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Pelsonian and Illyrian (Anisian, Middle Triassic) ammonoid faunas from the Bulog Group of Kovčezi, Durmitor Mountain, Dinarides (northern Montenegro)

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Abstract

Three different ammonoid assemblages of Anisian age are described from the Anisian Bulog Group of the Kovčezi section in the Durmitor Mountain (northern Montenegro/Dinarides). The Illyrian is represented by a succession belonging to the Komarani and Bulog Formations, together approximately 50 m thick. The Komarani Formation of late Illyrian age consists predominanty of oligomictic breccias and mass-transport deposits that contain redeposited Bulog Limestone blocks with Pelsonian ammonoids. Within the late Illyrian Bulog Formation above the Komarani Formation, two distinct condensed nodular limestone levels contain rich ammonoid faunas. In total 36 taxa could be determined, belonging to 24 genera of the Aplococeras avisianum and Nevadites secedensis zones. *Ptychites rugifer* (Oppel), *Megaphyllites obolus* Mojsisovics, *Parakellnerites rothpletzi* (Salomon), *Apleuroceras decrescens* (Hauer), *Proteusites labiatus* (Hauer), *Tropigastrites lahontanus* Smith, *Proarcestes pannonicus* (Mojsisovics) and *Proarcestes subtridentinus* (Mojsisovics), and the genus *Aristoptychites* are for the first time described from Montenegro (south Central Europe).

1. Introduction

Anisian ammonoid faunas of Montenegro (south Central Europe) have been described since more than a century (Martelli, 1904, 1905, 1906; Salopek, 1911; Simić, 1938; Čubrilović, 1940; Bešić, 1945, 1949; Petković and Miletić, 1953; Ljubović, 1976), predominantly of late Pelsonian to early Illyrian age. Some of these works belong to the classical literature on Middle Triassic ammonoids for the Western Tethys Realm (Martelli, 1904, 1906; Salopek, 1911).

Ammonoid faunas of the Kovčezi locality in the Durmitor Mountain (Fig. 1) were first described by Ljubović (1976), from red nodular limestones (Bulog Formation: Sudar et al., 2013, 2023a, b; Gawlick et al., 2023), who considered that the ammonoid-bearing part in the Bulog Limestone succession is of Ladinian age. After the new definition of the Anisian/Ladinian boundary (Brack et al., 2005), the emendation of the Bulog Formation and the introduction of the Bulog Group with the Bulog and Komarani Formations (Sudar et al., 2023b), the Kovčezi section was re-investigated in order to reconstruct the depositional history (Mrdak et al., 2024) and establish a more detailed biostratigraphic zonation based on ammonoids. From the whole middle to late Anisian shallow-water to deep-water succession with mass-transport deposits in the late Illyrian conodonts, ammonoids, algae

and foraminifers were analyzed and correlated (Mrdak et al., 2024). Within this study, three different ammonoid assemblages could be distinguished, one of late Pelsonian age in reworked Bulog Limestone blocks in the Komarani Formation, and two assemblages in cephalopod accumulation beds of the Bulog Formation of late Illyrian age.

In this paper, the newly discovered relatively rich, but only moderately preserved ammonoid faunas are described, consisting of a large number of taxa, but a low number of specimens, as typical for Bulog Formation faunas (Hauer, 1887, 1892, 1896; Martelli 1904, 1906; Salopek, 1911; Petković and Miletić, 1953). The ammonoid biostratigraphy is discussed in more detail, whereas the depositional environment of the Komarani and Bulog Formations and the correlation with other fossils (conodonts, algae, foraminifers) are the scope of another paper (see Mrdak et al., 2024). For more details on the depositional environment, facies, stratigraphic evolution of the formations of the Bulog Group interested readers are referred to Gawlick et al. (2023) and Sudar et al. (2023a, b and references therein).

2. Geological setting

In the Durmitor Mountain, with the Kovčezi locality (Fig. 1) as part of its Triassic sedimentary evolution, the complete Middle Triassic succession is reported to have a thickness of approximately 850 m (Mirković and Vujisić, 1989). The Anisian limestones, 250–350 m in thickness, are represented mainly by Pelsonian shallow water limestones of the Ravni Formation, and several tens of meters-thick deeper water red nodular limestones of the Bulog Formation. Outcrops of these rocks were partly described in detail by Mirković (1983). The overlying sedimentary succession is composed of different types of siliceous limestones and the Wetterstein Formation, traditionally considered to be Ladinian in age (Mirković, 1983; Mirković and Vujisić, 1989). In some areas of the mountain, Middle Triassic successions contain also thick volcanics (andesites and dacites), as well as their resediments (volcanic sandstones, breccias and tuffs). However, a total thickness of approximately 850 m as estimated by Mirković and Vujisić (1989) can be nowhere confirmed: the thickness of the Anisian-Ladinian limestone suc-

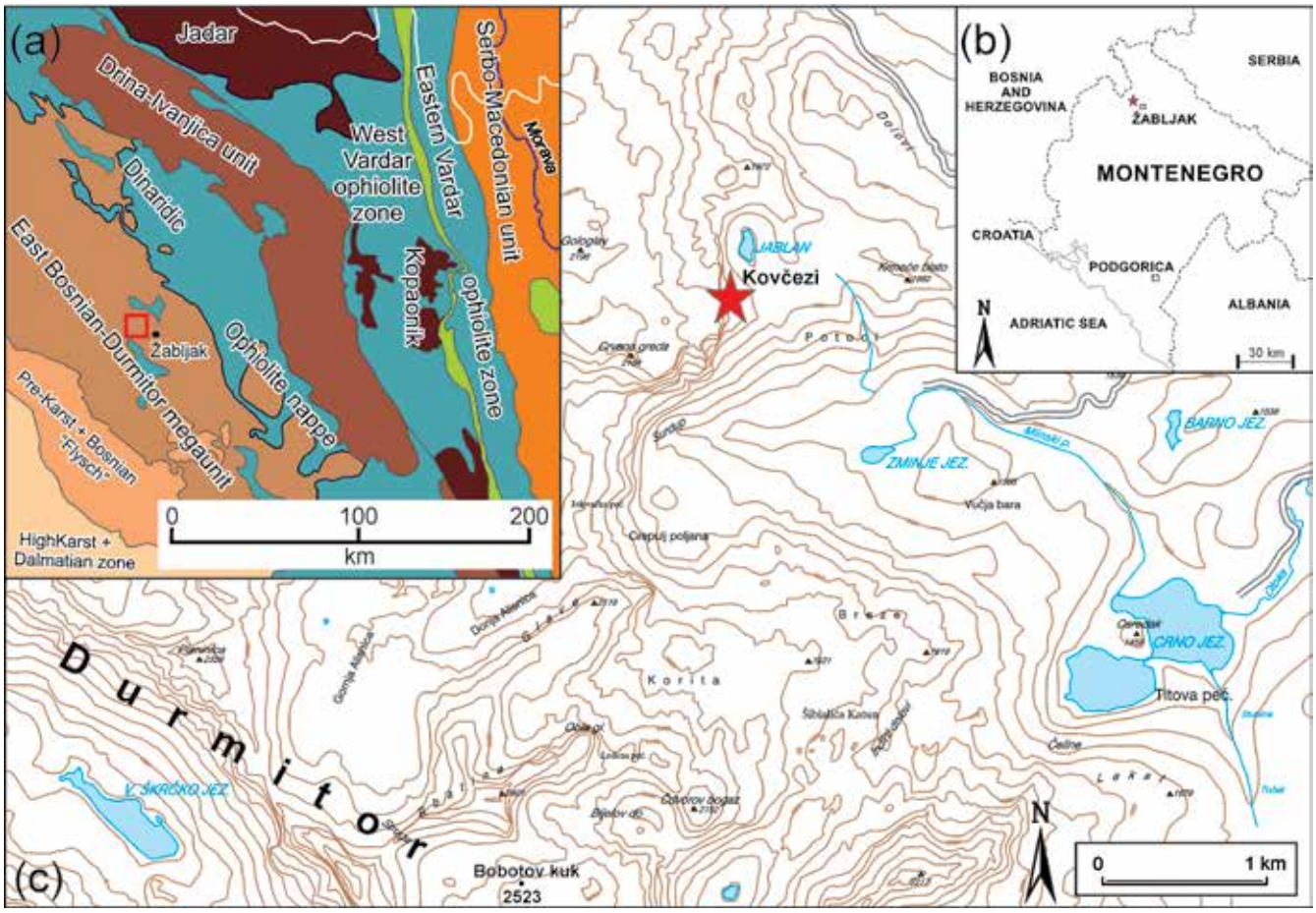

Figure 1: (a) General tectonic map of the study area between the Drina-Ivanjica unit in the north and the East Bosnian-Durmitor megaunit in the south roughly indicated by the red box (see C for geographical details) according to Schmid et al. (2008, 2020) (redrawn in the area of the Dinaridic Ophiolite nappe/East Bosnian-Durmitor megaunit after the results of Gawlick et al., 2017). Compare Schmid et al. (2020, Plate 1) with major changes for the Sava zone. For an explanation of the different units see Schmid et al. (2008, 2020), but compare Gawlick et al. (2017, 2020) and Djerić et al. (2024). **(b)** Geographic sketch map of Montenegro with position of the studied section in northern Montenegro. **(c)** Studied section Kovčezi located approximately 8 km northnorthwest of the city Žabljak marked by a star. **(b)** and **(c)** after Mrdak et al. (2024).

cession including the volcanics does not exceed 300 m (even if the shallow-water carbonates of the in fact Early Carnian Wetterstein Carbonate Platform is included), and the thickness of the Illyrian volcanics including the overlying volcanic sandstones varies between 10 and 200 meters. As the volcanics in some areas cover huge areas dissected by younger faults this maybe led to the calculation of a greater thickness.

The age of Anisian shallow-water limestones (Ravni Formation) is mostly determined by foraminifera and dasycladalean algae (Mirković, 1983 for an overview), and often constrained to be of Pelsonian or Illyrian age. However, the Ravni Carbonate Ramp demised in late Pelsonian times everywhere in the Dinarides, and a horst-and-graben structure was formed (Gawlick et al., 2023; Sudar et al., 2023a, b and references therein), also in the Durmitor Mountain (Mrdak et al., 2024). Whereas some parts of the Ravni Formation were uplifted and underwent karstification, in most other cases the Ravni Carbonate Ramp experienced a drowning, and the late Pelsonian condensed red nodular limestones of the Bulog Group were deposited. Therefore, an Illyrian age cannot be confirmed as also proven by the existence of late Pelsonian ammonoids in the Komarani Formation as described here. Ammonoids (Ljubović, 1976; Mirković, 1983) and conodonts (Sladić-Trifunović and Ljubović, 1975) were only rarely reported from the Anisian(-Ladinian) successions, with slightly more complete age assignment, until recently (Mrdak et al., 2024). Likewise, reconstructions of the depositional environment were also given only as general information (Mirković, 1983; Mirković and Vujisić, 1989).

A detailed sedimentological study including microfacies analysis of the Kovčezi succession (Fig. 2), as well as its position, have been described Mrdak et al. (2024). The studied section is situated near the city of Žabljak, approximatelly 8 km to the west in the Durmitor Mountain in the East Bosnian-Durmitor mega-unit (Fig. 1). Here, only a brief outline is given (Fig. 2). For a more detailed description the reader is refered to Mrdak et al. (2024).

The Illyrian part of the limestone succession has a total thickness of approximatelly 50 m (Fig. 2). First ten meters of the section are built by volcanic sandstones and tuffs,

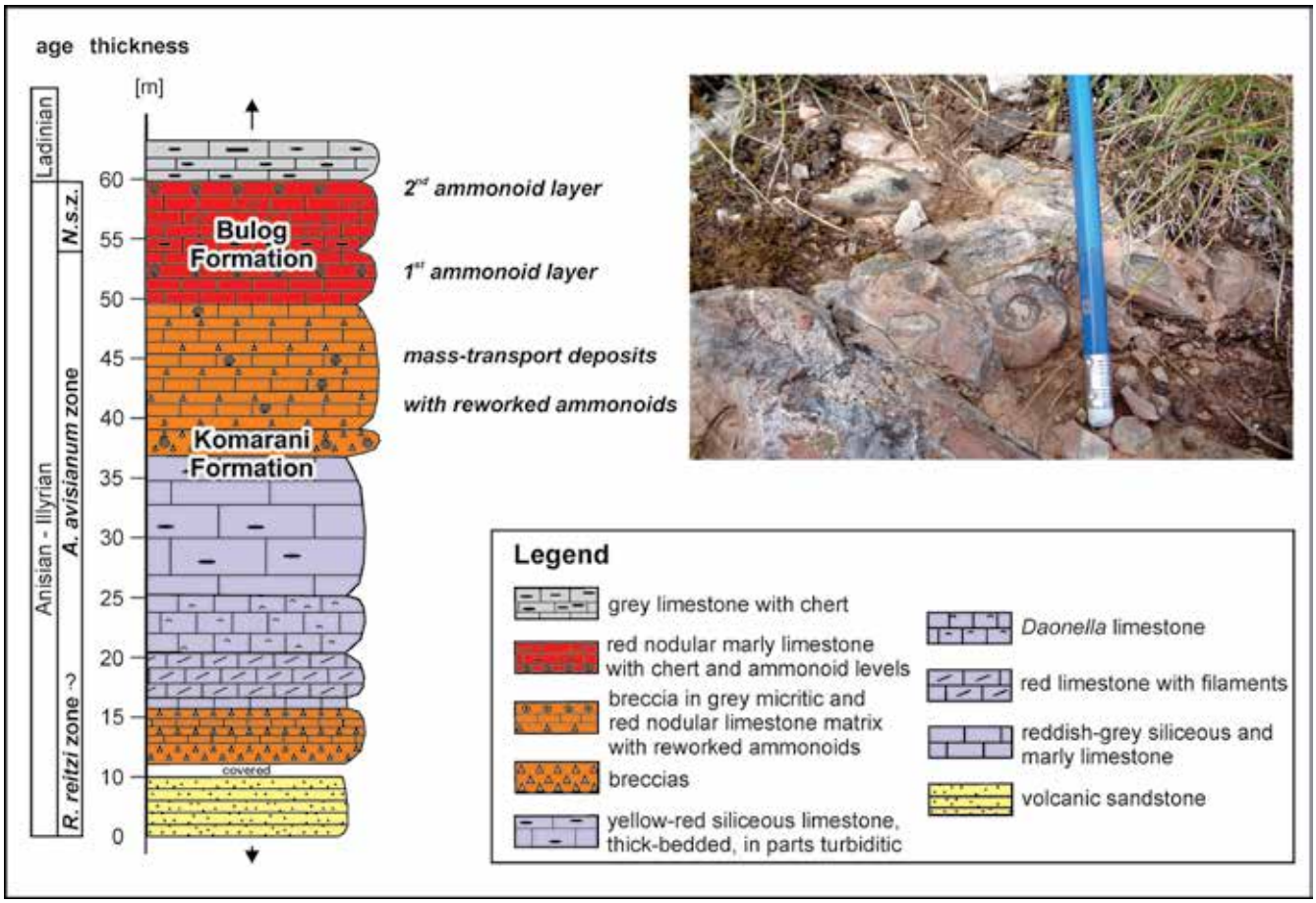

Figure 2: Upper Anisian to Ladinian sedimentary succession of the section Kovčezi and position of studied ammonoid faunas from the Komarani Formation and the Bulog Formation, simplified after Mrdak et al. (2024). Photo show N.s.z. = Nevadites secedensis Zone.

which overlie Middle Triassic volcanics in a thickness of more than 40 m. Above these sandstones, the Illyrian Bulog Group start with the Komarani Formation, first with 5 m thick oligomictic breccias, containing Ravni Formation components. These are followed by a 20 m thick series of reddish-grey to grey siliceous and marly limestones, containing chert nodules and carbonate turbidite layers. The Komarani Formation continues with mass-transport deposits (MTDs) and turbidites containing various older components of the Ravni and Bulog formations in a late Illyrian marly limestone matrix. The overlying red nodular limestone of the Bulog Formation, approximatelly 10 m in thickness, contain two distinct condensed horizons with rich ammonoid faunas. These are overlain by bedded red and grey limestones with cherts nodules and layers of Ladinian age.

Three distinct ammonoid assemblages from three different horizons could be recognized, based on their position in the section, as well as by their preservation for the material collected from rockfall. Late Pelsonian ammonoids have been collected from MTDs of the late Illyrian Komarani Formation, showing dissolvement and corrosion of the shells. This is in accordance with the age of this part of the succession given by Mrdak et al. (2024), determined by conodonts as part of the Aplococeras avisianum Zone. The first cephalopod accumulation bed in the red nodular limestones (Fig. 2) of the Bulog Formation slightly above the Komarani Formation contains taxa indicative for the Aplococeras avisianum Zone. Ammonoids from the second ammonoid-bearing nodular limestone level could only be collected from rockfall, but are easily recognizable due to their preservation, their lithology and their microfacies. Determined taxa are indicative for the Nevadites secedensis Zone of the late Illyrian.

3. Results and discussion

Three different ammonoid assemblages were recognized, one of late Pelsonian age, and two late Illyrian faunas (Fig. 2, Tab. 1). The late Pelsonian ammonoid fauna appears in redeposits (components and blocks) within the late Illyrian Komarani Formation of the section: *Acrochordiceras carolinae* Mojsisovics, *Acrochordiceras* sp., *Proarcestes* cf. *escheri* (Mojsisovics), and *Aristoptychites* sp. were collected out of blocks from coarse-grained breccia horizons. Only *Acrochordiceras carolinae* Mojsisovics can be considered as age indicative species, characteristic for the whole Pelsonian. Interestingly, the presence of the genus *Aristoptychites*, which is a relatively rare genus and not characteristic for the Western Tethyan Realm, may indicate at least an early Illyrian age. This age is not unusual, as the drowning sequence of the Ravni Carbonate Ramp starts generally with late Pelsonian red nodular limestones and deposition continues to the early-middle Illyrian. For example, this genus is mentioned from the Paraceratites trinodosus Zone of Epidauros by Tselepidis (2007) and Pomoni and Tselepidis (2013). The authors recognize that the genus *Aristoptychites* was found in condensed beds, but from the same zone they mention *Bulogites* and *Philippites* genera. These genera are mainly considered as part of Pelsonian faunas, which would point to a mixed and condensed assemblage, as often recognized in the drowning sequence of the Ravni Carbonate Ramp or the equivalent Steinalm Carbonate Ramp (Gawlick et al., 2021 and references therein). Since *Aristoptychites* sp. has been found in a breccia horizon in the Kovčezi section, which is dated as late Illyrian by conodont faunas (Mrdak et al., 2024), it is most likely that it is of a slightly different age than the rest of the ammonoids found in this level. However, it cannot be excluded that this genus is also present in the late Pelsonian, based on this finding and its presence in the Bulog Limestone of Greece (Pomoni and Tselepidis, 2013).

3.1. Aplococeras avisianum Zone

The Aplococeras avisianum Zone fauna from the overlying 1st ammonoid layer in the red nodular limestone succession (Fig. 2) of the Bulog Formation comprises *Ptychites rugifer* (Oppel), *Ptychites oppeli* Mojsisovics, *Flexoptychites acutus* (Mojsisovics), *Lanceoptychites indistinctus* (Mojsisovics), *Apleuroceras decrescens* (Hauer), *Proarcestes subtridentinus* (Mojsisovics), *Proarcestes boeckhi* (Mojsisovics), *Parakellnerites rothpletzi* (Salomon), *Tropigastrites lahontanus* Smith, *Arthaberites alexandrae* Diener, *Megaphyllites obolus* Mojsisovics, *Megaphyllites* cf. *sandalinus* (Mojsisovics), *Epigymnites* cf. *ecki* (Mojsisovics), *Discoptychites* ? *princeps* (Martelli), *Proteusites labiatus* (Hauer), *Longobardites* cf. *zsigmondyi* (Böckh), *Epikellnerites tamasi* Vörös, *Danubites floriani* (Mojsisovics), *Leiophyllites* cf. *taramellii* (Martelli), *Monophyllites wengensis* (Klipstein) and *Sturia* sp. As already indicated by Mrdak et al. (2024), the fauna comprises either long-ranging species or poorly known species in the published literature. The most problematic is the occurrence of *Proteusites labiatus* (Hauer) in this assemblage, since that genus is mainly considered as Pelsonian. However, this species is with certainty known only from Bosnia and Herzegovina, from the classical work of Hauer (1892) from the Bulog Limestone near Sarajevo. The author does not mention in which part of the section it is found, or which are the associated species found with it. Even though Hauer (1892) describes the genus *Proteusites* in this work, he places the new species in the genus *Ceratites*. Balini (1998) discussed that Bulog Limestone in Bosnia and Herzegovina contains ammonoids from four ammonoid zones, ranging from the Balatonites balatonicus to Nevadites secedensis zones. In that sense, true range of the species *Proteusites labiatus* (Hauer) is currently not sufficiently known. Likewise, *Apleuroceras decrescens* (Hauer) is until today known with certainty only from Bosnia and Herzegovina, assigned also to *Ceratites* by Hauer (1887). Since this species is in the present paper considered to belong to the genus *Apleuroceras*, and the only other species of this genus *Apleuroceras sturi* (Mojsisovics) is known

