Revision of haploceratid ammonoids from the Štramberk Limestone, Jurassic–Cretaceous boundary beds (Outer Western Carpathians)

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Haploceratids from the Štramberk Limestones represent three genera *Haploceras*, *Hypolissoceras*, and *Volanites*. The most species reach genus is *Haploceras.* The semi-involute shells of the local haploceratids are almost smooth or only with a specific sculpture bound to the ventral region near the peristome. The whorls tend to be weakly arched or flat. Statistical elaboration of H/D, U/D and B/D values during shell growth shows no significant differences between these values, except perhaps for U/D. The external morphology plays a decisive role in the generic and species identification of haploceratids. It is known that haploceratids form dimorphic pairs, as evidenced by the differently shaped peristomes in addition to the different shell sizes. Dimorphic pairs have been demonstrated as new in the Štramberk material for the pairs *Haploceras staszycii* (microconch, m) and *Haploceras elimatum* (macroconch, M), as well as *Hypolissoceras carachtheis* (m) and *Hypolissoceras woehleri* (M). *Haploceras tithonium* and *Volanites verrucosus* possessed dimorphic pairs but their counterparts have not been found in the Štramberk Limestone. With the exception of *Volanites verruciferus,* the species described here are of no stratigraphical importance. Their stratigraphic range is from the lower Tithonian to the lower Berriasian.

Key words: Ammonoidea, Haploceratidae, taxonomy, Štramberk Limestone, Silesian Unit, Štramberk area.

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Introduction

Palaeontological collections of Moravian-Silesian museums house a considerable number of macrofossils from the Štramberk Limestone collected by generations of collectors and available for studies. Significant part of the macrofossils from Štramberk are ammonites. Representatives of the family Haploceratidae constitute around 20% of all ammonites in these collections. The contributions by Oppel (1865) and Zittel (1868) concern primarily ammonites, including haploceratids from the Štramberk Limestone. These ammonites are taxonomically described in a monograph by Zittel (1868) and his ammonite collection, with only minor exceptions, was deposited in Munich, Germany (SNSB-BSPG).

In contrast to other groups of ammonites (see, e.g., Vašíček et al. 2018), haploceratids from Štramberk area were not investigated by any researchers, only with a minor exception of Václav Houša (in Špinar 1965). In recent years, especially during our so-called palaeontological salvage collecting in the Kotouč Quarry in Štramberk since 2002, haploceratids have been found again. Thanks to that abundant new material often found in well established stratigraphic levels we could investigate haploceratids in detail and check if they have any stratigraphical significance for distinguishing between Tithonian and Berriasian. The examined new material is represented by approximately one hundred favourably preserved, non-deformed specimens from our own collection and, from repositories of four Moravian-Silesian museums (Museum of Ostrava; Nový Jičín Regional Museum; Silesian Museum in Opava, and Moravian Museum in Brno). Additionally, we re-examined the specimens studied by Zittel (1868, 1870) and deposited in SNSB-BSPG.

From a large number of the ammonites deposited in Moravian-Silesian museums, we selected and loaned favourably preserved specimens of haploceratids with at least one

measurable shell diameter and other standard size parameters. We processed all of the new material under study in the Silesian and Moravian repositories (B, MM, PL, and Z) using an electric vibration needle (mainly removing rock matrix from the umbilici). A considerable obstacle in studying the museum collections of the Štramberk Limestone fauna is, however, are poorly documented accurate points of collecting of the specimens. The original labels contain usually only general locality name Stramberg (German spelling) or Štramberk (Czech spelling). In total, the material under this study displays 7 species of haploceratids. We give special attention to the possible sexual dimorphism in these ammonoids. We also discuss posssible matches of shells and aptychi in haploceratids.

Institutional abbreviations.—B, Museum of Ostrava, Czech Republic; MM and Ge, Moravian Museum in Brno, Czech Republic; PL, Nový Jičín Regional Museum, Czech Republic; Z, Silesian Museum in Opava, Czech Republic; SNSB-BSPG, Bayerische Staatssammlung für Paläontologie und Geologie, Munich, Germany.

Other abbreviations.—A, adventive lobe; B, whorl breadth; B/D, whorl breadth to the diameter ratio; D, diameter; Dmax, maximal diameter; E, external lobe; H, whorl height; H/D, whorl height to the diameter ratio; m, microconchs; M, macroconchs; U, umbilicus width; U_l, U_2, umbilical lobes; U/D umbilicus width to the diameter ratio.

Geological setting

The Štramberk Limestone is exposed in the form of carbonate megablocks (1 to 100 meter in size), breccias and conglomerates in several quarries (i.e., Kotouč, Municipal, Horní Skalka, and Castle Hill) in the immediate vicinity of the town of Štramberk (Figs. 1, 2). This unit represents deposits that formed during the latest Jurassic–earliest Cretaceous. Today, it is located in the Outer Western Carpathians. Block accumulations of the Štramberk Limestone form part of the continental-rise sediments of the Baška Facies in the Silesian Unit, which were deposited in the flysch trough of the Baška Subunit (for more details, see Picha et al. 2006).

The Štramberk Limestone represents sediments, formed on a carbonate platform during the Late Jurassic and earliest Cretaceous, along the northern Tethyan margin in the area of the Outer Western Carpathians. The Štramberk Limestone is whitish-grey in colour and was deposited in various settings across the carbonate platform and reef complex. The most common type of rock is biodetrital limestone. In some intervals sedimentary breccias occur with clasts up to some dozen of centimeters.

From about 1910 onwards, the quarry at Kotouč Hill has been the main source of macro- and microfossils that have been described in numerous palaeontological studies (see Vašíček and Skupien 2004, 2005 and references therein). The reefal limestone facies at the quarry varies widely, ranging from very coarse-grained to gravelly layers or lenses, formed by e.g., molluscan shells and corals, to very fine-grained micritic limestones and (most commonly) fine-grained biodetrital limestones (e.g., Houša and Vašíček 2004).

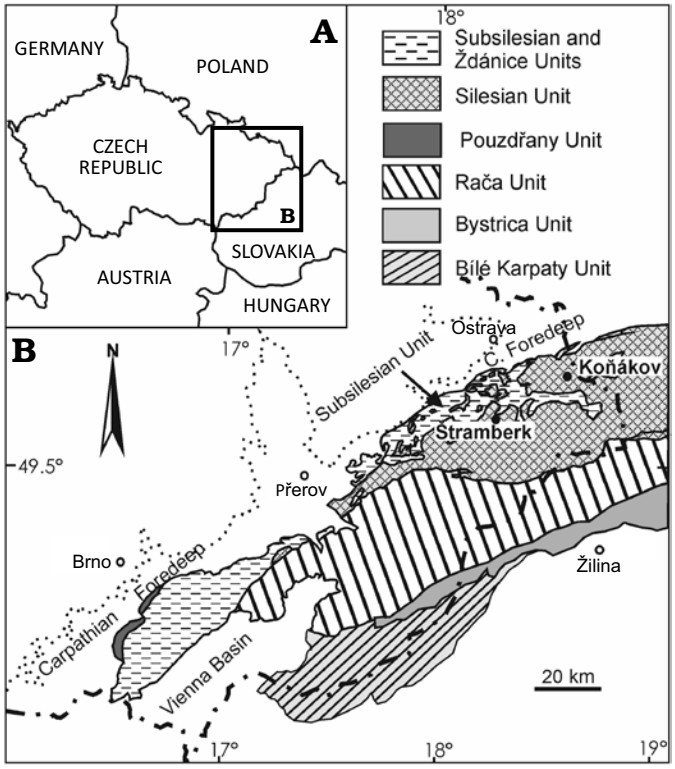


Fig. 1. **A**. Geographic location of the studied area. **B**. Tectonic map of the Outer Western Carpathian area of the Czech Republic (according to Skupien and Smaržová 2011).

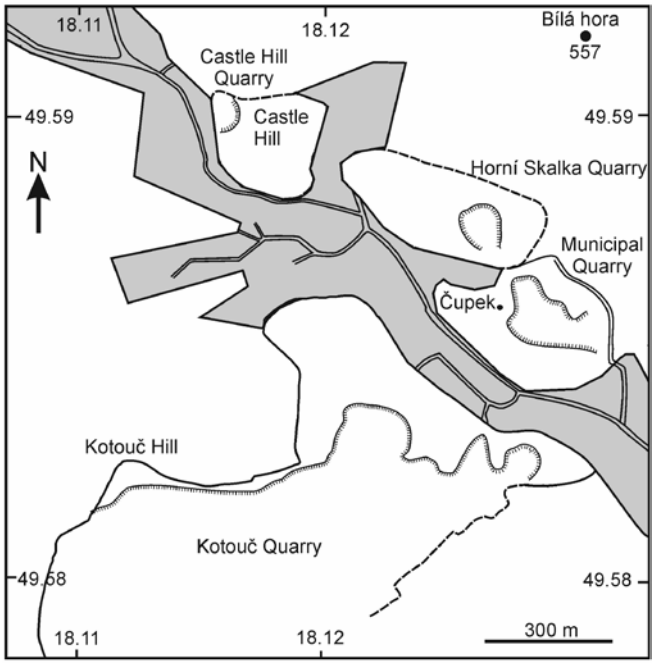


Fig. 2. Geographical setting of Štramberk Limestone quarries in the vicinity of Štramberk.

The age of the Štramberk Limestone was previously assumed to be the latest Kimmeridgian and Tithonian (e.g., Houša 1990; Houša in Houša and Vašíček 2004) but ammonites (Vašíček et al. 2013, 2017; Vašíček and Skupien 2013, 2014, 2016) from the limestone bodies indicate instead entire Tithonian and the earliest Berriasian.

Material

The advantage of ammonites from the Štramberk Limestone is their typically well-preserved, three-dimensional morphology without any deformation. In rare cases, their shells are only slightly deformed. These were not included in the statistical analysis. The core of our material comes from juveniles and ranges to adult specimens, with the diameter of the latter reaching almost 200 mm. There are three forms of proper preservation: recrystallized original tests, external and internal moulds (steinkerns). In the case of the last category, incomplete outer suture lines are usually preserved to various extents. Specimens are usually encased in detritic to coarse detritic, often organogenic limestone. In one specimen (Z1824) one side of the shell is covered by a sizeable number of small sessile remains of serpulid tubes, demonstrating that the ammonite shell had been lying on the bottom for quite a long time before it was covered with sediment.

The material processed by us is kept in museum collections and is designated in the systematic section below by means of an acronym of the relevant museum together with a deposit numbers marked on museum labels, as well as on individual specimens.

Historical background

The collection of ammnoids deposited now in SNSB-BSPG, was collected by a geologist Ludwig Hohenegger (1807–1854) mostly from a quarry below Castle Hill in Štramberk and from additional occurrences of Štramberk Limestone situated in the Silesian Unit of the Outer Western Carpathians, i.e., Koniakau (now Koňákov), Kotzobenz (now Chotěbuz), and Wilamowitz (now Wilamowice). Based on the Štramberk fauna, Oppel (1865) defined the Tithonian Stage. He identified and named some cephalopods from Štramberk Limestone, provided also brief descriptions but no illustrations. Subsequntly Zittel (1868) examined the collection of ammonites (and thus also haploceratids) from the Štramberk Limestone, described them in detail and illustrated—including the species established by Oppel in Zittel (1868) with no illustrations. Later on, Zittel (1870) created the genus *Haploceras*, which included *Ammonites carachtheis* and *Ammonites staszycii* established by Zejszner (1846). Zejszner (1846) illustrated these two species in his contribution on Tithonian brachiopods from Pieniny Klippen Belt, therefore he did not describe the ammonoids in detail. These species have been formally described in the monograph by Zittel (1870) and identified from the Štramberk Limestone. The name of the author of both species, however, have been provided in German spelling Zeuschner, while the original paper displays Polish spelling Zejszner.

In the 19th century and in the first half of the 20th century, the occurrence of Tithonian haploceratids under the generic name *Haploceras* was recorded in several localities throughout Europe. Breistroffer (1947) and subsequently many other authors proceeded to more specific, frequently different, varied and contradictory taxonomic concepts of haploceratids, above all in connection with *Ammonites carachtheis* at the subgeneric or generic level. Breistroffer (1947) defined the new subgenus *Hypolissoceras* with the type species *A. carachtheis.* Barthel (1962) assigned this latter species to *Glochiceras* Hyatt, 1900, a genus occurring in the Oxfordian and Kimmeridgian. Patrulius and Avram (1976) established the subgenus *Neoglochiceras* (synonym of *Hypolissoceras* Breistroffer, 1947); Olóriz Sáez (1978) used the subgenus *Lingulaticeras* Ziegler, 1958, for *A. carachtheis*; Sapunov (1979) used *Glochiceras*; Enay and Cecca (1986) added the new subgenus *Volanites* to the genus *Haploceras*; Főzy (1988) and lately Zeiss (2001) used subgenus *Hypolissoceras* for *A. carachtheis*. Kutek and Wierzbowski (1979, 1986) and Wierzbowski (1990) provided new data on the occurrence of several species of haploceratids, especially those from the lower and middle Tithonian strata of Rogoźnik (Pieniny Klippen Belt, Poland). Zeiss et al. (1994) referred to *A. carachtheis* as *Hypoglochiceras carachtheis*; however, the genus *Hypoglochiceras* has never been formally defined. Wright et al. (1996) included only two Cretaceous genera to the family Haploceratidae: *Haploceras* (and its synonyms) and *Neolissoceras.* Főzy and Scherzinger (2013) and Sarti (2020, 2024) reported also on some haploceratids from Trento Plateau (Southern Alp). All the species described in the papers by Sarti (2020, 2024) were classified in the genus *Haploceras*.

