The Late Devonian and Early Carboniferous ammonoids (Cephalopoda) from Milivojevića Kamenjar, Družetić (NW Serbia) and their stratigraphy

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The Late Devonian to Early Carboniferous olistolith near Družetić (north-western Serbia) contains the most species rich occurrence of Palaeozoic ammonoids known from the Balkan Peninsula. Four main faunal complexes are recorded, (1) a late Famennian assemblage with few clymeniids, (2) a species-poor indifferent Tournaisian assemblage, (3) two rather diverse early Late Viséan assemblages with about 15 species and (4) two latest Viséan/Serpukhovian assemblages with more than 20 species. The new genus Druzeticia and the following new species are described from the third faunal complex: Beyrichoceras Jadarense, Ubites Divnae, Ubites Novaki, Entogonites Serbicus, Druzeticia Decens and Prolecanites Stevanovici. The latest Viséan/Serpukhovian assemblages show very close relationships with the South Urals and both regions most probably belong to the same palaeogeographical realm. • Key words: Ammonoidea, Late Devonian, Early Carboniferous, Serbia, Družetić, stratigraphy.


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Records of Palaeozoic ammonoids from the Balkan Peninsula are very rare, and they are usually limited to a few specimens and species-poor assemblages. A Late Viséan ammonoid assemblage found north of Prača near Sarajevo (Bosnia and Herzegovina) by the miner Grimmer and described by Kittl (1904a, b) was for a long time the most diverse assemblage known from the entire area. Preservation of this material, however, is rather poor and does not allow for a very detailed analysis (Kostić-Podgorska 1958). This assemblage was remarkable because of the occurrence of the peculiar species Entogonites grimmeri, an ammonoid with tetragonally coiled inner whorls.

A second Palaeozoic ammonoid fauna was discovered by Renz (1910) near Attika (Greece), but this only contained the single species Pericleites Atticus. The stratigraphical age of this species is still unclear; Ruzhencev & Bogoslovskaya (1971) interpreted this as a Namurian species and described specimens from the South Urals, which they attributed to the same genus.

The discovery of a considerably diverse assemblage near Družetić (north-western Serbia; Fig. 1) in the late 1950’s replaced Prača as the most diverse ammonoid assemblage of the Balkan Peninsula (Stevanović & Kullmann 1962) and has occupied this position for the past fifty years (Korn et al. 2010a, b). After the original description, a complete revision of the ammonoid descriptions had not been achieved and this will now be introduced here.

The revision presented here is mainly based on new collections, which leads to a significant widening of the spectrum of ammonoid species from this section. The largely in-situ collected material also allows for a correlation of the succession of ammonoid species with the conodont stratigraphy.

Historical review

The study of Carboniferous ammonoids from Serbia begins with the discovery of the Milivojevića Kamenjar section in the village Družetić in 1956 by Petar Stevanović. At that time, the Carboniferous sedimentary succession within the area was poorly known, and hence the olistolithic nature of the limestone occurrences of Družetić has not been discovered. In a first report, Stevanović (1962) described the ammonoid-bearing beds as cephalopod limestone. At the same time, Kullmann studied the ammonoid faunas,

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which were presented in the context of stratigraphy and palaeogeography in a comprehensive monographic article (Stevanović & Kullmann 1962). In their study, two ammonoid layers with moderately rich assemblages were separated:

From the “lower layer” (which is in fact the stratigraphically younger horizon and belongs in the latest Viséan to Serpukhovian, see below), Stevanović & Kullmann (1962) listed the following species: “Prionoceras (Irinoceras) stevanoviCi Kullmann, 1962”, “Rhymnoceras gracilentum Ruzhencev, 1958”, “Proshumardites (Proshumardites) serbicus Kullmann, 1962”, “Proshumardites (Trigonoshumardites) wocklumerioides Kullmann, 1962”, “Pronorites uralensis uralensis Karpinsky, 1889”.

From the “upper layer” (which is in fact the stratigraphically older, early Late Viséan horizon), the authors listed the following species: “Cravenoceras cowlingense Bisat, 1932”, “Gastrioceras (Branneroceras) branneri Smith, 1896”.

Additionally, five species were reported to occur in both layers: “Cravenoceras arcticum subinvolutum Librovitch, 1938”, “Nuculoceras crenistriatoide Kullmann, 1962”, “Gastrioceras (Branneroceratoides) tetragonum Kullmann, 1962”, “Eoasianites europaicus Kullmann, 1962”, “Metacanites chancharensis (Ruzhencev, 1948)”.

Stevanović & Kullmann (1962) postulated two opinions about the stratigraphical age of these assemblages:

1) Both layers have the same stratigraphical age.
2) Both layers have a stratigraphical position in the “upper Eumorphoceras Stufe”.

Already Ruzhencev & Bogoslovskaya (1971, p. 37) commented on the taxonomic and stratigraphic characteristics of the assemblages from Družetić and criticised several of the generic identifications, such as the attribution of specimens to Gastrioceras rather than to Entogonites. They attributed the aforementioned species to the genera Dombarocanites, Uralopronorites, Irinoceras, Entogonites, Pericleites, Cravenoceras, Glaphyrrites, Nuculoceras and Rhymnoceras.

As will be shown below, both hypotheses by Stevanović & Kullmann (1962) will be refuted. The reasons for the misinterpretations, on which the two hypotheses are founded, may be explained by the following:

1) Stevanović & Kullmann (1962) obviously did not analyse the lithology of the limestone succession in great detail. Analysis of polished slabs or thin sections would have provided them with evidence (such as geopetal fabrics) for an inverted succession.

2) At the time of their studies, little was known about olistostromes; therefore Stevanović & Kullmann (1962) obviously did not consider the possibility that the occurrence at Milivojevića Kamenjar represents a reworked limestone block with inverted stratigraphic succession. However, doubts on the postulation that the limestone at this outcrop is entirely of Namurian age were, at that time, already put forward by Ivan Filipović (personal communication), who found Late Devonian microfossils (styliolinids, ostracods) in nodular limestone horizons at the top of the outcrop. This argument was dismissed by Stevanović & Kullmann (1962, footnotes on pp. 50 and 66), who insisted on a Namurian age for the entire outcrop on the basis of evidence from the ammonoid faunas.

3) The putative occurrence of some of the species [e.g., “Gastrioceras (Branneroceratoides) tetragonum”] in both layers (Stevanović & Kullmann 1962, pp. 48, 65) led those authors to assume that there is no difference in age between the two horizons. However, this statement can easily be refuted. – One of the results of the new investigation of the Milivojevića Kamenjar site (e.g., Korn et al. 2010a, b) and its ammonoids is that not a single species was found to occur in both horizons. The significant stratigraphic difference between the two assemblages makes it very unlikely that there are species, which are present in both of them. Mixing of samples in the outcrop may have caused an erroneous record of some of the species in the “lower horizon”. The species putatively occurring in both horizons were possibly the reason why J. Kullmann (in Stevanović & Kullmann 1962, p. 65) concluded, “the difference between the two beds is insignificant according to their faunas” (“… Unterschied zwischen diesen beiden Schichten infaunistischer Hinsicht unbedeutend.”). The species putatively occurring in both horizons were possibly the reason why J. Kullmann (in Stevanović & Kullmann 1962, p. 65) concluded, “the difference between the two beds is insignificant according to their faunas” (“… Unterschied zwischen diesen beiden Schichten infaunistischer Hinsicht unbedeutend.”).

4) The palaeogeographical distribution of Carboniferous ammonoid faunas was not well known in the early 1960’s. – The species list of Stevanović & Kullmann (1962) shows that names of species from very distant regions have been used (Korn et al. 2010b, 2012), the South Urals (3 species), Novaya Zemlya (1), Northern England.
(1) and the American Midcontinent (1). A further six species have been newly described. On the basis of this, Stevanović & Kullmann (1962, p. 86) concluded that the closest relationships are noticeable with the Urals. However, they also stated that the fauna from Družetić has an intermediate position between the “epicontinental and geosynclinal facies” of the Carboniferous occurrences in Europe.

5) The species-rich Viséan-Serpukhovian ammonoid assemblages from the South Urals were only fragmentarily described until the early 1960’s (e.g., Ruzhencev 1947, 1949, 1956; Librovitch 1957; Ruzhencev 1958). Only with the voluminous monographs by Ruzhencev & Bogoslovskaya (1971, 1978) did it become much easier to interpret less well-preserved material like the specimens from Družetić. – Several of the stratigraphically younger species newly described by Stevanović & Kullmann (1962) from Družetić were already known from the South Urals, but this was not fully recognised by the authors.

The rock succession of the Milivojevića Kamenjar section

The geological setting of the Milivojevića Kamenjar site has been described in detail by Korn et al. (2010a, b). At Milivojevića Kamenjar in Družetić, approximately 15 metres of sedimentary rocks, nearly exclusively carbonates, are exposed. The inverted bedding planes are inclined with 10 to 25° in a south-western direction. The succession can be subdivided into five units, in descending order (i.e. stratigraphically from older to younger) in the outcrop (Fig. 2):

Unit 1. Dark-grey, nodular flaser limestone (> 2 m) with high shale content, only poorly exposed. The limestone nodules and their macrofossil content are strongly deformed.

Unit 2. Grey, bedded and partly nodular limestone with minor shale content (0.95 m).

Unit 3. Dark-grey or light-grey, partly coarse-grained bedded limestone with high fossil content (0.65 m). Two fossil samples (DRZ1 and DRZ2, separated by a distance of about 20 cm) were taken from this “upper” (i.e., stratigraphically older) portion of succession. Particularly the stratigraphically younger sample DRZ1 is a coquina with a mass occurrence of ammonoids, but most of the specimens larger than 10 mm are crushed. From this unit, a number of ammonoid samples were obtained. The occurrence of macrofossils is very patchy; in some cases coquinas packed with ammonoids occur in more spartitic portions at several positions of the section.

Unit 4. Light-grey, thick-bedded or almost non-bedded non-fossiliferous micritic limestone (8.6 m).

Unit 5. Grey, well-bedded micritic nodular limestone (2.80 m are currently exposed) with minor shale content. From this unit, a number of ammonoid samples were obtained. The occurrence of macrofossils is very patchy; in some cases coquinas packed with ammonoids occur in more spartitic portions at several positions of the section.

Figure 2. Milivojevića Kamenjar section (from Korn et al. 2010b).

Material

More than 800 newly collected specimens, stored in the Cephalopod collection of the Museum für Naturkunde, Berlin (MB.C. prefix) are available for study besides about 120 ammonoid specimens stored in the Natural History Museum, Belgrade (BEO600-551.73:592-prefix). This material comes from four main intervals of the section:

Unit 1. – The nodular or flaser limestone of this unit is strongly affected by lateral and vertical tectonic deformation, and hence the fossil content is poorly preserved. Only some of the fragmentarily preserved ammonoids can be assigned to distinct genera and species. This material, which consists of 14 specimens, has a latest Famennian (Late Devonian) age. The assemblage can be assigned to the early Wocklumeria Stufe:

<table>
<thead>
<tr>
<th>Family</th>
<th>Genus</th>
<th>Species</th>
<th>Quantity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Linguaclymenia</td>
<td>similis</td>
<td>(Münster, 1839)</td>
<td>1 specimen</td>
</tr>
<tr>
<td>Linguaclymenia</td>
<td>sp.</td>
<td></td>
<td>1 specimen</td>
</tr>
</tbody>
</table>
cosmoceimeni indet. 6 specimens
Cymaclymenia sp. 5 specimens
Miminitoceras sp. 1 specimen

Unit 2. – Few ammonoids of unspecified Tournaisian age were collected from a single horizon at the top of the unit:

Imitoceras sp. 2 specimens

Unit 3. – Ammonoids were collected from two horizons, which differ only slightly in the species composition of the assemblages but markedly in the numbers of the individual specimens per species.

