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Early and Middle Callovian ammonites from the Pieniny Klippen Belt (Western Carpathians) in hiatal successions: unique biostratigraphic evidence from sediment-filled fissure deposits

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With 8 figures and 1 table

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Abstract: In the Pieniny Klippen Belt (West Carpathians), the upper Middle Jurassic (Callovian) sediments are mostly represented by deep-water radiolarites that were deposited in slope and basinal environments of the Kysuca Basin in the northwestern Tethys. The contemporaneous depositional conditions from shallow environments of the Czorsztyn Ridge are poorly known owing to the Upper Bathonian – Lower Oxfordian hiatus that is extensively developed in the Pieniny Klippen Belt. However, submarine fissures (neptunian dykes) related to extensional fracturing were filled with unlithified carbonate during this period and thus provide unique information about sediments and fossil assemblages that are otherwise missing in normal stratigraphic position. In hiatal successions, such sediments were not deposited on exposed surfaces owing to sediment bypassing and winnowing. The absence of borings and encrusters on the walls of the dykes indicates that such fissures were filled relatively rapidly with sediment, thus also enhancing preservation of fossil assemblages. In addition to brachiopods, bivalves, and gastropods, some dykes contain ammonites that represent biostratigraphic zones that were not recorded in the West Carpathians until now. They include the Lower Callovian Gracilis Zone and the Middle Callovian Coronatum Zone. Ammonite assemblages in the Callovian dykes are dominated by phylloceratids and lytoceratids. Ammonitina are almost exclusively represented by microconchs or juveniles. This size-selective preservation can reflect sorting of shells within fissures that eliminated large-sized microconchs and macroconchs, and/or higher susceptibility to damage of large-sized ammonites on the exposed sea-floor. Relatively rare kosmoceratid ammonites that are preserved in the Lower Callovian assemblages indicate that the Czorsztyn Ridge was situated within the area of the Subboreal influence.

Key words: Carpathians, Jurassic, Callovian, neptunian dykes, palaeobiogegraphy, ammonites, benthic community.

1. Introduction

The Pieniny Klippen Belt (PKB) is a compressed tectonic structure situated between the Central Carpathians and the Outer Carpathians, and located in the northwestern Tethys during the Jurassic. It represents a relict of a deep-water basin (Kysuca Basin) that was bordered in the northern parts by a pelagic carbonate platform (Czorsztyn Ridge with the so-called Czorsztyn Succession) and slope environments. Shallow-platform and slope deposits of the Czorsztyn Ridge record successions that contain abundant Lower

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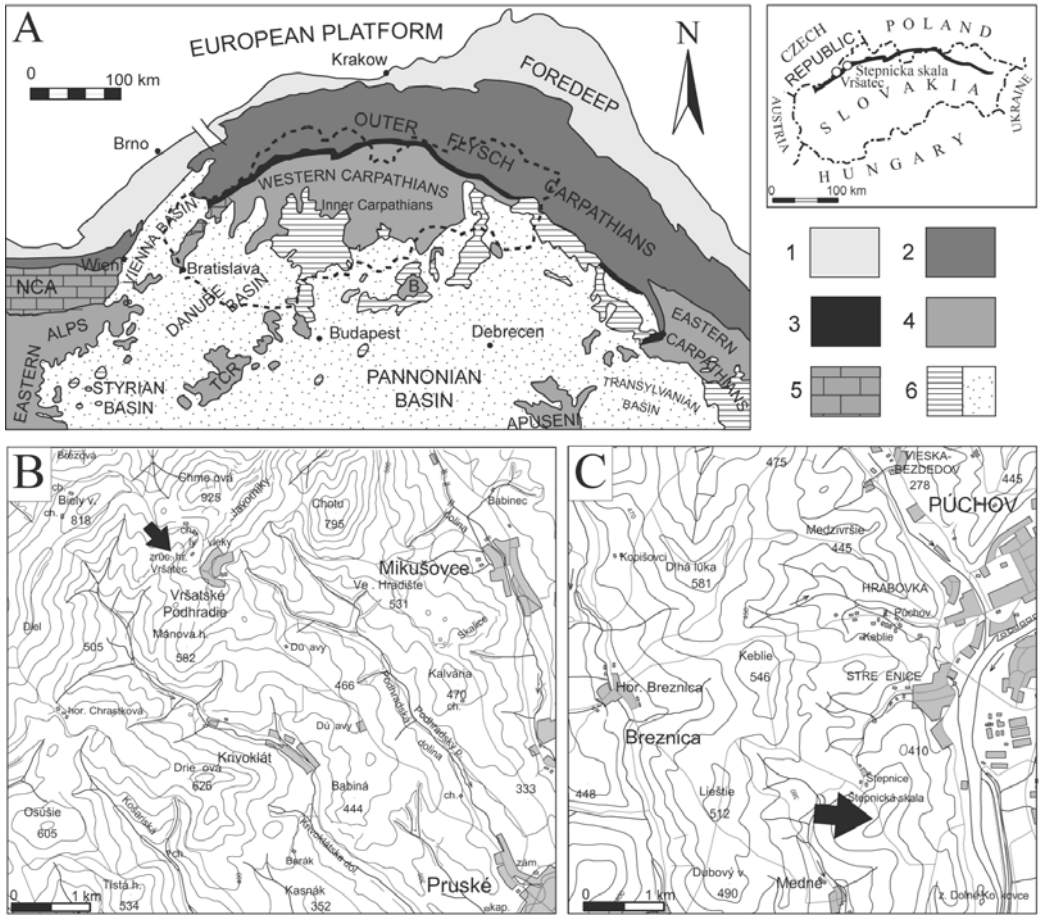

Fig. 1. Geographical and geological setting. A. Geological scheme of Central Europe, with the position of the Pieniny Klippen Belt (simplified from Kováč, 2000). B. Vršatec Klippen. C. Štepnická Skala. 1. Carpathian Foredeep. 2. Outer Flysch Belts. 3. Pieniny Klippen Belt. 4. Alpian-Carpathian-Dinaride and Pannonian internids. 5. Northern Calcareous Alps. 6. Neogene volcanics. B – Bükk, NCA – Northern Calcareous Alps, TCR – Transdanubian Central Range.

Jurassic (e.g. Rakús, 1993, 1995), Middle Jurassic (Schlögl & Rakús 2004; Schlögl et al. 2005, 2006; Wierzbowski et al. 1999) and Upper Jurassic macrofauna (Neumayr 1871a, b; Uhlig 1878, 1881; Kutek & Wierzbowski 1986). Several studies revealed presence of relatively long stratigraphic hiatuses in the Lower Bajocian (Krobicki & Wierzbowski 2004), in the Upper Bajocian (Wierzbowski et al. 2004), and especially in the Lower Callovian – Lower Oxfordian. The stratigraphic span of this last hiatus can be locally even longer, encompassing the uppermost Bajocian up to the Lower Tithonian. Similarly long hiatuses, frequently recorded by submarine hardgrounds of the Middle Jurassic – Oxfordian age, are captured by shallow-platform deposits in other parts of the northwestern Tethys (e.g. Santantonio 1993; Cecca et al. 2005; Collin et al. 2005; O'Dogherty et al. 2006). These hiatuses commonly correlate with extensive biosiliceous sedimentation and mark carbonate production crisis related to low rate of platform carbonate production and/or intense scouring current activity (Bartolini et al. 1996; Bartolini & Cecca 1999). The deposits corresponding to these intervals are almost completely absent in normal stratigraphic position in the Czorsztyn Succession in the whole Pieniny Klippen Belt. Lower Callovian and Upper Callovian ammonites that were described from the Czorsztyn Succession are represented by rare and poorly preserved specimens only (Wierzbowski et al. 1999).

However, new findings demonstrate that some Callovian deposits are preserved in sediment-filled fissures that are represented by neptunian dyke infillings (i.e., sheet-like carbonate deposits filling

fissures that originated by extensional fracturing of lithified sediment, e.g., Bouillin & Bellomo 1990; Lehner 1991; Winterer et al. 1991; Winterer & Sarti 1994; Martire 1996; Luczynski 2001; Wall & Jenkyns 2004). Neptunian dykes in the Czorsztyn Succession are relatively common but are mostly filled with micritic sediment with rare macroinvertebrate remains and their age assignment is based on microfacies composition with low temporal resolution (Mišík 1979). One of the few sections that were assumed to represent a continuous sedimentary Middle – Upper Jurassic succession is the Babiarzowa Skala section (Uhlig 1878, 1881). However, new findings indicate that the Uhlig's assemblages were also derived from thin neptunian dykes more or less parallel with stratification (Wierzbowski et al. 2005).

The aim of this study is to describe several dykes that (1) reveal information about composition of fossil assemblages that inhabited shallow platforms of the Pieniny Klippen Belt during the Callovian and were not preserved in normal stratigraphic position, (2) provide new insights into completeness and temporal resolution of the Czorsztyn Succession, and (3) allow paleobiogeographical comparisons with other fossil assemblages from neighbouring regions. Fossil assemblages in these neptunian dykes are characterized by the absence of larger ammonites and high abundance of microconchs and juveniles. Therefore, the composition of ammonite assemblages might be not representative of the contemporaneous ammonite associations owing to peculiar depositional environment and size-selective preservation and transport of ammonites in the dyke system.

2. Geological setting

In this study, we evaluate Callovian dyke deposits with ammonite assemblages that occur in the Štepnická Skala locality, and Bathonian – Callovian dyke deposits that were identified in the Vršatec locality. These two localities belong to the Czorsztyn Unit of the Pieniny Klippen Belt and are situated in the eastern part of Biele Karpaty Mts. in Western Slovakia (Fig. 1). The Vršatec locality consists of two blocks (klippen) – the Vršatec Castle Klippe in the southwestern part of the locality and the Vršatec-Javorníky Klippe in its north-eastern part (Schlögl et al. 2006). Dyke deposits with Callovian ammonites were found in the Vršatec Castle Klippe. The third locality with possibly Callovian ammonites, not treated in this study, is preserved in dykes in the Babiarzowa Skala section in the Polish part of the Pieniny Klippen Belt (Uhlig 1878, 1881; Wierzbowski et al. 2005).

3. Description of stratigraphic sections

3.1. Vršatec

The Vršatec locality is characterized by the presence of 15 m thick coral biohermal limestones and peribiohermal breccias of the Lower Bajocian (Vršatec Limestone, Fig. 2; Schlögl et al. 2006). They are overlain by thick complex of crinoidal limestones of upper Lower and Upper Bajocian (Smolegowa and Krupianka Formations). Thickness of crinoidal limestones attains 50 metres, although it can be laterally reduced to a few metres only. The top of crinoidal limestones is marked by a distinctive discontinuity with Fe-Mn hardground. The uppermost Bajocian to Lower Tithonian deposits are represented by the Bohunice and Czorstyn formations that consist of highly condensed micritic and red nodular limestones. Thickness of these deposits varies between 20 cm and 15 metres. These two formations also comprise the Callovian – Lower Oxfordian hiatus. The duration of the hiatus is variable, mostly encompassing the Callovian-Lower Oxfordian, but locally extending from the Upper Bajocian up to the Lower Tithonian. Their transition to overlying micritic and bioclastic deposits of the Dursztyn Formation (Tithonian – Berriasian) is relatively gradual, without any marked discontinuity. 26 m-thick Dursztyn Formation is terminated by an irregular surface with signs of subaerial exposure and karstification (Aubrecht et al. 2006). Neptunian dykes are mainly developed in biohermal limestones of the Vršatec Limestone and in crinoidal limestones of the Krupianka and Smolegowa Formations. The whole succession is in overturned position.

