertain whether it belongs to *H. rusticus* or is perhaps closer to some other species. The ribbing pattern, as far as can be seen, appears to be rather like that present on the beginning of the last whorl of one of the two *H. rusticus* figured by Hauer (1896, pl. IX, fig. 3). However, relatively well-developed umbilical nodes are comparable to the condition seen in *Halilucites obliquus* and its likely synonym *Halilucites intermedius*. These species, however, differ by being more involute in coiling and in the style of ribbing, which is very fine and exhibits very frequent bifurcation and intercalation. The ornamentation of *Halilucites arietitiformis*, which possesses rather simple, coarse ribbing and lacks umbilical or lateral nodes, is not comparable to the described specimen.

The opinion is here presented that the name *Halilucites zagoriensis*, given to this specimen by Salopek (1912), should be treated as a *nomen dubium* because its poor preservation obscures some of the key features necessary for a specific identification. Although it is here suggested that this specimen stands morphologically closest to *H. rusticus*, the combination of the umbilical nodosity comparable to that in *H. obliquus* with the coiling and the ribbing pattern like that seen in some *H. rusticus* supports the observation by Vörös (2018) that at least some of the various species of *Halilucites* may be somewhat indistinct. Currently, there is little evidence either in support or against the stratigraphic sepa-

ration of these morphotypes. The role of either intra-specific variability or evolutionary change as a source of their morphological differences therefore remains unknown.

Halilucites* cf. *arietiformis (Hauer, 1896)

Pl. 1, fig. 4.

- * 1896 *Ceratites* (*Hungarites*) *arietiformis* n. sp. — Hauer, p. 260, pl. X, figs 1–3.
- ? 1896. *Ceratites* (*Hungarites*?) *planilateratus* Hauer — Hauer, pp. 261–262, pl. 11, Figs 1–3.
- 1903 *Hungarites arietiformis* Hauer — Frech, Neue Cephalopoden, p. 13, pl. III, fig. 1.
- ? 1906 *Hungarites arietiformis* Hauer — Renz, Argolis (1), p. 388, unnumbered text-fig. on p. 386.
- ? 1907 *Ceratites* (*Halilucites*) sp. aff. *planilaterato* Hau. — Diener, pp. 59, 60, pl. V, fig. 3.
- ? 1910 *Hungarites arietiformis* Hauer (*Judicarites*) — Renz, p. 34, text-fig. 3.
- ? 1986 *Halilucites* cf. *arietiformis* (Hauer 1896) — Brack & Rieber, p. 204, pl. 2, figs 5, 6.
- 1993 *Halilucites arietiformis* — Gaetani (ed.), p. 118, pl. 13, fig. 6.
- 2002 *Halilucites* cf. *arietiformis* (Hauer) — Vörös, p. 488, pl. 2, fig. 2.
- ? 2007 *Halilucites rusticus* (Hauer, 1896) — Brack et al., p. 334, fig. 5/10.
- 2018 *Halilucites* cf. *arietiformis* (Hauer, 1896) — Vörös, pp. 101, 102, pl. XXIV, fig. 12.

Material: a single previously undescribed specimen (HPM 179), labelled as *Halilucites* cf. *rusticus*. It is preserved as a steinkern, with unequally preserved left and right side and a partially damaged venter. Collected at the Gregurić Breg locality.

Dimensions:

	D	H	h	U	W	w	W/H	U/D	SGR
HPM 179	50*	16.9*	13.4	20	-	11.3	-	0.4*	26*

Description. A small sub-evolute specimen of *Halilucites*. The whorl section is sub-rectangular and widest in the inner third of the flank. Flanks are slightly convex. The venter is wide and tri-carinate, with a blunt median keel bordered by lateral furrows which are bordered by high, carinate ventrolateral shoulders. The median keel is, where well preserved, higher than the lateral shoulders. The umbilical edge is rounded, and the umbilical wall is subvertical but not very high.

Flanks are ornamented by radial ribs. The ribbing is coarse and relatively sparse. Individual ribs are straight to very slightly sigmoid and are projected ventrally. They appear to be as wide as the interspaces. Most ribs are primary, with only some being intercalated in the inner part of the whorl, sometimes only slightly above the umbilical edge. No umbilical or lateral nodes are seen, with only very weak marginal swellings potentially being present.

The suture line very poorly preserved, likely ceratic.

Remarks. The relatively regular ribbing that lacks lateral and umbilical nodes, as well as the apparently sub-rectangular whorl section suggest this specimen can be referred to *Halilucites arietiformis*. It is, however, relatively poorly preserved, leading the present authors to use open nomenclature.

As already discussed by Vörös (2018), one of the specimens assigned by Brack et al. (2007) to *Halilucites rusticus* seems to represent *H. arietiformis* instead. Furthermore, a specimen from Argolis assigned to this taxon (Renz 1906; 1910) cannot be confirmed as such because it apparently somewhat differs in appearance from other specimens of *H. arietiformis* and is not illustrated in the diagnostic ventral view. It is here suspected, partially based on the apparently wrongly written species name (*arietiformis* instead of *arietiformis*), that there might have been some confusion with the unfortunately similarly named and superficially similar *Judicarites arietiformis* (Mojsisovics, 1882). Contrary to this assumption, Renz (1910) does not reference Mojsisovics when discussing this taxon. Therefore, this specimen's identification is questionable, and can only be confirmed by its re-examination.

A specimen from the Himalayas, figured and described by Diener (1907) and identified as possibly related to the doubtfully valid *Halilucites planilateratus*, may potentially also represent a specimen of *H. arietiformis*. However, this reference is, based on the description and the somewhat poor photographs, inconclusive.

PLATE 1

Uppermost Anisian ceratitids from the red nodular limestones of the Gregurić Breg locality.

Fig. 1 - *Halilucites* aff. *rusticus* (Hauer, 1896), specimen HPM 107, holotype of *Halilucites zagoriensis* Salopek, 1912; 1a, right lateral view, 1b, left lateral view, 1c, ventral view, 1d, apertural view.

Fig. 2 - *Halilucites rusticus* (Hauer, 1896), specimen HPM 108.2, partial phragmacone; 2a, left lateral view, 2b, ventral view.

Fig. 3 - *Halilucites rusticus* (Hauer, 1896), specimen HPM 108.1, partial body chamber and phragmacone; 3a, left lateral view, 3b, ventral view.

Fig. 4 - *Halilucites* cf. *arietiformis* (Hauer, 1896), specimen HPM 179; 4a, left lateral view, 4b, ventral view.

Fig. 5 - *Hungarites mojsisovicsi* (Roth, 1871), specimen HPM 109; 5a, left lateral view, 5b, apertural view.

Fig. 6 - *Nevadites* cf. *avenonensis* Brack & Rieber, 1993, specimen GPZ III 1651 (number shared with Pl. 2, fig. 4), partial body chamber and previous whorl; 6a, left lateral view, 6b, oblique left lateral view, 6c, ventral view, 6d, apertural view.

The scale bar is 5 cm for every specimen; each rectangle is 1 cm.

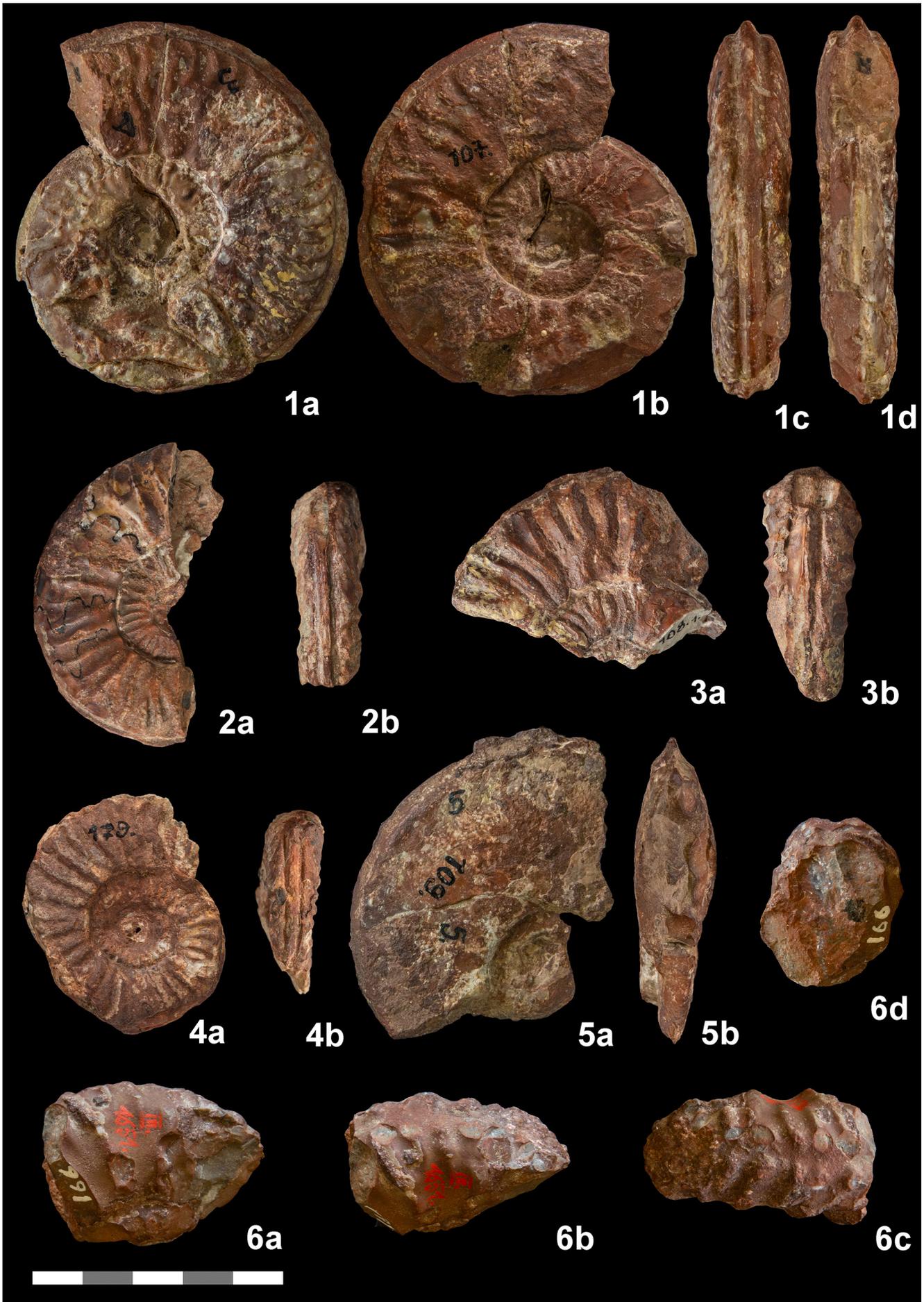


PLATE 1

Occurrence. *H. arietitiformis* has been identified in the Dinarides and the Balaton Highland, as well as probably in the Southern Alps and Argolis, and questionably also from the Himalayas. Its stratigraphic distribution is comparable to other species of *Halilucites*, occurring in the Avisianum subzone of the upper Reitzii zone and the Crassus subzone of the lower Secedensis zone.

Subfamily Nevaditinae Tozer, 1994
Genus *Nevadites* Smith, 1914

Type species: *Nevadites merriami* Smith, 1914

***Nevadites* cf. *avenonensis* Brack & Rieber, 1993**

Pl. 1, fig. 6.

1986 Group of *Nevadites reitzi* (Böckh 1872) — Brack & Rieber, p. 200, pl. 2, fig. 2, pl. 4, fig. 4.

* 1993 *Nevadites avenonensis* n. sp. — Brack & Rieber, p. 480, pl. 11, figs 9–12, pl. 12, figs 5, 6.

1993 *Nevadites avenonensis* n. sp. — Gaetani (ed.), p. 66, pl. 7, figs 6, 8.

2008 *Nevadites* cf. *avenonensis* Brack & Rieber, 1993 — Vörös et al., p. 331, pl. I, figs. 1, 3.

2018 *Nevadites* cf. *avenonensis* Brack & Rieber, 1993 — Vörös, pp. 113, 114, pl. XXX, figs. 2, 3.

Material: a single fragment likely pertaining to the body chamber (GPZ III 1651), with a small piece of the inner whorl also attached to the dorsal side. The specimen was stored under the same number as another specimen, which however belongs to *Falsanolcites* sp. Morphotype A. It was collected at the Gregurić Breg locality.

Dimensions:

	D	H	h	U	W	w	W/H	U/D	SGR
GPZ III 1651	-	25.3	-	-	21	-	0.83	-	-

Description. A moderate sized specimen of *Nevadites*. Whorls are characteristically subcircular, being only slightly taller than wide, and achieving their greatest width approximately at the middle of the flank. The flanks are convex. The venter is wide, basically flat, and slightly undulatory. No true ventrolateral shoulders are present, but the transition from flank to venter is clearly perceptible and marked by nodes. The umbilical edge is practically non-existent; the flank directly transitions into a somewhat steep, convex umbilical wall.

The flanks are ornamented by radial ribs and spiral rows of nodes. The ribbing is very coarse, with strong ribs being well spaced from each other. Primary ribs are rather straight and are slightly prorsiradiate. Secondary ribs arise as intercalations at the

varying heights of the flank, ranging from approximately the middle of the flank to above the lateral nodes, or as bifurcations on the lateral nodes. They are somewhat weaker than primary ribs. Three spiral rows of nodes are present: umbilical, lateral and external. The umbilical nodes are noticeable but rather weak and are positioned above the sloping umbilical wall. Lateral nodes occur above the middle of the flank, vary in strength and are distinctly present only on primary ribs. External nodes are prominent although damaged. Opposing external nodes stand in a corresponding position.

No external suture line is visible.

Remarks. Although fragmentary, our specimen shows marked similarities to the original photographs and the description of this taxon (Brack & Rieber, 1986; 1993; Gaetani 1993). Despite this, open nomenclature is still preferred in this case because of the specimen's fragmentary nature and the lack of precise stratigraphic data. The latter is of particular importance as the species *Reitziites ecarinatus* (Hauer, 1896), which occurs in older strata, shows considerable similarities to some of the *Nevadites* species from the Tethyan province (Vörös 2018). Despite this, there is no evidence that the specimen described herein possess four spiral rows of nodes, as in *R. ecarinatus*, which clearly distinguishes it from that taxon. Other tri-tuberculate alpine *Nevadites*, namely *N. crassiornatus* Brack & Rieber, 1993 and *N. secedensis* Brack & Rieber, 1993, differ from *N. avenonensis* by possessing different patterns of ornamentation, by having slightly concave ventral areas, and by apparently only having opposed external nodes in alternating positions.

Occurrence. The species has been previously reported from the Southern Alps and the Balaton highland and is now likely also known from the Dinarides. It is known from the Secedensis zone; following the Illyrian zonal scheme proposed by Vörös (2018), both the alpine and the Hungarian occurrence would fall under the Secedensis subzone of that zone.

Superfamily Clydonitoidea Hyatt, 1877

Family Trachyceratidae Hyatt, 1877

Subfamily Anolcitinae Mietto & Manfrin, 2008

Genus *Falsanolcites* Rieber & Brack, 2004

Type species: *Anolcites (Trachyceras) furcosus* (Mojsisovics, 1893)

Comments. From the original description of the genus and the included list of references (Rieber & Brack 2004), it is evident that the range of morphological variation of this genus is quite broad. The original authors propose that at least some of these variations are likely intraspecific. In doing so, they note a distinction between the two extreme forms in their studies samples: a “Coarse morphotype” and an “Involute morphotype”, as well as the existence of an “Intermediate morphotype”. Indeed, this proposed relationship and the characteristics of each morphotype agree with the Buckman’s First Rule of Covariation, which has been demonstrated to be a valid concept for many ammonoid species (Westermann 1966; Dagys & Weitschat 1993; Wiese & Schulze 2005; Monnet & Bucher 2005; Monnet et al. 2010; Wilmsen & Mosavina 2011; Monnet et al. 2015, etc.). Thus, it is likely that some of the species attributed to the genus *Falsanolcites* may not be distinct but represent various morphotypes of a single or multiple highly variable species.

However, it has not yet been exactly proposed or tested which of the currently recognized species of *Falsanolcites* may be grouped together in this manner. No potential populations of *Falsanolcites* have yet been morphometrically examined for variability. Such methods are also bound to have little utility in condensed Hallstatt-type limestones (including those at Gregurić Breg) due to their “mixed” and time averaged fauna, a problem which can also be exacerbated by suboptimal sampling conditions.

Secondly, not every distinction between the “Involute” and “Coarse” morphotypes is easily explainable by Buckman’s First Rule. Specifically, this appears true for the extent of the interruption of the ribs on the venter. The range of morphologies of this feature is difficult to interpret, as it is somewhat specific to this genus. It also tends to vary based on the preservation of the specimen (e.g., shell vs. steinkern of *F. recubariensis*), as well as ontogenetically (e.g., *F. furcosus*). Absence or presence of interruptions is also not linked to either “Involute” or “Coarse” morphotypes. Excellent examples are the very similar *F. gortanii* morph. *nodato* and *F. clapsavonum*, which differ almost exclusively in ventral morphology (Pisa 1966).

Because of the above-described problematics, it is currently very difficult to adequately identify whether morphological differences between

the many species of *Falsanolcites* are of taxonomic significance, or whether they represent variations of a lesser number of taxa. By necessity, this work must therefore take a typological approach. Differing morphotypes are assigned, when possible and with varying degrees of certainty, to already named species. Morphotypes not present in the literatures are simply designated with capital letters, as to not further complicate the specific composition of the genus. Only exceptionally, where thought of as likely, is the synonym of certain species discussed, e.g., in the case of *F. furcosus*.

Falsanolcites recubariensis (Mojsisovics, 1882)

Pl. 10, fig. 1.

- pars* 1882 *Trachyceras recubariense* — Mojsisovics, p. 114, pl. 7, fig. 1, non pl. 5, fig. 3.
 1886 *Trachyceras* cf. *recubariense* Mojs. — Polifka, p. 76-77, pl. 8, fig. 1-2.
 1899 *Protrachyceras* cfr. *recubariense* Mojs. — Tommasi, p. 25, pl. 3, fig. 4.
 non 1912 *Protrachyceras* ex aff. *recubariense* Mojs. — Salopek, p. 17, pl. 1, fig. 5.
 1966 *Trachyceras* (*Protrachyceras*) *recubariense* Mojs. — Pisa, pp. 646-652, pl. 72, p. 1-2, pl. 73, fig. 1-2, pl. n.t., fig. 3, 5.
 pars 1966 *Trachyceras* (*Protrachyceras*) *gredleri* Mojs. — Pisa, pp. 639-642, pl. 70, fig. 3 (non fig. 2, 4).
 non 1978 *Protrachyceras recubariense* (Mojsisovics) — Urlichs, p. 6-7, fig. 1, pl. 1, fig. 1.
 1986 *Eoprotrachyceras recubariense* (Mojs.) — Brack & Rieber, pl. 5, fig. 5.
 1993 *Eoprotrachyceras recubariensis* (Mojs.) — Gaetani (ed.), pl. 8, fig. 3, pl. 9, fig. 11-12.
 1995a “*Anolcites*” *recubariensis* (Mojsisovics, 1882) — Mietto & Manfrin, pl. 4, fig. 1, 3.
 1998 *Eoprotrachyceras* cf. *recubariense* (Mojsisovics) — Vörös, p. 53, 60, pl. 9, fig. 3.
 2007 *Falsanolcites recubariense* (Mojs.) — Brack et al., pl. 5, fig. 4.
 2018 *Falsanolcites recubariensis* (Mojsisovics, 1882) — Mietto et al., p. 237-238, pl. 2, fig. 1-3.

Material: a single partial specimen (HPM 15ž) collected at the Vlašić Brdo locality. Its outermost and the innermost whorls are preserved as a steinkern still attached to the host rock, while the other inner whorls and a small section of the last whorl are preserved as imprints of the shell. The latter were used to make casts, which enabled more detailed morphological comparisons.

Dimensions:

	D	H	h	U	W	w	W/H	U/D	SGR
HPM 15ž	47*	15.5	11.9	19.6	-	-	-	0.42*	30%*

Description. A small, sub-evolute *Falsanolcites*. Whorls are likely weakly to moderately compressed, sub-rectangular to sub-quadratic in section. The flanks are feebly convex, becoming rounded as they pass into the moderately wide venter. The um-

bilical edge is rounded, while the umbilical wall is almost vertical but relatively tall. On the venter, there is a wide and shallow, but clearly perceptible furrow.

The ornamentation is made up of spiral rows of nodes and radial ribs. There are four spiral rows of nodes present on the cast of the inner whorl: umbilical, lateral, marginal, and external. Lateral nodes are positioned in the inner third of the flank. Marginal and external nodes are very close to each other. The steinkern of the last whorl differs in that there appears to be additional swellings positioned at mid-flank, forming an incipient second lateral row of nodes. All the nodes are rounded in cross section. The ribbing is moderately coarse, slightly sigmoid with projected endings that terminate at the edge of the ventral furrow. The inner whorls are characterized by the bifurcation of secondary ribs below mid-flank, while the outer whorl shows dominant intercalation at around mid-flank. The ribs are rounded and wider than their interspace on the cast of the imprint, but narrow and acute on the steinkern, indicating the presence of a thickened pre-septal layer.

The external suture line is not visible.

Remarks. The specimen's morphology fits well with specimens described and illustrated in the examined literature, making its assignment to this taxon justified despite its incompleteness. It is particularly comparable to specimens described by Pisa (1966), which likewise exhibit a second lateral row of incipient node-like swellings.

The species is easily distinguished among other members of its genus and similar genera by the combination of its rather evolute coiling, possession of only four distinct, yet not particularly strongly expressed nodes (not counting the incipient swellings), and the possession of a perceptible ventral furrow. That said, the present authors agree with Mietto et al. (2018) in excluding the specimen figured and identified as *Protrachyceras* ex aff. *recubariense* by Salopek (1912) from this taxon; these specimens are described below as a separate morphotype.

Occurrence. *Falsanolcites recubariensis* is an important index fossil of the Recubariensis horizon/subzone of the Curionii zone. It is known from the Southern Alps, the Balaton Highlands, and now the Dinarides. Previous reports of this taxon from Croatia (Salopek, 1912) are likely misinterpreted (see above).

Falsanolcites furcosus (Mojsisovics, 1893)

Pl. 2, figs. 6, 7; Pl. 3, figs. 1, 2, 3.

- pars? 1882 *Trachyceras julium* E. v. Mojsisovics, pp. 103, 104, pl. XXXVII, fig. 2 (non pl. XIII, figs. 3, 4, 8).
- * 1893 *Anolcites (Trachyceras) furcosus* E. v. Mojsisovics, pp. 692, 693, pl. CC, fig. 1.
- ? 1900 *Anolcites furcosus* v. Mojsisovics — Diener, p. 12, pl. I, fig. 3.
- v 1912 *Anolcites furcosus* Mojs. sp. — Salopek, p. 16, pl. I, fig. 3.
- 1913 *Anolcites furcosus* Mojs. — Simionescu, p. 290, 300, pl. II, fig. 7.
- v 1936 *Anolcites furcosus* Mojs. var. — Salopek, p. 214, pl. I, fig. 2.
- ? 1966 *Trachyceras (Anolcites) julium* Mojs. — Pisa, pp. 661-665, pl. LXXIII, fig. 4, pl. LXXIV, fig. 3, 4, text pl., fig. 9.
- ? 1966 *Trachyceras (Anolcites) clapsavonum* Mojs. — Pisa, pp. 654-658, pl. LXXIV, figs. 1, 2, text pl., fig. 7.
- 2004 *Falsanolcites furcosus* (Mojs., 1893) — Rieber & Brack, figs. 2, 13, 21, 22, 27, 29.
- ? 2004 *Falsanolcites* group *furcosus*, coarse morphotype — Rieber & Brack, figs. 33, 34.
- ? 2004 *Falsanolcites* group *furcosus*, intermed. morphotype — Rieber & Brack, figs. 14, 31, 32.
- ? 2007 *Anolcites* aff. *julium* (Mojsisovics, 1882) — Tselepidis, pl. VIII, fig. 11.

Material: two small, well preserved specimens with shell (HPM 110.1, HPM 110.2); two large fragments of a body chamber of adults, one with shell (HPM 176) and one preserved solely as a steinkern (HPM 196G); and one relatively complete larger specimen preserved with shell (MKN 664). Collected from the red nodular limestones of Gregurić Breg.

Dimensions:

	D	H	h	U	W	w	W/H	U/D	SGR
HPM 110.2	28.3	9.5	6.9	11.9	9	-	0.95	0.42	38%
HPM 110.1	33.8	11.3	7.9*	14.6*	10.5	8.7*	0.93	0.43*	43%*
MKN 664	93.1	31.5	24.2	37.4	26*	-	0.83*	0.40	30%*
HPM 196G	120*	35.3	-	-	26	-	0.74	-	-
HPM 176	110*	42.2	-	-	34.2	-	-	-	-

Description. A large sub-evolute *Falsanolcites*. Whorls weakly to moderately compressed and almost subcircular in section in juveniles, tending to become moderately compressed oval in adults, achieving their greatest width in the inner third of the whorl height. The flanks are convex and gradually pass into a rather wide venter. The umbilical edge is well rounded, and passes discreetly into the subvertical to slightly divergent, moderately high umbilical wall.

The ornamentation is made up of radial ribs and spiral rows of nodes. At some point in growth, the juvenile specimens acquire five rows of more-

or-less prominent nodes: umbilical, first and second lateral, marginal and external. The umbilical and first lateral nodes are well developed and positioned close to each other. The second lateral, marginal and external nodes are equidistant. Second lateral nodes are the most weakly developed, while marginal and especially external nodes are rather strong. External nodes on the left and the right side of the venter are in the corresponding position. All nodes are distinctly rounded in cross section. In adults, most of the nodes fade as the ribbing becomes more robust, leaving only umbilical and external nodes clearly visible. The ribs are sigmoid, with projected ventral endings. They are wider than the interspaces and rounded when the shell is preserved, and acute and as wide as the interspaces in steinkerns. The ribbing is very coarse, especially in adults. The ribs bifurcate in the region of the umbilical nodes and the first lateral nodes; rarely, double bifurcation on both these nodes is present. Some of the ribs also intercalate in the inner half of the flank. The ribs distinctly cross the venter. There they are somewhat reduced in strength but tend to become stronger in adult individuals. On steinkerns, the weakening of the ribs on the venter is more pronounced than on the specimens with shell.

The external suture is not visible.

Remarks. *Falsanolcites furcosus* is the type species of the genus. In strict terms (cf. Mojsisovics 1893), it is characterised by evolute coiling, relatively low, only moderately compressed whorls, and strong and coarse ornamentation that includes five spiral rows of nodes and ribs that cross the venter. Some specimens could potentially have more than five rows of nodes (Diener, 1900), while in large specimens lateral and marginal nodes fade as ribs become more robust (Rieber & Brack 2004, figs. 27–29; this paper).

Herein, a potentially more inclusive concept of this species is proposed, with focus on the ventral rib morphology, and to a lesser extent the number of nodes. Namely, specimens referred to as the species *Anolcites julium* (Mojsisovics, 1882) and collected from the red limestones of Monte Clapsavon and other neighbouring localities in the Southern Alps (Mojsisovics 1882; Pisa 1966) are very similar to *F. furcosus* and are here suspected to represent a variety of this species. Most differences, such as slightly finer ornamentation, are minor and may represent individual variation. Coarse morphotypes

of *Falsanolcites* group *furcosus* from Monte Clapsavon illustrated by Rieber & Brack (2004), that specifically have ribs crossing the ventral area, could also represent a similar variant. Therefore, these specimens are herein listed in the synonymy with query, pending possible further revision of the material and more precise stratigraphic data.