(a) The stratigraphically older horizon is a dark-grey fossil-rich micrite, in which concentrations of fossils, particularly of ammonoids, occur sporadically. The fossils are well preserved but often fragmented caused by sedimentary transport. Most of the 310 specimens from this horizon are very small (less than 10 mm), but some specimens possess sizes of up to 80 mm. All are laterally deformed; deformation affected particularly the body chambers of the specimens. In specimens from this horizon, shell ornament is often very well preserved. The following species were newly collected from this horizon, which can clearly be attributed to the Entogonites Genus zone (Fig. 3):

Beyrichoceratoidea sp. 8 specimens
Bollandites sp. 1 specimen
Bollandocar sp. 1 specimen
Beyrichoceras jurdeense sp. nov. 19 specimens
Calgyirtoceras sp. 3 specimens
Ubites filipovici Korn & Sudar, 2010 119 specimens
Ubites diviae sp. nov. 19 specimens
Ubites novaki sp. nov. 1 specimen
Entogonites grimmeri (Kittl, 1904) 155 specimens
Entogonites tetragonus (Kullmann, 1962) 155 specimens
Entogonites praehelikous (Korn & Sudar, 2010) 6 specimens
Nomismoceras sp. 3 specimens
Druzeticia decens gen. et sp. nov. 81 specimens
Nomismoceras sp. 1 specimen
Prolecanites stenovici sp. nov. 70 specimens
Pronorites sp. 1 specimen
indet. juvenile specimens 19 specimens

(b) The stratigraphically younger of the two horizons is a light-grey sparite of about 30 cm thickness. This horizon is very rich in fossils, particularly in ammonoids, of which more than 350 specimens are available. Most of the specimens are very small (juvenile and adult specimens of Entogonites and juveniles of other genera). Details of the shell ornament are rarely preserved in this coarse-grained limestone, but deformation of the specimens is not significant. Most of the material attributed to the “upper horizon” by Stevanovic & Kullmann (1962) derives from this horizon. The following species were newly collected from this rock unit, which can clearly be attributed to the Entogonites Genus zone:

Beyrichoceratoidea sp. 1 specimen
Bollandites sp. 2 specimens
Beyrichoceras crenistriaeide (Kullmann, 1962) 12 specimens
Ubites filipovici Korn & Sudar, 2010 6 specimens
Ubites diviae sp. nov. 2 specimens
Ubites novaki sp. nov. 12 specimens
Entogonites grimmeri (Kittl, 1904) 44 specimens
Entogonites serbicous sp. nov. 8 specimens
Entogonites tetragonus (Kullmann, 1962) 155 specimens
Entogonites sp. 11 specimens
Nomismoceras sp. 6 specimens
Druzeticia decens gen. et sp. nov. 2 specimens
Prolecanites stenovici sp. nov. 70 specimens
Pronorites sp. 1 specimen
indet. juvenile specimens 19 specimens

Unit 5. – Ammonoids occur sporadically within an interval of about three metres thickness, but it is very difficult to obtain in-situ samples with high fossil content. Therefore, many float blocks with the same lithology were examined to acquire a larger amount of ammonoid specimens. The fossils occur usually in micritic, slightly nodular grey limestone that contains numerous limonitic veins, pressure solution surfaces. Most of the ammonoid specimens are strongly deformed or sheared and this deformation affected the body chambers of the specimens in particular. The phragmocones are usually filled with coarse calcite cement, which has often destroyed all inner structures such as shell walls and septa. Shell surfaces are often poorly preserved because of recrystallization and pressure solution, and hence species determination is difficult in many of these specimens. It is apparent that two complexes are represented (Fig. 3):

(a) The stratigraphically older complex is characterised by light grey to medium grey, partly spartic limestone with numerous limonitic and sideritic veins as well as pressure solution surfaces. From this complex, 105 newly collected specimens (in-situ and float collections) are available for study. The assemblage has a latest Viséan to early
Serpukhovian age. Most of the fossil content is strongly deformed; the assemblage is represented by the following species from new collections:

- **Irinoceras arcuatum** Ruzhencev, 1947 7 specimens
- **Hypergoniatites** sp. 1 specimen
- **Dombarites falcatooides** Ruzhencev & Bogoslovskaya, 1970 17 specimens
- **Dombarites liratus** Ruzhencev & Bogoslovskaya, 1971 6 specimens
- **Platygoniatites molaris** Ruzhencev, 1956 5 specimens
- **Platygoniatites omnilitratus** Ruzhencev & Bogoslovskaya, 1971 6 specimens
- **Cravenoceras** sp. 1 specimen
- **Lyrogoniatites tener** Ruzhencev & Bogoslovskaya, 1971 2 specimens
- **Lyrogoniatites** sp. 1 specimen
- **Pachylyroceras** sp. 3 specimens
- **Uralyroceras** sp. 1 specimen
- **Neoglyphioceras baccans** Ruzhencev & Bogoslovskaya, 1971 26 specimens
- **Neoglyphioceras litvinovichae** Ruzhencev & Bogoslovskaya, 1971 1 specimen
- **Neoglyphioceras** sp. 5 specimens
- **Lasitanites concavus** Ruzhencev & Bogoslovskaya, 1971 4 specimens
- **Ophilyroceras tersum** Ruzhencev & Bogoslovskaya, 1971 4 specimens
- **Dombarocanites catillus** Ruzhencev & Bogoslovskaya, 1971 6 specimens
- **Praedaraelites aktubensis** Ruzhencev & Bogoslovskaya, 1971 4 specimens
- **Uralopronorites mirus** Librovitch, 1949 3 specimens

(b) The stratigraphically younger complex is composed of dark grey, dense limestone without iron veins. Material from this unit is mainly available from the collection of the Natural History Museum, Belgrade (Stevanović & Kullmann 1962); almost no new material has become available. The assemblage has a late Serpukhovian age. It contains the following ammonoid assemblage from new collections:

- **Proshumardites uralicus** Librovitch, 1941 1 specimen
- **Rhymnoceras gracilentum** Ruzhencev, 1958 1 specimen

**Systematic palaeontology**

**Genus Linguaclymenia** Korn & Price, 1987

**Linguaclymenia similis** (Münster, 1839)

*Figure 4A*

- **Material.** – One deformed specimen.

- **Description.** – MB.C.25587 is a specimen of about 12 mm conch diameter (Fig. 4A). It is a laterally deformed, sub-evolute conch (uw/dm ~ 0.42) with rounded flanks and a ventrolateral groove at the end of growth. It displays coarse biconvex growth lines with a high ventrolateral projection typical for the species.

- **Remarks.** – This single specimen is the only clymeniid from Družetić and probably the first from the entire Balkan Peninsula that can be determined to the species level. There are some other specimens, but because of their poor preservation they can only be determined as either Linguaclymenia sp. or Kosmoclymeniidae indet.
Suborder Cyrtoclymeniina Korn, 2002
Superfamily Cyrtoclymeniaceae Hyatt, 1884
Family Cymaclymeniidae Hyatt, 1884
Subfamily Cymaclymeniinae Hyatt, 1884

Genus *Cymaclymenia* Hyatt, 1884

*Cymaclymenia* sp.
Figure 4B, C

**Material.** – Five fragmentary specimens, which because of their poor preservation can not be attributed to a distinct species.

**Remarks.** – Specimens MB.C.25586 and MB.C.25592.1 are fragments of specimens with about 15 and 20 mm conch diameter, which cannot be determined to the species level (Fig. 4B, C). According to the rather coarse growth lines and the lack of umbilical riblets it is close to *C. striata* (Münster). Specimen MB.C.25592.1 is an internal mould that shows rather strong protracting constrictions on the flank; in this character it resembles *C. semistriata* (Münster).

Order Goniatitida Hyatt, 1884
Suborder Tornoceratina Wedekind, 1914
Superfamily Prionocerataceae Hyatt, 1884
Family Prionoceratidae Hyatt, 1884
Subfamily Imitoceratinae Ruzhencev, 1950

Genus *Imitoceras* Schindewolf, 1923

*Imitoceras* sp.
Figure 5

**Material.** – Two specimens with about 30 mm conch diameter.

**Description.** – The poorly preserved specimen MB.C.25595.1 is slightly distorted and has 30 mm conch diameter. It is thickly discoidal (ww/dm ~ 0.55) with a closed umbilicus and a whorl expansion rate of 2.05. The suture line possesses a pouch E lobe that is less deep as the asymmetric A lobe. Both lobes are separated by an asymmetric, ventrally inclined ventrolateral saddle (Fig. 5).

Specimen MB.C.25595.2 is similar in size but somewhat crushed. It shows the shell surface, which is smooth except for barely visible, very delicate growth lines with convex course.

**Remarks.** – The material differs from most of the other species of the genus, such as *I. rotatorium* (de Koninck) by the relatively deep but less strongly pouchched external lobe. The conch shape also differs because the specimen described here has a rather low coiling rate (WER ~ 2.05), which is higher in most of the other species.

Genus *Irinoceras* Ruzhencev, 1947

*Irinoceras arcuatum* Ruzhencev, 1947
Figure 6

1947 *Irinoceras arcuatum* sp. nov.; Ruzhencev, p. 283, text-figs 1, 2b, c.
1962 *Prionoceras (Irinoceras) stevanovici* Kullmann sp. nov.; Kullmann in Stevanović & Kullmann, p. 73, pl. 1, fig. 1, text-fig. 1a, b.
1971 *Irinoceras arcuatum* Ruzhencev. – Ruzhencev & Bogoslovskaya, p. 150, pl. 3, figs 6, 7, pl. 6, fig. 1, text-fig. 16.

**Material.** – Seven specimens, ranging from 13 mm conch diameter (only one complete specimen) to fragments of specimens with 80 mm diameter, from new collections. Additionally four specimens in the Natural History Museum, Belgrade.

**Description.** – Holotype BEO600-551.73:592-453 of “*Prionoceras (Irinoceras) stevanovici*” (Kullmann in Stevanović & Kullmann 1962, pl. 1, fig. 1) is an undistorted specimen with 17 mm conch diameter. The specimen is thinly pachyconic (ww/dm = 0.62) with a nearly closed umbilicus.
(uw/dm = 0.05), a high aperture (WER = 2.20) and a broadly rounded venter. It is rather well preserved with suture line and shell ornament visible. The ornament has lamelllose coarse growth lines forming a low ventrolateral projection and a deep ventral sinus; the growth lines bifurcate on the inner flanks into two separate finer branches. There are no constrictions visible. The suture line possesses a strongly pouched external lobe and an asymmetric adventive lobe.

The smaller specimen MB.C.25688 (Fig. 6) has, at 13 mm conch diameter, similar conch proportions but a little more slender (ww/dm ~ 0.59). The ornament has lamellar growth lines that bifurcate on the inner flanks and form a very deep ventral sinus.

Discussion. – There is no real reason for a separation of the two species *Irinoceras arcuatum* and *I. stevanovici*. The slightly open umbilicus in the latter species is mainly caused by coarse preparation of the umbilicus and removal of the shell material in the holotype. In terms of the conch proportions, shell ornament and also the suture line, both species cannot be separated.

Superfamily Pericyclaceae Hyatt, 1900
Family Muensteroceratidae Librovitch, 1957

**Genus Beyrichoceratoides** Bisat, 1924

**Beyrichoceratoides** sp.

Figure 7

*Material.* – 14 specimens; conch diameter up to 12 mm. While the shell ornament is well preserved in the material, a suture line is not visible.

*Description.* – Specimen MB.C.25598 (Fig. 7A) is rather well preserved and shows the conch proportions and the ornament at 12 mm conch diameter. The conch is thinly pachyconic (ww/dm = 0.68) with a nearly closed umbilicus (uw/dm = 0.05), a rounded umbilical margin and a broadly rounded venter. The ornament consists of very delicate growth lines, which extend with a low dorsolateral projection, a higher ventrolateral projection and a moderately deep ventral sinus.

The smaller specimens MB.C.25669.1 (8.5 mm dm; Fig. 7B) and MB.C.25669.2 (5.6 mm dm; Fig. 7C) have
similar conch proportions but differ from specimen MB.C.25598 in the coarser growth lines.

Family Maxigoniatitidae Korn, Klug & Mapes, 1999

Genus Bollandites Bisat, 1952

Bollandites sp.

Figure 8

1962 Cravenoceras arcticum subinvolutum Librovitch. – Kullmann in Stevanović & Kullmann, p. 79, pl. 1, fig. 4.
1962 Eoasianites (Eoasianites) europaeus Kullmann n. sp.?; Kullmann in Stevanović & Kullmann, p. 94, pl. 2, fig. 9.

Material. – Three specimens; conch diameter up to 8 mm from new collections. Additionally, three specimens in the Natural History Museum, Belgrade.

