

## Original Article

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This work is dedicated to the memory of Herbert Summesberger (1939–2023), a very kind person and prominent student of Cretaceous stratigraphy and cephalopod palaeontology.

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# Scaphitid ammonites from the lower Maastrichtian of Nahoryany (western Ukraine) and discussion on the origin of *Hoploscaphites constrictus*

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## Abstract

The lower Maastrichtian (Upper Cretaceous) section at Nahoryany, south of Lviv (western Ukraine), has been known as a rich source of fossils since 1843. However, the section is not available since a long time ago and fossils collected from it can only be studied in museum collections. In the present paper, ammonites of the scaphitid genus *Hoploscaphites* are studied based on Nahoryany material, comprising *Hoploscaphites pumilus*, *H. constrictus* and *H. sp.* Specimens from Nahoryany in museum collections lack data on their provenance level within the section so it cannot be determined whether or not they occurred together or formed a succession; data on inoceramid bivalves indicate the presence of two successive zones at Nahoryany. Some specimens from Nahoryany here referred to as *H. pumilus* are similar to the controversial *H. constrictus anterior* from the lower Maastrichtian of Poland. This morphology suggests an ancestor–descendant relationship between *H. pumilus* and *H. constrictus*, a common species once considered as an informal index for the Boreal Maastrichtian in Europe. The inferred evolutionary transition from *H. pumilus* to *H. constrictus* was towards a less robust, recoiled shell, which would have enhanced the horizontal swimming ability and manoeuvrability of these cephalopods. Recoiling trends occurred in several lineages of Late Cretaceous scaphitids.

## Introduction

The classic palaeontological locality of Nahoryany (Nagórzany in Polish literature), south of Lviv in western Ukraine (Fig. 1), has long been known as a rich source of spectacular macrofossils of early Maastrichtian marine invertebrates. In the nineteenth century, these were sent out to many European museums. The first account of this locality and its fossils was published in the newspaper ‘Gazeta Lwowska’ (Kronenthal, 1843). The reader is referred to Kennedy & Summesberger (1987) and Machalski & Malchyk (2016) for historical overviews of the Nahoryany section. Today, it is impossible to collect fossils at Nahoryany, because the local quarries were abandoned near the end of the nineteenth century (Łomnicki, 1897). However, rich materials from this site are available for study in museum collections both in Ukraine and in western Europe (e.g., Kotsiubynskyi, 1958, 1968; Christensen, 1987; Kennedy & Summesberger, 1987; Bakayeva, 2011; Machalski & Malchyk, 2016).

Scaphitid ammonites, that is, representatives of the family Scaphitidae Gill, 1871, are a characteristic component of the Nahoryany fauna, having been studied and/or discussed in several papers (e.g., Kner, 1848, 1852; Alth, 1850; Geinitz, 1850; Favre, 1869; Mikhailov, 1951; Błaszkiwicz, 1980; Kennedy & Summesberger, 1987; Kennedy, 1993; Machalski & Odin, 2001; Machalski, 2019). Representatives of the two lineages distinguished by Machalski (2019) in the Maastrichtian of Europe are present in the Nahoryany collections. The first lineage comprises giant scaphitids, leading from *Hoploscaphites quadrispinosus* (Geinitz, 1850) through *Acanthoscaphites (Acanthoscaphites) tridens* (Kner, 1848) to *A. (Euroscaphites) varians blaszkiewiczzi* Jagt, et al., 1999, and *A. (E.) v. varians* (Łopuski, 1911). Both *H. quadrispinosus* and *A. (A.) tridens* occur at Nahoryany (Machalski & Malchyk, 2016). Another lineage, the focus of the present paper, comprises *Hoploscaphites pumilus* (Stephenson, 1941), which led to *H. constrictus* (J. Sowerby, 1817); this is here referred to as the *Hoploscaphites constrictus* lineage. The eponymous species is a common European taxon, established on early late Maastrichtian material from the Calcaire à *Baculites* of the Cotentin Peninsula, Manche, north-west France (see Kennedy, 1986; Walaszczyk & Kennedy, 2011). A group of mid- to late Maastrichtian taxa, e.g., *Hoploscaphites tenuistriatus* (Kner, 1848) or *H. schmidi* (Birkelund, 1982), are interpreted as short-lived offshoots of the main *H. constrictus* lineage (Machalski, 2005). Additionally, there are also rare records of North American immigrants from the European Maastrichtian (Jagt & Kennedy, 1994; Machalski et al., 2007).



**Figure 1.** Location of the Nahoryany site in western Ukraine.

In the past, *Hoploscaphites constrictus* was regarded as an informal index fossil for the Boreal Maastrichtian in Europe, having been even considered as one of the potential markers for the lower boundary of the stage as understood then (e.g., Schmid, 1955; Birkelund et al., 1984; Kennedy, 1984b; Schulz et al., 1984). Reference is made to Walaszczyk et al., (2002a, 2002b), Niebuhr et al. (2011), Machalski (2012a), Remin (2012), Walaszczyk et al. (2016) and Wilmsen et al. (2018) for correlations between the traditional position for the base of the Maastrichtian, which coincided with the base of the conventional belemnite *Belemnella lanceolata* Zone (e.g., Christensen, 1996), with its currently accepted location. The latter has been based on the Global Stratotype Section and Point for the lower boundary of Maastrichtian Stage at a level 115.2 m in the depositional succession exposed at Tercis les Bains, Landes, south-west France (Odin & Lamaurelle, 2001).

*Hoploscaphites constrictus* has also been claimed to represent an example of evolutionary stasis (Kennedy, 1989). However, subsequent studies have revealed that records from the lowermost Maastrichtian are, in fact, either based on *H. pumilus* or doubtful (Machalski & Odin, 2001; Machalski, 2019). It has also been demonstrated that younger representatives of the *H. constrictus* lineage may be subdivided into temporal subspecies, with the last one, *H. constrictus johnjagti* Machalski, 2005, briefly surviving Cretaceous–Paleogene boundary event (Machalski, 2005; Machalski & Heinberg, 2005; Machalski, 2012b).