The specimen labelled as *Anolcites* aff. *julium* by Tselepidis (2007), collected from the lower Ladinian layers of the red nodular limestones from Argolis, are also tentatively listed in the synonymy. Those specifically referred to *A. julium*, however, have less than five rows of nodes and a more subquadratic whorl section. They were also collected from lower layers pertaining to the *Nevadites* biohorizon, an equivalent of the Anisian Secedensis zone used for the western Tethys (Brack & Rieber 1993; Tselepidis 2007; Pomoni & Tselepidis 2013; Vörös 2018). They are therefore not included in the synonymy.

If the above proposed synonym is valid, the name *F. julium* technically has a priority over *F. furcosus*. However, the species *julium* is problematic in the sense that it was likely originally erected based on material belonging to multiple species (Mojsisovics 1882). Some specimens, as already mentioned, were collected from the red limestones of Monte Clapsavon and likely pertain to the same morphotype as those described by Pisa (1966) under the same name. These fossils certainly represent a species of *Falsanolcites* (cf. Rieber & Brack 2004). Other specimens, towards which Mojsisovics (1882) seemingly directed more attention, come from the platy limestones near Prezzo, Italy, which the author in question calls “Daonellenkalk”. From the same type of rocks, Mojsisovics (1882) illustrates specimens of *Protrachyceras archelaus* (Laube, 1869), *P. ladinum* (Mojsisovics, 1882), *Anolcites neumayri* (Mojsisovics, 1869), “*A.*” *judicarium* (Mojsisovics, 1869) and *Megjnoceras* (alt. *Frankites*) *regoledanus* (Mojsisovics, 1869). These ammonoids clearly indicate an upper Ladinian (Longobardian) age of these rocks. It is therefore very likely that *A. julium* from the “Daonellenkalk” is not *Falsanolcites*, but a member of another genus, likely the “true” *Anolcites*. As such, further research is necessary not only to test the synonym proposed herein, but also to resolve which specimen of *A. julium* constitutes the name bearing type.

Specimens of *Falsanolcites clapsavonum* (Mojsisovics, 1882) were originally identified from the same localities as *A. julium* but were only figured

for “Daonellenkalk”. This taxon also suffers the same problem as that taxon. This was, however, later resolved by Pisa (1966), who chose a neotype for this species. Specimens described and figured by that author from the area of Monte Clapsavon are members of *Falsanolcites*, making the specimens from “Daonellenkalk” of Prezzo unlikely to represent the same taxon. The nomenclatural combination *Falsanolcites clapsavonum* is thus justified.

The specimens of *F. clapsavonum* also share features with *F. furcosus*, namely five rows of nodes and ribs that cross the ventral area. The “double” bifurcation and/or appearance of intercalated ribs in between split ribs that Pisa (1996) considered characteristic for *F. clapsavonum* are also seen in the type specimen of *F. furcosus* (see Mojsisovics 1893; Rieber & Brack 2004), as well as in one of the specimens figured herein (Salopek 1936). *F. clapsavonum* is significantly different from *F. furcosus* based on more compressed whorls, more involute coiling, and finer and denser ornamentation. However, these differences might be explainable by Buckman’s First Rule of Covariation (Westermann 1966; Monnet et al. 2015) and could therefore be intraspecific. As such, specimens of *F. clapsavonum* figured by Pisa (1966), as well as some *Falsanolcites* from Monte Clapsavon figured by Rieber & Brack (2004) similar to this taxon, are tentatively listed in the synonym, pending more data. Further complicating this is the apparent close similarity between *F. clapsavonum* and *Falsanolcites gortani* morphotype *nodato* noted by Pisa (1966); the latter, however, has a furrow-like interruption on the venter. Once again, this problem necessitates further research beyond the scope of this paper.

Occurrence. Specimens of this species have been found at localities in the Southern and Northern Alps, the Dinarides, in Dobrogea, and potentially in Argolis. Their exact biostratigraphic position remains unknown, as they are yet to be reported from uncondensed, well studied stratigraphic sections. Most likely, based on other ammonoids associated with them (e.g., in red limestones of Monte Clapsavon), they come from lower Ladinian strata, but may potentially also be latest Anisian in age, as per the range of the genus (Rieber & Brack 2004).

Falsanolcites sp. Morphotype A

Pl. 2, figs. 3, 4.

- v 1912 *Protrachyceras* ex. aff. *recubariensis* Mojs. — Salopek, p. 17, pl. I, fig. 5.
- ? 1936 *Protrachyceras vouki* n. sp. — Salopek, pp. 217, 218, pl. II, fig. 1.
- v 1936 *Protrachyceras* sp. ind. ex aff. *vouki* — Salopek, p. 219.

Material: two specimens, likely preserved with the shell (HPM 170, GPZ III 1651). All were collected from the red nodular limestone of Gregurić Breg.

Dimensions:

	D	H	h	U	W	w	W/H	U/D	SGR
HPM 170	58.5	21.3	13.2	24	-	-	-	0.41	61%
GPZ III 1651	71.5	29.4	44*	27.5	29.6*	-	1.0	0.38	63%

Description. A moderate sized evolute *Falsanolcites*. Whorls are slightly depressed to very slightly compressed, with greatest width approximately at the middle of the whorl height. The flanks sensu stricto are almost flat to slightly convex but become very convex when passing into the very wide ventral area, which is convex to almost flat. This creates a rounded sub-rectangular to sub-quadrangle whorl section. On larger specimens, the venter becomes narrower. A very weak ventral furrow or a furrow-like interruption is sometimes present. Interestingly, the last whorl of the specimen GPZ III 1651 clearly shows a ventral furrow in the cross section of the steinkern, but on the shell it is significantly less per-

PLATE 2

Lower Ladinian (? uppermost Anisian) trachyceratids from the red nodular limestones of the Gregurić Breg locality.

- Fig. 1 - *Falsanolcites* cf. *gortanii* (Pisa, 1966), specimen GPZ III 1562; 1a, right lateral view, 1b, ventral view.
- Fig. 2 - *Falsanolcites* cf. *gortanii* (Pisa, 1966), specimen GPZ III 1652, lectotype of *Anolcites arminiae angusta* Salopek, 1936; 2a, right lateral view, 2b, apertural view.
- Fig. 3 - *Falsanolcites* sp. morphotype A, specimen HPM 170; 3a, right lateral view, 3b, ventral view.
- Fig. 4 - *Falsanolcites* sp. morphotype A, specimen GPZ III 1651; 4a, right lateral view, 4b, apertural view.
- Fig. 5 - *Falsanolcites* sp. morphotype B, specimen GPZ 195G; 5a, right lateral view, 5b, ventral view.
- Fig. 6 - *Falsanolcites furcosus* (Mojsisovics, 1893), specimen HPM 110.1; 6a, right lateral view, 6b, ventral view.
- Fig. 7 - *Falsanolcites furcosus* (Mojsisovics, 1893), specimen HPM 110.2; 7a, right lateral view, 7b, ventral view.
- Fig. 8 - *Falsanolcites* cf. *gortanii* (Pisa, 1966), specimen HPM 194G, partial body chamber and previous whorl; 8a, left lateral view, 8b, ventral view.
- Fig. 9 - *Meginoceras* (?) sp., specimen HPM 111M; 9a, left lateral view, 9b, ventral view.

Scale bars are 1 cm for each individual specimen.

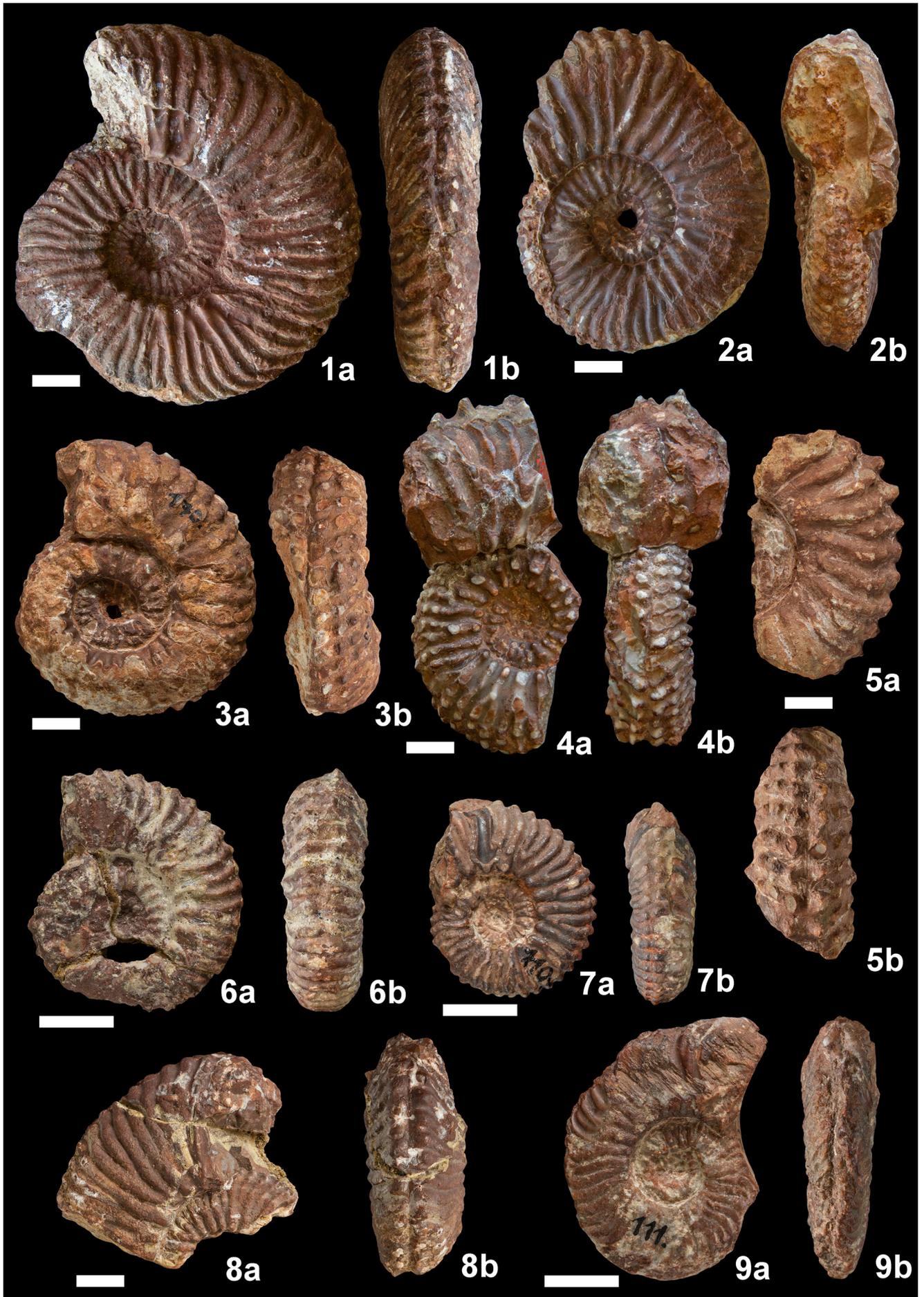


PLATE 2

ceptible. The umbilical edge is rounded, while the umbilical wall stands relatively tall and vertical.

The ornamentation consists of radial ribbing and spiral rows of nodes. The ribbing is coarse, with strong, well-spaced ribs that are approximately as wide as the interspaces. The ribs are rectiradial, slightly sigmoid or straight, and have projected ventral endings. The intercalation and bifurcation occur at the umbilical or first lateral rows of nodes, more frequently the latter. There are five rows of nodes present: umbilical, two lateral, marginal, and external. Umbilical nodes sometimes appear irregularly, being absent on some ribs. The first lateral nodes appear approximately at the half of the whorl height or slightly below it. The umbilical, first and second lateral nodes are equidistant and significantly more spaced from each other than the second lateral, marginal and external nodes, which are positioned very closely together. All ribs, including intercalations, possess at least these latter three rows of nodes, which are very strong, often spike-like. Because of the very wide ventral area at smaller whorl height, the marginal nodes are positioned so they are often not visible from lateral views. In a sense, they are positioned on the venter, alongside external nodes. The external nodes stand in an alternating position around the furrow-like interruption.

The external suture line is not exposed.

Remarks. As observed from the figures in the literature, the Gregurić Breg locality is, as of now, the only confirmed location where this morphotype occurs. It is suspected that this form may be the same taxon as *Protrachyceras vonki* Salopek, 1936, described at the same locality. The apparently very complete holotype of this species is, unfortunately, missing from its repository in the Croatian Natural History Museum and was not recovered during this research. As such, it is presumed lost. Because of the poor quality of figures illustrating this specimen, it is listed in the synonymy with query.

Because of this, as well as the condensed facies these fossils come from, the present authors currently abstain from referring these specimens to any particular species, and simply treat them as a different morphotype. Among other taxa, the apparently most similar are the specimens of *Falsanolcites* previously mistakenly referred to *Protrachyceras gredleri* (Mojsisovics, 1882) on multiple occasions (Mojsisovics 1882; De Toni 1913; Mietto & Manfrin 1995a). Although these ammonoids likewise

have a rather similar pattern of ornamentation in combination with a ventral furrow/furrow-like interruption, they have a different whorl section and are only sub-evolute in coiling. However, given the well-known possible range of variation known within ammonoid species, which was already proposed as possible for this genus (Rieber & Brack 2004), it is certainly possible that the few specimens collected at Gregurić Breg could possibly represent the more evolute, more strongly ornamented members of the same taxon.

Falsanolcites recubariensis (Mojsisovics, 1882), to which one of the specimens was initially referred with some scepticism (Salopek 1912), is similar in coiling but differs most prominently in having noticeably weaker ornamentation, and possessing only four spiral rows of nodes, only sometimes exhibiting a very weak fifth row of indistinct swellings.

Occurrence. As of now, this morphotype has only been reported at the Gregurić Breg locality, NW Croatia. Its exact biostratigraphic horizon is unknown due to the condensed rock facies it was collected from, coupled with the lack of bed-by-bed sampling. Most likely, it comes from the lower Ladinian (Fassanian), but may also be latest Anisian in age, as for the range of the genus (Rieber & Brack 2004).

Falsanolcites sp. Morphotype B

Pl. 2, fig. 5.

Material: a single partial fragment of a whorl (HPM 195G), likely of a body chamber preserved as a steinkern without the shell. Collected from red nodular limestone of Gregurić Breg.

Dimensions:

	D	H	h	U	W	w	W/H	U/D	SGR
HPM 195G	-	21.6	-	-	20.6	-	0.95	-	-

Description. A moderate sized *Falsanolcites*, likely sub-evolute to evolute in coiling. Whorl section is sub-circular to sub-polygonal, widest approximately at mid-flank. Flanks are convex and pass gradually into a relatively wide venter. The umbilical edge is rounded but pronounced, while the umbilical wall is almost vertical and of moderate height.

The ornamentation consists of radial ribbing and spiral rows of nodes. The ribbing is relatively sparse and coarse, with strong ribs. The ribs are slightly rectiradial and sigmoid. The bifurcation occurs at the umbilical and first lateral rows of

nodes, while intercalation occurs in the region of the first lateral nodes, approximately at mid-flank or slightly below. There are five rows of nodes: umbilical, two lateral, marginal, and external. The umbilical, the first and second lateral nodes are well spaced from each other, approximately equidistantly. The second lateral, marginal and external nodes are positioned relatively close to each other and are present on all ribs regardless of type. In particular, the marginal and external nodes are very pronounced and spike-like. All the nodes are rounded in cross section. The opposing external nodes stand in a corresponding position and are connected by weakened ribs that noticeably cross the venter.

The external suture line is not visible.

Remarks. Superficially, this morphotype is similar in appearance to specimens herein designated as *Falsanolcites* sp. Morphotype A but differs from them by having a more rounded whorl section and by having its opposing external tubercles clearly connected by weakened ribs that cross the venter. Taking the latter characteristic into account along with the pattern of nodes (5 rows total; second lateral, marginal and external positioned very close to each other), it can be compared to *Falsanolcites furcosus* (Mojsisovics, 1893), *F. clapsavonum* (Mojsisovics, 1882) and some specimens designated by Pisa (1966) as *Trachyceras (Anolcites) julium*. All these species, however, have much less pronounced, less spike-like nodes, while the second also has more compressed whorls. *Falsanolcites elisabethae* (Mojsisovics, 1893) has somewhat more spine-like, although still weaker nodes, but it also possesses more compressed whorls. Some resemblance is present with a specimen described and figured by Diener (1900) as *Anolcites furcosus*, but this specimen exhibits more than five rows of nodes. Therefore, this morphotype is somewhat unique among specimens figured in the relevant literature. It is, however, not described as a separate species, as the present authors hypothesise that it may represent a morphological variety of some of the species listed above.

Occurrence. As of now, this morphotype has solely been reported from red nodular limestones of Gregurić Breg, NW Croatia. Its exact stratigraphic horizon is unknown, but likely falls in the range of uppermost Anisian (Illyrian) Secedensis zone to lower Ladinian (Fassanian) Curionii zone, as per the range of the genus (Brack & Rieber 2004).

Falsanolcites cf. *rieberi* (Fantini Sestini, 1994)

Pl. 3, figs. 4 – 6; Fig. 9a.

- pars? 1882 *Trachyceras Riechthofeni* E. V. Mojsisovics — Mojsisovics, pl. XXXVII, fig. 5 (non pl. XXIII, figs. 4, 5).
 1993 *Eoprotrachyceras rieberi* Fantini Sestini, 1993 — Gaetani (ed.), pl. 8, figs. 1, 2.
 * 1994 *Eoprotrachyceras rieberi* sp. n. — Fantini Sestini, pp. 258, 259, pl. 3, figs. 1-4, text fig. 4h.
 1998 *Eoprotrachyceras rieberi* Fantini Sestini — Vörös, pl. VIII, figs. 6-7.
 2008 *Falsanolcites* cf. *rieberi* Fantini Sestini, 1994 — Vörös et al., pl. II, fig. 1.

Material: three specimens (GPZ IV 714, HPM 112, SM 2042) collected at the Gregurić Breg locality, preserved variably as steinkerns or with the shell. Two of them were not previously described, while one of them was identified as *Anolcites* cf. *luczkoi* by Salopek (1912), who interestingly suggested it may represent a separate species.

Dimensions:

	D	H	h	U	W	w	W/H	U/D	SGR
GPZ IV 714	79.5*	31.4	23.1*	25*	-	-	-	0.31*	36%*
HPM 112	91.6	45.3	23.1	23.2	26.6	19.2	0.59	0.25	96%
SM 2042	105	46.1	29.6*	29.3	-	-	-	0.28	56%*

Description. A large *Falsanolcites*, with coiling that possibly ontogenetically changes from sub-involute to sub-evolute. The whorl section is high oval, relatively compressed, with the maximum width of the whorl variably at the inner third or fourth of the whorl height. Flanks are either almost flat or feebly convex, and gradually pass into a venter that is relatively narrow for the genus, without ventrolateral shoulders. On the venter, a well-developed and distinct U-shaped ventral furrow can be seen. The umbilical edge of the best-preserved specimen is very distinct, but not sharp. The umbilical wall is moderately high.

The ornamentation consists of radial ribs and spiral rows of nodes. The ribbing is dense, with thin, relatively sharp ribs that vary in width compared to the interspaces; they are usually as wide or slightly narrower than the interspaces, depending on the specimen and the presence or absence of the shell. The ribs are generally straight to slightly sigmoid with ventrally projected endings. Secondary ribs arise as both intercalations and bifurcations. The intercalations vary in length, arising variably from just above the umbilicus to approx-

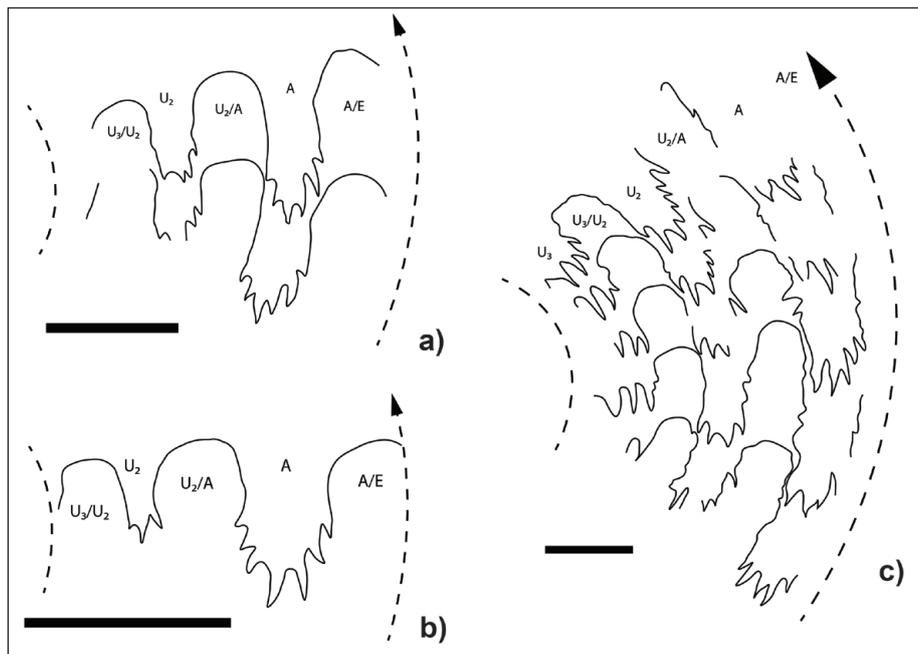


Fig. 9 - Suture lines of ammonoids with ceratitic or subammonitic sutures; a) *Falsanolcites* cf. *rieberi* (Fantini Sestini, 1994), specimen HPM 111; b) *Eoprotrachyceras dorae* (Salopek, 1912), lectotype specimen HPM 116.3; c) *Protrachyceras margaritosum* (Mojsisovics, 1882), specimen GPZ III 1560. Scale bars are 1 cm.

imately the half of the flank, and are sometimes inserted in between bifurcated ribs. The bifurcated ribs arise either in the inner third of the flank or at the umbilical nodes, variably between specimens. There are three rows of nodes: umbilical, marginal and external. The umbilical nodes are rather weak, but perceptible. The marginal nodes may be well marked or may be almost imperceptible. The external nodes are well marked and are rounded to slightly clavate in cross-section. The opposing external nodes stand in alternating positions, bordering the ventral furrow.

The external suture line (Fig. 9a) is ceratitic; the slight wrinkling of the saddles noted by Salopek (1912) is deceptive and a product of damage and recrystallization. Three lobes are well developed on the flank, with a fourth smaller one being visible near the umbilical margin. Together they likely pertain to E, A, U_2 and U_3 lobes, of which the A is the deepest. Three corresponding saddles are visible: A/E, U_2/A , and U_3/U_2 , with A/E being the tallest and generally largest among them.

Remarks. Although examined specimens generally fit well within the concept of the species established by Fantini Sestini (1994), they are nevertheless here treated with open nomenclature. The reasoning behind this stems from the general taxonomic problematics associated with the entirety of this genus, which were already discussed previously in this paper. Specifically, *F. rieberi* is somewhat difficult to clearly separate from *Falsanol-*

cites gortanii (Pisa, 1966). Based on the comments, descriptions and figures present in the relevant literature (see list of synonyms for these taxa), some main differences can be observed:

- 1) the coiling of *F. rieberi* is subinvolute in juveniles and tends to become more subevolute in larger forms, while it is sub-evolute even in juveniles of *F. gortanii*;
- 2) whorls of *F. rieberi* are higher, more compressed, and usually possess a somewhat narrower venter than in *F. gortanii*;
- 3) lateral tuberculation and swellings are not pronounced in *F. rieberi*, but weak lateral swellings/tuberculation may appear in *F. gortanii*;
- 4) the “true” ventral furrow seems to be present in *F. rieberi*, while *F. gortanii* possess only a very weakly pronounced furrow or merely a furrow-like interruption on the venter.

The difference in ribbing patterns noted by Fantini Sestini (1994), who stated that juvenile *F. rieberi* firstly only showed bifurcation of ribs in the region of the umbilical nodes and latter in growth transitioned to dominantly showing bifurcation in the inner third of the flank, whilst both patterns of bifurcation appeared interchangeably in *F. gortanii*, is potentially somewhat overgeneralized. In our sample, the exact ribbing pattern varies from specimen to specimen to an extent. Listed characters also clearly distinguish *F. rieberi* from all other, much more distinctly different species of *Falsanolcites*.

Based on the above discussed characteristics, these two species are here tentatively treated as separate. However, the extent of the variability of these characteristics within the genus *Falsanolcites* is currently unknown. Therefore, it is somewhat debatable if the way these specimens are herein grouped is optimal, as they already show considerable variation even within their potential species. The nomenclature of these taxa is therefore treated as open, pending possible revisions based on a larger sample size.

A small specimen from Monte Clapsavon, attributed by Mojsisovics (1882) to *Trachyceras richthofeni*, was regarded by Rieber & Brack (2004) as a member of *Falsanolcites*. Its apparently small umbilicus, as well as a similar whorl section and ornamentation suggest it may be a juvenile specimen of *F. rieberi*; herein, it is listed in the synonymy with a question mark.

Occurrence: *F. rieberi* has been identified from the localities in the Southern Alps, and likely also occurs at the Balaton Highland and in the Dinarides. Its biostratigraphic range seems to cover most of the Fassanian (lower Ladinian), as it occurs in the Perticaense, Recubariensis, and possibly the Curionii horizons/subzones of the Curionii Zone.

Falsanolcites cf. *gortanii* (Pisa, 1966)

Pl. 2, fig. 1, 2, 8.

- v 1912 *Anolcites arminiae* Mojs. Var. *angusta* nov. — Salopek, pp. 2014 – 2015, text fig. 8.
- * 1966 *Trachyceras* (*Protrachyceras*) *gortanii* — Pisa, p. 633-638, text-pl. fig. 4, pl. 81, figs 1-6.
- non 1993 *Protrachyceras gortanii* Pisa — Brack & Rieber, p. 486, pl. 13, figs 8-9.
- non 1993 *Protrachyceras gortanii* Pisa — Gaetani (ed.), pl. 9, figs 7, 10.
- ? 2004 *Falsanolcites* group *furcosus*, involute morphotype — Rieber & Brack, figs. 35, 36.
- ? 2007 *Falsanolcites* sp. — Brack et al., fig. 5.5.
- ? 2018 *Falsanolcites gortanii* (Pisa, 1966) — Mietto & Manfrin, p. 236, 237, pl. 1, fig. 8.

Material: three specimens of various completeness (GPZ III 1562, GPZ III 1652, HPM 194G). All preserve the shell and were all collected at the Gregurić Breg locality.

Dimensions:

	D	H	h	U	W	W	W/H	U/D	SGR
HPM 194G	-	27.3	-	-	21.7	-	0.79	-	-
GPZ III 1652	68.1	26.7	17.5	23.9	22.5	-	0.84	0.35	53%
GPZ III 1652	81.6	29.5	22.3	29.8	-	-	-	0.37	32%

Description. A moderate sized, sub-evolute *Falsanolcites*. The whorl section is moderately high oval, achieving greatest width in the inner part of the flank. The flanks are slightly to moderately convex and pass gradually into a relatively narrow venter. The venter possesses either a very weak ventral furrow, or a furrow-like interruption of the ribs. The umbilical edge is rounded but somewhat pronounced, while the umbilical wall is vertical and relatively tall.