3.2. Štepnická Skala

The Štepnická Skala section represents an abandoned quarry in the Bajocian – Kimmeridgian strata in overturned stratigraphic position. It is characterized by rapid lateral and vertical changes in bed thickness and sediment composition. 10 m-thick crinoidal limestones of the Smolegowa Formation (Fig. 3) are overlain by red nodular, poorly nodular or non-nodular micritic limestones, locally rich in crinods, belonging to the Czorsztyn and/or the Bohunice formations of the Early Bathonian to Early Callovian age. The boundary between crinoidal and nodular limestones is marked by a hardground with Fe-Mn encrusta-

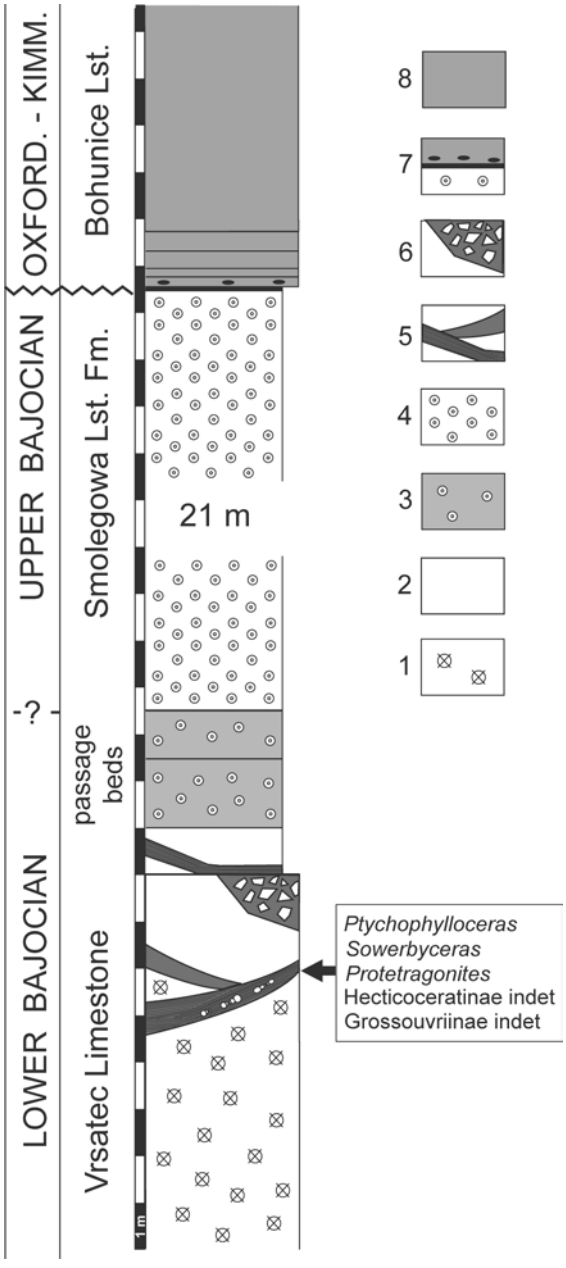

Fig. 2. Vršatec section. 1. Coral biohermal limestone. 2. Peribiohermal limestone. 3. Pink micritic limestones with dispersed crinoidal particles. 4. White crinoidal grainstones. 5. Neptunian dykes, with laminated or massive infillings. 6. Dykes and cavities with breccia infilling. 7. Hardground. 8. Red micritic limestones.

tions and *Frutexites*-like microbialites. A single specimen of *Bullatimorphitus* (*Kheraiceras*) gr. *bullatus* (D'Orbigny, 1846) was collected from the uppermost layer of nodular limestones, indicating the Lower Callovian Bullatus Zone. Locally, a several meters-thick set of crinoidal grainstones and packstones with cm-thick lenses rich in brachiopods (Štepnica Formation) overlies red nodular limestones. This shell-rich facies is unique because it probably captures the Callovian sediments that were deposited directly on the exposed sea bottom and not in protected neptunian dykes. Middle Oxfordian deposits are represented by ammonite shell beds, followed by micritic limestones with crinoids (*Saccocoma*), probably of Kimmeridgian age. Neptunian dykes are almost parallel with stratification and are located in the Smolegowa Formation and in red poorly nodular or non-nodular limestones of the Czorsztyn and/or Bohunice formations.

4. Description of neptunian dykes

4.1. Vršatec

In contrast to the the Vršatec-Javorníky Klippe with rare dykes and several decametres of the Middle Jurassic crinoidal limestones, the neptunian dykes are extensively developed in the Vršatec Castle Klippe that is characterized by the presence of locally highly reduced, several m-thick crinoidal limestones. The dykes are parallel, diagonal or perpendicular to normal bedding and are filled with red micrites or breccias with red micritic matrix (Fig. 2). Ammonites were collected from a diagonal dyke situated in the uppermost part of the biohermal Vršatec Limestone. It is a 60 cm-thick fissure with complex infilling consisting of finely laminated red mudstone to wackestone. Some laminae consist of densely-packed thin-shelled bivalves (*Bositra*). Non-laminated layers contain dense *Chondrites*-like bioturbation. One 5 cm-thick layer contains rare invertebrate macrofauna with gastropods and ammonites. They include *Ptychophylloceras* and other Phylloceratina, Lytoceratina, and small fragments of perisphinctid and hecticoceratid ammonites. Ammonite specimens are fragmented, coated with mineralized crusts, and smaller than 2 cm.

4.2. Štepnická Skala

Neptunian dyke 1 (ND-1)

A 45 cm-thick complex neptunian dyke is parallel with bedding. It shows a polyphase infilling with six layers that can be distinguished on the basis of microfacies composition.

Layer 1. A 15 cm-thick, red, indistinctly nodular wackestone/floatstone with dispersed crinoidal particles.

Layer 2. A 10 cm-thick red wackestone without macrofauna.

Layer 3. A 5 cm-thick red wackestone without macrofauna.

Layer 4. A 5 - 10 cm-thick reddish, well-sorted crinoidal grainstone, with crinoidal ossicles up to 2 mm, and with dispersed larger bioclasts, mainly ammonites, bivalves and brachiopods. Ammonites are small and fragmented, randomly oriented, showing polarity structures that are concordant with bedding. The fossil assemblage is dominated by Phylloceratina (*Sowerbyceras* cf. *subtortisulcatum* (Pompeckj, 1893), *Holcophylloceras* sp., *Ptychophylloceras* (*Tatrophylloceras*) sp.) and Lytoceratina (?*Protetragonites* sp.). Ammonitina, represented by Lissoceratidae, Oppeliidae, Reineckeiidae, Perisphinctidae, and Kosmoceratidae, are rare. The size of bioclasts does not exceed 5 cm. This facies is similar to crinoidal packstones and grainstones of the Štepnica Formation (Callovian). However, the relationship between the dyke and the Štepnica Formation remains uncertain owing to debris and vegetation cover.

Layer 5. A 10 cm-thick red wackestone/floatstone contains Mn oncoids up to 5 cm in a diameter and numerous brachiopods.

Layer 6. A 10 cm-thick red wackestone/floatstone with dispersed fragments of Mn crusts and tiny crinoidal debris.

Neptunian dyke 2 (ND-2)

An about 140 cm-thick dyke shows a polyphase infilling with at least 3 or 4 layers rich in ammonites. The rest of the dyke consists of red micritic limestone that laterally passes into laminated red limestone. Red micrites are represented by mudstones, wackestones and packstones with abundant thin-shelled bivalves (*Bositra*), ammonites, planktic algae (*Globochaete*), juvenile gastropods, common calcitized siliceous sponges, crinoids, benthic foraminifers, and rare smooth ostracods, brachiopod, bivalve, and aptychi fragments. Planktic foraminifers are locally also common. Larger bioclasts are generally bored, Fe-impregnated and encrusted. Ammonite fragments are locally dissolved and replaced by internal micrite. Lithoclasts are encrusted by microbial coatings and matrix is bioturbated.

Layer 1. A 30 cm-thick layer with incomplete and randomly oriented ammonites. The assemblage is dominated by Phylloceratina 93 %, especially by *Ptychophylloceras* (*Tatrophylloceras*) (62 %). The size of ammonites does not exceed 5 cm.

Layer 2. A 46 cm-thick, ammonite-rich bed can be subdivided in three layers:

Layer 2 A – lower part. Ammonites are well preserved and oriented concordantly with stratification. They are dominated by Phylloceratina (*Holcophylloceras, Ptychophylloceras* (*Tatrophylloceras*), *Adabofoloceras*, 47 %) and Lytoceratina, probably all belonging to the genus *Protetragonites* (46 %). Ammonitina represented by perisphinctid and reineckeiid taxa are rare (4 %). The size of ammonites does not exceed 7 cm.

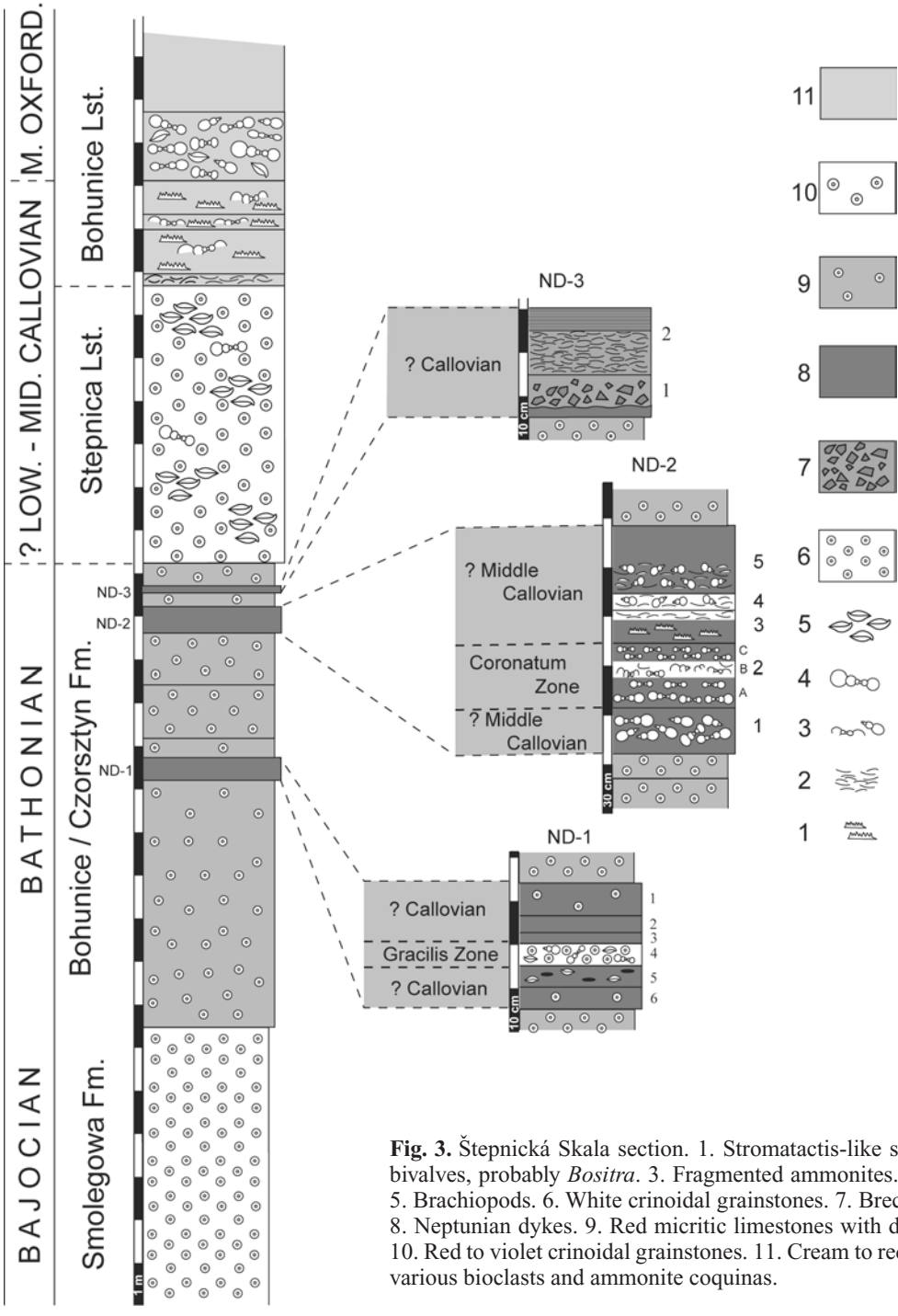

Fig. 3. Štepnická Skala section. 1. Stromatactis-like structures. 2. Thin-shelled bivalves, probably *Bositra*. 3. Fragmented ammonites. 4. Complete ammonites. 5. Brachiopods. 6. White crinoidal grainstones. 7. Breccia in the dyke infillings. 8. Neptunian dykes. 9. Red micritic limestones with dispersed crinoidal debris. 10. Red to violet crinoidal grainstones. 11. Cream to red micritic limestones with various bioclasts and ammonite coquinas.