Machalski & Odin (2001) proposed that *Hoploscaphites constrictus* descended, via transitional *H. constrictus anterior* Błazkiewicz, 1980, from *H. pumilus*, a species described originally from the upper Campanian of North America (Stephenson, 1941; Cobban, 1974; Kennedy & Cobban, 1993), but subsequently recorded also from the upper Campanian and lower Maastrichtian in France (Kennedy et al., 1986; Machalski & Odin, 2001; Odin et al., 2001). Discussions on that subject also involved specimens from Nahoryany, but results were not satisfactory. This is exemplified by a suite of specimens from Nahoryany assigned to *Scaphites constrictus* by Favre (1869, pl. 5, figs. 1, 2, 4), to *Hoploscaphites constrictus* by Kennedy & Summesberger (1987), tentatively affiliated with *H. c. anterior* by Błazkiewicz (1980), and with *H. pumilus* and *H. anterior* (raised to species level) by Machalski & Odin (2001).

In view of all the above, the aim of the present paper is twofold: (1) to reassess the taxonomy of specimens of the genus

*Hoploscaphites* Nowak, 1911 from Nahoryany and (2) to discuss the evolutionary origin and stratigraphical range of *Hoploscaphites constrictus*.

### Geological setting

There is limited data on the exact location and appearance of the Nahoryany outcrop, of which there are no traces in the present landscape as checked by myself in 2001. According to Kronenthal (1843), the Nahoryany section was located in a forest, two miles south of Lviv, on the right side of the road leading to the town of Stryj. The section was available in two quarries situated close to each other. At the quarries marls, limestones and sandstones were reportedly exposed; these yielded abundant fossils of marine invertebrates, including often large-sized cephalopod and bivalve specimens, which occasionally formed accumulations. Kner (1848), mentioned two quarries of a few ‘Klafter’ depths exposing alternating sandstones and limestones; the Viennese Klafter was equal to 1.896 m.

During examination of Nahoryany specimens, I did not come across any sandstone matrix; the ‘sandstones’ probably represented sandy limestones and marls. In Polish literature, the Nahoryany rocks were commonly referred to as the ‘opoka nagórzańska’ (‘Nahoryany opoka’, see e.g., Łomnicki, 1897; Siemiradzki, 1905; Syniewska, 1923). Opoka is a carbonate-siliceous rock that is widely distributed in Upper Cretaceous successions across Poland and Ukraine, but according to Jurkowska & Świerczewska-Gładysz (2022), its proper identification requires a petrological and mineralogical study.

The environmental setting of the Nahoryany succession has never been the subject of analysis. However, the admixture of sand, the abundance of large-sized molluscs and the presence of fossil accumulations point to deposition in a relatively shallow-water, turbulent environment (see Machalski & Malchyk, 2019, figure 3, for a facies model of Upper Cretaceous deposits in Poland and western Ukraine).

As far as the stratigraphy of the section is concerned, there are overviews in Mikhailov (1951), Pasternak et al., (1968, 1987), Kennedy & Summesberger (1987) and Machalski & Malchyk (2016). According to Pasternak et al., (1968, 1987), the Nahoryany section belonged to the ‘Poteleckaja svita’ of the lower Maastrichtian, characterised by the occurrence of ‘*Belemnella lanceolata* and *Acanthoscaphites tridens*’. These deposits are

overlain by the chalk succession of the ‘Lvivskaja svita’ (‘opoka lwowska’ or ‘Lviv opoka’ of authors) assigned to the conventional lower upper Maastrichtian *Belemnitella junior* Zone. See Christensen (1996, fig. 1) for conventional belemnite zonation of the Maastrichtian and Machalski & Malchuk (2016, fig. 4) for belemnite and inoceramid zonation of the upper Campanian and Maastrichtian successions in western Ukraine.

Inoceramid data published by Kotsiubynskiy (1958, 1968), revised by Walaszczuk et al. (2002a) and Machalski & Malchuk (2016), are of particular importance for the stratigraphy of the Nahoryany section (see also Walaszczuk et al., 2016). These data indicate that the Nahoryany section encompassed two inoceramid zones, namely the upper part of the lower Maastrichtian *Endocostea typica* Zone and the lower part of the lower/lowermost upper Maastrichtian *Trochoceras radius* Zone. The inoceramid-based stratigraphy is confirmed by analysis of giant scaphitid taxa associated, on the basis of a comparison with successions recorded from Poland (see Introduction). These suggest that the section at Nahoryany comprised the lower portion of the *E. typica* Zone as well (Machalski & Malchuk, 2016). The heterogeneous stratigraphical nature of the Nahoryany section was already postulated by Siemiradzki (1905), who suggested that what he regarded as ‘*Scaphites constrictus* and *tenuistriatus*’ occurred only in the upper levels of the ‘Nahoryany opoka’ (Siemiradzki, 1905, pp. 488–489).

The most recent revision of belemnites from Nahoryany brought results that were consistent with the inoceramid and ammonite data. Christensen (1987) identified *Belemnella (Pachybelemnella) inflata* (Arkhangelsky, 1912) in the Nahoryany collections. This species occurs in the *Belemnella lanceolata* and *Belemnella pseudobtusa* Zones as distinguished by Schulz (1979) in the Krons Moor section (north-west Germany). The currently accepted definition of the base of the Maastrichtian (Odin & Lamaurelle, 2001) coincides with the base of the *Belemnella pseudobtusa* Zone *sensu* Schulz at Krons Moor (Niebuhr et al., 2011, fig. 6). This is the base of the *Belemnella obtusa* Zone (*sensu* Niebuhr et al., 2011; see also Wilmsen et al., 2018), which in the Middle Vistula River section (central Poland) corresponds to the upper portion of the uppermost Campanian ‘*T. redbirdensis* Zone and to the lower Maastrichtian *E. typica* Zone in the inoceramid subdivision (Remin, 2012, fig. 2; see also Walaszczuk, 2004). Indeed, markers of the latter zone are well represented in the Nahoryany assemblage (Walaszczuk et al., 2002a; Machalski & Malchuk, 2016).