In remarks to the species *Haploceras elimatum* (Oppel Zittel, 1870), Barthel (1962) proposed that this species forms a dimorphic pair with *Ha. staszycii*. Olóriz Sáez (1978) described in detail Tithonian haploceratids from Spain. Enay and Cecca (1986) discussed in detail and in a somewhat non-traditional manner the evolution of Tithonian haploceratids. The basis of their analysis was *Haploceras* (*Haploceras*) *carachtheis*, which they considered as the evolutionary earliest species. First, they divided the collection of this species into two groups based on shell size and ornamentation. Furthermore, they subdivided *Ha. carachtheis* into smaller subgroups and named them morphs (e.g., *Ha. carachtheis* morph *elimatum*). In the framework of these morphs, they recognized microconchs (m) and macroconchs (M). For the species *Haploceras verruciferum*, Enay and Cecca (1986) established the new subgenus *Volanites.* Főzy (1988) subsequently studied the family Haploceratidae in detail, taking also into account possible dimorphism. He also defined a new species of *Haploceras cassiferum*. Interestingly, while establishing this new species, as well as discussing *Ha. verruciferum*, he did not mention

the subgenus *Volanites.* At the beginning of this millennium, Zeiss (2001) again studied haploceratids. Among other matters, he reported that *Ha. elimatum,* which should represent microconchs, has allegedly developed peristome with rostra and lappets in all growth stages. Főzy and Scherzinger (2013) reported some similar observations.

Recently, Hoedemaeker (in Hoedemaeker et al. 2016) revised the systematics of *Haploceras*. His conception reflected the opinions of Enay and Cecca (1986); he also used morph as a taxonomic category, and regarded *Haploceras carachtheis* morph *carachtheis* as a microconch and *Haploceras carachtheis* morph *elimatum* as a macroconch.

Systematic palaeontology

In the superfamily- to family-level conception of haploceratids, we follow the historical classification by von Zittel (1884), with modifications proposed by Wright et al. (1996) with the type genus *Haploceras*. At the suborder level, we did not follow the older taxonomy, by e.g., Hyatt (1900) or Callomon (1981). According to the character of the suture lines of haploceratids by Beznosov and Mikhailova (1983, 1991) we have classified the haploceratids in the suborder Haploceratina.

In the 20th century, several other genera were established for the Late Jurassic period. Among them, in the presented paper, besides *Haploceras*, the *Hypolissoceras* and *Volanites* are considered as separate genera. *Volanites* was originally not very clearly established as a subgenus of the genus *Haploceras* in Enay and Cecca (1986).

For favourably preserved specimens of haploceratids, the usual size parameters were measured in mm. For a description and illustration of outer suture lines, we use newer terminology from Korn et al. (2003).

Stratigraphic data and ammonite zonation are based primarily on the data from Enay and Cecca (1986), Zeiss (2001, 2003), and Főzy and Scherzinger (2013).

Order Ammonitida von Zittel, 1884

Suborder Haploceratina Beznosov & Mikhailova, 1983

Superfamily Haploceratoidea von Zittel, 1884

Family Haploceratidae von Zittel, 1884

Genus *Haploceras* Zittel, 1870

Type species: *Ammonites elimatus* Oppel, 1865; Štramberk, Czech Republic, Tithonian, by subsequent designation of Spath 1923: 14.

Remarks.—Adult members of the genus possess smooth or indistinctly ribbed shells with ribs best developed on the venter and on the upper half of whorl flanks. Indistinct fine lines are sometimes apparent even near the umbilicus. Wright et al. (1996: 10) consider, in accordance with previous conventions, a specimen of *Ammonites elimatus* as the type species of the genus *Haploceras*. In the generic description, Wright et al. (1996) stated that *Hypolissoceras* Breistroffer, 1947, with type species *Ammonites carachtheis* Zejszner, 1846, is a synonym of the genus *Haploceras.* Wright et al. (1996) again illustrated the specimen of Zittel (1868: pl. 15: 1a–c) in fig. 6/1c–e and stated that it is *Haploceras carachtheis*, which should be considered a microconch to *Haploceras elimatum*. We do not agree with this concept, as discussed in detail below.

Recently, Hoedemaeker has discussed the systematics of the genus *Haploceras* (in Hoedemaeker et al. 2016) and returned back to the concept of morphs by Enay and Cecca (1986). He regards *Haploceras carachtheis* morph *carachtheis* as the microconch corresponding to the macroconch *Ha. carachtheis* morph *elimatum*. He does not discuss the entirely different type of ribbings in *Ha. carachtheis* and *Ha. elimatum*, respectively.

Haploceras elimatum (Oppel, 1865)

Figs. 3A, 4A, 5, 6F, G.

1865 *Ammonites elimatus* Opp.; Oppel 1865: 549.
1868 *Ammonites elimatus* Opp.; Zittel 1868: 79, pl. 13: 1a–c (lectotype), 2, 3a, b, 4, 5a–c, 6, 7a, b.
1870 *Haploceras elimatum* Opp. sp.; Zittel 1870: 51, pl. 27: 7a, b.
1890 *Haploceras elimatum* Oppel; Toucas 1890: 576, pl. 13: 4.
1923 *Haploceras elimatum* (Oppel); Spath 1923: 14.
1925 *Haploceras elimatum* (Oppel); Spath 1925: 153, pl. 1: 1a–c.
1953 *Haploceras elimatum* Oppel; Arnould-Saget 1953: 8, pl. 1: 9a–c.
?1953 *Haploceras elimatum* Opp.; Slavin 1953: 54, pl. 1: 9.
1956 *Haploceras elimatum* (Opp.); Książkiewicz 1956: 211, pl. 25: 6, text-fig. 25.
1960 *Haploceras elimatum* Opp.; Collignon 1960: pl. 142: 536, 537.
1960 *Haploceras subelimatum* Font.; Collignon 1960: pl. 142: 538.
1960 *Haploceras elimatum* Oppel; Drushchits and Kudryavtsev 1960: 267, pl. 13: 1, text-fig. 71.
1962 *Haploceras elimatum* (Oppel); Barthel 1962: 11, pl. 1: 12–15 (= Zittel 1870: pl. 27: 7a, b), text-figs. 15–17.
1965 *Haploceras elimatum* (Oppel); Houša in Špinar 1965: fig. VIII/254.
1966a *Haploceras* (*Haploceras*) *elimatum*; Wiedmann 1966a: 76, pl. 1: 1a, b.

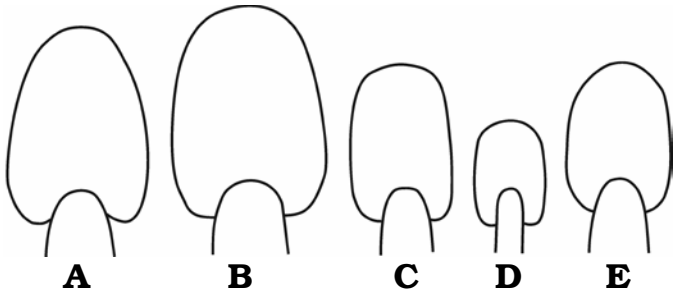


Fig. 3. Whorl sections of haploceratid ammonoids from Štramberk, Czech Republic, Tithonian–lower Berriasian. **A**. *Haploceras elimatum* (Oppel, 1865), SNSB-BSPG AS III 800 (Zittel 1868: pl. 13: 1a) at H = 33 mm. **B**. *Haploceras staszycii* (Zejszner, 1846), SNSB-BSPG AS III 805 (Zittel 1870: pl. 27: 3a) at H = 37 mm. **C**. *Haploceras tithonium* (Oppel, 1865), SNSB-BSPG AS III 798 (Zittel 1868: pl. 14: 2a) at H = 25 mm. **D**. *Hypolissoceras carachtheis* (Zejszner, 1846), SNSB-BSPG AS III 47 (Zittel 1868: pl. 15: 1c) at H = 17 mm. **E**. *Hypolissoceras woehleri* (Oppel, 1865), MM 06 at H = 27 mm.

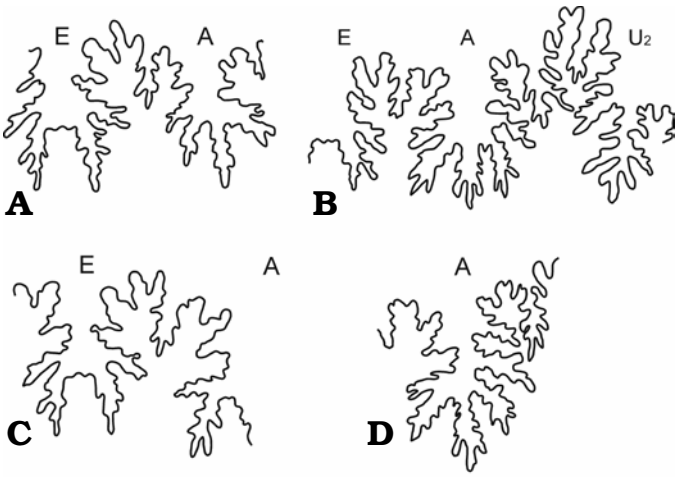


Fig. 4. Suture lines of haploceratid ammonoids from Štramberk, Czech Republic, Tithonian–lower Berriasian. **A**. *Haploceras elimatum* (Oppel, 1865). Almost complete outer suture line of Z4224 at H = 11.5 mm. **B**. *Haploceras staszycii* (Zejszner, 1846). Substantial part of outer suture line of PL5061 (6th level, middle) at H = 14 mm. **C**. *Haploceras tithonium* (Oppel, 1865). Outer and adventive lobes with accompanying saddles of PL5113 at H = 15 mm. **D**. *Hypolissoceras woehleri* (Oppel, 1865). Adventive lobe with parts of accompanying saddles of MM08 at H = 15 mm. A, adventive lobe; E, external lobe; U2, umbilical lobe.

1966b *Haploceras* (*Haploceras*) *elimatum* (Oppel); Wiedmann 1966 b: 61, text-figs. 42b, 43a.
1968 *Haploceras* (*Haploceras***)** *elimatum* (Oppel); Wiedmann 1968: pl. 1: 3a, b.
1970 *Haploceras elimatum* (Oppel); Patrulius et al. 1970: 138, pl. 2: 11a, b, ?fig. 10.
1976 *Haploceras* **(***Haploceras*) *elimatum* (Oppel); Avram 1976: 34, pl. 8: 1a, b.
1978 *Haploceras elimatum* (Oppel); Olóriz Sáez 1978: 12, pl. 1: 2, 3.
1979 *Haploceras elimatum* (Oppel); Sapunov 1979: 42, pl. 7: 1, 2a, b, text-fig. 4/5 (with synonymy).
1983 *Haploceras* (*Haploceras*) *elimatum* (Oppel); Vašíček 1983: 97, pl. 3: 1.
1984 *Haploceras elimatum* (Oppel); Rossi 1984: 88, pl. 31: 11, 12.
1986 *(Haploceras (Haploceras) carachtheis* (M) (Zeuschner) morph *elimatum*; Enay and Cecca 1986: pl. 4: 3, 4a, b, 5a, b; non pl. 4: 1a, b, 2a, b (= *Haploceras staszyci* Zejszner).
1988 *Haploceras* (*Haploceras*) *elimatum* (Oppel); Főzy 1988: 51, pl. 2: 1, non pl. 2: 2, 3 (= *Haploceras tithonium* Oppel).
?1994 *Haploceras elimatum* (Oppel); Főzy et al. 1994: 158, pl. 1: 10.
?1994 *Haploceras elimatum* (Oppel); Zeiss et al. 1994: 1: 4.
1995 *Haploceras elimatum* (Oppel); Főzy 1995: 136, pl. 20: 9.
1996 *Haploceras elimatum* (Oppel); Wright et al. 1996: 10: 6/1a, b (= Zittel 1868: pl. 13: 1a, b).
1997 *Haploceras* (*Haploceras*) *carachtheis* Zeuschner morph *elimatum* (Oppel); Benzaggagh and Atrops 1997: pl. 4: 3.
1999 *Haploceras* cf. *elimatum* (Oppel); Fatmi and Zeiss 1999: 39, pl. 43: 1.
non 1999 *Haploceras elimatum* (Oppel); Kvantaliani 1999: 74, pl. 5: 4 (= *Haploceras staszyci* Zejszner).
2000 *Haploceras* ex gr. *elimatum* (Oppel); Arkadiev et al. 2000: 99, pl. 2: 6a–c.
2001 *Haploceras* (*Haploceras*) *elimatum* (Oppel); Zeiss 2001: 37, pl. 5: 6, 7.
2005 *Haploceras elimatum* (Oppel); Boughdiri et al. 2005: 309, pl. 2: 1.
2009 *Haploceras elimatum* (Oppel); Klein et al. 2009: 257 (with synonymy).
2013 *Haploceras elimatum* (Oppel); Főzy and Scherzinger 2013: 214, pl. 4: 5a, b, ?pl. 5: 11, ? pl. 6: 7.
2013 *Haploceras elimatum* (Oppel); Szives and Főzy 2013: 294, pl. 3: 3.
2016 *Haploceras carachtheis* morph *elimatum* (Oppel); Hoedemaeker et al. 2016: 169, pl. 17: 7, 8.
2017 *Haploceras elimatum* (Oppel); Főzy 2017: pl. 27: 5, pl. 35: 7.
2020 *Haploceras elimatum* (Oppel); Sarti 2020: 86.
2024 *Haploceras elimatum* (Oppel); Sarti 2024: 86.

Type material: Lectotype SNSB-BSPG AS III 800 was designated by Spath (1925), originally figured by Zittel (1868: pl. 13: 1 a–c).

Type locality: Štramberk Limestone, Štramberk, Czech Republic.