Description. – Specimen BEO600-551.73:592-474 is a slightly deformed specimen with 12 mm conch diameter. It is thickly pachyconic (ww/mm ~ 0.80) and subevolute (uw/mm ~ 0.35) with a steep umbilical wall and a very wide and broadly rounded venter. The ornament shows fine growth lines with a shallow lateral sinus and a broad ventral projection. The suture line is barely visible with a very narrow external lobe and a broadly rounded ventrolateral saddle (broader than in text-fig. 3b of Kullmann in Stevanović & Kullmann 1962).

Specimen MB.C.25634 is a small specimen with 5.4 mm conch diameter (Fig. 8). It is thickly pachyconic (ww/mm = 0.75) and evolute (uw/mm = 0.50) with a narrowly rounded umbilical margin that delimits the broad venter. The specimen has rather coarse lamellar growth lines, which form a lateral sinus on the umbilical wall and form a broad and low ventral projection.

Discussion. – It is clear that the specimens, for morphological and also stratigraphical reasons, cannot be assigned to Cravenoceras. The small individuals closely resemble juvenile material of the genus Bollandites particularly known from the British Isles (Korn & Tilsley 2006). The small specimens have, with their wide umbilicus and broad flattened venter, also some resemblance with juvenile specimens of the genus Calygirtyoceras.

Genus Bollandoceras Bisat, 1952

Bollandoceras sp.

Figure 9

Material. – One specimen.

Description. – Specimen MB.C.25680 has a conch nearly 10 mm in diameter and is thickly discoidal and narrowly umbilicate (ww/dm ~ 0.55; uw/dm ~ 0.25) with subparallel flanks and a broadly rounded venter. The ornament has lamellar growth lines with biconvex course (Fig. 9).

Genus Beyrichoceras Foord, 1903

Beyrichoceras jadarense sp. nov.

Figure 10A–C

Holotype. – Specimen MB.C.25668; illustrated here in Fig. 10A.

Type locality and horizon. – Milivojevića Kamenjar site in Družetić (NW Serbia); sample 2009-DRZ2, Ubites filipovicici horizon, Entogonites Genus Zone.

Material. – 10 moderately well preserved but often strongly deformed specimens; conch diameter up to 70 mm.

Etymology. – Named after the Jadar River area, the region with the type locality.
**Diagnosis.** – Species of *Beyrichoceras* with thinly pachyconic conch (ww/dm ~ 0.60) and very narrow umbilicus (uw/dm ~ 0.05) at 20 mm conch diameter; conch discoidal (ww/dm ~ 0.45) with very narrow umbilicus (uw/dm ~ 0.05) at 40 mm dm. Umbilical margin narrowly rounded. Ornament with about 200 fine spiral lines forming a spider-web pattern; growth lines biconvex already at 15 mm dm.

**Description.** – Specimen MB.C.25668 is a strongly deformed but otherwise rather well preserved specimen of about 43 mm conch diameter (Fig. 10B). It is fully covered with well-preserved shell material, which is ornamented by delicate spiral lines (about 100 from umbilicus to midventer) and even finer, biconvex growth lines. These growth lines possess a low dorsolateral projection, a very shallow lateral sinus, a low ventrolateral projection and a shallow ventral sinus.

The smaller specimen MB.C.25668.2 (~ 20 mm dm) is also strongly deformed but allows the reconstruction of conch proportions (Fig. 10C). It is thinly pachyconic (ww/dm ~ 0.60) with an almost closed umbilicus. The entire specimen is covered with shell material and the main component of the ornament is spiral ornamentation (about 200 spirals from umbilicus to umbilicus), which forms a spider-web pattern. The spirals are usually less wide than their interspaces but coarser than the fine growth lines. It is noticeable that the spirals are already perfectly developed at the beginning of the last preserved volution, i.e., at an approximate conch diameter of 15 mm. Already at this stage and thereafter, the growth lines show a biconvex course with low dorsolateral and ventrolateral projections and a deeper ventral sinus.

**Discussion.** – The new species differs from the other Serb-ian species *B. crenistriatoide* (compare Fig. 10D) in having a thinly pachyconic, involute conch (ww/dm ~ 0.70; uw/dm ~ 0.05) at 12–20 mm dm; aperture low (WER ~ 1.65). Shell ornament with crenulated growth lines up to 18 mm conch diameter, thereafter fine spiral lines. Course of the growth lines with shallow lateral sinus and low and wide ventral projection.

**Beyrichoceras crenistriatoide** (Kullmann, 1962)

*Figure 10D, E*

1962 *Nuculoceras crenistriatoide* Kullmann sp. nov.; Kullmann *in* Stevanović & Kullmann, p. 82, pl. 1, figs 5, 6.

**Holotype.** – Specimen BEO600-551.73:592-483 (Natural History Museum, Belgrade); illustrated by Stevanović & Kullmann (1962, pl. 1, fig. 5).

**Type locality and horizon.** – Milivojevića Kamenjar site in Družetić (NW Serbia); “upper horizon” of Stevanović & Kullmann (1962), probably *Entogonites tetragonus* horizon, *Entogonites Genus Zone*.

**Material.** – 12 specimens in the new collection with conch diameters up to 21 mm. Additionally about 12 specimens in the Natural History Museum, Belgrade.

**Diagnosis.** – Species of *Beyrichoceras* with a thinly pachyconic, involute conch (ww/dm ~ 0.70; uw/dm ~ 0.05) at 12–20 mm dm; aperture low (WER ~ 1.65). Shell ornament with crenulated growth lines up to 18 mm conch diameter, thereafter fine spiral lines. Course of the growth lines with shallow lateral sinus and low and wide ventral projection.

**Description.** – Holotype BEO600-551.73:592-483 (Kullmann *in* Stevanović & Kullmann 1962, pl. 1, fig. 5) is a slightly distorted specimen with a maximum diameter of almost 16 mm. At 12 mm conch diameter, it is thinly pachyconic (ww/dm ~ 0.70) with a nearly closed umbilicus (uw/dm ~ 0.05). The specimen is completely covered with shell, which shows very fine growth lines with clear lateral sinus and a flat, moderately high ventral projection. A sul-ture line is not visible. The conch is filled with dark-grey calcite cement and the shell is dark brown; it most probably comes from the *Entogonites tetragonus* horizon.

Specimen MB.C.25650.1 is a rather well preserved and only slightly deformed specimen with 21 mm conch diameter (Fig. 10D). It is thinly pachyconic (ww/dm ~ 0.70) and involute (uw/dm ~ 0.05) with a low aperture (WER ~ 1.65). Flanks and venter are broadly rounded. Most of the specimen is covered with shell material, which shows a change in the ornament during the last preserved volution. At the
Representatives of the genus *Beyrichoceras* from Družetić; lateral and dorsal views. • A – *Beyrichoceras jadarense* sp. nov., holotype MB.C.25668.1 from sample 2009-DRZ2; × 1.5. • B – *Beyrichoceras jadarense* sp. nov., paratype MB.C.25686 from loose block 2010-2; × 1.5. • C – *Beyrichoceras jadarense* sp. nov., paratype MB.C.25668.2 from sample 2009-DRZ2; × 1.5. • D – *Beyrichoceras crenistriatoide* Kullmann, 1962, specimen MB.C.25650.1 from loose block 2012-36; × 2.5. • E – *Beyrichoceras crenistriatoide* Kullmann, 1962, specimen MB.C.25650.2 from loose block 2012-36; × 2.5.

Figure 10. Representatives of the genus *Beyrichoceras* from Družetić; lateral and dorsal views. • A – *Beyrichoceras jadarense* sp. nov., holotype MB.C.25668.1 from sample 2009-DRZ2; × 1.5. • B – *Beyrichoceras jadarense* sp. nov., paratype MB.C.25686 from loose block 2010-2; × 1.5. • C – *Beyrichoceras jadarense* sp. nov., paratype MB.C.25668.2 from sample 2009-DRZ2; × 1.5. • D – *Beyrichoceras crenistriatoide* Kullmann, 1962, specimen MB.C.25650.1 from loose block 2012-36; × 2.5. • E – *Beyrichoceras crenistriatoide* Kullmann, 1962, specimen MB.C.25650.2 from loose block 2012-36; × 2.5.
beginning, there are wide-standing and slightly crenulated growth lines, which form a shallow lateral sinus and turn forward for a low and wide ventral projection, the growth lines, then become finer and densely spaced. At the end of the volution, at a conch diameter of 19 mm, fine spiral lines develop out of stronger crenulation of the growth lines, which still extend with the lateral sinus and ventral projection.

Specimen MB.C.25650.2 has 18 mm conch diameter (Fig. 10E) and is generally similar to specimen MB.C.25650.1 (Fig. 10D). It is slightly stouter (ww/dm ~ 0.75) and has a cuboid whorl profile.

Discussion. – According to Kullmann (in Stevanović & Kullmann 1962), this species was found in the “lower” as well as the “upper” fauna. However, our new collections demonstrate that this species is restricted to the stratigraphically older of the assemblages, where it co-occurs with Entogonites. Specimen BEO600-551.73:592-484, which putatively comes from the “lower horizon”, has a lithology that assigns it to the “upper horizon” (i.e., Entogonites tetragonus horizon).

Suture lines are usually not preserved in this material, but it can be stated that the shell ornament with the rather fine growth lines does not belong to Nuculoceras (which shows an ornament with strong riblet-like growth lines) but to Beyrichoceras. The suture line figured by Kullmann (in Stevanović & Kullmann 1962) does not contradict an assignment to Beyrichoceras.

Kullmann (in Stevanović & Kullmann 1962) had only small individuals up to 18 mm conch diameter available for study and hence was not aware of the spirally ornamented subadult and adult stage.

However, it appears to be clear that at this growth stage clear ornamental differences separate B. crenistriatoide from the new species B. jadarense. In B. crenistriatoide, the ornament is still dominated by growth lines extending with a ventral projection, while in B. jadarense sp. nov. there is already an ornament dominated by spiral lines and the growth lines are biconvex with a ventral sinus.

Family Entogonitidae Ruzhencev & Bogoslovskaya, 1971

Genus Ubites Korn & Sudar, 2010

Type species. – Ubites filipovici Korn & Sudar, 2010.

Diagnosis. – Entogonitidae with complex ontogeny. Inner whors evolve, adult whors with narrower umbilicus caused by stronger whorl overlap. Inner whors circularly coiled. Shell ornament with sharp biconvex riblets; inner whors with sharp dichotomizing or intercalating ribs. Ventrolateral projection of riblets low in the adult stage, ventral sinus moderately deep. Deep steinkern constrictions in the subadult and adult stage.


Discussion. – The three species within the genus Ubites show some morphological range, particularly in the width of the umbilicus. The narrowly umbilicated Ubites novaki sp. nov. shows, in the conch proportions, close similarities to representatives of the genera Boilandites and Bollandoceras, but differs in the dichotomizing riblets.

Ubites differs from Entogonites in the regularly coiled inner whors and in the ontogenetic development, which shows an adult stage in which the uw/dm ratio is significantly reduced.

Ubites filipovici Korn & Sudar, 2010

Figure 12A–I

1962 Gastrioceras (Branneroceras) branneri branneri Smith. – Kullmann in Stevanović & Kullmann, p. 86, pl. 2, fig. 1.

2010a Ubites.filipovici Korn & Sudar. – Korn et al., p. 362, text-fig. 6.

Holotype. – Specimen MB.C.19130.1, illustrated here in Fig. 12A.
**Type locality and horizon.** – Milivojevića Kamenjar section, Družetić (NW Serbia); sample DRZ 2, *Ubites filipovici* horizon, *Entogonites* Genus Zone.

**Material.** – 125 specimens in the new collections and two specimens in the Natural History Museum, Belgrade; conch diameter up to 16.5 mm.

**Diagnosis.** – Species of *Ubites* with a thinly discoidal, evolute conch (ww/dm = 0.35–0.45; uw/dm = 0.50–0.55) at 8 mm dm; conch thinly discoidal, evolute (ww/dm = 0.40; uw/dm = 0.47) at 16 mm dm. Aperture low (WER = 1.50–1.60) in the adult stage.