## Material and methods

The present study is based on 18 specimens, which are housed in State Museum of Natural History of the National Academy of Sciences of Ukraine (SMNH-PZ-K) at Lviv (Ukraine), as well as nine specimens at GeoSphere Austria (GSA), formerly Geologische Bundesanstalt, Vienna, Austria. Some of the specimens from the GSA collections were illustrated by Favre (1869) and Kennedy & Summesberger (1987). The SMNH specimens studied have never been published, as far as I can tell.

The terminology of the scaphitid conch (Fig. 2A–D) essentially follows that used by Machalski (2005, 2021) and Machalski & Odin (2001). The dimorphism of each species, presumably of a sexual nature, is accepted. The dimorphs are referred to as macroconchs (M) and microconchs (m) (Fig. 2). Macroconchs typically attain much larger sizes at maturity, have high-whorled body chambers and commonly bear an umbilical bulge (swell) on the dorsal wall of the shaft. Such shells are traditionally interpreted as females. The

microconchs, are typically smaller (but not always, as seen by the giant specimen illustrated in Fig. 2C). They are characterised by low-whorled body chambers and concave umbilical walls lacking a bulge, and are regarded as males (e.g., Makowski, 1962; Cobban, 1969; Kennedy, 1986; Machalski, 1996, 2005, 2021; Landman et al., 2012; Klug et al., 2015). In view of the fact that the material has been largely distorted during diagenesis, only the length of the shell (= maximum diameter in Machalski, 2005, 2021) is measured for complete individuals.

As is typical of remains of ectocochleate cephalopods in the porous carbonate facies of the European Upper Cretaceous (Malchuk et al., 2017; Janiszewska et al., 2018; Machalski, 2021), all specimens studied are preserved as moulds (steinkerns). More specifically, the Nahoryany specimens are composite moulds with the external ornament superimposed on the internal mould following dissolution of the aragonitic shell and subsequent compaction. Specimens illustrated in Figure 3 were coated with ammonium chloride prior to photography. Line drawings of specimens are largely based on restored (retrodeformed, where needed) individuals from the published collections.

## Taxonomy

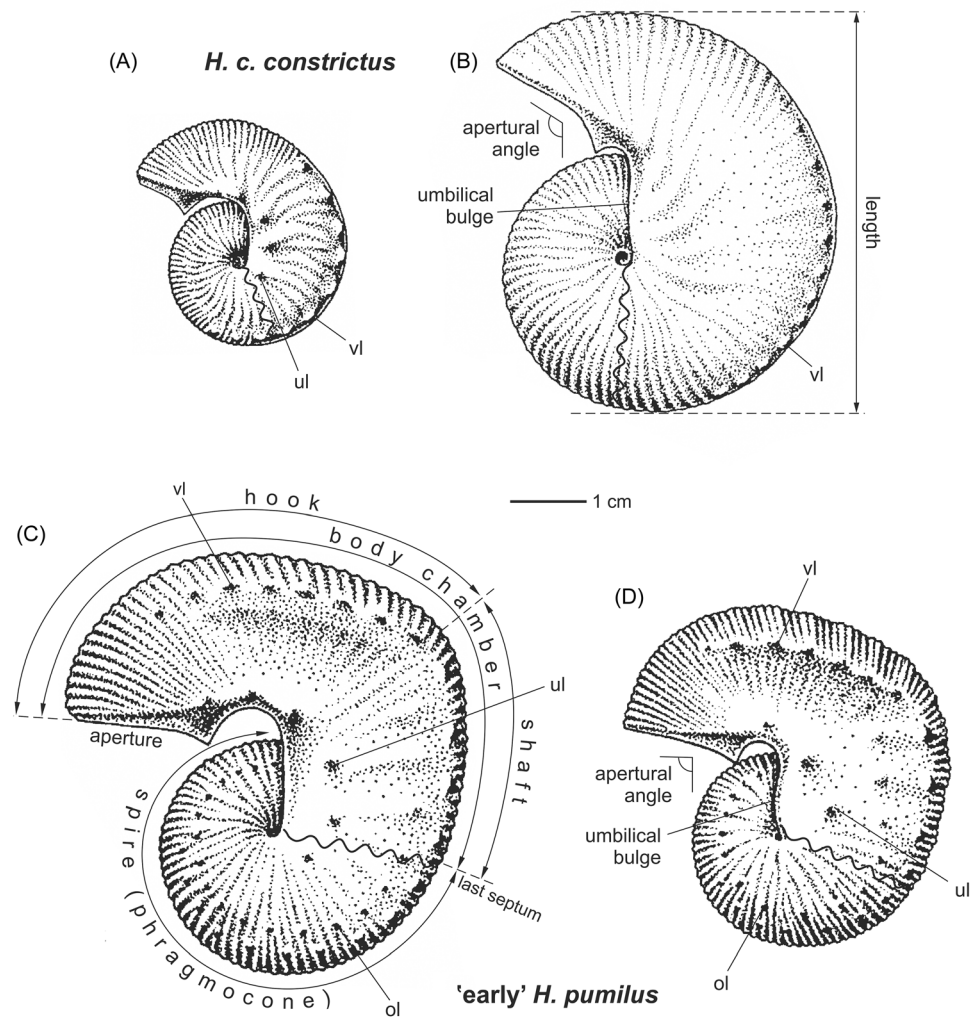
Three morphologically different groups of specimens are discernible in the material studied. These are assigned here to *Hoploscaphites pumilus*, *H. constrictus* and *H. sp.*