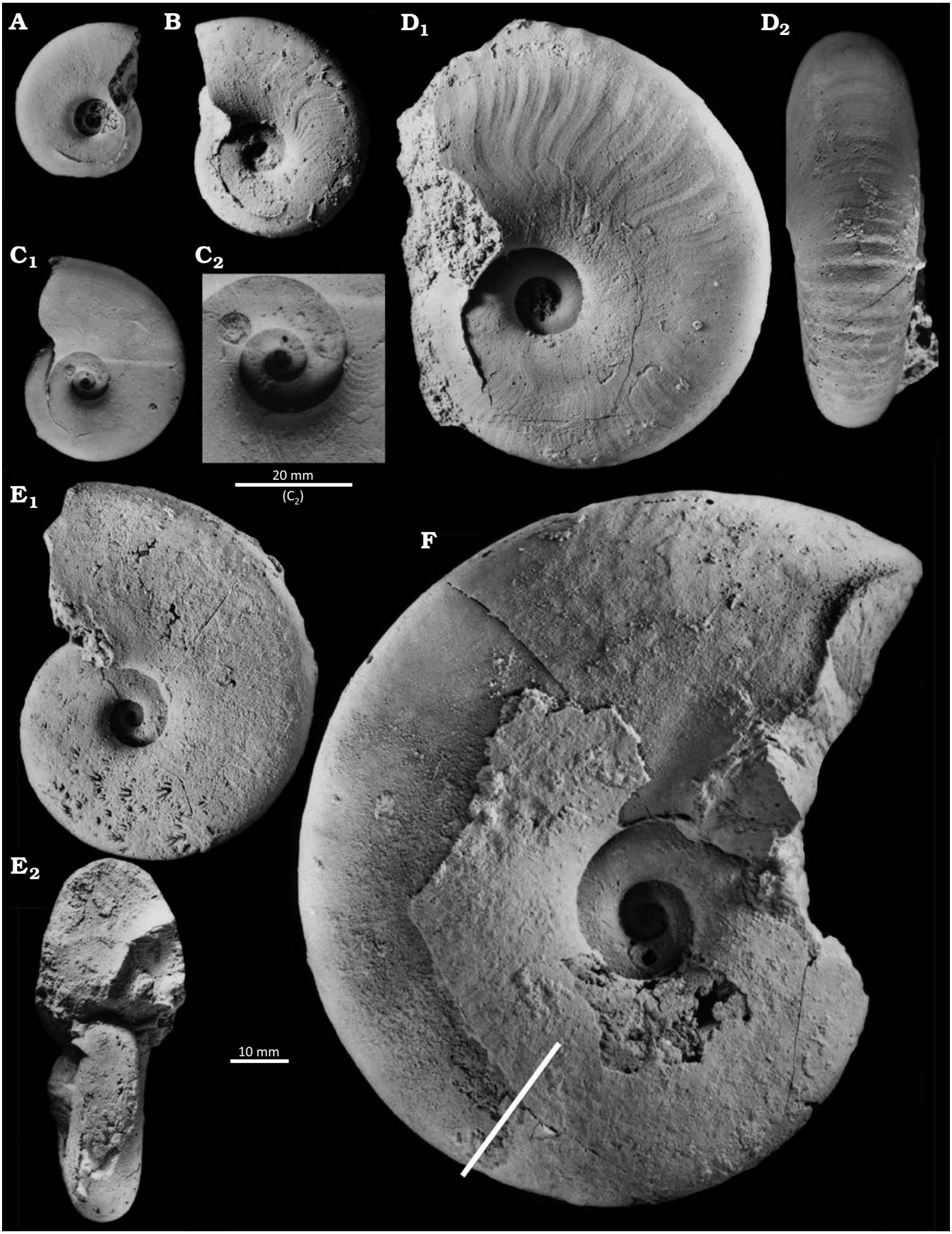
Type horizon: Tithonian or lower Berriasian.

Material.—In addition to the favourably preserved and published specimens deposited in Munich (SNSB-BSPG AS III 800–802), more than 30 other non-deformed specimens with sizes ranging from approximately 20 to 200 mm with various degrees of preservation quality were studied. Some specimens deposited in the Moravian-Silesian museums are phragmocones (some with preserved incomplete suture lines), and others are phragmocones with incomplete body chambers. The best preserved specimens are PL2520, PL5056, PL5058, PL5107–5112, B13569, B13831, Z1824, Z4224,. However, no completely preserved specimens have been found.

Description.—All specimens are semi-involute, with high, medium-broad whorls and a comparatively narrow umbilicus. The flanks of the whorl are arched. The whorl reaches its greatest breadth relatively close to the umbilical seam. The whorl declines from the area of the greatest arch to the umbilicus more steeply but continuously. No edge is developed on the line of coiling, but there is a narrow, strongly arched zone. Judging from the steinkerns, it is evident that the whorl still plunges inside below the line of coiling so that between the ultimate and penultimate whorls, an empty gap remains in the steinkerns. The flanks of the whorl decline gradually towards the venter. The venter is medium-broad and strongly arched.

The exceptionally well-preserved is medium-sized specimen PL5108 has a recrystallized original shell (Fig. 5D) and in comparison to others, is more conspicuously ribbed. Relatively broad, blunt, and rather widely placed ribs are present mainly on the upper half of the whorl in *Haploceras elimatum*. The ribs are S-shaped. Near the line of coiling, ribs are faint and concavely bent to the aperture in a short zone. At approximately half the whorl height, the blunt ribs are clearly convexly bent and on the outer side, again concave in a wide shallow arch. Over the venter, the ribs pass without interruption and are slightly inclined towards the peristome. On the original shells, small, fine, dense lines (Fig. $5C_2$) are usually preserved near the umbilicus. On the flanks and on the venter, as with the steinkerns, the ribs are usually only slightly pronounced. Very often, ribbing is not preserved at all, and thus, the specimens seem to be or are smooth.

Zittel (1868: pl. 13: 2, 7) illustrated a peristome for two specimens. The smaller specimen, reaching a diameter of approximately 70 mm, has a simpler peristome than the larger specimen. The larger one, with a diameter of approximately 125 mm, displays a peristome with a well expressed lappet.


A
B
D1
D2
C1
C2
20 mm
(C2)
E1
F
E2
10 mm

← Fig. 5. Haploceratid ammonoid *Haploceras elimatum* (Oppel, 1865) from Kotouč Quarry, Tithonian–lower Berriasian, Upper Jurassic–Lower Cretaceous, from author's own findings in the quarry or from the collection of Lubomir Martinásek (Kopřivnice, Czech Republic). **A**. PL5058, phragmocone with original test. **B**. PL5112, specimen with original test and with beginning of body chamber, lateral view. **C**. PL5110, phragmocone with original test, lateral view (C_1), detail of sculpture around umbilicus (C_2). **D**. PL5108, specimen with the original test and with a part of body chamber, lateral (D_1) and ventral (D_2) views. **E**. PL5107, external mould with beginning of body chamber in lateral view (E_1), view on the area near aperture (E_2). **F**. PL5109, internal mould in lateral view, with the body chamber inclusive of peristome (with rest of original test around umbilicus). The straight line perpendicular to periphery of specimen shows the margin between body chamber and phragmocone.

Almost entire outer suture line is preserved on the juvenile specimen Z4224 (D = 28.5 mm). The external lobe E bears a non-high secondary saddle of rectangular shape. The E/A saddle is two-branched, with its external branch higher than its internal branch. The mentioned saddle is lower than the A/U saddle. Adventive lobe A is broad and four finger-shaped at the base. On specimen B13831, an incomplete suture line (E and A) is preserved as well.

Measurements.—The parameters we measured on both juvenile and adult specimens (we measured approximately 30 specimens, see SOM 1, 2, in Supplementary Onine Material available at http://app.pan.pl/SOM/app70-Vasicek_Skupien_SOM.pdf). The lectotype at D = 61.3 mm (Dmax ca. 70 mm) has H/D = 0.49, U/D = 0.22, B/D = 0. 34. Across the entire size range of the shells, the ratios of the measured parameters remain in similar range: H/D ranges 0.46–0.50, U/D ca. 0.20–0.23, B/D ca. 0.33–0.38. It statistical investigations we initially set an arbitrary boundary between juvenile and adult specimens at a value around the diameter D of ca. 60 mm for practical reasons. In Fig. 7A–C, we have labelled the smaller specimens as "microconchs", and the larger ones as "macroconchs". The regression lines are similar in all cases, and the calculated correlation coefficients R are close to 1. Therefore it is implausible to define any statististically meaningful boundary between small and large specimens (see Fig. 7). We conclude therefore that all measured specimens belong to the macroconch category. The terminal size of the adult specimens is around the diameter of 105 mm. These results agree with data of Zeiss (2001).

Remarks.—We could not found any differences neither in the measured parameters nor their morphology and ornamentation between small and large specimens. The peristome in the small specimen illustrated as a drawing by Zittel (1868: pl. 13: 2) does not accurately reflect reality. Its shape, especially the size of the lappet is somewhat reduced. In contrast, in the peristome of the specimen illustrated by Zittel (1868: pl. 13: 7a), a seemingly unrealistic robust lappet is shown. Less conspicuous lappets in large specimens of *Ha. elimatum* are indicated by growth lines on the flank of the whorls of most specimens, as illustrated in Fig. 5F. This is also valid for the imperfectly preserved peristome of our adult specimen shown in Fig. 5F, which reaches a size similar to that of the specimen in Zittel (1868: pl. 13: 7). Growth lines, which should highlight the conspicuous lappet, are missing also in the lectotype.

Fontannes (1879) established *Haploceras subelimatum*, which according to its illustration (Fontannes 1879: pl. 2: 6) differs from *Ha. elimatum* merely in having narrower whorls. This is also confirmed by the data of B/D values (around 0.27–0.37) in the specimens reported by Sarti (2020). In contrast, *Ha. subelimatum* as illustrated by Collignon (1960: pl. 142: 538) did not have narrow whorls, and thus, it can be regarded as *Ha. elimatum.* According to a table showing the measurements of the specimens described by Kvantaliani (1999) as *Ha. elimatum,* the specimens have broader whorls and narrower umbilicus than both aforementioned species and apparently belong to *Ha. staszycii.*

Stratigraphic and geographic range.—*Haploceras elimatum* is known from the whole Mediterranean area from North Africa to the Himalayas and from Madagascar (for more information, see Főzy and Scherzinger 2013). According to figure in Enay and Cecca (1986: fig. 4), which marks the ammonite zonation of the Tithonian, *Ha. elimatum* has a considerably wide stratigraphic range from the basal Tithonian to the lower Berriasian inclusive (see also Sarti 2020). The lectotype comes from an unspecified part of the Štramberk Limestone in Štramberk. The lower Berriasian occurence is mentioned, e.g., by Arnould-Saget (1953), Olóriz Sáez (1978), Vašíček and Skupien (2013), and Szives and Főzy (2013). Spath (1925) stated that in Madagascar, this species occurs in the Kimmeridgian, but Collignon (1960) corrected it to the lower Tithonian (though also with an imprecise stratigraphy).

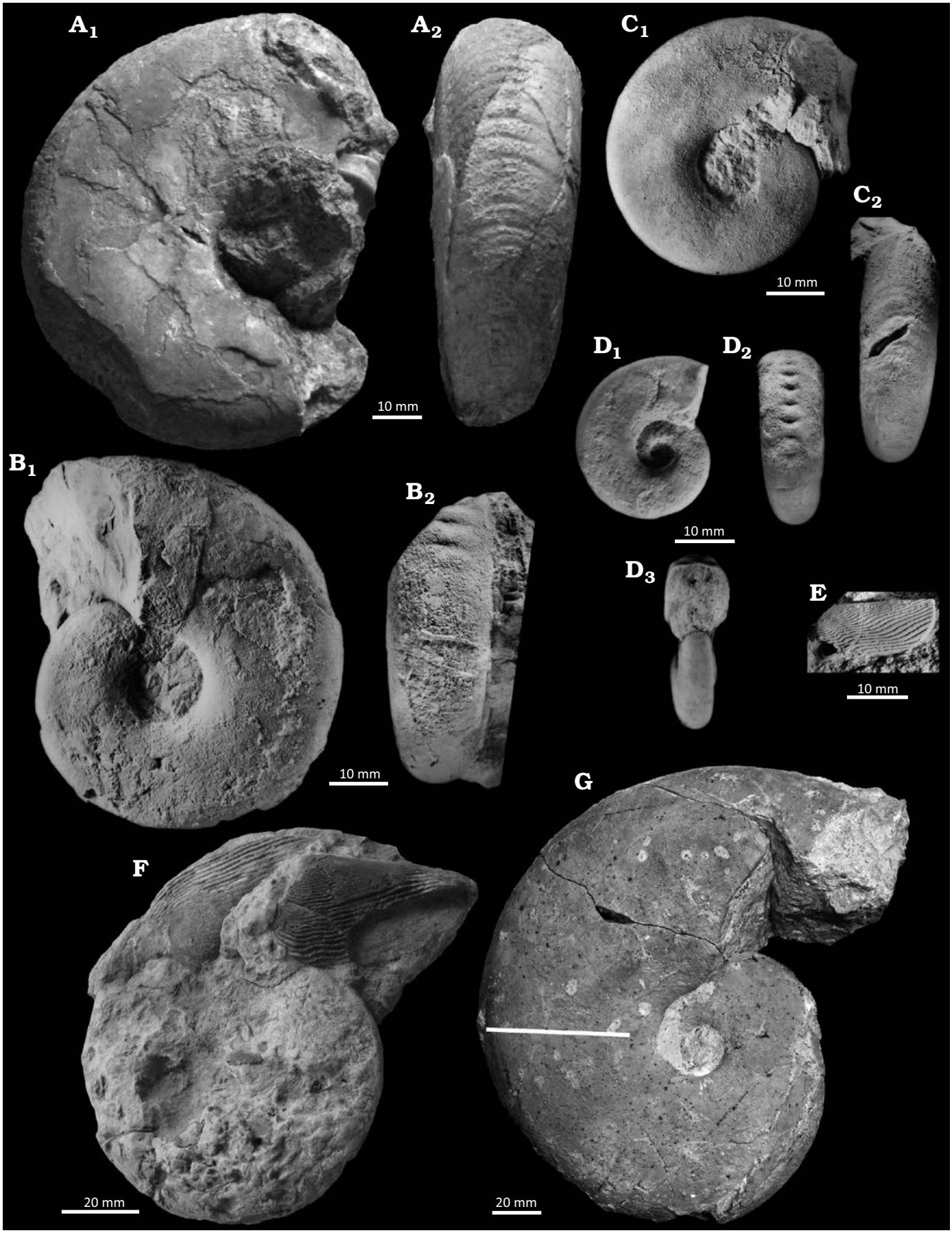
Our specimens from the Kotouč Quarry occur, according to the other accompanying ammonites, in both the lower and upper Tithonian (especially locality 4 in Vašíček and Skupien 2016), as well as sporadically in the lower Berriasian (Vašíček and Skupien 2013).