The ornamentation is made up of radial ribbing and spiral rows of nodes. The ribbing is relatively dense and moderately coarse, but slightly varies from specimen to specimen. The ribs are either slightly wider or approximately as wide as the interspaces, rectiradiate and sigmoid to varying degrees. Although the general pattern of ribbing is variable, the bifurcation and intercalation occur in the periumbilical area or anywhere between the inner third of the flank and the mid flank. Double bifurcation is sometimes present, occurring once in the periumbilical area and once in the inner third of the flank, as is the insertion of intercalated ribs between the ribs bifurcated in the periumbilical area. There are at least three spiral rows of nodes: umbilical, marginal and external. The umbilical nodes are more-or-less pronounced, while the marginal nodes are usually weak. The external nodes are rounded in cross section, and opposing ones stand in an alternating position on the edge of the weak furrow or a furrow-like interruption. Sometimes, but not in all specimens, there is an irregularly appearing swelling in the inner third of the flank, usually where the ribs bifurcate.

The external suture line is not visible.

Remarks. The comparison between *F. gortanii* and *F. rieberi* was already discussed for the latter species. All the mentioned characteristics in that part of the text can be used to separate *F. gortanii* from most other species of *Falsanolcites*. However, *F. gortanii*, especially the tuberculate morphotype *nodato*, is particularly similar in coiling, whorl section and ornamentation to *Falsanolcites clapsavonum* (Mojsisovics, 1882). This was already noted by Pisa (1966), who also designated a neotype for *F. clapsavonum*. The main difference between these taxa is the morphology of the venter. The ribs of *F. gortanii* are ventrally interrupted by a weak furrow or a furrow-like structure, while the opposing external tubercles stand in an alternating position. In *F. clapsavonum*,

the ribs cross the venter and connect the opposing external tubercles, which stand in a corresponding position. Because of this Pisa (1966) originally attributed *F. gortanii* to *Trachyceras* (*Protrachyceras*), while *F. clapsavonum* was attributed to *Trachyceras* (*Anolcites*). Whether or not this feature is intraspecifically variable or not is a part of a larger taxonomic problem of this genus, which was already discussed.

One of the specimens from the literature (Brack & Rieber 1993, pl. 13, fig. 8, 9; Gaetani 1993, pl. 9, figs. 7, 10) attributed to *Falsanolcites gortanii* morphotype *nodato*, then referred to the genus *Protrachyceras*, does not belong to this taxon. This was noted in the original description of the genus *Falsanolcites* by Rieber & Brack (2004), in the description of the fig. 9. Because of the appearance of intercalated and bifurcated ribs in the region of the second lateral and marginal nodes, both of which are positioned well above the middle of the flank, this specimen instead likely pertains to either *Protrachyceras* or *Eoprotrachyceras*.

A nomenclatural problem arises for this taxon as well. Namely, *Anolcites arminiae* var. *angusta* Salopek, 1936, a name which pertains to at least one of the specimens herein regarded to be the same taxon as *F. gortanii*, technically has priority over it. According to the article 45.6.4. of the ICZN Code, *Anolcites arminiae* var. *angusta* is a subspecies, as Salopek (1936) does not mention it is infrasubspecific. As such, it is technically available, can be elevated to the rank of the species, and transferred to the genus *Falsanolcites*, resulting in the combination *Falsanolcites angustus* (Salopek, 1936). If regarded as the same taxon as *F. gortanii*, the latter becomes its junior synonym.

This approach is, however, not opted for in this work. Firstly, the taxonomy of the genus *Falsanolcites*, as already discussed, is not completely resolved because of the likely potential for significant intraspecific variability of its species. As such, much of this taxonomy is currently somewhat subjective; a future researcher could potentially regard some of these specimens as being distinct from *F. gortanii*. This is simultaneously the reason why open nomenclature is herein used for this species. In this current taxonomic state, it is perhaps best not to cause further confusion by replacing the more cited name with an obscure one. However, it is strongly encouraged that, if a future comprehensive revision of this genus finds that the species with these

matching characteristics is valid, the name *Falsanolcites angustus* (Salopek, 1936) should ultimately be used for it. The holotype of this species would be GPZ 1652, which likely pertains to the specimen illustrated by Salopek (1912, text fig. 8); the body chamber was subsequently damaged, which is why the original measurements and those presented here differ. The smaller specimen described and measured by Salopek (1912) was not located, however.

Occurrence. *F. gortanii* has been identified at localities in the Southern Alps, and likely also occurs in the Dinarides. In terms of biostratigraphy, it has yet to be identified in well correlated stratigraphic sections. However, it was found associated with *Falsanolcites* (alt. *Eoprotrachyceras*) *gervasuttii* (Fantini Sestini, 1994) in at least one locality (Mietto et al. 2018). In uncondensed ammonoid lenses of the Esino limestone, the latter taxon occurs in the same lenses as *F. recubariensis* (see Jadoul et al. 1992; Fantini Sestini 1994). At Monte San Giorgio, it possibly occurs immediately above the layer with *Chieseiceras chiesense* (see Brack et al. 2005). This data suggests that *F. gortanii* occurs throughout the Curionii zone.

Subfamily Arpaditinae Hyatt, 1900

Genus *Meginoceras* McLearn, 1930

Type species: *Steinmannites* (*Meginoceras*) *meginae* McLearn, 1930

PLATE 3

Lower Ladinian (? uppermost Anisian) trachyceratids from the red nodular limestones of the Gregurić Breg locality.

Fig. 1 - *Falsanolcites furcosus* (Mojsisovics, 1893), specimen HPM 196G, partial body chamber; 1a, left lateral view, 1b, ventral view.

Fig. 2 - *Falsanolcites furcosus* (Mojsisovics, 1893), specimen HPM 176, partial body chamber; 2a, left lateral view, 2b, ventral view.

Fig. 3 - *Falsanolcites furcosus* (Mojsisovics, 1893), specimen MKN 664; right lateral view.

Fig. 4 - *Falsanolcites* cf. *rieberi* (Fantini Sestini, 1994), specimen HPM 112; 4a, left lateral view, 4b, right lateral view, 4c, ventral view, 4d, apertural view.

Fig. 5 - *Falsanolcites* cf. *rieberi* (Fantini Sestini, 1994), specimen SM 2042; left lateral view.

Fig. 6 - *Falsanolcites* cf. *rieberi* (Fantini Sestini, 1994), specimen GPZ IV 714; intermediate between *F. cf. rieberi* and *F. cf. gortanii*; 6a, left lateral view, 6b, ventral view.

The scale bar is 5 cm for every specimen; each rectangle is 1 cm.

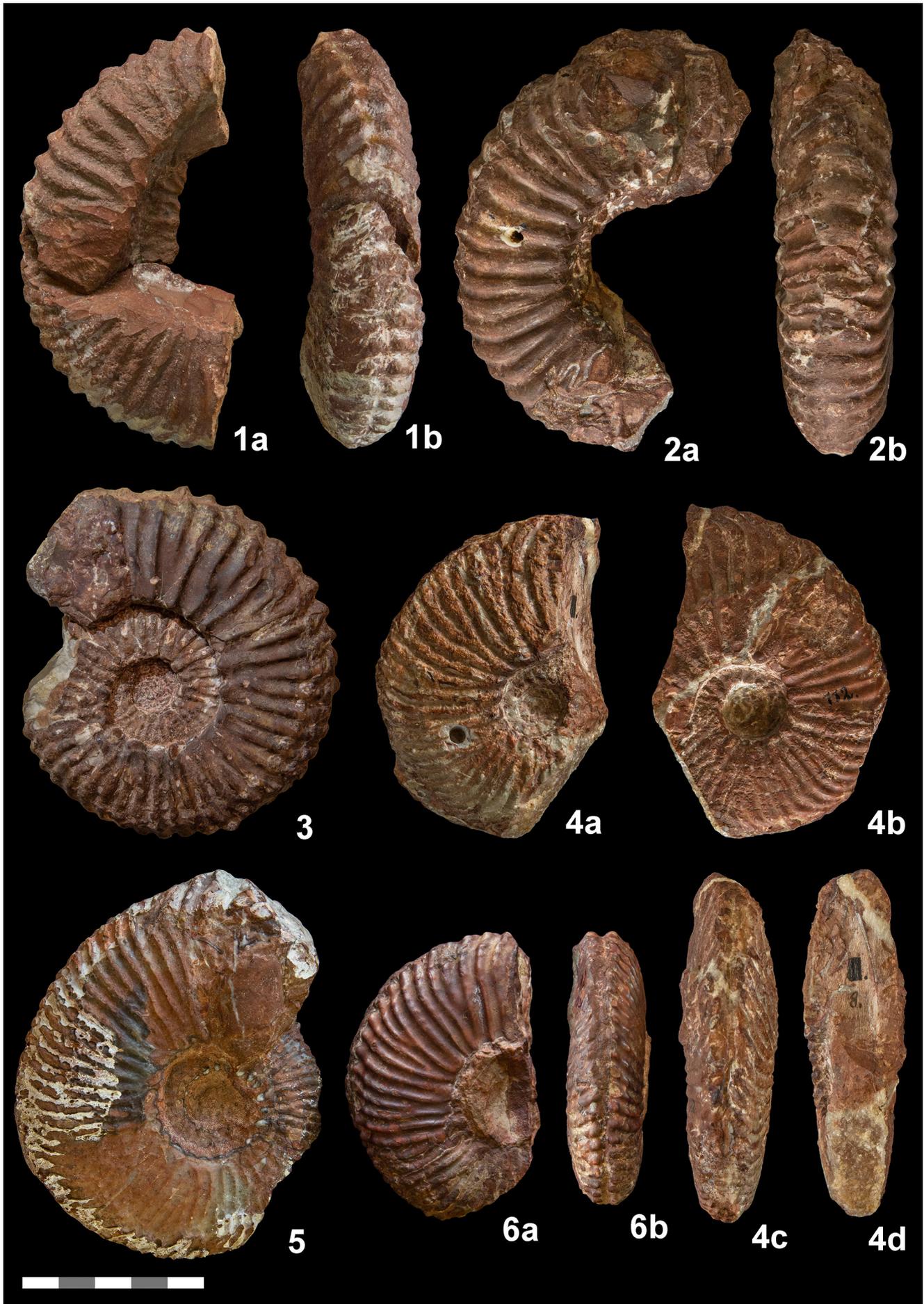


PLATE 3

***Meginoceras* (?) sp.**

Pl. 2, fig. 9.

V 1912 *Anolcites* cfr. *Richthofeni* Mojs. – Salopek, p. 16.

Material: a single small, poorly preserved specimen preserved with the shell (HPM 111), collected at the Gregurić Breg locality and originally identified as *Anolcites* cf. *richthofeni* by Salopek (1912).

Dimensions:

	D	H	h	U	W	W	W/H	U/D	SGR
HPM 111	34.9	12.7*	9.8*	12.4	9.2	-	0.72	0.36	30%

Description. A small specimen possibly belonging to the genus *Meginoceras*. Whorl section is oval and likely widest in the inner third of the flank or lower, and with feebly convex flanks. The venter is damaged but is apparently moderately narrow, with a clear ventral furrow. Raised marginal keels do not appear to be present. The umbilical edge is subrounded but very pronounced, and the umbilical wall is moderately tall and vertical.

The ornamentation consists of radial ribbing and spiral rows of nodes. Ribs are gently sigmoid with strongly projected ventral endings. They are rounded, relatively flat and are slightly wider than the interspaces. Most ribs are primary, but sporadic bifurcation at the umbilical edge and the mid-flank is also present. The nodes are very weak, almost absent, and consist of a row of tiny external nodes bordering the ventral furrow, and possibly of a row of swellings at the umbilical edge. The number of external nodes compared to the number of ribs cannot be established.

The external suture line is not visible.

Remarks. The original referral of this small specimen to *Anolcites richthofeni* (Mojsisovics, 1882) by Salopek (1912) is highly problematic. Originally, three illustrated specimens were assigned to this species (then *Trachyceras richthofeni*), but no holotype was designated (Mojsisovics 1882). Of these, the smallest and the only three dimensionally preserved one, found at Mt. Clapsavon, belongs to the genus *Falsanolcites* and is not the same taxon as the other two (Rieber & Brack 2004). The two remaining specimens show neither the ventral morphology nor a suture line, and their stratigraphic position is not precisely known, which makes them difficult to classify. As a result, subsequent researchers used the species *richthofeni* as a “wastebasket taxon” for many, often fragmentary densely ribbed specimens lacking distin-

ct nodes. Some of these can, like one of the original specimens, be classified as *Falsanolcites* (see Tommasi 1899; De Toni 1913; Rieber & Brack 2004), while others belong to *Frankites* (see Frech 1903; Ogilvie-Gordon 1927; cf. Mietto et al. 2008). Most recently, He & Wang (1997) described and illustrated two partial specimens, one of which preserves a suture line with frilled saddles, leading them to assign the species *richthofeni* to the genus *Paratrachyceras*. Apart from the latter genus being problematic in and of itself (see remarks for “*Anolcites*” cf. *laczkoii* below), it must be noted that the second specimen illustrated by these authors possibly belongs to the genus *Frankites*, which means these specimens are likely not conspecific (Mietto et al. 2008). Better preserved specimens have shown that *T. richthofeni* belongs to the genus *Maclearnoceras*, which is here accepted (Urlich 1977; Mietto & Manfrin 1995b, pers. correspondence 2022).

The specimen herein redescribed, although somewhat poorly preserved, does not show as close of a resemblance to *Maclearnoceras richthofeni* as was originally interpreted by Salopek (1912). Although his referral is understandable from a historical point of view, the morphologically closest taxa appear to be the more evolute species of the arpaditine genus *Meginoceras*, such as *Meginoceras aylardi* (McLearn, 1947). Although arpaditines typically possess elevated keels bordering the ventral furrow, they are not present in all arpaditine taxa and are often relatively unpronounced or even absent in various species of *Meginoceras* (see Tozer 1994). As such, this specimen is herein interpreted as potentially belonging to the genus *Meginoceras*.

Occurrence. The occurrence of *Meginoceras* in the Tethyan province is somewhat enigmatic. It has been reported, although not figured, from strata in Spiti, Himalaya (Balini et al. 1998; Krystin et al. 2004), and has been figured, although not described, from localities in Anatolia (Chen et al. 2016, fig. 1G). The Tethyan species *Ammonites (Trachyceras?) regoledanus* Mojsisovics, 1869, often cited as a *Frankites*, has also recently been suggested to likely also represent a species of *Meginoceras* due to its furrowed venter (Mietto et al. 2008; Mietto & Manfrin, pers. correspondence 2022). Its biostratigraphic range in the Tethyan province therefore appears to span the Longobardicum and Neumayri subzones (Archelaus zone), and the lower parts of the Regoledanus zones (Mietto et al. 2012, fig. 11; Mietto & Manfrin, pers. correspondence 2022).

Subfamily Protrachyceratinae Tozer, 1971

Comments. Tozer (1980) defined the genus *Eoprotrachyceras* based on the possession of a ceratitic suture line, compared to a sub-ammonitic to ammonitic suture of a “true” *Protrachyceras*. This distinction, although rather straightforward, is complicated by the fact that the exact distinction between these types of suture lines is somewhat difficult to define, as transitional forms appear to be present. Some “classic” *Protrachyceras* species variably exhibit transitional, only slightly crenulated saddles in some specimens, while others show “typical” indented saddles, as seems to be the case for specimens of *P. pseudoarchelaus*, *P. steinmanni*, *P. margaritosum* and *P. sikanianum* (Mojsisovics 1882; Toula 1898; Frech 1903; De Toni 1913; Arthaber 1915; Salopek 1912, 1936; Rossi Ronchetti 1960; Brack & Rieber 1993; Tozer 1994). Furthermore, in terms of biostratigraphy (Fig. 8), there is some evidence that, at least in the Tethyan province, protrachyceratine species with a more-or-less ceratitic suture lines, although typical, are not entirely restricted to the lower Ladinian stage (Brack & Rieber 1993; Fantini Sestini 1994). Also complicating this is the possible intraspecific and ontogenetic variability of the suture line. For example, among other ceratitids, *Hungarites mojsisovicsi* (Roth, 1871), *Parakellnerites boeckhi* (Roth, 1871), *Lardaroceras krysztyni* Balini, 1992, and *Rieppelites boletzkyi* Monnet & Bucher, 2005 clearly show variably indented saddles (ceratitic to sub-ammonitic) between individuals. Species of the genera *Billingsites* and *Gymnotoceras* exhibit an ontogenetic change from slightly crenulated sub-ammonitic, almost ceratitic suture lines towards ammonitic ones (Balini 1992; Monnet & Bucher 2005; Vörös 2018). Therefore, the evolution, as well as inter- and intraspecific variability of the suture line among protrachyceratine ammonoids currently remains understudied, with hints at it being potentially more complicated than usually assumed. Consequently, generic distinctions currently employed may not be entirely adequate. Specific cases for protrachyceratine species present in the studied sample are discussed for each taxon independently.

Genus *Eoprotrachyceras* Tozer, 1980

Type species: *Eoprotrachyceras matutinum* Tozer, 1980

Eoprotrachyceras cf. *curionii* (Mojsisovics, 1882)

Pl. 4, figs. 5, 6.

- * 1882 *Trachyceras Curionii* E. v. Mojsisovics — Mojsisovics, pp. 116, 117, pl. XIV, fig. 4.
- 1898 *Protrachyceras Curionii* Mojs. — Toula, pl. 1, fig. 2.
- 1903 *Trachyceras Curionii* Mojs. nut. nov. *rubra* (*Protrachyceras*) — Frech, pp. 22-24, pl. IV, fig. 1., text figs. 7, 9.
- 1903 *Trachyceras Curionii* Mojs. (*Protrachyceras*) Typ. — Frech, pl. IV, fig. 2.
- v 1912 *Protrachyceras Curionii* Mojs. var. — Salopek, pl. V, fig. 1.
- 1913 *Protrachyceras Curionii* Mojs. — Simionescu, pp. 290, 291, 351, fig. 16.
- 1914 *Protrachyceras Curionii* Mojs. — Horn, pp. 19, 20, pl. 1, figs. 3, 4.
- 1927 *Protrachyceras Curionii* Mojsisovics. — Ogilvie-Gordon, p. 51, pl. VI, fig. 11.
- non? 1962 *Trachyceras* (*Protrachyceras*) *curionii* Mojs. var. *ramonensis* Parnes, n.var. — Parnes, pp. 42, 43, pl. 8, fig. 1-4 [? = *Eoprotrachyceras ramonensis* (Parnes, 1962)].
- ? 1966 *Trachyceras* (*Protrachyceras*) *curionii* Mojs. — Pisa, pp. 630-633, pl. LXX, fig. 1.
- 1986 *Eoprotrachyceras curionii* (Mojs.) — Brack & Rieber, pl. 5, fig. 4.
- pars? 1993 *Eoprotrachyceras curionii* (Mojs.) — Gaetani (ed.), pl. 8, figs. 7, 8.
- 1994 *Trachyceras curionii* Mojsisovics, 1882 — Balini, pl. 2, figs. 1, 2, pl. 3, fig. 1.
- non? 1995 *Eoprotrachyceras curionii* (Mojsisovics, 1878) — Goy, pl. 2, fig. 1 [? = *Eoprotrachyceras ramonensis* (Parnes, 1962)].
- 1995a *Eoprotrachyceras curionii* (Mojsisovics, 1882) — Mietto & Manfrin, pl. III, fig. 5, pl. IV, fig. 6.
- non? 1996 *Eoprotrachyceras curionii* (Mojsisovics, 1878) — Goy & Pérez-López, fig. 3.6 [? = *Eoprotrachyceras ramonensis* (Parnes, 1962)].
- 1998 *Eoprotrachyceras curionii* (Mojsisovics) — Vörös, pl. IX, figs. 1, 2, 4.
- ? 1998 *Eoprotrachyceras* cf. *curionii* (Mojsisovics) — Vörös, pl. IX, fig. 5.
- ? 2004 *Eoprotrachyceras curionii* (Mojs., 1882) — Rieber & Brack, fig. 8.
- non? 2005 *Eoprotrachyceras curionii* (Mojsisovics) *ramonensis* Parnes, 1962 — Pérez Valera, pl. 2, fig. 2, pl. 5, fig. 1-2, pl. 6, fig. 1, pl. 9, figs. A, C, fig. 4D [? = *Eoprotrachyceras ramonensis* (Parnes, 1962)].
- 2008 *Eoprotrachyceras* cf. *curionii* (Mojsisovics, 1882) — Vörös et al., pl. 1, fig. 5.
- non? 2016 *Eoprotrachyceras curionii* (Mojsisovics) — Pérez Valera et al., fig. 3A, specimen in fig. 4 [? = *Eoprotrachyceras ramonensis* (Parnes, 1962)].
- non? 2016 *Eoprotrachyceras curionii* (Mojsisovics, 1882) — Pérez Valera, pp. 196-209, pl. 39, fig. 1.; pl. 40, figs. 1, 2; pl. 41, figs. 1, 2, 3; pl. 42, figs. 1, 2; pl. 43, figs. 1, 2, 3; pl. 44, figs. 1, 2; pl. 45, fig. 1; pl. 46, fig. 5; pl. 47, fig. 1; fig. 3.1.51 [? = *Eoprotrachyceras ramonensis* (Parnes, 1962)].
- 2018 *Eoprotrachyceras curionii* (Mojsisovics, 1882) — Mietto et al., pp. 238, 240, pl. 2, fig. 4.
- 2018 *Eoprotrachyceras* cf. *curionii* (Mojsisovics, 1882) — Mietto et al., p. 240, pl. 2, fig. 5.

Material: two relatively poorly preserved fragments of the body chamber (HPM 140, SM 2009), one of which was previously described by Salopek (1912). Both collected at the Gregurić Breg locality.

Dimensions:

	D	H	h	U	W	W	W/H	U/D	SGR
HPM 140	-	74.9	-	-	-	-	-	-	-
SM 2009	-	61.2*	-	-	60.9	-	0.995	-	-

Description. A large *Eoprotrachyceras*. Whorls are sub-rectangular in section, with slightly convex flanks, reaching their greatest width approximately in the inner third of the whorl height. The relatively flat and wide venter is bordered by rounded, more-or-less distinct ventrolateral shoulders. A distinct ventral furrow is present. The morphology of the umbilicus is not discernible due to the state of preservation.

Ornamentation consists of radial ribbing and spiral rows of nodes. The ribs are prorsiradiate and generally straight or projected. They are narrower than the interspaces and are strong and sparse. The intercalation or bifurcation occurs at the second lateral row of nodes, as well as in the periumbilical area. There are, as far as can be seen, five spiral rows of nodes: umbilical, two lateral, marginal, and external. The first lateral row of nodes, as well as the second to a lesser extent, are difficult to observe on the specimen HPM 140, likely due to very poor preservation; on the specimen SM 2009, poor preservation somewhat obscures the umbilical nodes. The marginal nodes sit on the rounded lateral shoulders, while the external ones are positioned on the venter and the opposing ones stand in alternating positions around the ventral furrow. The external nodes are distinctly clavate.

The external suture line is not seen.

Remarks. The specimens described and re-described herein are poorly preserved, which is why they are treated with open nomenclature. Nevertheless, the relatively coarse, sparse ribbing and the apparent intercalation and bifurcation of ribs at the second lateral row of nodes are characteristic of the species *E. curionii* (*sensu stricto*). Additionally, the almost sub-rectangular whorl section, with pronounced but rounded lateral shoulders, fits well with the original illustrations by Mojsisovics (1882) and subsequent authors, although Brack & Rieber (1986) note that *E. curionii* from their samples show certain variability of this feature, as well as in ornamentation. This variability is noticeable in some specimens described by Frech (1903) as *E. curionii* mut. *rubra*, which are more robust and with a more oval whorl section than Mojsisovics' original but are nevertheless here interpreted as representing the same taxon.

Gaetani (1993) illustrates two specimens labelled as *E. curionii*. The first (pl. 8, fig. 7) exhibits typical features of this taxon, while the second (pl.

8, fig. 8), whose ornamentation was later schematically illustrated by Rieber & Brack (2004, fig. 8), has significantly denser ribs which exhibit atypical bifurcation and intercalation. Both specimens occur in the same stratum and locality. Similar specimens include the *E. curionii* illustrated and described by Pisa (1966), and *E. cf. curionii* illustrated by Vörös (1998). Since it is difficult to gauge whether these specimens are within the range of intraspecific variability of this species by the data from literature alone, they are provisionally listed in the synonymy with a question mark.

Specimens referred to *E. curionii* from the Sephardic province (Parnes 1962; Goy 1995; Goy & Pérez-López 1996; Pérez Valera 2005; Pérez Valera et al. 2016; Pérez Valera 2016), sometimes more specifically attributed to the subspecies *E. curionii ramonensis* Parnes, 1962, are somewhat controversial. Specifically, certain conodont workers (Chen et al. 2015, Chen et al. 2016) and ammonoid workers (Mietto et al. 2018) objected to the specific identification of these ammonoids. Even Parnes (1962) originally suggested his juvenile specimen may belong to a separate species. Others disagreed (Plasencia et al. 2016), threatening these specimens as validly attributed to *E. curionii*. Chen et al. (2016) offered compelling arguments against the referral to *E. curionii*; these specimens, although possessing a similar pattern of ribbing and whorl section, are usually more involute and possess very small and particularly clavate external and marginal tubercles, as well as the apparently more pronounced lateral tuberculation. Although these differences could be explained by intraspecific variation, as attempted by Plasencia et al. (2016), this is difficult to justify in absence of a clear morphological overlap between specimens from the Tethyan and the Sephardic province. Therefore, the specimens from the Sephardic province are herein tentatively not considered to be *E. curionii*, with *Eoprotrachyceras ramonensis* perhaps being a more appropriate name for them, although present authors maintain these two taxa are likely very closely related.

Occurrence. *E. curionii* is a widely recognized and often cited taxon that has been recognized from various localities in the Southern Alps, Balaton Highland, Dobrogea, and now very likely in the Dinarides. The reported occurrences from the Sephardic province (Israel, Spain) are questionable and discussed above. Biostratigraphically, this spe-

cies is very important as its first occurrence marks the beginning of the Ladinian stage in the Tethyan province (Brack et al. 2005); simultaneously, this occurrence marks the beginning of the Curionii zone, of which this taxon is an index fossil. The taxon is apparently limited to the lower part of this zone (Curionii horizon/subzone).

***Eoprotrachyceras doraе* comb. nov. (Salopek, 1912)**

Pl. 4, figs. 1 – 3; Fig. 9b.

v* 1912 *Protrachyceras Doraе* n. sp. — Salopek, p. 18, pl. II, fig. I.

Type specimens: lectotype is HPM 116.3; paratypes are HPM 116.1 and HPM 116.2.

Stratum typicum: condensed red-to-grey nodular limestone, uppermost Anisian to lower upper Ladinian in age.

Locus typicus: north-western Croatia, Samoborsko gorje, Gregurić Breg.

Repository: Croatian Natural History Museum, Zagreb (HPM = Hrvatski prirodoslovni muzej)

Dimensions:

	D	H	h	U	W	W	W/H	U/D	SGR
HPM 116.1	44.3*	15.2*	12.6	16.5	-	11.2	-	0.37	21%*
HPM 116.2	50.3	20.3	14.2	15.8*	-	-	-	0.31*	43%
HPM 116.3	61.1*	24.4	15.5*	21.2	-	12.5	-	0.35*	57%

Revised diagnosis. A. small to moderately sized sub-evolute *Eoprotrachyceras*, distinguished as such by bifurcation or intercalation of ribs in the upper part of the flank, the presence of a ventral furrow and a ceratitic suture line. Additional characteristic features of the conch are the sub-rectangular whorl section without the pronounced ventrolateral shoulders and a relatively wide ventral area. Ornamentation is characterized by the increase from four to five rows of spiral nodes. The most diagnostic character is the unique pattern of ribbing: primary ribs, characterized by the presence of umbilical nodes, alternate with long intercalatory ribs which almost reach the umbilical edge but lack the umbilical nodes, such that for every primary rib there is at usually at least one, but sometimes even two intercalatory ribs. The suture line (Fig. 9b) is ceratitic with only two lobes on the flank (A, U2), with A being the largest and most developed one. The external lobe (E) is very small and restricted to the ventral area, while the small lobe U3 sits on the

umbilical wall. Accordingly, there are three saddles on the flank (A/E, U2/A, U3/U2); all of them are of similar height. (Sture line taken at H=17mm)

Additional description. The flanks are mostly flat, but gradually curve into the wide ventral area in the upper third of the flank. The umbilical edge is rounded, while the umbilical wall stands moderately tall and is vertical. Of the five rows of nodes, the umbilical, second lateral, marginal and external are quite distinguishable, while the first lateral row is not as perceptible; this row appears last during growth. The external nodes stand in an alternating position around the ventral furrow, and are distinctly clavate in the holotype, while in the coarsely ornamented paratypes they are more rounded in cross section. The ribs are slightly adorally curved and ventrally projected in the lectotype, while they are slightly sigmoid in more coarsely ornamented paratypes. The ribs are slightly narrower than the interspaces in the lectotype, while being approximately as wide as the interspaces in the paratypes. Apart from the diagnostic long intercalatory ribs, intercalation and bifurcation occur at the first and especially second lateral nodes.