### *Hoploscaphites pumilus* (Stephenson, 1941)

#### Description

Nine specimens from GSA collections are assigned here (Fig. 3A–V). Mature microconchs (m), five in total, are identified on the basis of the low whorl of the shaft and the straight or concave umbilical wall (Fig. 3A–E, K–N, S). A distinct gap between the hook and spire is seen in some individuals (Fig. 3L). Some are compressed with flat flanks (Fig. 3A–C), while others are notably depressed and robust in appearance (Fig. 3K–N). The robust specimens are typified by sharply defined ventrolateral and umbilical shoulders and a trapezoidal cross-section of the shaft, resulting from a marked concavity of the flank at the shaft-hook transition. These specimens have also more inflated venters on the hook than on the shaft (compare Fig. 3K,N). Regular and dense ribbing is present over the entire venter. The best-preserved, relatively undistorted microconch (Fig. 3C) is 31 mm long, with an apertural angle close to normal. This is the original of Favre (1869, pl. 5, fig. 1), reillustrated by Kennedy & Summesberger (1987, pl. 6, figs. 16–18). Another, much more distorted microconch (Fig. 3K–N) was illustrated by Favre (1869, pl. 5, fig. 4) and Kennedy & Summesberger (1987, pl. 6, figs. 19–21).

Mature macroconchs (M), four in total, are identified based on the high whorl of the body chamber (Fig. 3F–J, O–R, T–V). The best-preserved one (Fig. 3T–V) is the original of Favre (1869, pl. 5, fig. 2), reillustrated by Kennedy & Summesberger (1987, pl. 6, figs. 13–15). It is a compressed individual, 51 mm long, with a distinct umbilical bulge, flat flanks, rather close contact of the spire and hook, an apertural angle close to normal, and abundant ventrolateral tubercles ranging up to the aperture. Although fragmentary and distorted, a much smaller macroconch (Fig. 3F–H) seems to be similar in proportions and morphology. In contrast, other specimens identified here as macroconchs by virtue of their high-whorled body chambers (e.g., Fig. 3O–R) are strongly depressed, with concave flanks of the shaft and a trapezoidal cross-section at the shaft-hook transition, sharing these characters



**Figure 2.** Morphological terms used to describe scaphitid conchs. A, B. *Hoploscaphites constrictus*. A – microconch; B – macroconch (based on several specimens from the lower upper Maastrichtian Calcaire à *Baculites* of the Contentin Peninsula, illustrated by Kennedy, 1986). C, D. *Hoploscaphites pumilus*. C – giant microconch, characterised by the low height of the shaft whorl; D – macroconch. Specimens C and D are based on specimens from the upper Campanian Saratoga Chalk, illustrated by Kennedy & Cobban, 1993, fig. 17/17–19 for C and fig. 16/22–26 for D. vl – ventrolateral tubercles, ul – umbilical tubercles, ol – outer lateral tubercles.

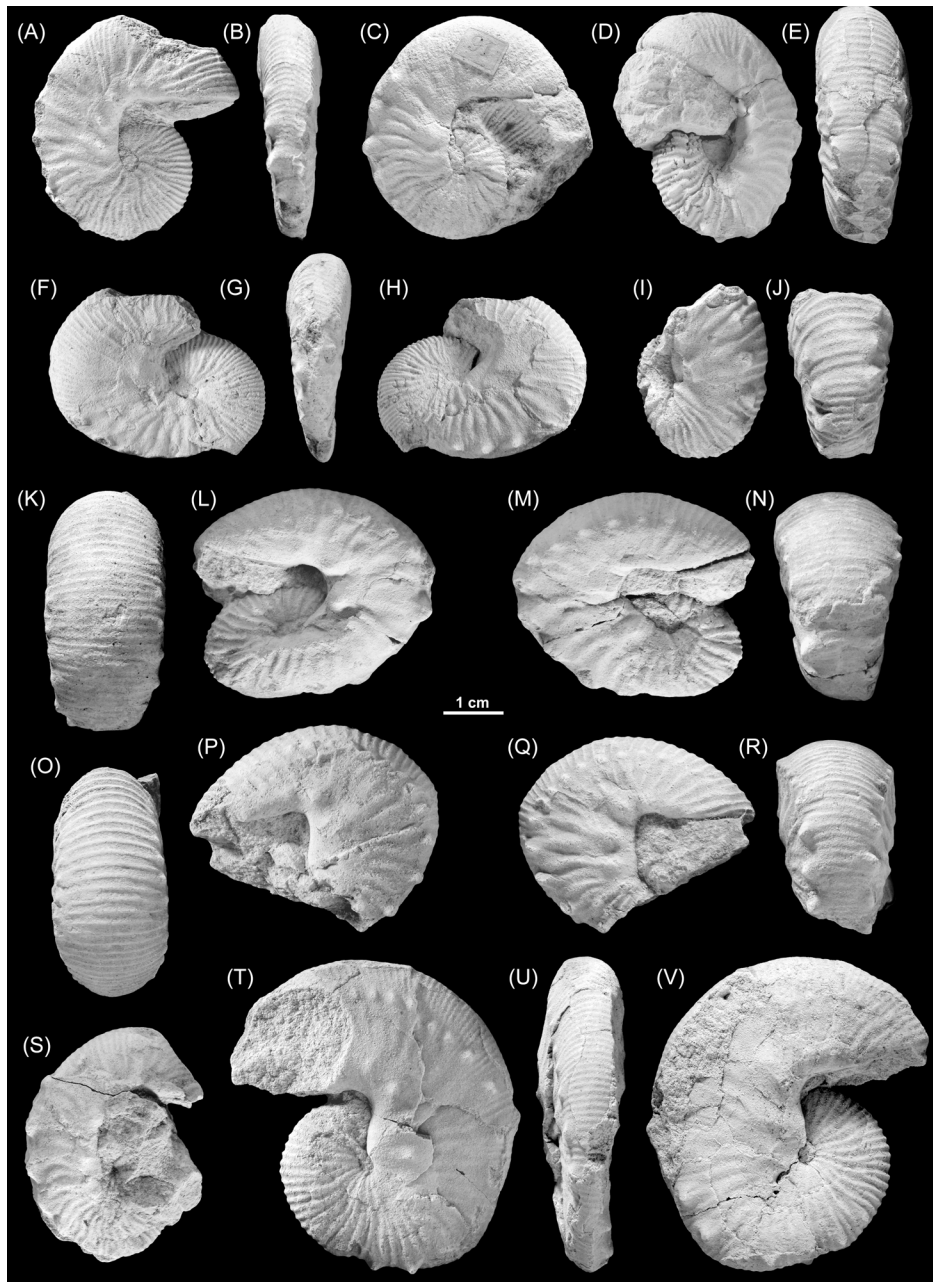
with the robust microconchs. This is best seen when comparing the microconch in Figure 3K–N and the macroconch in Figure 3O–R. The latter reveals another distinctive feature, namely a break in the pattern of ventrolateral tuberculation corresponding to a change in the geometry of the final whorl. The ventrolateral tubercles are rather distant on the older part of the shaft and more closely spaced over the younger portion of the shaft and hook. This change seems to be associated with an abrupt change in whorl convexity, resulting in the ‘hump-backed’ outline of the specimen (Fig. 3O–R).