Layer 2 A – upper part. Ammonites are well preserved, well sorted, and oriented concordantly, with shell size up to 6 cm. The assemblage is dominated by abundant phylloceratid ammonites (34 %) and less common lytoceratid ammonites (19 %), which are represented by the same taxa as in the lower part of the layer. One 3 cm-thick interval is dominated by Ammonitina (47 %) that are almost exclusively represented by Hecticoceratinae (11 %) and Grossouvriinae (31 %). Lissoceratidae are rare (4 %). This layer contains rare gastropods, bivalves and belemnites.

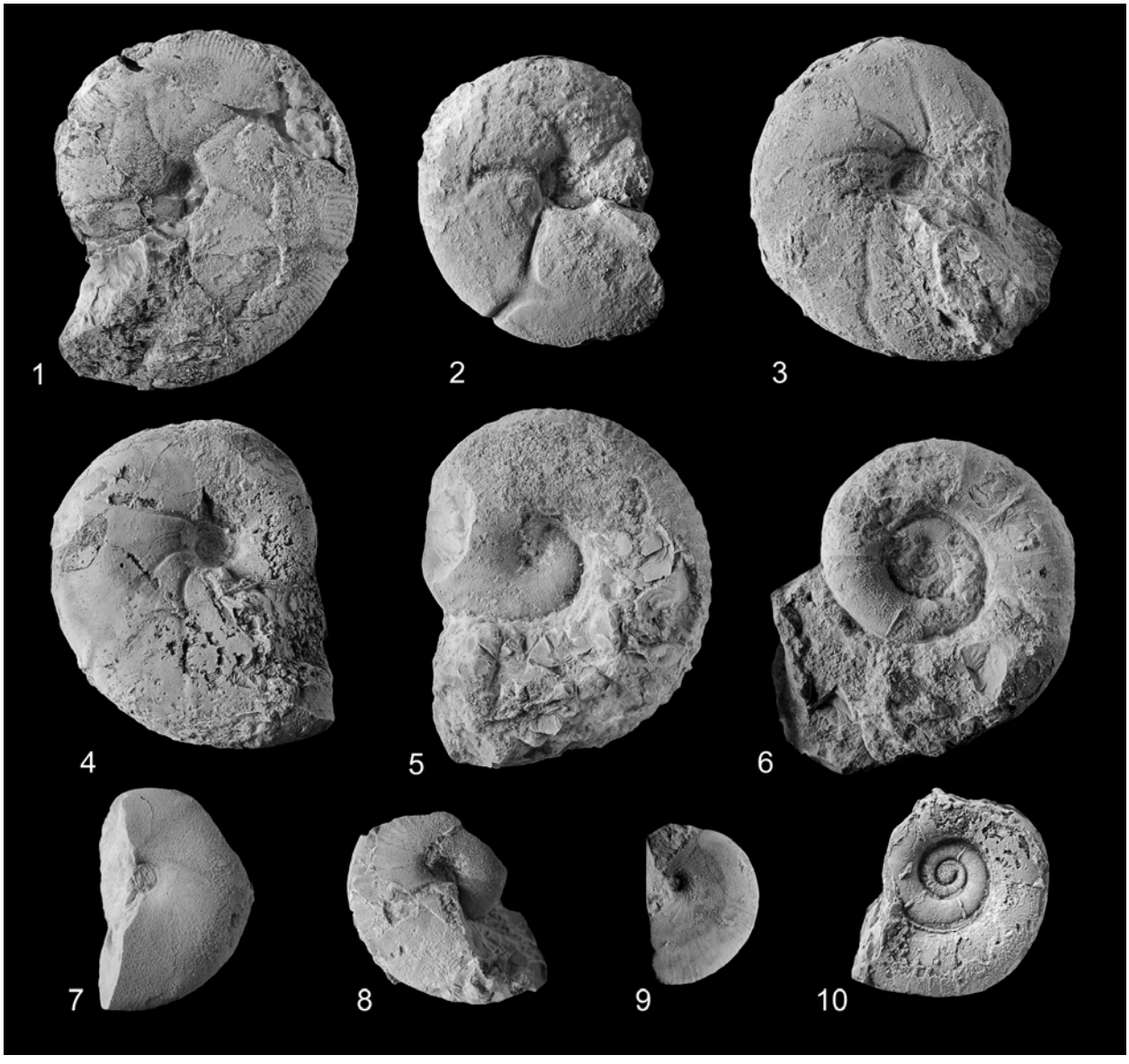

Fig. 4. 1-2 – *Holcophylloceras zignodianum* (D'ORBIGNY, 1848). **3-4, 7** – *Ptychophylloceras* (*Tatrophylloceras*) *euphyllum* (NEUMAYR, 1870). **5, 8** – *Adabofoloceras* sp., on the bigger specimen, part of the body chamber was removed to see the morphology of the internal whorls. **6, 10** – *Protetragonites* sp. **9** – *Adabofoloceras subobtusum* (KUDERNATSCH, 1852). Except specimen of Fig. 4.9 the all other specimens come from the Štepnická Skala ND-2, late Middle Callovian. The specimen 4.9 comes from the Vršatec, Upper Bathonian or Callovian in age. Natural size.

Layer 2 B. Grainstone with bioclasts, mainly ammonites up to 1 cm, randomly oriented, fragmented.

Layer 2 C. Wackestone and packstone composed mainly of randomly oriented juvenile ammonites, with polarity structures concordant with bedding.

Layer 3. A 20 cm-thick red wackestone/floatstone with stromatactoid structures and dispersed ammonite fragments.

Layer 4. A 10 cm-thick grainstone formed by thin-shelled bivalves and dispersed ammonite fragments.

Layer 5. A 40 cm-thick wackestone-packstone with thin-shelled bivalves and dispersed ammonite fragments in the lower part, and red wackestone without macrofossils in the upper part.

Neptunian dyke 3 (ND-3)

This 26 cm-thick dyke consists of two, 10 cm and 16 cm thick layers.

Layer 1. The base of the layer represents a host rock formed by packstones and wackestones with thin-shelled bivalves (*Bositra*). Angular clasts that occur in the dyke were derived from such rock type during its fracturing and opening. The matrix of the breccia is represented either by laminated or bioturbated mudstone. Some laminae have a peloidal texture and faecal pelets occur in the burrow infillings. Ostracods of the genus *Pokornyopsis* that typically occur in cryptic (cave) habitats are common in the matrix.

Layer 2. The lower part represents laminated mudstone to wackestone with various bioclasts, with their long axis oriented parallel to stratification. Larger bioclasts are often bored and Fe-impregnated. Ammonite fragments are often dissolved and shell walls are filled with internal micrite. The upper part of this layer is formed by laminated mudstone. Ribbed ostracods (*?Pokornyopsis*) are abundant.

4. Systematic palaeontology

Type specimens are housed in the collection of the Slovak National Museum in Bratislava (SNM Z …), other ammonites are stored in the Department of Geology and Paleontology, Faculty of Sciences, Comenius University in Bratislava (coll. Schlögl), and brachiopods (coll. Tomašových) and bivalves (coll. Golej) in the Geological Institute, Slovak Academy of Sciences in Bratislava. Ammonite shell measurement data are summarized in Tab. 1.

Family Phylloceratidae Zittel, 1884
Subfamily Phylloceratinae Zittel, 1884

Remarks: Phylloceratina and Lytoceratina represent the major part of the fossil assemblages. In the Štepnická Skala section (ND-2), the *Ptychophylloceras* (*Tatrophylloceras*) *euphyllum* (Neumayr, 1870) (Fig. 4.3, 4.4, 4.7) is the most abundant taxon. It is accompanied by less abundant *Holcophylloceras zignodianum* (D'Orbigny, 1848) (Fig. 4.1, 4.2) and rare *Adabofoloceras*, probably represented by a new species (Fig. 4.5, 4.8). This genus is represented in the Vršatec locality by *A. subobtusum* (Kudernatsch, 1852) (Fig. 4.9). The Štepnická Skala ND-1 yielded *Sowerbyceras* cf. *subtortisulcatum* (Pompeckj, 1893) and juvenile *Holcophylloceras* and *Tatrophylloceras*.

Family Lytoceratidae, Neumayr, 1875
Subfamily Lytoceratinae Neumayr, 1875

Remarks: This subfamily is represented by small (juvenile) individuals that probably belong to a single species of the genus *Protetragonites* (Fig. 4.6, 4.10). They are characterized by a circular whorl section and megastries. There are four megastries per whorl up to a diameter of 20-25 mm, but they become more numerous later.

Family Haploceratidae Zittel, 1884
Genus *Lissoceras* Bayle, 1879

Lissoceras voultense (Oppel, 1865)
Figs. 5.1, 5.2, 6.1

1865 *Ammonites voultensis*. – Oppel, p. 319.
1905 *Haploceras voultensis* Oppel. – Lee, p. 32, pl. 1, fig. 7.
1924 *Lissoceras voultense* (Oppel). – Roman, p. 47, pl. 2, figs. 1, 1a.

Material: Four specimens with an incomplete body-chamber, and several fragments.

Description: Moderately involute discoidal ammonite with a highly oval whorl-section. Maximum width is just above the umbilical margin. Ventral part rounded and slightly arched.

Remarks: There are three other species described from Callovian and Oxfordian of Europe, including *Lissoceras jullieni* (Douvillé, 1914), *Lissoceras rollieri* (de Loriol,

Fig. 5. 1-2 – *Lissoceras voultense* (Oppel, 1865). **3** – *Horioceras* sp. nov. aff. *depereti* (Lemoine, 1932). **4** – *Hecticoceras* (*Lunuloceras*) cf. *paulowi* (de Tsytovitch, 1911). **5** – *Hecticoceras* (*Lunuloceras*) sp. 1. **6-7** – *Hecticoceras* (*Lemoineiceras*) gr. *submatheyi* (Lee, 1905). **8** – Kosmoceratidae juv. indet. (one specimen). **9-11** – *Hecticoceras* (*Lunuloceras*) gr. *metomphalum* (Bonarelli, 1894). **12** – *Hecticoceras* (*Brightia*) sp. **13-14** – Reineckeiidae indet. **15** – *Hecticoceras* (*Prohecticoceras*) gr. *zieteni* (de Tsytovitch, 1911). **16** – *Hecticoceras* (?) sp. [m]. Except specimens of Fig. 5.3 and 5.13, the all other specimens come from the Štepnická Skala ND-2, Middle Callovian, Coronatum Zone. The specimens of Fig. 5.3 and 5.13 come from ND-1, Lower Callovian, probably Gracilis Zone. Except 8b (x2), all specimens are in natural size.

Fig. 5 (Legend see p. 62)

1898) and *Lissoceratoides erato* (D'Orbigny, 1850). However, *Lissoceras jullieni*, described from the Callovian of Calvados is not a Lissoceras but an oppeliid ammonite. Its ventrum bears a low keel and upper part of the flank is ribbed. This species was also figured by Jeannet (1951: 103, pl. 31, figs. 1-2, text-figs. 233-234) from Herznach (N Switzerland), but in this case it probably belongs to *L. voultense. Lissoceras rollieri* is a Late Oxfordian species known from Jura Bernois (W Switzerland) and Herznach. Its morphology is indistinguishable from the Oppel's species and it is also very similar to Callovian "*L. jullieni*" of Jeannet (non Douvillé, 1914) from Herznach. *L. voultense* differs from *Lissoceratoides erato* (according to Oppel (1865) and Lee (1905)) because it possesses more convex whorls and 2 auxiliary lobes only (for details see Enay & Gauthier 1994).

Stratigraphic position: Lower – Middle Callovian, Štepnická Skala ND-1 and ND-2.

Family Oppeliidae Bonarelli, 1894
Subfamily Distichoceratinae Hyatt, 1900
Genus *Horioceras* Munier-Chalmas, 1892

Horioceras sp. nov. (aff. *Horioceras depereti* Lemoine, 1932)
Figs. 5.3, 6.2

Material: One specimen with adult body chamber.