Another locality with *Ha. elimatum* in the Czech Republic is an abandoned quarry near the municipality of Roštín (Rača Nappe of the Magura Unit), namely, in a block conglomerate with grey marly limestones that, according to the accompanying ammonites, belong to the lower Tithonian (Vašíček 1983). Other historical occurrences in the Silesian Unit of the Outer Western Carpathians are known from so-called exotic conglomerates, in which the main component is Štramberk Limestone, in the localities of Koňákov, Chotěbuz, and other (Hohenegger 1861).

Haploceras staszycii (Zejszner, 1846)

Figs. 3B, 4B, 8A–D.

1846 *Ammonites Staszycii* Zejszner 1846: pl. 4: 3a–c.
1870 *Haploceras Staszycii* Zeuschner; Zittel 1870: 50, pl. 27: 2a, b, 3a, b (neotype), non figs. 4, 5 (?).
1876 *Haploceras Staszycii* Zeuschn.; Gemmellaro 1876: 34, pl. 7: 1–3.
1879 *Haploceras staszycii* Zeuschner; Fontannes 1879: 11, pl. 2: 4a, b.
1960 *Haploceras staszycii* Zeuschn.; Collignon 1960: pl. 142: 539.


A1
A2
C1
C2
10 mm
D1
D2
10 mm
B1
B2
D3
E
10 mm
10 mm
G
F
20 mm
20 mm

← Fig. 6. Haploceratid ammonoids from Tithonian–lower Berriasian, Upper Jurassic–Lower Cretaceous. **A**, **B**. *Hypolissoceras woehleri* (Oppel, 1865). **A**. Holotype AS III 811 (real state of preservation), external mould, Štramberk, in lateral (A_1) and ventral (A_2) views. **B**. Z4171, external mould, Štramberk, in lateral (B_1) and ventral (B_2) views. **C**. *Volanites verruciferus* (Zittel, 1869), Z2981b, external mould, Štramberk, in lateral (C_1) and ventral (C_2) views. **D**. *Hypolissoceras subtilius* (Zittel, 1870), Z2767a, external mould, Štramberk, in lateral (D_1) and ventral (D_2) views, view of the area of peristome (D_3). **E**. *Beyrichilamellaptychus beyrichi beyrichi* (Oppel, 1865), Ge0001, lateral view, from Měchová et al. (2010: fig. 9B), Kurovice. **F**, **G**. *Haploceras elimatum* (Oppel, 1865). **F**. Specimen with *Punctaptychus punctatus* (Zittel, 1868) in the body chamber, AS III 339, in lateral view, from Barthel (1962), according to Barthel's hand-written label: "*H. elimatum* (Oppel) mit erhaltenen Aptychen, Tithon, Le Pouzin, Typloc. zu Toucas 1890". **G**. Z1824, specimens carrying the calcitic shells of serpulid worms (white dots), Štramberk. The straight line perpendicular to periphery of specimen shows the margin between body chamber and phragmocone. Photos Kristýna Mezihoráková (Ostrava, Czechia), exept A, ZV; and G. Ondřej Malek, (Green Gas DPB, Paskov, Czechia).

1970 *Haploceras stazsycii* (Zeuschner); Patrulius et al. 1970: 138, pl. 2: 9a, b.
1976 *Haploceras* (*Haploceras*) *staszycii* (Zeuschner); Avram 1976: 35, pl. 8: 4a, b.
1978 *Haploceras staszycii* (Zeuschner); Olóriz Sáez 1978: 15, pl. 1: 1a, b.
1979 *Haploceras staszycii* (Zejszner); Sapunov 1979: 43, pl. 7: 3a, b, text-fig. 4/6.
1980 *Haploceras staszici* (Zejszner); Malinowska et al. 1980: 444, pl. 136: 5.
?1984 *Haploceras staszycii* (Zeuschner); Rossi 1984: 89, pl. 31: 8.
1986 *Haploceras* (*Haploceras*) *carachtheis* (M) Zeuschner) morph *elimatum*; Enay and Cecca 1986: pl. 4: 1a, b.
1986 *Haploceras* (*Haploceras*) *carachtheis* (M) (Zeuschner) morph *staszycii*; Enay and Cecca 1986: pl. 4: 2a, b.
1988 *Haploceras* (*Haploceras*) *staszycii* (Zeuschner); Főzy 1988: 53, text-fig. 7 (with additional synonymy).
1999 *Haploceras elimatum* (Oppel); Kvantaliani 1999: 74, pl. 5: 4.
1994 *Haploceras staszycii* (Zeuschner); Zeiss et al. 1994: 370, pl. 1: 1.
2001 *Haploceras* (*Haploceras*) *staszycii* (Zeuschner); Zeiss 2001: 38, pl. 5: 1-3.
2002 *Haploceras* (*Haploceras*) *carachtheis* (Zeuschner) *staszycii* (Zeuschner); Pavia et al. 2002: 233: 159.
2020 *Haploceras staszycii* (Zeuschner); Sarti 2020: 87, pl. 3: 5.
2024 *Haploceras staszycii* (Zeuschner); Sarti 2024: 87, pl. 3: 5.

Type material: The holotype of Zejszner (1846) according to Malinowska et al. (1980: 444) was lost. They designated as a lectotype the specimen from Zittel (1870: pl. 27: 3, i.e., SNSB-BSPG AS III 805) from Rogoźnik. But according to the ICZN she designated neotype rather than lectotype.

Type locality: Rogoźnik, Poland.

Type horizon: Pieniny Klippen Zone, Rogoża Coquina Member, Fallauxi ammonite Zone, lower Tithonian.

Material.—The material under this study consists of 8 specimens from Moravian-Silesian museums (e.g., Z1585, Z1484, MM 010, MM Ge30259, B13570, PL2447, PL5059, and PL5061). The set was supplemented by direct study of originals in the Zittel collection housed in Munich (SNSB-BSPG AS III 803, 805, 806). The initial half of the ultimate whorl of the specimen PL5059 belongs, according to the visible suture line, to the phragmocone, and the final half to the body chamber.

Description.—Semi-involute specimens, with a high, relatively broad whorl and a narrow umbilicus. The low umbilical wall declines obliquely to the line of coiling. It continuously passes through a rounded zone to the slightly arched flanks of the whorl. The flanks also pass through a rounded zone to the medium-broad venter. On the juvenile specimen PL2447 and further on the adult specimen Z1484, a siphonal furrow is preserved on the phragmocone. The shell is

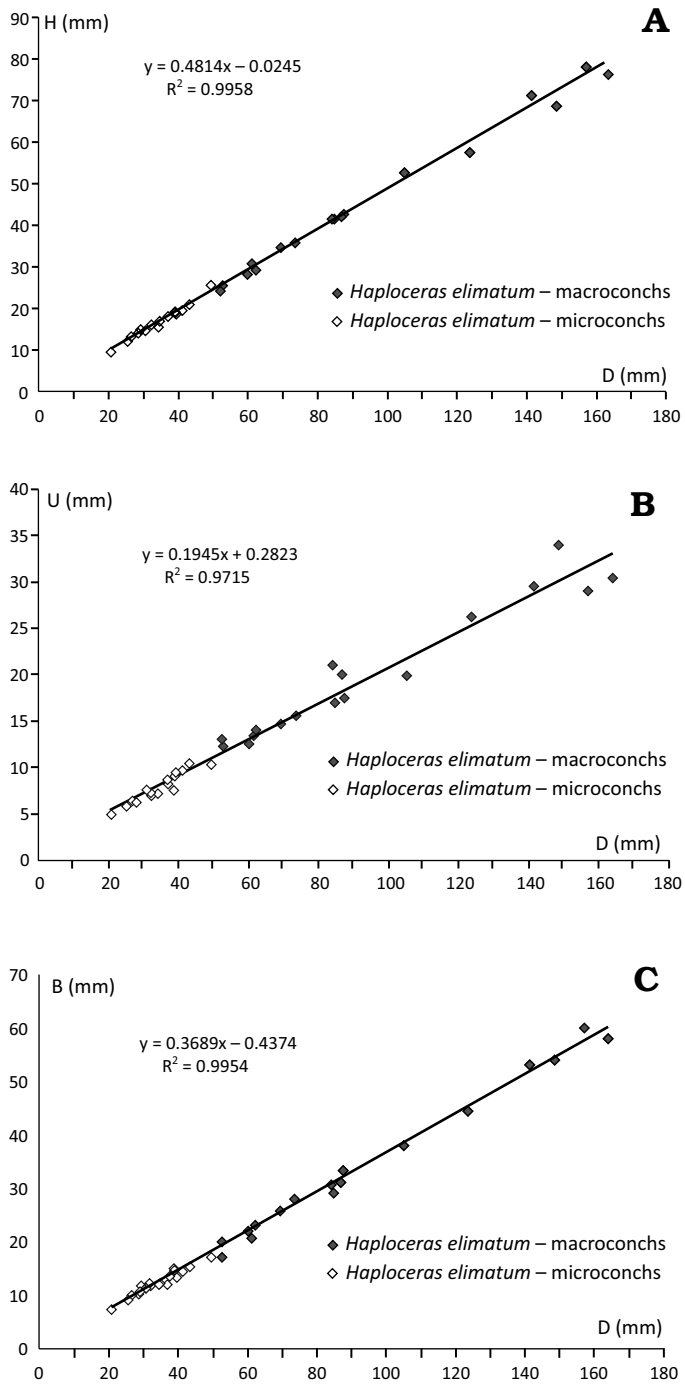
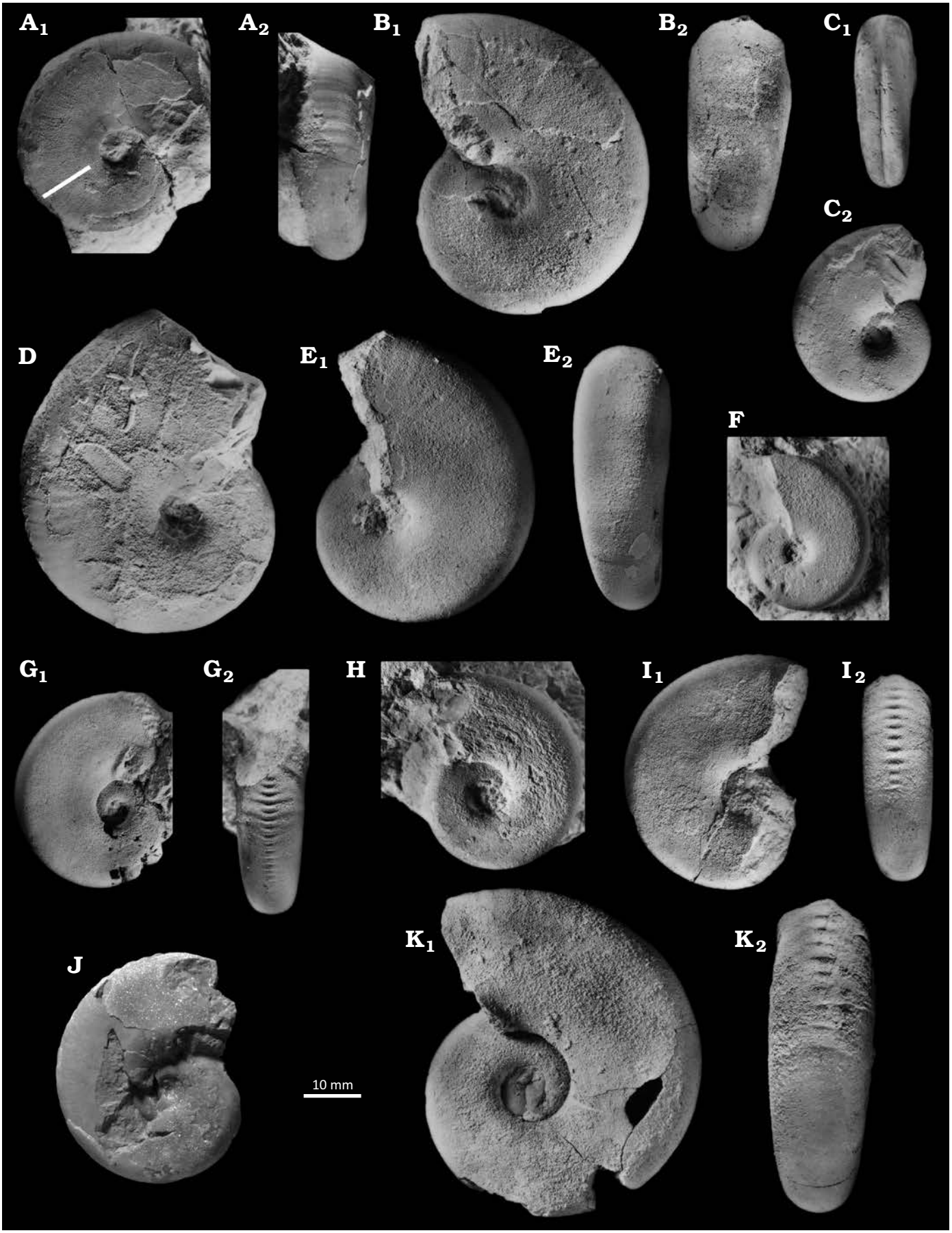


Fig. 7. Relationship between size parameters of *Haploceras elimatum* (Oppel, 1865) macroconchs and microconchs. **A**. Height (H) of whorl on diameter (D). **B**. Umbilicus breadth (U) on diameter, **C**. Whorl breadth (B) on diameter.