#### Discussion

The material described above matches that of *Hoploscaphites pumilus* described from the upper Campanian Nacatoch Sand of Navarro County (Texas), Saratoga Chalk of Hempstead County (Arkansas) and Navesink Formation at Atlantic Highlands (New Jersey), all in the USA (Stephenson, 1941; Cobban, 1974; Kennedy & Cobban, 1993) and that from the upper Campanian and lower Maastrichtian of the D’Avezac and Les Vignes units as exposed at Tercis les Bains, France (Machalski & Odin, 2001; Odin et al., 2001). There is also a record of ‘*Scaphites* aff. *pumilus* Stephenson’ from the upper Campanian of Tajikistan, Middle Asia (Atabekyan & Khakimov, 1976, pl. 8, figs. 1, 2), which remains to be verified.

The Saratoga Chalk material of *H. pumilus* is the most representative in view of its good preservation and abundance. The Saratoga specimens are characterised by a distinctive, rather robust ‘hump-backed’ shell, trapezoidal cross-section of the shaft, an apertural angle close to normal and the occasional presence of an additional row of tubercles next to the ventrolateral ones (outer lateral tubercles; Fig. 2). One of the Saratoga specimens interpreted as a macroconch by Kennedy & Cobban (1993, fig. 17/17–19) has been reinterpreted by Machalski & Odin (2001) as a giant microconch, marking a notable reversal in the microconch vs macroconch size-relationship typical for scaphitids and other ammonites (Fig. 2). In contrast, the Tercis les Bains material is more variable, comprising ‘Saratoga-type’ specimens in the uppermost Campanian part of the succession (Odin et al., 2001, pl. 1, figs. 9–10, 11–13) and a mixture of ‘Saratoga-like’ specimens (e.g., Machalski & Odin, 2001, pl. 1, figs. 3, 4, 30–31, 36) with more slender, less ‘hump-backed’ individuals in the lower Maastrichtian portion of the section (Machalski & Odin, 2001, pl. 1, figs. 15–16, 25, 26), which is in the *Endocostea typica* Zone (Walaszczyk et al., 2002b).

Some of the robust Nahoryany specimens, especially a microconch illustrated in Figure 3K–N, and a macroconch in Figure 3O–R, have close counterparts in the Saratoga material of *H. pumilus* illustrated by Kennedy & Cobban (1993, figs. 16–17). The only significant differences are that (1) none of the Nahoryany



**Figure 3.** *Hoploscaphites pumilus* from the lower Maastrichtian of Nahoryany. A, B. GSA2006/086/0002 (m); A – lateral view. B – ventral view. C. GSA1869/006/0011/01 (m), lateral view. D, E. GSA2006/086/0007 (m); D – lateral view, E – ventral view. F–H. GSA2006/086/0001 (M); F, H – lateral view, G – ventral view. I, J. GSA2006/086/0006 (M), I – lateral view, J – ventral view. K–N. GSA1869/006/0011/03 (m); K – ventral view of hook, L, M – lateral views, N – ventral view of shaft. O–R. GSA1869/006/0011/04 (M); O – ventral view of hook, P, Q – lateral views, R – ventral view of shaft. S. GSA2006/086/0008 (m), lateral view. T–V. GSA1869/006/0011/02 (M); T, V – lateral views, U – ventral view of shaft. m – microconch; M – macroconch.