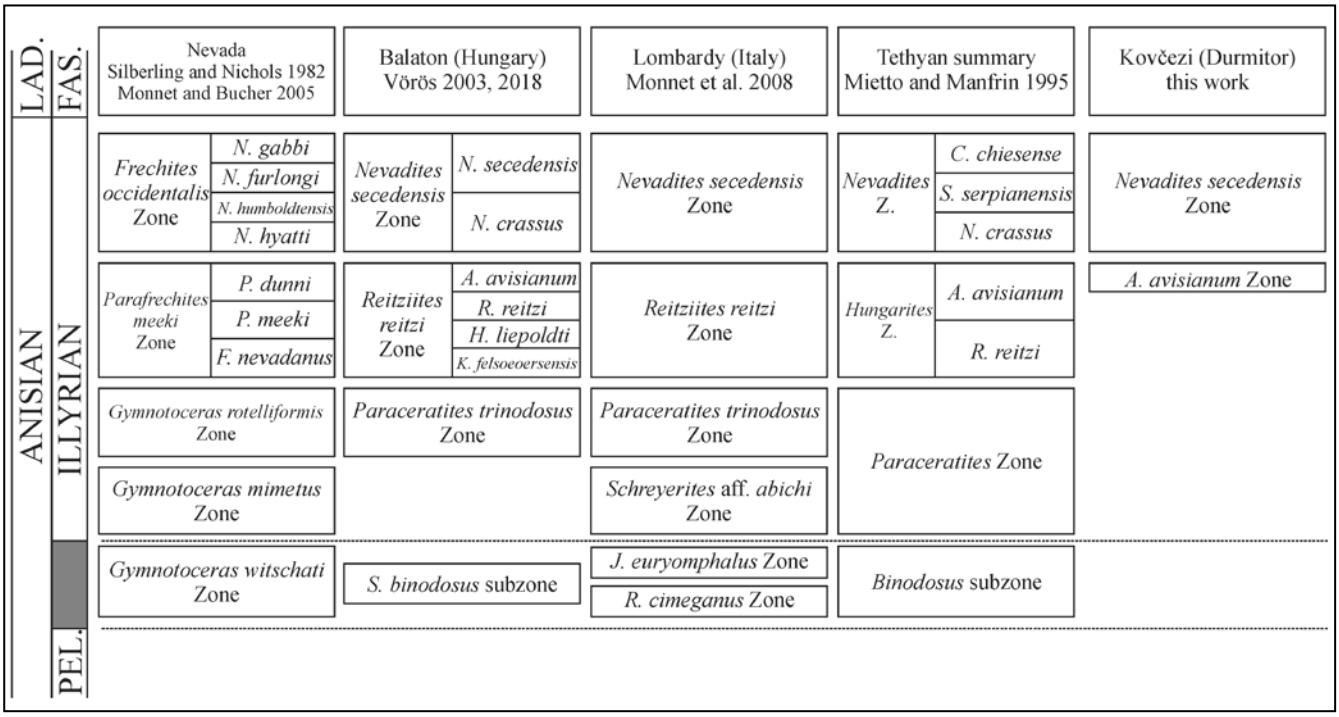

Figure 3: Biostratigraphic correlation chart of the late Anisian, i.e. Illyrian ammonoid zones with Kovčezi section. Gray shaded area indicates ammonoid zones that are included into Pelsonian (Mietto and Manfrin 1995; Vörös 2003) or Illyrian (Monnet et al. 2008) by different authors.

from the Ladinian Protrachyceras archelaus Zone, it also represents a poorly documented genus for age assignment. *Tropigastrites lahontanus* Smith also represents one of poorly known species, found for the first time in Western Tethys Realm. Monnet and Bucher (2005) reported this species from the Gymnotoceras rotelliformis Zone of Nevada, which is the equivalent of Paraceratites trinodosus Zone. However, intermediate specimens to a younger *Tropigastrites louderbacki* (Hyatt and Smith) are reported by Silberling and Nichols (1982) also from the lower part of Parafrechites meeki Zone (equivalent of the lower Reitziites reitzi Zone). Since these are two very close species, it may be that *Tropigastrites lahontanus* Smith can be an element in the younger faunas as well. Likewise, the presence of the genus within the Western Tethys Realm is only reported by Manfrin et al. (2005), also within the Aplococeras avisianum Zone. Other rare species, such as *Ptychites rugifer* (Oppel), *Arthaberites alexandrae* Diener, *Megaphyllites obolus* Mojsisovics, *Discoptychites* ? *princeps* (Martelli) and *Danubites floriani* (Mojsisovics), are mainly known from condensed sections which need future re-investigation. Assignment of this fauna to the Aplococeras avisianum Zone is primarily based on the co-occurrence of *Parakellnerites rothpletzi* (Salomon), *Epikellnerites tamasi* Vörös and *Epigymnites* cf. *ecki* (Mojsisovics) by comparison with the Balaton Highland in Hungary (Vörös, 2018). A similar assemblage is also described from the Dolomites (Italy) by Manfrin et al. (2005), where *Parakellnerites rothpletzi* (Salomon), *Longobardites zsigmondyi* (Böckh), *Tropigastrites* sp. and *Epigymnites* sp. co-occur within the Aplococeras avisianum Zone fauna (Fig. 3). Two meters above this level, conodont fauna indicative for the latest Illyrian according to Krystyn (1983) are described in Mrdak et al. (2024).

3.2. Nevadites secedensis Zone

The Nevadites secedensis Zone ammonoid fauna from the highest part of the Bulog Formation of the Kovčezi locality comprises *Monophyllites wengensis* (Klipstein), *Flexoptychites flexuosus* (Mojsisovics), *Flexoptychites angustoumbilicatus* (Böckh), *Flexoptychites* aff. *studeri* (Hauer), *Gymnites incultus* (Beyrich), *Discoptychites* cf. *megalodiscus* (Beyrich), *Discoptychites* ? sp., *Chieseiceras* sp., *Joannites* cf. *tridentinus* (Mojsisovics), *Proarcestes pannonicus* (Mojsisovics), *Sturia sansovinii* (Mojsisovics), and *Arcestes* ? sp. found only in the rockfall. As mentioned before, preservation of these ammonoids is different from the rest of the specimens. This assemblage comprises mostly long ranging species not truely indicative for age assignment at the biozone level. However, genera *Chieseiceras* and *Joannites* are until today not known from strata older than the uppermost Illyrian. Conodont faunas indicate also a latest Illyrian age of this part of the section (Mrdak et al., 2024).

3.3. Ammonoid assemblages

The described ammonoid faunas contain taxa mostly characteristic for the Western Tethyan Realm, or truly cos-

Table 1

Determined taxa	Reworked Pelsonian fauna	Aplococeras avisianum fauna	Nevadites secedensis fauna	Sum.
Acrochordiceras carolinae Mojsisovics	1			1
Acrochordiceras sp.	1			1
Proarcestes cf. *escheri* (Mojsisovics)	3			3
Aristoptychites sp.	1			1
Ptychites rugifer (Oppel)		1		1
Ptychites oppeli Mojsisovics		2		2
Flexoptychites acutus (Mojsisovics)		1		1
Lanceoptychites indistinctus (Mojsisovics)		1		1
Apleuroceras decrescens (Hauer)		1		1
Proarcestes subtridentinus (Mojsisovics)		1		1
Proarcestes boeckhi (Mojsisovics)		2		2
Parakellnerites rothpletzi (Salomon)		1		1
Tropigastrites lahontanus Smith		1		1
Arthaberites alexandrae Diener		1		1
Megaphyllites obolus Mojsisovics		1		1
Megaphyllites cf. *sandalinus* (Mojsisovics)		2		2
Epigymnites cf. *ecki* (Mojsisovics)		1		1
Discoptychites ? *princeps* (Martelli)		1		1
Proteusites labiatus (Hauer)		1		1
Longobardites cf. *zsigmondyi* (Böckh)		2		2
Epikellnerites tamasi Vörös		1		1
Danubites floriani (Mojsisovics)		2		2
Leiophyllites cf. *taramellii* (Martelli)		2		2
Monophyllites wengensis (Klipstein)		2	2	4
Sturia sp.		1		1
Flexoptychites flexuosus (Mojsisovics)			1	1
Flexoptychites angustoumbilicatus (Böckh)			1	1
Flexoptychites aff. *studeri* (Hauer)			1	1
Gymnites incultus (Beyrich)			1	1
Discoptychites cf. *megalodiscus* (Beyrich)			1	1
Discoptychites ? sp.			1	1
Chieseiceras sp.			1	1
Joannites cf. *tridentinus* (Mojsisovics)			1	1
Proarcestes pannonicus (Mojsisovics)			1	1
Sturia sansovinii (Mojsisovics)			1	1
Arcestes ? sp.			1	1

Table 1: List of ammonoid taxa collected from the different horizons of the Kovčezi section in the Durmitor Mountain and their number of specimens per bed..

mopolitan species such as *Acrochordiceras carolinae* Mojsisovics, *Sturia sansovinii* (Mojsisovics) and *Monophyllites wengensis* (Klipstein). Some of the determined species are also rare elements of Western Tethyan Realm ammonoid assemblages, e.g. *Arthaberites alexandrae* Diener, *Megaphyllites obolus* Mojsisovics, *Danubites floriani* (Mojsisovics), which results in a relatively poor knowledge of their biostratigraphic ranges. Other species are known exclusively from one locality, such as *Discoptychites* ? *princeps* (Martelli) from Montenegro (Martelli, 1906), or additionally with some doubtful occurrences, like *Proteusites labiatus* (Hauer) and *Apleuroceras decrescens* (Hauer), known from Bulog Limestone of Bosnia and Herzegovina (Hauer, 1892) but reported also from Greece (Frech, 1907; Renz, 1910). To this list *Joannites tridentinus* (Mojsisovics) and *Leiophyllites taramellii* (Martelli) should be added, known so far from Italy, and Bosnia and Herzegovina, and Montenegro respectively. Another peculiarity is the presence of the genus *Aristoptychites*, registered in the Western Tethyan Realm only in Greece until now (Tselepidis, 2007; Pomoni and Tselepidis, 2013). On the other hand, the red limestones of the Kovčezi section contains also species that have not been found in the Western Tethyan Realm so far, e.g. *Ptychites rugifer* (Oppel) and *Tropigastrites lahontanus* Smith, known only from India and China (Oppel, 1865; Diener, 1895a; Wang and He, 1981), and Nevada (and tentatively East Timor) respectively (Smith, 1914; Nakazawa and Bando, 1968; Monnet and Bucher, 2005 and references therein). However, *Arthaberites alexandrae* Diener, a species known almost entirely from Western Tethys Realm, is also found in China (Wang and He, 1981). Likewise, *Gymnites incultus* (Beyrich) is described from India (Diener, 1907), and *Longobardites zsigmondyi* (Böckh) is also present in Nevada (Monnet and Bucher, 2005). The reason for their absence in the areas between these distant localities can currently be explained by the lack of data from these areas.

In the present paper we use the term Aplococeras avisianum Zone (Mojsisovics et al., 1895) as redefined by Assereto (1969). However, although at that time this zone was generally placed into the Ladinian near to the Anisian/Ladinian boundary as used until 2005, Assereto placed the Aplococeras avisianum Zone below the Reitziites reitzi Zone, but as a separate ammonoid zone. In the subsequent years the Aplococeras avisianum Zone has been incorporated as upper part of the Reitziites reitzi Zone (Mietto and Manfrin, 1995; Vörös, 2003), without any distinction or clear definition (Balini et al., 2010; Jenks et al., 2015 and references therein), or as a subzone within it (Vörös, 2014, 2018), and placed therefore in the in fact not clearly defined "middle Illyrian". Mietto and Manfrin (1995) separated Reitzi and Avisianum subzones within their Hungarites Zone. However, if the species are to be used as zonal markers, then their Avisianum subzone should be used as a separate zone, as originally defined by Mojsisovics et al. (1895), and later revised by Assereto (1969). Likewise, Mietto et al. (2003) state that *Aplococeras avisianum* (Mojsisovics) does not overlap with *Reitziites reitzi* (Böckh) anywhere in the Southern Alps and the Balaton Highland. Recently, Vörös (2018) reported that these two species overlap at Balaton, distinguishing there *Reitziites reitzi* morphotype *cholnokyi* together with *Aplococeras avisianum* (Mojsisovics). However, this co-occurrence can be considered problematic, since Brack and Rieber (1993) synonymised *Trachyceras cholnokyi* described by Frech (1903) with *Reitziites reitzi* based on the fact that they have the same ornamentation and whorl section on inner whorls, i.e. in the earlier ontogenetic stages. Contrary to this, Balini (1998) demonstrated that small to medium specimens of Ptychitidae for example cannot be certainly assigned to a specific genus (*Flexoptychites* or *Lanceoptychites*) in these early stages, making the recognition of a species impossible. Vörös (2018) states that there are transitional forms in the Balaton Highland, and he distinguishes the *cholnokyi* morphotype as a more slender form of *Reitziites reitzi*. For example, transitional forms are also described between *Tropigastrites lahontanus* Smith and *Tropigastrites louderbacki* (Hyatt and Smith) by Silberling and Nichols (1982). The first species occurs within the uppermost Gymnotoceras rotelliformis Zone, and the second within the earliest Parafrechites meeki Zone, with end variants of these species being present in lower or upper levels respectively, but they are still considered as separate species. In Balaton, *Reitziites reitzi* (Böckh) does not occur in the Avisianum subzone, whereas *Reitziites reitzi* morphotype *cholnokyi* (Frech) is found within Reitzi and Avisianum subzones (Vörös, 2018). If morphotype *cholnokyi* is actually a different species of the genus, than *Reitziites reitzi* (Böckh) and *Aplococeras avisianum* (Mojsisovics) do not overlap in the Balaton Highland, as stated by Mietto et al. (2003). This would then justify the use of the later species as a zonal marker. In any case, sections in the Balaton Highland (Vörös, 2018), as well as northern Italy (Mietto et al., 2003) contain more complete ammonoid records, where these questions can be resolved. The question raised here is whether the faunas with *Aplococeras avisianum* (Mojsisovics) should have the status of a separate zone, or if they should still be considered a subzone within the Reitziites reitzi zone.

Another controversy is currently the use of Aplococeras avisianum Zone as a part of middle or late Illyrian. However, since the conodonts of this age are mainly described as late Illyrian (Mrdak et al., 2024 for an overview, following Krystyn, 1983), in order to correlate the ammonoid and conodont zonations, the First Appearance Datum (FAD) of *Aplococeras avisianum* (Mojsisovics) could be proposed as the base of late Illyrian, as was previously done in the Bagolino section for the base of the Ladinian by Mietto et al. (2003). In this sense, faunas with *Aplococeras avisianum* (Mojsisovics) should be considered a separate zone. For geological reasons and correlation with other organisms groups (e.g., conodonts, radiolarians – Krystyn, 1983, Kozur, 2003) we plead for an independent Aplococeras avisianum Zone which should be incorporated into the late Illyrian.

Ammonoid specimens were collected from condensed

Table 2

Determined taxa	Inv. Number	D	H	W	U	H/D	W/D	U/D
Arthaberites alexandrae Diener	CG/K-30/20	53.2	28.9	? 11	5.3	54.3	? 20.7	10
Megaphyllites obolus Mojsisovics	CG/K-31/20	19.5	12.6	6.8	0	64.6	34.9	0
Acrochordiceras carolinae Mojsisovics	CG/K-9/20	105.3	53.5	X	20.2	50.8	X	19.2
Epikellnerites tamasi Vörös	CG/K-24/20	? 33	? 13.4	? 9.7	? 10.3	? 40.6	? 29.4	? 31.2
Danubites floriani (Mojsisovics)	CG/K-46/20	49.5	14.1	12.3	23.7	28.5	24.8	47.9
Apleuroceras decrescens (Hauer)	CG/K-16/20	56.1	20.7	16.1	21.4	36.9	28.7	38.1
Longobardites cf. *zsigmondyi* (Böckh)	CG/K-33/20	41	23.9	4	0	58.3	9.8	0
Ptychites rugifer (Oppel)	CG/K-1/20	56.1	38.3	36.8	7.4	68.3	65.6	13.2
Ptychites oppeli Mojsisovics	CG/K-7/20	X	48.3	X	12.3	X	X	X
	CG/K-36/20	73.6	41.3	? 28.7	9.3	56.1	? 39	12.6
Aristoptychites sp.	CG/K-43/20	? 75.7	? 43.7	? 47.0	X	? 57.7	? 62.1	X
Flexoptychites acutus (Mojsisovics)	CK/K-37/20	? 59.9	? 33.2	? 20.8	? 7.7	? 55.4	? 34.7	? 12.9
Flexoptychites angustoumbilicatus (Böckh)	CG/K-39/20	59.4	31.7	? 16.9	8.1	53.4	? 28.5	13.6
Flexoptychites aff. *studeri* (Hauer)	CG/K-42/20	172.3	99.4	60.6	19.1	57.7	35.2	11.1
Discoptychites ? *princeps* (Martelli)	CG/K-47/20	265	138	88.4	35.9	52.1	33.4	13.5
Proteusites labiatus (Hauer)	CG/K-26/20	41.8	17.3	X	14.6	41.4	X	34.9
Tropigastrites lahontanus Smith	CG/K-29/20	45.2	12.8	14.5	21.6	28.3	32.1	47.8
Proarcestes pannonicus (Mojsisovics)	CG/K-12/20	? 39.2	? 17.7	? 32.6	? 4.5	? 45.2	? 83.2	? 11.5
Proarcestes subtridentinus (Mojsisovics)	CG/K-45/20	58.6	35.5	35.7	6.1	60.6	60.9	10.4
Proarcestes boeckhi (Mojsisovics)	CG/K-22/20	46.7	29.6	33.7	5.5	63.4	72.2	11.8
Joannites cf. *tridentinus* (Mojsisovics)	CG/K-27/20	75.7	40.2	33.7	5.8	53.1	44.5	7.7
Leiophyllites cf. *taramellii* (Martelli)	CG/K-21/20	39.8	9	6.9	23.1	22.6	17.3	58

Table 2: Measurements of determined taxa from the Kovčezi section.

layers, which can result in cases in a collection of time-mixed faunas. However, conodont sampling excluded this in the Kovčezi section. As shown by Mrdak et al. (2024, Fig. 4), underlying MTD's of the Komarani Formation contain conodonts from the Aplococeras avisianum Zone, directly above the 1st cephalopod accumulation bed deposited. From the Bulog Limestone above the 1st cephalopod-rich level two samples contain conodonts from the Nevadites secedensis Zone (compare Krystyn, 1983). These two samples are below the 2nd cephalopod-rich layer. Since the 1st cephalopod-rich bed does not contain any ammonoid taxa that would indicate the Nevadites secedensis Zone, it is interpreted to belong to an earlier Aplococeras avisianum Zone. Likewise, several taxa found within it that might be conisidered problematic for this age, e.g. *Proteusites labiatus* (Hauer) or *Tropigastrites lahontanus* Smith, cannot represent older elements, since the underlying MTD's also belong to Aplococeras avisianum Zone.

4. Systematic palaeontology

Systematic descriptions follow the classification given by Tozer (1981), as well as by Vörös (2003, 2018) and Monnet and Bucher (2005). For all specimens wherever measurements were possible, dimensions of the diameter of the shell (D), whorl height (H), whorl width (W) and umbilical diameter (U) are given in milimeters and for H/D, W/D and U/D in percentages of D (Tab. 2).

Each specimen has an inventory number, which consists of abbreviations for the locality (CG/K – Crvena greda/Kovčezi), number of the specimen and the abbreviations for the year when it was collected (e.g., CG/K-1/20). All described specimens are stored at the Geological Survey of Montenegro in Podgorica. The occurence for the specimens with only a generic determination is not given.

Class Cephalopoda Cuvier, 1797
Superorder Ammonoida Hoffmann, 2022
Order Ceratitida Hyatt, 1884
Superfamily Noritoidea Karpinsky, 1889
Family Noritidae Karpinsky, 1889
Genus *Arthaberites* Diener, 1900

Type species: *Arthaberites alexandrae* Diener, 1900

***Arthaberites alexandrae* Diener, 1900**
Figure 4a–d

1900 *Arthaberites Alexandrae* nov. sp. Diener, p. 18, Pl. 2, Figure 4.

1911 *Arthaberites Katzeri* n. sp. Turina, p. 248, Pl. 5, Figures 1–2.

1912 *Arthaberites Katzeri* n. sp. Turina, p. 689, Pl. 42, Figures 1–2.

1934 *Arthaberites alexandrae* – Spath, p. 282, Figure 99.

1964 *Arthaberites alexandrae* – Kollárová-Andrusovová, p. 234, Pl. 11, Figures 1–3.

p 1981 *Arthaberites alexandrae* – Wang and He, p. 292, Pl. 2, Figures 1–2 (non Figs. 3–5).

Material: One completely preserved specimen (CG/K-30/20).

Description: Specimen medium in size, compressed, involute, platycone, round in shape. The whorl section is lenticular, with maximum thickness in the middle of the section. The venter is tabulate, with angular ventral shoulders towards the flanks, which are slightly convex. The umbilicus is very small, rounded, covered by sediment. The ornamentation consists of very weak, barely noticable sinuous growth lines. At mid-flank, one very weakly developed spiral strigation is present. Suture line with very wide first and second lateral lobe, and elongated saddles, characteristic for the genus. The dimensions of the studied specimen are given in Table 2.

Discussion: This species is very similar in its outline to the genus *Norites*, as already discussed by Diener (1900) and Spath (1934), differing only in the shape of the suture line, which represents practically the only criteria for their differentation. Since the suture line was not uncovered when the first report on the new ammonoid faunas from the Kovčezi section was published (Đaković et al. 2023), it was wrongfully determined as *Norites gondola*. Likewise, only one of the specimens described from China by Wang and He (1981) represents *Arthaberites alexandrae*, whereas the other figured specimen probably belongs to *Norites gondola*, as indicated in the synonymy list.

The specimen from the Kovčezi section is the only specimen so far described on which the weak ornamentation can be observed, i.e. sinuous growth lines and one spiral strigation (Fig. 4c). The ornametation is very delicate, so it is possible that it is not preserved in previously described examples. In this sense, *Arthaberites alexandrae* shows most resemblance to *Bosnites*, from which it differs by being more involute and less compressed. Spiral strigation of Kovčezi specimen is in this sense consistent with weak spiral row of nodes in the mid-flank of *Bosnites*. This, as well as characteristic suture line of these genera, might be a reason enough to distinguish them as part of a different subfamily within Noritidae in the future. However, since these are both very rare representatives of Anisian fauna, more material is needed to confirm such an interpretation.

Occurrence: *Arthaberites alexandrae* Diener is known from the Illyrian of Austria (Diener, 1900), Bosnia and Herzegovina (Turina, 1911, 1912), Montenegro (Spath, 1934), Slovakia (Kollárová-Andrusovová, 1964), and China (Wang and He, 1981).

Superfamily Megaphyllitoidea Mojsisovics, 1896
Family Megaphyllitidae Mojsisovics, 1896
Genus *Megaphyllites* Mojsisovics, 1879

Type species: *Ammonites jarbas* Münster, 1841

***Megaphyllites obolus* Mojsisovics, 1882**

Figure 4e–h

? 1876 *Ammonites Jarbas* – Benecke, p. 311, Pl. 24, Figures 10–11.