A1
A2
B1
B2
C1
C2
D
E1
E2
F
G1
G2
H
I1
I2
J
K1
K2
10 mm

← Fig. 8. Haploceratid ammonoid *Haploceras staszycii* (Zejszner, 1846) from Štramberk, Tithonian–lower Berriasian, Upper Jurassic–Lower Cretaceous. **A**. PL5059, lateral view (A_1), ventral view demonstrating the ribbing on external mould (A_2), Kotouč Quarry, debris on the 9th level. The straight line perpendicular to periphery of specimen show the margin between body chamber and phragmocone. **B**. Z1585, lateral (B_1) and ventral (B_2) views. **C**. PL2447, specimen with the siphonal groove, ventral (C_1) and lateral (C_2) views. **D**. MM010, lateral view. **E**, **F**. *Haploceras tithonium* (Oppel, 1865). **E**. PL5113, internal mould with incomplete outer suture line, lateral (E_1) and ventral (E_2) views, Kotouč Quarry, site No. 4 on the 8th level (Vašíček and Skupien 2016). **F**. PL5115, juvenile specimen, lateral view, Kotouč Quarry. **G**–**J**. *Hypolissoceras carachtheis* (Zejszner, 1846). **G**. Z1385 internal mould, lateral view (G_1) with rest of peristome by umbilicus, ventral view (G_2). **H**. B12689, external mould in lateral view. **I**. Z2981a external mould in lateral (H_1) and ventral (H_2) views. **J**. SNSB-BSPG AS III 47, lateral view of the lectotype (real state of preservation), Koňákov. **K**. *Hypolissoceras woehleri* (Oppel, 1865), MM06, external mould, lateral (K_1) and ventral (K_2) views. The straight lines perpendicular to periphery of specimen show the margin between body chamber and phragmocone. Photos Kristýna Mezihoráková (Ostrava, Czechia); except J, Alexander Nützel (SNSB-BSPG).

smooth at the beginning. On the body chambers in the specimens under study or where the original shell is peeled off to expose the steinkern, faint, blunt to indistinct, and relatively closely spaced ribs are visible.

Measurements.—The 16 measurable specimens range from 29 to 83 mm in diameter (SOM 3). The Dmax of PL5059 is 44.0 mm; the end of the phragmocone is present at a D of approximately 32.0 mm. According to our measurement from a copy of the illustration of the lost Zejszner's holotype (1846: pl. 4: 3a, b), at Dmax = 56.5 mm, H = 27.2 (0.48), U = 10.0 (0.18), B = 21.7 (0.38). Neotype SNSB-BSPG AS III 805 at D = 73.6 mm shows H/D = 0.51, U/D = 0.19, B/D = 0.36. Values of H/D in the material under study range from 0.47–0.52, U/D from 0.17–0.22, B/D from 0.36–0.41. The regression lines H/D, U/D, B/D of *Ha. staszycii* are accompanied by the microconch lines of *Ha. elimatum* in the graphs (Fig. 9A–C). The only clear difference in the course of the two regression lines is evident for the U/D values.

Remarks.—Malinowska et al. (1980: 444) stated that the holotype of *Ha. staszycii* disappeared and established the lectotype (but actually neotype). *Haploceras staszycii* reaches a medium size. Characteristic features include a relatively narrow umbilicus. Ribbing, if preserved, is usually weakly developed with regard to the smaller sizes of specimens of *Ha. staszycii*. *Haploceras tithonium* (Oppel, 1865) is a species that reaches a minor size of specimens and has higher whorls.

Stratigraphic and geographic range.—Enay and Cecca (1986) state that the stratigraphic range is Hybonotum to Ponti zones. Zeiss (2001) mentions the Tithonian of the Tethyan area with emphasis on the upper Tithonian. With regard to the assumption that *Ha. staszycii* forms a dimorphic pair with *Ha. elimatum*, the stratigraphic range should be identical to that of *Ha. elimatum,* i.e., the Tithonian to lower Berriasian. This argument is supported by specimens in Kvantaliani (1999) from Crimea, determined, however, as *Ha. elimatum*. *Haploceras staszycii* occurs in many localities of the Mediterranean and sub-Mediterranean areas. The neotype comes from Rogoźnik in Poland (lower Tithonian of the Pieniny Klippen Zone); it is also known from France, Italy, Romania, Hungary, Crimea, and Madagascar.

Our own collections from Kotouč Quarry come from Level 8 from locality 4 (Vašíček and Skupien 2016) with accompanying ammonites from the Fallauxi and Microcanthum ammonite zones and from the debris on Level 9.

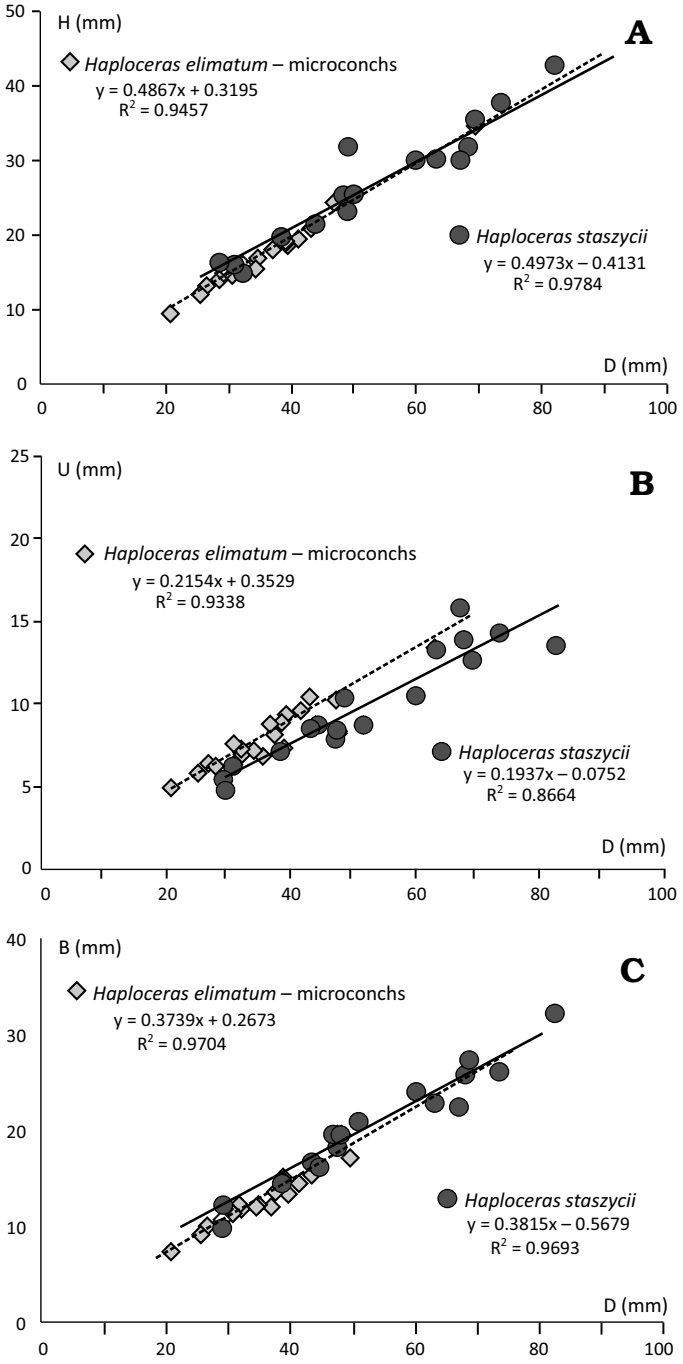


Fig. 9. Relationship between size parameters of *Haploceras elimatum* (Oppel, 1865) microconchs and *Haploceras staszycii* (Zejszner, 1846). **A**. Height (H) of whorl on diameter (D). **B**. Umbilicus breadth (U) on diameter. **C**. Whorl breadth (B) on diameter.

Haploceras tithonium (Oppel, 1865)

Figs. 3C, 4C, 8E, F.

1865 *Ammonites tithonius* Opp.; Oppel 1865: 549.
1868 *Ammonites tithonius* Opp.; Zittel 1868: 82, pl. 14: 1a, b (lectotype), 2a–c, 3a, b.
1953 *Haploceras tithonium* Opp.; Slavin 1953: 53, pl. 3: 11, 12, text-fig. 4
1978 *Haploceras tithonium* (Opp.); Olóriz Sáez 1978: 20, pl. 1: 4a, b, 5.
1988 *Haploceras (Haploceras) tithonium* (Oppel); Főzy 1988: 53, text-fig. 8.
2020 *Haploceras tithonium* (Zittel); Sarti 2020: 90, pl. 4: 2A, B.
2024 *Haploceras tithonium* (Zittel); Sarti 2024: 90, pl. 4: 2A, B.

Type material: Lectotype (established herein) SNSB-BSPG AS III 797 from Hohenegger collection in Munich, originally figured by Zittel (1868: pl. 14: 1) as *Ammonites tithonius* Oppel.

Type locality: Štramberk Limestone, Castle Hill in Štramberk, Czech Republic.

Type horizon: Tithonian or lower Berriasian.

Material.—Three specimens present in the Hohenegger collection in Munich (SNSB-BSPG AS III 797–799) and four favourably preserved specimens, partly preserved as steinkerns, partly as external moulds, or with a recrystallized original shell (PL5061, PL5113, PL5115, Z2761).

Description.—Specimens of small- to medium-sized, semi-involute, with high, medium-broad whorls and with a narrow umbilicus. The flanks of the whorl are slightly arched. They reach the greatest breadth at approximately one-third of the whorl height. From this height, the flanks slope gradually to the umbilicus. Near the umbilicus, a rather sharp transition to the steeper part of the whorl declining to the line of coiling is observed. Near the venter, the flanks of the whorl are separated unclearly from the venter. The venter is slightly arched and medium-broad.

Our specimens appear to be smooth or, rarely, very thin indistinct ribbing is observed.

Remarks.—The remains of weak, dense ribbing are clear in the area around the line of coiling in Zittel's (1868: pl. 14: 1a) specimen SNSB-BSPG AS III 797, desinated here as lectotype.

In the juvenile specimen PL5061, three lobes (E, A, U_2) are favourably preserved. In specimen PL5113, part of the outer suture line is preserved with the external lobe, adjacent saddle E/A and part of the adventive lobe. The preserved part is essentially identical to the suture line of *Ha. elimatum*. A more completle external suture of *Ha. tithonium* is also illustrated by Slavin (1953: text-fig. 4).

Measurements.—The lectotype: D = 61.0 mm has H/D = 0.565, U/D = 0.13, B/D = 0.38. Eight specimens under study have sizes from 25 to 55 mm in diameter. The other six specimens under study range 21.6 to 54.2 mm in diameter. Their parameters are as follows: H/D = 0.51–0.56, U/D = 0.13–0.19, B/D = 0.35–0.38 (SOM 4). In Z2761, the phragmocone ends at a diameter D = 42 mm.

Remarks.—The flanks of the whorl of the specimen illustrated by Zittel (1868: pl. 14: 2a, b) are not as flat in cross-section as illustrated in Zittel's fig. 2a. *Haploceras tithonium* is characterised—in contrast to other species in this genus—by a narrower umbilicus and a high and relatively slender whorl. Vígh (1984: 176, pl. 1: 1a, b) described *Haploceras tithonium perumbilicatum* as a new morphologically similar subspecies that differs from *Ha. tithonium* in having a smaller whorl height (H/D = 0.44), broader umbilicus (U/D = 0.23) and narrower whorl (B/D = 0.32). It could, under the name *Haploceras perumbilicatum*, represent a dimorphic counterpart of *Ha. tithonium*. With regard to the sizes of both taxa, however, it is not possible to determine which of them is a macroconch and which is a macroconch.

Stratigraphic and geographic range.—Data on the stratigraphic position of *Ha. tithonium* are relatively scarce. Enay and Cecca (1986) state the uppermost lower Tithonian from Spain, and Főzy (1988), the upper Tithonian from Hungary. According to Slavin (1953), *Ha. tithonium* occurs abundantly in the Upper Jurassic of the Ukrainian Carpathians.

Our dated collection from the Štramberk Limestone in the Kotouč Quarry on Level 6 corresponds to the basal upper part of the lower Tithonian. The specimens described by Zittel (1868) come from Štramberk Limestone of the currently abandoned quarry below Castle Hill in Štramberk.

Genus *Hypolissoceras* Breistroffer, 1947

Type species: *Ammonites carachtheis* Zejszner, 1846 (pl. 4: 1) by monotypy. Tatra Mountains in Poland, probably lower Tithonian.

Remarks.—The genus is characterised in particular by a series of short, small ribs (crenulations) limited to the venter of adult specimens.

Hypolissoceras carachtheis (Zejszner, 1846)

Figs. 3D, 8G–J.

1846 *Ammonites carachtheis* Zejszner 1846: pl. 4: 1a–d.
1868 *Ammonites carachtheis* Zeuschner; Zittel 1868: 84, pl. 15: 1a-e, ?2a, b, ?3a, b.
1879 *Haploceras carachtheis* Zeuschner; Fontannes 1879: 10, pl. 2: 3a, b.
1880 *Ammonites* (*Haploceras*) *carachtheis,* Zeuschner; Favre 1880: 29, pl. 2: 10.
1890 *Haploceras carachtheis* Zeuschner sp.; Toucas 1890: 577, pl. 13: 5a, b, pl. 15, ?fig. 7a, b; non fig. 8 (= ?*Ha. leiosoma* Oppel).
1893 *Haploceras carachtheis* Zeuschn.; Retowski 1893: 242, pl. 9: 10, ?11.
1953 *Haploceras carachtheis* Zeuschner; Arnould-Saget 1953: 7, pl. 1: 8a, b, 11a, b.
non 1960 *Haploceras carachtheis* Zeuschner; Drushchits and Kudryavcev 1960: 268, pl. 13: 2a, b (= ?*Ha. staszycii*), ?3a, b, ?text-fig. 72.
1962 *Glochiceras carachtheis* (Zejszner); Barthel 1962: 17, pl. 2: 1–4, pl. 3: 1–3 (figs. 1, 2 = Zittel 1868, pl. 15: 1d, e): 6, 7; text-fig. 3c; non pl. 3: 4, 5.
1965 *Glochiceras carachtheis* (Zeuschner); Houša in Špinar 1965: fig. VIII-255.
1976 *Haploceras* (*Neoglochiceras*) *carachtheis* (Zeuschner); Avram 1976: 36, pl. 8: 9a, b.
?1976 *Haploceras* (*Haploceras*) aff. *elimatum* (Oppel); Avram 1976: pl. 8: 10a, b.