Description: Microconch with a compressed whorl-section, slightly convex flanks, rounded umbilical edge, and almost vertical and low umbilical wall. The shell is completely smooth up to a diameter of 22-23 mm. Later, large clavi appear on the ventro-lateral edge, accompanied by very weak ventral keel. The clavi are low and rounded and alternate either side of the venter. The clavi can be observed at least up to a diameter of 30 mm (the specimen is damaged on its ventral side). The last 90° of the body chamber has a highly oval whorl-section with flattened venter and angular ventro-lateral margins, without clavi or keel, but with very shallow, almost indistinct lateral groove. Although the specimen seems to be an adult there are no lappets on its aperture, but this can be also due to incomplete preservation. The body chamber occupies 110° of the last whorl.

Remarks: *Horioceras* is a rather rarely described species. The best known is the *Horioceras baugieri* (D'Orbigny, 1847), a small sized species of Late Callovian age (Athleta – Lamberti zones, Palframan 1967; Gauthier & Elmi 1994). The clavi are locally pointed, and are more pronounced than in our specimen. In addition, the venter on the body chamber is rounded and not flattened. Baloge & Cariou (2001) described another small-sized *Horioceras* from the Lower – Middle Callovian boundary beds from Deux-Sèvres (W France). With the exception of its stratigraphical position, this taxon is almost indistinguishable from *H. baugieri*. *Horioceras mitodaense* Kobayshi, 1935 from the Callovian of Japan is similar in its overall shape and size to *H. baugieri*, although the clavi disappear earlier in the ontogeny and the lateral ornamentation is absent. *Horioceras depereti* Lemoine, 1932 from the Anceps and Athleta zones of Chanaz (E France) is a species of larger size than *H. baugieri* and *H. mitodaense*. It possesses rounded clavi and lateral groove, similar to our specimen. Based on personal observations of the original material, *H. depereti* has a scaphitoid coiling in the adult stage and a very weak ventral keel up to the adult aperture. It has similarly flattened venter as our specimen, with angular ventro-lateral margins. However, it has a scaphitoid shape because its coiling is more evolute and the whorl height on the beginning of body chamber expands very rapidly up to the last clavi, where it abruptly becomes lower. The last clavi are very large and strong.

Stratigraphic position: The specimen is associated with *Jeanneticeras*, whose stratigraphic range is restricted to Lower Callovian, and with Reineckeiidae that appear in abundance in the Grossouvrei Subzone (Thierry et al. 1997). Therefore, the stratigraphic position of this new species in the Štepnická Skala ND-1 corresponds to the upper part of Lower Callovian, Gracilis Zone.

Subfamily Hecticoceratinae Spath, 1928
Genus *Jeanneticeras* Zeiss, 1956

Jeanneticeras sp.

Material: Two small fragments.

Description: Moderately involute ammonite with almost flat to very slightly convex flanks. Umbilical edge is rounded. The ornamentation of flanks consists of poorly visible concave external ribs, and a line of strong, rounded tubercles on the ventro-lateral margin. Venter is fastigate with keel.

Remarks: The overall morphology, mainly characterized by the presence of the weak external ribbing, and the tubercles on the ventro-lateral margin are diagnostic for the genus *Jeanneticeras*.

Stratigpraphic position: *Jeanneticeras* occurs in the Lower Callovian (Elmi 1967), Gracilis Zone of the Štepnická Skala ND-1.

Genus *Hecticoceras* Bonarelli, 1894
Subgenus *Prohecticoceras* Spath, 1928

Hecticoceras (*Prohecticoceras*) gr. *zieteni* (de Tsytovitch, 1911)
Figs. 5.15, 6.3

1911 *Hecticoceras Zieteni* n. sp. – de Tsytovitch, p. 25, pl. 1, fig. 2.
1956 *Hecticoceras* (*Zieteniceras*) *zieteni* (de Tsytovitch). – Zeiss, p. 26, pl. 1, fig. 17.

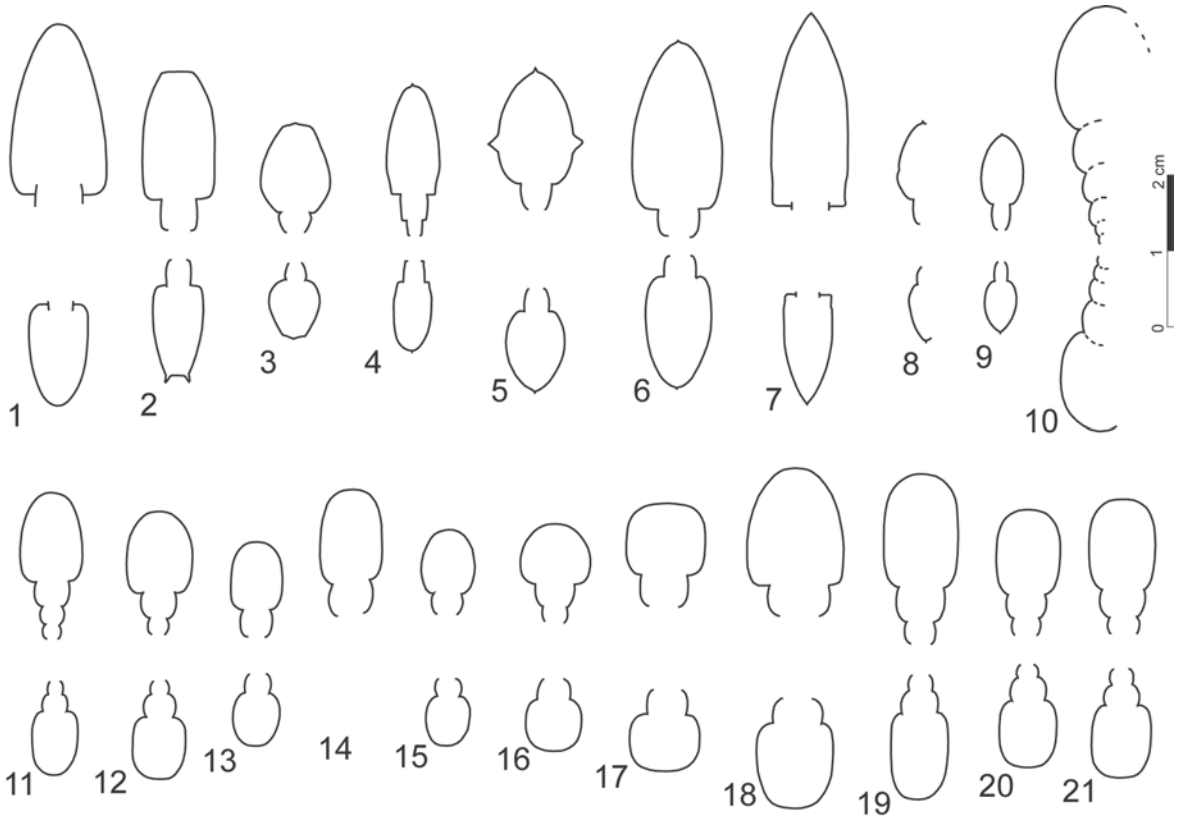

Fig. 6. Whorl cross-sections. **1** – *Lissoceras voultense* (Oppel, 1865), Fig. 5.1. **2** – *Horioceras* sp. nov. aff. *depereti* (Lemoine, 1932), Fig. 5.3. **3** – *Hecticoceras* (*Prohecticoceras*) gr. *zieteni* (de Tsytovitch, 1911), Fig. 5.15. **4-5** – *Hecticoceras* (*Lunuloceras*) gr. *metomphalum* (Bonarelli, 1894), Figs. 5.10-11. **6** – *Hecticoceras* (*Lunuloceras*) cf. *paulowi* (de Tsytovitch, 1911), Fig. 5.4. **7** – *Hecticoceras* (*Lunuloceras*) sp. 1, Fig. 5.5. **8** – *Hecticoceras* (*Brightia*) sp., Fig. 5.12. **9** – *Hecticoceras* (*Lemoineiceras*) gr. *sub-matheyi* (Lee, 1905), Fig. 5.6-7. **10** – *Choffatia* (*Grossouvria*) *kontkiewiczi kontkiewiczi* (Siemiradzki, 1894), Fig. 8.10. **11** – *Choffatia* (*Grossouvria*) *kontkiewiczi composita* (Pfaehler-Erath, 1938), Fig. 7.7. **12** – *Choffatia* (*Grossouvria*) ex. gr. *kontkiewiczi* (Siemiradzki, 1894), Fig. 7.11. **13** – *Choffatia* (*Grossouvria*) sp. nov. 1, Fig. 7.3. **14** – *Choffatia* (*Grossouvria*) *vahica* sp. nov., holotype, Fig. 8.1. **15** – *Choffatia* (*Grossouvria*) aff. *tenella* (Teisseyre, in Mangold, 1971, fig. 139), Fig. 8.4. **16** – *Choffatia* (*Grossouvria*) sp. nov. indet. aff. *Ammonites convolutus* Quenstedt, 1849, form 1, Fig. 8.7. **17** – *Choffatia* (*Grossouvria*) sp. nov. indet. aff. *Ammonites convolutus* Quenstedt, 1849, form 2, Fig. 8.8. **18** – *Flabellisphinctes* (*Flabellia*) *tsytovitchae* Mangold, 1971, Fig. 7.1. **19** – *Flabellisphinctes* (*Flabellia*) *tuberosus* Mangold, 1971, Fig. 7.4. **20-21** – *Flabellisphinctes* (*Flabellia*) *elmii* sp. nov. 20. Paratype, Fig. 7.3. 21. Holotype, Fig. 7.2.

1967 *Hecticoceras* (*Prohecticoceras*) *zieteni* (de Tsytovitch, 1911). – Elmi, p. 615, text-figs. 132-136, pl. 6, fig. 12 (cum syn.).

Material: One specimen with an incomplete part of body chamber.

Description: Moderately involute *Prohecticoceras* with a compressed whorl-section, relatively large and keeled venter, and falcoid ribbing. Very low peri-ventral keels are situated between siphonal line and ventro-lateral edge. Umbilical wall is very low, umbilical edge is rounded. Prorsiradiate internal ribs start on the umbilical edge and continue either as simple ribs or as bifurcated ribs. They are strongest at the bifurcation point situated near 1/3 of the flanks. The external ribs are concave and end on the ventro-lateral edge, forming small tubercles.

Remarks: *H.* (*P.*) *zieteni* from the Coronatum Zone shows similar lateral keels, but differs in more evolute coiling, a slightly different cross-section, and a marked umbilical edge. This species shows, however, a large intraspecific variability encompassing also forms similar to the described specimen. *H.* (*P.*) *lemoinei* (Zeiss, 1956) is a Lower Callo-

vian species with similar ornamentation and coiling. However, its ventral side is large and the keel is separated from the ventro-lateral tubercles by clear depressions.

Stratigraphic position: Middle Callovian, Coronatum Zone, Štepnická Skala ND-2. Its complete stratigraphic range seems to be larger, ranging from the upper Lower Callovian (Lemoine 1932; Zeiss 1956).

Hecticoceras (*Lunuloceras*) gr. *metomphalum* (Bonarelli, 1894)
Figs. 5.9-5.11, 6.4-6.5

1971 *Harpoceras punctatum* Stahl sp. – Neumayr, p. 28, pl. 9, fig. 8.
1894 *Hecticoceras* (*Lunuloceras*) *metomphalum* n. f. – Bonarelli, p. 90.

Material: Four incomplete specimens partially still with the calcitized shell.

Remarks: This taxon has a rather large intraspecific morphological variability, ranging from compressed and involute forms up to evolute and heavily ornamented forms. Several authors proposed subdivision on the subspecies level (Zeiss 1956), introducing *H.* (*L.*) *metomphalum multicostatum* (de Tsytovitch, 1911) for compressed forms with numerous external ribs, or *H.* (*L.*) *metomphalum acuticosta* (de Tsytovitch, 1911) for the forms with strong internal ribs. All these taxa can represent similar forms whose differences could be explained by large intraspecific variability. More evolute forms show a less compressed whorl section, stronger external ribbing, internal ribs reduced to a strong peri-umbilical tubercles, and low umbilical wall. In contrast, more involute forms have a more compressed whorl section; internal ribs are well visible and terminated by low and prolonged tubercles or bullae. In addition, external ribs are thinner, and umbilical edge is well developed with a higher umbilical wall.