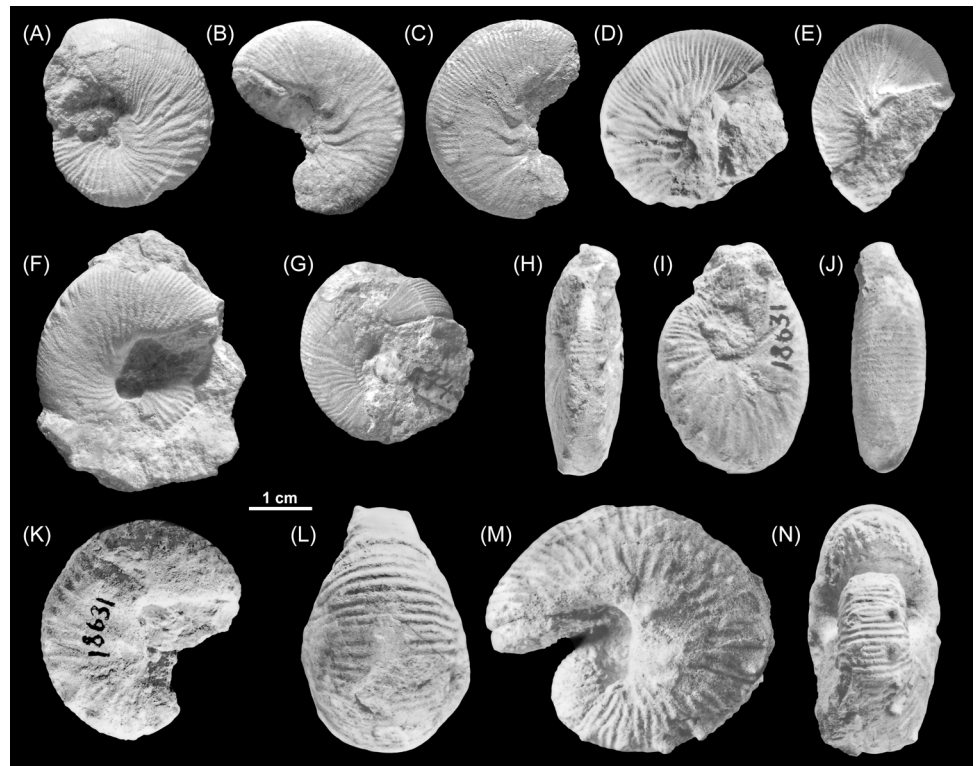
specimens reveal an additional row of tubercles and (2) the Nahoryany microconchs never exceed in size the associated macroconchs.

The distorted, fairly large microconch specimen figured by Kner (1852, pl. 15, fig. 13) under the name of ‘*Scaphites constrictus* d’Orb. Var.’ seems to represent the ‘Saratoga-like’ morphology as well; it might even possess an additional row of tubercles as pointed out by Machalski & Odin (2001).

Amongst the compressed Nahoryany specimens, the microconch in Figure 3A,B and the macroconch in Figure 3T–V are close in their appearance to several of the Tercis les Bains specimens, as exemplified by a microconch from a level 10 cm above the Campanian–Maastrichtian boundary (Machalski & Odin, 2001, pl. 1, figs 15, 16) and a macroconch from a level 50 cm below this boundary (Machalski & Odin, 2001, pl. 1, figs. 25, 26).

The compressed specimens from Nahoryany and Tercis les Bains are also close in their morphology to *Hoploscaphites*

*constrictus anterior* Błaszkiwicz, 1980 from the lower Maastrichtian of the Miechów Upland, southern Poland; this is from the upper part of the inoceramid *Endocostea typica* Zone (Agata Jurkowska, personal communication, 2018). Indeed, Błaszkiwicz (1980) placed specimens from Nahoryany illustrated by Favre (1869) in the synonymy of *H. c. anterior*, albeit with a query. Błaszkiwicz (1980) differentiated this subspecies from the nominate one, among other things, by its smaller apertural angle and less close contact of the body chamber and spire. It must be noted, however, that Błaszkiwicz (1980) illustrated only two well-preserved macroconch specimens of his subspecies, which differ in several ways from each other. The holotype (Błaszkiwicz, 1980, pl. 18, figs. 4–6), from Polichno near Pińczów, has an open apertural angle, unlike the Saratoga specimens of *H. pumilus*, but similar to *H. constrictus* material from the lower upper Maastrichtian Calcaire à *Baculites* of Cotentin (Kennedy, 1986). Indeed, the latter author regarded *H. c. anterior* as a synonym of



**Figure 4.** Scaphitid ammonites, *H. constrictus* (A–G) and *H. sp.* (H–N), from the lower Maastrichtian of Nahoryany. A. SMNH-PZ-K-9716/2 (M), lateral view. B, C. SMNH-PZ-K-9716/5 (M), lateral views. D. SMNH-PZ-K-9718/2 (M?), lateral view. E. SMNH-PZ-K-9716/4 (m), lateral view. F. SMNH-PZ-K-9716/1 (m), lateral view. G. SMNH-PZ-K-9716/3 (m), lateral view. H–J. SMNH-PZ-K-9716/3; H – ventral view of spire, I – lateral view, J – ventral view of hook. K. SMNH-PZ-K-9718/3 (M), lateral view, L–N. SMNH-PZ-K-9720 (M); L – ventral view of hook, M – lateral view, N – adapertural view. m – microconch; M – macroconch.

*H. c. constrictus*. Another macroconch of *H. c. anterior* from Śladów (Błaszkiwicz, 1980, pl. 18, figs. 9–10) has, however, an apertural angle that is close to normal and a slightly ‘hump-backed’ shell outline, like the Tercis les Bains and Nahoryany macroconchs of *H. pumilus* discussed above. These characters led Machalski & Odin (2001) and Machalski (2019) to postulate that *H. constrictus* evolved from *H. pumilus*. However, in opposition to the conclusions reached by Machalski & Odin (2001), *H. constrictus anterior* is still regarded herein as a doubtful taxon, awaiting revision based on more abundant material from the type locality, which is inaccessible today.

### *Hoploscaphites constrictus* (Sowerby, 1817)

#### Description

Six individuals from the SMNH collections are assigned here (Fig. 4A–G), two of these being undoubted macroconchs (Fig. 4A–C) and another one probably a macroconch as well (Fig. 4D); the remaining specimens are microconchs in view of their low whorl of the shaft (Fig. 4E–G). The specimens are rather small when compared to Nahoryany material assigned to *H. pumilus*.