1976 *Haploceras* (*Neoglochiceras*) *carachtheis* (Zeuschner); Patrulius and Avram 1976: 168, pl. 3: 8.
1978 *Haploceras* (*Lingulaticeras*) *carachtheis* Zeuschner; Olóriz Sáez 1978: 124, pl. 10: 6a, b, 7, 8.
?1979 *Glochiceras* (*Glochiceras*) *carachtheis* (Zejszner); Sapunov 1979: 64, pl. 14: 2a, b.
1980 *Glochiceras* (*Glochiceras*) *carachtheis* (Zejszner); Malinowska et al. 1980: 445, pl. 136: 7a–c.
1983 *"Haploceras" carachteis* (Zeuschner); Cecca et al. 1983: 114, pl. 1: 3.
1983 *Haploceras* (*Neoglochiceras*) *carachtheis* (Zejszner); Vašíček 1983: 98, pl. 3: 2, 3.
1984 *Haploceras carachtheis* (Zeuschner); Cecca et al. 1984: pl. 6: 1.
1986 *Haploceras* (*Haploceras*) *carachtheis* (m) (Zeuschner), resp. *Haploceras* (*Haploceras*) *carachtheis* (m) (Zeuschner) morph *carachtheis*; Enay and Cecca 1986: 49, pl. 2: 1a–c, 3a, b, 4a, b, ?5a, b, 7, ?8a, b, 9a, b, 10a, b; non pl. 2: 2; pl. 3: ?6a, b, 7a, b, 8a, b, ?9a, b, 10a, b, 11a, b, 12a, b, ?13a,b, 14a, b, 15a, b, 18a, b; non pl. 3: 1, 2a, b (= *Haploceras woehleri*), non pl. 3: 16a, b, 17a, b, 19a, b.
1986 *Glochiceras carachtheis* (Zeusch.); Kutek and Wierzbowski 1986: tab. 2.
1988 *Haploceras carachtheis* (Zeuschner); Főzy 1988: 59, pl. 3: 3, 4.
1989 *Haploceras carachtheis* (Zeuschner); Khimshiashvili 1989: 31, pl. 9: 3, 5, 7.
1990 *Haploceras carachtheis* (Zeusch.); Wierzbowski 1990: fig. 3.
1991 *Haploceras* (*Haploceras*) *carachtheis* (m) (Zeuschner) morph *carachtheis*; Cecca and Enay 1991: pl. 1: 8a, b.
1994 *Haploceras carachtheis* (Zeuschner); Főzy et al. 1994: 158, pl. 1: 16, 22.
?1994 *Haploceras (Hypoglochiceras) carachtheis* (Zeuschner); Zeiss et al. 1994: 370, pl. 2: 3.
1995 *Haploceras carachtheis* (Zeuschner); Főzy 1995: 136, pl. 20: 12.
1996 *Haploceras carachtheis* (Zeuschner); Wright et al. 1996: 10: 6/1c–e.
?2001 *Haploceras* (*Hypolissoceras*) *carachtheis* (Zeuschner); Zeiss 2001: 38, pl. 5: 4, 5.
?2004 *Haploceras carachtheis* (Zeuschner); Ettachfini 2004: 155, pl. 5: 1.
2013 *Haploceras carachtheis* (Zeuschner); Főzy and Scherzinger 2013: 215, pl. 4: 4a, b, ?fig. 3a, b, ?pl. 5: 1a, b, 2, 10.
2013 *Haploceras carachtheis* (Zeuschner); Szives and Főzy 2013: 295, pl. 4: 3.
non 2016 *Haploceras carachtheis* morph *carachtheis* (Zeuschner); Hoedemaeker et al. 2016: 168, pl. 17: 4–6 (= *Hypolissoceras leiosoma* Oppel).
2017 *Haploceras carachtheis* (Zeuschner); Főzy 2017: pl. 1: 3a, b, ?pl. 32, fig 1a, b.
2020 *Haploceras carachtheis carachteis* (Zeuschner); Sarti 2020: 91, pl. 4: 7.
?2020 *Haploceras carachtheis leiosoma* (Zittel); Sarti 2020: 91, pl. 4: 6A, B.
2024 *Haploceras carachtheis leiosoma* (Zittel); Sarti 2024: 91, pl. 4: 6A, B.

Type material: Holotype of Zejszner (1846) is apparently lost (Malinovska et al. 1980). Neotype (established herein) SNSB-BSPG AS III 47, originally figured by Zittel (1868: pl. 15: 1a–e) as *Ammonites carachtheis* Zejszner, 1846, and figured herein in Fig. 8J. The Zittel's (1868) depiction of this specimen is partly idealized (compare with Fig. 8J).

Type locality: Štramberk Limestone, locality of Koňákov (formerly Koniakau), Czech Republic (the locality no longer available).

Type horizon: Tithonian or lower Berriasian.

Material.—Four specimens from Zittel (1868) and Barthel (1962) collections (SNSB-BSPG AS III 45, 48, 49; SNSB-BSPG AS III 47 is the neotype) and eight relatively complete specimens preserved as external moulds (B12689, Z1503, Z2981a, PL4370, Ge30342, Ge30344b) and a steinkern with the remnant of peristome (Z1385).

Description.—Semi-involute specimens, rather small in size, with high, medium-broad whorls and a narrow umbilici. The flanks of the whorl are flat to slightly arched. In the area of the umbilicus, a funnel-shaped zone is observed. On the best-preserved steinkern, it is obvious that the base of the whorl ends in a narrowly rounded shape, and the whorl still continues below to the dorsum in the shape of a narrow, slot-like form. The flat venter is clearly separated from the flanks by a rounded zone.

The inner whorls are smooth. On favourably preserved juvenile specimens, growth lines can be observed on the upper parts of the whorl. In adult specimens, short ventral ribs are present in the siphonal area in the final fifth of the ultimate whorl.

Measurements.—Specimens under our study have maximum diameter of approximately 42 to 44 mm. The phragmocones usually terminate at diameters ranging from approximately 23 to 26 mm, and on the specimen in Cecca and Enay (1991: pl. 1: 8), even at 35 mm. In the specimens from Štramberk, the first ventral ribs appear at D = 30–36 mm. Our own measurement of 13 specimens was supplemented with several values from Sarti (2020) data (SOM 5). Parameters: H/D = 0.46–0.51, U/D = 0.17–0.22, B/D = 0.32–0.34, and B/H = 0.65–0.71. Neotype with diameter D = 44.0 mm has H/D = 0.46, U/D = 0.23, B/D = 0.315.

Remarks.—Based on information obtained from Lidia Malinowska in 1980 (see Vašíček 1983: 99), the type material, i.e., the holotype of *Hy. carachtheis* presented by Zejszner (1846), which was merely illustrated without diagnosis, is lost. Historically, the closest material to the non-existent type specimen is the specimen depicted in Zittel (1868), pl. 15: 1a–e. For this reason, we designate it as a neotype herein.

The basic features of *Hy. carachtheis* include a narrow umbilicus and slender whorls with flat flanks. The main morphological feature is the onset of ribbing confined to the venter that appears on the final half to third of the body chamber at a shell diameter of more than 30 mm. The favourably preserved specimens bear a complexly formed peristome. On the venter, a short rostrum is present, and on the flanks, conspicuous, tongue-shaped lappets occur. The whole peristome is usually bounded by a clear constriction that is accompanied by a swollen rib on the front side. The preserved portion of the peristome indicates that the specimens Z1385 (see Fig. 8G_1 here) and Z2981a (Fig. 8I_1) represents adult individuals.

The umbilicus is mostly narrow (U/D less than 0.23), whereas broader umbilici are commonly reported in the literature (e.g., Zittel 1868, for SNSB-BSPG AS III 47 in pl. 15/1d, e; Zeiss 2001; Főzy and Scherzinger 2013). Due to the lack of comparative material, it is not clear whether this is

a case of species variability or a case of different species. *Haploceras carachtheis,* considered by us as a microconch of *Hypolissoceras woehleri* (Oppel, 1865)*,* is compared with *Hy. woehleri* in the description of the latter species.

Stratigraphic and geographic range.—*Haploceras carachtheis* occurs in almost the whole Mediterranean and the sub-Mediterranean area, from the Himalayas to northwestern and eastern Africa. According to Enay and Cecca (1986), it occurs from the lower Tithonian (Hybonotum Zone) to the lower Berriasian inclusive. The lower Berriasian occurences are also mentioned by, e.g., Arnould-Saget (1953), Patrulius and Avram (1976), and Szives and Főzy (2013) with a detailed analysis of *Ha. carachtheis* occurrences.

Specimens described by Zittel (1868) come from the Štramberk Limestone in Štramberk and from Koňákov. We could not find this species in Štramberk area ourselves. In the Czech Republic, it is also known from the lower Tithonian of the Magura Group of nappes in Roštín (Vašíček 1983).

Hypolissoceras woehleri (Oppel, 1865)

Figs. 3E, 6A, B, 4D, 8K.

1865 *Ammonites Wöhleri* Opp.; Oppel 1865: 549.
1868 *Ammonites Wöhleri* Opp.; Zittel 1868: 84, pl. 14: 4a, c.
1986 *Haploceras* (*Haploceras*) *carachtheis* (m) (Zeuschner) morph *carachtheis*; Enay and Cecca 1986: 49, pl. 3: 1, 2a, b.
?1988 *Haploceras* (*Hypolissoceras*) *carachtheis* (Zeuschner); Főzy 1988: 59, pl. 3: 3, 4.
1988 *Haploceras* **(***Haploceras*) *wohleri* (Oppel); Főzy 1988: 55, pl. 3: 1, 2, text-fig. 9.

Type material: The holotype by monotypy (SNSB-BSPG AS III 811) is a poorly preserved specimen (Zittel 1868: pl. 14: 4). The original illustration of which is quite idealized. The body chamber is almost completely preserved but the phragmocone is missing. The peristome, i.e., both the rostrum and especially the flank, is distorted. The greater part of the holotype (with exception of the area around peristome, where on both sides, remains of the original shell occur) is a steinkern. There is a prominent granulation on the venter, however, this is very likely a product of diagenesis.

Type locality: Štramberk Limestone, Štramberk, Czech Republic.

Type horizon: Tithonian or lower Berriasian.

Material.—In addition to the holotype, more than 10 adult specimens preserved as external moulds and one specimen with remains of the original test, partly split off from the body chamber (Z1817), are available. The best-preserved museum specimens are Z2305, Z4171, Z4206, Z4210, MM 04, MM 06–09, and Ge30355.

Description.—Specimens semi-involute, rather large in size, with relatively high whorls with slightly arched flanks, and a visibly, although unclearly, separated venter. The umbilicus is relatively narrow. The flanks of the whorl, which reach the greatest breadth at approximately the lower fifth of its height, decline steeply without any edge to the line of coiling. Around the umbilicus, a funnel-like shape is observed. The venter is only slightly arched.

The inner whorls are smooth. At the beginning of the final part of the ultimate whorl, unclear ribs may be seen on the venter. Near the peristome in all larger specimens, at least several (approximately 4–7) short, widely spaced, relatively strong blunt ventral ribs appear.

Suture line. On specimen MM08, some incomplete suture lines bound by merely an adventive lobe A and adjacent parts of saddles are preserved. The lobe is strongly articulated, formed similarly to the suture lines of the genus *Haploceras.*

Measurements.—The holotype reaches diameter of approximately 117 mm. Because of imperfect preservation, the measurements are rather ambiguous; at D = 116.0 mm, H is ca. 58.5 mm (0.50), U ca. 23.0 mm (0.20), B ca. 42.5 mm (0.37). The largest specimen from the Moravian-Silesian collection (Z4171) reaches a diameter of only approximately 61 mm. By

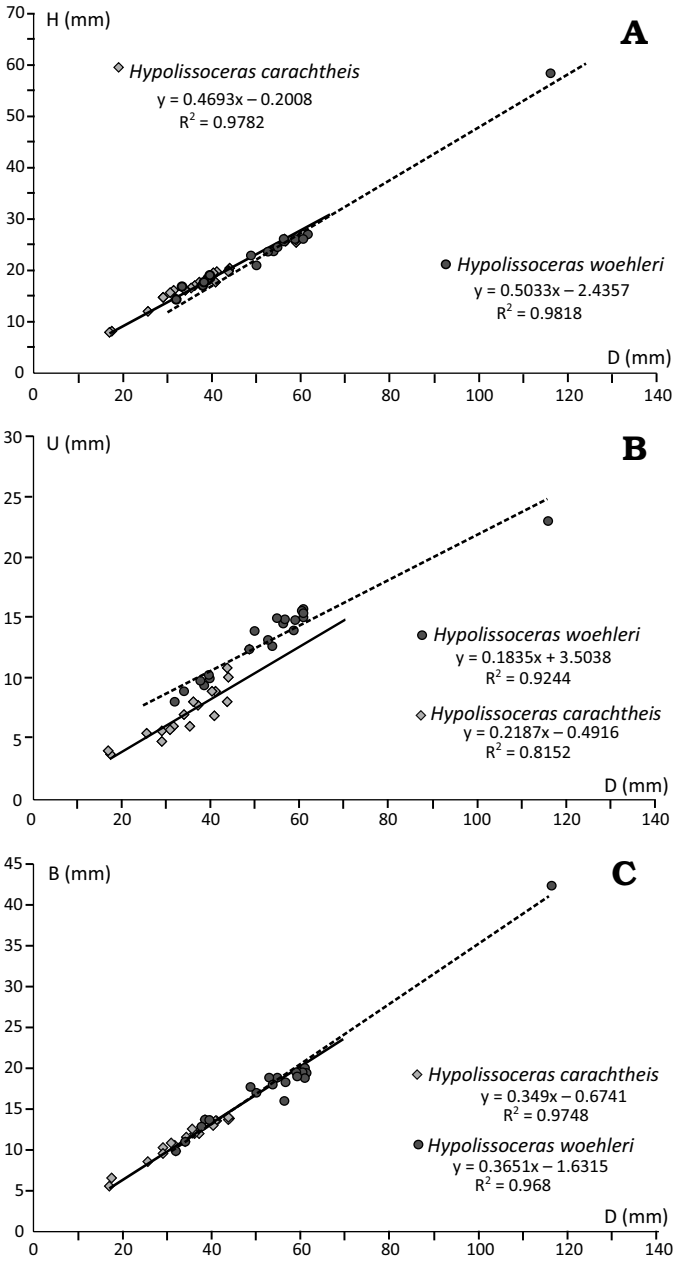


Fig. 10. Relationship between size parameters of *Hypolissoceras carachtheis* (Zejszner, 1846) and *Hypolissoceras woehleri* (Oppel, 1865). **A**. Height (H) of whorl on diameter (D). **B**. Umbilicus breadth (U) on diameter. **C**. Whorl breadth (B) on diameter.