**Description.** – Holotype MB.C.19130.1 is an incomplete, slightly distorted specimen with 16 mm conch diameter; it demonstrates a rapid ontogenetic change from the evolute juvenile stage into the adult morphology (Fig. 12A). This change takes place within only one volution, in which the whorl height becomes significantly larger. At 16 mm dm, the flanks are slightly flattened and the umbilical margin is subangular. The last volution shows the excellently preserved shell ornament, consisting of sharp riblets, of which three stand within one millimetre. Every second of these riblets is intercalated near the umbilical margin; the main riblets begin on the umbilical wall and form a sharp elongate node on the umbilical margin. The riblets form a shallow sinus on the umbilical margin, a low projection in the inner flank area, a very shallow sinus on the midflank, a low ventrolateral projection, and a moderately deep ventral sinus. Parallel to the growth lines extend two shell constrictions standing approximately 120° apart. They begin in the inner flank area and extend with the same depth across flanks and venter.

The smaller paratype MB.C.19130.2 (8.1 mm conch diameter) represents the juvenile growth stage, in which the conch is still evolute (uw/dm = 0.51). The whorls are wide (ww/wh = 1.42) and crescent-shaped in this stage, and flanks and venter are regularly rounded. The shell ornament shows about 50 sharp riblets; between these, finer intercalatory riblets begin in the inner flank area. The riblets extend almost linearly across the inner flanks, bend forward to form a moderately high ventrolateral projection, and then turn back for a moderately deep ventral sinus (Fig. 12D).

Small specimens such as paratype MB.C.19130.4 (5.5 mm conch diameter) display similar conch morphology and shell ornament (Fig. 12C). This specimen is more widely umbilicate (uw/dm = 0.55) than the larger ones.

**Discussion.** – Kullmann (in Stevanović & Kullmann 1962) had only two small specimens, and he attributed these, probably because of the dichotomising ribs, to the North American Morrowan (late Bashkirian) index species *Brannerceras branneri*. This determination did not consider the small size of the Serbian specimens, which only superficially resemble juveniles of *B. branneri*. The reconstruction of the suture line by Kullmann (in Stevanović & Kullmann 1962, fig. 4a) cannot be confirmed, as the figured specimen does not show a clear suture line. *U. filipovici* Korn & Sudar is similar to *U. pseudocyclus*, but that species has, at 16 mm diameter (i.e. the same size as the holotype of *U. filipovici*), less sharp riblets with a more linear course across flanks and venter. The umbilicus is wider in *U. pseudocyclus* (uw/dm = 0.47, in contrast to 0.42 in *U. filipovici*). *U. pseudocyclus* co-occurs, at the type locality Mundubbera (Queensland), with species of the genera *Irinoceras*, *Bollandites*, *Maxigioniates* and *Cantabricanites*, which can be taken as evidence for an early Late Viséan age similar to *U. filipovici*.

*U. divnae* sp. nov. has, at a comparable conch diameter, a much narrower umbilicus than *U. filipovici* (at 8 mm conch diameter: uw/dm = > 0.50 in *U. filipovici* but < 0.40 in *U. divnae*).

**Ubites divnae** sp. nov.

**Figure 12J–L**

**Holotype.** – Specimen MB.C.25654.1; illustrated in Fig. 12J.

**Type locality and horizon.** – Milivojevića Kamenjar section, Družetić (NW Serbia); loose block 36, *Entogonites tetragonus* horizon, *Entogonites* Genus Zone.

**Material.** – 21 specimens; conch diameter up to 12 mm.

**Etymology.** – Named after Divna Jovanović (Belgrade, Serbia) for her engagement in the field collections.

**Diagnosis.** – Species of *Ubites* with a thickly discoidal, sub-evolute conch (ww/dm = 0.50; uw/dm = 0.35–0.40) at 8 mm dm. Aperture low (WER = 1.50–1.60) in the adult stage.
Ubites novaki sp. nov.

Description. – Holotype MB.C.25639.1 (8.3 mm conch diameter; Fig. 12J) is a deformed specimen with rather well-preserved shell ornament. The conch is thickly discoidal and subevolute in this growth stage (ww/dm ~ 0.53; uw/dm ~ 0.38) with a low coiling rate (WER ~ 1.55). It has a straight umbilical wall, a narrowly rounded umbilical margin and flanks converging to the broadly rounded venter. The shell ornament shows fine and densely spaced primary riblets, between whose secondary riblets are intercalated near the umbilicus. The riblets have a biconvex course with equally low dorsolateral and ventrolateral projections, a very shallow lateral sinus and a shallow ventral sinus. Two shell constrictions arranged in 90° distance follow the course of the growth lines.

Paratype MB.C.25667.1 is an incomplete specimen with 7 mm conch diameter (Fig. 12K); it is thickly discoidal and subevolute (ww/dm = 0.50; uw/dm = 0.38) and closely resembles the holotype.

Discussion. – Ubites divnae sp. nov. closely resembles U. filipovici in the shell ornament with biconvex riblets dichotomizing near the umbilicus, but the conch shape offers clear characters for a separation. U. divnae differs from U. filipovici in the narrower umbilicus (uw/dm > 0.50 at 8 mm dm) in U. filipovici but < 0.40 in U. divnae).

A similar species is U. novaki sp. nov., but this species has a narrower umbilicus (uw/dm ~ 0.30 at 8 mm dm) than U. divnae (uw/dm ~ 0.40 at 8 mm dm).

Ubites novaki sp. nov.

Figure 12M–O

1962 Cravenoceras cowlingense Bisat. – Kullmann in Stevanović & Kullmann, p. 78, pl. 1, fig. 3.

Holotype. – Specimen MB.C.25639.1; illustrated in Fig. 12M.

Type locality and horizon. – Milivojevića Kamenjar section, Družetić (NW Serbia); float block, Entogonites tetragonus horizon, Entogonites Genus Zone.

Material. – 13 newly collected specimens and three specimens in the Natural History Museum, Belgrade; conch diameter up to 13 mm.

Etymology. – Named after Matevž Novak (Ljubljana, Slovenia) for his engagement in the field collections.

Diagnosis. – Species of Ubites with a thickly discoidal to thinly pachyconic, subinvolute conch (ww/dm ~ 0.60; uw/dm ~ 0.30) at 8 mm dm. Aperture low (WER ~ 1.65) in the adult stage.

Description. – Holotype MB.C.25639.1 is a weakly deformed specimen with nearly 10 mm conch diameter (Fig. 12M). It is thickly discoidal (ww/dm nearly 0.60) and subinvolute (uw/dm nearly 0.30); it possesses a steep umbilical wall, a narrowly rounded umbilical margin and a weakly depressed whorl cross-section (ww/wh nearly 1.50) with a broadly rounded venter. The shell ornament shows coarse growth lines, which sometimes are strengthened like fine riblets. They extend with a weakly biconvex course with low projections and shallow sinuses across flanks and venter. The shell has also constrictions arranged in angles of 90°; they follow the course of the growth lines and are deepest in the midflank area.

Paratype MB.C.25639.2 shows the morphology of the smaller stage. It is 6.5 mm in diameter and covered with shell material (Fig. 12O). It has an umbilicus of about a third of the conch diameter and a broadly rounded venter. The growth lines are coarse like riblets; they extend with low dorsolateral and ventrolateral projections across the flank and form a ventral sinus that is slightly deeper than the lateral sinus. Deep shell constrictions are arranged in angles of 90°.

The smaller paratype MB.C.25618.1 has, at 6 mm conch diameter, conch proportions similar to the holotype (Fig. 12N). It shows the well-preserved shell ornament with rather coarse, riblet-like growth lines, extending with a very low dorsolateral projection, a very shallow lateral sinus, a low ventrolateral projection and a rather narrow and shallow ventral sinus. Riblets are intercalated in the inner flank area. The last volution possesses eight short constrictions on the flank; these constrictions lead to the impression that the areas between them are raised like broad and rounded nodes.

Figure 12. Representatives of the genus Ubites from Družetić; lateral and dorsal views; all × 4. • A–I – Ubites filipovici Korn & Sudar, 2010; A – holotype MB.C.19130 from sample 2008-DRZ2; B – paratype MB.C.19130.5 from sample 2008-DRZ2; C – paratype MB.C.19130.3 from sample 2008-DRZ2; D – paratype MB.C.19130.2 from sample 2008-DRZ2; E – paratype MB.C.19129.1 from sample 2008-DRZ2; F – paratype MB.C.19130.7 from sample 2008-DRZ2; G – specimen MB.C.25633 from loose block 2010-3; H – specimen MB.C.25676.1 from sample 2009-DRZ2; I – specimen MB.C.25676.2 from sample 2009-DRZ2. • J–L – Ubites divnae sp. nov.; J – holotype MB.C.25654.1 from loose block 2012-36; K – paratype MB.C.25667.1 from sample 2008-DRZ2; L – paratype MB.C.25638 from block 2010-DRZ1. • M–O – Ubites novaki sp. nov.; M – holotype MB.C.25639.1 from block 2010-DRZ1; N – paratype MB.C.25618.1 from sample 2009-DRZ2; O – paratype MB.C.25639.2 from block 2010-DRZ1.
**Discussion.** – The specimen figured by Kullmann (in Stevanović & Kullmann 1962, pl. 1, fig. 3) cannot, on the basis of conch shape and ornament, be assigned to the genus *Cravenoceras*. All characters plus the stratigraphical occurrence speak for identification of the specimen as an *Ubites* species, which together with similar species co-occurs with *Entogonites*.

*Ubites novaki* sp. nov. has similarities with *U. divnae*; both species resemble each other in the course of the growth lines and in the conch proportions, but *B. novaki* has a narrower umbilicus (uw/dm ~ 0.30 at 8 mm dm) than *U. divnae* (uw/dm ~ 0.40 at 8 mm dm).

There are also some similarities to representatives of the genera *Bollandites* and *Bollandoceras*. *Bollandites rileyi* Korn & Tilsley for instance has similar conch morphology.

**Genus Entogonites Kittl, 1904**

*Type species.* – *Tetragonites Grimmeri* Kittl, 1904 (by monotypy).

**Diagnosis.** – Entogonitidae with simple ontogeny. Adult whorls slightly narrower umbilicate; inner whorls tetragonally coiled.


**Entogonites grimmeri** (Kittl, 1904)

*Figure 13A–H*

1904a *Tetragonites Grimmeri* nov. gen. n. f.; Kittl, p. 677, pl. 21, figs 18–24.

1958 *Nomismoceras grimmeri* (Kittl). – Kostić-Podgor ska, p. 28, pl. 15, figs 1–4.

1962 *Gastrioceras (Branneroceratoides) tetragonum* Kullmann sp. nov. – Kullmann in Stevanović & Kullmann, p. 88, pl. 2, figs 5, 6 (only).


1988 *Entogonites grimmeri* (Kittl). – Korn, p. 47, pl. 5, figs 1–4 (see for more synonymy).


**Material.** – 46 specimens in the new collection and five specimens in the Natural History Museum, Belgrade.

**Description.** – Specimen MB.C.25620.1 is about 8 mm in conch diameter and represents the growth stage, in which the tetragonal coiling is transformed into regular coiling (Fig. 13B). The specimen is thinly discoidal (ww/dm = 0.38) and evolute (uw/dm = 0.49) with a depressed whorl profile (ww/wh = 1.48). The ornament shows almost 40 sharp primary ribs on the last volution; they are straight on the flank and turn forward to a rather high ventrolateral projection. On the venter they run with a sharp, chevron-shaped sinus. The ribs bifurcate in the outer flank area, but in some places intercalatory ribs can also be seen.

Of the smaller specimens, it is particularly MB.C.25747 (Fig. 13D) that deserves attention. It has a diameter of 6 mm and is laterally deformed. The conch is thinly discoidal (ww/dm = 0.39) and subevolute (uw/dm = 0.42). The coiling is strikingly tetragonal with a square-shaped umbilicus. The last volution has about 35 sharp ribs, which dichotomize on the outer flank.

**Discussion.** – *Entogonites grimmeri* has originally been described from flattened material collected in the vicinity of Prača near Sarajevo (Bosnia and Herzegovina) by Kittl (1904a, b), a locality only 110 km southwest from Družetić. The morphology of the specimens suggests that the species occurs at both places.

Among the *Entogonites* species from Družetić, *E. grimmeri* has the strongest tetragonal coiling and the sharpest ribs with the highest ventrolateral projection.

**Entogonites serbicus** sp. nov.

*Figure 13I–K*

**Holotype.** – Specimen MB.C.25597, illustrated in Fig. 13I.

**Type locality and horizon.** – Milivojevića Kamenjar section, Družetić (NW Serbia); float block, *Entogonites tetragonum* horizon, *Entogonites Genus Zone*.