1882 *Megaphyllites obolus* Mojsisovics, p. 192, Pl. 53, Figures 3–5.

1960 *Megaphyllites* cf. *sandalinus* – Pavlović, p. 213, Pl. 2, Figure 1.

Material: One completely preserved specimen (CG/K-31/20).

Description: Specimen small, involute, moderately compressed, elliptical in shape. The whorl section is subrectangular in shape with maximum thickness in the middle of the section. The venter is rounded, with gradual transition towards the flanks, which are almost straight. The umbilicus is occluded. The ornamentation consists of delicate growth lines, not entirely preserved. The suture line only partly uncovered, phylloid, characteristic of the genus. The dimensions of the studied specimen are given in Table 2.

Discussion: Mojsisovics (1882) described this species as very close to *Megaphyllites sandalinus*, differing mainly in the shape of the suture line. Likewise, specimens he shows differ from *M. sandalinus* in the shape of the whorl section, which is closer to *Megaphyllites jarbas*. He included in the new species also the specimen described by Benecke (1876), which is here only tentatively included, since the figures shown in the publication resemble *M. sandalinus* more, and the suture line is not presented.

The specimen from Vareš (Bosnia and Herzegovina) described by Pavlović (1960) as *Megaphyllites* cf. *sandalinus* is in the present paper considered to belong to *Megaphyllites obolus* based on the description and photos of the specimen, which are very similar to the specimen from the Kovčezi section.

Occurrence: The species has so far been known from the Anisian (Aplococeras avisianum Zone) and Ladinian (Protrachyceras archelaus Zone) of Italy (Mojsisovics, 1882), and the Anisian of Bosnia and Herzegovina (Pavlović, 1960).

***Megaphyllites* cf. *sandalinus* (Mojsisovics, 1869)**

Figure 4i–k

1869 *Phylloceras sandalinum* Mojsisovics, p. 585, Pl. 15, Figure 4.

1882 *Megaphyllites sandalinus* – Mojsisovics, p. 191, Pl. 53, Figures 1–2.

1892 *Megaphyllites sandalinus* – Hauer, p. 32, Pl. 10, Figure 3.

1960 *Megaphyllites sandalinus* – Pavlović, p. 213, Pl. 1, Figures 5–6.

? 1968 *Megaphyllites sandalinus* – Meço, p. 74, Pl. 1, Figure 7.

1979 *Megaphyllites sandalinus* – Mihajlović-Pavlović, p. 107, Pl. 3, Figure 2.

2007 *Megaphyllites sandalinus* – Tselepidis, p. 197, Pl. 12, Figure 9.

Material: Two broken specimens (CG/K-35/20 and CG/K-44/20).

Description: Specimen small, involute, compressed, elliptical in shape. The whorl section is subrectangular in shape with maximum thickness in the middle of the section. The venter is rounded, with gradual transition towards the flanks, which are straight. The umbilicus is occluded. Shell smooth, without ornamentation. The suture line only partly uncovered, phylloid, characteristic of the genus. Due to poor preservation, dimensions can not be measured.

Discussion: Specimens from the Kovčezi section are very similar to all previous descriptions of *Megaphyllites sandalinus*. However, because of poor and fragmentary preservation, they are left in open nomenclature.

Occurrence: *Megaphyllites sandalinus* (Mojsisovics) is known from the Anisian of Austria (Mojsisovics, 1882), Bosnia and Herzegovina (Hauer, 1892; Pavlović, 1960), Serbia (Mihajlović-Pavlović, 1979), and Greece (Tselepidis, 2007). The occurence in Albania (Meço, 1968) can only tentatively be considered, since it is based on a poor photo. Likewise, the species has been reported from the Anisian of Montenegro by different authors (Salopek, 1911; Čubrilović and Matejić, 1940; Bešić, 1949), but was not figured in any of the publications.

Superfamily Ceratitoidea Mojsisovics, 1879

Family Acrochordiceratidae Arthaber, 1911

Genus *Acrochordiceras* Hyatt, 1877

Type species: *Acrochordiceras hyatti* Meek, 1877

***Acrochordiceras carolinae* Mojsisovics, 1882**

Figure 5a–b

p 1877 *Acrochordiceras hyatti* Meek, p. 124, Pl. 11, Figure 5 (non Fig. 5a).

1882 *Acrochordiceras Carolinae* Mojsisovics, p. 141, Pl. 28, Figure 14, Pl. 36, Figure 3.

1882 *Acrochordiceras Fischeri* Mojsisovics, p. 142, Pl. 33, Figure 8.

1882 *Acrochordiceras pustericum* Mojsisovics, p. 143, Pl. 6, Figure 4.

1887 *Acrochordiceras Damesi* – Hauer, p. 22, Pl. 5, Figure 2.

1892 *Acrochordiceras enode* Hauer, p. 272, Pl. 7, Figure 1.

1895a *Acrochordiceras* sp. ind. Diener, p. 22, Pl. 4, Figure 2.

1896a *Acrochordiceras undatus* Arthaber, p. 79, Pl. 7, Figures 7–8.

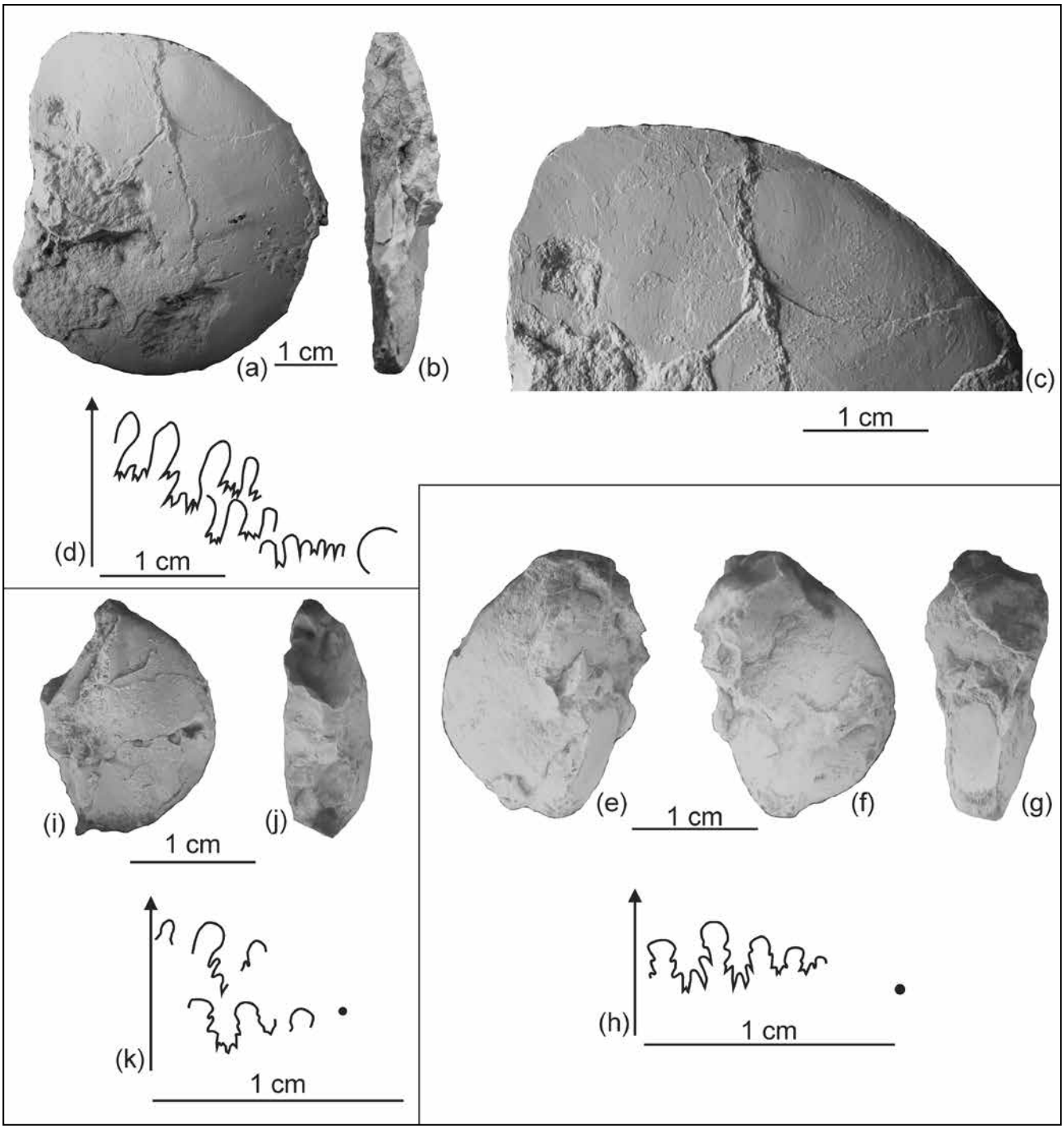

Figure 4: (a–d) *Arthaberites alexandrae* Diener, CG/K-30/20; **(e–h)** *Megaphyllites obolus* Mojsisovics, CG/K-31/20; **(i–k)** *Megaphyllites* cf. *sandalinus* (Mojsisovics), CG/K-44/20.

1896a *Acrochordiceras* nov. spec. indet. Arthaber, p. 81, Pl. 7, Figure 10.

1896a *Acrochordiceras erucosum* Arthaber, p. 82, Pl. 7, Figure 9.

1896b *Acrochordiceras undatum* – Arthaber, p. 226, 235, Pl. 27, Figure 2.

non 1896 *Acrochordiceras Halili* nov. spec. Toula, p. 168, Pl. 19, Figure 10.

1905 *Acrochodiceras hyatti* – Hyatt and Smith, p. 178, Pl. 23, Figures 8–11.

1905 *Acrochordiceras Carolinae* – Airaghi, p. 249, Pl. 8, Figure 6.

1905 *Acrochordiceras undatum* – Airaghi, p. 251, Pl. 8, Figure 4.

1905 *Acrochordiceras enode* – Airaghi, p. 252, Pl. 8, Figure 2.

1906 *Acrochordiceras Portisi* sp. nov. Martelli, p. 132, text-Figure. 4, Pl. 6, Figure 2.

1911 *Acrochordiceras Ippeni* Arthaber, p. 271, Pl. 24, Figure 11.

1913 *Acrochordiceras* cf. *enode* – Diener, p. 61, Pl. 7, Figure 7.

1913 *Acrochordiceras* cf. *Haueri* – Diener, p. 63, Pl. 7, Figure 8.

1914 *Acrochordiceras bithynicum* Arthaber, p. 179, Pl. 14, Figure 2.

? 1914 (?) *Acrochordiceras* sp. Arthaber, p. 180, Pl. 13, Figure 9, Pl. 14, Figure 1.

non 1914 *Acrochordiceras Halili* – Arthaber, p. 181, Pl. 14, Figures 3–4.

1914 *Acrochordiceras Haueri* – Arthaber, p. 182, text-Figure 12; Pl. 14, Figures 5–6.

1914 *Acrochordiceras pustericum* – Arthaber, p. 183, text-Figure 13; Pl. 14, Figure 7.

? 1914 *Acrochordiceras Endrissi* Arthaber, p. 184, Pl. 15, Figure 1.

p 1914 *Acrochordiceras hyatti* – Smith, p. 39, Pl. 4, Figures. 8–11, Pl. 15, Figure 5 (non Fig. 5a).

? 1934 *Acrochordiceras* (*Epacrochordiceras*) *portisi* – Spath, p. 404, Pl. 18, Figure 2.

1949 *Acrochordiceras damesi* – Bešić, p. 143, Pl. 9, Figure 1.

1953 *Acrochordiceras enode* – Petković and Miletić, p. 11, Pl. 1, Figure 1, text-Figure 16.

? 1960 *Acrochordiceras* sp. indet. Kummel, p. 6, Pl. 1, Figure 1.

1960 *Acrochordiceras enode* – Pavlović, p. 215, Pl. 2, Figure 6.

non 1973 *Acrochordiceras* cf. *carolinae* – Pelosio, p. 153, Pl. 17, Figure 3a–b.

1980 *Acrochordiceras carolinae* – Gu et al., p. 350, Pl. 2. Figures 12–13.

1980 *Acrochordiceras undatum* – Gu et al., p. 350, text-Figure 6c; Pl. 2, Figures 4–5 and 10–11.

1980 *Acrochordiceras fischeri* – Gu et al., p. 351, text-Figure 6b; Pl. 2, Figures 8–9.

1980 *Acrochordiceras balarama* – Gu et al., p. 351, text-Figure 6a; Pl. 2, Figures 14–16.

1982 *Acrochordiceras* cf. *A. carolinae* – Silberling and Nichols, p. 22, text-Figure 14; Pl. 5, Figures 8–9.

1987 *Acrochordiceras* cf. *carolinae* – Vörös, p. 56, Pl. 2, Figure 3.

non 1988 *Acrochordiceras* cf. *halili* – Prlj and Mudrenović, p. 16, Pl. 5, Figure 5.

non 1988 *Acrochordiceras* (*Epiacrochordiceras*) *enode* – Prlj and Mudrenović, p. 16, Pl. 5, Figure 7.

1988 *Acrochordiceras bythinicum* – Fantini Sestini, p. 54, text-Figure 11a, Pl. 9, Figure 4.

non 1988 *Acrochordiceras halili* – Fantini Sestini, p. 54, text-Figure 11b, Pl. 10, Figure 2.

1988 *Acrochordiceras haueri* – Fantini Sestini, p. 55, text-Figure. 11e, Pl. 10, Figures 1 and 3.

1988 *Epacrochordiceras pustericum* – Fantini Sestini, p. 55, text-Figure 11c, Pl. 11, Figure 3.

1991 *Acrochordiceras* cf. *carolinae* – Tatzreiter and Vörös, p. 252, Pl. 2, Figure 2.

1991 *Acrochordiceras undatum* – Tatzreiter and Vörös, p. 256, Pl. 2, Figure 5a–b.

2003 *Acrochordiceras carolinae* – Vörös, p. 83, text-Figure A13; Pl. A1, Figures 11–14.

2005a *Acrochordiceras carolinae* – Monnet and Bucher, p. 16, Pl. 2, Figures 5–9.

2007 *Acrochordiceras carolinae* – Jenks et al., pl. 17, Figures D–E; Pl. 35, Figures E–F.

2007 *Acrochordiceras* sp., Jenks et al., Pl. 18, Figures G–H.

2008 *Acrochordiceras* cf. *carolinae* – Stiller and Bucher, p. 552, Figure 3a–b.

2010 *Acrochordiceras carolinae* – Monnet et al., p. 973, Pl. 6–11, text-Figure 12.

2022 *Acrochordiceras carolinae* – Vörös et al., p. 706, Pl. 2, Figures 2–3.

Material: One poorly preserved, but almost complete specimen (CG/K-9/20).

Description: Specimen large, moderately involute, moderately compressed, elliptical in shape. The whorl section is subtriangular in shape. The venter is rounded. The flanks are convex and pass gradually towards the arched venter. The umbilicus is medium sized, rounded and deep, with rounded shoulders towards the flanks. The ornamentation consists of rectiradiate, slightly concave, strong ribs, that pass to the venter. The suture line is partly preserved, subammonitic, characteristic of the species. The dimensions of the studied specimen are given in Table 2.

Discussion: Monnet et al. (2010) did a thorough revision of the genus *Acrochordiceras*, describing the species *Acrochordiceras carolinae* as highly variable one, including all described species of Pelsonian age in it. The specimen from the Kovčezi section is most similar with slender forms that do not bear nodes, previously described as *Acrochordiceras pustericum*, and *Acrochordiceras enode*.

In the present paper, the species *Acrochordiceras halili* is excluded from the synonymy for *Acrochordiceras carolinae*, which was also doubted by Monnet et al. (2010). Figured specimens of this species in published literature (Toula, 1896; Arthaber, 1914; Fantini Sestini, 1988) all resemble more *Acrochordiceras hyatti* of Bithynian age, in shape of the shell (slender forms) and especially the suture line. Likewise, Fantini Sestini (1988) describes it from late Bithynian to early Pelsonian of Turkey. Until today *Acrochordiceras carolinae* is not known from Bithynian, whereas *Acrochordiceras hyatti* Meek is not found in the Pelsonian. For now it is not clear if *Acrochordiceras halili* is a synonym of *Acrochordiceras hyatti* Meek or a separate species, which would need to be controlled with new material and data, but based on its descriptions and suture line it should not be included in *Acrochordiceras carolinae* Mojsisovics either.

Occurrence: *Acrochordiceras carolinae* Mojsisovics represents a cosmopolitan form during Pelsonian, described from Austria, Hungary, Bosnia and Herzegovina, Montenegro, Italy, Turkey, China, India, Nevada, among others (Monnet et al. 2010 for an overview; Martelli 1906, Bešić 1949, and Petković and Miletić 1953 for the localities in Montenegro).

***Acrochordiceras* sp.**
Figure 5c

Material: One partly preserved internal mold (CG/K-8/20).

Description: Part of a large, moderately compressed specimen. Whorl section high oval. The venter is rounded. The flanks are slightly convex and pass gradually towards the venter. The ornamentation consists of rectiradiate, slightly concave, strong ribs, that pass to the venter. Only one node is preserved on the umbilical margin, from which three ribs arise. Due to poor preservation, dimensions could not be measured.

Discussion: Described specimen probably belongs to *Acrochordiceras carolinae*, but due to poor preservation it is determined only at a genus level.

Family Ceratitidae Mojsisovics, 1879
Subfamily Paraceratitinae Silbering, 1962
Genus *Epikellnerites* Vörös, 2018

Type species: *Ceratites angustecarinatus* Hauer, 1896

***Epikellnerites tamasi* Vörös, 2018**
Figure 5d–g
1896 *Ceratites Bosnensis* Hauer, p. 254, Pl. 7, Figures 13–14.
1904 *Ceratites trinodosus* – Martelli, p. 80, Pl. 5, Figure 1.
p 1914 *Popinites bosnensis* – Salopek, p. 11, Pl. 3, Figure 2b and c (non Fig. 2a), Pl. 7, Figure 1.
p 1993 *Kellnerites bosnensis* – Brack and Rieber, p. 470, Pl. 5, Figure 10 (non Figs. 7–9 and 13–14).
1998 *Kellnerites* cf. *bosnensis* – Petek, p. 131 and 138, Pl. 3, Figure 3 (non Figs. 1–2).
2018 *Epikellnerites tamasi* Vörös, p. 67, Pl. 7, Figures 3–4.

Material: One partial specimen (CG/K-24/20).

Description: Specimen small, moderately involute, moderately compressed. The whorl section sub-trapezoidal in shape, with maximum thickness near the umbilical margin. The venter is almost fastigate, with a sharp keel. The flanks are slightly convex and pass gradually towards the venter. The umbilicus is medium sized, relatively deep, with subrounded shoulders towards the flanks. The ornamentation consists of strong, prorsiradiate, projected ribs, that bear four rows of nodes. Rare secondary ribs are also developed. The umbilical nodes are less developed than the first and second row of lateral nodes, which are stronger. Near the ventrolateral margin, the ribs almost disappear, where the nodes develop as projected clavi on the margin. Suture line is not preserved. Due to poor preservation, measured dimensions should be considered only tentatively (Tab. 2).

Discussion: The specimen from the Kovčezi section shows most resemblance to the one described by Hauer (1896) as *Ceratites bosnensis*, which Vörös (2018) assigned to the newly described species *Epikellnerites tamasi*.

Occurrence: *Epikellnerites tamasi* Vörös is known from the Anisian of Bosnia and Herzegovina (Hauer, 1896), Montenegro (Martelli, 1904), Croatia (Salopek, 1914), Italy (Brack and Rieber, 1993), Slovenia (Petek, 1998), and Hungary (Vörös, 2018).

Genus *Parakellnerites* Rieber, 1973

Type species: *Parakellnerites frauenfelderi* Rieber, 1973

Parakellnerites rothpletzi (Salomon, 1895)
Figure 5h–j
1895 *Balatonites Rothpletzi* nov. sp. Salomon, p. 199, Pl. 6, Figure 12.
1993 *Parakellnerites rothpletzi* – Brack and Rieber, p. 466, Pl. 4, Figures 1–17.
2005 *Parakellnerites rothpletzi* – Manfrin et al., p. 495, Figure 9: 29–34.
2018 *Parakellnerites* cf. *rothpletzi* – Vörös, p. 92, Pl. 15, Figures 5–8.

Material: One partial specimen (CG/K-28/20).

Description: Specimen small, involute, moderately compressed. The whorl section is subtriangular in shape, with maximum thickness near the umbilical margin. The venter is fastigate and arched, with sub-angular transition towards the flanks which are almost straight. The umbilicus is small, round and deep, with a perpendicular umbilical wall, covered by sediment. The ornamentation consists of weak prorsiradiate, sinuous ribs with sinuous secondary ribs and growth lines between them, and weak nodes between umbilical margin and mid-flank, as well as on the ventrolateral margin. Nodes on the flanks are developed only on the primary ribs, whereas the somewhat projected nodes on the ventrolateral margin are also developed on the secondary ribs. The suture line is not preserved. Due to poor preservation, dimensions could not be measured.

Discussion: Even though only a fragment of the shell is preserved, the specimen from Kovčezi is well comparable to the stronger ornamented specimens described by Brack and Rieber (1993), which is in accordance with their opinion that this is a very variable species.
Vörös (2018) described the specimens from Balaton

as *Parakellnerites* cf. *rothpletzi*, leaving it in open nomenclaure due to poor preservation. However, all the important characteristics of the species are noted by the author, so it is in the present paper considered that it should be a certain occurence of *Parakellnerites rothpletzi*.

Occurrence: The species is known from the Anisian Reitziites reitzi and Aplococeras avisianum Zones of Italy (Salomon, 1895; Brack and Rieber, 1993; Manfrin et al., 2005), and Hungary (Vörös, 2018).

Subfamily Nevaditinae Tozer, 1994
Genus *Chieseiceras* Brack and Rieber, 1986

Type species: *Trachyceras chiesense* Mojsisovics, 1882

Chieseiceras sp.
Figure 5k-l

Material: One poorly preserved fragment (CG/K-20/20).