Stratigraphic position: Middle Callovian, Coronatum Zone, Štepnická Skala ND-2. This polymorphic species is known from the Anceps to Lamberti zones (Zeiss 1956).

Hecticoceras (*Lunuloceras*) cf. *paulowi* (de Tsytovitch, 1911)
Figs. 5.4, 6.6

1911 *Hecticoceras Paulowi* n. sp. – de Tsytovitch, p. 69, pl. 17, figs. 8, 10-12, pl. 8, figs. 2-3.
1956 *Hecticoceras* (*Lunuloceras*) *paulowi* (de Tsytovitch). – Zeiss, p. 44, pl. 1, fig. 11 (cum syn.).

Material: One incomplete specimen.

Description: Moderately involute shell, with slightly convex flanks, relatively large venter with a thin and low keel, and falcoid ribs. Umbilical edge is poorly marked and rounded, umbilical wall is steep. Radiate to slightly prorsiradiate and low internal ribs are long, without real tubercles, divided around the middle of the flanks in two or three concave external ribs. These external ribs become slightly larger near the ventro-lateral line, but without tubercles.

Remarks: The shell is characterized by its involute coiling and long internal ribs. The type specimen of *H.* (*L.*) *paulowi* shows more falcoid ribbing and a more pronounced keel.

Stratigraphic position: Middle Callovian, Coronatum Zone, Štepnická Skala ND-2. Zeiss (1956) considers this species as being typical of the Athleta Zone, but its occurrence in the Middle Callovian was confirmed by other authors (Lemoine 1932; Mangold 1971).

Hecticoceras (*Lunuloceras*) sp. 1
Fig. 5.5, 6.7

Material: One incomplete specimen.

Description: Moderately involute shell is characterized by a strongly compressed whorl section with a sharp and keeled venter. Flanks are only slightly convex, umbilical edge is well marked with a relatively high and vertical umbilical wall. Prorsiradiate internal ribs are better visible around the 1/3 of the flanks where they become stronger, but without a real tubercle or bullae. The external ribs pass rapidly from a relatively dense concave ribs to large and dense ribs on the last whorl.

Remarks: The venter is very sharp but the keel is not clearly developed, which is a rare feature among the Middle Callovian *Hecticoceras*. There are no identical forms of the same age. This taxon may represent a new species.

Stratigraphic position: Middle Callovian, Coronatum Zone, Štepnická Skala ND-2.

Hecticoceras (?) sp. [m]
Fig. 5.16

Material: One specimen with an incomplete part of body-chamber.

Description: Evolute shell with a highly oval whorl-section and distinctly keeled venter. Umbilical wall is very low and vertical. Bullate prorsiradiate internal ribs appear on the umbilical edge, terminating in a low tubercle or bullae near the 1/3 of the flanks where strong and concave external ribs begin.

Remarks: This specimen probably represents a micro-conch belonging to the subgenus *Lemoineiceras* or *Putealiceras* from the Middle Callovian group of *H.* (*P.*) *punctatum* (see Zeiss 1956).

Stratigraphic position: Middle Callovian, Coronatum Zone, Štepnická Skala ND-2.

Hecticoceras (*Brightia*) sp.
Figs. 5.12, 6.8

Material: One well-preserved but incomplete specimen with calcitized shell.

Description: Evolute shell possesses convex flanks, sharply keeled venter, and falcoid ribbing. Umbilical wall is vertical and very low. Prorsiradiate internal ribs are short and without a tubercle. There is a very shallow lateral groove below the middle part of the flank where the external ribs start. The internal ribs pass the groove with a lappet-like projection that reflects the shape of temporary apertures. Therefore, the concave external ribs are strongly adorally curved just above the spiral groove, terminating on the ventro-lateral margin without tubercles. Venter bears a low but distinct and sharp keel.

Remarks: The subgenus *Brightia* is characterized by presence of rounded or oval venter, a clearly developed keel, absence of ventro-lateral tubercles, ventrally projected external ribs, and peristome with lappets. The presence of spiral groove distinguishes this subgenus from the subgenus *Lemoineiceras*.

Stratigraphic position: Middle Callovian, Coronatum Zone, Štepnická Skala ND-2.

Hecticoceras (*Lemoineiceras*) gr. *submatheyi* (Lee, 1905)
Figs. 5.6-5.7, 6.9

1905 *Hecticoceras sub-matheyi*, nov. sp. – Lee, p. 22, pl. 1, fig. 10.
1956 *Hecticoceras* (*Lunuloceras*) *sub-matheyi* (Lee). – Zeiss, p. 37, pl. 1, fig. 13 (*cum syn.*).

Material: Three specimens with partly preserved calcitized shell.

Description: Small evolute shell with a compressed whorl section. Umbilical edge is well marked, umbilical wall is very low. Flanks are regularly convex. Venter with distinct keel, visible also on the inner whorls (diameter = 12 mm). Internal ribs well visible at this diameter, concave, strongly adorally projected near the 1/3 of the flanks, without tubercles. External ribs are very thin. The point of rib division is situated below the mid-flank. Later in the ontogeny, the external ribs become slightly stronger, but the internal ribs are less marked, and intercostal space is reaching twice the rib width. The aperture of the most complete specimen (Fig. 5.6) shows thin lateral lappet-like projections.

Remarks: The species is very close to *H.* (*L.*) *brightii* (Pratt, 1841) because they share a very similar type of ribbing, widely spaced internal ribs and numerous external ribs. The difference is related to less evolute coiling of *H.* (*L.*) *brightii*.

Stratigraphic position: Middle Callovian, Coronatum Zone, Štepnická Skala ND-2. Zeiss (1956) mentioned the stratigraphic range from the Anceps Zone to Athleta zones.

Family Kosmoceratidae Haug, 1887

Kosmoceratidae juv. indet.
Fig. 5.8a-b

Material: Two small specimens, representing inner whorls of one relatively complete specimen and one incomplete specimen with small part of ventral part.

Remarks: A juvenile specimen with bifurcated ribs and a row of tubercles at the point of rib division, situated in the middle part of the flank. Slightly prorsiradiate primary ribs appear on the umbilical wall. Secondary ribs are interrupted by small tubercles near the mid-venter. The opposite tubercles are interconnected by a single and low radiate rib crossing the venter.

Stratigraphic position: Lower Callovian, Gracilis Zone, Štepnická Skala ND-1.

Family Reineckeiidae Hyatt, 1900, emend. Spath, 1928

Reineckeiidae indet.
Figs. 5.13-5.14

Remarks: Small and fragmented specimens occur in both dykes at the Štepnická Skala locality. Taxonomy of this group is predominantly based on morphological traits that are visible on adult specimens only. The ornamentation of the inner whorls is highly variable and thus hardly diagnostic for species determination. However, we note some differences between the specimens collected in the Lower Callovian dyke and the specimen found in the Middle Callovian dyke. The latter are represented by a unique specimen with a depressed whorl section and strong, radiate primary ribs, starting from the umbilical seam and terminating in strong pointed tubercles (Fig. 5.13). The tubercles mark the division point of ribs. There are generally three radiate secondary ribs starting from a single tubercle. These ribs are less pronounced but not completely interrupted near the mid-ventral line. This specimen probably belongs to some species of *Reineckeia or Loczyceras*.

With exception of one specimen, the reineckiid from the Lower Callovian dyke are represented by innermost whorls only. The larger specimen shows radiate to slightly prorsiradiate primary ribs, forming a tiny tubercle in the point of rib bifurcation (Fig. 5.14). Few intercalated ribs are present. Venter is regularly rounded, with the secondaries clearly interrupted on the ventral line. Other specimens show a depressed whorl section, prorsiradiate primaries, tubercles at the point of rib division are absent, and the secondaries are clearly interrupted on the ventral line.

Stratigraphic position: Lower Callovian, probably Gracilis Zone, Štepnická Skala ND-1 and Middle Callovian Coronatum Zone, Štepnická Skala ND-2

Family Perisphinctidae Steinman, 1890
Subfamily Grossouvriinae Spath, 1931
Genus *Choffatia* Siemiradzki, 1898
Subgenus *Grossouvria* Siemiradzki, 1898

Choffatia (*Grossouvria*) sp. ex. gr. *kontkiewiczi* (Siemiradzki, 1894)
Fig. 6.12, 7.11

Material: Two adult specimens partly covered with calcitized shell.

Description: Evolute form with a long stage with parabolic nodes, also present at the beginning of the adult body chamber. Primary ribs are radiate or slightly prorsiradiate. On the body chamber, primary ribs are bifurcated, rarely polygyrate, and intercalatory ribs are common. The point of bifurcation is situated above the middle part of the flanks. Secondaries are slighty rursiradiate. Adult body chamber is more compressed than the phragmocone, with an oval whorl-section, and with almost flat or only slightly convex flanks. There are two or three shallow constrictions on the last whorl. Aperture bears lateral lappets.

Remarks: Morphological characters place these specimens between *C.* (*G.*) *kontkiewiczi kontkiewiczi* (Siemiradzki, 1894), *C.* (*G.*) *kontkiewiczi composita* (Pfaehler-Erath, 1938) and *C.* (*G.*) *kontkiewiczi incomposita* (Pfaehler-Erath, 1938).

Stratigraphic range: Middle Callovian, Coronatum Zone, Štepnická Skala ND-2.

Choffatia (*Grossouvria*) *kontkiewiczi kontkiewiczi* (Siemiradzki, 1894)
Figs. 6.10, 8.10

1894 *Perisphinctes kontkiewiczi* n. sp. – Siemiradzki, p. 513, pl. 38, figs. 3-4.
1971 *C.* (m. *Grossouvria*) *kontkiewiczi kontkiewiczi* (Siemiradzki), 1894. – Mangold, p. 179, figs. 135-136; pl. 8, figs. 2-5 (*cum syn.*).
?2003 *Choffatia kontkiewiczi* (Siemiradzki, 1894). – Majidifard, p. 129, pl. 11, figs. 4, 6, 8, 10; pl. 13, fig. 4.

Material: Two specimens; one adult specimen with lappets, covered with calcitized shell.

Description: This subspecies is characterized by its larger size relative to other subspecies, a diagnostic whorl-section shape in the adult stage and high abundance of parabolic ribs, which occur also on the innermost whorls. Primary ribs are radiate or slightly prorsiradiate, giving generally two or three secondary ribs near the 2/3 of the flanks. The point of rib division descends near the middle parts of the flanks on the adult body chamber. The intercalatory ribs are present. The whorl-section is circular on the innermost whorls, but becomes more oval at the end of the phragmocone. The whorl-section is high-oval with regularly convex flanks on the body chamber. The adult aperture bears lateral lappets accompanied by a shallow peristomal constriction.

Remarks: This subspecies can be distinguished by its size, which is largest among all subspecies of *C.* (*G.*) *kontkiewiczi*, by its high-oval cross section on the adult body chamber, and regularly convex whorl-sides.

Stratigraphic position: Middle Callovian, Coronatum Zone, Štepnická Skala ND-2. The whole stratigraphic range is upper Anceps and Coronatum zones (sensu Mangold 1971).

Choffatia (*Grossouvria*) *kontkiewiczi composita* (Pfaehler-Erath, 1938)
Figs. 6.11, 7.7-7.10

1938 *Grossouvria curvicosta* (Oppel) var. *composita* n. var. – Pfaehler-Erath, p. 5, pl. 1, figs. 1a, 1b.
1971 *C.* (m. *Grossouvria*) *kontkiewiczi composita* (Pfaehler-Erath), 1938. – Mangold, p. 175, fig. 137; pl. 15, fig. 6 (cum syn.).

Material: Five adult specimens, four of which are complete and have apertures.