**Material.** – 8 specimens up to 16 mm conch diameter.

**Etymology.** – Named after the country of Serbia.

**Diagnosis.** – Species of *Entogonites* with a thinly discoidal conch (ww/dm = 0.35–0.40), moderately wide umbilicus (uw/dm = 0.35–0.40) and broadly rounded venter at 8 mm conch diameter. Aperture moderately low (WER = 1.80–1.90). Inner whorls with very weak tetragonal coiling.
Figure 13. Representatives of the genus *Entogonites* from Družetić, lateral and dorsal views; all × 4. • A–H – *Entogonites grimmeri* (Kittl, 1904); A – specimen MB.C.25599.1 from sample 2008-DRZ1; B – specimen MB.C.25601.1 from sample 2009-DRZ1; C – specimen MB.C.25602.2 from sample 2009-DRZ1; D – specimen MB.C.25599.2 from sample 2008-DRZ1; E – specimen MB.C.25599.3 from sample 2008-DRZ1; F – specimen MB.C.25599.4 from sample 2008-DRZ1; G – specimen MB.C.25599.5 from sample 2008-DRZ1; H – specimen MB.C.25596 from float. • I–K – *Entogonites serbicus* sp. nov.; I – holotype MB.C.25597 from float; J – paratype MB.C.25600 from sample 2008-DRZ1; K – paratype MB.C.25635 from loose block 2010-DRZ1. • L–O – *Entogonites tetragonus* (Kullmann, 1962); L – specimen MB.C.18128.1 from sample 2008-DRZ1; M – specimen MB.C.19128.2 from sample 2008-DRZ1; N – specimen MB.C.25636 from block 2010-DRZ1; O – specimen MB.C.19128.5 from sample 2008-DRZ1.
Shell ornament with 30 rounded and ventrolaterally dichotomising ribs. Ventrolateral projection of ribs low, ventral sinus shallow.

**Description.** – Holotype MB.C.25597 is the largest available specimen with 16 mm conch diameter and shows the adult conch morphology and ornament (Fig. 13I). The conch is extremely discoidal (ww/dm = 0.27) and subevolute (uw/dm = 0.32) with a whorl expansion rate of 2.00. The umbilical margin is rounded; the flanks stand subparallel and are delimited by a subangular ventrolateral margin from the rounded venter. The ornament changes during the last growth interval. In the largest growth stage (which is only visible in a short growth interval), it consists of sharp dense riblets. The last well-preserved half volution shows 25 sharp ribs on the flank. They have a protracted direction on the flank and dichotomize in the middle of the flank, from here they continue as slightly weaker ribs, which form a pronounced ventrolateral projection and turn back to a chevron-shaped ventral sinus. Another half volution earlier, 20 sharp ribs can be counted. In this stage, the ribs are straight on the flank.

Paratype MB.C.25600.1 is a fairly well-preserved steinkern specimen with 9 mm conch diameter (Fig. 13J). It is thinly discoidal (ww/dm = 0.38) and subinvolute (uw/dm = 0.39). During the last half volution, the umbilicus opens and the uw/dm ratio increases from 0.35 to 0.39. The umbilical margin is rounded and the flanks converge towards the broadly rounded venter that is limited from the flanks by a weakly angular shoulder. About 30 rounded riblets are present on the last volution; these riblets show a very shallow lateral sinus and bend forward toward a low ventrolateral projection. The ribs become much weaker in the ventrolateral area, where they bifurcate into weaker branches.

Paratype MB.C.25635 has almost the same conch proportions (Fig. 13K). It has slightly sharper ribs than the holotype.

**Discussion.** – *Entogonites serbicus* sp. nov. belongs to the species of the genus with a relatively narrow umbilicus. Similarly involute are *E. burbankensis* (which possesses strongly tetrangular inner whorls) and *E. nasutus* (with very low ventrolateral projection of the ribs). Of the Serbian species, *E. serbicus* is the one with the least tetrangular coiling of the inner whorls.

**Entogonites tetragonus** (Kullmann, 1962)

Figures 13L–O

1962 *Gastrioceras (Branneroceratoides) tetragonus* Kullmann sp. nov.; Kullmann in Stevanović & Kullmann, p. 88, pl. 2, figs 2–4 (only).

1971 *Entogonites tetragonus* (Kullmann); – Ruzhencev & Bogoslovskaya, p. 37.

2010a *Entogonites tetragonus* (Kullmann). – Korn et al., p. 361, text-fig. 5.

**Holotype.** – Specimen BEO600-551.73:592-476 (Natural History Museum Belgrade), illustrated by Stevanović & Kullmann (1962, pl. 2, fig. 2).

**Type locality and horizon.** – Milivojevića Kamenjar site in Družetić (NW Serbia); “upper horizon” of Stevanović & Kullmann (1962), *Entogonites Genus Zone*.

**Material.** – The holotype and about 20 paratypes in the Natural History Museum Belgrade (some of which are poorly preserved) and additionally 157 newly collected specimens; conch diameter up to 9.5 mm.

**Diagnosis.** – Species of *Entogonites* with a thinly discoidal conch (ww/dm = 0.35–0.40), wide umbilicus (uw/dm = 0.45–0.50) and slightly flattened venter at 8 mm conch diameter. Aperture moderately high (WER = 1.80–1.90). Inner whorls with moderate tetrangular coiling. Shell ornament with 35 moderately strong, rounded and ventrolaterally dichotomising ribs per volution. Ventrolateral projection of ribs low, ventral sinus moderately deep.

**Description.** – Holotype BEO600-551.73:592-476 (Kullmann in Stevanović & Kullmann 1962, pl. 2, fig. 2) is a relatively well-preserved specimen with nearly 9 mm conch diameter. It is extremely discoidal (ww/dm = 0.34) and evolute (uw/dm = 0.46). The specimen has about 35 rounded ribs on the last volution. They have a straight radial course on the flank and in the ventrolateral area turn forward to form a rather low projection and a shallow ventral sinus.

Specimen MB.C.19128.1 is a rather well preserved specimen with 8.5 mm conch diameter (Fig. 13L). It is thinly discoidal and evolute (ww/dm = 0.36; uw/dm = 0.46) and possesses a moderately high aperture (WER = 1.83). The inner whorls show inconspicuous tetrangular coiling. About 30 rounded ribs can be counted on the last volution; they extend in a linear course across the inner flank and bifurcate on the outer flank. The apertural branch forms a rather high ventrolateral projection and a shallow sinus on the venter.

The other, smaller specimens are similar in conch shape and ornament. Some of them, such as specimen MB.C.19128.2 (7 mm dm; Fig. 13M) and MB.C.19128.5 (4.2 mm dm; Fig. 13O) possess constrictions extending parallel to the riblets. The tetrangularly coiled stage ends at about 6 mm conch diameter.

**Discussion.** – *E. tetragonus* is the type species of the subgenus *Gastrioceras (Branneroceratoides)* Kullmann, 1962, which was erroneously regarded as a Namurian genus by...
Kullmann (in Stevanović & Kullmann 1962). The figured, strongly fragmentary suture line with a putatively acute adventive lobe and a parallel-sided external lobe (Kullmann in Stevanović & Kullmann 1962, text-fig. 4b, unfortunately no specimen number was given) is obviously incorrect in these respects; it is clear that the subgenus has to be put in synonymy with *Entogonites*.

Not all of the specimens listed by Kullmann (in Stevanović & Kullmann 1962) do in fact belong to this species; two of the figured ones (figs 5 and 6 of pl. 2) show a narrower umbilicus and a more pronounced projection of the ribs; they must be regarded as *E. grimmeri*.

*E. tetragonus* differs from *E. grimmeri* in the less developed tetrangular coiling of the inner whorls. The riblets in *E. tetragonus* are less sharp when compared with *E. grimmeri*. *E. nasutus* also has weakly tetrangular inner whorls, but in this species the umbilicus is much narrower (uw/dm = 0.35) than in *E. tetragonus* (uw/dm = 0.45). *E. borealis* has a narrower umbilicate conch than *E. tetragonus*, and *E. saharensis* possesses sharper ribs with higher ventrolateral projections.

Superfamily Nomismocerataceae Librovitch, 1957
Family Nomismoceratidae Librovitch, 1957
Genus *Nomismoceras* Hyatt, 1884

*Nomismoceras* sp.

![Figure 14. *Nomismoceras* sp. from Družetić; lateral and dorsal views of specimen MB.C.25666 from sample 2008-DRZ2; × 4.](image)

*Material.* – Six specimens up to 6 mm conch diameter.

*Description.* – Specimen MB.C.25666 (Fig. 14) is, with 6 mm conch diameter, the largest of the available specimens. It is extremely discoidal (ww/dm = 0.30) and subevolute (uw/dm = 0.40) with a low whorl embracing rate and a high aperture (WER = 2.20). The whorl profile shows, on the last half volution, a rounded umbilical wall; the whors are widest in the inner flank area and show a wide and shallow spiral groove on the outer flank and a broadly rounded venter. The shell ornament shows very delicate growth lines, which extend with a dorsolateral projection and a deep lateral sinus across the flank.

Superfamily Goniatitaceae Hyatt, 1884
Family Goniatitidae Hyatt, 1884
Genus *Hypergoniatites* Ruzhencev & Bogoslovskaya, 1970

*Hypergoniatites* sp.

![Figure 15. *Hypergoniatites* sp.; suture line of specimen MB.C.25741 from Družetić; loose block 2012-29, at ~ 17 mm wh; × 3.0.](image)

*Material.* – Only one fragmentary specimen.

*Description.* – The single fragment MB.C.25741 is poorly preserved. At a whorl height of about 17 mm, it shows a suture line with a very narrow, V-shaped E lobe, an acute ventrolateral saddle and a slightly asymmetric A lobe (Fig. 15). While there is no doubt about the genus attribution, an assignment to a distinct species is impossible.

Family Delepinoceratidae Ruzhencev, 1957
Subfamily Dombaritininae Kullmann, 2007
Genus *Dombarites* Librovitch, 1957

*Dombarites falcatoides* Ruzhencev & Bogoslovskaya, 1970

![Figure 16A, B, D, F, G](image)

*Material.* – Six specimens up to 6 mm conch diameter.

*Description.* – Specimen MB.C.25666 (Fig. 14) is, with 6 mm conch diameter, the largest of the available specimens. It is extremely discoidal (ww/dm = 0.30) and subevolute (uw/dm = 0.40) with a low whorl embracing rate and a high aperture (WER = 2.20). The whorl profile shows, on the last half volution, a rounded umbilical wall; the whors are widest in the inner flank area and show a wide and shallow spiral groove on the outer flank and a broadly rounded venter. The shell ornament shows very delicate growth lines, which extend with a dorsolateral projection and a deep lateral sinus across the flank.

Family Delepinoceratidae Ruzhencev, 1957
Subfamily Dombaritininae Kullmann, 2007
Genus *Dombarites* Librovitch, 1957

*Dombarites falcatoides* Ruzhencev & Bogoslovskaya, 1970

*Material.* – Only one fragmentary specimen.

*Description.* – The single fragment MB.C.25741 is poorly preserved. At a whorl height of about 17 mm, it shows a suture line with a very narrow, V-shaped E lobe, an acute ventrolateral saddle and a slightly asymmetric A lobe (Fig. 15). While there is no doubt about the genus attribution, an assignment to a distinct species is impossible.
Material. – 17 specimens ranging in their diameters from 5 mm to 80 mm from new collections. Many of the specimens are rather poorly preserved and species attribution of some of the material may not be completely clear. There are at least two specimens in the Natural History Museum, Belgrade.

Description. – Specimen MB.C.25733 is a fragment of a large specimen of about 80 mm conch diameter (Fig. 16A). Although incompletely preserved it is obvious that the conch was rather stout (ww/dm ~ 0.60). It shows a poorly preserved shell ornament, which possesses about 45 rather coarse spiral lines (umbilicus to midventer) as well as rhythmically strengthened growth lines producing a conspicuous falcate ornament. At the largest diameter, a shallow shell constriction is visible.

MB.C.25745 is a specimen of about 48 mm conch diameter. It has a strongly deformed body chamber but a less deformed phragmocone (Fig. 16B). The conch shape is, at about 35 mm dm, thickly pachyconic (ww/dm ~ 0.75). The ornament of the specimen shows spiral lines nearly as wide as their interspaces.