D = 60.8 mm H/D is 0.435, U/D = 0.25, B/D = 0.33. Its phragmocone ends at D = 46 mm. The first ventral ribs appear at D = 53–60 mm. Usual parameters in the collection under study are as follows: H/D = 0.43–0.47, U/D = 0.24–0.26, B/D = 0.32–0.36. Főzy (1988) reports specimens larger in size, i.e., with a diameter of up to 146 mm. The measurements for constructing the charts on Fig. 10 are listed in SOM 6.

Remarks.—With reference to the morphology of the holotype, we assume that *Hy. woehleri* represents a macroconch to *Hy. carachtheis. Hypolissoceras woehleri* differs from *Hy. carachtheis* above all in different shell size. Figure 10A–C shows that the H/D and B/D values for both species are almost identical. A smaller difference is evidenced only by U/D values (Fig. 10B). The ventral ribs of *Hy. woehleri*, as shown by specimens from the Moravian Museum, begin only at shell diameters of approximately 53 to 60 mm, whereas in *Hy. carachtheis,* they begin at diameters of approximately 30–36 mm. The holotype of *Hy. woehleri* (Dmax of 117 mm) with ambiguously measurable parameters differs somewhat from the just-described macroconchs in the ratios H/D, U/D, and B/D. This is probably associated with the smaller sizes of specimens in the collection under study and with unfavourable preserved parameters of the holotype.

Stratigraphic and geographic range.—In contrast to *Hy. carachtheis*, data on the stratigraphic range and geographical distribution of *Hy. woehleri* are limited. The holotype comes from not well constrained stratigraphic position of Štramberk Limestone in Štramberk (probably from the currently non-existent Castle Quarry). According to Főzy (1988), this species occurs in the "middle" and upper Tithonian in Hungary. Given that we assume these species form a dimorphic pair, the stratigraphic range of *Hy. woehleri* should be the same as that for microconchs.

The holotype of *Hy. woehleri* comes from Štramberk, and the specimen in Enay and Cecca (1986: pl. 3: 1) from Le Pouzine, France (Fallauxi Zone). The specimens from the Moravian-Silesian museums lack detailed geographic and stratigraphic information.

Hypolissoceras subtilius (Zittel, 1870)

Fig. 6D.

1870 *Haploceras carachtheis* var. *subtilior*; Zittel 1870: 54, pl. 27: 11a–c.

1986 *Haploceras carachtheis* var. *subtilior*; Enay and Cecca 1986: 39, text-fig. 4.

?1986 *Haploceras* (*Haploceras*) *carachtheis* (m) (Zeuschner); Enay and Cecca 1986: pl. 2: 8a, b, pl. 3: 8a, b.

Type material: Holotype (by monotypy) SNSB-BSPG AS III 42 (Zittel 1870: pl. 27: 11)

Type locality: Rogoźnik, Poland.

Type horizon: Pieniny Klippen Zone, Rogoża Coquina Member, Fallauxi ammonite Zone, lower Tithonian.

Material.—Holotype and a single weathered, slightly corroded external mould (Z2767a), both small in size.

Description.—The semi-involute specimen has a medium-high whorl and a medium-broad umbilicus. The flanks of the whorl are slightly arched. The greatest breadth of the whorl is close to its base. From the mentioned area, the whorl declines, through a rounded zone, continuously to the line of coiling. The umbilical wall is very low. The flanks slope gradually to the venter. In the more juvenile part, the flanks pass continuously to a rounded venter; in the final part of the ultimate whorl, the venter is slightly arched with an indication of its separation from the flanks.

The juvenile half of the ultimate whorl is smooth. At the beginning of the second half, indistinct ribs are seen on the venter. Only in the vicinity of the aperture, 7 straight and very short but distinctive ventral ribs are observed. On the unphotographed, more poorly preserved opposite side, remains of the peristome are visible; they indicate that it is probably an adult specimen.

Measurements.—The holotype preserved as a steinkern has a maximum diameter of 23 mm. At D = 22.9 mm, H = 9.9 mm (0.43), U = 6.1 mm (0.27), and B mm = 7.0 (0.305). Specimen Z2767a reaches a maximum diameter of 30 mm. At D = 30.0 mm, H =12.6 mm (H/D = 0.42), U = 9.3 mm (U/D = 0.31), B = 9.4 mm (B/D = 0.31), and B/H = 0.75. The first ventral ribs appear at a D of approximately 27 mm.

Remarks.—*Hypolissoceras subtilius* differs from the similar small-sized *Hypolissoceras leiosoma* (Oppel in Zittel, 1868) in having a much broader umbilicus and smaller height and breadth of whorls. Adult specimens with the preserved peristome, designated by Enay and Cecca (1986: pl. 2: 8, pl. 3: 8) as *Ha. carachtheis* (m), probably also belong to *Hy. subtilius*.

Stratigraphic and geographic range.—According to Enay and Cecca (1986: text-fig. 4) *Hy. subtilius* occurs sporadically in the uppermost lower Tithonian (Ponti Ammonite Zone) in Spain, The holotype comes from Rogoźnik in Poland, most likely from the lower Tithonian. Z2767a from the museum collection in Opava is labelled with the locality name Štramberk only.

Genus *Volanites* Enay and Cecca, 1986

Type species: Due to the fact that Enay and Cecca (1986) did not fulfill all the prescribed requirements when determining the type species, we designate *Ammonites verruciferus* Zittel in Benecke 1869 herein, represented by the lectotype specimen SNSB-BSPG AS III 809, originally figured by Zittel (1870: pl. 27: 8). Tithonian, Volano, Italy.

Volanites verruciferus (Zittel, 1869)

Fig. 6C.

1869 *Ammonites verruciferus* Zittel in Benecke 1869: 145.

1870 *Haploceras verruciferum* Meneghini sp.; Zittel 1870: 52, pl. 27: 8 (lectotype), 9, 10.

1890 *Haploceras verruciferum* Meneghini sp.; Toucas 1890: 577, pl. 13: 7.

1978 *Haploceras verruciferum* Meneghini; Olóriz Sáez 1978: 23, pl. 1: 6–8.

1983 *Haploceras verruciferum* (Meneghini) in Zittel; Cecca et al. 1983: 116, pl. 1: 4.

1984 *Haploceras verruciferum* (Meneghini); Rossi 1984: 90, pl. 31: 7, pl. 32: 7.
1986 *Haploceras (Volanites) verruciferum* (Zittel); Enay and Cecca 1986: 48, pl. 1: 2-8, pl. 2: 11–15; non pl. 1: 1 and 9 (= *Haploceras cassiferum* Főzy, 1988).
?1986 *Haploceras verruciferum* (Zittel); Sarti 1986: 490, pl. 1: 6.
?1986 *Haploceras* cf. *verruciferum* (Men.); Kutek and Wierzbowski 1986: tab. 2.
1988 *Haploceras (Hypolissoceras) verruciferum* (Zittel); Főzy 1988: 63, pl. 4: 3, 4, pl. 5: 1, pl. 6: 3–6, text-figs 13, 14 (cum syn.).
1989 *Haploceras (Volanites) verruciferum* Zittel; Khimshiashvili 1989: 31, pl. 9: 2.
1990 *Haploceras verruciferum* (Zittel); Főzy 1990: 327, pl. 1: 10, 11.
non 1991 *Haploceras (Volanites) verruciferum* (Zittel); Cecca and Enay 1991: 45, pl. 2: 1–4 (= ?*V. cassiferum* Főzy).
1994 *Haploceras verruciferum* (Zittel); Főzy et al. 1994: 158, pl. 1: 23.
1994 *Haploceras (Volanites) verruciferum* (Zittel); Zeiss et al. 1994: 370, pl. 2: 1.
1995 *Haploceras verruciferum* (Zittel); Főzy 1995: 136, pl. 20: 4, 7.
2002 *Haploceras (Volanites) verruciferum* (Zittel); Pavia et al. 2002: 234, figs. 160/1–3, ?4.
2013 *Haploceras verruciferum* (Zittel); Főzy and Scherzinger 2013: 216, pl. 5: 6–8, 12, ?pl. 4: 1, 2a,b, ?pl. 5: 9.
2017 *Haploceras verruciferum* (Zittel); Főzy 2017: pl. 1: 1, pl. 12: 3, pl. 23: 1, pl. 32: 17.
2020 *Haploceras (Volanites) verruciferum* (Zittel); Sarti 2020: 82, pl. 3: 3A, B, 4A, B.
2024 *Haploceras (Volanites) verruciferum* (Zittel); Sarti 2020: 82, pl. 3: 3A, B, 4A, B.

Type material: The lectotype (SNSB-BSPG AS III 809) originally designated by Enay and Cecca (1986: 49).

Type locality: Volano, Italy.

Type horizon: Tithonian or lower Berriasian.

Material.—Two specimens from Zittel collection (SNSB-BSPG AS III 807 and SNSB-BSPG AS III 809—lectotype), one relatively well-preserved juvenile external mould (Z2981b) without peristome. The specimen Z2981b is labelled only with the locality of Štramberk.

Description.—Semi-involute specimens, with medium-high whorls and a medium-broad umbilicus. The flanks of the ultimate whorl are moderately arched. They are broadest near the whorl base. From that point, the whorl declines, through a low rounded zone, to the line of coiling. The flanks of the whorl decline gradually towards the venter. The venter is rounded and separated from the flanks of the whorl.

The ultimate whorl is smooth. In one specimen (Z2981b) only blunt ribs convexly bent towards the peristome are observed.

Measurements.—The specimens of *V. verruciferus* illustrated in Zittel (1870: pl. 27: 8–10) reach, according to our measurements, sizes of 42–62.5 mm in diameter. In the studied small collection there are two size extreme specimens: the smallest with diameter about 38 mm, the largest with diameter 105 mm. The parameters of specimens in SOM 7 are as follows: H/D = 0.38–0.44, U/D = 0.30–0.33, and B/D = 0.29–0.32. The lectotype by D = 62.5 mm has H/D = 0.44, U/D = 0.30, B/D = 0.27. The largest specimen or The only specimen in our own collection (or Moravian-Silesian collections) has maximum size 51 mm.

Remarks.—We found only one specimen that should belong to *V. verruciferus* in the Moravian-Silesian collections studied by us. Judging from its size, it is a juvenile specimen without the characteristic final swollen rib on the venter near the peristome. However, the size parameters and morphology are similar to those of *V. verruciferus*. In other regions, a similar species but larger species, *Volanites cassiferus* (Főzy, 1988) occurs together with *V. verruciferus.* According to Főzy (1988), *V. cassiferus* reaches a diameter of approximately 100 mm or more. Főzy's (1988) specimen J-8048 from Lókút section (Hungary) has measurements of H/D = 0.43, U/D = 0.27, and B/D = 0.30 at D = 105 mm. In accordance with Főzy (1988) and Főzy and Scherzinger (2013), we assume that *V. cassiferus* represents a macroconch of the microconch represented by *V. verruciferus.*

Stratigraphic and geographic range.—According to data in the literature, *V. verruciferus* occurs abundantly in the Mediterranean area (Verruciferus Zone) of southern Spain, southeastern France, Sicily, northern Italy, Hungary (Bakony, Gerecse), and Abkhazia. Főzy's (1988) type material of *V. cassiferus* comes from the lower Tithonian of Lókút section, Hungary. According to Zeiss et al. (1994) and Zeiss (2003), *V. verruciferus* was previously considered an index species in the higher part of the lower Tithonian or near base of middle Tithonian. Detailed stratigraphic position of the specimen found in the area around Štramberk is not known.

Discussion

Considerable inconsistency in the classification of haploceratids is evident at the species and generic levels. In the present paper we propose an integrated concept based on dimorphic pairs of haploceratids. We recognize herein four dimorphic pairs, namely micro- and macroconchs, designated by us with individual species names. We abolished previous classification of the genus *Haploceras* based on subdivision into subgenera (Enay and Cecca 1986).

Our classification is based on the direct study of approximately one hundred favourably preserved specimens from the Štramberk Limestone and deposited in Moravian-Silesian museums, specimens collected by us, and study of published materials in which the morphology is sufficiently documented (including type series of Zittel 1868, 1870).

We furthermore performed the statistical analysis of the parameters H/D, U/D, and B/D based on the well-preserved specimens. We evaluated also other characters, e.g., whorl cross-sections, peristome shape, and sculpture. Several well-preserved steinkerns allowed the drawing of septal suture lines.