Description: Evolute, densely ribbed subspecies with numerous parabolic ribs persisting up to the beginning of the body chamber. Whorl-section is circular on the inner whorls, and oval and laterally compressed on the body

Fig. 7. 1a-c – *Flabellisphinctes* (*Flabellia*) *tsytovitchae* Mangold, 1971. **2-3** – *Flabellisphinctes* (*Flabellia*) *elmii* sp. nov. 2a, b:. Holotype, SNM Z 24 749. 3: Paratype, SNM Z 24 750. **4-5**a, b – *Flabellisphinctes* (*Flabellia*) *tuberosus* Mangold, 1971. **6**a, b – *Flabellisphinctes* (*Flabellia*) sp. **7-10** – *Choffatia* (*Grossouvria*) *kontkiewiczi composita* (Pfaehler-Erath, 1938). **11**a, b – *Choffatia* (*Grossouvria*) ex. gr. *kontkiewiczi* (Siemiradzki, 1894). **12-13** – *Choffatia* (*Grossouvria*) sp. All specimens come from the Štepnická Skala ND-2, Middle Callovian, Coronatum Zone. Figs. 7.1b,c, 7.2b, 7.5b, 7.6b, 7.11b and 7.13 with marked ornamentation represent plaster casts. Natural size.

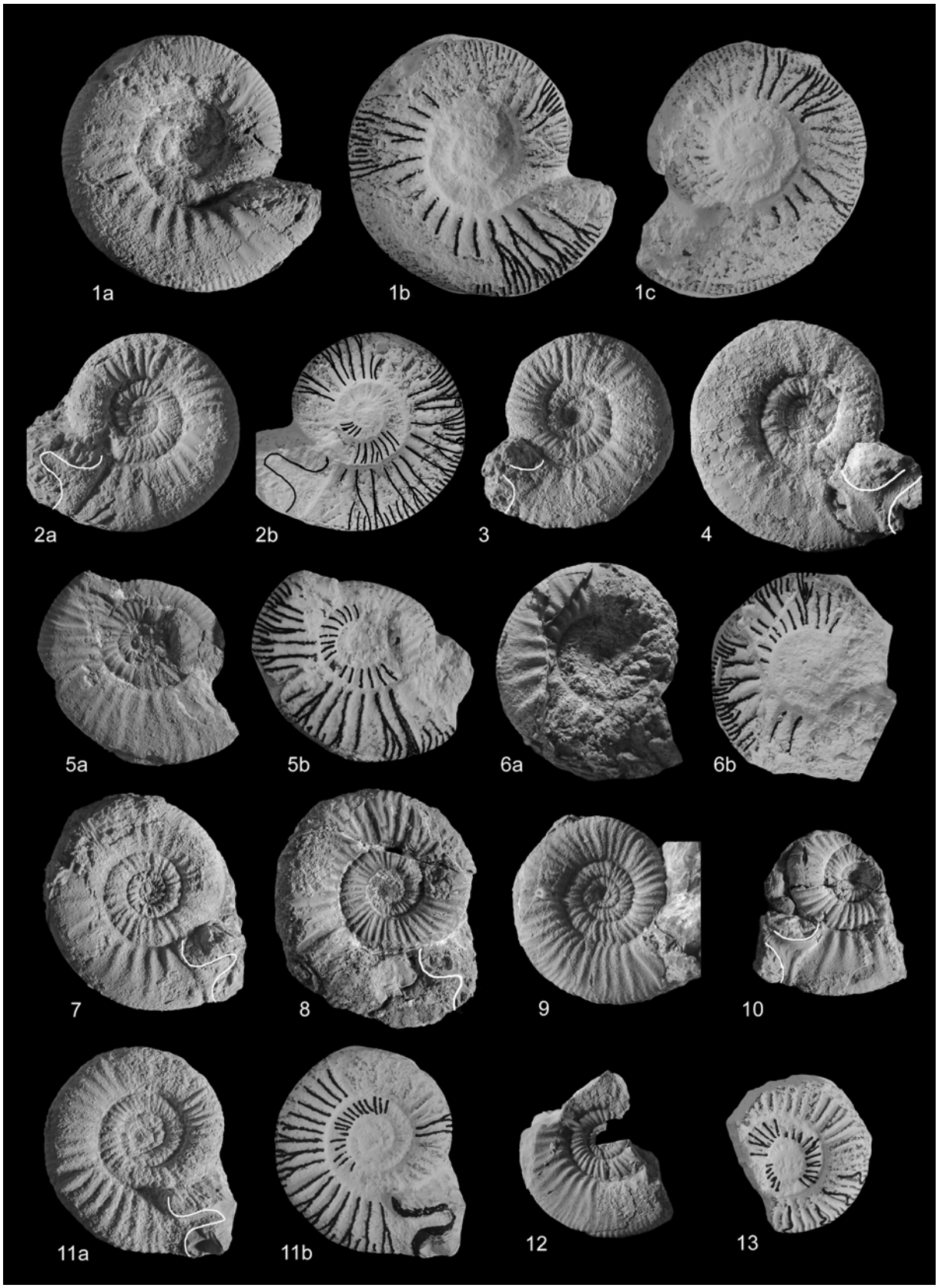

Fig. 7 (Legend see p. 68)

chamber. Dense radiate to slightly prorsiradiate primary ribs appear on the umbilical line. The umbilical wall and margin form one continuous and regularly rounded structure. On the phragmocone, the primary ribs are bifurcated on the 2/3 of the flanks, secondaries are slightly rursiradiate, intercalatory ribs are present, but rare. On the body chamber, the primary ribs branch to 2 or 3 secondary ribs, separated by intercalatory ribs. Aperture bears large and shallow peristomal constriction and lateral lappets.

Remarks: General characters of the described specimens are well comparable with the description of this subspecies by Mangold (1971: p. 176).

Stratigraphic range: Middle Callovian, Coronatum Zone, Štepnická Skala ND-2. Species of the Anceps Zone, rarely known also from the lower Coronatum Zone (Mangold 1971).

Choffatia (*Grossouvria*) sp. nov. 1
Figs. 6.13, 8.3

Material: One adult specimen with aperture.

Description: Small sized, evolutely coiled *Grossouvria* with a circular whorl-section on the phragmocone, which becomes compressed on the body chamber. On the inner whorls, the ornamentation consists of dense, thin, slightly prorsiradiate primary ribs, which become weaker on the adult body chamber. Parabolic ribs with ventro-lateral parabolic nodes are abundant up to the beginning of the body chamber. Due to their relative abundance, the ribbing pattern is irregular. Only the last 90° of the adult body chamber is devoid of parabolic ribs. The point of rib division is situated very high on the phragmocone, near the ventro-lateral margin. The ribs on the last 90° of the body chamber are bifurcated. Each one is separated from the following one by two intercalatory ribs, converging towards the bifurcation point of the neighbouring rib but never join it, which give to ribs a quadriplicate or virgatotome appearance. The final aperture bears a shallow peristomal constriction and lateral lappets.

Remarks: This small-sized species with the peculiar ornamentation on the body chamber substantially differs from all other Middle Callovian members of the genus *Grossouvria*, but because of the unique specimen available we prefer to keep its taxonomic status open.

Stratigraphic range: Middle Callovian, Coronatum Zone, Štepnická Skala ND-2.

Choffatia (*Grossouvria*) *vahica* sp. nov.
Figs. 6.14, 8.1-8.2

Etymology: According to the Slovak Váh River. The type locality Štepnická Skala is situated on the right side of the Middle Váh Valley.

Holotype: SNM Z 24 747, Fig. 8.1.

Paratype: Internal whorls, SNM Z 24 748, Fig. 8.2.

Type locality: Štepnická Skala locality, Pieniny Klippen Belt, West Carpathians, Slovakia.

Type horizon: Czorsztyn Limestone Formation, Štepnická Skala ND-2, Middle Callovian Coronatum Zone.

Diagnosis: Evolutely coiled ammonite with a circular cross-section of inner whorls and a more compressed cross-section of the body chamber with almost flat whorl sides. Ornamentation on the inner whorls is formed by numerous and very thin parabolic ribs. Body chamber bears regular, bifurcated or polygyrate ribs.

Description: Evolute shell with shallow umbilicus, a rounded whorl section on inner whorls, but compressed with almost flat flanks on the bodychamber. Very thin and dense ornamentation consists of thin primary ribs, which are simple or bifurcate between the middle parts and the 2/3 of the flanks, and rarely polygyrate and numerous intercalatory ribs. Parabolic ribs are very abundant, crossing the primary and the secondary ribbing, which gives an irregular and chaotic style of ribbing on the phragmocone. The primaries are radiate to slightly prorsiradiate, starting already on the umbilical wall, which is rounded and low. The secondaries are thin, slightly rursiradiate. In the smaller immature specimen, there are five parabolic ribs per 1/4 of the last preserved whorl, each separated by 4-5 secondary ribs on the ventral area. Constrictions are not visible, probably absent. The primary ribs become stronger on the last third of the preserved whorl. This feature is well seen on the holotype. The body chamber bears regularly spaced primary ribs, bifurcating near the 2/3 of the flanks. There is one intercalatory rib per one bifurcated or polygyrate rib.

Remarks: There are no other *Grossouvria* with similarly ornamented internal whorls. Thin ornamentation and abundance of parabolic ribs is typical of *Indosphinctes* (*Elatmites*) *steinmanni* (Parona & Bonarelli, 1897), but this species does not belong to *Grossouvria* and is stratigraphically older, ranging from the Koenigi Zone to the Patina zones. In addition, in contrast to *Grossouvria*, the ornamentation of the innermost whorls in this species shows a zigzag pattern.

Stratigraphic position: Middle Callovian, Coronatum Zone, Štepnická Skala ND-2.

Choffatia (*Grossouvria*) sp. aff. *Perisphinctes planus* Siemiradzki in Lee, 1905
Figs. 8.5-8.6

?1905 *Perisphinctes planus* Siemiradzki – Lee, p. 39, pl. 1, fig. 12.

Material: Two incomplete specimens.