Remarks. Among multiple novel ammonoid species named by Salopek (1912; 1936) during his explorations of the Gregurić Breg locality, this is the the only one based on more than one specimen and simultaneously exhibiting enough diagnostic and clearly preserved characteristics of the conch and the suture line. As such, it is here revised and re-diagnosed according to more modern standards and considered a valid taxon.

The species, with its ceratitic suture line, a clearly present ventral furrow and secondary ribs that occur above the mid-flank, can confidently be referred to *Eoprotrachyceras*. Comparisons can also be made with some species of *Falsanolcites*, but morphological features of the conch, and especially the ribbing pattern, do not support its inclusion into that genus. Among the members of *Eoprotrachyceras*, no species closely matches its unique pattern of ornamentation. The typical western Tethyan species of the genus, *E. curionii*, chiefly differs in possessing massive ribs that are more spaced from each other and secondary ribs which dominantly occur as intercalations or splits at the second lateral row of nodes; these characters are even seen in juvenile specimens of *E. curionii* (cf. Mietto et al. 2018), making it very unlikely *E. doraе* represents

juveniles of the former species. Specimens from the Sephardic province often classified as *E. curionii ramonensis*, here considered to represent a separate species from *E. curionii*, are comparatively more involute, have very delicate and clavate external and marginal nodes and differ in terms of ornamentation in much of the same ways as the “true” *E. curionii*. Another Sephardic taxon, *Protrachyceras wabrmani* Parnes, 1962, which was recently interpreted as belonging to *Eoprotrachyceras* (see Pérez Valera 2016), is more involute and has a different ribbing pattern. The Canadian *Eoprotrachyceras matutinum* Tozer, 1980 has a different ribbing pattern and can have six instead of just five rows of nodes, while *E. gibsoni* Tozer, 1994 is much more involute, with higher and more compressed whorls of a different shape, denser and weaker ornamentation, and with more numerous nodes of which the lateral ones fade on the last whorl. The Nevadan *Eoprotrachyceras americanum* (Mojsisovics, 1886) is more involute and has a differing pattern of ornamentation that is generally like that of *E. curionii*, while its ventral furrow appears to be relatively unpronounced. *Eoprotrachyceras labontabum* (Smith, 1914) is different from *E. dorae* in similar ways to the previous species but matches it more closely in coiling. “*Eoprotrachyceras*” *dunni* (Smith, 1914) has a different pattern of ribbing, is more involute, and lacks a true ventral furrow, making it transitional between *Paranevadites* and *Eoprotrachyceras* and likely a member of a separate genus (Silberling & Nichols, 1982). Lastly, *Eoprotrachyceras meeki* (Mojsisovics, 1882) and *Eoprotrachyceras subsperum* (Meek, 1877) are both more involute, have more compressed whorls of a different shape, and have different patterns of ornamentation; the former has six or seven spiral rows of nodes, while the latter has only four, of which the lateral ones are enlarged and occur sporadically, with both species having relatively weak ribbing.

The most diagnostic feature of *E. dorae*, its long, intercalated ribs that create an alternating pattern of umbilical nodes, is comparable to the morphology originally noted in the description of *Protrachyceras margaritosum* (Mojsisovics, 1882). Otherwise, the latter taxon is clearly significantly different, and it also appears that this feature is likely variable for this species and not present on every specimen (see description of *P. margaritosum* below for details). Since both the compressed lectotype and the more massive paratypes of *E. dorae*

exhibit this pattern of ribbing, it is considered diagnostic for this taxon.

Occurrence. As of the writing of this text, *E. dorae* has only been described from the Gregurić Breg locality in NW Croatia. The taxon was also mentioned as present at the Vlašić Brdo locality by Sakač (1994), yet this specimen has not been identified in any of the studied collections; this occurrence is therefore dubious and unsubstantiated. The exact biostratigraphic position of the species is unfortunately unknown due to the condensed facies it was recovered from, but it is safe to hypothesise that it likely belongs, like the other members of its genus, to the lower Ladinian stage (Fassanian substage), although this needs to be confirmed by more material from better stratigraphic sections.

Eoprotrachyceras nov. sp. indet.

Pl. 4, fig. 4.

v 1912 *Protrachyceras* cf. *pseudo-Archelaus* Boeckh. — Salopek, pp. 18, 19, pl. I, fig. 6.

Material: a single crushed and asymmetrically preserved steinkern (HPM 114), partially covered by shell fragments. It was collected from red nodular limestones of the Gregurić Breg locality and referred by Salopek (1912) to *Protrachyceras* cf. *pseudoarchelaus*.

Dimensions:

	D	H	h	U	W	W	W/H	U/D	SGR
HPM 114	78.6*	30.1	-	24	18.8*	-	0.62*	0.31	-

PLATE 4

Lower Ladinian trachyceratids from the red nodular limestones of the Gregurić Breg locality.

Fig. 1 - *Eoprotrachyceras dorae* (Salopek, 1912), lectotype specimen HPM 116.3; 1a, right lateral view, 1b, ventral view.

Fig. 2 - *Eoprotrachyceras dorae* (Salopek, 1912), paratype specimen HPM 116.2; 2a, left lateral view, 2b, ventral view.

Fig. 3 - *Eoprotrachyceras dorae* (Salopek, 1912), paratype specimen HPM 116.1; 3a, left lateral view, 3b, ventral view.

Fig. 4 - *Eoprotrachyceras* nov. sp., specimen HPM 114; 4a, right lateral view, 4b, ventral view (specimen is laterally crushed).

Fig. 5 - *Eoprotrachyceras* cf. *curionii* (Mojsisovics, 1882), specimen SM 2009, fragment of the body chamber; 5a, left lateral view, 5b, ventral view.

Fig. 6 - *Eoprotrachyceras* cf. *curionii* (Mojsisovics, 1882), specimen HPM 140, fragment of the body chamber; 6a, right lateral view, 6b, oblique apertural view (specimen damaged).

Scale bars are 1 cm for figs. 1 – 4, and 5 cm for figs. 5 and 6. Each rectangle is 1 cm.

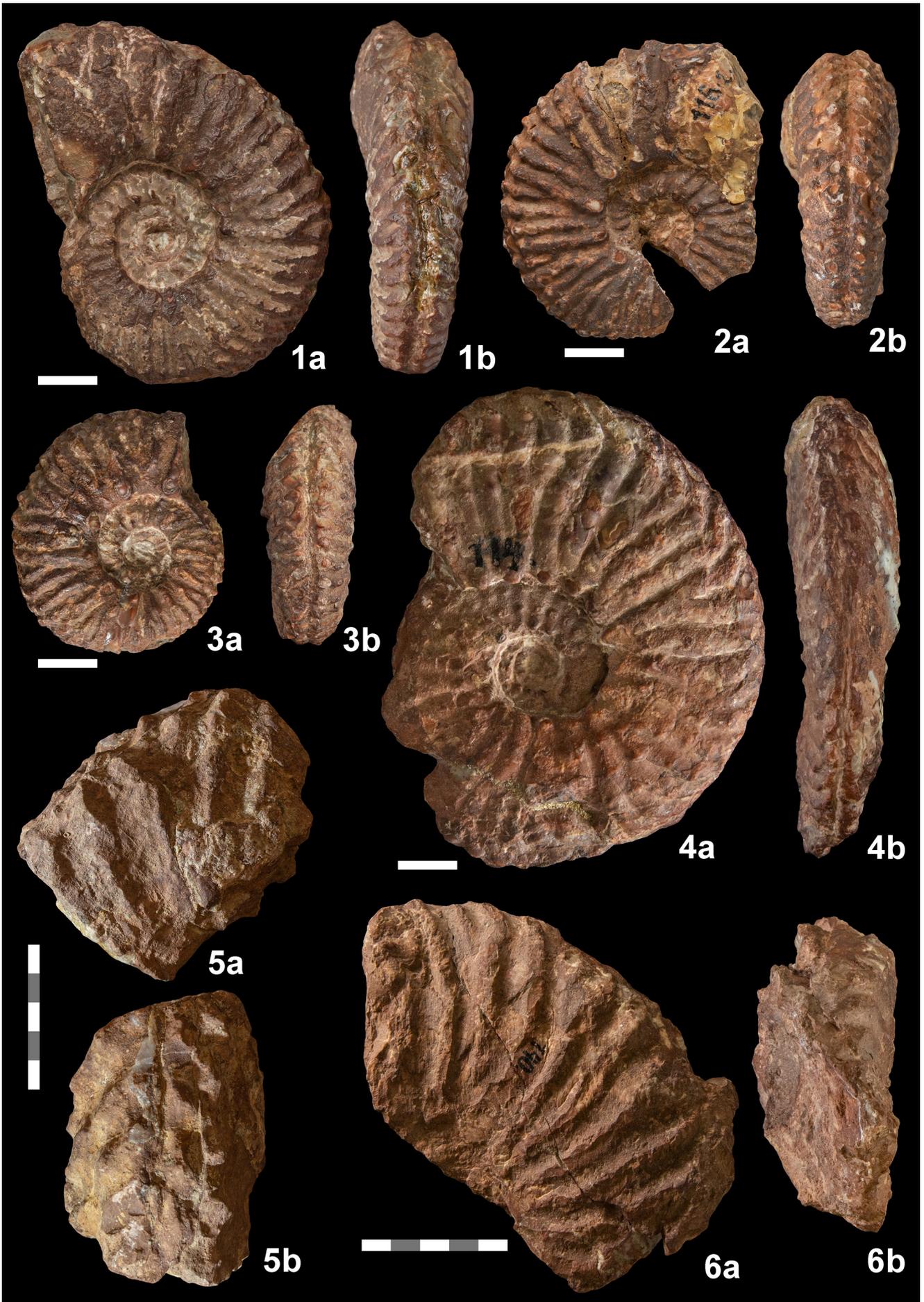


PLATE 4

Description. A moderately sized sub-involute *Eoprotrachyceras*. The flanks appear to be flat and pass gradually into the ventral area, without pronounced ventral shoulders. The venter is damaged but possesses a distinct ventral furrow. The umbilical edge is rounded but pronounced, and the umbilical wall is tall and vertical. Most of the relative dimensions are unknown due to severe crushing.

The ornamentation consists of radial ribbing and spiral rows of nodes. The ribs are rather flat, rounded, and wide, often wider than the interspaces. They are very clearly sigmoid and have rather strongly projected ventral endings. Bifurcation and intercalation appear to occur in varying positions on the flank. The ribs at first bear six spiral rows of nodes, which are at first equidistant. At the end of the preserved body chamber, a seventh row of incipient lateral nodes appear, and an interspace between the first and the second lateral nodes forms. The umbilical and the external nodes appear to be the most pronounced. The external nodes are very distinctly spirally elongated, while the other rows remain rounded in cross section.

The ceratitic suture line is only partially preserved and very difficult to observe. Of the elements, the saddle U_2/A and the lobe A are visible and decently preserved. The lobe is denticulate at its base, but the saddle remains rounded and with no major crenulations or incisions.

Discussion. The unique pattern of nodes and the very wide ribs, coupled with a ceratitic suture line, indicate that this specimen is a new, yet undescribed species of *Eoprotrachyceras*. This was confirmed by other contacted researchers (Mietto & Manfrin, pers. correspondence 2022), who are in possession of much better material from the Southern Alps which is in preparation for publication. As such, this new species is not named in this paper and is not discussed in further detail. However, a suspicion that some of the previously described specimens of various *Protrachyceras* species might belong to this or a similar taxon should be raised (see *Protrachyceras* cf. *pseudoarchelaus* for more detail). No further specimens are, however, currently referred to this taxon.

Occurrence. This species is currently known from a single specimen in the Dinarides and more unpublished specimens in the Southern Alps. At the second locality, the species occurs in condensed facies spanning the Recubariensis subzone and the

Margaritosum zone. It therefore occurs in an interval straddling the potential Fassanian – Longobardian boundary (Mietto & Manfrin, pers. correspondence 2022).

Genus *Protrachyceras* Mojsisovics, 1893

Type species: *Trachyceras archelaus* Laube, 1869.

Comments. McLearn (1943) described in more detail a species he had named previously, *Protrachyceras sikanianum* McLearn, 1930, from the Ladinian strata of British Columbia. In his work, the author notes the apparently remarkable intraspecific variability among the members of the species. More compressed forms sometimes, but not always, develop a comparatively high number of tubercles (often developed into bullae or clavi) and generally have weaker and denser ornamentation. Less compressed, more evolute forms retain six rows of tubercles throughout the ontogeny and exhibit stronger, more sparse ornamentation. The evolute, less compressed form was named *Protrachyceras sikanianum* var. *zawmae* McLearn, 1930. Later, Tozer (1994) briefly described this species and figured more specimens, interpreting *P. sikanianum* in a broader sense and considering most Canadian *Protrachyceras*, which were found in three successive ammonoid zones but apparently showed no significant differences between each of them, to belong to this taxon. In doing so, specimens with a varying degree of involution, compression of the whorls, strength of the ornamentation, as well as with varying number and relative position of tubercles and certain differences in the suture line, were all considered conspecific.

Such an interpretation, although far from being unknown among other ammonoid species, is remarkably different from how species of *Protrachyceras* from the Tethyan province are typically treated. Although Tozer (1994) compares compressed, involute forms of *P. sikanianum* with *P. longobardicum*, and evolute, massive forms with *P. archelaus*, the figured specimens reveal an even greater degree of morphological variation of the conch. An equivalent taxonomic situation in the Tethyan province would be the synonymy of *P. archelaus*, *P. ladinum*, *P. pseudoarchelaus*, *P. longobardicum* and *P. steinmanni*. If future testing of such a scenario, preferably through statistical methods, points to its validity, it could

potentially significantly reduce the diversity of the Tethyan species of *Protrachyceras*. Also important is the notion that in the Canadian Triassic, *Protrachyceras sikanianum* is not used as a zonal indicator, as it occurs in multiple zones; in the Tethyan province, species of *Protrachyceras* are almost always treated as very important index fossils (Fig. 8). This, along with potential taxonomic inconsistencies between the Canadian and Tethyan members of the genus, hampers global correlation of Ladinian strata. Although the findings of McLearn (1943) and Tozer (1994) are certainly suggestive, species of *Protrachyceras* are herein classified typologically, according to their “classic” distinctions, pending a future, likely necessary taxonomic revision.

Protrachyceras margaritosum (Mojsisovics, 1882)

Pl. 5, fig. 5; Fig. 9c.

- * 1882 *Trachyceras margaritosum* E. v. Mojsisovics. — Mojsisovics, pp. 127–128, pl. 82, fig. 1.
- v 1936 *Protrachyceras* sp. ind. ex aff. *margaritosum* Mojs. — Salopek, pp. 221–222, text fig. 10.
- 1993 (*Eo-*)*Protrachyceras margaritosum* (Mojs., 1882) — Brack & Rieber, pp. 484, text fig. 17h, pl. 13, figs. 6, 7.
- 1993 [*Eo-*] *Protrachyceras margaritosum* (Mojs., 1882) — Gaetani (ed.), pl. 9, fig. 9.
- 1994 *Protrachyceras* cf. *margaritosum* (Mojsisovics) — Fantini Sestini, pl. 2, fig. 3.
- 1995a *Protrachyceras margaritosum* (Mojsisovics, 1882) — Mietto & Manfrin, pl. 4, fig. 2, 4.
- non 2007 *Eoprotrachyceras* cf. *margaritosum* (Mojsisovics, 1882) — Tselepidis, pp. 162–163, pl. 8, fig. 1, 2 [= *Falsanolites* sp.].
- 2007 (*Eo-*)*Protrachyceras margaritosum* (Mojsisovics, 1882) — Brack et al., fig. 5.1.
- 2018 *Protrachyceras margaritosum* (Mojsisovics, 1882) — Mietto et al., pp. 240–241, pl. 2, fig. 7.

Material: two specimens, one from the red nodular limestone at the Gregurić Breg locality (GPZ III 1560) and one from the tuffaceous deposits of the Radilovec Jaruga locality (HPM 10492/7). The first is slightly asymmetrical in terms of the umbilical width and the whorl height but seems to not be deformed post-mortem and is potentially palaeopathological, while the second is asymmetrically preserved and significantly deformed. Specimen GPZ III 1560 was already described by Salopek (1936), while HPM 10492/7 was only passingly mentioned by Sakač (1994).

Dimensions:

	D	H	h	U	W	w	W/H	U/D	SGR
HPM 10492/7	62.5	27.4	16.3	18.8	-	-	-	0.30	68%
GPZ III 1560	120.9	55.3	31.2	34.4	36.5	24.0	0.66	0.28	77%

Description. A large, sub-involute *Protrachyceras*. The whorl section is high oval, widest in the

inner fourth of the whorl section and with gently convex flanks which curve into a moderately wide venter, without distinct ventrolateral shoulders. The ventral area becomes slightly wider through ontogeny. A distinct and pronounced ventral furrow is present. The umbilical edge is rounded but pronounced, while the umbilical wall stands tall and vertical.

The ornamentation consists of radial ribbing and spiral rows of nodes. The ribs are straight or slightly sigmoid and with projected ventral endings. The ribbing, although of moderate strength, is relatively dense. The ribs are narrower than the interspaces and are generally relatively thin. Bifurcation and intercalation occur somewhat irregularly in the region of the umbilical and various lateral nodes. At smaller sizes, up to the whorl height of approximately 25 mm, there are seven rows of nodes present: umbilical, four lateral, marginal, and external. This number increases to eight, and at larger sizes it appears to reach as much as ten by the insertion of additional rows of lateral nodes. Characteristically, all the rows of nodes are approximately equidistant and of similar strength; the umbilical and external nodes are sometimes slightly larger. The external nodes are distinctly clavate, and the opposing external nodes stand in an alternating position on the edge of the ventral furrow.

The external suture line can be observed on the larger specimen (Fig. 9c). Where well preserved, it appears to be sub-ammonitic, with highly denticulate lobes and saddles with denticulate flanks and slightly crenulated tops. Some saddles have tops that are, however, almost smooth, resembling the ceratitic condition. In total, there are four lobes present: E, A, U₂ and U₃. However, only the latter three are preserved and visible in their entirety. In turn, three saddles are present, E/A, U₂/A and U₃/U₂, but the first one is poorly preserved or is not seen at all. The A lobe is by far the deepest and the most developed one. The saddles E/A and U₂/A cannot be compared in size and the degree of denticulation because of the poor preservation of the former.

Remarks. Comparison with various illustrated and described specimens of *Protrachyceras* has shown that the above-described specimens fit well with those assigned to *P. margaritosum*. The most characteristic feature of this species, separating it from other members of the genus, is the very high number of equidistant spiral nodes of mostly simi-

lar strength, which appear rather early in ontogeny and allow even the rather poorly preserved specimen HPM 10492/7 to be referred to this taxon. The larger GPZ III 1560 departs slightly from the holotype of this species, which was described and figured by Mojsisovics (1882), by being more involute and, consequently, having higher and more compressed whorls. However, due to the very similar ornamentation, these differences are unlikely to be taxonomically significant, as *P. margaritosum* illustrated throughout the literature also vary in this aspect. Another difference is the lack of the alternating umbilical nodes, present only on some ribs; this feature, specifically highlighted as important by Mojsisovics (1882), is likewise probably variable and is not present in all *P. margaritosum* figured in the literature. Even though Salopek (1936) originally suggested that GPZ III 1560 was only related to *P. margaritosum*, the present authors are of the opinion this specimen is indeed referable to this taxon.

The suture line (Fig. 9c) of GPZ III 1560 departs from the suture line of *P. margaritosum* illustrated by Brack & Rieber (1993) in that it possesses noticeably less denticulated saddles. However, even this specimen shows markedly less developed saddle denticulation than some later members of the genus, such as *P. archelaus*, *P. ladinum* or *P. longobardicum*. The suture line of the holotype illustrated by Mojsisovics (1882) is more comparable to that of GPZ III 1560, although Fantini Sestini (1994) states that the suture line of the holotype is apparently not figured correctly. Due to the great resemblance of the ornamentation of these specimens, it is most parsimonious to suggest these variations of the suture line are likely intraspecific, and not taxonomically significant; similar examples among other ceratitids are listed in the comments for the subfamily Protrachyceratinae. The present authors also agree with Brack & Rieber (1993), Fantini Sestini (1994) and Mietto et al. (2018) that this taxon does not belong to *Eoprotrachyceras*, as suggested by Tozer (1980).

The small specimen assigned to *Eoprotrachyceras* cf. *margaritosum* by Tselepidis (2007) almost certainly does not belong to this taxon, both because of the significantly different morphology and its stratigraphic position. Rather, it is either referable to an indeterminate species of *Eoprotrachyceras* or *Falsanolcites*.

Occurrence. *P. margaritosum* has been identified from multiple localities in the Southern Alps, and now from two localities in the Dinarides. The Greek occurrence described by Tselepidis (2007) is almost certainly misidentified. It is likely one of the earliest occurring *Protrachyceras* in the Tethyan province, as it appears in horizons stratigraphically above those of the Curionii zone, and below horizons containing other “true” *Protrachyceras* (see Brack & Rieber 1993; Fantini Sestini 1994; Mietto & Manfrin 1995a). As such, its occurrence can be placed in its own Margaritosum zone.

***Protrachyceras* cf. *pseudoarchelaus* (Böckh, 1872)**

Pl. 5, figs. 1–3, 6.

- * 1872 *Trachyceras pseudoarchelaus* n. sp. — Böckh, pp. 153, 154, pl. X, fig. 15.
- 1873 *Trachyceras pseudoarchelaus* n. sp. — Böckh, pp. 165, 166, pl. X, fig. 15.
- 1882 *Trachyceras pseudo-Archelaus* Boeckh — Mojsisovics, pp. 121, 122, pl. XIX, fig. 4; pl. XX, fig. 2.
- 1896 *Protrachyceras pseudo-Archelaus* Boeckh sp. — De Lorenzo, p. 148, pl. XX, fig. 19.
- ? 1898 *Protrachyceras anatolicum* n. f. — Toula, pp. 26–34, unnumbered pl., figs. 1, 7.
- 1898 *Protrachyceras pseudo-Archelaus* Böckh sp. — Toula, pl. I, fig. 4.
- 1899 *Protrachyceras pseudo-Archelaus* Boeckh. — Tommasi, pp. 26, 27, pl. IV, fig. 2.
- 1903 *Trachyceras Pseudo-Archelaus* Böckh (*Protrachyceras*). — Frech, pp. 25, 26, fig. 10a; fig. 7β.
- 1903 *Trachyceras Pseudo-Archelaus* var. nov. *glabra* (*Protrachyceras*). — Frech, p. 26, pl. V, fig. 2.
- 1908 *Trachyceras Psudo-Archelaus* Boeckh (*Protrachyceras*) — Frech & Renz, pl. XVII, fig. 1.
- 1910 *Trachyceras (Protrachyceras) pseudo-Archelaus* Boeckh. — Renz, p. 50, pl. IV, fig. 1.
- non 1912 *Protrachyceras* cf. *pseudo-Archelaus* Boeckh. — Salopek, pp. 18, 19, pl. I, fig. 6 [= *Eoprotrachyceras* sp. nov.].
- 1913 *Protrachyceras pseudo-Archelaus* Boeckh. — De Toni, pp. 138, 139, only pl. X, fig. 5.
- ? 1927 *Protrachyceras* cf. *pseudo-Archelaus* Boeckh sp. — Ogilvie Gordon, pp. 59, 60, pl. VII, fig. 6.
- v 1936 *Protrachyceras pseudo-archelaus* Boeckh sp. — Salopek, pp. 219, 220, pl. III, fig. I.
- v pars 1936 *Protrachyceras* sp. ind. aff. *pseudo-archelaus* Boeckh. — Salopek, pp. 220, 221.
- non 1952 *Trachyceras* cf. *pseudo-archelaus* Mojsisovics. — Leonardi & Polo, p. 15, pl. II, fig. 31.
- 1966 *Trachyceras (Protrachyceras) pseudo-archelaus* Boeckh. — Pisa, pp. 642–646, pl. LXX, figs. 6, 7; unnumbered pl., fig. 6.
- non 1983 *Protrachyceras pseudo-archelaus* (Boeckh) — Wang, p. 157, pl. I, figs. 1, 2, 9, 10.
- 1998 *Eoprotrachyceras* ? *pseudoarchelaus* (Böckh) — Vörös, pl. XI, fig. 1, 2.

Material: four specimens, in various states of preservation and completeness, but all of them most likely at least partially preserving the shell. All were collected from the red nodular limestones at Gregurić Breg.

Dimensions:

	D	H	h	U	W	w	W/H	U/D	SGR
HPM 139	133	51.7	38.7	42.6	-	-	-	0.32	34%
HPM 141	-	92.1	-	-	67	-	0.73	-	-
SM 2008	149.1	67.5	41.9	39.7	-	-	-	0.27	61%
SM 2057	223.8*	100*	76.3	47.5*	-	41?	-	0.21*	31%

Description. Large to very large protrachyceratines, varying in involution from sub-involute to sub-evolute. Whorl section is high oval, with greatest width at either the inner third of the flank or approximately at half-flank. The flanks are slightly convex and gradually curve into a moderately wide venter, which possess a distinct ventral furrow. The umbilical edge is not sharp but is very distinctly marked, while the umbilical wall variably stands either subvertical, vertical or overhanging, sometimes changing ontogenetically in that order on the same specimen (e.g., HPM 139).

Ornamentation is made up of radial ribbing and spiral rows of nodes, both showing considerable morphological variability. The ribs are mostly prorsiradiate, straight to sigmoid or even slightly bi-concave. They between being similarly wide or narrower than the interspaces; the two states are even seen on the same specimen (HPM 139). They vary in strength and density from quite strong and sparse to relatively weak and dense. Their cross section is either acute or rounded, but always relatively raised and not flattened. Intercalation and bifurcation variably appear in the regions of umbilical and various lateral tubercles. There are seven spiral rows of tubercles: umbilical, four lateral, marginal, and external. In some specimens all the rows of nodes are of approximately the same strength, while in others the umbilical, the external and the marginal nodes (e.g., HPM 141) dominate over the lateral ones. In some specimens, the rows are approximately equidistant (e.g., HPM 141, SM 2057), while in others there is a clear interspace between the umbilical and first lateral rows (e.g., HPM 139, SM 2008). Some specimens show bullate lateral nodes (e.g., HPM 139, HPM 141). The external nodes are clearly clavate, and the opposing external nodes stand in an alternating position bordering the ventral furrow.

The suture line is either not seen or not preserved adequately on most specimens. Only the

specimen HPM 139 shows a slightly better preserved saddles U_2/A and U_3/U_2 on its inner whorls, which are crenulated or even slightly incised.