Description: Specimen represents only a small piece of the internal mold of the outer whorl. The whorl section is trapezoidal. The venter is wide and concave, with a marked margin towards the flanks which are convex. The ornamentation consists of strong rectiradiate ribs, one row of weak lateral nodes between mid-flank and ventrolateral margin, and one row of prominent nodes developed on the end of the ribs at the ventrolateral margin. Suture line is not preserved.

Discussion: Preserved characteristics of the specimen CG/K-20/20 are all well developed in the type species *Chieseiceras chiesense* (Mojsisovics), as described by Brack and Rieber (1986). However, it represents only a small fragment on which the suture line is not preserved, hence it is determined on a genus level.

Superfamily Danubitoidea Spath, 1951
Family Danubitidae Spath, 1951
Subfamily Danubitinae Spath, 1951
Genus *Danubites* Mojsisovics, 1893

Type species: *Celtites floriani* Mojsisovics, 1882

Danubites floriani (Mojsisovics, 1882)
Figure 5m–q
1882 *Celtites Floriani* Mojsisovics, p. 145, Pl. 28, Figures 5–7, Pl. 31, Figure 4.
1976 *Celtites floriani* – Ljubović, p. 206, Pl. 3, Figure 3.
1979 *Celtites floriani* – Mihajlović-Pavlović, p. 102, Pl. 2, Figure 1.

Material: One completely preserved specimen (CG/K-46/20) and one fragment (CG/K-14/20).

Description: Shell medium in size, compressed, evolute, elliptical in shape. The whorl section is subrectangular, with maximum thickness in the middle of the section. The venter is slightly fastigate, with rounded transition towards the flanks which are straight. The umbilicus is large, elliptical and shallow, with rounded umbilical wall. The ornamentation consists of strong radial ribs, which start at the umbilical margin towards the venter, where they are slightly projected, but do not cross the venter. Sometimes on inner whorls, the ribs are joined at the umbilical margin, but they do not form nodes. On the outer whorl secondary ribs can be formed, starting slightly above the umbilical margin, being as already at mid-flank as strong as primary ribs. The suture line is ceratitic, very simple, with broad saddles and indented lobes. The dimensions could only be measured on the specimen CG/K-46/20 (Tab. 2).

Discussion: The specimen CG/K-46/20 is slightly more evolute then the ones shown by Mojsisovics (1882), and has somewhat stronger ornamentation, whereas all other characteristics are very similar. Even though only a fragment, the specimen CG/K-14/20 shows all the important characteristics described for the species, except for the suture line which is not preserved.

Occurrence. The species is known from the Anisian of Austria (Mojsisovics, 1882), Serbia (Mihajlović-Pavlović, 1979) and Montenegro (Ljubović, 1976). Hauer (1892) and Spath (1951) also mentioned this species from Bosnia and Herzegovina, but did not figure the specimens.

Family Aplococeratidae Spath, 1951
Genus *Apleuroceras* Hyatt, 1901

Type species: *Ceratites sturi* Mojsisovics, 1882

Apleuroceras decrescens (Hauer, 1887)
Figure 6a–c
1887 *Ceratites decrescens* Hauer, p. 24, Pl. 5, Figure 3.

Material: One completely preserved specimen (CG/K-16/20).

Description: Shell medium in size, compressed, moderately evolute, elliptical in shape. The whorl section is subquadratic, with maximum thickness in the middle of the section. The venter is rounded, with gradual transition towards the flanks, which are almost straight. The umbilicus is medium-sized, elliptical, relatively deep, with rounded shoulders. The ornamentation consists of very weak radial folds, barely noticeable. The suture line is not preserved. The dimensions of the studied specimen are given in Table 2.

Discussion: Despite missing suture line, described specimen shows all other important characteristics of the species described by Hauer (1887).

After original description, other authors (Renz, 1910;

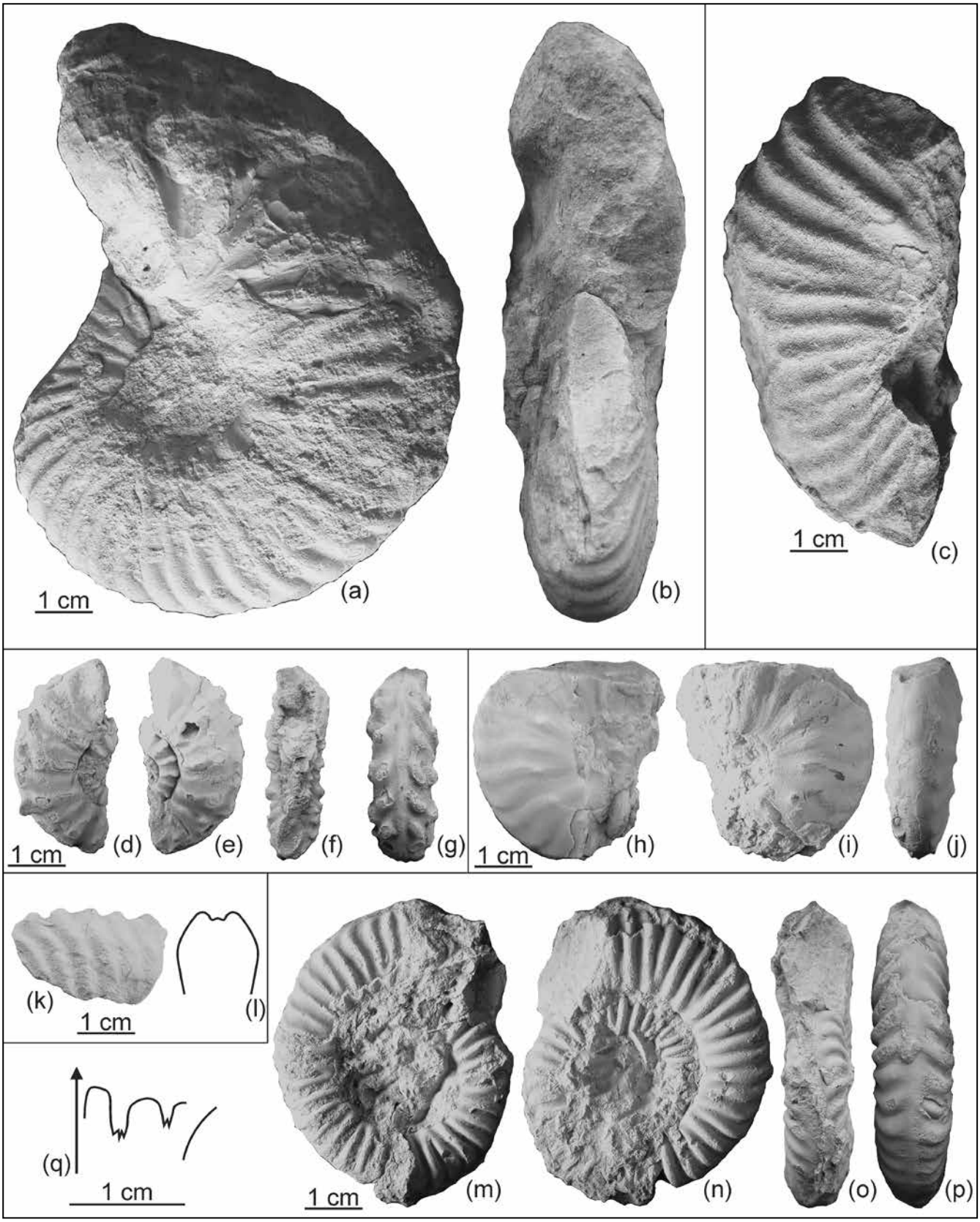

Figure 5: (a–b) *Acrochordiceras carolinae* Mojsisovics, CG/K-9/20; **(c)** *Acrochordiceras* sp., CG/K-8/20; **(d–g)** *Epikellnerites tamasi* Vörös, CG/K-24/20; **(h–j)** *Parakellnerites rothpletzi* (Salomon), CG/K-28/20; **(k–l)** *Chieseiceras* sp., CG/K-20/20; **(m–q)** *Danubites floriani* (Mojsisovics), CG/K-46/20.

Salopek, 1911) considered it belongs to the genus *Proteites*, which is a synonym of *Proteusites*. However, later authors disregarded original Hauer's opinion that this species shows similarities to *Ceratites Sturi* which was later chosen by Hyatt (1900) as the type species for the genus *Apleuroceras*. Opinion given in the present paper is that this species should be assigned to this genus, based on overall similarity with the type species, as well as the shape of the suture line shown by Hauer.

Occurrence: *Apleuroceras decrescens* (Hauer) has so far been known only from the Anisian of Bosnia and Herzegovina (Hauer, 1887). Renz (1910) reported it from the Anisian of Greece, but he did not figure the specimens, so this occurrence can only tentatively be accepted.

Family Longobarditidae Spath, 1951
Subfamily Longobarditinae Spath, 1951
Genus *Longobardites* Mojsisovics, 1882

Type species: *Longobardites breguzzanus* Mojsisovics, 1882

Longobardites cf. *zsigmondyi* (Böckh, 1873)
Figure 6d–e
1874 *Ammonites* (*Sageceras*) *Zsigmondyi* – Böckh, p. 177, Pl. 4, Figure 14.
1882 *Longobardites Zsigmondyi* – Mojsisovics, p. 185, Pl. 52, Figure 4.
1901 *Longobardites parvulus* Reis, p. 92, Pl. 4, Figures 28–31, Pl. 7, Figure 15.
1907 *Longobardites parvulus* – Reis, p. 117, Pl. 1, Figures 5–8.
1963 *Longobardites zsigmondyi* – Assereto, p. 71, Pl. 8, Figure 2.
1966 *Longobardites* (*Longobardites*) *zsigmondyi* – Assereto, p. 974, Pl. 68, Figures 2–6.
1973 *Longobardites* (*Longobardites*) *zsigmondyi* – Rieber, p. 64, Pl. 17, Figure 15.
1973 *Longobardites* (*Longobardites*) cf. *zsigmondyi* – Rieber, p. 64, Pl. 17, Figure 13.
1982 *Longobardites* cf. *L. zsigmondyi* – Silberling and Nichols, p. 51, Pl. 21, Figures 26–28.
1998 *Longobardites zsigmondyi* – Vörös, p. 20, 26, 31, 38, 42 and 48, Pl. 5, Figure 9.
2005 *Longobardites zsigmondyi* – Monnet and Bucher, p. 50, Pl. 31, Figures 10–13.
2018 *Longobardites zsigmondyi* – Vörös, p. 132, Pl. 40, Figures 10–11.

Material: Two incomplete fragments (CG/K-33/20 and CG/K-34/20).

Description: Specimens small to medium in size, compressed, extremely involute, oxycone, elliptical in shape. The whorl section is lenticular, with maximum thickness in the middle of the section. The venter is acute, and the flanks are convex. The umbilicus is occluded. Shell is smooth, without ornamentation. The suture line is not preserved. Due to poor preservation, the dimensions could only be measured on specimen CG/K-33/20 (Table 2).

Discussion: Specimens from the Kovčezi section show most resemblance to smaller specimens of *Longobardites zsigmondyi* described in the synonymy list. However, due to poor preservation and the fact that the suture line could not be observed, they are left in open nomenclature.

Occurrence: *Longobardites zsigmondyi* (Böckh) has been known from the upper Anisian of Hungary (Böckh, 1874; Mojsisovics, 1882; Vörös, 1987, 2018), Italy (Assereto, 1963, 1966), Switzerland (Rieber, 1973), and Nevada (Silberling and Nichols, 1982; Monnet and Bucher, 2005).

Superfamily Pinacoceratoidea Mojsisovics, 1879
Family Gymnitidae Waagen, 1895
Subfamily Gymnitinae Waagen, 1895
Genus *Gymnites* Mojsisovics, 1882

Type species: *Ammonites incultus* Beyrich, 1867

Gymnites incultus (Beyrich, 1867)
Figure 6f–h
1867 *Ammonites incultus* Beyrich, p. 132, Pl. 3, Figure 1.
1882 *Gymnites incultus* – Mojsisovics, p. 233, Pl. 54, Figures 1–3.
1904 *Gymnites incultus* – Martelli, p. 104, Pl. 5, Figures 9–10.
1907 *Gymnites incultus* – Diener, p. 109, Pl. 14, Figures 1–2.
1953 *Gymnites* (*Anagymnites*) *incultus* – Petković and Miletić, p. 10, Pl. 1, Figure 7.
1967 *Gymnites incultus* – Jacobshagen, p. 28, Pl. 2, Figure 2.
1968 *Gymnites incultus* – Meço, p. 87, Pl. 5, Figures 1–3.
1988 *Gymnites incultus* – Prlj and Mudrenović, p. 21, Pl. 3, Figure 1.
1998 *Gymnites incultus* – Petek, p. 134 and 140, Pl. 5, Figure 3.
2007 *Epigymnites incultus* – Tselepidis, p. 238, Pl. 35, Figures 4–5, Pl. 36, Figures 1–5.

Material: One fragment of the outer whorl (CG/K-41/20).

Description: Preserved part of a large specimen, evolute, compressed. The whorl section is high oval, elliptical to subtrigonal in shape, with maximum thickness close to the umbilical margin. Venter is rounded, with gradual transition towards the flanks, which are convex. The umbilicus was large and shallow, with rounded umbilical shoulders. Ornamentation consists of poorly preserved,

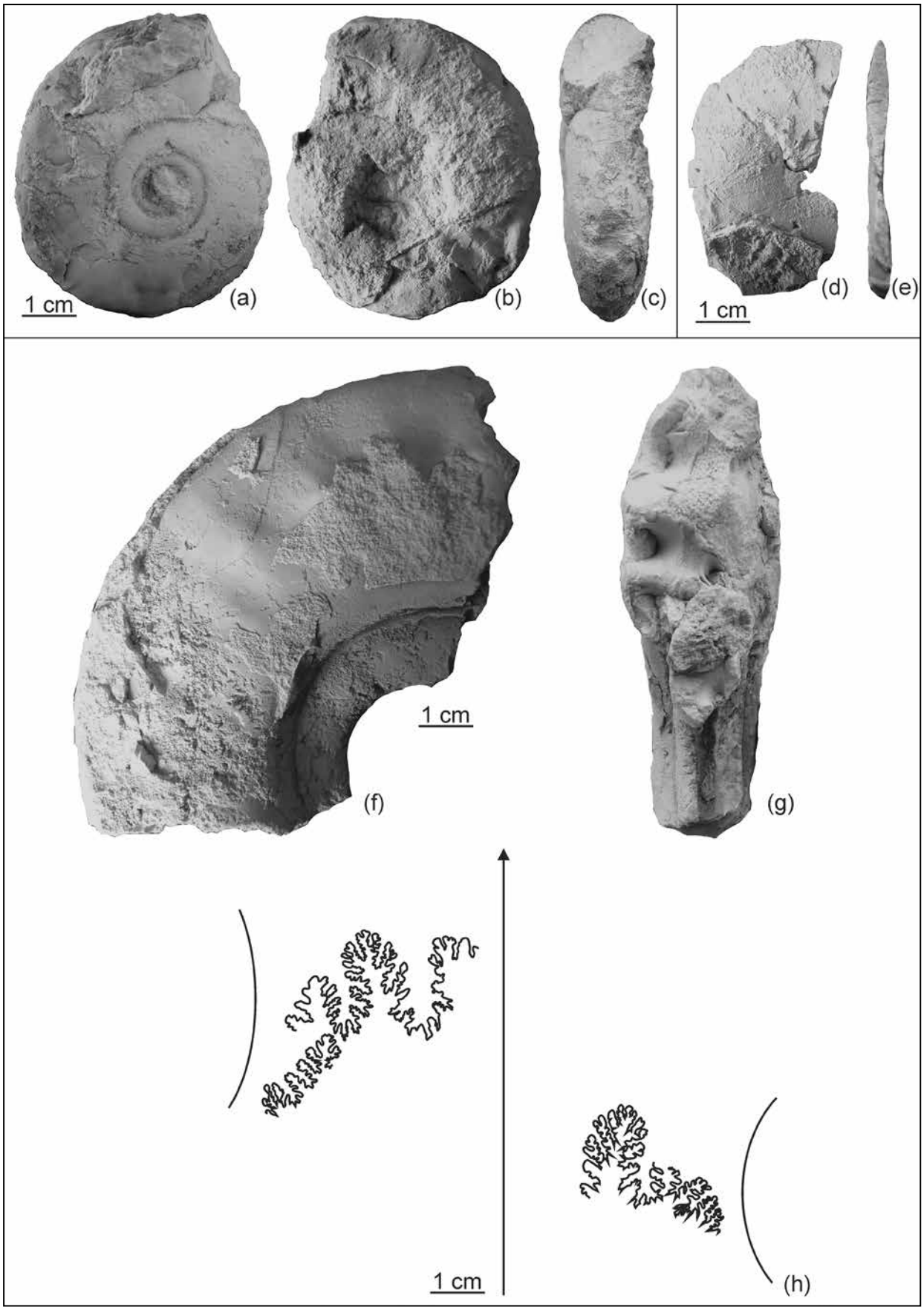

Figure 6: (a–c) *Apleuroceras decrescens* (Hauer), CG/K-16/20; **(d–e)** *Longobardites* cf. *zsigmondyi* (Böckh), CG/K-33/20; **(f–h)** *Gymnites incultus* (Beyrich), CG/K-41/20.

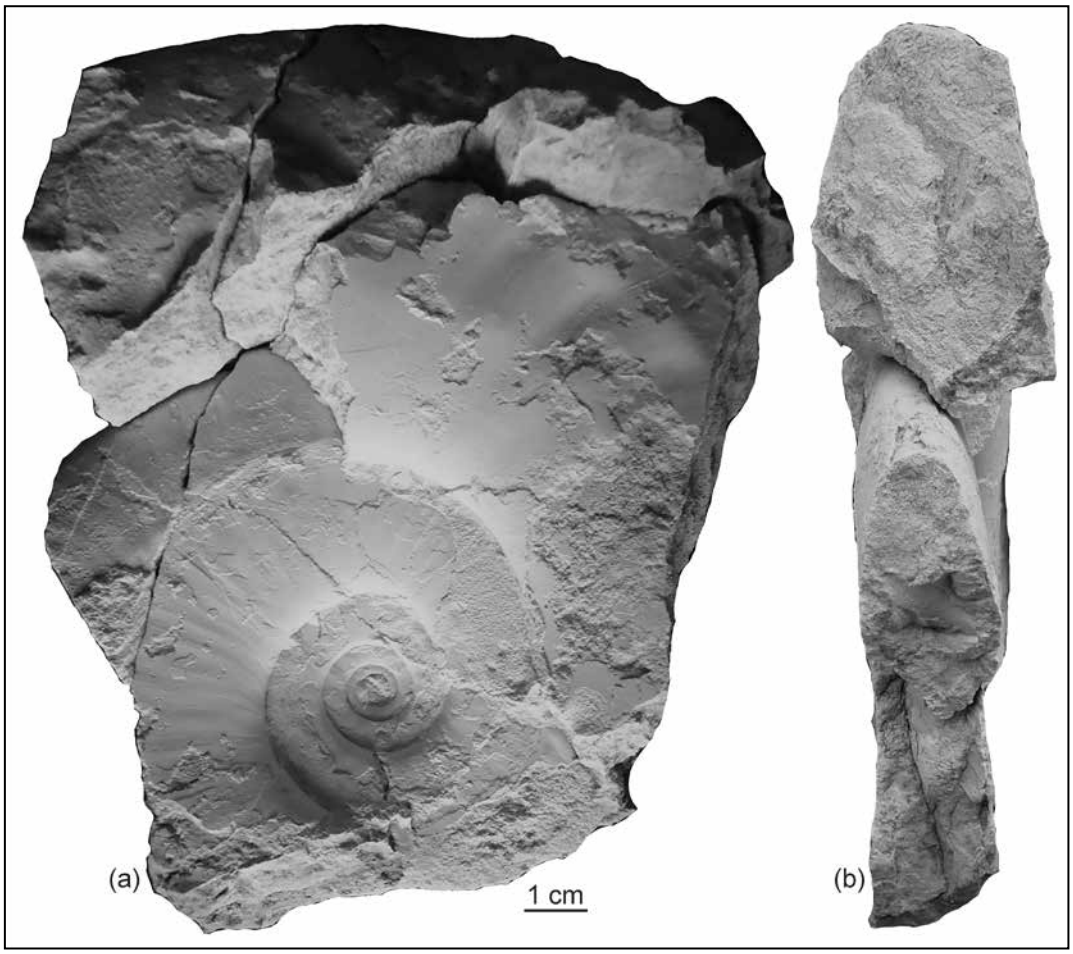

Figure 7: (a–b) *Epigymnites* cf. *ecki* (Mojsisovics), CG/K-40/20.

weak radial folds. Suture line ammonitic, very complex, characteristic of the genus. Due to poor preservation, dimensions could not be measured.

Discussion: Even though the specimen from the Kovčezi section is only a fragment, described characteristics and the suture line completely fit the species *Gymnites incultus*, which is one of the most common species in the Anisian of the Dinarides. Described ornamentation is more characteristic for some other species of the genus, e.g. *Gymnites obliquus*. However, such features are also present in the specimens shown by other authors such as Martelli (1904).

Occurrence: *Gymnites incultus* (Beyrich) is known from the upper Anisian of Austria (Beyrich, 1867; Mojsisovics, 1882), Montenegro (Martelli, 1904; Petković and Miletić, 1953), Greece (Jacobshagen, 1967; Tselepidis, 2007), Albania (Meço, 1968), Croatia (Prlj and Mudrenović, 1988), Slovenia (Petek, 1998), and India (Diener, 1907).