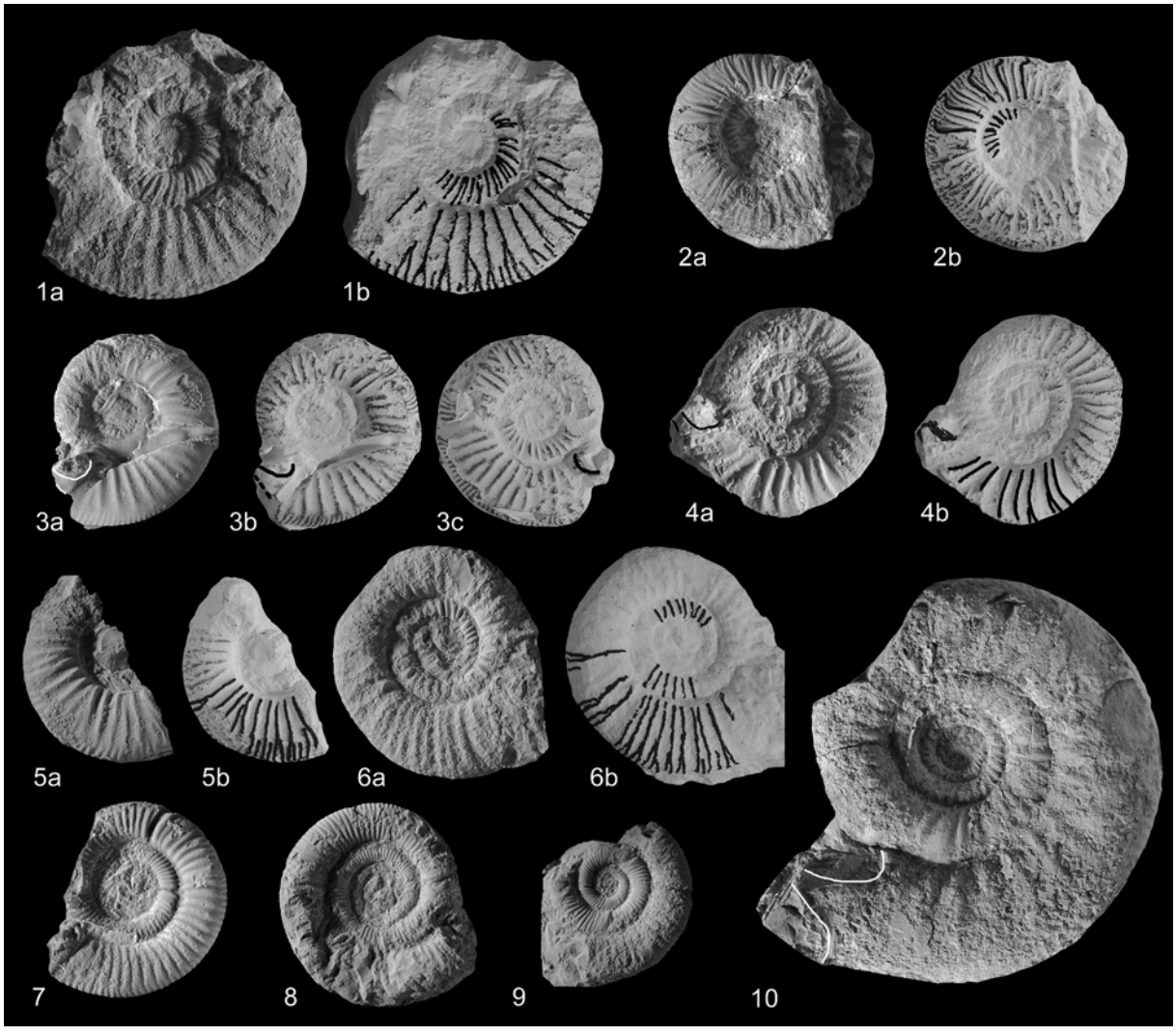

Fig. 8. 1-2 – *Choffatia* (Grossouvria) *vahica* sp. nov. 1a, b:. Holotype, SNM Z 24 747. 2a, b:. Paratype, SNM Z 24 748. **3** a-c – *Choffatia* (*Grossouvria*) sp. nov. 1. **4** a, b –. *Choffatia* (*Grossouvria*) aff. *tenella* (Teisseyre, in Mangold, 1971). **5-6** – *Choffatia* (*Grossouvria*) sp. aff. *Perisphinctes planus* Siemiradzki in Lee, 1905. **7-9** – *Choffatia* (*Grossouvria*) sp. nov. indet. aff. *Ammonites convolutus* Quenstedt, 1849. **10** – *Choffatia* (*Grossouvria*) *kontkiewiczi kontkiewiczi* (Siemiradzki, 1894). All specimens come from the Štepnická Skala ND-2, Middle Callovian, Coronatum Zone. Figs. 8.1 b, 8.2 b, 8.3 b, c, 8.4 b, 8.5 b, 8.6 b with marked ornamentation represent plaster casts. Natural size.

Description: These specimens are characterized by dense ribbing on the phragmocone, which persists as dense also at the beginning of the adult body chamber. The division point of radiate to prorsiradiate primary ribs is situated higher on the flanks, the ribs are generally bifurcated, rarely polygyrate, intercalatory ribs are rare. Three constrictions per whorl are relatively shallow, and almost parallel with ribbing.

Remarks: In terms of dense ribbing persisting up to the beginning of the body chamber, this species is similar to the specimen figured by Lee (1905, pl. 1, fig. 12) under the name *Perisphinctes planus* Siemiradzki, 1898). The original description of this taxon was based on the material of Quenstedt (1885, pl. 81, figs. 15-19). However, the fig. 19 was used by Teisseyre (1889: 594) for the type specimen of *P. tenellus* and other specimens belong to *Choffatia* (*Grossouvria*) *evexa* (Quenstedt, 1885) (for more details see Mangold, 1971: 186). The specimen described and figured by Lee (1905) differs from both aforementioned species and represents another, probably still unknown taxon.

Stratigraphic position: Middle Callovian, Coronatum Zone, Štepnická Skala ND-2.

Choffatia (*Grossouvria*) aff. *tenella* (Teisseyre, in Mangold 1971, fig. 139)
Figs. 6.15, 8.4

1971 *C.* (m. *Grossouvria*) *tenella* (Teiss.) – Mangold, p. 188, fig. 139.

Material: One almost complete adult specimen.

Description: Very evolute shell with only a slightly compressed whorl-section on the body chamber. A bifurcation of primary ribs situated very high on the flanks, near the ventro-lateral margin, is a characteristic trait. Radiate or slightly prorsiradiate primary ribs appear on the umbilical edge. Umbilical wall is very low. Ribbing on the inner whorls is rather thin, accompanied by parabolic ribs. Adult aperture is enlarged in the region where lateral lappets begin. Numerous large constrictions on the last quarter of the body chamber mark the position of temporary subadult apertures.

Remarks: Among the Middle Callovian *Grossouvria*, only *G. tenuis* (Siemiradzki, 1894) shows similar morphology, but the bifurcation point is situated lower on the flanks, and the type specimen is not complete, thus the morphology of its adult body chamber remains unknown. Another small-sized species *C.* (*G.*) *polonica* (Siemiradzki, 1894) has more densely-spaced ribs and the division point of ribs is also situated lower on the flanks. Probably the most similar species is represented by *C.* (*G.*) *tenella* (Teisseyre, in Mangold 1971, fig. 139), which is characterized by more evolute coiling and the division point placed higher on the flanks.

Stratigraphic position: Middle Callovian, Coronatum Zone, Štepnická Skala ND-2.

Choffatia (*Grossouvria*) sp. nov. indet. aff. *Ammonites convolutus* Quenstedt, 1849
Figs. 6.16-6.17, 8.7-8.9

?1849 *Ammonites convolutus*. – Quenstedt, pl. 13, fig. 5.
?1849 *Ammonites convolutus interruptus*. – Quenstedt, pl. 13, fig. 3.
?1911 *Perisphinctes* (*Grossouvria*) sp. ind. – Till, p. 30, pl. 7, fig. 1.

Material: Three specimens partly covered with calcitized shell.

Description: Extremely evolute, serpenticone shells with large and shallow umbilicus. Umbilical wall and edge are regularly rounded. The whorl section is subquadrate during the ontogeny owing to slightly flattened venter and flanks. There are two morphotypes differing in the density of ribbing. In the first morphotype, primary ribs are less dense, radiate to slightly prorsiradiate on the inner whorls, and slightly concave on the bodychamber. The ribs appear near the umbilical seam and bifurcate near the ventro-lateral margin (2/3 of the flanks). Secondary ribs are slightly rursiradiate. There are three prorsiradiate constrictions per whorl, almost concordant with the ribbing. The second morphotype is densely ribbed; thinner primaries also start on the umbilical line. These primary ribs are radiate, either simple, or bifurcate at the same height of the flanks as in the first morphotype. The simple and bifurcating ribs alternate regularly. The thickness of primary and secondary ribs is very similar. There are three strong slightly prorsiradiate constrictions per whorl. Parabolic ribs are present but rare on both morphotypes.

Remarks: These specimens are comparable with *A. convolutus* described by Quenstedt (1849: 13, fig. 5), and *A. convolutus interruptus* Quenstedt (1849, pl. 13, fig. 3, not 4). These taxa share similar evolute coiling, the same type of dense ribbing, and three narrow but incised constrictions per whorl. The *A. convolutus interruptus* Quenstedt (1849: 13, fig. 3) is an adult microconch with aperture bearing strong peristomal constriction and lateral lappets. Similar specimens were also found in the Callovian of Villany (Hungary). Till (1911) described *Perisphinctes* (*Grossouvria*) sp. indet (pl. 7, fig. 1), probably a macroconch with densely ribbed, constricted inner whorls and more coarsely-ribbed last whorl. This species was collected in the Anceps and Athleta zones. It is possible that the Hungarian material represents the macroconch form of the Quenstedt's species.

Stratigraphic position: Middle Callovian, Coronatum Zone, Štepnická Skala ND-2.

Genus *Flabellisphinctes* Mangold & Elmi, 1966
Subgenus *Flabellia* Mangold, 1971

Flabellisphinctes (*Flabellia*) *elmii* sp. nov.
Figs. 6.20-6.21, 7.2-7.3

Holotype: SNM Z 24 749, Fig. 7.2.

Paratype: SNM Z 24 750, Fig. 7.3.

Etymology: After the recently deceased French ammonite specialist Serge Elmi.

Type locality: Štepnická Skala locality, Pieniny Klippen Belt, West Carpathians, West Slovakia.

Type horizon: Czorsztyn Limestone Formation, Neptunian dyke ND-2, Middle Callovian, Coronatum Zone.

Diagnosis: Small-sized *Flabellia* with a circular section of inner whorls and compressed high-oval section of adult body chamber, dense, slightly prorsiradiate primary ribs and parabolic ribs up to the beginning of the body chamber.

Description: Evolutely coiled shell with shallow umbilicus. Inner whorls with a circular cross section, body chamber compressed with a highly oval cross section. Umbilical wall is very low, regularly rounded, passing to lateral sides without a marked umbilical edge. Slightly prorsiradiate primary ribs appear on the umbilical wall. Parabolic ribs are present, 7-8 per 3/4 of the whorl on the inner whorls, continuing up to the beginning of the body-chamber. Division point of primary ribs on the inner whorls is situated higher on the flanks. On the body chamber, the ribs branch lower on the flanks. Virgatotome, polygyrate and bifurcated ribs irregularly alternate, and intercalated ribs are present (Fig. 7.2). Aperture bears a marked peristomal constriction and lateral lappets near the middle of the aperture height. Suture line is invisible due to calcitization.

Remarks: This new species shows the main character of the subgenus, the virgatotome ribs on the bodychamber, but these alternate with polygyrate and bifurcated ribs. This species can be easily distinguished from other species of the subgenus by its small size and a relatively dense primary ribbing on the body chamber. The morphologically closest species *F.* (*F.*) *tsytovitchae* Mangold, 1971 from the lower part of Coronatum Zone, Obductum Subzone differs in larger size, more evolute coiling, and more spaced primary ribs on the body chamber. *F.* (*F.*) *lineatus* Mangold, 1971 shows the same coiling as the new species but it is also larger-sized, with thin and dense ribs on the bodychamber, often branching near the umbilical margin. *F.* (*F.*) *tuberosus* Mangold, 1971 differs in coarser and less dense primary ribbing on the body chamber.

Stratigraphic position: Middle Callovian, Coronatum Zone, Štepnická Skala ND-2.

Flabellisphinctes (*Flabellia*) *tsytovitchae* Mangold, 1971
Figs. 6.18, 7.1a-c

1971 *F.* (m. *Flabellia*) *tsytovitchae* nov. sp. – Mangold, p. 195, figs. 142-143; pl. 16, figs. 7-8.
2003 *Flabellisphinctes* (*Flabellia*) *tsytovitchae* Mangold, 1970 [m] – Majidifard, p. 138, pl. 13, figs. 1-2, 5.

Material: Two incomplete adult specimens, partially covered by calcitized shell.

Description: Evolutely coiled ammonites with a highly oval whorl section of the adult body chamber, low and vertical umbilical wall, and marked umbilical edge. Ornamentation consists of prorsiradiate primary ribs, which are relatively dense up to the end of the preserved part of the body chamber. They show the virgatotome, polygyrate or polyploke division. Aperture is broken.

Remarks: These specimens are well comparable to the Mangold's figures and description of the species.

Stratigraphic position: Middle Callovian, Coronatum Zone, Štepnická Skala ND-2; Coronatum Zone, Baylei Subzone sensu Mangold (1971).

Flabellisphinctes (*Flabellia*) *tuberosus* Mangold, 1971
Figs. 6.19, 7.4-7.5

1971 *F.* (m. *Flabellia*) *tuberosus* nov. sp. – Mangold, p. 196, figs. 144-145; pl. 15, figs. 3-4; pl. 16, figs. 3- 4.

Material: One complete adult specimen partially covered with calcitized shell, one fragmented and partly deformed specimen.

Description: This species is characterized by a more compressed whorl-section on the last quarter of the phragmocone and especially on the body chamber, which shows relatively flat whorl sides, and less densely-spaced primary ribs. The parabolic ribs persist up to the adult body chamber, the last one can be observed as far as 1/4 of the whorl length from the final aperture. Peristomal constriction is large and shallow on the flanks but thin and deeply incised on the ventral side. Adult aperture bears long lateral lappets.

Remarks: The specimens are well comparable with the Mangold's figures and description.

Stratigraphic position: Middle Callovian, Coronatum Zone, Štepnická Skala ND-2. Coronatum Zone, Baylei Subzone sensu Mangold (1971).