Based on the overall analysis of the available material and literature sources, we recognize four dimorphic pairs in the framework of three genera in Tithonian/early Berriasian haploceratids. The first pair is formed by *Ha. elimatum* (macroconchs) and *Ha. staszycii* (microconchs). The two species

when preserved as external moulds, bear similar indistinct ribbing patterns on the venter and the flanks of the whorls. While the macroconchs reach diameters of up to 200 mm, microconchs reach diameters of only 80 mm. The microconchs have slightly broader whorls and somewhat narrower umbilicus (see Fig. 9). This dimorphic pair was already suggested by Barthel (1962: 12). The position of *Ha. subelimatum* (Fontannes, 1879) remains uncertain from the point of view of dimorphism, with specimens of a similar size. It has clearly narrower whorls than the two previous species.

The second possible dimorphic pair in *Haploceras* are *Ha. tithonium* and *Ha. perumbilicatum* Vígh, 1984. In this case, we have only specimens of *Ha. tithonium* in our own collection. Nevertheless, we consider *Ha. tithonium perumbilicatum* established by Vígh (1984), to be a dimorphic pair. The two morphologically similar species differ in the height and breadth of the whorls as well as in the breadth of the umbilicus. With reference to the insufficiently known maximum sizes of both species (according to the published data, approximately 50 mm in both cases), it is not yet possible to decide which species represents a macroconch and which a microconch.

The third pair is formed by *Hypolissoceras carachtheis* and *Hy. woehleri.* Zejszner's original holotype (*Hy. carachtheis*) is lost, and thus we designated its neotype herein. Both species are characterised by specific ribbing that is developed only on the venter. *Hyppolisoceras carachtheis* (microconch) attains a smaller size, less than ca. 55 mm, while *Hy. woehleri* (macroconch) reaches a size of 120 to 140 mm. The cross-sections of whorls are also somewhat different; in *Hy. carachtheis*, the whorls are slenderer, whereas in *Hy. woehleri*, the whorls are lower, and the umbilicus is broader.

Another less perfectly clear dimorphic pair, due to the shortage of our own material, is based on accounts from published data. In accordance to Főzy (1988) and Főzy and Scherzinger (2013), we treat *Volanites verruciferus* and *V. cassiferus* (Főzy 1988: 59) as a possible dimorphic pair. *Volanites verruciferus* (microconch) reaches a maximum size of almost 70 mm, whereas *V. cassiferus* (macroconch) reaches a maximum size of approximately 100 mm.

In the collections of haploceratids from Štramberk deposited in the Moravian-Silesian museums, specimens very small in size (less than 30 mm) are missing, in contrast to the haploceratids from the Štramberk Limestone published by Zittel (1868, 1870) and from some other European localities. This may be explained by the fact that small specimens of ammonites were not attractive to the collectors of fossils in the Štramberk area. The exception in museum material is a single, small specimen of *Hypolissoceras subtilius* (originally *Haploceras carachtheis* var. *subtilior* Zittel, 1870). Its dimorphic pair could be *Hypolissoceras leiosoma* (Oppel in Zittel, 1868), with a distinctly narrower umbilicus. In both species, ventral ribbing or crenulation are less noticeable than that of *Hy. carachtheis*.

Peristomes are rarely preserved in Tithonian haploceratids; however, still and ample number of specimens of various sizes displays them, e.g., Zittel (1868: pl. 13: 2, 4, 7; pl. 14: 4b, ?5; pl. 15: 1b, 1e). Peristomes in his lithographic tables are usually complicated in nature and were usually drawn more or less embellished and even idealized. They are characterised by a rostrum on the venter and robust lateral tongue-shaped lappets. This holds true especially for the large specimens of *Ha. elimatum* (Zittel 1868: pl. 13: 7a) and *Hy. woehleri* (Zittel 1868: pl. 14: 4b) that are considered macroconchs. But it should be underlined that such terminal modifications of the aperture are normally typical of microconchs. It is possible that specimens like these started as females with a macroconchiate shape, but then changed their sex to males and finally formed the characteristic lappets. Examples of such phenomena were first described in Parent et al. (2008) and more extensively discussed by Frau and Boursicot (2021). Complicated peristomes were also illustrated by other authors as well (e.g., Barthel 1962: pl. 3: 1, 2; Olóriz Sáez 1978: pl. 10: 6a; Enay and Cecca 1986: pl. 2: 1, 8, 9; pl. 3: 1, 4; Zeiss 2001: pl. 5: 4), which should be considered as typical of microconchs.

In haploceratids, the possibility for sexual dimorphism is discussed in several papers (e.g., Zeiss 2001; Főzy and Scherzinger 2013). The theory of dimorphism and possible polymorphism was analysed thoroughly by Matyja (1986). Based on the study of Oxfordian ammonites, Matyja reported the possibility of trimorphism, where in addition to microconchs and macroconchs, specimens smaller than microconchs with lappets may occur. Such form named miniconchs, i.e., miniature specimens are considered by Matyja (1986) as an evidence of polymorphism. The haploceratids studied by us do not provide sufficient material to reach similar conclusions, although our material includes several small shells of *Ha. elimatum.* Our knowledge of dimorphic pairs, in the case where pairs cannot be established according to their peristomes, is based on different sizes of shells, similarity of sculpture, smaller differences in the parameters H/D, U/D, and B/D. The crowding of septa, demonstrating the adulthood of individuals, is proven in our material merely in several large steinkerns of *Ha. elimatum* and never in small specimens.

In the majority of Tithonian haploceratids, suture lines were already known in the period of publication of the monographs by Zittel (1868, 1870). The suture line of *Ha. elimatum*, illustrated by Zittel (1868: pl. 13: 6) has saddles accompanying lobe E drawn somewhat differently. Zittel's right saddle by E has the all partial branches practically similar, typical specimens have the branches of different size. We regard the suture line of a juvenile specimen in Wiedmann (1966b: text-tab. 43a) with a trifid lobe A as an authoritative suture line for *Ha. elimatum*. Specimen Z4224, illustrated here in Fig. 4A, bears the same suture line. The suture line of *Ha. staszycii* illustrated by Zittel (1870) in pl. 27: 6, and in our Fig. 4B appears to be the same as that of *Ha. elimatum*.

The suture line of *Ha. tithonium* in Zittel (1868: pl. 14: 2b, c) is not drawn reliably. A suture line of the same type is well-illustrated by Slavin (1953: text-fig. 4). This suture line

and the incomplete suture line of our specimen from Level 6 (Fig. 4C) are similar to the suture line of *Ha. elimatum*.

The suture line of *Hypolissoceras carachtheis* in the lost holotype was drawn by Zejszner (1846: pl. 4: 1d) and Zittel (1868) states that Zejszner's illustration is not reliable. Zittel (1868: pl. 15: 3a, b) illustrated the suture line of *Hy. carachtheis* from a whorl fragment of his specimen. Neither Barthel (1962) nor Vašíček et al. (2018) succeeded in finding the latter specimen, which should be deposited in SNSB-BSPG. It cannot be determined if the suture lines of *Hy. carachtheis* illustrated by Zittel (1868) differ from the suture lines of the genus *Haploceras.* The same is true for the suture line of *Hy. woehleri,* in which only an adventive lateral lobe is preserved (Fig. 4D).

The incomplete suture line of *Volanites verruciferus,* which is illustrated by Zittel (1870: pl. 27: 10), if reliable, differs slightly from the suture lines of the two previously mentioned genera in terms of the shapes of most saddles and lobes.

Olóriz Sáez (1976: text-fig. on p. 33) summarily illustrates the suture lines of quite a number of species of haploceratids. However, due to the small scale of the illustrated suture lines and their schematic nature, they are not very helpful.

Statistics.—The measured values of the parameters (H, U, and B) in representatives of the genera *Haploceras* (*Ha. elimatum*, *Ha. staszycii*) and *Hypolissoceras* (*Hy. carachtheis*, *Hy. woehleri*) were compared in relation to the diameter (D) using multivariate regression analysis (see Shea and Vecchione 2002 for details on the statistical procedure). Statistical analyses were performed using the Excel software package. The dependence is expressed by the regression lines and the coefficient R^2 determination (Hammer and Harper 2006). All measured values, from which the graphs were constructed, are presented in SOM 1–6. We have created statistical charts to compare dimension parameters between macroconchs and microconchs in *Ha. elimatum* (Fig. 7); between microconchs *Ha. elimatum* and *Ha. staszycii* (Fig. 9); and between *Hy. carachtheis* and *Hy. woehleri* (Fig. 10).

A statistical proof of the dependence of whorl height and whorl breadth to diameter shows a high significant linear correlation (R^2 more then 0.9). In the case of *Ha. elimatum*, the difference between microconchs and macroconchs cannot be observed. All measured specimens therefore belong to the macroconch category. In the adult specimens, the phragmocone ends at a diameter of approximately 105 mm. In the case of the macroconch, it is only possible to observe greater variability between the umbilicus breadth from a diameter of 80 mm.

The comparison of the microconch *Ha. elimatum* and *Ha. staszycii* (Fig. 9A–C), displays noticeable difference in umbilicus breadth. In the case of *Ha. staszyci*, the umbilicus breadth is smaller than in *Ha. elimatum*. It is also possible to observe more significant variability (linear correlation is 0.87).

Based on its morphology we assume that the holotype of *Hy. woehleri* represents a macroconch of *Hy. carachtheis. Hypolissoceras woehleri* differs from *Hy. carachtheis* above all in different shell size (Fig. 10A–C). Similarly, the difference in umbilicus breadth of *Hy. carachtheis* and *Hy. woehleri* is also noticeable. In the case of *Hy. carachtheis*, the umbilicus breadth is smaller than in *Hy. woehleri*.

Stratigraphy.—The majority of ammonoid specimens from the Štramberk Limestone from the Silesian Unit do not have accurate localizations and thus their stratigraphic positions are not known. It can be inferred from the data in the literature that the most stratigraphically important species described here is *Volanites verruciferrus,* which is usually given as an equivalent of the Semiforme Ammonite Zone from the higher part of the lower Tithonian (see, e.g., Zeiss et al. 1994; Zeiss 2003). Most data on the stratigraphic range are for the species *Haploceras elimatum* and *Hypolissoceras carachtheis.* Both species are, according to data based on our collection and in the literature, known from the whole Tithonian to the lower Berriasian. The occurrence of *Ha. elimatum* in the lower Berriasian is also confirmed by our newest findings in the Kotouč Quarry (Vaňková et al. 2019).

Aptychi.—Another peculiarity of the haploceratids is a strongly calcified lower element of the jaw apparatus in their body chambers. It consists of two symmetrical valves known as aptychi. In recent years, Engeser and Keupp (2002) and Schweigert (2009), among others documented their occurences. Thick-walled, ribbed calcite valves of aptychi, preserved in pairs, are most likely found in situ only in ammonites of the family Haploceratidae in Štramberk Limestone. Such examples with aptychi are usually only seldom illustrated in the literature. Finds of isolated (dispersed) specimens of aptychi are, in contrast, quite common.

In the Tithonian, specimens that belong, in the parataxonomic classification of aptychi (e.g., Měchová et al. 2010) to the genera *Punctaptychus* Trauth, 1927, and *Beyrichilamellaptychus* Turculet, 1994, occur more frequently. Some other genera from this artificial classification, similar to the latter genus, are included under the older common name lamellaptychi or in accordance with the proposal of Engesser and Keupp (2002), in aptychophoran aptychi (from Aptychophora), also occur.

In the collection of haploceratids processed by Barthel (1962), deposited in SNSB-BSPG, a specimen not illustrated by Barthel (1962) but labelled *Haploceras elimatum* (Tithonian from Le Pouzin) possesses two valves of *Punctaptychus punctatus* (Zittel, 1868) in the body chamber. Although the valves are not in paired positions (see Fig. 6F), with reference to their sizes (length L of ca. 48 mm) and the size of the body chamber of the ammonite, this finding can be regarded as evidence that the genus *Haploceras* is a bearer of aptychi of the genus *Punctaptychus.* Similarly, aptychi *Beyrichilamellaptychus beyrichi* (Oppel, 1865) may belong to *Hypolissoceras woehleri* based on equivalent dimensions of the body chamber and the maximum sizes of the valves (see an example in Fig. 6E).

The stratigraphic range of dimorphic pairs of the species of genera given here, i.e., *Haploceras* and *Hypolissoceras*, is from the Tithonian to the lower Berriasian. This corresponds essentially to the same time span of occurrence of aptychi of *P. punctatus* and *B. beyrichi,* for which Engeser and Keupp (2002) proposed the informal name Aptychophora.

Conclusions

According to our understanding, the haploceratids from the Štramberk Limestone belong to three genera: *Haploceras*, *Hypolissoceras*, and *Volanites*. A total of seven species have been identified and described. In the case of the lost holotypes, we designated lectotypes or neotypes.

Smooth juvenile and adult specimens of *Haploceras elimatum* analysed statistically as possible "microconchs" and "macroconchs" actually belong all to the to the macroconch of *Ha. elimatum*.

Haploceratids form dimorphic pairs. In our material, the dimorphism is evidenced by *Haploceras staszycii* (m) with *Ha. elimatum* (M)*,* another pair is probably *Haploceras tithonium* with *Haploceras subelimatum*. The latter species is absent from our material. The determination of dimorphism is based on published data but we could not determine which species is macroconch and which is microconch.

A statistically documented dimorphic pair is also formed by *Hypolissoceras carachtheis* (m) and *Hypolissoceras woehleri* (M).

We assume that another dimorphic pair consists of *Volanites verruciferus* (m) and *Volanites cassiferus* (M). We were unable to find both species in Štramberk during our own sampling. The Silesian Museum in Opava has a single juvenile specimen deposited, possibly belonging to *V. verruciferus*.

From a stratigraphic point of view, the most important species should be *V. verruciferus*, sometimes considered as an index species. According to literature data, it occurs at the level of the Semiforme Ammonite Zone (base of the middle Tithonian).

The other haploceratid species described here from the Štramberk Limestone have a broad stratigraphic range from the lower Tithonian to the lower Berriasian inclusive. They are insignificant for the determination of the J/K boundary and detailed stratigraphy.

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