Remarks. *Protrachyceras pseudoarchelaus* is, as it currently stands, a relatively poorly defined species, despite being rather frequently cited. Originally, it was coined for specimens most notably characterized by the presence of seven spiral rows of nodes, of which the external, marginal, and umbilical were the most pronounced (Böckh 1872; 1873; Mojsisovics 1882). Additionally referred specimens differed in coiling, whorl section shape, and the characteristics of the ornamentation. Very notable are the multiple examples in which specimens, usually but not necessarily of larger dimensions, possess more than seven (eight or nine) rows of tubercles (Tommasi 1899; Frech 1903; De Toni 1913; Pisa 1966). One such specimen, with eight tubercles, was reported from the Gregurić Breg locality by Salopek (1936) but was neither illustrated nor could be identified during this research.

Also problematic is the apparent very high variability of the suture line. The holotype specimen did not have its suture line exposed (Böckh 1872; 1873), while subsequent authors figured and described everything from practically ceratitic suture lines (Mojsisovics 1882; Toulia 1898; Tommasi 1899; Pisa 1966), suture lines with slightly crenulated saddles (Frech 1903; De Toni 1913; Vörös 1998), and subammonitic/ammonitic suture lines with denticulated saddles (Frech 1903). Since most of these specimens come from localities where more precise stratigraphic analyses were not performed during collecting, it remains a mystery whether all these differences are a result of interspecific variability, ontogeny, or if specimens referred to *P. pseudoarchelaus* potentially belong to multiple species, or even genera. For instance, one of the specimens (HPM 114) from the Gregurić Breg locality originally described by Salopek (1912) and referred to this species is likely a member of an unnamed species of *Eoprotrachyceras* (Mietto & Manfrin, pers. correspondence 2022). Another specimen of *P. pseudoarchelaus* from the same locality (HPM 139) is clearly a true *Protrachyceras* due to its crenulated saddles in the inner whorls. However, an ontogenetic change of saddle crenulation, seen in some other species of the genus (e.g., see *Protrachyceras margaritosum* and *P. steinmanni* sections), may also occur in this species (Mietto & Manfrin, pers. correspondence 2022).

Material described and redescribed in this paper, as can be seen from the description, is rather variable in every feature except the presence of seven spiral rows of nodes. Given that this species is perhaps one of the most taxonomically problematic among the “classic” Tethyan *Protrachyceras* species, the classification of the Gregurić Breg specimens is left open, pending future revisions of this taxon. Even so, it should be compared to other similar *Protrachyceras* species. *P. longobardicum*, whose smaller specimens also exhibit seven rows of tubercles, has eight distinct, equidistant tubercles in adult specimens. This species is also usually even more compressed, more involute, finely ribbed, and distinctly shows a very high number of external versus umbilical tubercles due to frequent splitting and intercalation of ribs. Subadult *P. steinmanni* also have seven rows of nodes, but the species is extremely weakly ribbed and has a distinct pattern of tuberculation. *P. margaritosum* is most easily distinguished by possessing a very high number (up to ten) of equidistant tubercles of similar strength, even relatively early in ontogeny. *P. archelaus*, *P. spitiense* and *P. irregulare* have only six tubercles, are more massively ornamented, and have lower and thicker whorls and a wider venter. *P. ladinum* is more involute and has only six spiral rows of tubercles.

Protrachyceras anatolicum Toulou, 1898 from Turkey is in many ways comparable to *P. pseudoarchelaus*, but since it is based on a single specimen found in an isolated secondary deposit, little can be concretely said about it. Specimens described and figured by Ogilvie-Gordon (1927) are not sufficiently preserved for species level identification. A specimen figured and briefly described by Leonardi & Polo (1952) is almost certainly not *P. pseudoarchelaus*, as the fauna they described is Carnian in age. Smaller specimens figured and described by Wang (1983) appear to not be very similar to *P. pseudoarchelaus*, and may not even be *Protrachyceras* (e.g., their opposing external nodes are not in an alternating position).

Occurrence. Specimens that can be referred to *P. pseudoarchelaus* have been identified from localities in the Balaton Highland, the Southern Alps, the Dinarides, and in Argolis. Specimens from China are most likely misidentified. It is a Longobardian species and apparently occurs in the Longobardicum subzone of the Archelaus zone, as well as possibly in the Margaritosum zone (Mietto & Manfrin 1995a; Vörös 1998).

Protrachyceras steinmanni (Mojsisovics, 1882)

Pl. 5, fig. 4; Fig. 10.

- * 1882 *Trachyceras steinmanni* E.v Mojsisovics — Mojsisovics, p. 109, pl. LXXXI, figs. 10, 11.
 1915 *Trachyceras (Protrachyceras) steinmanni* Mojs. — Arthaber, p. 133, pl. XVI, fig. 5.
 1960 *Trachyceras (Protrachyceras) steinmanni* Mojsisovics 1882. — Rossi Ronchetti, pp. 28, 29, pl. IV, figs. 7, 9; text fig. 2.
 1971 *Trachyceras (Protrachyceras) steinmanni* Mojsisovics — Yurttaş-Özdemir, p. 71, pl. II, figs. 4, 5.
 1992 *Protrachyceras steinmanni* (Mojsisovics) — Jadoul et al., pl. 23, fig. 5.
 1993 *Protrachyceras steinmanni* (Mojs., 1882) — Brack & Rieber, pp. 484 – 486, pl. 13, figs. 1, 4 – 5; fig. 17g.
 1993 *Protrachyceras steinmanni* (Mojs., 1882) — Gaetani (ed.), pl. 9, figs. 2, 6.
 1994 *Protrachyceras steinmanni* (Mojsisovics) — Fantini Sestini, pl. 4, fig. 1.
pars 1998 *Eoprotrachyceras ? steinmanni* (Mojsisovics) — Vörös, pl. XIII, fig. 1, non fig. 2 [= *Protrachyceras* sp. indet.].

Material: a single almost complete steinkern (SM 2007), somewhat poorly preserved and partially still covered by the matrix. The shell is likely also partially preserved. Collected at the Gregurić Breg locality.

Dimensions:

	D	H	h	U	W	w	W/H	U/D	SGR
SM 2007	141.7	75.9	39.5*	26.3*	-	-	-	0.19*	92%*

Description. A large, involute *Protrachyceras*. Whorl section is very high oval, apparently being widest in the periumbilical area. Flanks are feebly convex and pass gradually into a relatively narrow

PLATE 5

Ladinian trachyceratids from the red nodular limestones of the Gregurić Breg locality.

Fig. 1 - *Protrachyceras* cf. *pseudoarchelaus* (Böckh, 1872), specimen SM 2008; right lateral view.

Fig. 2 - *Protrachyceras* cf. *pseudoarchelaus* (Böckh, 1872), specimen HPM 139; 2a, right lateral view, 2b, ventral view.

Fig. 3 - *Protrachyceras* cf. *pseudoarchelaus* (Böckh, 1872), specimen HPM 141, fragment of the body chamber; 3a, left lateral view, 3b, apertural view, 3c, ventral view.

Fig. 4 - *Protrachyceras steinmanni* (Mojsisovics, 1882), specimen SM 2007; left lateral view.

Fig. 5 - *Protrachyceras margaritosum* (Mojsisovics, 1882), specimen GPZ III 1560; 5a, left lateral view, 5b, apertural view, 5c, ventral view.

Fig. 6 - *Protrachyceras* cf. *pseudoarchelaus* (Böckh, 1872), specimen SM 2057; 6a, left lateral view, 6b, ventral view.

The scale bar is 5 cm for every specimen; each rectangle is 1 cm.

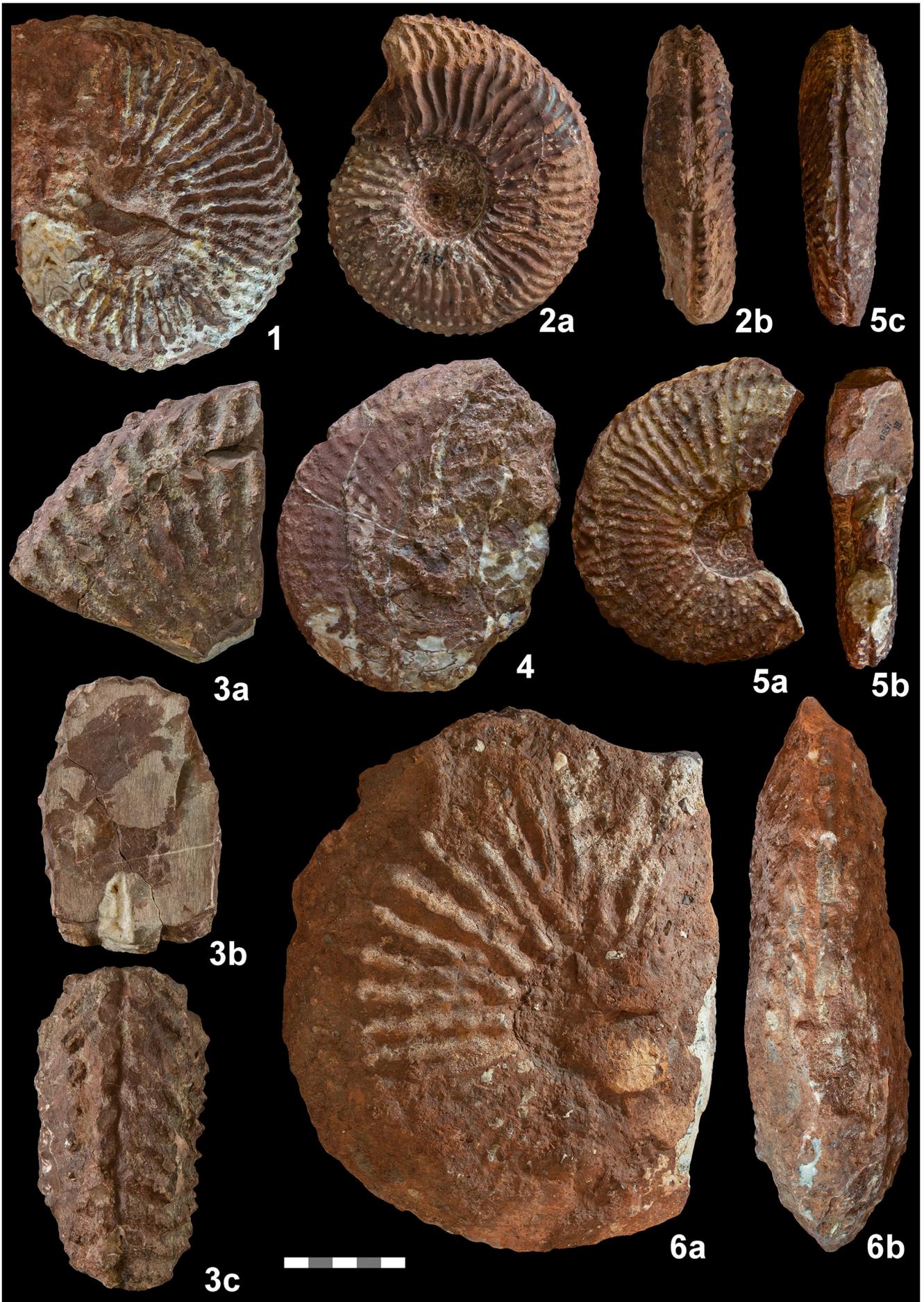


PLATE 5

venter. The ventral furrow is present but is poorly preserved and partially obscured by the matrix infill. The umbilicus is narrow but is also filled in by the sediment.

Ornamentation consists of spiral rows of nodes and radial ribbing. The nodes are small and weak, but perceptible. There are eight rows of nodes: umbilical, five laterals, marginal and external. The umbilical nodes are poorly visible on the left side of the steinkern, but are somewhat more perceptible on the right side, which is otherwise poorly preserved. The first lateral row of nodes is positioned some distance away from the umbilical row, while the second, third and fourth rows are characteristically very close together; the third row is also noticeably weaker than the rest. The fifth lateral row of nodes is again positioned some distance away from the fourth lateral row; this row, the marginal and the external rows are equidistant. Therefore, the rows of nodes are not all equidistant and are of differing strengths. Lateral nodes are blunt and rounded in cross section, while the morphology of the poorly preserved umbilical, marginal and external nodes is not clear; the external nodes may be somewhat clavate. The ribs are extremely weak, rounded, as wide as the interspaces and gently sigmoid. Based on the nodes, the secondary ribs seem to occur, but not very frequently, and it is difficult to ascertain whether they are split or intercalated.

The external suture is visible on the beginning of the last whorl, but is, due to the surface erosion, preserved relatively unevenly and poorly, making it difficult to figure; because of this, a photograph of the visible parts of the suture is shown in Fig. 10. Despite the state of preservation, the suture line is clearly not ceratitic, but appears to be at least sub-ammonitic or even ammonitic, with serrated lobes and clearly crenulated saddles, where preserved more favourably. Four clearly developed lobes can be seen (likely E, A, U₂ and U₃), with three saddles between them. The septal interspace is relatively narrow.

Remarks. This specimen represents the first report of this taxon from the Gregurić Breg locality. Although the specimen is preserved somewhat poorly and not entirely prepared, the distinct pattern of very weak nodes coupled with the very weak ribbing is very characteristic and differentiates this species from all other Tethyan species of *Protrachyceras*. The most similar Tethyan species is *Protrachyceras*

longobardicum, which, however, has more frequent secondary ribs and nodes that are equidistant and more-or-less of similar strength. *Protrachyceras ladinum* is also similarly involute and compressed but has only six spiral rows of nodes, while *Protrachyceras margaritosum* often has more than eight rows of nodes which are all approximately equidistant and is usually more evolute and generally more robust. Lastly, *Protrachyceras parinaense* Fantini Sestini, 1994 has similarly weak ribs, but adults have nine instead of seven to eight rows of nodes, which are large and often spirally elongated, resembling the condition seen in *Sirenotrachyceras*. The specimen described herein agrees in proportions and ornamentation with other specimens collected from localities in the Southern Alps (Mojsisovics 1882; Rossi Ronchetti 1960; Jadoul et al. 1992; Brack & Rieber 1993; Gaetani 1993; Fantini Sestini 1994). However, the suture line, although poorly preserved, clearly departs from that illustrated for some other specimens in the literature (Rossi Ronchetti 1960; Rieber & Brack 1993) in that it has clearly crenulated saddles (Fig. 10), contrary to the almost ceratitic sutures of these specimens. Since these specimens otherwise agree with *P. steinmanni* in external morphology, they are here considered to belong to the same taxon. The source of the variation of the suture line is therefore likely intraspecific, and the marked difference in size between these specimens suggests it might be ontogenetic. Since the Gregurić Breg specimen is the largest of these and shows evidence of at least a sub-ammonitic suture line, this species is kept in the genus *Protrachyceras*.

One of the specimens illustrated by Vörös (1998, pl. XIII, fig. 2) possesses ornamentation that shows little resemblance to that typical of *P. steinmanni* and is here considered to represent and indeterminate species of *Protrachyceras*. Specimens from Anatolia (Arthaber 1915; Yurttas-Özdemir 1971) are here tentatively listed in the synonymy without any special notation but should be mentioned as they appear to be more evolute than other examples and possess a suture line with very incised saddles. No dimensions of the specimen whose suture line was illustrated are given. More research beyond the scope of this paper is needed to resolve this species' noted inconsistencies and reveal the true scope of its intraspecific variability.

Occurrence. Specimens of *P. steinmanni* have been identified at the localities in the Southern Alps,

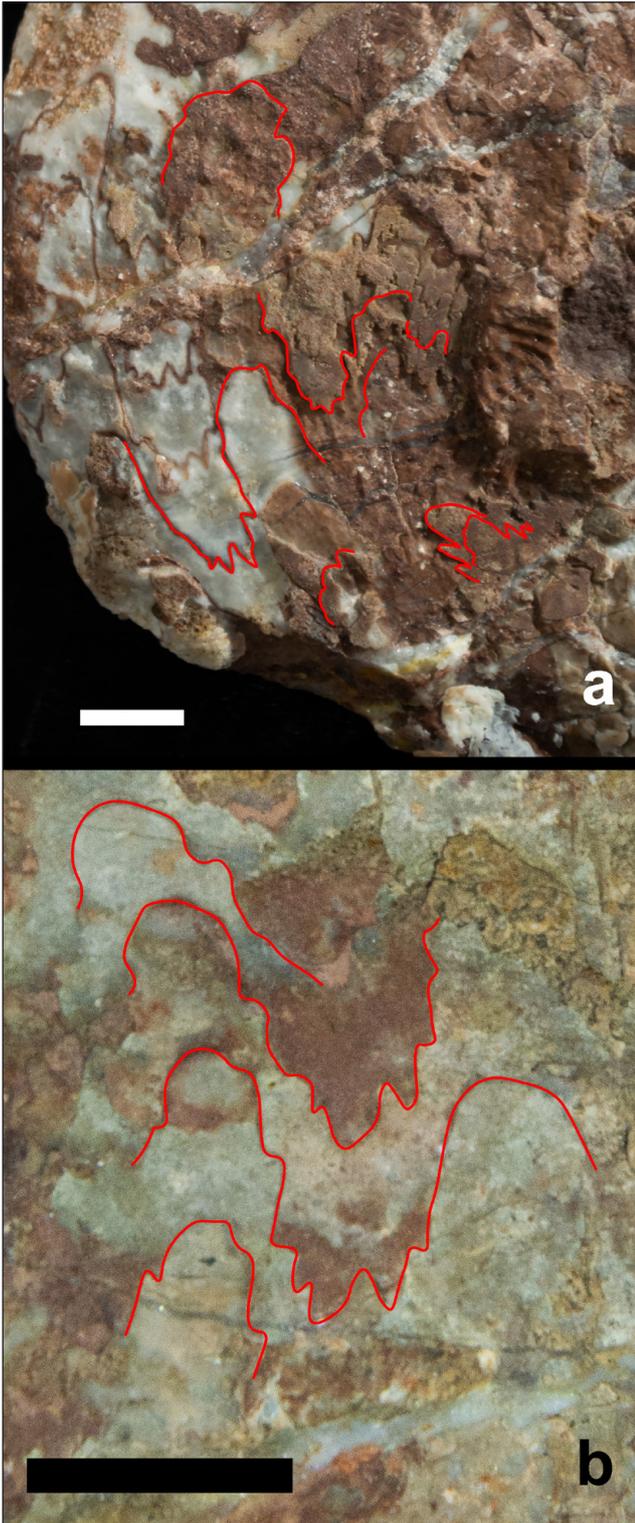


Fig. 10 - Poorly preserved suture line of *Protrachyceras steinmanni* (Mojsisovics, 1882), specimen SM 2007. Parts of the suture exhibiting marked saddle crenulations are highlighted in red; a) left lateral side; b) right lateral side. Scale bars are 1 cm.

as well as probably at the Balaton Highland and in Anatolia, potentially in Argolis (Krystin 1983; no specimens illustrated), and now also in the Dinarides. Its exact stratigraphic range has yet to be

precisely established; it undoubtedly occurs in the Longobardicum zone (equivalent of the lower Archelaus zone) of the Fassanian (upper Ladinian), but also potentially in the Margaritosum (previously Gredleri) zone (Krystin 1983; Brack & Rieber 1993; Fantini Sestini 1994; Mietto & Manfrin 1995a). Precise biostratigraphy of this part of the Ladinian unfortunately remains poorly known in the western Tethys, and its zonation is discussed elsewhere in the text.

Protrachyceras longobardicum (Mojsisovics, 1882)

Pl. 6, fig. 3.

- * 1882 *Trachyceras longobardicum* E. v. Mojsisovics. — Mojsisovics, pp. 126, 127, pl. XVIII, figs. 4, 5; pl. XX, fig. 1; pl. XXII, fig. 5.
 1898 *Protrachyceras longobardicum* Mojs. — Toula, pl. I, fig. 6.
 1903 *Trachyceras longobardicum* Mojs. (*Protrachyceras*) — Frech, p. 27, pl. VI, fig. 3.
 1907 *Protrachyceras* cf. *longobardicum* v. Mojsisovics. — Diener, pp. 95, 96, pl. XII, fig. 1.
 1908 *Protrachyceras* cf. *longobardicum* Mojs. — Diener, pp. 24, 25, pl. I, fig. 6; pl. II, figs. 4, 5.
 1913 *Protrachyceras longobardicum* Mojs. — Simionescu, p. 290, text figs. 14, 15.
 1913 *Protrachyceras longobardicum* Mojs. — De Toni, pp. 140, 141, pl. X, figs. 2-4.
 1914 *Protrachyceras longobardicum* Mojs. — Horn, pp. 35, 36, pl. I, fig. 6.
 1914 *Protrachyceras* cf. *longobardicum* (Mojs.) — Horn, p. 37, pl. I, fig. 8.
 1927 *Protrachyceras longobardicum* Mojsisovics. — Ogilvie Gordon, p. 52, pl. VI, fig. 13.
 ? 1960 *Trachyceras* (*Protrachyceras*) cf. *longobardicum* — Rossi Ronchetti, pp. 26, 27, pl. IV, figs. 4-6.
 1971 *Trachyceras* (*Protrachyceras*) *longobardicum* Mojsisovics — Yurttaş-Özdemir, pp. 72, 73, pl. I, figs. 1, 2, 6; pl. II, fig. 6.
 1994 *Protrachyceras longobardicum* (Mojsisovics). — Fantini Sestini, pl. 4, fig. 4.
 1995a *Protrachyceras longobardicum* (Mojsisovics, 1882) — Mietto & Manfrin, pl. V, fig. 2.
 1998 *Protrachyceras longobardicum* (Mojsisovics) — Vörös, pl. XI, fig. 3; pl. XII, fig. 1, 6.
 2003 *Protrachyceras* cf. *longobardicum* (Mojsisovics) — Pálffy et al., fig. 5i.
 non 2003 *Protrachyceras longobardicum* Mojs. — Xu et al., pl. IV, fig. 12.

Material: a single small, partially preserved specimen (HPM 193G), likely partially covered with the shell. Collected at the Gregurić Breg locality.

Dimensions:

	D	H	h	U	W	w	W/H	U/D	SGR
HPM 193G	45*	-	-	8.8*	-	-	-	0.20*	-

Description. A small, involute specimen of *Protrachyceras*. Whorls are very high oval, possibly even sub-triangular in section, widest in the perium-

bilical area. Flanks are almost flat. The venter appears narrow, but other details are either not preserved or obscured by the matrix. Details of the umbilical edge and wall are obscured by the matrix.

Ornamentation consists of spiral rows of nodes and radial ribbings. The nodes are small but perceptible, and all are of approximately equal strength. They come in seven distinct rows: umbilical, four lateral, marginal, and external. All the rows of nodes are equidistant. The lateral, marginal and external nodes greatly outnumber the umbilical ones, indicating substantial splitting and/or intercalation of secondary ribs. The ribs themselves are extremely weak and barely visible. Numerous secondary ribs are present, but the weakness of the ribs makes it difficult to ascertain whether they are intercalated, bifurcated or both.

The external suture line is not visible.

Remarks. Although poorly preserved, observable features indicate that this is a young specimen of *P. longobardicum*. It is particularly comparable to other younger specimens of the species, such as those figured by Mojsisovics (1882), Frech (1903) and De Toni (1913). The lower number of nodes (seven instead of the typical eight in larger specimens) is explainable by the early ontogenetic stage of these specimens. *P. longobardicum* can easily be distinguished from other species of the genus by its involute coiling, very tall and compressed whorls, as well as by its weak ornamentation consisting of seven to eight equidistant rows of weak nodes and of ribs which often intercalate or split, resulting in external and marginal nodes greatly outnumbering the umbilical ones. The most similar species in the western Tethys is *P. steinmanni*, which differs chiefly by less frequent intercalation and splitting of ribs, and a different arrangement of nodes, where not all rows are equidistant.

A specimen described and figured by Rossi Ronchetti (1960) and identified as *Trachyceras* (*Protrachyceras*) cf. *longobardicum*, is rather fragmentary and somewhat poorly figured and is listed in the synonymy with query. A specimen figured by Xu et al. (2003) as belonging to *P. longobardicum* seems to, as far as can be discerned from the rather poor figures, not belong to this species due to the more robust and less numerous tuberculation.

Occurrence. *P. longobardicum* has been identified at localities in the Southern Alps, the Balaton Highland, in Argolis (Renz 1910), in Dobrogea, in

Anatolia, likely in the Himalayas, and now also in the Dinarides. Occurrences in Southern China are probably misidentified. It is a Longobardian (upper Ladinian) species, and an index species of the Longobardicum subzone, here considered the lower part of the Archelaus zone.

Protrachyceras ladinum (Mojsisovics, 1882)

Pl. 6, fig. 1; Pl. 11, fig. 3.

- 1843 *Ammonites aequinodosus* — Klipstein, p. 121, pl. 7, fig. 1.
 non 1869 *Trachyceras aequinodosum* Klipstein sp. — Laube, pp. 73-74, pl. 39, fig. 5 [= *Sirenotrachyceras hadwigae* (Mojsisovics, 1893)].
 * 1882 *Trachyceras ladinum* E. v Mojsisovics — Mojsisovics, p. 125, pl. 14, fig. 2; pl. 15; pl. 16, fig. 1; pl. 22, fig. 1; pl. 23, fig. 2-3; pl. 36, fig. 2; non pl. 19, fig. 5.
 1898 *Protrachyceras ladinum* Mojs. — Toula, pl. I, fig. 5.
 1903 *Protrachyceras ladinum* Mojs. — Frech, p. 26, pl. 6, fig. 1.
 1908 *Protrachyceras ladinum* v. Mojsisovics. — Diener, pp. 23, 24, pl. I, figs. 2, 4, 5.
 1913 *Protrachyceras ladinum* Mojs. — Simionescu, pp. 289-290, pl. 3, fig. 4.
 1914 *Protrachyceras ladinum* Mojs. — Horn, pp. 38-40, pl. I, fig. 9.
 ? 1927 *Protrachyceras ladinum* Mojsisovics — Ogilvie Gordon, p. 60, pl. 7, fig. 7.
 non 1952 *Trachyceras* cf. *ladinum* Mojsisovics — Leonardi & Polo, pl. 2, fig. 32-35 [= *Sirenites* sp.].
 1960 *Trachyceras* (*Protrachyceras*) *ladinum* Mojsisovics 1882. — Rossi Ronchetti, pp. 25, 26, pl. IV, figs. 1, 2.
 non 1962 *Trachyceras* (*Protrachyceras*) *ladinum* Mojs. var. *parana* Parnes n. var. — Parnes, pp. 43-45, pl. 8, fig. 11-16 [= *Protrachyceras negevensis* Parnes, 1986].
 non? 1973 *Protrachyceras ladinum* Mojs. — Mu et al., pl. V, figs. 15, 16 [? = *Protrachyceras archelaus* (Laube, 1869)].
 1977 *Protrachyceras* cf. *ladinum* (Mojsisovics) — Urlichs, p. 1, fig. 1.
 1985 *Protrachyceras ladinum* (Mojsisovics) — Parnes et al., p. 661-662, pl. 2, fig. 9-11.
 1986 *Protrachyceras ladinum amplum* n. ssp. — Parnes, p. 36, pl. 22, figs. 4-6; pl. 23, figs. 10, 11.
 1997 *Protrachyceras ladinum* Mojs. — He & Wang, p. 338, 339, pl. I; text fig. 2.
 1998 *Protrachyceras ladinum* (Mojsisovics) — Vörös, pl. XII, fig. 7, 8, 9; pl. XIII, fig. 3-4; pl. XIV, fig. 1.
 ? 1998 *Protrachyceras archelaus* (Laube) — Vörös, pl. XIV, fig. 2.
 non 2003 *Protrachyceras* cf. *ladinum* Mojs. — Xu et al., pl. II, fig. 9.
 non 2003 *Protrachyceras ladinum* Mojs. — Xu et al., pl. II, fig. 15.
 2017 *Protrachyceras ladinum* (Mojsisovics, 1882) — Urlichs, pp. 177-180, pl. 4, figs. 1-4.