Specimen S4 is a well-preserved, rounded-triangularly coiled individual of 12.5 mm conch diameter (Kullmann in Stevanović & Kullmann 1962, pl. 4, fig. 1). It is thickly pachyconic (ww/dm ~ 0.80) with a very narrow umbilicus (uw/dm ~ 0.10). The shell ornament shows about 80 spirals and growth lines as strong as spirals; the growth lines extend with a rather deep lateral sinus and a wide ventral projection. Three shell constrictions are deepest on the flanks. The suture line is not visible.

The smallest available specimen MB.C.25690.1 is thickly globular (ww/dm = 1.07) with a nearly closed umbilicus (Fig. 16G). The specimen shows triangular coiling caused by three deep constrictions arranged 120° apart. The shell ornament shows dominant biconvex growth lines (with a very shallow ventral sinus) and finer spiral lines.

Discussion. – The material of Dombarites from the South Ural (Ruzhencev & Bogoslovskaya 1971) is much better preserved than the material from Družetić, and hence a comparison is rather difficult. It is obvious that some of the specimens attributed by Kullmann (in Stevanović & Kullmann 1962) to ‘‘Proshumardites (Trigonoshumardites) wocklumeroides’’ do in fact belong to Dombarites.

**Dombarites liratus** Ruzhencev & Bogoslovskaya, 1971

Figures 16C, E, 17

1962 Proshumardites (Trigonoshumardites) wocklumeroides Kullmann nov. subgen. et nov. sp.; Kullmann in Stevanović & Kullmann, p. 98, pl. 3, fig. 3 (only).

1971 Dombarites liratus sp. nov.; Ruzhencev & Bogoslovskaya, p. 232, pl. 18, figs 1–5.

Material. – Six specimens ranging in their diameters from 28 mm to 70 mm from new collections; preservation of the specimens is moderately good. There is at least one specimen in the Natural History Museum, Belgrade.

Description. – Specimen BEO600-551.73:592-471 is a slightly distorted specimen with 38 mm conch diameter. The conch is pachyconic (ww/dm ~ 0.70) with a narrow umbilicus (uw/dm ~ 0.10). The specimen shows few shell remains with about 80–90 fine spirals being separated by wider interspaces. The suture line is well visible; it has a V-shaped E lobe and a median saddle of more than half the height of the external lobe depth. The ventrolateral saddle is acute; the flanks of the adventive lobe are inflexed with angular and very short secondary lobes.

Specimen MB.C.25731.1 is a comparatively well preserved, only slightly deformed individual of 26 mm diameter displaying the ornament of the recrystallized shell (Fig. 16C). The conch is thinly pachyconic and involute (ww/dm = 0.67; uw/dm = 0.13) with broadly rounded venter. A total of 40 spiral lines can be counted from the umbilicus to the midventer; their width equals the width of their interspaces. Three barely visible shell constrictions standing about 90 degrees apart are visible in the midflank area. The suture line shows a V-shaped E lobe with a median saddle as high as half of the E lobe depth and very narrow, V-shaped prongs. The ventrolateral saddle is acute and the A lobe is slightly asymmetric with a weak inflexion of the ventral flank (Fig. 17B).

Specimen MB.C.25697 is the fragment of a specimen with maximally 30 mm conch diameter; it is very similar to specimen MB.C.25731.1. Parts of an inner volution are visible; this possesses finer spiral lines than the outer whorl (Fig. 16E).

Discussion. – Preservation of the material is sufficient for an attribution to *D. liratus*, as the falcate ornament typical for the otherwise similar species *D. parafalcatoïdes* is absent. The main difference to the co-occurring *D. falcatoïdes* is the slender conch.

Genus Proshumardites Rauser-Tschernoussowa, 1928

**Proshumardites uralicus** Librovitch, 1941

Figure 18

1941 Proshumardites uralicus sp. nov.; Librovitch, p. 153, pl. 40, fig. 9, text-fig. 43.

1962 Proshumardites (Proshumardites) serbicus Kullmann nov. spec.; Kullmann in Stevanović & Kullmann, p. 96, pl. 3, fig. 1, text-fig. 6a.
1962 *Proshumardites (Trigonoshumardites) wocklumeroides* Kullmann subgen. nov. et sp. nov.; Kullmann in Stevanović & Kullmann, p. 98, pl. 3, figs 2, 4, 5, text-fig. 6b (only).


**Material.** – One fragment from new collections. A suite of about 20 specimens (of which some are poorly preserved) is stored in the collections of the Natural History Museum, Belgrade.

**Description.** – The holotype of *"Proshumardites (Proshu-
mardites) serbicus Kullmann, 1962", specimen S1, is an individual with about 55 mm conch diameter and it was prepared with a strong acid treatment. It is embedded in dark grey dense limestone without iron stains. The conch is, at 48 mm conch diameter, thinly pachyconic (ww/dm ~ 0.65) with a very narrow umbilicus (uw/dm ~ 0.13) and a weakly depressed whorl profile (ww/wh ~ 1.25). Few shell remains are preserved with wide-standing, fine lamellar growth lines that show a rursiradiate course on the flank. The external suture line is visible in parts and can be obtained from two positions at 43 and 48 mm conch diameter. The external lobe has nearly straight flanks and narrow V-shaped prongs; the height of the median saddle is not clear but it is possibly more than 60% of the E lobe depth. The ventrolateral saddle is barely visible in the specimen but obviously not completely acute. On the flank follows the adventive lobe, which is trifurcate with a large primary prong and small claw-shaped secondary prongs (Fig. 18A).

The holotype of “Proshumardites (Trigonoshumardites) wocklumerioides” Kullmann, 1962”, specimen BEO600-551.73:592-444, is a specimen also embedded in dark grey dense limestone without iron stains; shell remains are preserved on one side and the other side was etched for preparation of the suture line. At a conch diameter of 21.7 mm, the conch is thinly pachyconic (ww/dm = 0.73) and the umbilicus is nearly closed (uw/dm = 0.06). The whorl profile is horseshoe-shaped with broadly rounded venter and a low aperture (WER = 1.54). The shell ornament shows 80 fine spirals (from umbilicus to umbilicus) with interspaces about five times wider than the lines; the growth lines are very fine. The suture line is visible at a conch width of about 14 mm. It shows a Y-shaped E lobe with weakly asymmetric lanceolate prongs and a median saddle slightly higher than the E lobe depth. The ventrolateral saddle is very narrow and subacute and the A lobe is trifurcated with a larger V-shaped primary prong and two asymmetric, claw-shaped secondary prongs (Fig. 18B).

Discussion – Ruzhencev & Bogoslovskaya (1971) regarded the two Serbian species as synonyms of P. uralicus. These authors did not see any difference between P. uralicus and P. wocklumerioides and argued that the development of the ornament (i.e., losing the spiral lines at a diameter of about 35 mm) and also the conch dimensions speak for a synonymy of the three species.

It is questionable if all specimens regarded by Kullmann (in Stevanović & Kullmann 1962) as “Proshumardites (Trigonoshumardites) wocklumerioides” really belong to Proshumardites. Doubts can be raised particularly for the specimens BEO600-551.73:592-471 (Kullmann in Stevanović & Kullmann 1962, pl. 3, fig. 3), which has a Dombarites-like A lobe and S4 (pl. 4, fig. 1), which shows a reticulate shell ornament with equally strong growth lines and spiral lines. Furthermore, the small triangularly coiled specimens are very unlikely to belong to P. uralicus; most probably they are the juvenile individuals of Dombarites falcatooides.

Family Delepinoceratidae Ruzhencev, 1957

Genus Platygoniatites Ruzhencev, 1956
Platygoniatites molaris Ruzhencev, 1956

Figures 19A, 20A

1956 Platygoniatites molaris sp. nov.; Ruzhencev, p. 158, text-figs 1–3.
1971 Platygoniatites molaris Ruzhencev. – Ruzhencev & Bogoslovskaya, p. 217, pl. 12, figs 2, 3, pl. 13, figs 2–4.

Material. – Five strongly deformed specimens between 40 and 75 mm conch diameter.

Description. – MB.C.25742 (Fig. 19A) is a partly crushed and deformed specimen of about 75 mm conch diameter with a very narrow umbilicus (uw/dm ~ 0.14). Shell ornament is barely visible except for fine spiral lines on the outer flank; the flanks of the steinkern are smooth. Poorly preserved wrinkle layer structures can be seen on the outer flank.

Figure 19. Representatives of the genus Platygoniatites from Družetić; lateral and dorsal views. • A – Platygoniatites molaris Ruzhencev, 1958, specimen MB.C.25742 from loose block 2012-30; × 1. • B – Platygoniatites omninitiratus Ruzhencev & Bogoslovskaya, 1971, specimen MB.C.25730 from loose block 2012-13; × 1.5. • C – Platygoniatites omninitiratus Ruzhencev & Bogoslovskaya, 1971, specimen MB.C.25749.1 from float; × 1.5. • D – Platygoniatites omninitiratus Ruzhencev & Bogoslovskaya, 1971, specimen MB.C.25692.1 from sample 2009-C; × 1.5. • E – Platygoniatites omninitiratus Ruzhencev & Bogoslovskaya, 1971, specimen MB.C.25749.2 from float; × 2.5.

Platygoniatites molaris Ruzhencev, 1956

Figures 19A, 20A

1956 Platygoniatites molaris sp. nov.; Ruzhencev, p. 158, text-figs 1–3.
1971 Platygoniatites molaris Ruzhencev. – Ruzhencev & Bogoslovskaya, p. 217, pl. 12, figs 2, 3, pl. 13, figs 2–4.

Material. – Five strongly deformed specimens between 40 and 75 mm conch diameter.

Description. – MB.C.25742 (Fig. 19A) is a partly crushed and deformed specimen of about 75 mm conch diameter with a very narrow umbilicus (uw/dm ~ 0.14). Shell ornament is barely visible except for fine spiral lines on the outer flank; the flanks of the steinkern are smooth. Poorly preserved wrinkle layer structures can be seen on the outer flank.

Figure 20. Suture lines of Platygoniatites from Družetić; all × 2.5. • A – Platygoniatites molaris Ruzhencev, 1958, specimen MB.C.25748 from float, at 17.2 mm ww, 17.5 mm wh. • B – Platygoniatites omninitiratus Ruzhencev & Bogoslovskaya, 1971, specimen MB.C.25730 from loose block 2012-13, at 14.7 mm ww, 14.2 mm wh.
Specimen MB.C.25748 is a fragment of a strongly deformed specimen with about 50 mm conch diameter. At a diameter of 30 mm, the conch is thickly discoidal and involute (ww/dm ~ 0.50; uw/dm ~ 0.07) with a broadly rounded venter. In this stage the suture line possesses a very wide external lobe with slightly asymmetric lanceolate prongs, a narrowly rounded ventrolateral saddle, and a slightly asymmetric adventive lobe with inflexed flanks (Fig. 20A).

Specimen MB.C.25716 is a somewhat crushed specimen with nearly 40 mm conch diameter. The inner whorl (~ 24 mm dm) shows fine spiral lines on the flank, but on the outer whorl (~ 36 mm dm) the spirals appear to be restricted to the venter.

**Platygoniatites omniliaratus** Ruzhencev & Bogoslovskaya, 1971

Figures 19B–E, 20B

1971 *Platygoniatites omniliaratus* sp. nov.; Ruzhencev & Bogoslovskaya, p. 216, pl. 11, figs 1–5, pl. 12, fig. 1, pl. 13, fig. 1.

**Material.** – Six moderately well preserved specimens between 10 and 40 mm conch diameter.

**Description.** – Specimen MB.C.25730 is a rather well preserved specimen with 40 mm diameter (Fig. 19B). The conch is thickly discoidal (ww/dm ~ 0.50) and involute (uw/dm = 0.08) with subparallel flanks and a continuously rounded venter. Large parts of the specimen are covered with shell material, which shows 50 sharp spiral lines from the umbilicus to the midventer. These spirals are half as wide as their interspaces and possess a fine granulation where they are crossed by the sharp growth lines. The growth lines are biconvex with low lateral projections (of which the dorsolateral projection is higher than the ventrolateral) and a rather deep ventral sinus. The suture line (Fig. 20B) of the same specimen shows a very wide E lobe with wide, weakly asymmetric prongs and a very narrow median saddle that reaches more than half the height of the E lobe depth. The ventrolateral saddle is nearly symmetric tectiform with parallel flanks in the middle part. The adventive lobe is weakly asymmetric and more strongly curved on the ventral side.