Genus *Epigymnites* Diener, 1916

Type species: *Gymnites ecki* Mojsisovics, 1882

Epigymnites cf. *ecki* (Mojsisovics, 1882)

Figure 7a–b

1882 *Gymnites Ecki* Mojsisovics, p. 238, Pl. 60, Figure 3.
1895 *Gymnites Ecki* – Salomon, p. 191, Pl. 8, Figure 1.
1910 *Gymnites Ecki* – Renz, p. 39, Pl. 4, Figure 2.
? 1960 *Epigymnites ecki* – Rossi Ronchetti, p. 37, Pl. 8, Figure 4.
1968 *Gymnites ecki* – Meço, p. 88, Pl. 5, Figure 4.
1973 *Gymnites* cf. *ecki* – Rieber, p. 71, Pl. 16, Figure 8.
1994 *Epigymnites ecki* – Fantini Sestini, p. 269, Pl. 1, Figure 1.
1998 *Epigymnites ecki* – Vörös, p. 45, Pl. 16, Figure 3.
2007 *Epigymnites ecki* – Tselepidis, p. 237, Pl. 35, Figure 3.
2018 *Epigymnites ecki* – Vörös, p. 136, Pl. 41, Figures 4–5.
2020 *Epigymnites ecki* – Smirčić et al., p. 79, Figure 6.4.

Material: One almost completely preserved specimen (CG/K-40/20).

Description: Specimen large, moderately evolute, compressed. The whorl section is high oval, elliptical in shape, with maximum thickness in mid-section. Venter is rounded, with gradual transition towards the flanks, which are convex. The umbilicus is large and shallow, with rounded umbilical shoulders. Ornamentation consists of poorly preserved, very weak radial folds. Slightly above mid-flank, only two blunt nodes are visible. Suture

line partly preserved, ammonitic, very complex. Due to poor preservation, dimensions could not be measured.

Discussion: Specimen from the Kovčezi section is very similar to all specimens of *Epigymnites ecki* in published literature, in shape of the shell and shape of the suture line. However, the most important characteristic of the species, i.e. a row of blunt nodes in mid-flank is practicaly missing, probably due to poor preservation. Because of this it is left in open nomenclature.

Occurrence: *Epigymnites ecki* (Mojsisovics) has been known from the upper Anisian and lower Ladinian of Italy (Mojsisovics, 1882; Salomon, 1895; Fantini Sestini, 1994), Greece (Renz, 1910; Tselepidis, 2007), Albania (Meço, 1968), Switzerland (Rieber, 1973), Hungary (Vörös, 1998, 2018), and Croatia (Smirčić et al., 2020).

Superfamily Ptychitoidea Mojsisovics, 1882
Family Ptychitidae Mojsisovics, 1882
Genus *Ptychites* Mojsisovics, 1875

Type species: *Ammonites rugifer* Oppel, 1865

Ptychites rugifer (Oppel, 1865)
Figure 8a–c
1865 *Ammonites rugifer* Oppel, p. 293, Pl. 85, Figures 2–3.
1895a *Ptychites rugifer* – Diener, p. 64, Pl. 22, Figures 1–2, Pl. 23, Figures 1–2, Pl. 24, Figures 1–2.
1981 *Ptychites rugifer* – Wang and He, Pl. 4, Figures 1–2.
? 2002 *Ptychites rugifer* – Waterhouse, p. 37, Pl. 7, Figures 1–2, 4 and 7, Pl. 8, Figures 1 and 8.

Material: One completely preserved specimen (CG/K-1/20).

Description: Shell medium in size, globose, involute and elliptical in shape. The whorl section is oval, with maximum thickness near the umbilicus. Venter is rounded, with gradual transition towards the flanks, which are convex. The umbilicus is rounded and small, covered with sediment. The ornamentation consists of weak radial folds with broad depressions between them. The suture line is partly preserved, ammonitic, characteristic of the genus. The dimensions of the studied specimen are given in Table 2.

Discussion: The specimen from the Kovčezi section shows great resemblance to the species described by Oppel (1865), especially with the specimens shown by Diener (1895a). Mojsisovics (1882) considered that *Ptychites rugifer* does not have related species within the Mediterranean species. However, *Ptychites eusomus* Beyrich is morphologicaly very similar, and despite having a different suture line, is probably very closly related to *Ptychites rugifer*.

The specimens shown by Waterhouse (2002) can only tentatively be included in this species, due to very poor preservation.

Occurrence: The species has so far been known only from the Illyrian of India (Oppel, 1865; Diener, 1895a), and China (Wang and He, 1981).

Ptychites oppeli Mojsisovics, 1882
Figure 8d–i
1882 *Ptychites Oppeli* Mojsisovics, p. 248, Pl. 71, Figures 1 and 3, Pl. 72, Figures 1–2.
1904 *Ptychites Oppeli* – Martelli, p. 114, Pl. 9, Figures 1–3.
1910 *Ptychites Oppeli* – Renz, p. 28, text-Figure. 2.
1964 *Ptychites oppeli* – Čelebić, p. 26, Pl. 1, Figure 2.
1968 *Ptychites oppeli* – Venzo and Pelosio, p. 119, Pl. 14, Figures 13–17, Pl. 15, Figures 1 and 3–5, Pl. 16, Figure 1.
1968 *Ptychites oppeli* – Meço, p. 75, Pl. 1, Figures 1–3.
1984 *Ptychites oppeli* – Leithner and Krystyn, p. 190, Pl. 1, Figure 2.
1988 *Ptychites oppeli* – Prlj and Mudrenović, p. 17, Pl. 5, Figure 4.
2010 *Ptychites oppeli* – Vörös, p. 12, Pl. 2, Figure 7.

Material: Two almost completely preserved specimen (CG/K-7/20 and CG/K-36/20).

Description: Shell medium in size, globose, involute and round to elliptical in shape. The whorl section is oval, subtriangular, with maximum thickness near the umbilicus. Venter is rounded, with gradual transition towards the flanks, which are almost straight. The umbilicus is rounded and small, with rounded umbilical shoulders, moderately deep. The ornamentation consists of strong radial folds with depressions of similar width between them. The folds appear at the umbilical margin, become strongest at the mid-flank and disappear before the venter. The suture line is ammonitic. The dimensions of studied specimens are given in Table 2.

Discussion: Specimens from the Kovčezi section are most similar to the ones shown by Mojsisovics (1882), and Venzo and Pelosio (1968). Differences of this species and other representatives of the genus are already discussed by Vörös (2010).

Occurrence: The species is known from the Anisian of Austria (Mojsisovics, 1882; Leithner and Krystyn, 1984), Montenegro (Martelli, 1904), Greece (Renz, 1910), Bosnia and Herzegovina (Čelebić, 1964), Italy (Venzo and Pelosio, 1968), Albania (Meço, 1968), Croatia (Prlj and Mudrenović, 1988), and Hungary (Vörös, 2010).

Genus *Aristoptychites* Diener, 1916

Type species: *Ammonites gerardi* Blanford, 1863

Aristoptychites sp.
Figure 9a–b

Material: One very poorly preserved specimens (CG/K-43/20).

Description: Specimen large, involute, round in shape. The whorl section subtriangular, with maximum thickness near the umbilicus. The venter is acutely rounded, without distinct transiton towards the flanks, which are slightly convex. The umbilicus cannot be observed, since it is covered by sediment. The ornamentation consists of weak radial folds. The suture line is not preserved. Due to poor preservation, measured dimensions should be considered only tentatively (Table 2).

Discussion: Described specimen is assigned to the genus *Aristoptychites* based on the shape of the shell, the shape of the whorl section and ornamentation. However, due to poor preservation and missing suture line, clear identification is not possible.

Genus *Flexoptychites* Spath, 1951

Type species: *Ptychites flexuosus* Mojsisovics, 1882

Flexoptychites flexuosus (Mojsisovics, 1882)
Figure 9c

1882 *Ptychites flexuosus* Mojsisovics, p. 261, Pl. 63, Figures 2–8, Pl. 64, Figures 1–3, Pl. 66, Figures 2–3.

1904 *Ptychites flexuosus* – Martelli, p. 125, Pl. 10, Figures 2–7.

1910 *Ptychites flexuosus* – Renz, p. 25, text-Figure 1.

1913 *Ptychites flexuosus* – Toula, p. 663, Pl. 24, Figure 9.

1913 *Ptychites flexuosus* – Simionescu, p. 342 and 367, Pl. 8, Figure 7.

1914 *Ptychites flexuosus* – Arthaber, p. 144, Pl. 13, Figure 1.

? 1931 *Ptychites flexuosus* – Živković, p. 90, Pl. 5, Figure 1.

? p 1936 *Ptychites studeri – plexuosus* – Stefanoff, p. 151, Pl. 1, Figures 11–12 (non Pl. 2, Figures 1–2).

? 1953 *Ptychites flexuosus* – Petković and Miletić, p. 7, Pl. 1, Figure 2.

1964 *Ptychites Flexuosus* – Čelebić, p. 25, Pl. 3, Figure 2.

1964 *Flexoptychites flexuosus* – Kollárová-Andrusová, p. 236, Pl. 11, Figures 4–5.

1968 *Flexoptychites flexuosus* – Venzo and Pelosio, p. 127, Pl. 16, Figure 18, Pl. 17, Figure 9.

1968 *Ptychites flexuosus* – Meço, p. 76, Pl. 3, Figure 8, Pl. 4, Figure 1–4.

1988 *Flexoptychites flexuosus* – Prlj and Mudrenović, p. 19, Pl. 5, Figure 2.

1992 *Flexoptychites flexuosus* – Sakač, p. 32, Pl. 5, Figure 4.

1998 *Flexoptychites flexuosus* – Petek, p. 132 and 139, Pl. 4, Figures 1–5.

2010 *Flexoptychites flexuosus* – Vörös, p. 13, Pl. 3, Figures 4–5.

2018 *Flexoptychites flexuosus* – Vörös, p. 140, Pl. 43, Figures 1–3.

Material: One partly and poorly preserved specimen (CG/K-38/20).

Description: Specimen medium in size, moderately compressed, involute and rounded in shape. The whorl section is high oval. Venter is rounded, without distinct transiton towards the flanks, which are slightly convex. The umbilicus is small and rounded, covered by sediment. The ornamentation consists of sinuous folds, which are strongest at mid-flank, with depressions of similar width between them. Suture line is not preserved. Due to poor preservation, dimensions could not be measured.

Discussion: Even though the specimen from the Kovčezi section is poorly preserved, it can without doubt be assigned to *Flexoptychites flexuosus*, because it presents most of the characteristics of this species, one of the most common and best described of the genus.

The opinions in the synonymy list mostly follow the discussion of Vörös (2018). However, specimens shown by Stefanoff (1936) in plate 2, Figures 1 and 2, are in the present paper considered not to belong to *Flexoptychites flexuosus*, as they are more similar to the genus *Ptychites*, looking like they are more globose.

Occurrence: *Flexoptychites flexuosus* (Mojsisovics) represents one of the most common species in the Anisian of Austria (Mojsisovics, 1882), Montenegro (Martelli, 1904), Greece (Renz, 1910), Bosnia and Herzegovina (Toula, 1913), Romania (Simionescu, 1913), Bosnia and Herzegovina (Čelebić, 1964), Turkey (Arthaber, 1914), Italy (Venzo and Pelosio, 1968), Slovakia (Kollárová-Andrusová, 1964), Albania (Meço, 1968), Croatia (Prlj and Mudrenović, 1988), Slovenia (Petek, 1998), and Hungary (Vörös, 2010, 2018), and tentatively from Serbia (Živković, 1931), and Bulgaria (Stefanoff, 1936).

Flexoptychites acutus (Mojsisovics, 1882)
Figure 9d–e

1882 *Ptychites acutus* Mojsisovics, p. 263, Pl. 64, Figure 4, Pl. 65, Figure 1, Pl. 66, Figure 5–6 (? Fig. 4).

1901 *Ptychites acutus* – Reis, p. 93, Pl. 5, Figures 3–13, Pl. 7, Figures 16–27.

p 1903 *Ptychites acutus* – Frech, p. 13, Pl. 1, Figure 2b (non 2a).

1904 *Ptychites acutus* – Martelli, p. 128, Pl. 11, Figures 5–6.

1910 *Ptychites acutus* – Renz, p. 26, Pl. 1, Figure 8.

1913 *Ptychites acutus* – Simionescu, p. 341 and 367, Pl. 5, Figure 2.

? 1963 *Flexoptychites acutus* – Assereto, p. 80, Pl. 9, Figure 3.

1964 *Ptychites acutuc* – Čelebić, p. 23, Pl. 1, Figure 1.

1967 *Flexoptychites acutus* – Casati and Gnaccolini, p. 137, Pl. 10, Figure 7.

1973 *Flexoptychites acutus* – Rieber, p. 71, Pl. 17, Figures 21 and 24.

1988 *Flexoptychites acutus* – Prlj and Mudrenović, p. 20, Pl. 4, Figure 4, Pl. 5, Figure 1.

1996 *Flexoptychites acutus* – Fantini Sestini, p. 223, Pl. 1, Figure 1.

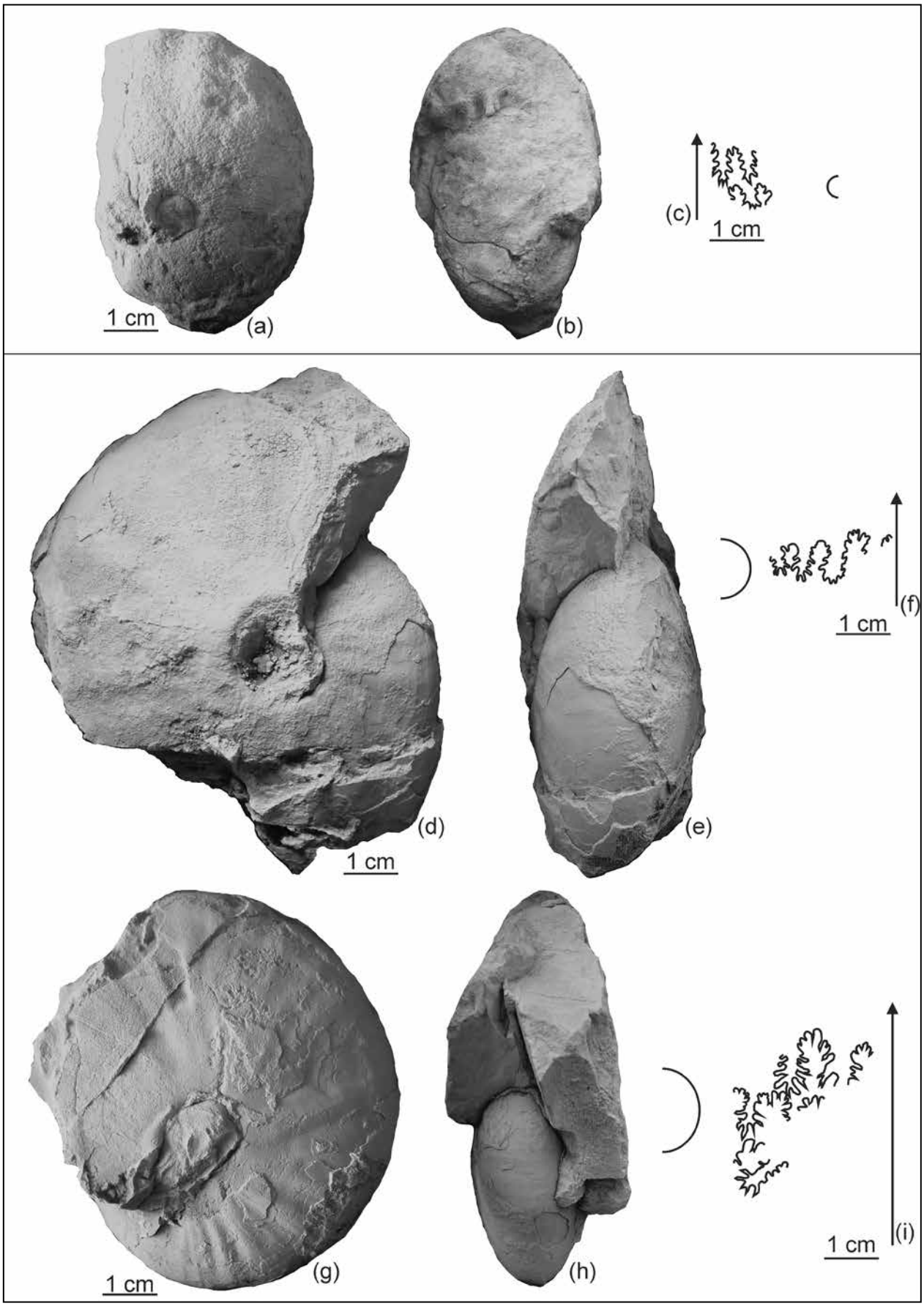

Figure 8: (a–c) *Ptychites rugifer* (Oppel), CG/K-1/20; **(d–i)** *Ptychites oppeli* Mojsisovics, **(d–f)** CG/K-7/20; **(g–i)** CG/K-36/20.

1998 *Flexoptychites acutus* – Petek, p. 133 and 140, Pl. 5, Figure 1.

2007 *Flexoptychites acutus* – Tselepidis, p. 222, Pl. 28, Figure 3, Pl. 29, Figures 1–4.

non 2010 *Flexoptychites acutus* – Vörös, p. 13, Pl. 4, Figures 1–2.

2023 *Flexoptychites acutus* – Vidaković et al., p. 532, Pl. 10, Figure 2, Pl. 11, Figures 1–2 and 6.

Material: One partly preserved specimen (CK/K-37/20).

Description: Specimen medium in size, compressed, involute. The whorl section is high oval, subtrigonal, with maximum thickness near the umbilicus. Venter is rounded, without distinct transition towards the flanks, which are slightly convex. The umbilicus is small and rounded, moderately deep, with rounded shoulders and perpendicular wall, covered by sediment. The ornamentation consists of weak, slightly sigmoid folds. Fine growth lines are also preserved in one part of the shell. Suture line partly uncovered, ammonitic. Due to poor preservation, measured dimensions should be considered only tentatively (Table 2).

Discussion: As already indicated by Balini (1998), when describing the new genus *Lanceoptychites*, *Flexoptychites acutus* (Mojsisovics) does not have an acute venter, despite its name. In this sense, specimens described and shown by Vörös (2010) cannot be included in this species, which was already noticed by Vidaković et al. (2023), who considered them as *Lanceoptychites* sp. In the present paper they are considered to belong to the type species of this genus *Lanceoptychites velox*.

Occurrence: *Flexoptychites acutus* (Mojsisovics) represents one of the most common species in the Anisian of Austria (Mojsisovics, 1882), Hungary (Frech, 1903), Montenegro (Martelli, 1904), Greece (Renz, 1910; Tselepidis, 2007), Romania (Simionescu, 1913), Bosnia and Herzegovina (Čelebić, 1934), Italy (Casati and Gnaccolini, 1967; Fantini Sestini, 1996), Switzerland (Rieber, 1973), Croatia (Prlj and Mudrenović, 1988; Vidaković et al., 2023), and Slovenia (Petek, 1998).

Flexoptychites angustoumbilicatus (Böckh, 1872)
Figure 9f–h

1872 *Arcestes angusto-umbilicatus* Böckh, p. 149, Pl. 8, Figures 7–8, Pl. 9, Figure 9.

1873 *Arcestes angusto-umbilicatus* Böckh, p. 160, Pl. 8, Figures 7–8, Pl. 9, Figure 9.

1875 *Arcestes angusto-umbilicatus* – Stürzenbaum, p. 258, Pl. 5, Figure 3.

1882 *Ptychites angusto-umbilicatus* – Mojsisovics, p. 257, Pl. 65, Figures 5–6, Pl. 66, Figure 1.

p 1882 *Ptychites noricus* Mojsisovics, p. 258, Pl. 64, Figure 5 (non Pl. 64, Figure 6).

1903 *Ptychites anguste-umbilicatus* – Frech, p. 13, Pl. 1, Figure 1.

1904 *Ptychites anguste-umbilicatus* – Martelli, p. 123, Pl. 12, Figure 4.

1968 *Flexoptychites angusto-umbilicatus* – Venzo and Pelosio, p. 130, Pl. 17, Figures 8, 10–11 and 13 (?).

non 1997 *Flexoptychites angustoumbilicatus* – Urlichs and Kurzweil, p. 4, Figures 2–3.

2010 *Flexoptychites* cf. *angustoumbilicatus* – Vörös, p. 14, Pl. 3, Figure 1.

2018 *Flexoptychites angustoumbilicatus* – Vörös, p. 139, Pl. 42, Figures 1–5.

Material: One completely preserved specimen (CG/K-39/20).

Description: Specimen medium in size, compressed, involute and elliptical in shape. The whorl section is high, acutely oval, with maximum thickness near the umbilicus. Venter is moderately acute, without distinct transiton towards the flanks, which are slightly convex. The umbilicus is small and rounded, moderately deep, with rounded shoulders and almost perpendicular wall. The ornamentation consists of sinuous folds which start at the umbilical margin, are strongest at mid-flank, and disappear near the venter. Between them, two to three weak secondary folds are developed. Suture line partly uncovered, ammonitic. The dimensions of the studied specimen are given in Table 2.

Discussion: *Flexoptychites angustoumbilicatus* (Böckh) is easily distinguishable from other species of the genus by its characteristic ornamentation, which is present in the specimen from the Kovčezi section. The species has been discussed in detail by Vörös (2018) and his opinion is accepted in the present paper.

Occurrence: *Flexoptychites angustoumbilicatus* (Böckh) is known from the Anisian of Hungary (Böckh, 1872, 1873; Stürzenbaum, 1875; Frech, 1903; Vörös, 2010, 2018), Austria (Mojsisovics, 1882), Montenegro (Martelli, 1904), and Italy (Venzo and Pelosio, 1968).

Flexoptychites aff. *studeri* (Hauer, 1857)
Figure 10a–b

1857 *Ammonites Studeri* Hauer, p. 146, Pl. 1, Figures 1–4.

1867 *Ammonites Studeri* – Beyrich, p. 123, Pl. 1, Figure 5.

1882 *Ptychites Studeri* – Mojsisovics, p. 260, Pl. 63, Figure 1.

1904 *Ptychites Studeri* – Martelli, p. 127, Pl. 12, Figure 1.

1913 *Ptychites Studeri* – Toula, p. 659, Pl. 23, Figure 4.

1963 *Flexoptychites studeri* – Assereto, p. 86, Pl. 11, Figure 5.

? 1988 *Flexoptychites studeri* – Prlj and Mudrenović, p. 19, Pl. 4, Figure 1.

2007 *Flexoptychites studeri* – Tselepidis, p. 226, Pl. 30, Figure 2, Pl. 32, Figure 1.