Material: two specimens; a partial steinkern (HPM 10493/8) still partially covered by the limestone matrix and collected at the Vlašić Brdo locality, and a fragment (SM 2050) preserved with the shell and collected at the Gregurić Breg locality.

Dimensions:

	D	H	h	U	W	w	W/H	U/D	SGR
HPM 14093/8	88.8	46	27.3	15.5	32.5*	17.5	0.70*	0.17	68%
SM 2050	-	39.7	-	-	-	-	-	-	-

Description. A moderate-sized, sub-involute *Protrachyceras*. Whorls are high, thickest in the lower third of their height and high oval in section. The feebly convex flanks gradually pass into a narrow venter, which possesses a distinct ventral furrow. The umbilicus is narrow, but its other characteristics are obscured by the matrix infill on both specimens.

The ornamentation consists of spiral rows of nodes and radial ribbing. The nodes come in six distinct rows of equal strength: umbilical, three lateral, marginal, and external. The umbilical nodes cross over the edge of the umbilicus. The three lateral rows of nodes are equidistant among themselves, but they are separated from the umbilical nodes by a clear interspace. An interspace also exists between the third lateral and the marginal row, but it is markedly narrower. The external nodes on the opposing sides of the ventral furrow are in alternating positions and are slightly clavate. All the other nodes are round in cross section. The ribs are relatively weak, apparently as wide as the interspaces. They are straight to slightly sigmoid, with slightly projected ventral endings. Due to the weak ribbing of the specimen HPM 14093/8, it is not possible to determine whether secondary ribs appear as intercalations or if they are bifurcated, but they seem to appear in the regions of all the nodes except marginal and external. The specimen SM 2050 exhibits bifurcation at the umbilical and third and fourth lateral nodes.

Specimen HPM 14093/8 show a poorly preserved suture line. As far as it can be seen, there are four lobes present on the flanks. Three saddles are also visible on the flanks, as well as one on the umbilical edge. The best-preserved yet still very weathered saddle, likely pertaining to U_2/A , is crenulated in the upper part, and serrated at the base.

Remarks. The above-described morphology agrees quite well with the characteristics attributed to this species in its original description (Mojsisovics 1882) and the subsequent revision (Urlichts 2017). *Protrachyceras ladinum* corresponds to the more involute, compressed morphotypes of the genus, making it comparable to *Protrachyceras steinmanni* (Mojsisovics, 1882) and *Protrachyceras longobardicum* (Mojsisovics, 1882), from which it is most clearly distinguished by possessing only six spiral rows of nodes in adult specimens. The same number of nodes can be observed in species such as *P. archelaus* (Laube, 1869), *P. spitiense* Diener, 1908, and *P.*

irregulare Fantini Sestini, 1994, which are, however, clearly distinguishable by their significantly coarser, more pronounced ornamentation, lower and thicker whorls and their more evolute coiling.

The specimen figured by Ogilvie Gordon (1927) is poorly preserved and is listed in the synonymy with query. A specimen figured by Mu et al. (1973) appears to be rather strongly ornamented and possess wide whorls with a broad venter, and as such is perhaps closer to *P. archelaus*. A specimen referred to *P. archelaus* by Vörös (1998) appears to be rather involute and rather weakly ornamented and is tentatively suggested to be closer to *P. ladinum*; the crucial ventral view was, however, not figured.

Occurrence. This species is typical for the Longobardian substage of the Ladinian, and is known across the Tethyan province, occurring in the Southern Alps, the Balaton Highlands, the Dinarides, as well as in Dobrogea, Israel, Himalayas, and in China. Its exact biozonal provenance is, however, not yet entirely clear. While its redescription states that it occurs in the Neumayri subzone and the Regoledanus zone (Urlichts 2017), likely following the data presented by Mietto & Manfrin (1995a, b), it is worth noting that there are at least two instances (Fantini Sestini 1994; Vörös 1998) in which this species was reported to co-occur with *Protrachyceras longobardicum*, the marker of the Longobardicum subzone of the Archelaus zone. This extends the range of *P. ladinum* into this lower subzone.

Subfamily uncertain

Genus uncertain

***"Anolcites" cf. laczkoi* (Diener, 1899)**

Pl. 6, fig. 2.

- * 1899 *Anolcites Laczkói* nov. sp. — Diener, pp. 13, 14, pl. I, fig. 7.
- 1903 *Trachyceras (Anolcites) Laczkói* Dien. — Frech, pp. 29, 30, pl. VI, fig. 4.
- 1908 *Anolcites cf. laczkói* Diener. — Diener, pp. 26, 27, pl. I, fig. 8.
- non 1913 *Anolcites laczkói* Dien. — De Toni, pp. 144, 145, pl. XI, fig. 4 [= *Falsanolcites* sp.].
- v 1936 *Anolcites laczkói* Dien. var. *falcoidea* n. — Salopek, pp. 216, 217, text fig. 9.
- 1998 *Protrachyceras laczkói* (Diener) — Vörös, pl. XIII, fig. 6; pl. XV, fig. 4.

Material: a single partial steinkern (HPM 112) preserving parts of the body chamber and the phragmacone. It serves as a holotype of *Anolcites laczkói* var. *falcoidea*, established by Salopek (1936). Collected from the red nodular limestones of Gregurić Breg.

Dimensions:

	D	H	h	U	W	w	W/H	U/D	SGR
HPM 112	>90*	40.8	-	-	-	-	-	-	-

Description. A moderate sized trachyceratid, likely sub-involute in coiling. The whorl section is high oval to elliptical, with the maximum whorl width at approximately the half of the whorl height on the body chamber, and in the inner third of the whorl height on the inner preserved whorl. The flanks are almost flat in the inner part of the whorl and become convex as they gradually pass into a narrow ventral area. The umbilical edge is rounded, and the moderately tall umbilical wall stands vertical to slightly overhanging.

The ornamentation is made up of spiral rows of nodes and radial ribs. On the inner whorl, there appear to be two rows of very weak nodes: the umbilical and external, with possible very weak lateral swelling in the lower part of the flank. Characteristically, all the nodes almost completely fade on the body chamber, leaving only very weak swellings, of which the umbilical ones are the more noticeable; external swellings are almost imperceptible. The umbilical swellings are bullate and adorally curved. The ribbing is relatively fine and dense and is characteristically biconcave because of the curvature of the umbilical swellings. Ribs are acute and approximately as narrow as the interspaces. On the inner whorl, ribs are interrupted on the venter. On the body chamber, the ribs gradually become weaker ventrally and either cross the venter with significantly diminished strength, or do not cross the venter at all. In both cases, a very narrow and shallow furrow-like interruption is present, bordered by external swellings. Bifurcation is rare and occurs anywhere from the inner third of the flank to approximately the middle of the flank on the body chamber, while on the inner preserved whorl there is also some bifurcation at the umbilical swellings. The intercalated ribs are more common, with intercalation occurring mostly in the inner third or at the middle of the flank. Short, intercalated ribs that originate above the middle of the flank are rare, but a few of them can be seen on the body chamber.

The external suture line is seen on the inner whorl but is very poorly preserved, so its type cannot be determined.

Remarks. As already pointed out by Salopek (1936), this unusual ammonoid resembles spe-

cimens of the somewhat obscure taxon *Anolcites laczkoi* Diener, 1903. Its unusual venter, showing a narrow and shallow furrow-like interruption that lacks clearly discernible margins, but which is, however, sometimes crossed by very weak ribs, as well as its lack of any “true” nodes, except for the weak umbilical and external swellings, fits well with the original description and illustrations. However, the most notable difference is the very sigmoid, almost biconcave morphology of the ribs, which is very clearly not as pronounced in the original figures and other figured specimens. This character inspired Salopek (1936) to erect a new variant based on the specimen in question, dubbed *Anolcites laczkoi* var. *falcoidea*. Here, it is not treated as a separate taxon, as the low number of described specimens makes it unclear how individually or ontogenetically variable the rib morphology truly is. Open nomenclature is also employed for the same reason.

Two other middle Triassic Tethyan ammonoid taxa also appear to be similar. The first is *Chiešicerias perticaense* Brack & Rieber, 1986, which shows a deceptively similar style of ornamentation. This taxon differs from the herein described specimen primarily by a different, more subtrapezoidal whorl section and by the different ventral morphology, in which the opposing external nodes are more spaced from each other, and the consequently wider, flat-

PLATE 6

Ladinian (? uppermost Anisian) trachyceratids and pinacoceratoids from the red nodular limestones of the Gregurić Breg locality.

Fig. 1 - *Protrachyceras ladinum* (Mojsisovics, 1882), specimen SM 2050 embedded in the host rock, body chamber fragment; 1a, left lateral view, 1b, ventral view.

Fig. 2 - “*Anolcites*” cf. *laczkoi* Diener, 1899, specimen HPM 113, holotype of *Anolcites laczkoi falcoidea* Salopek, 1936, partial body chamber and previous whorl; 2a, left lateral view, 2b, ventral view.

Fig. 3 - *Protrachyceras longobardicum* (Mojsisovics, 1882), specimen HPM 193G embedded in the host rock; left lateral view.

Fig. 4 - *Japonites raphaeliszoja* (Tommasi, 1899), specimen HPM 134; 4a, right lateral view, 4b, apertural view.

Fig. 5 - *Parapinacoceras* sp., specimen HPM 137, holotype of *Gymnites intermedius* Salopek, 1912; 5a, left lateral view, 5b, apertural view.

Fig. 6 - *Japonites raphaeliszoja* (Tommasi, 1899), specimen HPM 171; 6a, right lateral view, 6b, apertural view.

Fig. 7 - *Japonites raphaeliszoja* (Tommasi, 1899), specimen GPZ 6.11; right lateral view.

The scale bar is 5 cm for every specimen; each rectangle is 1 cm.

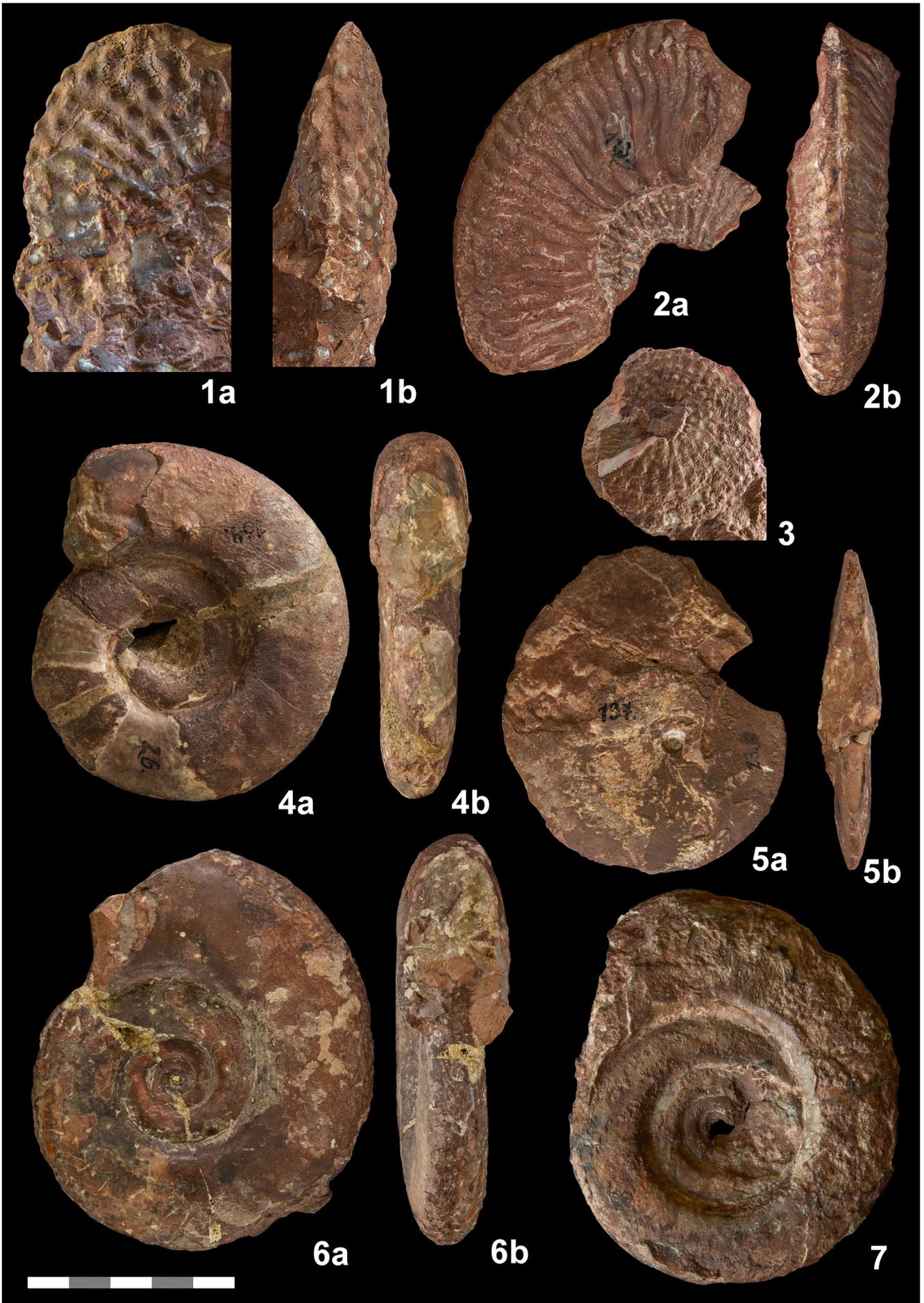


PLATE 6

ter venter is smooth and not crossed by ribs. The suture line of this taxon is also ceratitic instead of sub-ammonitic, and ribs tend to become straighter rather than more sigmoid through ontogeny (Brack & Rieber 1986; Fantini Sestini 1994).

The second apparently similar taxon is the obscure *Protrachyceras mascagni* Tornquist, 1898. The similarity between *P. mascagni* and *A. laczkói* var. *falcoidea* was recently pointed by Mietto et al. (2018), noting the apparently very similar ventral morphologies. However, it is difficult to draw any meaningful comparisons, as the figures in Tornquist (1898) are rather poor, and the holotype has unfortunately been destroyed (Mietto et al. 2018). In the same work, Mietto et al. (2018) also considered *Protrachyceras lermani* Parnes, 1986, originally described by Parnes (1962) as *Protrachyceras* cf. *mascagni*, to be taxonomically connected with *P. mascagni* and *A. laczkói* var. *falcoidea*, once again noting the apparently similar ventral morphology. This proposal is here rejected, as *Protrachyceras lermani* possess a different ribbing pattern, five spiral rows of nodes and a clearly different ventral morphology; in the view of the present authors, this species is clearly substantially different. The proposal by Vörös (2018) that *P.* cf. *mascagni* represents a potential specimen of *Chieseiceras chiesense*, also appears unlikely for much of the same reasons.

Generic and familiar identity of “*A.*” *laczkói* is also not entirely clear. The original referral to *Anolcites*, as well as to any Anolcitinae in general, is questionable due to the sub-ammonitic character of the suture line. Species of the genus *Maclearnoceras* Tozer, 1963, as well as the possibly congeneric Chinese *Frankites leyeensis* He & Wang, 1997, superficially appear comparable to “*A.*” *laczkói*. However, the latter attains a significantly larger size, has a sub-ammonitic instead of a ceratitic suture line, a noticeably different venter, a different ribbing pattern, and the tuberculate inner whorls, diagnostic for *Maclearnoceras*, are currently unknown for this taxon. Members of the so far endemic Chinese subfamily Haoceratinae, especially *Haoceras xingyiensis* Zou et al., 2015, are superficially similar and possess a similar suture line, but are also much smaller, have a distinctly furrowed venter, and a different ribbing pattern. The morphology of the venter, and the low number of very weak nodes also make it unlikely it belongs to *Protrachyceras*, to which it was most recently referred (Vörös 1998).

An interesting proposal (Salopek 1936; McLearn 1947) that this taxon may belong to *Paratrachyceras* is complicated by the fact that the coiling of the Carnian *Paratrachyceras hofmanni* (Böckh, 1872), the type species of that genus, is very involute and its conch is very discoidal. Furthermore, although the long list of species belonging to this genus given by Arthaber (1915) was later revised and severely reduced by McLearn (1947), some of them are currently rather conclusively classified into at least two unrelated genera known from differing stratigraphic intervals, *Meginoceras* and *Frankites*. *Paratrachyceras* is, therefore, an example of a “wastebasket” taxon and, consequently, any referral of species to it in the lack of its thorough revision is unwise at best. As such, it remains possible that the species *laczkói* represents its own, previously undescribed genus.

Occurrence. “*A.*” *laczkói* occurs at the localities in the Balaton Highland, as well as probably in the Dinarides and the Himalayas. The single occurrence from the Southern Alps is likely a misidentified *Falsanolcites* (see De Toni 1913; Rieber & Brack 2004). Little is known about its exact stratigraphic range, but Vörös (1998) identified specimens occurring in the same beds as *Protrachyceras archelaus*, *P. ladinum* and *P. longobardicum*, indicating it likely occurs at least in the Longobardicum subzone of the Archelaus zone.

Superfamily Pinacoceratoidea Mojsisovics, 1879
Family Japonitidae Tozer, 1971
Genus *Japonites* Mojsisovics, 1893

Type species: *Ceratites ? planiplicatus* Mojsisovics, 1888.

Japonites raphaeliszoja (Tommasi, 1899)

Pl. 6, figs. 4, 6, 7; Pl. 11, fig. 5; Fig. 11a.

- * 1899 *Gymnites Raphaelis Zoja* n. sp. — Tommasi, pp. 41, 42, pl. 6, fig. 5-6.
- 1908 *Japonites argivus* Frech — Frech & Renz, p. 457, pl. 18, fig. 1,3.
- 1910 *Gymnites Raphaelis Zojae* Tommasi (*Japonites*) — Renz, p. 41, pl. 2, fig. 2,10,12.
- v 1912 *Gymnites* (?) *Raphaelis Zojae* Tomm. sp. — Salopek, pp. 25,26, pl. 2, fig. 3.
- non 1915 *Japonites Raphaelis Zojae* Tommasi — Welter, pp. 123 – 125, pl. 10, fig. 1, 2 [= *Japonites* sp.].
- non 1915 *Japonites Raphaelis Zojae* Tommasi — Welter, pp. 123 – 125, pl. 10, fig. 3, 4 [= *Japonites asseretoi* Fantini Sestini 1981].
- non 1970 *Japonites raphaelis-zojae* (Tommasi) — Bender, pp. 448, 449, pl. IV, fig. 1 [= *Japonites asseretoi* Fantini Sestini 1981].
- ? 2007 *Japonites raphaelis-zojae* (Tommasi, 1899) — Tselepidis, pp. 241-243, pl. XXXVII, fig. 2; pl. XXXVIII, fig. 1.

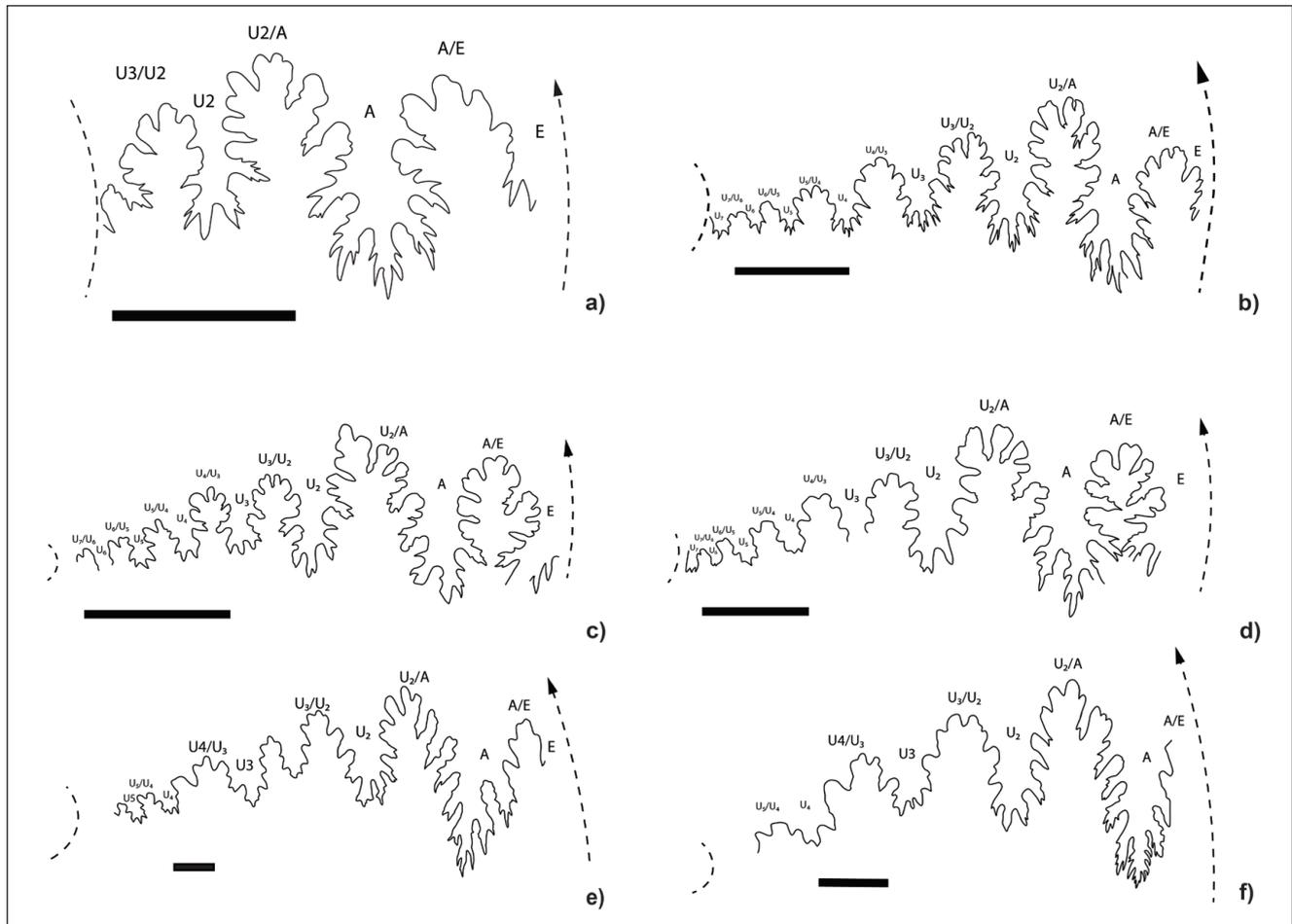


Fig. 11 - Suture lines of ammonoids with ammonitic sutures; a) *Japonites raphaeliszoja* (Tommasi, 1899), specimen HPM 171; b) *Flexoptychites acutus* (Mojsisovics, 1882), specimen HPM 10489; c) *Parasturia emmrichi* (Mojsisovics, 1882), specimen HPM 138; d) *Parasturia emmrichi* (Mojsisovics, 1882), specimen HPM 151.1; e) *Discoptychites* sp., specimen HPM 18ž (Vlašić Brdo locality); f) *Discoptychites* sp., specimen HPM 153.2 (Gregurić Breg locality). Sutures of *Discoptychites* are somewhat simplified due to preservation. Scale bars are 1 cm.

Material: four specimens, three from the Gregurić Breg locality (HPM 134, HPM 171, GPZ 6.11.) and one from the Vlašić Brdo locality (HPM 10490/5), all at least partially preserved with the shell. The specimen found at Vlašić Brdo was previously reported by Sakač (1994), where it was mistakenly attributed to *Monophyllites* cf. *wengensis*. Gregurić Breg specimens were described by Salopek (1912).

Dimensions:

	D	H	h	U	W	w	W/H	U/D	SGR
HPM 10490/5	85.7	26	20.2	39.5	-	-	-	0.46	29%
HPM 134	89.6	28.3	23.3	37	21.9	18.1	0.77	0.42	21%
HPM 171	98.5	33.1	25.8	39.6	23.5	18.7	0.70	0.40	28%
GPZ 6.11	98.5	30.3	21.1*	47.1	20.3	16.5	0.67	0.48	44%*

Description. A medium sized, evolute *Japonites*. Each whorl encompasses the previous one by about a half of its whorl height. Whorls are slow growing, thickest in the periumbilical area, with flat to feebly convex flanks, and with a high oval whorl

section that tends to become sub-rectangular on the body chamber of some specimens (e.g., HPM 134). The venter is rounded and moderately narrow to moderately wide. Umbilical edge is rounded, while the umbilical wall is rather high and sloping at an angle. Flanks are ornamented with very faint, wide folds.

The suture line is partially visible on the specimens HPM 171 (Fig. 11a) and HPM 10490/5, and to a lesser extent on HPM 134. It is weakly ammonitic, and is comprised of three pronounced lobes (E, A, U₂), while the remaining umbilical lobe-like elements are significantly reduced in size and the degree of frilling. These elements have an oblique course compared to the rest of the suture and are partially positioned on the umbilical edge and wall. The lobe A is significantly deeper than both A and U₂. There are three pronounced saddles on the flank (A/E, U₂/A, U₃/U₂); saddle U₂/A is the tallest one.

Remarks. Inclusion of the taxonomic description of this species serves primarily to correct the irregularities in its nomenclature. Since most of the literature dealing with this taxon is rather old, the exact taxonomic name pertaining to this species has fluctuated. Most of the works, including the original description, write the name of the species as a trinomen, but without implying the existence of sub-species level taxa anywhere in the text. Also, the suffix of the third component of the name has fluctuated between “-a” and “-ae”. Therefore, it is proposed, according to articles 32.5.1 and 32.5.2.2. of the ICZN code, that the name of this species should be written down as follows: *Japonites rasphaeliszoja* (Tommasi, 1899).

It must also be noted that the suture line drawn by Salopek (1912, pl. 2, fig. 3c) is likely a composite taken from various whorl heights of the specimen HPM 171. Although individual elements are drawn very competently, the course and the proportions of the suture line are slightly misleading. The small umbilical lobe-like elements are more obliquely positioned compared to the rest of the suture line, like in the condition typical for *Gymnites*, but less developed and fewer in number. The saddle E/A in the illustration also appears to be somewhat too short compared to the A/U2.

Specimens figured by Tselepidis (2007) show typical features of *J. rasphaeliszoja*, especially at smaller diameters, but are notable for possessing a single row of spirally elongated *Epigymnites*-like swellings on the flanks of the last whorl. The author explained this as an ontogenetic change, as these specimens are notably larger than most previously reported ones. However, specimens from the Gregurić Breg and Vlašić Brdo localities are in a similar size range as those of Tselepidis (2007), and yet do not show this type of ornamentation. Although individual variation cannot be discredited with certainty, it is possible that the Greek specimens represent a different taxon and are therefore listed in the synonymy with query.

Occurrence. This taxon is known from localities in the Southern Alps, the Dinarides, and potentially in Argolis. Its biostratigraphic range is not very well constrained, but it appears to occur along with other Ladinian and uppermost Anisian ammonoids (Tommasi 1899; Bucher 1989), and a potential occurrence from Argolis has been constrained to the equivalent of the Secendensis zone (Tselepi-

dis 2007; Pomoni & Tselepidis 2013). Possible lower Anisian occurrences of this taxon (e.g., Welter 1915; Bender 1970) are very likely misinterpreted and belong to separate species (Fantini Sestini 1981; Bucher 1989).