The best-preserved macroconch is shown in Figure 4A. It is 30 mm long, almost circular in lateral view and has a distinct umbilical swelling and flat flanks covered with delicate ribs; barely discernible traces of two or three ventrolateral tubercles are seen in the middle portion of the shaft. Delicate flexuous riblets cover the hook, and the apertural angle is open (*c.* 120°). Another specimen (Fig. 4B,C) is closely similar in morphology and size (32 mm in length), with an open apertural angle as well. The specimen bears more accentuated ventrolateral tubercles than the preceding one; umbilical bullae are also visible. The ornament of the incomplete specimen in Figure 4D is stronger.

The best-preserved microconch (Fig. 4F) is of comparable size to the macroconchs, sharing with them faint traces of tuberculation

in the middle of the shaft and an open apertural angle. The other two microconchs (Fig. 4E,G), both distorted and fragmentary, are very finely ribbed with no tubercles at all; poor preservation precludes interpretation of the apertural angle.

#### Discussion

All specimens described above share rather small dimensions, delicate ornament with feeble or missing ventrolateral tuberculation and an open umbilical angle, where this can be seen. They were placed in the same box in the SMNH collections and labelled ‘*Scaphites tenuistriatus*’. Indeed, the fine, occasionally thread-like ribbing of these individuals recalls that of *Hoploscaphites tenuistriatus* (Kner, 1848). This species was recorded from Nahoryany by Kennedy & Summesberger (1987). However, their specimen actually came from the younger chalk succession of the ‘Lvivskaja svita’, representing the conventional lower upper Maastrichtian *Belemnitella junior* Zone (Machalski & Odin, 2001; Machalski, 2005).

The specimens discussed above match well some of the specimens of *Hoploscaphites constrictus* from the *stratum typicum* of this species, namely the lower upper Maastrichtian Calcaire à *Baculites* of Cotentin (Kennedy, 1986; Walaszczyk & Kennedy, 2011). The French material shows a remarkable variability in size and style of ornamentation of both dimorphs (Kennedy, 1986), and in contrast to the Nahoryany material is represented by internal rather than composite moulds, but all these specimens share an open apertural angle and relatively short shaft when compared to *H. pumilus*, especially in macroconchs. The Nahoryany specimens match particularly well the suite of small and finely ornamented Cotentin specimens illustrated by Kennedy (1986, pl. 14, figs. 1–9). It should be noted that amongst the specimens figured in Kennedy (1986) only that in his plate 14, figs. 1–4 is an undoubted microconch, the remaining ones better

interpreted as very small macroconchs, as judged by the presence of an umbilical bulge.

Two of the specimens from the GSA Nahoryany collections illustrated by Kennedy & Summesberger (1987, pl. 6, figs. 6–7 and 8–9) as *H. constrictus*, both undoubted microconchs (not localised by myself in the collections), share the characters of the SMNH specimens discussed herein. All in all, it seems that only small (with length of around 30 mm) and finely ornamented representatives of this species occur at Nahoryany. For comparison, the type material of the species from Cotentin ranges from 22 to 68 mm in shell length (Kennedy, 1986).

### *Hoploscaphites* sp.

#### Description

Depressed macroconch individuals from SMNH collections, three in total, are assigned here (Fig. 4H–J, K, L–N). The stout specimen illustrated in Figure 4L–N is 40 mm long, typified by strong flank ribs, prominently swollen inner flanks and ventrolateral tubercles ranging all around the ventrally exposed portion of the adult shell, including particularly strong tubercles on the entire exposed phragmocone (spire). The same extent of tuberculation is visible in the specimen shown in Figure 4H–J. The specimen illustrated in Figure 4L–N is relatively undistorted and has an apertural angle close to normal. The specimen in Figure 4H–J is heavily distorted; incidentally it shows a great similarity to the (lost) specimen illustrated by Kner (1848, pl. 1, fig. 4) as ‘*Scaphites compressus* d’Orbigny’, which is a specific name coined for a Coniacian scaphitid (see Kennedy, 1984a).

#### Discussion

The two macroconchs (Fig. 4H–J, L–N) are utterly different from what is referred to here as *H. pumilus* and *H. constrictus*. Instead, they share their strong ‘all-around’ ventrolateral tuberculation with some early Maastrichtian North American scaphitids. These are *Hoploscaphites sargklofak* Landman, et al., 2015, *H. macer* Landman et al., 2019 and *H. criptonodosus* (Riccardi, 1983). However, the similarity is probably of a superficial nature, because the undeformed Nahoryany specimen (Fig. 4L–N) differs from each of the above-mentioned North American species in having an apertural angle that is close to normal. Specimen in Figure 4K lacks the spire but most probably belongs to this group too.

### Discussion on the origin and range of *Hoploscaphites constrictus*

The subject of the present paper provides an opportunity to discuss the evolutionary origin and stratigraphical range of *Hoploscaphites constrictus*. As pointed out in Introduction, this widespread and common European scaphitid ammonite was considered as an informal ‘guide fossil’ for the European Maastrichtian as its stratigraphical extent was regarded to be (almost) equal to the range of the Maastrichtian Stage, in the old definition. In order to test this view, an overview of the stratigraphical ranges of the first appearance datum (FAD) of *H. constrictus* is presented below. The recently elaborated inoceramid stratigraphy of the Maastrichtian Stage (Walaszczyk et al., 2002a, 2002b; Walaszczyk, 2004; Walaszczyk et al., 2010, 2016; Walaszczyk & Kennedy, 2011; Machalski & Malchuk, 2016; Jagt & Jagt-Yazykova, 2018) is accepted as a convenient basis for calibration of scaphitid ranges (Fig. 5).