? 2018 *Flexoptychites* cf. *studeri* – Vörös, p. 138, Pl. 41, Figure 7.

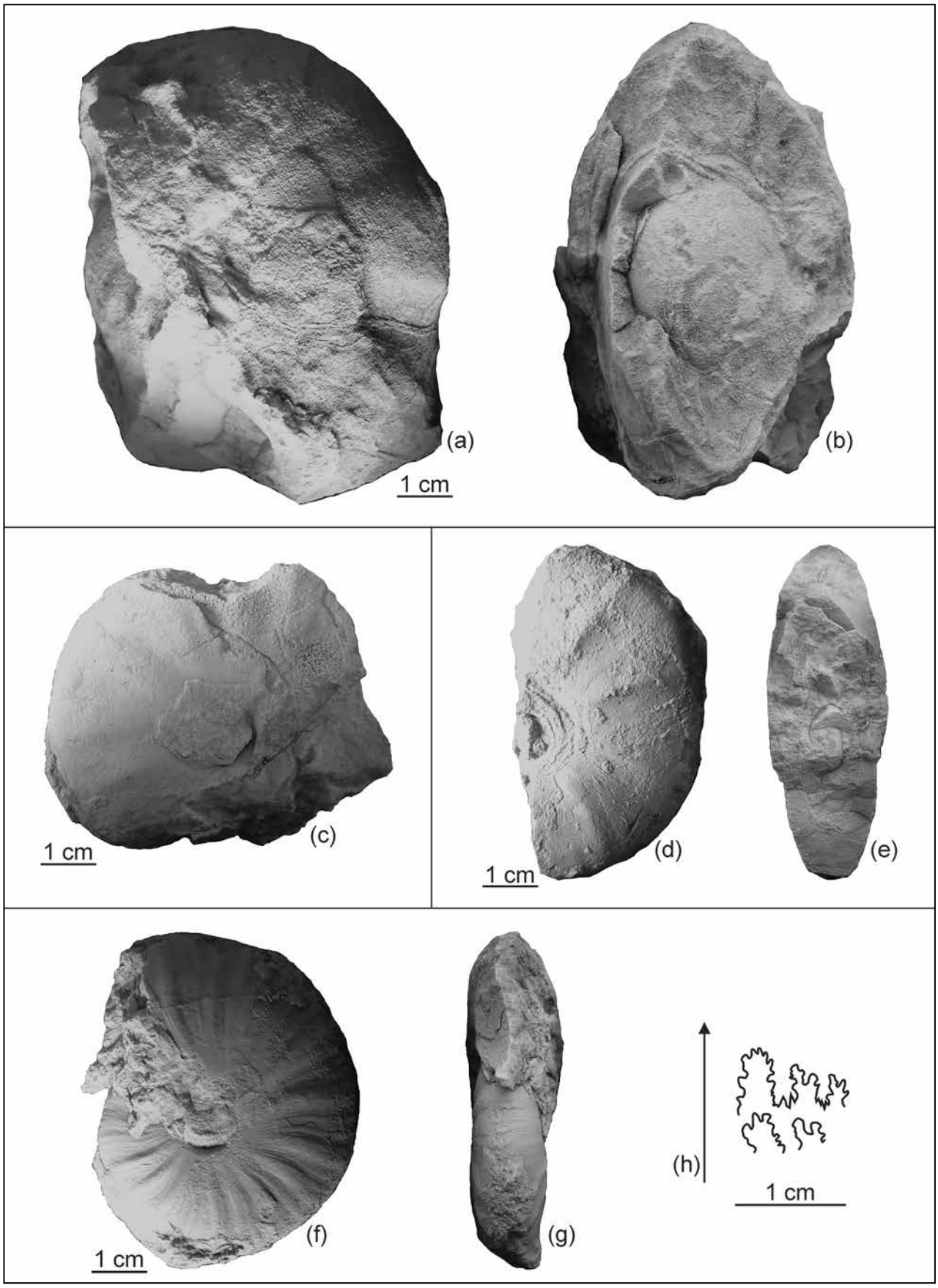

Figure 9: (a–b) *Aristoptychites* sp., CG/K-43/20; **(c)** *Flexoptychites flexuosus* (Mojsisovics), CG/K-38/20; **(d–e)** *Flexoptychites acutus* (Mojsisovics), CG/K-37/20; **(f–h)** *Flexoptychites angustoumbilicatus* (Böckh), CG/K-39/20.

Material: One almost completely, but poorly preserved specimen (CG/K-42/20).

Description: Specimen large, compressed, involute, elliptical in shape. The whorl section is high oval, subtriagonal, with maximum thickness near the umbilicus. Venter is rounded, without distinct transition towards the flanks, which are almost straight. The umbilicus is small and rounded, with rounded shoulders, covered by sediment. The ornamentation consists of weak, slightly rectiradiate folds. Fine growth lines are also preserved. Suture line partly uncovered, ammonitic. The dimensions of the studied specimen are given in Table 2.

Discussion: Described specimen shows great resemblance to *Flexoptychites studeri*, especially in having slightly rectiradiate folds. However, it has higher H/D ratio and lower U/D ratio than the specimens described in literature. Its poor preservation prevents the description of a new species, and allows only a determination that indicates it is closely related to the species described by Hauer (1857).

Occurrence: *Flexoptychites studeri* (Hauer) is known from the Illyrian of Austria (Hauer, 1857; Beyrich, 1867), Italy (Mojsisovics, 1882; Assereto, 1963), Montenegro (Martelli, 1904), Bosnia and Herzegovina (Toula, 1913), and Greece (Tselepidis, 2007), and tentatively Croatia (Prlj and Mudrenović, 1988), and Hungary (Vörös, 2018).

Genus *Lanceoptychites* Balini, 1998

Type species: *Lanceoptychites velox* Balini, 1998

Lanceoptychites indistinctus (Mojsisovics, 1882)
Figure 11a
1882 *Ptychites indistinctus* Mojsisovics, p. 263, Pl. 67, Figures 1–2.
? 1904 *Ptychites* cf. *indistinctus* – Martelli, p. 130, Pl. 12, Figure 3.
non 1964 *Ptychites indistinctus* – Čelebić, p. 25, Pl. 2, Figure 1.
1998 *Lanceoptychites indistinctus* – Balini, p. 156, text-Figures 10–11, Pl. 3, Figure 1.
2010 *Lanceoptychites indistinctus* – Vörös, p. 16, Pl. 3, Figure 3.

Material: One almost completely preserved specimen (CG/K-15/20).

Description: Specimen large, compressed, involute and elliptical in shape. The whorl section is high, subtriangular, with maximum thickness near the umbilicus. Venter is subacute, becoming high oval later, without distinct transiton towards the flanks, which are slightly convex. The umbilicus is small and rounded, shallow, with rounded shoulders. The ornamentation consists of very weak radial folds which are strongest at mid-flank. Suture line is not uncovered. Dimensions were not measured, because the whorl section is damaged.

Discussion: Although the specimen from the Kovčezi section is damaged in the last whorl part, the subacute venter that becomes rounded and its ornamentation are enough to assigne it *Lanceoptychites indistinctus* without reservation.

Occurrence: *Lanceoptychites indistinctus* (Mojsisovics) has surely been known from the Anisian of Austria (Mojsisovics, 1882; Balini, 1998), and Hungary (Vörös, 2010).

Family Sturiidae Kiparisova, 1958
Genus *Sturia* Mojsisovics, 1882

Type species: *Amaltheus Sansovinii* Mojsisovics, 1869

Sturia sansovinii (Mojsisovics, 1869)
Figure 11b–d
1869 *Amaltheus Sansovinii* Mojsisovics, p. 580, Pl. 18, Figures 1–2.
1882 *Sturia Sansovinii* – Mojsisovics, p. 241, Pl. 49, Figures 5–7, Pl. 50, Figure 1.
1892 *Sturia Sansovinii* – Hauer, p. 283, Pl. 10, Figure 7.
1895a *Sturia Sansovinii* – Diener, p. 61, Pl. 15, Figure 1.
1904 *Sturia Sansovinii* – Martelli, p. 102, Pl. 6, Figure 5.
1913 *Sturia Sansovinii* – Simionescu, p. 338 and 367, Pl. 7, Figure 8.
1913 *Sturia Sansovinii* – De Toni, p. 167, Pl. 13, Figures 1–2.
? 1931 *Sturia Sansovinii* – Živković, p. 91, Pl. 1, Figure 3.
? 1960 *Sturia sansovinii* – Kummel, p. 5, Pl. 1, Figure 2.
1968 *Sturia sansovinii* – Shevyrev, p. 216, Pl. 18, Figure 5.
p 1968 *Sturia sansovinii* – Meço, p. 82, Pl. 7, Figures 4–5 (non Pl. 8, Fig. 3).
1969 *Sturia* sp. – McLearn, p. 8, Pl. 12, Figure 2.
? 1994 *Sturia sansovinii* – Tozer, p. 132, Pl. 46, Figure 11.
1995 *Sturia sansovinii* – Shevyrev, p. 57, Pl. 7, Figures 8–9.
2007 *Sturia sansovinii* – Tselepidis, p. 228, Pl. 32, Figures 2–6.
2023 *Sturia sansovinii* – Vidaković et al., p. 482, Pl. 8, Figure 4.

Material: One partly preserved specimen (CK/K-19/20).

Description: Fragment of a large, extremely involute specimen. The whorl section is elliptical in shape in earlier stages, later becoming lense shaped, with maximum thickness at mid-section. Venter subrounded in earlier stages, becoming subacute later, without a distinct transition towards the flanks, which are convex. The ornamentation consists of characteristic strigation, developed on the entire flank. Suture line ammonitic, very complex, characteristic of the genus. Due to poor and fragmentary preservation, the dimensions could not be measured.

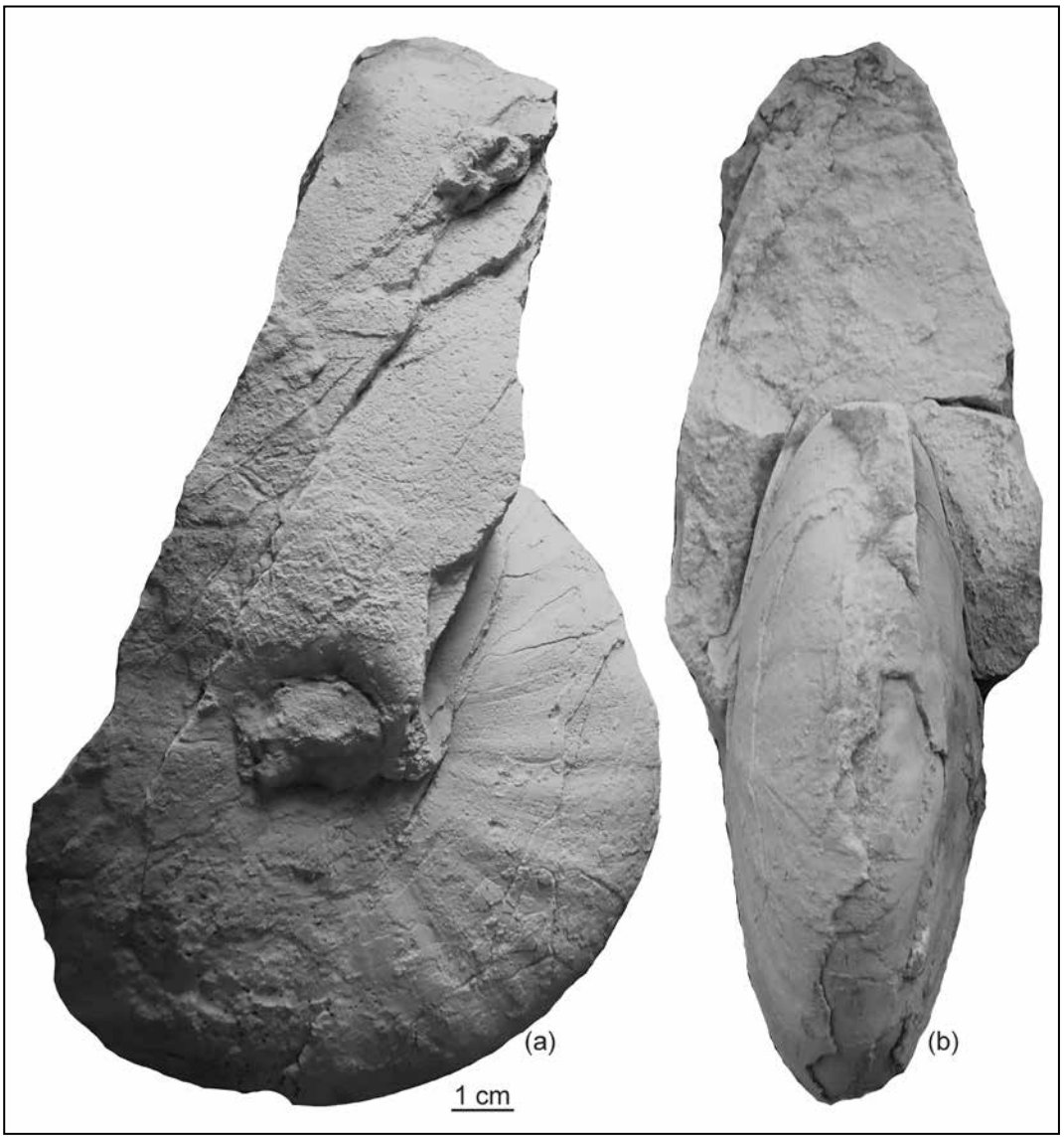

Figure 10: (a–b) *Flexoptychites* aff. *studeri* (Hauer), CG/K-42/20.

Discussion: Even though it is only a fragment of the shell, characteristic whorl section, ornamentation and suture line are well preserved and enough for a definite determination of this specimen as *Sturia sansovinii*.

Occurrence: *Sturia sansovinii* (Mojsisovics) represents a cosmopolitan form during Illyrian, described from Austria (Mojsisovics, 1869, 1882), Bosnia and Herzegovina (Hauer, 1892), Montenegro (Martelli, 1904), Romania (Simionescu, 1913), Italy (De Toni, 1913), Albania (Meço, 1968), Greece (Tselepidis, 2007), Croatia (Vidaković et al., 2023), Russia (Shevyrev, 1968, 1995), India (Diener, 1895a), and Canada (McLearn, 1969).

Sturia sp.
Figure 11e

Material: One fragment of the shell (CG/K-18/20).

Description: Fragment of a large specimen. The whorl section is elliptical, with maximum thickness at mid-section. Venter rounded, without a distinct transition towards the flanks, which are straight. The ornamentation consists of characteristic strigation, developed on the entire flank. Suture line partly preserved, ammonitic. Due to poor and fragmentary preservation, the dimensions could not be measured.

Discussion: Described chacarteristics would indicate that this specimen belongs to *Sturia semiarata* Mojsisovics, especially the shape of the whorl section and straight flanks. However, this species has smooth flanks, with strigation only on venter and near umbilicus. Because of this and due to poor preservation, it can only be determined at a genus level.

Genus *Discoptychites* Diener, 1916

Type species: *Ammonites megalodiscus* Beyrich, 1867

Discoptychites cf. *megalodiscus* (Beyrich, 1867)
Figure 12a–b

1867 *Ammonites megalodiscus* Beyrich, p. 135, Pl. 2.

1882 *Ptychites megalodiscus* – Mojsisovics, p. 253, Pl. 77, Figure 1, Pl. 78, Figures 1–2.

1896 *Ptychites megalodiscus* – Toula, p. 174, Pl. 21, Figure 1.

1907 *Ptychites megalodiscus* – Reis, p. 137, Pl. 3, Figure 2, Pl. 4, Figure 2.

1913 *Ptychites megalodiscus* – Toula, p. 677, Pl. 23, Figure 1.

1936 *Ptychites megalodiscus* – Stefanoff, p. 152, Pl. 2, Figures 7–8.

1979 *Ptychites megalodiscus* – Mihajlović-Pavlović, p. 108, Pl. 3, Figure 4.

1984 *Discoptychites megalodiscus* – Leithner and Krystyn, p. 190, Pl. 2, Figure 1.

2010 *Discoptychites megalodiscus* – Vörös, p. 10, Pl. 4, Figure 3.

2022 *Discoptychites megalodiscus* – Vörös et al., p. 710, Pl. 3, Figure 1.

Material: One poorly preserved fragment (CG/K-5/20).

Description: Fragment of a large, involute specimen. The whorl section is broad, triangular, with maximum thickness near the umbilicus. Venter is acute and the flanks are only slightly convex. Suture line is ammonitic, but eroded and very poorly preserved. Due to poor and fragmentary preservation, the dimensions could not be measured.

Discussion: Specimen from the Kovčezi section shows important characteristics similar to *Discoptychites megalodiscus* (whorl section, venter, dimensions), but since the umbilicus and the suture line are not preserved, it is left in open nomenclature.

Occurrence: *Discoptychites megalodiscus* (Beyrich) is known from the Anisian of Austria (Beyrich, 1867; Mojsisovics, 1882; Leithner and Krystyn, 1984), Turkey (Toula, 1896), Bosnia and Herzegovina (Toula, 1913), Bulgaria (Stefanoff, 1936), Serbia (Mihajlović-Pavlović, 1979) and Hungary (Vörös, 2010; Vörös et al., 2022).

Discoptychites ? *princeps* (Martelli, 1906)
Figure 12c–d

1906 *Ptychites princeps* Martelli, p. 147, Pl. 8, Figure 4, Pl. 9, Figure 1.

non 1988 *Ptychites princeps* – Prlj and Mudrenović, p. 18, Pl. 1, Figure 1.

Material: One completely preserved specimen (CG/K-47/20).

Description: Specimen large, involute and elliptical in shape. The whorl section is broad, subtriangular, with maximum thickness at the umbilical margin. Venter is subacute and the flanks are only convex. The umbilicus is small in comparison to the rest of the shell, rounded, covered by sediment. Umbilical wall is almost perpendicular, with rounded shoulders. The ornamentation consists of very weak radial folds, barely noticable. Suture line is not preserved. The dimensions of the studied specimen are given in Table 2.

Discussion: The species described by Martelli (1906) shows all the important characteristics of the genus *Discoptychites*, i.e. subacute venter, subtriangular whorl section and distinct umbilical wall. Likewise, the suture line shown by the author is well comparable to other representatives of the genus. However, even though the whorl section is subtriangular in shape, it is somewhat lower and is more similar to *Aristoptychites*. Hence, this species is only tentatively assigned to *Discoptychites*.

The specimen shown by Prlj and Mudrenović (1988) has a different whorl section and rounded venter, that is not comparable with the material described by Martelli (1906) or the specimen from the Kovčezi section, and is in the present paper considered not to belong to this species.

Occurrence: *Discoptychites* ? *princeps* (Martelli) has been known only from the Illyrian of Montenegro (Martelli, 1906).

Discoptychites ? sp.
Figure 13a–c

Material. One poorly preserved fragment (CG/K-17/20).

Description. Fragment of a large, involute specimen. The whorl section is broad, subtriangular, with maximum thickness near the umbilicus. Venter is subacute, with gradual transition towards the flanks, which are convex. The suture line is only partialy preserved, damaged by erosion. Due to poor and fragmentary preservation, the dimensions could not be measured.

Remarks. Described specimen has a different whorl section than other representatives of *Discoptychites*. However, partial suture line, even though it is damaged by erosion, is very characteristic and does not differ much from e.g. *Discoptychites megalodiscus* (Beyrich) or *Discoptychites dux* (Giebel). Hence, it has been assigned to *Discoptychites*, but only tentatively.

Superfamily Nathorstitoidea Spath, 1951
Family Proteusitidae Spath, 1951
Genus *Proteusites* Hauer, 1887

Type species: *Proteusites kellneri* Hauer, 1887

Proteusites labiatus (Hauer, 1892)

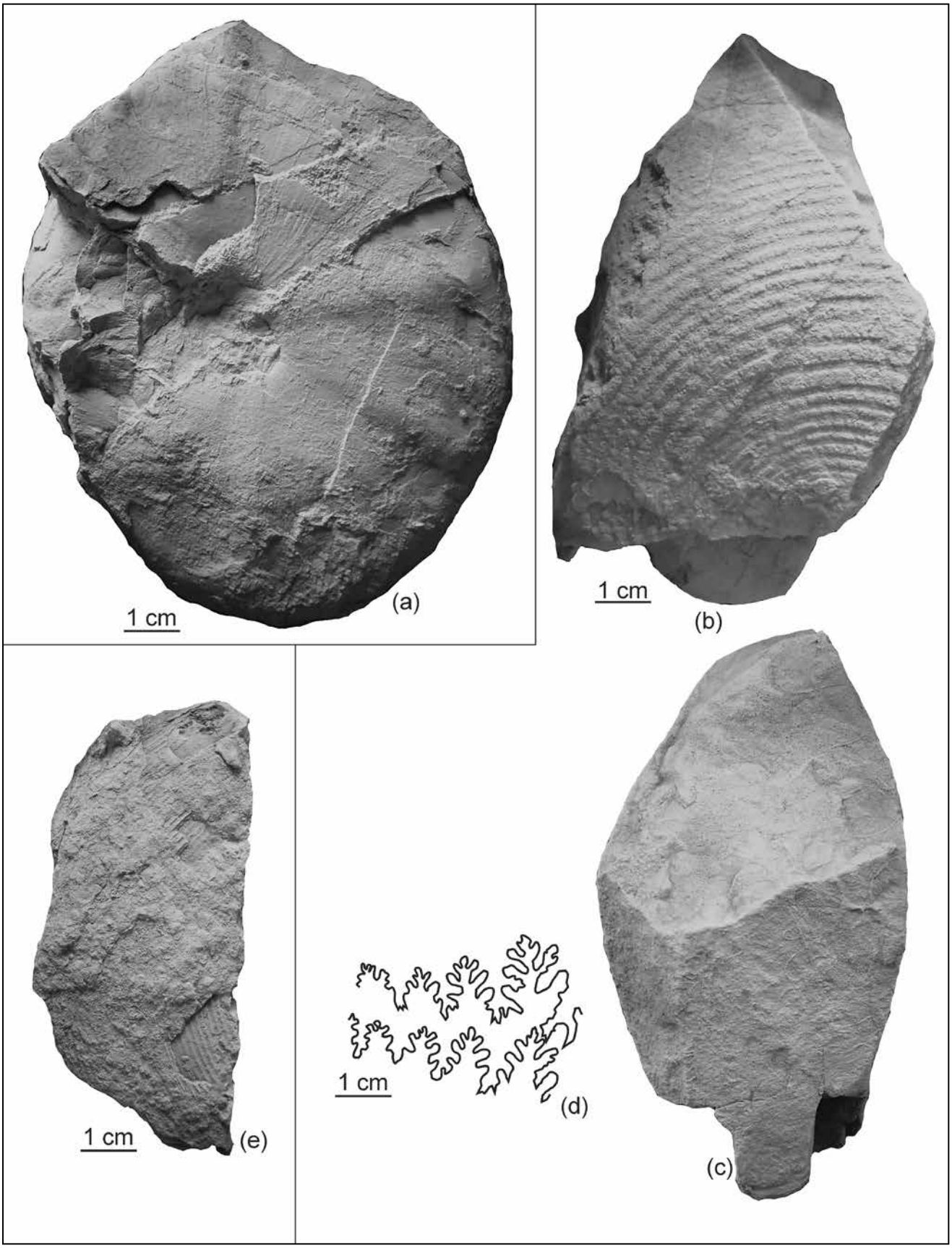

Figure 11: (a) *Lanceoptychites indistinctus* (Mojsisovics), CG/K-15/20; **(b–d)** *Sturia sansovinii* (Mojsisovics), CG/K-19/20; **(e)** *Sturia* sp., CG/K-18/20.