Family Gymnitidae Waagen, 1895

Comments. At the studied localities, multiple species (Tabs. 1,2; Pl. 7) of both *Gymnites* and *Epigymnites* are present, as is *Parapinacoceras aspidoides* (Diener, 1900). Special attention should be given to the species *Gymnites ubligi* Salopek, 1912 and *Gymnites bosnensis* var. *nodosa* Salopek, 1936. The holotype of *G. ubligi* (Pl. 7, fig. 1) is very fragmentary but preserves a body chamber with an elliptical whorl section, very faint folds and rounded, relatively large and spaced nodes in the middle of the flank. *G. bosnensis* var. *nodosa* is represented by three specimens. The holotype (Pl. 7, fig. 7) is a rather compressed specimen with elliptical whorls ornamented by very small, densely packed rounded nodes positioned above the middle of the flank on the last whorl. The

PLATE 7

Uppermost Anisian and Ladinian gymnitids from the red nodular limestones of the Gregurić Breg locality.

- Fig. 1 - *Gymnites* (?) *ubligi* Salopek, 1912, holotype specimen HPM 2, fragment of a body chamber and a pervious whorl; 1a, right lateral view, 1b, apertural view.
 Fig. 2 - *Gymnites bosnensis* Hauer, 1887, specimen SM 2025; 2a, left lateral view, 2b, apertural view.
 Fig. 3 - *Gymnites* cf. *incultus* (Beyrich, 1865), specimen GPZ III 1649, phragmacone; 3a, left lateral view, 3b, ventral view, 3c, apertural view.
 Fig. 4 - *Epigymnites* cf. *ecki* (Mojsisovics, 1882), specimen HPM 175, partial phragmacone; 4a, left lateral view, 4b, ventral view, 4c, apertural view.
 Fig. 5 - *Epigymnites credneri* (Mojsisovics, 1882), specimen GPZ III 1645; right lateral view.
 Fig. 6 - *Gymnites* (?) “*bosnensis nodosa*” Salopek, 1936, paratype specimen HPM 172; 6a, right lateral view, 6b, apertural view.
 Fig. 7 - *Gymnites* (?) “*bosnensis nodosa*” Salopek, 1936, holotype specimen HPM 149; 7a, left lateral view, 7b, ventral view, 7c, apertural view.
 Fig. 8 - *Parapinacoceras aspidoides* (Diener, 1900), specimen HPM 153.1, phragmacone; 8a, right lateral view, 8b, left lateral view.
 Fig. 9 - *Epigymnites* cf. *peciensis* (Toula, 1913), specimen HPM 136, fragment of a phragmacone; 9a, left lateral view, 9b, apertural view.

The scale bar is 5 cm for every specimen; each rectangle is 1 cm.

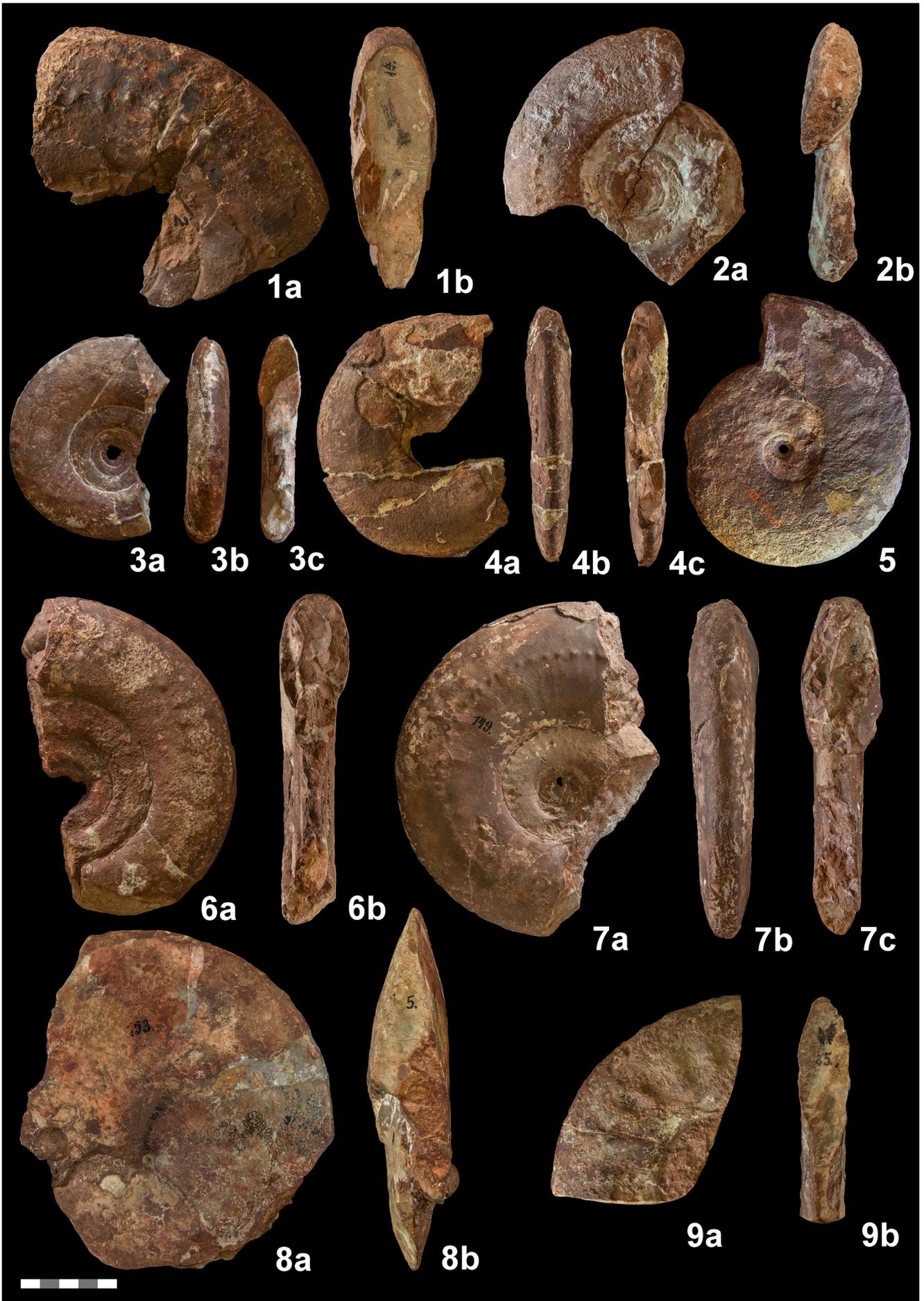


PLATE 7

paratype (Pl. 7, fig. 6) is more evolute, has a more oval, almost sub-rectangular whorl section with a significantly wider venter and similar, but slightly larger and somewhat more spaced nodes which are positioned approximately in the middle of the flank. The third specimen is stored in the Samobor Museum (Pl. 7, fig. 2), and is evolute, shows distinctly spirally elongated nodes on the body chamber, and preserves a *Gymnites*-like suture line with an undivided saddle A/E. As such, it represents a true specimen of *Gymnites bosnensis* Hauer, 1887.

The two former specimens of *G. bosnensis* var. *nodosa* and the holotype of *G. ubligi* are problematic as they either do not preserve entire suture lines or lack them at all. They all possess a spiral of rounded nodes, but otherwise differ significantly, to the point that it is difficult to ascertain if they are members of the same genus. The holotype of *G. bosnensis* var. *nodosa* appears to be comparable to "*Gymnites*" *breuneri* (Hauer, 1849) but is slightly more involute. The holotype of *G. ubligi*, on the other hand, has comparable ornamentation to the Nevadan *Epigymnites alexandrae* (Smith, 1914), but differs in whorl section. These specimens are herein tentatively left in their respective species and subspecies, but only questionably attributed to the genus *Gymnites*, awaiting the discovery of similar, more complete material.

Genus *Parapinacoceras*

Type species: *Pinacoceras aspidoides* Diener, 1900

Parapinacoceras sp.

Pl. 6, fig. 4.

v 1912 *Gymnites* (?) *intermedius* n. sp. — Salopek, pp. 24, 25, pl. II, fig. 2.

Material: a single specimen from the Gregurić Breg locality. It is preserved as a steinkern, but still partially covered by the shell.

Dimensions:

	D	H	h	U	W	w	W/H	U/D	SGR
HPM 137	78.5	45.9	27	5.6	12.3	8.7	0.27	0.07	70%

Description. A moderate sized, very involute *Parapinacoceras*. The flanks are almost flat and pass into an acute venter. The whorl section is very high and very compressed sub-ovoid, with its greatest width being located approximately in the inner fourth of the whorl, slightly above the periumbilical

area. The very narrow umbilicus has a rounded but very prominent umbilical edge, while the moderately high umbilical wall is vertical. There is no perceptible ornamentation on the flanks.

The external suture line is relatively poorly preserved, but is ammonitic, with incised lobes and saddles. There are at least six primary lobes visible on the flank, with six corresponding lobes. The saddle A/E is bipartite, divided by a secondary lobe-like element; it is also the tallest and most developed saddle. Salopek (1912, pl. II, fig. 2c) illustrated the suture line very well.

Remarks. This small, very flat, involute and discoidal specimen is certainly not a member of the genus *Gymnites*. Its suture line is also slightly simplified due to surface damage, but even so shows little resemblance to the "true" *Gymnites*. As noted by Salopek (1912), this suture line shows some similarities to *Buddhaites rama* (Diener, 1895) and *Parapinacoceras subclausus* (Hauer, 1887). The resemblance to juvenile *Buddhaites* is even clearer when compared to the small specimens of *Buddhaites hagei* (McLearn, 1946) illustrated by Tozer (1994). The differences between juvenile and adults of that species, notably simpler denticulation, less divided saddle A/E and less numerous umbilical elements in juveniles, is almost exactly what differentiates *G. (?) intermedius* from the adults of *Buddhaites* and *Parapinacoceras*. These two genera are closely related, with the former recently considered to be a subgenus of the latter (Rein & Werneburg 2010). Since *Buddhaites* is unknown from the western Tethys and occurs in strata older than those at Gregurić Breg, the Gregurić Breg specimen is herein referred to *Parapinacoceras* sp., and the name *G. intermedius* is considered a nomen dubium.

Superfamily Ptychitoidea Mojsisovics, 1882

Family Ptychitidae Mojsisovics, 1882

Genus *Flexoptychites* Spath, 1951

Type species: *Ptychites flexuosus* Mojsisovics, 1882

Flexoptychites acutus (Mojsisovics, 1882)

Pl. 10, fig. 2; Pl. 11, figs., 1, 2, 6; Fig. 11b.

* 1882 *Ptychites acutus* E. v. Mojsisovics. — Mojsisovics, p. 263, pl. LXIV, fig. 4, pl. LXV, figs. 5, 6, ? fig. 4.

1901 *Ptychites acutus* Mojs. var. (?) — Reis, p. 93, pl. V, fig. 3-13; pl. VII, figs. 16-27.

? 1903 *Ptychites acutus* Mojs. — Frech, p. 13, pl. I, fig. 2.

1904 *Ptychites acutus* Mojsisovics 1882 — Martelli, p. 128, pl. XI, figs. 5, 6.

- 1910 *Ptychites acutus* Mojsisovics — Renz, p. 26, pl. I, fig. 8.
 ? 1913 *Ptychites flexuosus* Mojs. - *acutus* Mojs. — Toula, pp. 667-671., pl. XXIV, fig. 9.
 1913 *Ptychites acutus* Mojs. — Simionescu, pp. 341, 367, pl. V, fig. 2, text fig. 73.
 v 1914 *Ptychites acutus* Mojs. — Salopek, p. 20.
 ? 1963 *Flexoptychites acutus* (Mojsisovics), 1882. — Assereto, p. 80, pl. IX, fig. 3.
 1967 *Flexoptychites acutus* (Mojsisovics, 1882) — Casati & Gnaccolini, p. 137, pl. 10, fig. 7.
 1973 *Flexoptychites acutus* (Mojsisovics, 1882) — Rieber, p. 71, pl. 17, figs. 21, 24; text fig. 19ad.
 v 1988 *Flexoptychites acutus* (Mojsisovics), 1882 — Prlj & Mudrenović, p. 20, pl. IV, fig. 4; pl. V, fig. 1.
 non 1992 *Flexoptychites* cf. *acutus* (Mojsisovics), 1882 — Sakač, p. 33; [= *Discoptychites megalodiscus* (Beyrich, 1867); *Flexoptychites* sp.]
 1996 *Flexoptychites acutus* (Mojsisovics, 1882) — Fantini Sestini, p. 223, pl. 1, fig. 1.
 1998 *Flexoptychites acutus* (Mojsisovics, 1882) — Petek, pp. 133, 140, pl. 5, fig. 1.
 2007 *Flexoptychites acutus* (Mojsisovics, 1882) — Tselepidis, pp. 222-224, pl. XXVIII, fig. 3; pl. XXIX, figs. 1-4.
 non 2010 *Flexoptychites acutus* (Mojsisovics, 1882) — Vörös, p. 13, pl. IV, fig. 1, 2 [= *Lanceoptychites* sp.]
 2018 *Flexoptychites acutus* (Mojsisovics, 1882) — Đaković, pp. 191-193, fig. 109.
 non 2018 *Flexoptychites* cf. *acutus* (Mojsisovics, 1882) — Vörös, pp. 141, 142, pl. XLIII, fig. 4 [= *Lanceoptychites* sp.]

Material: four specimens, collected from the Kolići and Vlašić Brdo localities. All of them are preserved as steinkerns. Two of the specimens, HPM 10489/4 and HPM 10ž, were already mentioned by Sakač (1994) as *Flexoptychites flexuosus* and *Flexoptychites* sp., respectively.

Dimensions:

	D	H	h	U	W	w	W/H	U/D	SGR
HPM 10ž	65*	-	27.1	6.3	-	-	-	-	-
HPM 10489/4	89.5	44.7	33.8	11	-	-	-	0.12	32%
HPM 14ž	104.1	-	38.4	10.5	-	-	-	0.1	-
HPM 17ž	216	-	84.4	-	-	-	-	-	-

Description. Medium sized to very large, involute *Flexoptychites*. Whorls are high and narrow, high oval in section, and are widest slightly above the periumbilical area. The venter is rather narrow but is clearly rounded. The umbilicus is narrow and step-shaped in the best-preserved specimen (HPM 10489/4). The umbilical edge is rounded, while the umbilical wall is subvertical. Flanks are ornamented with weak sigmoid folds, which begin slightly above the umbilical edge and end before the contact with the ventral area. Specimen HPM 10489/4 has noticeably stronger folds than the other specimens, although their surface preservation is somewhat poorer; HPM 17ž (Pl. 11, fig. 7) may have no folds, but its surface is rather poorly preserved. Intercalary folds of the same strength as primary folds are also present

on the specimen HPM 10489/4 (Pl. 11, fig. 1), which has a density of the folds of approximately 7 per half-whorl. The same specimen also shows folds which are less sigmoid near the beginning of the last whorl.

The suture line (Fig. 11b), ammonitic in character, is typical for the genus. Eight lobes are present in total, with lobe A being the deepest and the most complexly divided one. Lobes, as well as saddles, progressively become smaller and less divided towards the umbilicus. Saddle U_2/A is the tallest one, significantly oversizing the neighbouring saddles A/E and U_3/U_2 . Saddle A/E is not constricted at the base, as the relatively small lobe E does not closely approach the neighbouring lobe A. The septal interspaces are not very narrow.

Remarks. Amongst the species of the genus, *F. acutus* is generally distinguished by relatively narrow and high whorls which terminate in a markedly narrow but rounded venter. This interpretation of the ventral morphology agrees with the original descriptions and illustrations (Mojsisovics 1882) and was later confirmed by Balini (1998). As such, specimens with very acute or fastigate ventral areas and those with lanceolate whorl sections (cf. Balini 1998) are not included into this taxon. These include a specimen figured by Assereto (1963) and those figured by Vörös (2010, 2018). Additionally, the original description and the general concept of this species in the literature implies the presence of sparse, weak sigmoid folds, a step-shaped umbilicus, and an external suture line with eight lobes on the flanks. However, the validity of this species was questioned multiple times by various authors, specifically regarding its relationship with undoubtedly closely related *Flexoptychites flexuosus* (Mojsisovics, 1882) and *Flexoptychites studeri* (Hauer, 1857) (see Diener 1900; Reis 1901; Frech 1903; Martelli 1904; Renz 1910; Urlichs & Kurzweil 1997). Some authors have even gone as far as to synonymize two or three of these species (Hauer 1887; Turina 1912; Toula 1913), while more recent works once again opted to interpret these taxa as separate (Gugenberger 1927; Assereto 1963; Vörös 2010, 2018; etc.).

This taxonomic problem is clear from the material described and illustrated in the literature and was observed first-hand in the specimens of *Flexoptychites* available for study, most of which were collected and previously briefly described by Salopek (1914) and stored in the Croatian Natural History Museum. Morphological features typically used to diagnose these taxa appear, in many cases, apparently almost con-

tinuously variable. Because of this, it is often exceedingly difficult to clearly define the morphological boundaries between specimens of *F. acutus* and the more compressed variants of both *F. flexuosus* and *F. studeri*. Significant inconsistency is thus present in the literature regarding the naming of specimens which possess differing combinations and degrees of expression of various morphological features.

Further complications arise when comparing *F. acutus* with *Lanceoptychites noricus* (Mojsisovics, 1882). It is important to note that the usage of the term “lanceolate whorl section” in the redescription of *L. noricus* by Manfrin et al. (2005) does not appear to match the usage of the same term in the original description of the genus *Lanceoptychites* by Balini (1998). Namely, Balini (1998) only uses this terminology for the whorl sections which show a marked, concave narrowing towards the venter, which is apparently absent in *L. noricus* (Manfrin et al., 2005; Mietto & Manfrin, pers. correspondence 2022). Because of this, as well as the very similar ornamentation, adult specimens of *L. noricus* illustrated by Manfrin et al. (2005) are remarkably comparable to the original illustrations of *Flexoptychites acutus* by Mojsisovics (1882). Juvenile specimens of *L. noricus* are, however, distinct from most other ptychitids in showing a clearly subacute venter very early in their ontogeny. Since both taxa apparently occur in the same strata (Manfrin et al. 2005, tab. 1), it may sometimes be difficult to clearly discern between their adult forms, easily causing misidentifications and raising the possibility that a part of the type series of *F. acutus* may belong to *L. noricus* instead.

As tempting as it might be to simply synonymize some of the discussed taxa, the opinion of the present authors is that this should be avoided without their comprehensive revision, accompanied by the application of modern morphometric methods and, especially, correlation with stratigraphic data. Therefore, our specimens are here simply dubbed *Flexoptychites acutus*, as they are closest to the original concept of that species.

Specimens of *Flexoptychites angustoumbilicatus* (Böckh, 1872), which often show a rather similar compressed whorl section and the narrower venter like that of *F. acutus*, can be easily distinguished from it by their very characteristic ornamentation comprised of alternating sets of primary and secondary folds of differing strengths. Because of the possible presence of this morphology, a specimen figured by Toulou (1913) and interpreted as “*Ptychites flexuosus-acutus*”, a

composite name used for *F. acutus* as merely a variant of *F. flexuosus*, may in fact belong to *F. angustoumbilicatus*, and is therefore listed in the synonymy with query.

Sakač (1992) described, but did not illustrate, two specimens from the Brotnja locality (Lika, Croatia) that he identified as *F. cf. acutus*. However, only one of these specimens (HPM 10420/6) can be ascribed to the genus *Flexoptychites*. The venter of this specimen is wider than is expected for *F. acutus*, and it possesses very weak sigmoid folds and a funnel-shaped umbilicus. Because of the taxonomic problems and uncertainties described above, identification of this specimen beyond the genus *Flexoptychites* is not possible. The other specimen (HPM 10421/7) shows practically no ornamentation, has a triangular whorl section, a very narrow but rounded venter, and a suture line typical for the genus *Discoptychites*. Therefore, it demonstrably represents a smaller-sized specimen of *Discoptychites megalodiscus*.

Occurrence. *Flexoptychites acutus* is known from the localities in the Southern Alps, the Northern Calcareous Alps, the Dinarides, from Argolis, from Dobrogea, and possibly from the Balaton Highland. Stratigraphically, it occurs exclusively in Anisian strata, as do the other species of the genus. According to the literature, its first occurrence is apparently in the Trinodosus subzone, while its last occurrence is most likely during the Crassus subzone of the Secedensis zone, which would restrict it to the Illyrian substage (Mietto & Manfrin 1995a; Fantini Sestini 1996; Vörös 2014, 2018). Some data from Argolis, although potentially problematic due to being derived from condensed red nodular limestones, may indicate that the species’ first occurrence might be as low as the Balatonicus zone of the Pelsonian (Tselepidis 2007; Pomoni & Tselepidis 2013).

Flexoptychites sp.

Pl. 8, fig. 8.

v 1912 *Ptychites Gretae* n. sp. — Salopek, p. 27, pl. IV, fig. 1.

Material: at least three specimens, ranging from moderate to large in size and at least partially preserved with the shell. More specimens may be present, but their poor preservation makes it unable to exclude referral to the similar *Parasturia*.

Remarks. *Ptychites gretae* Salopek, 1912 is based on a large but poorly preserved specimen. Originally compared to ptychitids of the “*rugifer* group” (genus *Ptychites sensu stricto*) by Salopek (1912), it is clear from

its rather compressed conch, a relatively narrow venter, and its sutural characteristics that this is a large specimen of *Flexoptychites*. The suture line drawn by Salopek (1912, pl. 4, fig. 1c) is a composite from multiple whorl heights, but accurately illustrates morphology and proportions of elements. The specimen, however, exhibits no truly diagnostic characters and cannot be identified to the species level. The name *P. gretae* Salopek 1912 is, therefore, a nomen dubium. This specimen is simply listed under *Flexoptychites* sp. and is not described in further detail. Several other indeterminate *Flexoptychites* specimens also occur at this locality.

Genus *Parasturia* Spath, 1951

Type species: *Meekoceras emmrichi* Mojsisovics, 1882

Parasturia emmrichi (Mojsisovics, 1882)

Pl. 8, figs. 1-3, 6-7; Fig. 11c, d.

- * 1882 *Meekoceras Emmrichi* E. v. Mojsisovics — Mojsisovics, p. 219, pl. I, fig. 4.
- 1901 *Beyrichites Emmrichi* Mojs. spec. var. — Reis, p. 100, pl. VI, fig. 19; pl. VII, fig. 32.
- 1907 *Beyrichites Emmrichi* var. *lateumbilicatus* Reis. — Reis, pp. 136, 137, text fig. 13.
- v 1912 *Ptychites* cf. *Ublig* Mojs. — Salopek, p. 26.
- v 1912 *Ptychites* cf. *angusto-umbilicatus* Boeckh. — Salopek, p. 27.
- 1997 *Flexoptychites angustoumbilicatus* (Böckh) — Urlich & Kurzweil, p. 4, figs. 2, 3.
- 2005 *Parasturia emmrichi* (Mojsisovics, 1882) — Manfrin et al., p. 500, figs. 10/9-14.
- 2018 *Parasturia* cf. *emmrichi* (Mojsisovics, 1882) — Vörös, pp. 142, 143, pl. XLIII, fig. 5; text fig. 83

Material: five specimens collected from the red nodular limestones of the Gregurić Breg locality, most apparently still partially covered by the shell but otherwise of a variable state of preservation and completion. Originally described by Salopek (1912) but misidentified as belonging to various species of *Ptychites*.

Dimensions:

	D	H	h	U	W	w	W/H	U/D	SGR
HPM 138	108.9	60.8	42.7	5.4	-	-	-	0.05	42%
HPM 151.1	160.9*	84.7*	65	11.2	41	25.9	0.48*	0.07	30%
HPM 151.2	146.8	77.5	57.2	13.7	38	29.7	0.49	0.09	35%
HPM 174.2	-	95.1	-	-	46	-	0.48	-	-
GPZ III 742	134.5*	71.5*	50	13*	-	-	-	0.1*	43%*

Description. A large, very involute *Parasturia*. The whorl section is very high oval to sub-triangu-

lar, as the whorls are variably widest approximately in the inner fourth of the whorl height, or in the periumbilical area. The flanks are very slightly convex. The venter is narrow but rounded. There is a tendency for the whorl section to become more inflated and for the venter to become somewhat less narrow in larger specimens. The funnel-shaped umbilicus is very narrow, sometimes nearly occluded, but exact dimensions vary. The umbilical edge is rounded but quite pronounced, while the umbilical wall is often rather tall and sub-vertical to vertical; larger specimens have higher umbilical walls.

Flanks are ornamented by sigmoid primary radial folds. Although their strength varies from specimen to specimen, they are usually very weak and only readily perceptible in the ventral portion of the flank. In larger specimens, the folds almost completely fade away, and are only slightly more perceptible in the lower part of the flank. There are between seven and nine of them on the half whorl.

The external suture line (Fig. 11c, d) is ammonitic, with strongly denticulate lobes and saddles, and with a narrow septal interspace. There are eight lobes present on the flank. The lobe A is the most developed and deepest, but E and U₂ lobes, while smaller, are also rather strongly developed. Characteristically, the E lobe is large and almost touches the A lobe, making the A/E lobe “strangled” at the base. The U₂/A saddle is significantly taller than the neighbouring A/E lobe, while other saddles gradually decrease in height towards the umbilicus.

Remarks. After examining the original material, it was determined that most of the ptychid specimens described by Salopek (1912) can be placed into this genus. This includes specimens originally identified as *Ptychites* cf. *ubligi* and *Ptychites* cf. *angustoumbilicatus*. Where preserved, the suture line clearly pertains to that of *P. emmrichi*, especially the wonderfully illustrated example by Urlich & Kurzweil (1978), which was originally misidentified as *Flexoptychites angustoumbilicatus*. The morphology of the conch of most specimens is similar and appears to follow the ontogenetic progression described by Manfrin et al. (2005), although there is variation in the strength of ornamentation and, especially, the size of the umbilicus. This variation, although possibly caused by temporal evolutionary changes due to the very condensed nature of the facies from which these specimens originate, is nevertheless treated as most likely intraspecific.

The original drawing of the suture line of this taxon (Mojsisovics 1882) is rather simplified compared to those found on other specimens (e.g., Ulrichs & Kurzweil 1997; this paper), but is still proportionally rather similar. The large E lobe and the consequentially strangled saddle A/E are unmistakable. The present authors were unable to personally check the holotype of *P. emmrichi*, but correspondence with experts who have done so (Vörös, pers. correspondence 2022; Mietto & Manfrin, pers. correspondence 2022) and examination the photographs suggests that the simplified suture line is likely a result of invasive preparation. One of the herein described specimens, HPM III 742, has parts of its steinkern slightly worn; there, the suture is rather noticeably simpler than just beneath the shell. Therefore, it is here deemed likely that the apparently simplified suture line of the holotype of *P. emmrichi* is not representative of the “true” complexity of the suture line of this taxon.

This has possibly led to some confusion in the literature. Perhaps most notably, Zakharov et al. (2015) erected a new species *Parasturia primorica*, based on a single small specimen. This taxon is certainly not a member of *Parasturia*, as its subammonitic suture is not only significantly simpler but bears absolutely no other resemblance to that of *P. emmrichi*. In addition, the specimen bears spiral ribs on its surface, which are not a characteristic of *Parasturia*. Taking this into account, it is somewhat perplexing why this taxon was even considered as a member of this genus. Another proposed additional species of the genus, *Parasturia acutata* Shevryev, 1995, has a suture line that is comparable with those of the genus *Discoptychites*, especially the suture line of the original *D. megalodiscus* as figured by Beyrich (1867, pl. II, fig. 1). As such, it is unlikely this species belongs to *Parasturia*. As a result, the genus is currently still monospecific.