Specimens MB.C.25749 (Fig. 19C) and MB.C.25692.1 (Fig. 19D) are deformed individuals with nearly 27 mm and 24 mm diameter, respectively. Their approximated conch proportions are: ww/dm ~ 0.58, uw/dm ~ 0.08. Both show the shell ornament similar to specimen MB.C.25730 with biconvex, sharp growth lines and stronger, granulated spirals. The shell has an ornament with about 45 sharp spiral lines (umbilicus to midventer) and three prominent shell constrictions about 120° apart.

The small specimen MB.C.25749.2 is a juvenile, deformed specimen of 9 mm conch diameter (Fig. 19E); the estimated conch proportions are: ww/dm ~ 0.85, uw/dm ~ 0.14. It is covered with shell. About 40 fine spiral lines can be counted from the umbilical margin to the midventer, they are narrower than the interspaces. Three well-visible shell constrictions appear in a short distance from the umbilical margin, they are most prominent in the midflank area. The outer flank is occupied by a wrinkle structure.

**Remarks.** – The material from Družetić shows the same conch proportions as the Uralian material and the conch ornament does not show significant differences. Despite the comparatively poor preservation of the Serbian material, a specific identification can be stated quite confidently.

Superfamily Somoholitaceae Ruzhencev, 1938
Family Glaphyritidae Ruzhencev & Bogoslovskaya, 1971

**Genus Syngastrioceras** Librovitch, 1938

**Syngastrioceras europaeum** (Kullmann, 1962)

Figure 21

1962 *Eoasianites (Eoasianites) europaeus* Kullmann sp. nov.; Kullmann in Stevanović & Kullmann, p. 92, pl. 2, figs 7, 8.

**Holotype.** – Specimen BEO600-551.73:592-455 (Stevanović Coll.; Natural History Museum Belgrade); illustrated by Stevanović & Kullmann (1962, pl. 2, fig. 8).

**Type locality and horizon.** – Milivojevića Kamenjar site in Družetić (NW Serbia); “lower horizon” of Stevanović & Kullmann (1962), probably *Fayettevillea-Delepinoceras* Genus Zone.

**Material.** – Five specimens in the Natural History Museum Belgrade. New material has not been discovered.

**Description.** – Holotype BEO600-551.73:592-455 from Kullmann (*in* Stevanović & Kullmann 1962, pl. 2, fig. 8) is a rather poorly preserved fragment embedded in dark grey dense limestone. It is, at 48 mm conch diameter, thinly pachyconic (ww/dm ~ 0.67) with a wide umbilicus (uw/dm ~ 0.52) and a strongly depressed whorl profile (ww/wh ~ 2.90). The umbilical margin is narrowly rounded and the broad venter is broadly rounded (Fig. 21A). Shell remains are not visible; one steinkern constriction turns forward to form a broad ventral projection. The suture line has a pouched external lobe with narrow lanceolate prongs, the ventrolateral saddle is weakly angular and the adventive lobe is widely lanceolate with flanks nearly parallel in the upper part (Fig. 21B).

Paratype BEO600-551.73:592-456 (Kullmann *in* Stevanović & Kullmann 1962, pl. 2, fig. 7) is a deformed steinkern specimen of about 28 mm conch diameter. The specimen suffered from rough preparation, and hence the conch dimensions cannot be obtained precisely. It appears that the conch is wider than in the holotype but the umbilicus is narrower. One steinkern constriction turns forward to form a broad ventral projection. The suture line has a pouched external lobe with narrow lanceolate prongs, the ventrolateral saddle is weakly angular and the adventive lobe is widely lanceolate with flanks nearly parallel in the upper part (Fig. 21B).

**Discussion.** – Kullmann (*in* Stevanović & Kullmann 1962, p. 94) described a specimen of only 4 mm diameter as “*Eoasianites (Eoasianites) europaeus*?”. This specimen comes from the “upper horizon” (*Entogonites* Genus Zone); it belongs in the genus *Bollandites*, but specific attribution is impossible. Ruzhencév & Bogoslovskaya (1971, p. 37) regarded the species as an early representative in the evolution of the genus *Glaphyrites*. However, the shapes of the external lobe and the ventrolateral saddle speak for an attribution to the genus *Syngastrioceras*.

Superfamily Neoglyphiocerataceae Plummer & Scott, 1937

Family Cravenoceratidae Ruzhencév, 1957

Subfamily Cravenocerinaceae Ruzhencév, 1957

**Genus Cravenoceras Bisat, 1928**

**Cravenoceras sp.**

Figure 22

**Material.** – One fragmentary specimen.

**Description.** – The single specimen MB.C.25720 is poorly preserved with a conch diameter of about 30 mm. It can only be said that the conch is thickly discoidal with a slightly opened umbilicus. The suture line allows attribution to the genus *Cravenoceras*; it shows a narrow V-shaped E lobe with slightly sinusous flanks, a rounded, weakly tectiform ventrolateral saddle and a nearly symmetric A lobe with curved flanks (Fig. 22).

Subfamily Lyrogoniatitinae Ruzhencév & Bogoslovskaya, 1971

**Genus Lyrogoniatites Miller & Furnish, 1940**

**Lyrogoniatites tener** Ruzhencév & Bogoslovskaya, 1971

Figure 23A

1971 *Lyrogoniatites tener* sp. nov.; Ruzhencév & Bogoslovskaya, p. 277, pl. 29, figs 1–4.

**Material.** – Two specimens, 6 and 25 mm in diameter.

**Description.** – Specimen MB.C.25699.1 is an incomplete and only slightly deformed, fairly well preserved specimen with 24 mm dm (Fig. 23A). The conch is thinly pachyconic (ww/dm ~ 0.65) and subevolute (uw/dm ~ 0.30); the umbilical wall is steep and flat, the umbilical margin is subangular, flanks and venter are broadly rounded. The shell ornament shows spiral lines as the most important elements; there are 20 of such spirals between the umbilical margin and the midventer. They are crossed by much finer growth lines, which extend almost linearly across the flanks and slightly turn forward to form a very low, wide ventral projection. The shell surface shows three constrictions, which follow the growth lines in their course. After the last of
these constrictions, the shell ornament changes in the way that spirals are lacking; instead the growth lines become slightly coarser.

Genus *Tympanoceras* Ruzhencev, 1958

*Tympanoceras* sp.

**Figure 23B**

**Material.** – One deformed specimen.

**Description.** – Specimen MB.C.25751 (Fig. 23B) is strongly deformed and the conch proportions can only be estimated. The conch appears to be rather slender (ww/dm ~ 0.45) and subinvolute (uw/dm ~ 0.25). Three constrictions can be seen on one volution; they extend radially and form a shallow ventral projection.

Family Neoglyphioceratidae Plummer & Scott, 1937

Genus *Neoglyphioceras* Brüning, 1923

*Neoglyphioceras baccans* Ruzhencev & Bogoslovskaya, 1971

**Figure 24A**

1971 *Neoglyphioceras baccans* sp. nov.; Ruzhencev & Bogoslovskaya, p. 313, pl. 35, figs 2–4.

**Material.** – 26 specimens; diameters ranging from 4 mm to 17 mm.

**Description.** – MB.C.25723.1 is a laterally deformed specimen with 17 mm diameter; the conch is thinly pachyconic and subevolute (ww/dm ~ 0.65; uw/dm ~ 0.33) with broadly rounded venter and steep umbilical wall. The entire specimen is covered by strongly recrystallized shell material. 20 coarse spiral lines are present between the umbilical wall and the midventer; they are as wide as their interspaces. One weak and slightly protracting shell constriction is visible on the midflank (Fig. 24A).

*Neoglyphioceras litvinovichae* Ruzhencev & Bogoslovskaya, 1971

**Figure 24B**

1971 *Neoglyphioceras litvinovichae* sp. nov.; Ruzhencev & Bogoslovskaya, p. 317, pl. 36, figs 1–3.

**Material.** – Only one specimen.

**Description.** – MB.C.25736 is a fragment of a laterally distorted and crushed specimen of 20 mm diameter; the conch is thinly discoidal (ww/dm ~ 0.40) and involute (uw/dm ~ 0.09) with nearly parallel flanks and a narrowly rounded venter. A small area shows the shell ornament, this possesses 40 fine spiral lines from the umbilical margin to the midventer. The spiral lines show nearly identical distances and are slightly narrower than their interspaces. Fine biconvex growth lines cross the spiral lines; their course parallels a shell constriction, which is most prominent on the inner flank. The steinkern is smooth but shows a biconvex constriction, which is more prominent than the shell constriction and visible on flank and venter. The two constrictions show a distance of approximately 90° (Fig. 24B).

*Neoglyphioceras* sp.

**Figure 24C**

**Material.** – Five poorly preserved specimens between 6 and 10 mm conch diameter.
Description. – Specimen MB.C.25701 (Fig. 24C) has 10 mm diameter and is thickly discoidal (ww/dm = 0.55) with a narrow umbilicus (uw/dm = 0.13). It possesses sharp spiral lines (30 from umbilicus to umbilicus), which are crossed by much finer growth lines. These turn slightly forward on the flank to form a moderately high ventrolateral projection and a very shallow ventral sinus.

Genus Lusitanites Ruzhencev & Bogoslovskaya, 1971

Lusitanites concavus Ruzhencev & Bogoslovskaya, 1971

Figure 25

1971 Lusitanites concavus sp. nov.; Ruzhencev & Bogoslovskaya, p. 325, pl. 37, figs 5, 6.

Material. – Four specimens which range between 11 and 23 mm conch diameter.

Description. – MB.C.25713.1 is a fragmentary specimen of 22.5 mm diameter, which on one side is entirely covered with strongly recrystallized shell material. The last whorl is deformed, but the conch proportions at 20 mm diameter can be estimated as follows: ww/dm ~ 0.40, uw/dm ~ 0.10. The shell ornament shows 18 sharp spiral lines from the umbilical margin to the midventer; these spirals are about half as wide as their interspaces. The shell surface and the steinkern do not show constrictions (Fig. 25A).

The smaller specimen MB.C.25717 has a 12 mm conch diameter and is only slightly deformed (Fig. 25B). It is thinly discoidal (ww/dm ~ 0.42) with a very narrow umbilicus (uw/dm ~ 0.15) and a very low aperture (WER ~ 1.50). The shell ornaments shows about 20 rounded spiral lines (umbilicus to midventer) and finer growth lines. One curved constriction can be seen on the flank.

Figure 25. Lusitanites concavus Ruzhencev & Bogoslovskaya, 1971 from Družetić; lateral and dorsal views. • A – specimen MB.C.25713.1 from loose block 2011-1; × 2. • B – Specimen MB.C.25717 from float (foot of the rock); × 2.5.

Family Rhynocerotidae Ruzhencev & Bogoslovskaya, 1971

Genus Ophilyroceras Ruzhencev & Bogoslovskaya, 1971

Ophilyroceras tersum Ruzhencev & Bogoslovskaya, 1971

Figure 26A–C


Material. – Four moderately well preserved but fragmentary specimens between 15 and 24 mm conch diameter.

Description. – Specimen MB.C.25702.1 is a strongly deformed conch with about 24 mm diameter (Fig. 26A). It is extremely discoidal and subevolute (uw/dm ~ 0.40) with a laterally compressed whorl profile. The shell ornament consists of coarse spiral lines, which are a little wider than their interspaces. From umbilicus to midventer, about 24 spirals can be counted. The steinkern is
smooth except for barely visible impressions of the spiral lines and a forward-bending constriction, which forms a moderately high ventrolateral projection and a shallow ventral sinus.

The smaller specimens MB.C.25702.2 (~12 mm dm; Fig. 26B) and MB.C.25732 (~15 mm dm; Fig. 26C) differ from the preceding specimen in the presence of distinct shell constrictions. At this stage, the whorl profile is depressed or circular.

**Genus Rhymnoceras Ruzhencev, 1958**

**Rhymnoceras gracilentum Ruzhencev, 1958**

Figure 26D

1958 *Rhymnoceras gracilentum* sp. nov.; Ruzhencev, p. 294, text-figs 1e–z, 2e.
1962 *Rhymnoceras gracilentum* Ruzhencev. – Kullmann in Stevanović & Kullmann, p. 75, pl. 1, fig. 2, text-fig. 3a.