Figure 13d–f
1892 *Ceratites labiatus* Hauer, p. 266, Pl. 5, Figure 1.
? 1907 *Proteites labiatus* – Frech, p. 9, Pl. 2, Figure 4.

Material: One almost completely preserved specimen (CG/K-26/20).

Description: Specimen medium in size, moderately involute, round in shape. The whorl section is subtrapezoidal, with maximum thickness close to the umbilical margin. The venter is rounded, with gradual transition towards the flanks, which are slightly convex. The umbilicus is medium-sized, elliptical, in earlier stages deep with a perpendicular umbilical wall, becoming shallow later, with inclined, rounded wall. The ornamentation consists of very weak radial folds, more pronounced on the umbilicus. Constrictions are also noticable on parts of the specimen. The suture line is ceratitic, very simple, with slightly monophyllic saddles. The dimensions of the studied specimen are given in Table 2.

Discussion: The specimen from the Kovčezi section fits very well with the smaller specimen shown by Hauer (1892, pl. 5, fig. 1d–f). Frech (1907) describes *Proteusites labiatus* from the Anisian of Greece, but shows only its suture line, so this finding can only tentatively be included in the present species.

Occurrence: *Proteusites labiatus* (Hauer) has been known from the Anisian of Bosnia and Herzegovina (Hauer, 1892), and tentatively from Greece (Frech, 1907).

Genus *Tropigastrites* Smith, 1914

Type species: *Tropigastrites trojanus* Smith, 1914

Tropigastrites lahontanus Smith, 1914
Figure 13g–i
1914 *Tropigastrites lahontanus* Smith, p. 28, Pl. 19, Figures 14–15.
1914 *Tropigastrites halli* – Smith, p. 27, Pl. 18, Figures 11–12, Pl. 88, Figures 14–15.
1914 *Tropigastrites rothpletzi* Smith, p. 31, Pl. 19, Figures 1–7 and 22–23, Pl. 87, Figures 24–26.
1914 *Tropigastrites neumayri* – Smith, p. 29, Pl. 18, Figures 15–17.
? 1968 *Tropigastrites* aff. *lahontanus* – Nakazawa and Bando, p. 109, Pl. 5, Figure 7.
1982 *Tropigastrites lahontanus* – Silberling and Nichols, p. 54, Pl. 26, Figures 5–17.
2005 *Tropigastrites lahontanus* – Monnet and Bucher, p. 52, Pl. 30, Figures 11–13.

Material: One almost completely preserved specimen (CG/K-29/20).

Description: Specimen medium in size, moderately evolute, round in shape. The whorl section is subtriangular, with maximum thickness near the umbilicus. The venter is acute, fastigate, with rounded transition towards the flanks which are convex. The umbilicus is large in comparison to the rest of the shell, rounded, deep and with rounded shoulders. The ornamentation consists of strong radial ribs that start at the umbilical margin and disappear at mid-flank. They are stronger on inner whorls. The suture line is ceratitic to subammonitic, damaged by erosion. On one side of the specimen it has rounded saddles and indented lobes, whereas on the other side it is only partly uncovered, showing slightly serrated first lateral saddle and indented lateral lobe. The dimensions of the studied specimen are given in Table 2.

Discussion: Silberling and Nichols (1982) commented on *Tropigastrites lahontanus* and its similarities with *Tropigastrites louderbacki* (Hyatt and Smith), assigning more slender and more evolute forms to *Tropigastrites lahontanus*, reviewing also other species described by Smith (1914). Their opinions were later accepted by Monnet and Bucher (2005). In the present paper, only the specimens that were for sure considered to belong to *Tropigastrites lahontanus* by mentioned authors, are considered to belong to this species. Also, a specimen from East Timor, described as *Tropigastrites* aff. *lahontanus* by Nakazawa and Bando (1968) is tentatively included in this species, with the remark that the form of the figured specimen is similar to Smith's species, but the drawing of the suture line is very different.

The specimen from the Kovčezi section has greater W/D ratio than what is proposed by Silberling and Nichols (1982) for *Tropigastrites lahontanus* (23–30 %), but still less than for *Tropigastrites louderbacki* (35–40 %), and U/D ratio is closer to *Tropigastrites lahontanus*. The shape of the suture line on one side is close to the type specimen of the species, but it may be that it is eroded and damaged. The shape of partly uncovered suture line on the other side of the specimen is very similar to specimens described by Smith (1914) as *Tropigastrites rothpletzi*, which Silberling and Nichols (1982) and Monnet and Bucher (2005) synonymized with *Tropigastrites lahontanus*. However, this suture line is also similar to representatives of *Tropigymnites*, especially the type species *Tropigymnites planorbis* (Hauer). Silberling and Nichols (1982) describe *Tropigastrites lahontanus* as variable species and the specimen from the Kovčezi section fits these variations, but a more thorough revision of the entire genus and comparison with other similar genera, based on larger material, is needed in the future.

Occurrence: *Tropigastrites lahontanus* Smith is until today known from the late Anisian of Nevada (Smith, 1914; Silberling and Nichols, 1982; Monnet and Bucher, 2005). The occurence in the Illyrian of East Timor (Nakazawa and Bando, 1968) should be taken only tentatively.

Superfamily Arcestoidea Mojsisovics, 1875
Family Arcestidae Mojsisovics, 1875

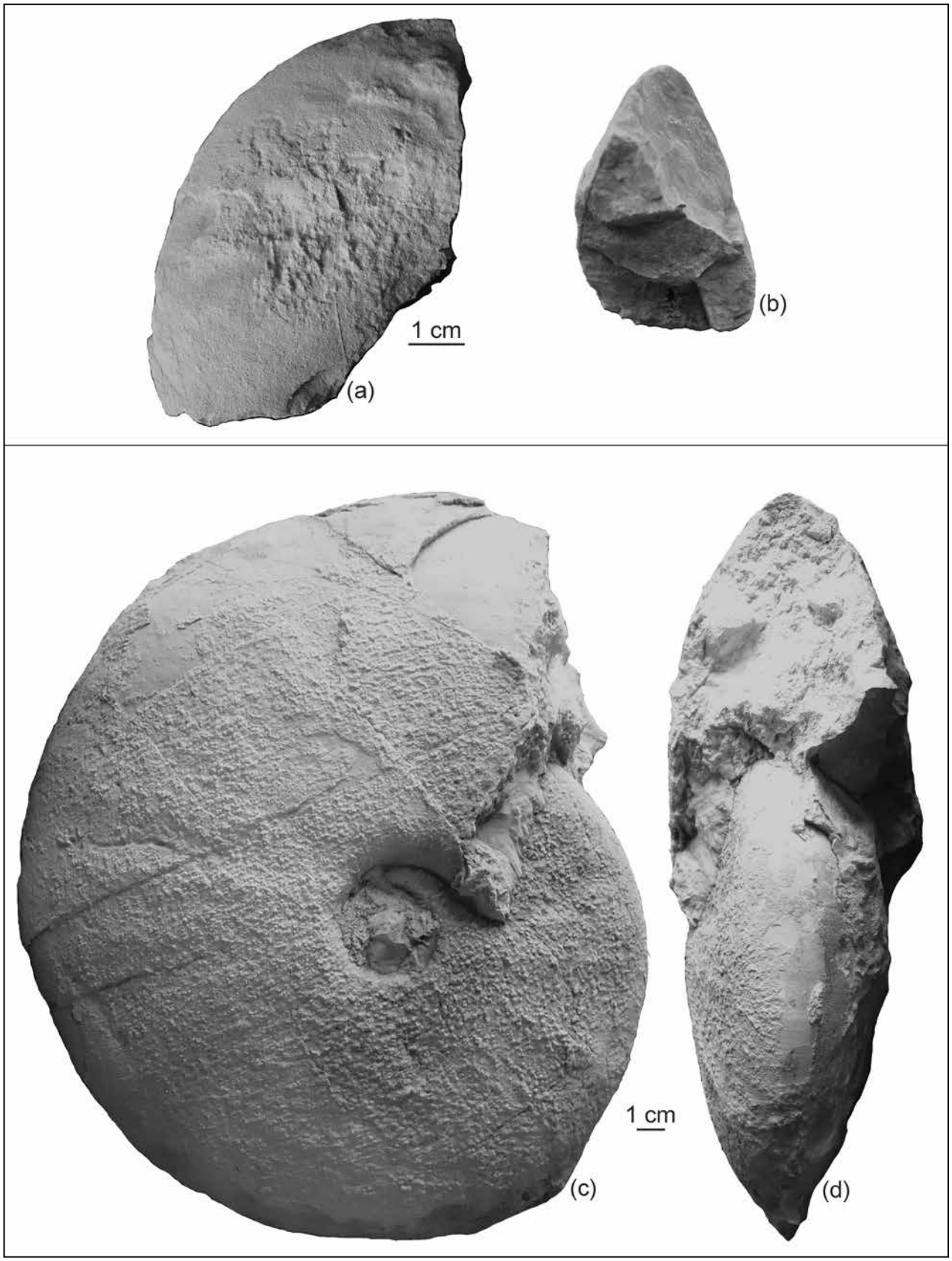

Figure 12: (a–b) *Discoptychites* cf. *megalodiscus* (Beyrich), CG/K-5/20; **(c–d)** *Discoptychites* ? *princeps* (Martelli), CG/K-47/20.

Genus *Arcestes* Suess, 1865

Type species: *Ammonites galeiformis* Hauer, 1850

Arcestes ? sp.
Figure 13j

Material: One very poorly preserved specimen (CG/K-6/20).

Description: Specimens large, involute, globose, round in shape. The whorl section is subtriangular, with maximum thickness near the umbilicus. The venter is rounded and the flanks are straight. The umbilicus is small in comparison to the rest of the shell, rounded. Shell smooth, without ornamentation. The suture line is ammonitic, damaged by erosion, but characteristic for the family. Due to poor preservation, dimensions were not measured.

Discussion: The specimen has general characteristics of the genus *Arcestes*. However, even though most of them could be observed and described, poor preservation prevents certain determination, so the assignement to the genus is also doubtfull.

Genus *Proarcestes* Mojsisovics, 1893

Type species: *Arcestes bramantei* Mojsisovics, 1869

Discussion: The genus *Proarcestes* includes a large number of species, often based on minor differences, as already indicated by Vidaković et al. (2023). The same can be observed also on the material from the Kovčezi section. However, based on published literature, we distinguished several species of the genus, even though their differences can also represent intraspecific variations. Thorough revision of the genus is needed to resolve these problems, but *Proarcestes* specimens from the Kovčezi section do not allow such analysis, and it is not the scope of the present paper.

Proarcestes cf. *escheri* (Mojsisovics, 1875)
Figure 14a
1882 *Arcestes Escheri* – Mojsisovics, p. 162, Pl. 46, Figures 7–9.
1914 *Proarcestes Escheri* – Arthaber, p. 170, Pl. 15, Figure 6.
2007 *Proarcestes Escheri* – Tselepidis, p. 179, Pl. 9, Figure 6.

Material: Three partly and very poorly preserved specimens (CG/K-4/20, CG/K-10/20 and CG/K-11/20).

Description: Specimens medium in size, involute, globose, round in shape. The whorl section is oval, with maximum thickness near the umbilicus. The venter is rounded and the flanks are convex. The umbilicus is small in comparison to the rest of the shell, rounded, deep and with rounded shoulders. Shell smooth, without ornamentation. The suture line is not preserved. Due to poor preservation, dimensions were not measured.

Discussion: Described specimens are very similar in form to the ones mentioned in the synonymy. However, poor preservation and missing suture line, prevent the clear determination, so they are left in open nomenclature.

Occurrence: *Proarcestes escheri* (Mojsisovics) has been known from the Anisian of Austria (Mojsisovics, 1882), the Pelsonian of Turkey (Arthaber, 1914) and the Illyrian of Greece (Tselepidis, 2007).

Proarcestes pannonicus (Mojsisovics, 1870)
Figure 14b–c
1882 *Arcestes pannonicus* – Mojsisovics, p. 159, Pl. 45, Figures 6–7.
1962 *Arcestes* (*Proarcestes*) *pannonicus* var. *termierae* Dufour, p. 847, Pl. 21b, Figure 4.

Material: One poorly preserved specimen (CG/K-12/20).

Description: Specimen small, involute, globose, round in shape. The whorl section is oval, with maximum thickness near the umbilicus. The venter is rounded and the flanks are straight, passing gradually towards the venter. The umbilicus is small in comparison to the rest of the shell, rounded, deep and with rounded shoulders. The ornamentation consists of very weak growth lines. The suture line partly preserved, ammonitic, characteristic of the genus. Due to poor preservation, measured dimensions should be considered only tentatively (Table 2).

Discussion: Even though the specimen is poorly preserved, its general shape and partly uncovered suture line are considered enough to determine it at a species level.

Occurrence: *Proarcestes pannonicus* (Mojsisovics) has been known from the early Ladinian of Hungary (Mojsisovics, 1882) and Greece (Dufour, 1962). The species is also mentioned from the Ladinian of Austria (Alma, 1926), but it is not figured in the publication.

Proarcestes subtridentinus (Mojsisovics, 1882)
Figure 14d–e
1882 *Arcestes subtridentinus* Mojsisovics, p. 156, Pl. 43, Figures 1–3, Pl. 44, Figures 1–3.
1914 *Proarcestes subtridentinus* – Arthaber, p. 172, Pl. 17, Figure 10.

Material: One completely preserved specimen (CG/K-45/20).

Description: Specimen medium in size, involute, globose, elliptical in shape. The whorl section is oval, with

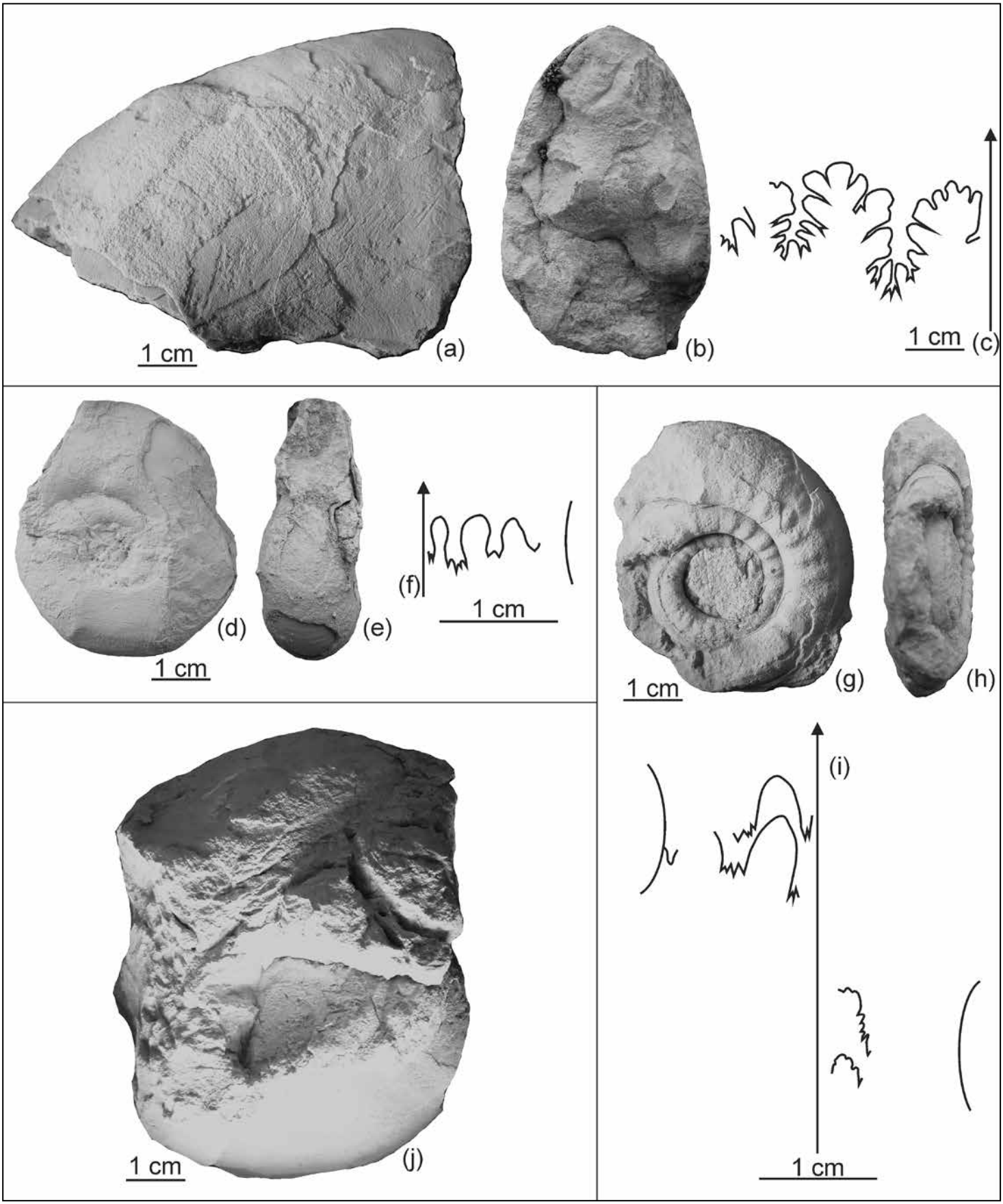

Figure 13: (a–c) *Discoptychites* ? sp., CG/K-17/20; **(d–f)** *Proteusites labiatus* (Hauer), CG/K-26/20; **(g–i)** *Tropigastrites lahontanus* Smith, CG/K-29/20; **(j)** *Arcestes* ? sp., CG/K-6/20.

maximum thickness at mid flank. The venter is rounded and the flanks are convex, passing gradually towards the venter. The umbilicus is small in comparison to the rest of the shell, rounded, covered by sediment. Two marked, rectiradiate constrictions are present. The suture line is not preserved. The dimensions of the studied specimen are given in Table 2.

Discussion: Described specimen is very similar to the species figured by Mojsisovics (1882), especially the ones shown in plate 43. It differs from the ones in plate 44, as well as the one figured by Arthaber (1914) in being more robust and having a different shape of the whorl section, which could be a characteristic of later ontogenetic stage.

Occurrence: *Proarcestes subtridentinus* (Mojsisovics) has until today been known from the Anisian of Turkey (Arthaber, 1914), and the Ladinian of Italy and Hungary (Mojsisovics, 1882). The species is also mentioned from the Anisian of Bosnia and Herzegovina (Hauer, 1892), but it is not figured.

Proarcestes boeckhi (Mojsisovics, 1882)
Figure 15a–d
1882 *Arcestes Boeckhi* Mojsisovics, p. 157, Pl. 44, Figure 4.
1913 *Proarcestes subtridentinus* – De Toni, p. 148, Pl. 12, Figure 1.
1976 *Arcestes boeckhi* – Ljubović, p. 204, Pl. 1, Figure 3.
1976 *Arcestes munsteri* – Ljubović, p. 208, Pl. 3, Figures 1–2.
1988 *Arcestes* (*Proarcestes*) *boeckhi* – Prlj and Mudrenović, p. 17, Pl. 5, Figure 3.

Material: One completely preserved specimen (CG/K-22/20) and one fragment (CG/K-23/20).

Description: Specimen medium to large, involute, globose, round in shape. The whorl section is oval, with maximum thickness near the umbilical margin. The venter is rounded and the flanks are slightly convex, passing gradually towards the venter. The umbilicus is small in comparison to the rest of the shell, rounded, covered by sediment. Broad, marked, rectiradiate constrictions are present. The suture line is not preserved. The dimensions were measured only for the specimen CG/K-22/20 (Tab. 2).

Discussion: Described specimens show great similarities to the species figured by Mojsisovics (1882), especially in the shape of the whorl section, which is different from other representatives of the genus.

The specimens from the Kovčezi section previously described by Ljubović (1976) and determined as *Arcestes boeckhi* and *Arcestes munsteri* are very similar and are regarded as the same species in the present paper. Specimens assigned to *Arcestes munsteri* by the author show the same whorl section present in the specimen CG/K-22/20.

Occurrence: *Proarcestes boeckhi* (Mojsisovics) is known from the Middle Triassic of Italy (Mojsisovics, 1882; De Toni, 1913), Hungary (Mojsisovics, 1882), Montenegro (Ljubović, 1976), and Croatia (Prlj and Mudrenović, 1988).

Family Joannitidae Mojsisovics, 1882
Genus *Joannites* Mojsisovics, 1879

Type species: *Nautilus cymbiformis* Wulfen, 1793

Joannites cf. *tridentinus* (Mojsisovics, 1869)
Figure 15e–g
1882 *Joannites* (?) *tridentinus* – Mojsisovics, p. 168, Pl. 47, Figure 1.
? 1927 *Joannites tridentinus* – Ogilvie Gordon, p. 53, Pl. 6, Figure 15.