5. Associated macrofauna

In addition to crinoids in the Štepnická Skala ND-1 and thin-shelled bivalves of the genus *Bositra* in the Vršatec locality, ammonites are the most common macrofossils in the neptunian dyke infillings. Brachiopods represent the second most abundant group in the Štepnická Skala ND-2, followed by common bivalves and rare gastropods. Brachiopod assemblage is exclusively composed of pedunculate species. *Septocrurella sanctaeclarae* (Roemer, 1870) (40 %) and *Monticlarella rollieri* (Wisniewska, 1932) (24 %) are abundant. They are associated with less common *Linguithyris vicaria* (Szajnocha, 1881) (11 %), *Aulacothyris* sp. (11%) and *Karadagithyris decipiens* (Eudes-Deslongchamps, 1879) (9 %), and by rare *Praelacunosella* aff. *dumortieri* (Szajnocha, 1879) (3 %) and *Capillirhynchia* aff. *furcillata* (von Buch, 1835) (2 %). Bivalves are less abundant and poorly diverse. The epibyssate bivalve *Plagiostoma rupicola* (Uhlig, 1881) (70 %) is common, accompanied by the free-lying/mobile species *Entolium* (*Entolium*)

corneolum (Young & Bird, 1828) (20 %), "*Inoceramus*" sp. (8 %) and "*Isoarca*" sp. (2 %). Free-lying *Bositra* can be locally very abundant (Vršatec).

6. Biostratigraphic implications

Ammonite assemblages are preserved in neptunian dykes that were developed and filled up during a long phase of sediment bypassing and synsedimentary erosion that locally lasted from the Late Bajocian to the Early Tithonian in the Pieniny Klippen Belt. The age of the Štepnická Skala ND-1 dyke corresponds to the upper part of the Lower Callovian, most probably to the Gracilis Zone because (1) the hecticoceratid *Jeanneticeras* is limited to Lower Callovian, and (2) reineckeiid ammonites appear in the Gracilis Zone (Thierry et al. 1997). The assemblage from the Štepnická Skala ND-2 dyke is stratigraphicaly younger. This dyke contains numerous and diverse Ammonitina, composed mainly of Hecticoceratinae and Grossouvriinae. First, the presence of the subgenus *Flabellia* indicates the Coronatum Zone of upper Middle Callovian (Mangold 1971). Second, *C.* (*G.*) *kontkiewiczi kontkiewiczi* is also typical of this zone, more precisely of the Baylei Subzone (although it appears already in the uppermost Anceps Zone). The stratigraphic ranges of hecticoceratid ammonites based on studies of Zeiss (1956), Lemoine (1932) and Elmi (1967) mainly indicate a time span from the Anceps Zone up to the Athleta zones for the Štepnická Skala ND-2 dyke. The age of the assemblage from the Štepnická Skala ND-2 thus likely corresponds to the Coronatum Zone (upper Middle Callovian).

The stratigraphic position of the neptunian dyke from the Vršatec locality remains less constrained. The fossil assemblage indicates Upper Bathonian or Callovian because hecticoceratid ammonites co-occur with the *Sowerbyceras* and with a microfacies rich in thin-shelled bivalves (*Bositra*). In the Western Carpathians, this microfacies is consistently restricted to the Toarcian – Callovian and is replaced by the *Globuligerina* microfacies in the Lower Oxfordian. The main distribution of the genus *Sowerbyceras* is Callovian – Kimmeridgian, although it was rarely mentioned also from Bajocian or Bathonian (Joly 2000).

7. Palaeobiogeographic implications

During the Callovian-Oxfordian, a long-term eustatic sea level rise was associated with rapid sea-floor spreading rates, changes in ocean circulation and ocean chemistry (Haq et al. 1988; Hallam 1989; Corbin et al. 2000; Cecca et al. 2005; Rais et al. 2007; Louis-Schmid et al. 2007). These changes were coupled with changes in palaeoceanographic conditions via the reopening of migration corridors for marine faunas, allowing the spreading of ammonites and other marine organisms (Enay & Mangold 1982; Cariou et al. 1985). The overlap between the Subboreal and Submediterranean Provinces is generally characterized by the southward migration of the Subboreal Kosmoceratidae and the northward migration of Tethyan Reineckeiidae during the Callovian. During the Late Callovian and Oxfordian, Cardioceratidae migrated southward from the Boreal Province and the Tethyan Perisphinctidae and Oppeliidae migrated northward (Cariou et al. 1985).

Palaeomagnetic data acquired from different sections from Slovakian, Polish and mainly Ukrainian localities suggest that the Pieniny Klippen Basin migrated to the south during the Callovian-Oxfordian owing to the rapid opening of an oceanic domain on the north side of the Czorsztyn Ridge (Lewandowski et al. 2005, 2006). The Bajocian-Bathonian palaeomagnetic inclinations indicate that the Czorsztyn Ridge was situated on the southern margin of European Craton. However, the Middle Oxfordian-Kimmeridgian data already indicate a significant separation of the Czorsztyn Ridge from European Craton (for details see Lewandowski et al. 2005).

Fossil assemblages of the neptunian dykes show affinities to the Submediterranean Province and are largely dominated by phylloceratid and lytoceratid ammonites. These pelagic taxa that preferred open oceanic conditions consistent with the Czorsztyn Ridge are accompanied by Perisphinctidae (Grossouvriinae) and Oppeliidae (mainly Hecticoceratinae). Reineckeiidae seems to be more abundant in the Lower Callovian than in the Middle Callovian. However, ammonite assemblages preserved in the Callovian-Oxfordian fissure fillings of the Czorsztyn Succession suggest that the Czorsztyn Ridge was situated within or near the southern limit of the Subboreal and Boreal provinces. First, abundant, probably lowermost Middle Oxfordian cardioceratids occur in neptunian dykes from the Vršatec Klippen (Schlögl et al. 2001), and cardioceratids occur also in the Middle Oxfordian (Transversarium Zone) of the Štepnická Skala locality (not published). Second, the presence of Kosmoceratidae in the Callovian dyke deposits also demonstrates the close proximity of the Czorsztyn

Ridge to the Subboreal Province. Two juvenile kosmoceratid specimens were found in the Štepnická Skala ND-1 (this study), and another kosmoceratid ammonite was figured by Uhlig (1881, pl. 7, fig. 6 a, b) from the Babierzowa Skala section as *Reineckeia greppini* Oppel. His figure shows a microconch of small size with two rows of tubercles and flattened mid-ventral area, morphologicaly similar to some less densely ribbed, and more evolute morphotypes of *Kepplerites* (*Toricellites*) *lahuseni* (Parona & Bonarelli, 1897). The originally proposed Callovian age of this faunal assemblage is now under reconsideration (in collaboration with Wierzbowski).

Subboreal ammonites do not occur in the Middle Callovian deposits of the Czorsztyn Ridge, although the Middle and the Lower Callovian assemblages might be biased by size-selective preservation of ammonites when exposed on the sea-floor and/or size sorting during their transport in dyke systems. The presence of micritic sediment in dykes indicates that the Callovian hiatuses are related to sediment bypassing, winnowing, and erosion rather than to complete starvation and/or sediment dissolution (e.g., Rais et al. 2007). The absence of bioerosion and encrustations on the walls of the neptunian dykes indicate that such fissures were filled relatively rapidly with sediment, thus also enhancing preservation of fossil assemblages. For example, rapid burial can reduce the likelihood of shell disintegration owing to dissolution and bioerosion (Powell et al. 1989). Sediment-filled fissures can also provide preservation traps in hardgrounds environments subjected to intense sediment scouring (e.g., Fürsich 1979; Vennin 2007) and thus hostile for in situ fossil preservation. Ammonites that inhabited the Czorsztyn Ridge during Late Callovian and Early Oxfordian time intervals remain completely unknown because deposits of such age were not detected in the Czorsztyn Unit.

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Table 1. Measurements: D – max. diameter; O – umbilical diameter; H – whorl height at max. D; E – whorl width at max. D (near the adult aperture if possible); H' – whorl height on the opposite side of the whorl (180° from H); E' – whorl width on the opposite side of the whorl (180° from E).

	D	O	H	E	H′	E′	O/D	E/H	E′/H′
F. (F.) elmii sp. nov., holotype. Fig. 7.2	34.50	14.50	11.20	8.80	8.90	7.80	0.42	0.79	0.88
F. (F.) elmii sp. nov., paratype. Fig. 7.3	36.90	14.90	11.90	8.80	9.60	7.90	0.40	0.74	0.82
F. (F.) tsytovitche, Fig. 7.1	45.00	17.80	15.20	13.00	11.00	10.10	0.40	0.86	0.92
F. (F.) tuberosus, Fig. 7.4	42.80	17.40	14.60	9.60	11.30	7.60	0.41	0.66	0.67
F. (F.) tuberosus, Fig. 7.5	38.50	16.00	14.00	7.70	9.50	7.80	0.42	0.55	0.82
C. (G.) vahica sp. nov., holotype. Fig. 8.1	38.00	15.00	12.00	7.50			0.39	0.63	
C. (G.) aff. tenella, Fig. 8.4	28.40	13.80	8.30	7.20	6.20	5.70	0.49	0.87	0.92
C. (G.) sp. nov. 1, Fig. 8.3	27.20	10.70	9.00	7.00	6.90	6.00	0.39	0.78	0.87
C. (G.) k. composita, Fig. 7.7	37.40	16.20	11.70	8.30	8.40	6.00	0.43	0.71	0.71
C. (G.) k. composita, Fig. 7.8	41.00	18.10	14.00		10.00	8.70	0.44		0.87
C. (G.) k. composita, Fig. 7.9	33.20	14.30	10.40	9.60	8.00	7.20	0.43	0.92	0.90
C. (G.) k. composita (not figured)	44.50	18.40	13.00	9.40			0.41	0.72	
C. (G.) k. kontkiewiczi, Fig. 8.10	56.00	26.00	16.00	12.50	13.00	11.00	0.46	0.78	0.85
C. (G.) sp. ex. gr. k., Fig. 7.11	34.70	15.70	10.40	8.40	7.80	6.80	0.45	0.81	0.87
C. (G.) sp. nov. indet. aff. Ammonites convolutus. Fig. 8.8	30.10	15.60	7.90	9.50	5.80	7.50	0.52	1.20	1.29
C. (G.) sp. nov. indet. aff. Ammonites convolutus. Fig. 8.7	28.30	14.20	7.50	8.40	5.80	8.60	0.50	1.12	1.48
H. (L.) sp. 1, Fig. 5.5	55.20	12.40	27.00	10.70	15.50	6.70	0.22	0.40	0.43
H. (Brightia) sp., Fig. 5.12	27.00	10.80	9.50	6.50	6.70	4.00	0.40	0.68	0.60
H. (L.) gr. sub-matheyi, Fig. 5.6	26.40	10.30	9.30	5.70	6.70	4.40	0.39	0.61	0.66
H. (P.) gr. zieteni, Fig. 5.15	29.00	9.20	12.00	9.40	7.90	6.90	0.32	0.78	0.87
H. (L.) gr. metomphalum, Fig. 5.11	35.00	11.80	14.40	7.00	8.90	5.00	0.34	0.49	0.56
H. (L.) gr. metomphalum, Fig. 5.10	43.00	15.10	15.00	10.00	11.80	7.80	0.35	0.67	0.66
H. (L.) gr. metomphalum, Fig. 5.9	37.50	9.80	17.50	6.50	11.40	6.10	0.26	0.37	0.54
H. (L.) cf. paulowi, Fig. 5.4	46.30	8.80	22.40	12.00	14.60	8.40	0.19	0.54	0.58
Horioceras sp. nov., aff. *depereti*, Fig. 5.3	40.60	11.40	16.80	9.70	12.10	6.80	0.28	0.58	0.56
Lissoceras voultense, Fig. 5.1	52.00	13.40	22.00	12.50	14.30	7.50	0.26	0.57	0.52
Lissoceras voultense, Fig. 5.2	31.80	8.10	14.70	6.20	9.40	4.80	0.25	0.42	0.51
Lissoceras voultense, ND-2 (not figured)	29.60	7.50	13.80	6.00	9.10	4.60	0.25	0.43	0.51