Lastly, it is worth noting that Vörös (2018) expressed doubt about the referral of specimens figured by Reis (1901; 1907) to *Parasturia emmrichi*, partially due to the low quality of figures, but also partially due to the apparently different characteristics of the suture line. However, the author in question seems to have mistakenly attributed the figured suture line (Reis 1907, text. fig. 12) of *Beyrichites interplicatus* Reis, 1901 to *Beyrichites emmrichi* var. *lateumbilicatus* Reis, 1907. In fact, Reis (1901, 1907) did not figure any suture line for his specimens of

Beyrichites emmrichi. As such, these examples are tentatively listed in the synonymy without a special notation.

Occurrence. *P. emmrichi* has been identified from localities in the Southern Alps, the German Muschelkalk, and likely the Balaton Highland, and has now been recognized in the Dinarides. It is characteristic for the uppermost Anisian Secedensis zone and for the lower Ladinian (Fassanian), but may have potentially appeared earlier, in the Avisianum subzone of the uppermost Reitzi zone.

Family Sturiidae Kiparisova, 1958

Genus *Discoptychites* Diener, 1916

Type species: *Ammonites megalodiscus* Beyrich, 1867

Discoptychites sp.

Pl. 8, fig. 5; Pl. 11, fig. 7; Fig. 11e, f.

Material: two individuals: a large, partially preserved specimen (HPM 18ž) with the recrystallized shell collected at the Vlašić Brdo locality, and a smaller poorly preserved steinkern (HPM 153.2) collected at the Gregurić Breg locality. Both specimens only preserve the phragmacone.

Dimensions:

	D	H	H	U	W	w	W/H	U/D	SGR
HPM 18ž	>260,6*	>131.2*	-	-	-	-	-	-	-
HPM 153.2	151.4*	82*	63.4	6*	50	30	0.61*	0.04*	29%*

PLATE 8

Ladinian and uppermost Anisian discoidal ptychitoids from the red nodular limestones of the Gregurić Breg locality.

Fig. 1 - *Parasturia emmrichi* (Mojsisovics, 1882), specimen HPM 138; right lateral view.

Fig. 2 - *Parasturia emmrichi* (Mojsisovics, 1882), specimen GPZ III 742; 2a, left lateral view, 2b, apertural view.

Fig. 3 - *Parasturia emmrichi* (Mojsisovics, 1882), specimen HPM 174.2, fragment of a body chamber and the previous whorl; apertural view.

Fig. 4 - *Sturia sansovinii* (Mojsisovics, 1882), specimen HPM 207G; 4a, right lateral view, 4b, apertural view.

Fig. 5 - *Discoptychites* sp., specimen HPM 153.2; 5a, right lateral view, 5b, apertural view.

Fig. 6 - *Parasturia emmrichi* (Mojsisovics, 1882), specimen HPM 151.2; 6a, right lateral view, 6b, apertural view.

Fig. 7 - *Parasturia emmrichi* (Mojsisovics, 1882), specimen HPM 151.1; 7a, right lateral view, 7b, apertural view.

Fig. 8 - *Flexoptychites* sp., specimen HPM 152, holotype of *Ptychites gretae* Salopek, 1912; 8a, left lateral view, 8b, apertural view.

The scale bar is 5 cm for every specimen; each rectangle is 1 cm.



PLATE 8

Description. Large to very large, involute *Discoptychites*. Conch is discoidal, with very high whorls that appear thickest near or slightly above the edge of the umbilicus. Flanks are very slightly convex, making the whorl section sub-triangular. The venter of HPM 153.2 is rounded and narrow, but broad for the genus. The size of the umbilicus, as well as the characteristics of the umbilical edge and wall, cannot be accurately assessed due to poor preservation. No ornamentation can be observed.

The suture line (Fig. 11e, f) is ammonitic, with complexly divided saddles and lobes. There are likely six or seven lobes present on the flanks. Lobe A is the deepest and the most complex one. Saddle U_2/A is the tallest one. Of note is the very pronounced bipartite division of the lobes U_3/U_2 and U_4/U_3 by a very pronounced accessory lobe-like element; the latter state is present in both specimens while the first is missing in HPM 153.2. Specifically, the saddle U_3/U_2 is divided asymmetrically, with the umbilical part being markedly narrower than the ventral part.

Remarks. Characteristics of the suture, in combination with the discoidal shape and the large size, clearly indicate that these specimens belong to the widespread Anisian genus *Discoptychites*. Exact specific affinity is, however, not possible to determine. Both specimens have poorly preserved suture lines and umbilical areas, and the venter is entirely missing on the large Vlašić Brdo specimen. The specimen HPM 153.2 definitely does not belong to *D. megalodiscus*, as it exhibits a noticeably broader venter and thicker whorls. Preserved portions of the suture lines of the two specimens exhibit some differences, indicating that they might potentially belong to different species, if these are not caused by ontogenetic or interspecific differences.

The suture line of the larger specimen shows affinity with that of the species *Discoptychites oenensis* Sakač, 1992, which is known from the Anisian deposits of the Brotinja locality. Sakač (1992) based his diagnosis primarily on the occurrence of a “solitary, narrow first auxiliary saddle” which has, according to the author, “not been observed in any of the described ptychites”. Based on the examination of the holotype and the paratype of this species, it was determined that this “auxiliary saddle” is the same element here interpreted as an umbilical part of the bipartite saddle U_3/U_2 of the specimen described above. This interpretation is founded on the fact

that the lobe-like element, although very complex, is noticeably shallower than the “true” lobes surrounding it, and therefore not interpreted as such. It is also important to note that the bipartite character of this saddle is significantly less pronounced in the paratype of *D. oenensis*. Furthermore, it is not true that this characteristic of the suture is unique to this supposed species, as similar sutural elements, appearing in multiple species of the genus, were figured in the literature predating the naming of *D. oenensis* (Beyrich 1867; Mojsisovics 1882; Martelli 1906; Reis 1907; Toulou 1913; Ishibashi 1978). Of note is the appearance of this character, although somewhat less pronounced, in the drawings of the suture of the holotype of *D. megalodiscus* (Beyrich, 1867), a species whose conch morphology is practically indistinguishable from that of *D. oenensis*. Therefore, it is very probable that both specimens of *D. oenensis* belong to *D. megalodiscus* instead, with the appearance of bipartite saddles being either individually or, more probably, ontogenetically variable.

Occurrence. Species of the genus *Discoptychites* show an almost cosmopolitan distribution, being present in the Tethyan and Panthalassan provinces, as well as in the Germanic basin. Species from the Boreal province have been proposed, although their describing authors expressed some doubt about

PLATE 9

Miscellaneous uppermost Anisan and Ladinian ammonoids from the red nodular limestones of the Gregruić Breg locality.

- Fig. 1 - *Proarcestes ombonii* Tommasi, 1899, specimen HPM 120, phragmacone; 1a, right lateral view, 1b, apertural view.
 Fig. 2 - *Monophyllites wengensis* (Klipstein, 1843), specimen GPZ III 1657; left lateral view.
 Fig. 3 - *Sageceras walteri* (Mojsisovics, 1882), specimen HPM 123.1; 3a, left lateral view, 3b, ventral view.
 Fig. 4 - *Proarcestes subtridentinus* (Mojsisovics, 1870), specimen HPM 119.1, phragmacone; 4a, left lateral view, 4b, apertural view.
 Fig. 5 - *Joannites* sp., specimen HPM 178; 5a, right lateral view, 5b, ventral view.
 Fig. 6 - *Sturia semiarata* Mojsisovics, 1882, specimen HPM 133, phragmacone; 6a, left lateral view, 6b, ventral view.
 Fig. 7 - *Praepinacoceras damesi* (Mojsisovics, 1882), specimen HPM 127.2; 7a, right lateral view, 7b, apertural view.
 Fig. 8 - *Procladiscites* aff. *brancoi* Mojsisovics, 1882, specimen HPM 124.1; 8a, left lateral view, 8b, ventral view.
 Fig. 9 - *Procladiscites* aff. *brancoi* Mojsisovics, 1882., specimen HPM 124.5 partially covered by host rock, right lateral view.
 Fig. 10 - *Psilocladiscites molaris* (Hauer, 1887), specimen HPM 121.2, phragmacone; 10a, left lateral view, 10b, apertural view.
 Scale bars are 1 cm for each individual specimen.



PLATE 9

their generic affinity (Bychkow et al. 1976). The genus is constrained to the strata of the Anisian stage, likely appearing in the Pelsonian substage and going extinct during the Illyrian, at the end of the Reitzi zone according to the data from the Balaton Highland (Vörös 2014; 2018).

Superfamily Arcestoidea Mojsisovics, 1875

Family Arcestidae Mojsisovics, 1875

Genus *Proarcestes* Mojsisovics, 1893

Type species: *Arcestes bramantei* Mojsisovics, 1869

Proarcestes spp.

Pl. 9, figs. 1, 4; Pl. 10, figs. 6, 7.

Material: at least 53 specimens of various sizes and states of preservation collected at the Gregurić Breg (49), Vlašić Brdo (3) and Kolići (1) localities. Additionally, as many as 13 Gregurić Breg specimens may belong here but can equally represent members of the genus *Joannites*, since the suture lines are not visible.

Remarks. The members of the genus *Proarcestes* in the western Tethys are at present a source of taxonomic confusion. The list of available species names is vast, with new species often being based on relatively minor differences. Many of these were identified by Salopek (1912) at the Gregurić Breg locality. For most of the species of this genus the stratigraphic ranges are not entirely or precisely known, due in no small part to the fact many of them were first described from condensed red nodular limestones. The taxonomic revision of Tethyan *Proarcestes* was announced (Fantini Sestini 1994; 1996), but never followed up on. The species of *Proarcestes* occurring in North American strata clearly show a degree of individual variation and morphological changes through ontogeny. However, differences between the successive species may not be readily apparent (Silberlin & Nichols 1982; Monnet & Bucher 2005). It is therefore difficult to ascertain which, if any, of the species present in the studied sample may be synonymous. Therefore, although specimens of *P. subtridentinus* (Mojsisovics, 1870) look markedly different to those of, for an extreme example, *P. ombonii* Tommasi, 1899, they are all here simply listed as *Proarcestes* spp., awaiting further revisions of the genus.

Family Joannitidae Mojsisovics, 1882

Genus *Joannites* Mojsisovics, 1879

Type species: *Nautilus cymbiformis* Wulfen, 1793

Joannites sp.

Pl. 9, fig. 5.

v 1912 *Joannites* ind. aff. *tridentinus* Mojs. — Salopek, p. 20.

Material: at least six specimens of various sizes, most at least partially preserved with the shell. Additionally, as many as 13 Gregurić Breg specimens may belong here but can equally represent members of the genus *Proarcestes*, since the suture lines are not visible.

Remarks. Salopek (1912) identified several specimens he attributed to the genus *Joannites*. In agreement, it is suspected, based on some partially preserved suture lines showing a bipartite saddle A/E, that these are likely early members of the genus *Joannites*. These specimens are more compressed but still comparable to some species of *Proarcestes* in their dimensions. Since suture lines are rarely visible in these ammonoids due to their long body chambers, this poses an identification problem for some of the arcestid specimens in the studied sample.

Family Cladiscitidae Zittel, 1884

Subfamily Procladiscitinae Gamsjäger, 1982

PLATE 10

Miscellaneous ammonoids from various Middle Triassic localities of the Žumberak Mts.

Fig. 1 - *Falsanolites recubariensis* (Mojsisovics, 1882), specimen HPM 15ž; 1a, right lateral view, 1b, ventral view, 1c, ventral view of the inner whorl cast, 1d, lateral view of the inner whorl cast; Vlašić Brdo locality.

Fig. 2 - *Flexoptychites acutus* (Mojsisovics, 1882), specimen HPM 10ž, embedded into host rock; 2a, right lateral view, 2b, ventral view; Kolići locality.

Fig. 3 - *Gymmites* cf. *incultus* (Mojsisovics, 1882), specimen HPM 10487; right lateral view; Vlašić Brdo locality.

Fig. 4 - *Protrachyceras margaritosum* (Mojsisovics, 1882), specimen HPM 10492; left lateral view; Radilovec Jaruga locality.

Fig. 5 - *Monophyllites* sp., specimen HPM 12ž, body chamber fragment and an imprint; left lateral view; Radilovec Jaruga locality.

Fig. 6 - *Proarcestes* sp., specimen HPM 10491, phragmacone; 6a, left lateral view, 6b, apertural view.

Fig. 7 - *Proarcestes* sp., specimen HPM 11ž, phragmacone partially embedded in the host rock; 7a, left lateral view, 7b, ventral view.

The scale bar is 5 cm for every specimen; each rectangle is 1 cm.

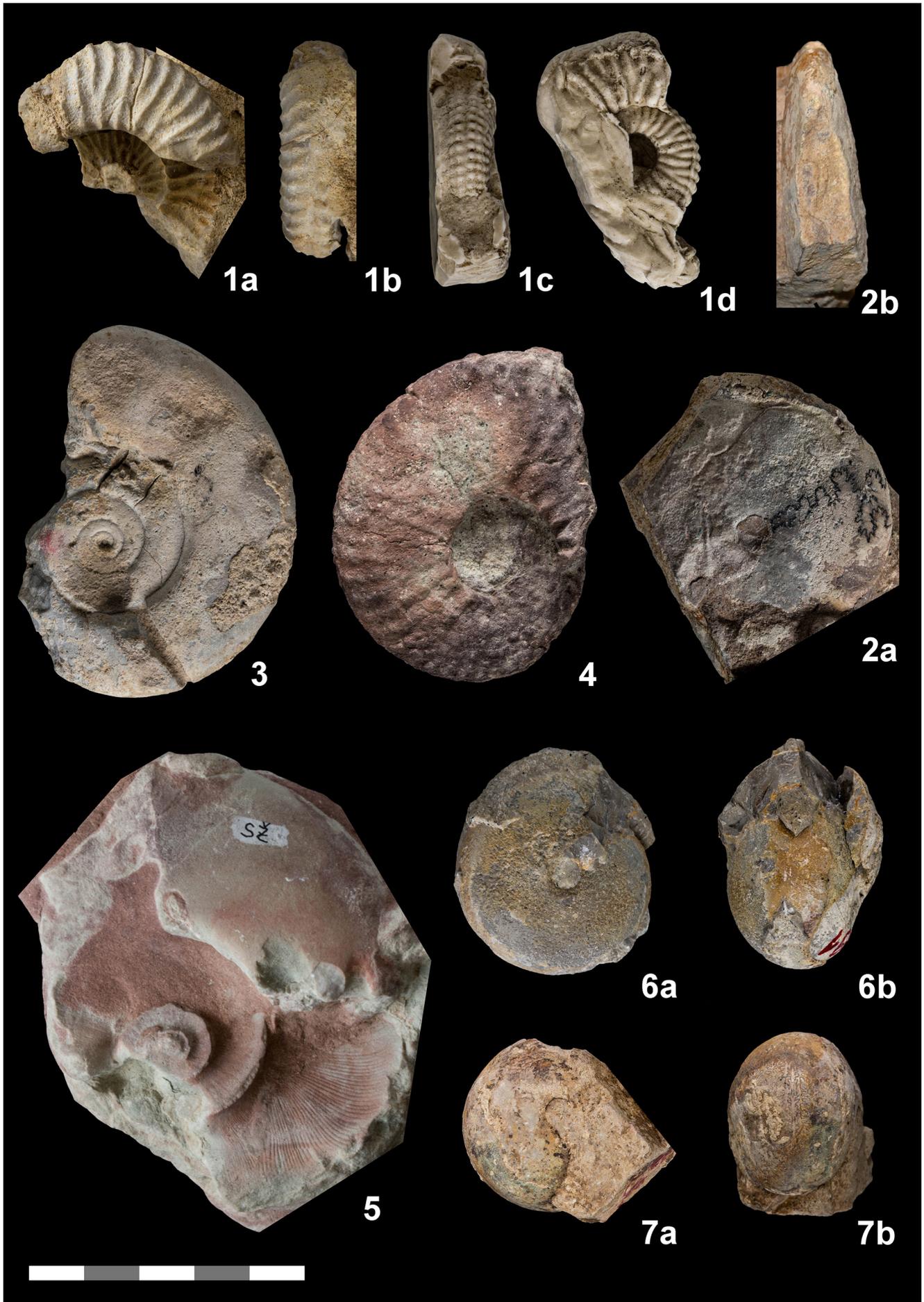


PLATE 10

Genus *Procladiscites* Mojsisovics, 1882

Type species: *Procladiscites brancoi* Mojsisovics, 1882

Procladiscites* aff. *brancoi Mojsisovics, 1882

Pl. 9, figs. 8, 9.

v 1912 *Procladiscites (Hypocladiscites) brancoi* Mojs. sp. — Salopek, p. 21.

Material: five small specimens from the Gregurić Breg locality, all of which are fully or partially preserved with the shell.

Remarks. Several small specimens originally identified as *Procladiscites (Hypocladiscites) brancoi* are herein considered to likely only be related to it. Originally based on specimens collected at Schreyeralm, *P. brancoi* was thought by Mojsisovics (1882) to belong to his conception of the “*Ceratites trinodosus*” zone. It is now known that this author also erroneously included taxa belonging to the earlier Pelsonian substage (e.g., *Balatonites*, *Acrochordiceras*) into this zone. Likewise, several latter works (Wang 1985; Mietto & Manfrin 1995a; Germani 1997; Tselepidis 2007; Pomoni & Tselepidis 2013), as well as the personal observations of the present authors based on a yet undescribed locality in Croatia, seem to suggest *P. brancoi* occurs in upper Bythinian, Pelsonian and possibly lower Illyrian strata. This stratigraphic interval is, based on the associated ammonoids, not recorded in the red nodular limestones of Gregurić Breg. Therefore, it is likely that specimens collected at this locality belong to a different, yet still comparable (both in conch morphology and the suture line) species of *Procladiscites*.

Genus *Psilocladiscites* Mojsisovics, 1896

Type species: *Procladiscites molaris* Hauer, 1887

Psilocladiscites molaris (Hauer, 1887)

Pl. 9, fig. 10.

* 1887 *Procladiscites molaris* n. sp. — Hauer, pp. 30, 31, pl. IV, fig. 3.
v 1912 *Phyllocladiscites crassus* Hauer. — Salopek, pp. 20, 21.

Material: five small specimens collected at the Gregurić Breg locality. They are preserved as steinkerns with small patches of poorly preserved shell.

Remarks. Salopek (1912) described four specimens he identified as *Phyllocladiscites crassus* (Hauer, 1887). The same author also considered both *Procla-*

discites molaris (Hauer, 1887) and *Procladiscites connectens* (Hauer, 1892) to be synonymous with that taxon. While the latter synonymy is likely, as both species undoubtedly belong in the genus *Phyllocladiscites*, the synonymy of *Pb. crassus* and the species *molaris* is more problematic. The latter taxon has been postulated as the type species of the genus *Psilocladiscites* Mojsisovics, 1896, which Gamsjäger (1982) redefined as near identical in whorl section and sutural morphology to *Phyllocladiscites* but lacking the distinctive spiral ridges of the that taxon. Salopek (1912) suggested that this difference may be an artifact of poor preservation. This is unlikely, as the holotype of *Ps. molaris* is apparently preserved well enough for Hauer (1887) to discern fine growth lines. The Gregurić Breg specimens, however, are mostly preserved as steinkerns, with poorly preserved shell fragments partially still being present. The spiral ridges are apparently absent, but it is not clear if this is an artefact of preservation. Therefore, the Gregurić Breg specimens herein are tentatively considered to belong to *Psilocladiscites molaris*.

Occurrence. This species is surely known from the Dinarides and was also reported from Greece but was not illustrated (Renz 1910). These occurrences are all from condensed Hallstatt-type limestones not sampled bed-by-bed, meaning that this species' exact stratigraphic range is not known, although the Bosnian occurrence is very likely Anisian. Mietto & Manfrin (1995a) report this species from the Ladinian Longobardicum zone, but do not list the locality or provide an illustration of a specimen.

PLATE 11

Miscellaneous Middle Triassic ammonoids from the Vlašić Brdo locality.

Fig. 1 - *Flexoptychites acutus* (Mojsisovics, 1882), specimen HPM 10489, phragmacone; 1a, left lateral view, 1b, ventral view.

Fig. 2 - *Flexoptychites acutus* (Mojsisovics, 1882), specimen HPM 14ž; 2a, right lateral view, 2b, apertural view (body chamber is crushed).

Fig. 3 - *Protrachyceras ladinum* (Mojsisovics, 1882), specimen HPM 10493, embedded in the host rock; 3a, right lateral view, 3b, ventral view.

Fig. 4 - *Sturia* sp., specimen HPM 16ž, embedded in the host rock; 4a, left lateral view, 4b, ventral view.

Fig. 5 - *Japonites raphaeliszoja* (Tommasi, 1899), specimen HPM 10490, embedded in the host rock; right lateral view.

Fig. 6 - *Flexoptychites acutus* (Mojsisovics, 1882), specimen HPM 17ž; 7a, right lateral view, 7b, apertural view.

Fig. 7 - *Discoptychites* sp., specimen HPM 18ž; right lateral view.

The scale bar is 5 cm for every specimen; each rectangle is 1 cm.

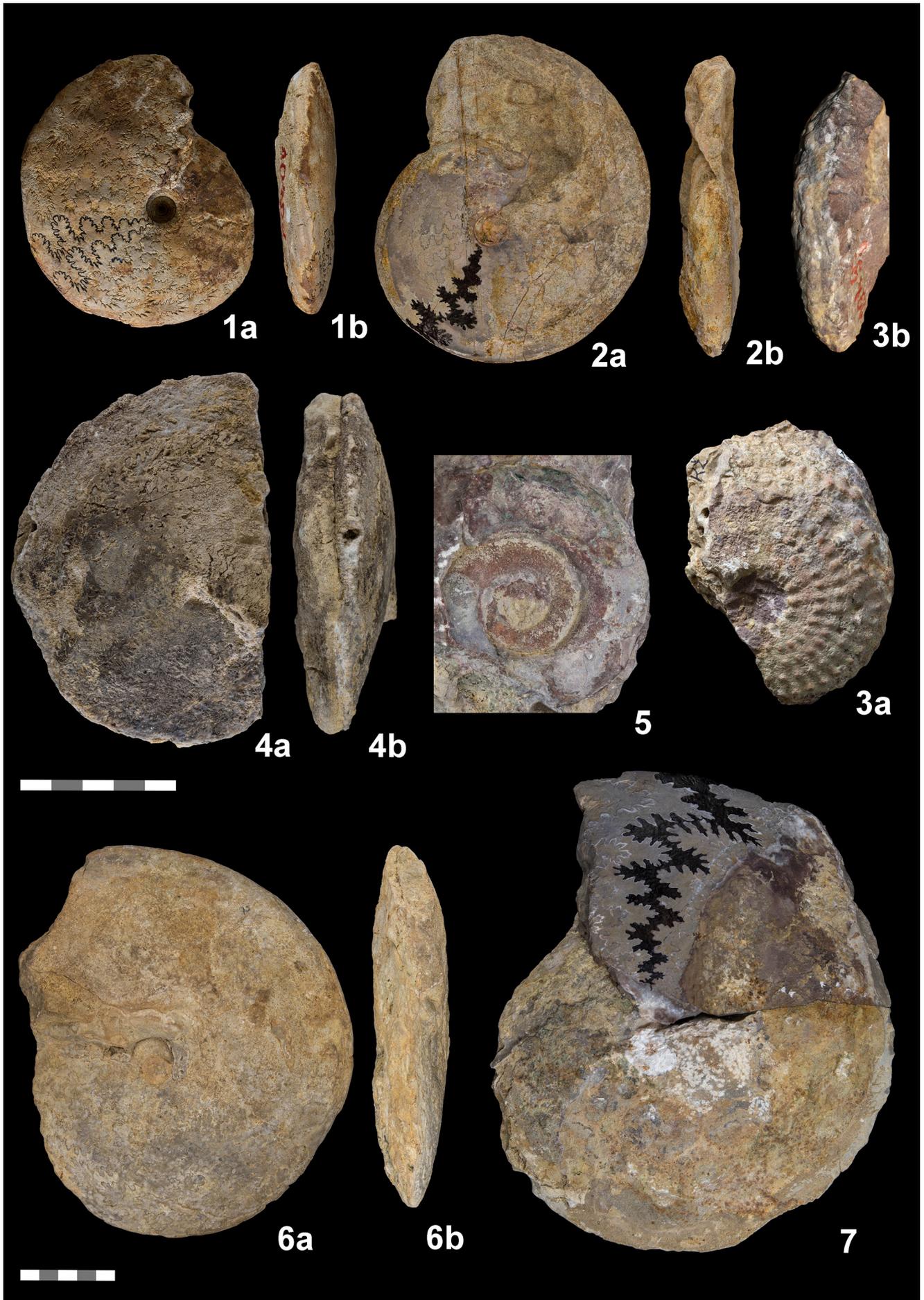


PLATE 11

CONCLUSION

Several key points can be drawn from the research presented in this paper:

Most of the taxa collected from the localities in the Samobor and Žumberak Mts. were redescribed; key findings significant for their taxonomy are summarized here. Firstly, several well-known genera, including *Halilucites*, *Falsanolcites*, *Eoprotrachyceras*, *Protrachyceras*, *Proarcestes*, and *Flexoptychites*, likely require a general, detailed taxonomic revision, ideally based on modern methods (morphometry, phylogenetic analysis, analysis of ontogeny, etc.). Some of the species of these genera, as well as some others (e.g., *Japonites raphaeliszgoja*), require more precise biostratigraphic constraints. "*Anolcites*" *laczkoi* Diener, 1899 potentially represent a member of an unnamed and undescribed genus. Although its presence in the western Tethyan province has been implied, this work presents further evidence of the genus *Meginoceras* from this paleogeographic region, otherwise much more well-known from the Canadian Ladinian.

A slightly modified preliminary zonal and subzonal scheme of the Ladinian is proposed for the western Tethys, to incorporate most of the already published data from the well-studied sections. The potential for further improvement of the Ladinian subdivision is recognized. The Margitosum zone (previously Gredleri zone) requires further sampling. The superposition of the Longobardicum and Neumayri subzones (here considered parts of the Archelaus zone) should be recognized in a single section. Most importantly, further discussion on the Fassanian – Longobardian boundary is required.

At the Gregurić Breg locality, the Hallstatt-type facies horizon most likely spans from the Avisianum subzone (uppermost Reitzi zone, upper Illyrian) to the Longobardicum subzone (Archelaus zone, "middle" Longobardian). The overlying thinly bedded limestones with *Daonella lommeli* are most likely latest Ladinian in age, although better preserved ammonoid remains are required for more precise dating. The lower part of the basal section is likely Illyrian (*Trinodosus* and Reitzi zones), and potentially upper Pelsonian.

Ammonoids collected at the Mt. Žumberak localities (Vlašić Brdo, Kolići, Radilovec Jaruga) indicate that the upper, limestone rich part of

this succession spans from at least the Avisianum subzone (upper Reitzi zone, upper Illyrian) to the Longobardicum subzone (Archelaus zone, "middle" Longobardian). Although these results agree with the radiolarian data from the lower, chert rich part of the succession (Goričan et al. 2005), more ammonoids, especially Anisian taxa, are needed to better understand the timing of the basinal deposition. There is potential for future studies of these localities to provide valuable data on the Ladinian ammonoid biostratigraphy.

Based on superposition, the Medven Draga dolostones, capping the Middle Triassic basal successions, cannot be ruled out as at least partially early Carnian in age. Most parsimoniously, they should be regarded as latest Ladinian –? early Carnian in age.

In spite of further room for the improvement of the subdivision of the Ladinian, this work demonstrates the utility of decades of research on Middle Triassic ammonoid biostratigraphy. Although ammonoids herein examined and described were historically not sampled bed-by-bed in well-exposed sections, the knowledge gained from other localities allows their usage as valuable biostratigraphic indicators in otherwise stratigraphically challenging localities.

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