Material: One completely, poorly preserved specimen (CG/K-27/20).

Description: Specimen large, involute, compressed, elliptical in shape. The whorl section is high oval, subtriangular, with maximum thickness near the umbilical margin. The venter is rounded and the flanks are almost straight, passing gradually towards the venter. The umbilicus is small in comparison to the rest of the shell, rounded, covered by sediment. Broad, marked, rectiradiate constrictions that are slightly convex are present. The suture line is not preserved. The dimensions of the studied specimen are given in Table 2.

Discussion: Described specimen is very similar to *Joannites tridentinus*, differing only in having more numerous constrictions, whereas other characteristics are practically the same. In regard to the number of constrictions, it is most similar to *Joannites* ? *batyolcus* described by Böckh (1873) and also figured by Mojsisovics (1882). However, constrictions on this species are biconcave, unlike the specimen from Kovčezi. It might be that *Joannites* cf. *tridentinus* from the Kovčezi section represents a new species, but poor preservation and missing suture line prevents such determination.

Joannites tridentinus figured by Ogilvie Gordon (1927) can only tentatively be included in this species, since the figure shown in the publication is very different from the ones shown by Böckh (1873) and Mojsisovics (1882).

Occurrence: *Joannites tridentinus* (Mojsisovics) has until today been known from the Middle Triassic of Italy (Mojsisovics, 1882).

Order Phylloceratida Arkell, 1950
Superfamily Phylloceratoidea Zittel, 1884
Family Palaeophyllitidae Hyatt, 1900
Genus *Leiophyllites* Diener, 1915

Type species: *Monophyllites suessi* Mojsisovics, 1882

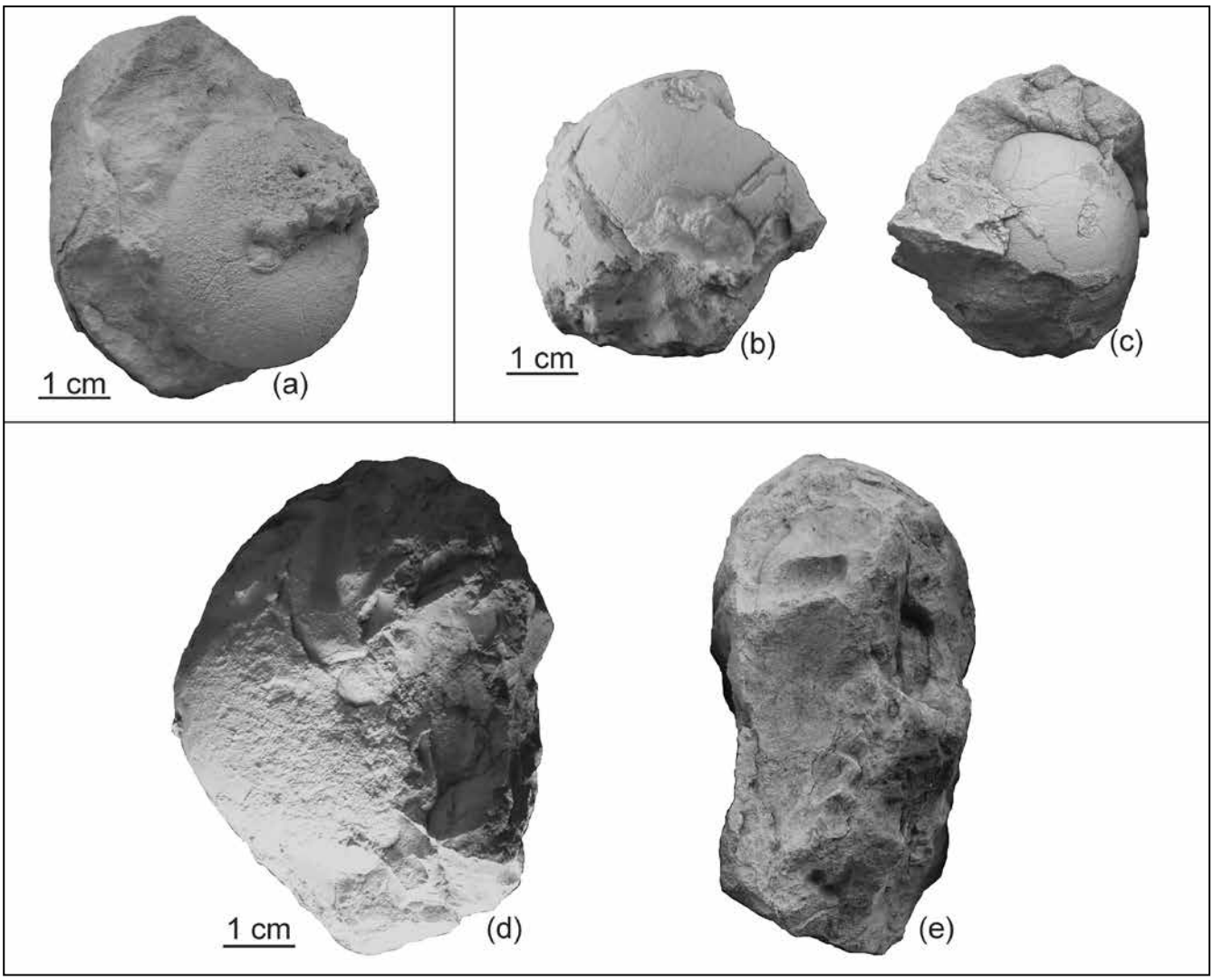

Figure 14: (a) *Proarcestes* cf. *escheri* (Mojsisovics), CG/K-10/20; **(b–c)** *Proarcestes pannonicus* (Mojsisovics), CG/K-12/20; **(d–e)** *Proarcestes subtridentinus* (Mojsisovics), CG/K-45/20.

Leiophyllites cf. *taramellii* (Martelli, 1906)
Figure 15h–i
1906 *Monophyllites taramellii* Martelli, p. 135, Pl. 6, Figures 3–4.
1934 *Leiophyllites taramellii* – Spath, p. 305, Pl. 6, Figure 2.
non 1968 *Leiophyllites taramellii* – Meço, p. 84, Pl. 1, Figure 10.

Material: One almost completely preserved specimen (CG/K-21/20) and one fragment (CG/K-32/20).

Description: Specimens small, evolute, serpenticone, round to elliptical in shape. The whorl section is subrectangular, with maximum thickness at mid-section. The venter is rounded, with rounded ventral shoulders towards the flanks which are convex. The umbilicus is large, taking more than one half of the shell, shallow, with rounded umbilical shoulders. The suture line is monophyllic, very simple. Due to fragmentary preservation, the dimensions were measured only on the specimen CG/K-21/20 (Tab. 2).

Discussion: Specimens from the Kovčezi section are completely evolute, which is similar to the species described by Martelli (1906). However, elliptical shape of one of the specimens, probably due to preservation, as well as fragmentary preservation of the other specimen, prevents an accurate determination, so they are left in open nomenclature.

Occurrence: *Leiophyllites taramellii* (Martelli) is until today known from the upper Anisian of Montenegro (Martelli, 1906), and Bosnia and Herzegovina (Spath, 1934).

Family Ussuritidae Hyatt, 1900
Genus *Monophyllites* Mojsisovics, 1879

Type species: *Ammonites sphaerophyllus* Hauer, 1851

Monophyllites wengensis (Klipstein, 1843)
Figure 16a–e

1843 *Ammonites Wengensis* Klipstein, p. 120, Pl. 6, Figure 11.

1851 *Ammonites sphaerophyllus* Hauer, p. 113, Pl. 1, Figure 11.

1869 *Phylloceras sphaerophyllum* – Mojsisovics, p. 586, Pl. 16, Figure 2.

1872 *Phylloceras boeckhi* – Böckh, p. 158, Pl. 10, Figures 18–19.

1873 *Phylloceras boeckhi* – Böckh, p. 171, Pl. 10, Figures 18–19.

1882 *Monophyllites sphaerophyllus* – Mojsisovics, p. 206, Pl. 79, Figures 1–3.

1882 *Monophyllites wengensis* – Mojsisovics, p. 207, Pl. 78, Figures 10–12.

1899 *Monophyllites wengensis* – Tommasi, p. 33, Pl. 4, Figure 5.

1904 *Monophyllites sphaerophyllus* – Martelli, p. 99, Pl. 8, Figure 3, Pl. 9, Figure 6.

1904 *Monophyllites wengensis* – Martelli, p. 101, Pl. 8, Figure 4.

1906 *Monophyllites wengensis* – Martelli, p. 135, Pl. 8, Figure 1.

1910 *Monophyllites Wengensis* var. *sphaerophylla* – Renz, p. 22, Pl. 1, Figure 4.

1910 *Monophyllites Wengensis* – Renz, p. 46, Pl. 3, Figures 1–2.

1913 *Monophyllites Wengensis* var. *sphaerophylla* – Renz, p. 561, Figure 7.

p 1914 *Monophyllites billingsianus* – Smith, p. 48, Pl. 22, Figures 1–5 (non Pl. 5, Figs. 3–4, Pl. 48, Figs. 8–9).

1927 *Monophyllites wengensis* – Ogilvie-Gordon, p. 53, Pl. 6, Figure 16.

1931 *Monophyllites wengensis* – Živković, p. 95, Pl. 7, Figure 1.

1934 *Monophyllites wengensis* – Spath, p. 288, Pl. 17, Figure 4.

1938 *Monophyllites sphaerophyllus* – Simić, p. 217, Pl. 18, Figure 3.

1953 *Monophyllites* (*Leiophyllites*) *sphaerophyllus* – Petković and Miletić, p. 9, Pl. 1, Figure 4.

1963 *Monophyllites sphaerophyllus* – Assereto, p. 87, Pl. 10, Figure 3, Pl. 11, Figure 3.

? 1964 *Monophyllites sphaerophyllus* – Čelebić, p. 29, Pl. 4, Figure 3.

1968 *Monophyllites sphaerophyllus* – Meço, p. 91, Pl. 5, Figures 5–6, Pl. 6, Figures 1–3, Pl. 7, Figures 1–3.

1976 *Leiophyllites* (*Monophyllites*) *agenor* – Ljubović, p. 203, Pl. 1, Figure 2.

1988 *Monophyllites sphaerophyllus* – Prlj and Mudrenović, p. 22, Pl. 1, Figure 2.

1995 *Monophyllites wengensis* – Shevyrev, p. 138, Pl. 24, Figure 2.

2007 *Monophyllites sphaerophyllus* – Tselepidis, p. 253, Pl. 39, Figures 11–12, Pl. 40, Figures 1–6.

2007 *Monophyllites wengensis* – Tselepidis, p. 255, Pl. 40, Figures 7–11, Pl. 41, Figure 3.

2010 *Monophyllites wengensis* – Vörös, p. 18, Pl. 4, Figure 6.

Material: Two incomplete but well preserved specimens (CG/K-2/20 and CG/K-25/20) and two fragments (CG/K-3/20 and CG/K-13/20).

Description: Specimens medium to large in size, evolute, round to elliptical in shape. The whorl section is subtrapezoidal in shape, with maximum thickness at the umbilical margin. The venter is rounded, arched and the flanks are straight, passing gradually towards the venter. The umbilicus is large, taking approximately one third of the shell, deep, with perpendicular umbilical wall and rounded shoulders. Ornamentation consists of fine, densely spaced and projected growth lines. The suture line is monophyllic, very complex, characteristic for the species. Due to fragmentary preservation of the specimens, the dimensions cannot be measured.

Discussion: Vörös (2010) already indicated that *Monophyllites sphaerophyllus* is a junior synonym of *Monophyllites wengensis*, which represents a nomenclatorial problem, since *M. spaerophyllus* is a type species of the genus. However, if the rule of priority is to be followed, then *M. spaerophyllus* should stay the type species of the genus. Similar to this, *Pseudosageceras* sp. indet. (Diener, 1895b) is still a type species for the Early Triassic *Pseudosageceras*, even though it has subsequently been synonymized with *Pseudosageceras multilobatum*.

Shevyrev (1995) correctly synonymized part of the material described as *Monophyllites billingsianus* by Smith (1914, pl. 22, figs. 1–5) with *Monophyllites wengensis*, since *M. billingsianus* represents a more involute species.

Occurrence: *Monophyllites wengensis* (Klipstein) represents a cosmopolitan form described from Pelsonian, Illyrian and Ladinian of Austria, Hungary, Italy, Montenegro, Greece, Serbia, Bosnia and Herzegovina, Albania, Croatia, Nevada, among others (Shevyrev, 1995 for an overview; Martelli, 1904, 1906, Simić, 1938, Petković and Miletić, 1953, and Ljubović, 1976 for the localities in Montenegro).

5. Conclusion

Results of detailed palaeontological and biostratigraphic investigations of collected ammonoids of the Kovčezi section in Montenegro are:

- Three different Anisian ammonoid assemblages were recognized, one of late Pelsonian age from the mass-transport deposits of the late Illyrian Komarani Formation, and two of Illyrian age from cephalopod beds of the Bulog Formation limestones. The ammonoid assemblages belong to the late Illyrian Aplo-

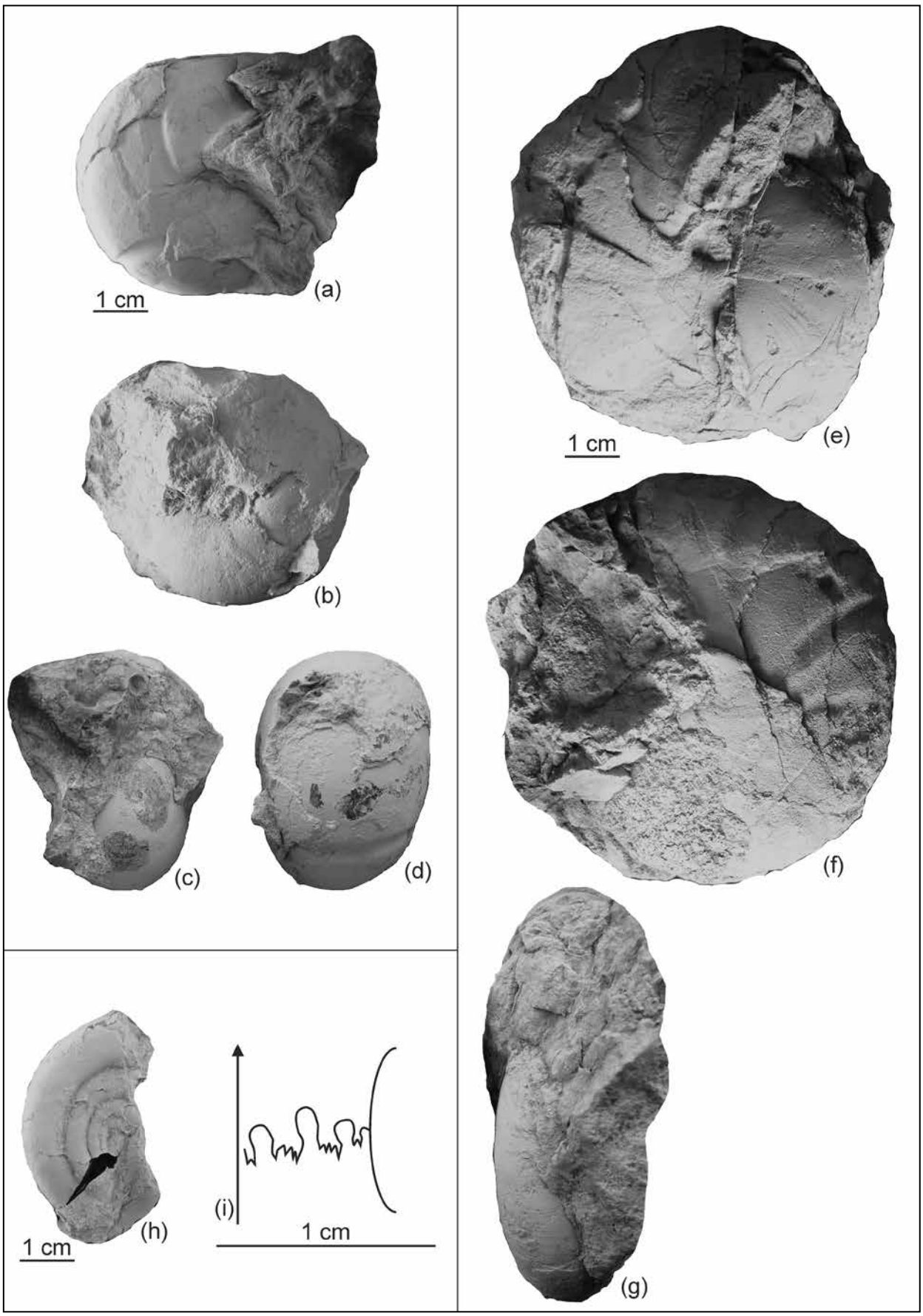

Figure 15: (a–d) *Proarcestes boeckhi* (Mojsisovics), CG/K-22/20; **(e–g)** *Joannites* cf. *tridentinus* (Mojsisovics), CG/K-27/20; **(h–i)** *Leiophyllites* cf. *taramellii* (Martelli), CG/K-21/20.

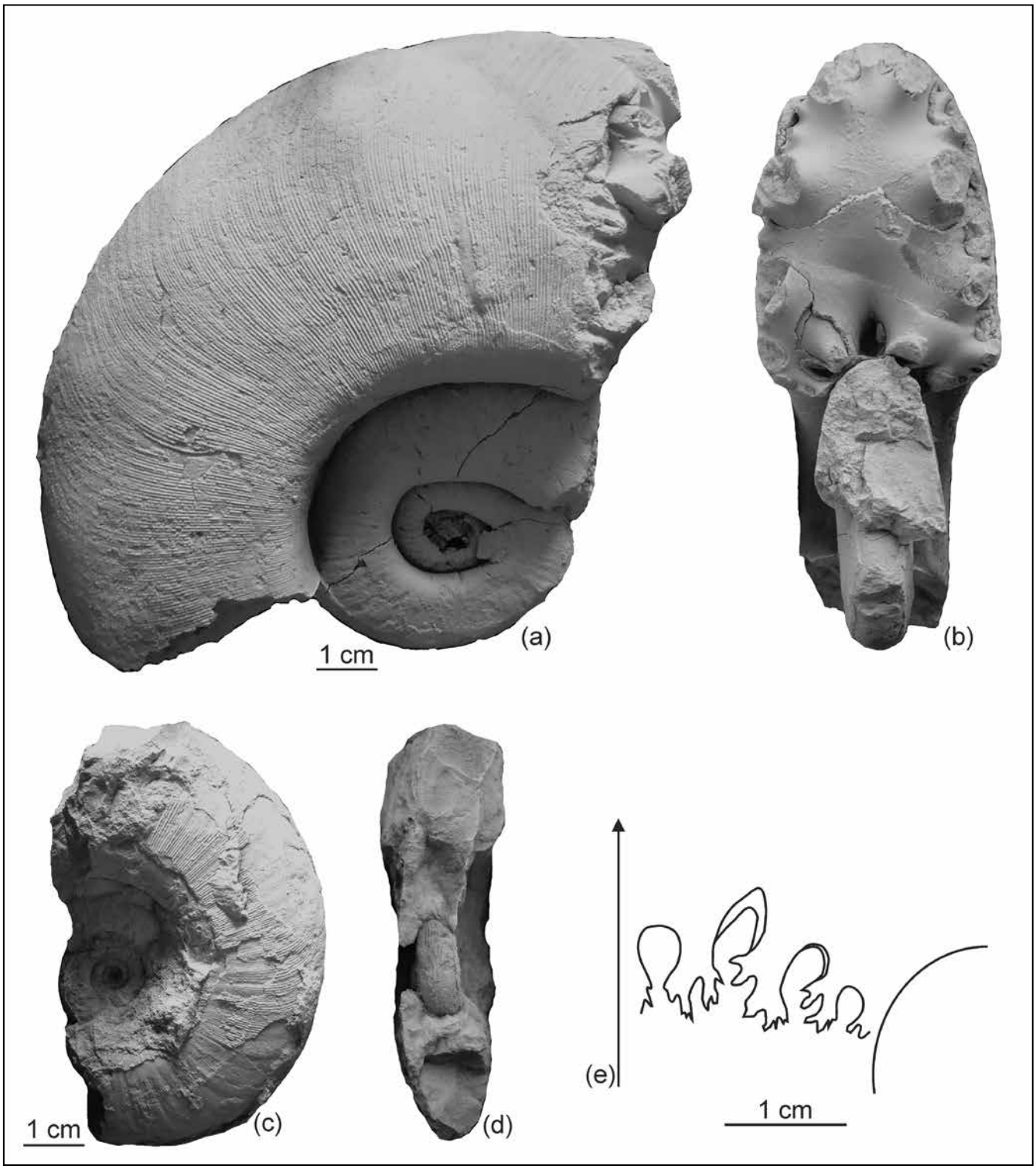

Figure 16: *Monophyllites wengensis* (Klipstein) **(a–b)** CG/K-2/20; **(c–e)** CG/K-25/20.

coceras avisianum Zone and the Nevadites secedensis Zone, respectively.

- *Tropigastrites lahontanus* Smith and *Ptychites rugifer* (Oppel) have for the first time been documented in the Western Tethyan Realm, and *Megaphyllites obolus* Mojsisovics, *Parakellnerites rothpletzi* (Salomon), *Apleuroceras decrescens* (Hauer), *Proteusites labiatus* (Hauer), *Proarcestes pannonicus* (Mojsisovics) and *Proarcestes subtridentinus* (Mojsisovics) are for the first time described from the Bulog Formation of Montenegro. *Aristoptychites* sp. represents only the second finding of this genus in the Western Tethyan Realm, previously known only from Greece.

The results point out that for several relatively unex-

plored species further detailed studies are needed from the rare late Illyrian ammonoid-bearing sections in the Western Tethys Realm. The results of this study clearly demonstrate that even after 150 years of intense research still several open questions remain on the way to a stable correlation of ammonoid zones worldwide. The new findings of ammonoid species not known from the Western Tethys Realm show the importance to restudy also known sections with ammonoids and to investigate new faunas from so far unknown or only incomplete documented localities.

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