**Material.** – One specimen from new collections and three specimens in the Natural History Museum, Belgrade.

**Description.** – Specimen BEO600-551.73:592-486 (Kullmann in Stevanović & Kullmann 1962, pl. 1, fig. 2) is a deformed specimen of about 20 mm conch diameter; it is extremely discoidal (ww/dm ~ 0.30) and widely umbilicate (uw/dm ~ 0.55) with a rounded, slightly depressed whorl profile (ww/wh ~ 1.15) and a moderately low coiling rate (WER ~ 1.75). The specimen shows a coarse reticulate shell ornament consisting of spiral lines (about 30 from umbilicus to umbilicus) and coarse, riblet-like growth lines (which extend with a forward direction on the flank and a very shallow ventral sinus) with approximately equal strength. Several constrictions are visible on the shell; they are accompanied by a bulge on the apical side. The steinkern shows only radial riblets.

The smaller specimen MB.C.25752 (Fig. 26D) has, at a diameter of 16 mm, very similar conch dimensions. It is fully covered with shell showing the reticulate ornament with protracting riblet-like growth lines and coarse spiral lines.

**Superfamily and family uncertain**

**Druzeticia gen. nov.**

**Type species.** – *Druzeticia decens* gen. et sp. nov.

**Derivation of name.** – Named after Družetić, the village where the section Milivojevića Kamenjar is located.

**Diagnosis.** – Small ammonoids with thickly discoidal to pachyconic conch and nearly closed umbilicus. Ornament with coarse and sharp radial riblets and delicate spiral lines between the riblets.

**Included species.** – *decens*: *Druzeticia decens* gen. et sp. nov.; Serbia.

**Discussion.** – This new enigmatic genus can at current state and without knowledge of the suture line not be attributed to any of the Carboniferous ammonoid families. In the conch shape and ornament, there are some superficial similarities to the families Prionoceratidae and Goniatitidae.

**Druzeticia decens sp. nov.**

Figure 27

**Holotype.** – Specimen MB.C.25670.1, illustrated in Fig. 27A.

**Type locality and horizon.** – Milivojevića Kamenjar site in Družetić (NW Serbia); sample 2009-DRZ2, *Ubites filipovići* horizon, *Entogonites* Genus Zone.

**Material.** – 83 specimens with conch diameters up to 10 mm.

**Etymology.** – After the Latin *decens* (= graceful), because of the small, nicely ornamented conch.

**Diagnosis.** – As for the genus.

**Description.** – Holotype MB.C.25670.1 (Fig. 27A) is the best of the numerous specimens and it is, with 9 mm conch diameter, one of the largest individuals. It is a pachyconic conch (ww/dm ~ 0.73) with a nearly closed umbilicus (uw/dm ~ 0.08). The conch is thickest near the umbilicus, from where the flanks converge towards the broadly rounded venter. The shell ornament consists of two elements, (1) rather coarse riblets, which have a weakly protracted but otherwise linear direction on the flank and form a low and wide ventral projection and (2) very fine spiral lines, which are visible between the riblets and stand in distance of about 0.5 mm. The shell surface shows two constrictions, which in their course largely follow the growth lines.

The material shows some variability with respect to the thickness of the conch. Paratypes MB.C.25670.2 (Fig. 27B) and MB.C.25670.3 (Fig. 27C) have, at the same diameter, a more slender conch (ww/dm ~ 0.55), but differences may
also be caused by deformation. However, the two specimens show also variability in the strength of the riblets; in paratype MB.C.25670.3 they are much finer and more densely spaced that in the holotype and paratype MB.C.25670.2. Both specimens show one constriction. The smaller paratypes MB.C.25670.4 and MB.C.25670.5 (Fig. 27D, E) with about 7 mm diameter are stout with an extremely narrow umbilicus. Both possess fine riblets, which in their course are more strongly bent forward in paratype MB.C.25670.5. Specimen MB.C.25670.4 does not show constrictions, but MB.C.25670.5 has three constrictions spaced in distances of 120 degrees. The smallest specimens have a conch diameter of 3 mm; they do not significantly differ in their morphology from the larger ones, except for a slightly wider umbilicus.

Remarks. – The new species does not closely resemble any known ammonoid species. Unfortunately, a suture line could not be seen in the material, and hence a clear
attribution of the new species to an ammonoid family is not possible.

Order Prolecanitida Miller & Furnish, 1954
Suborder Prolecanitina Miller & Furnish, 1954
Superfamily Prolecanitaceae Hyatt, 1884
Family Prolecanitidae Hyatt, 1884

Genus Prolecanites Mojsisovics, 1882

Prolecanites stevanovici sp. nov.
Figures 28, 29

1962 Metacanites chancharensis (Ruzhencev). – Kullmann in Stevanović & Kullmann, p. 103, pl. 4, fig. 5 (only).

Holotype. – Specimen MB.C.25657.1; illustrated in Fig. 28A.

Type locality and horizon. – Milivojevića Kamenjar section, Družetić (NW Serbia); from sample 2012-DRZ2, Ubites filipovici horizon, Entogonites Genus Zone.

Material. – 78 newly collected specimens up to 62 mm conch diameter; also three specimens in the Natural History Museum, Belgrade.

Etymology. – Named after Petar Stevanović (1914–1999) who discovered the fossil locality.

Description. – Holotype MB.C.25657.1 is a deformed but otherwise rather well-preserved specimen of 62 mm diameter (Fig. 28A), in which the conch proportions can be estimated as follows (without deformation of the last volute): the conch is extremely discoidal and subevolute (ww/dm ~ 0.22, uw/dm ~ 0.40) with a compressed whorl profile (ww/wh ~ 0.60) and rapidly expanding whorls (WER ~ 2.50). The whorl cross section is compressed and oval in the penultimate whorl; it becomes laterally flattened with subparallel flanks in the last volute, where the umbilical wall is steeper. The shell appears to be smooth, but fine convex growth lines are visible in the inner whorls.
Smaller specimens such as paratypes MB.C.25673.1 (Fig. 28B) with 13 mm conch diameter and MB.C.25637 (Fig. 28C) with 10 mm conch diameter have similar conch proportions but possess a wider whorl profile (ww/wh ~ 0.90 and 1.00, respectively). The first specimen shows the well-preserved shell ornament, which consists of fine growth lines extending with a projection on the flank and a wide and very shallow ventral sinus.

A suture line can be seen in the small specimen MB.C.25683.1 at 4.5 mm whorl height (Fig. 29). The dominant sutural element is the very large and pouched E lobe, which is much deeper than the slightly pouched, blunt A lobe. The lateral lobe is pouched and continuously rounded.

**Discussion.** – Obviously, the new species is, with a ww/dm ratio of about 0.22 and a ww/wh ratio of about 0.60 at 40 mm conch diameter, the most slender species of the genus. The species *P. discoides* (Foord & Crick) for instance shows ratios of 0.30 and 0.80–0.90 in this growth stage, similar ratios can be seen in most of the other species of *Prolecanites*.

**Genus Dombarocanites Ruzhencev, 1949**

*Dombarocanites catillus* Ruzhencev & Bogoslovskaya, 1971

Figure 30

1971 *Dombarocanites catillus* sp. nov.; Ruzhencev & Bogoslovskaya, p. 135, pl. 1, figs 8, 9.

**Material.** – Six rather poorly preserved specimens from new collections; they range between 12 and 30 mm in diameter.

**Description.** – Specimen MB.C.25747 belongs to the better preserved specimens; it has 30 mm conch diameter and is extremely discoidal (ww/dm ~ 0.26) with a rather wide umbilicus (uw/dm ~ 0.43). The whorl profile is compressed and the shell surface appears to be smooth (Fig. 30A).

Family Daraelitidae Tchernow, 1907

**Genus Praedaraelites Schindewolf, 1926**

*Praedaraelites aktubensis* Ruzhencev, 1949

Figure 31

1949 *Praedaraelites aktubensis* sp. nov.; Ruzhencev, p. 740, text-figs 1i–n, 2e, 3c.

1962 *Metacanites chancharensis* (Ruzhencev). – Kullmann in Stevanović & Kullmann, p. 103, pl. 4, fig. 4 (only).

1971 *Epicanites aktubensis* (Ruzhencev). – Ruzhencev & Bogoslovskaya, p. 132, pl. 1, figs 10–13, pl. 2, figs 1, 2.

**Material.** – Five rather strongly deformed specimens of 20 to 30 mm conch diameter from new collections and about five specimens in the Natural History Museum, Belgrade.

**Description.** – MB.C.25737.1 is a poorly preserved deformed specimen with 32 mm diameter (Fig. 31B). The conch is extremely discoidal and subinvolute (uw/dm ~ 0.25) with oval, compressed whorl cross section. The shell surface is smooth.

Specimen BEO600-551.73:592-455 (Kullmann in Stevanović & Kullmann 1962, pl. 4, fig. 4) is a rather well-preserved individual with 27 mm conch diameter (Fig. 31C). It is extremely discoidal (ww/dm ~ 0.30) and subevolute (uw/dm ~ 0.32) with a high aperture (WER ~ 2.35). The specimen is almost entirely covered with nearly smooth shell and the suture line is not visible.

Specimen MB.C.25750 (Fig. 31A) is a specimen of about 30 mm conch diameter, of which particularly the body chamber is strongly deformed. It is extremely discoidal and subevolute (ww/dm ~ 0.30; uw/dm ~ 0.33) with a compressed oval whorl profile at 25 mm diameter. The shell surface appears to be smooth.

**Remarks.** – Parts of the suture line are only visible in
specimen MB.C.25709 they show a serrated adventive lobe and an inflated ventrolateral saddle. The absence of suture lines in the other specimens may prevent clear assignment to the genus *Praedaraelites*, but the whorl expansion rate of 2.35 (about 2.80 in *Dombarocanites chancharensis* at the same conch diameter) and the combination of a comparatively narrow umbilicus with a rather wide whorl profile and a rather high embracing rate of the whorls speaks for assignment to this genus rather than in *Dombarocanites*.

**Superfamily Medlicottiaceae Karpinsky, 1889**
**Family Pronoritidae Frech, 1901**
**Genus *Uralopronorites* Librovitch, 1949**

*Uralopronorites mirus* Librovitch, 1949

**Figure 32**

1949 *Uralopronorites mirus* sp. nov.; Librovitch in Ruzhencev, p. 63, pl. 1, figs 10–15, text-figs 24, 25.
1962 *Pronorites uradensis uradensis* Karpinsky. – Kullmann in Stevanović & Kullmann, p. 107, pl. 4, fig. 6, text-fig. 7b.

**Material.** – Three poorly preserved fragments from new collections; their species attribution is not clear. There are additionally about eight specimens in the Natural History Museum, Belgrade.

**Description.** – Specimen BEO600-551.73:592-463 (Kullmann in Stevanović & Kullmann 1962, pl. 4, fig. 6) is incomplete; the conch is thinly discoidal (ww/dm ~ 0.40) and subinvolute (uw/dm ~ 0.17) at 25 mm diameter. The flanks of the specimen are flat and separated from the nearly flat venter by a subangular ventrolateral margin (Fig. 32A). Five successive suture lines show a very narrow external lobe, a deep and pouchèd, asymmetric adventive lobe that is deeper than the lateral lobe and five further lobes on the flank (Fig. 32B).

**Acknowledgements**

We particularly acknowledge Divna Jovanović, Ivan Filipović (both Belgrade) and Matevž Novak (Ljubljana) for their intense assistance in the field. Aleksandra Stevanović made the collections of the Natural History Museum, Belgrade available for study. Dieter Korn acknowledges the Deutsche Forschungsgemeinschaft (DFG project Ko1829/8-1) for financial support. Special thanks to J. Eiven Stenzel (Berlin) for preparation and Ana Suchocka (Berlin) for photography of the specimens. We further thank Sonny A. Walton (Potsdam) for checking the language of the manuscript and Claude Monnet (Lille) and an anonymous reviewer for constructive suggestions.

**References**

Foord, A.H. 1903. Monograph of the Carboniferous Cephalopoda of Ireland, Part V, Containing the families Glyphioceratidae (concluded) and Prol ine cintidae, with title-page and index. *Transactions of the Palaeontographical Society* 57, 147–234.
### List of co-occurrences of ammonoid species in samples and loose blocks from new collections.

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**Appendix**

List of co-occurrences of ammonoid species in samples and loose blocks from new collections.