The Nahoryany section is not very conclusive with respect to the stratigraphical ranges of the species involved. Based on inoceramid and ammonite data, the section encompassed two zones, namely the lower Maastrichtian *Endocostea typica* Zone and the lower part of the lower/lowermost upper Maastrichtian *Trochoceras radius* Zone (Walaszczyk et al., 2002a; Machalski & Malchuk, 2016; Walaszczyk et al., 2016). The exact provenance level of the studied scaphitid specimens is not available on museum labels. Therefore, it is not known whether they occurred together or formed a succession. It is only certain that *H. constrictus* appeared in one of these two inoceramid zones. For comparison, the *stratum typicum* of the species, the Calcaire à *Baculites* of Cotentin, represents the lower upper Maastrichtian ‘*Inoceramus*’ *ianjoanensis* Zone (Walaszczyk & Kennedy, 2011).

At Tercis les Bains, there are no unequivocal records of *H. constrictus* from correlatives of the *E. typica* Zone (Machalski & Odin, 2001), the base of which is a good proxy for the Campanian–Maastrichtian boundary (Walaszczyk et al., 2002b).

At Krons Moor (north-west Germany), most of the specimens identified as *H. constrictus* by Niebuhr (2003, pl. 7, figs. 2–4) are regarded here as equivocal in view of their poor preservation and lack of diagnostic characteristics. These doubtful individuals include two specimens (Niebuhr, 2003, pl. 7, figs 2, 5) found in the interval c. 3.5–4 m above the base of the conventional *Belemnella lanceolata* Zone, regarded formerly as the base of the Maastrichtian Stage in Europe. The only indisputable specimen of *H. constrictus* from Krons Moor is a single macroconch from the *Belemnella obtusa* Zone (Niebuhr, 2003, pl. 7, fig. 4), which is equivalent to the *E. typica* Zone (Remin, 2012).

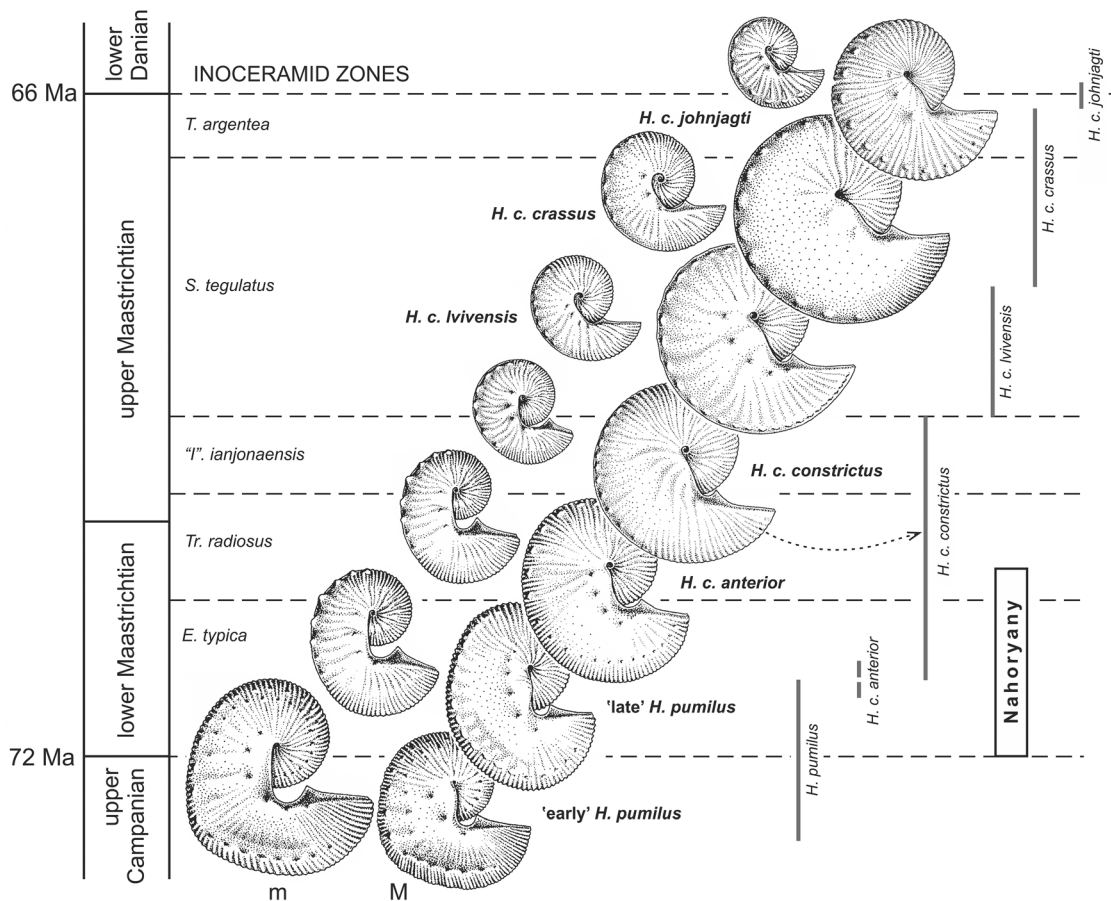
At Krampen near Neuberg (Steiermark, Austria), the undoubtedly early Maastrichtian ammonite fauna contains *H. constrictus*, but its precise dating is equivocal (Kennedy & Summesberger, 1986, see also Machalski et al., 2007). Moreover, it has not yet been calibrated against the inoceramid zonation. Some of the specimens regarded as *H. constrictus* by Kennedy & Summesberger (1986, pl. 16, figs. 8, 9 and 13) have subsequently been reinterpreted by Machalski et al. (2007) as an unknown *Hoploscaphites* species with North American affinities. However, the remaining specimens illustrated as *H. constrictus* by Kennedy & Summesberger (1986, pl. 16, figs. 1–5, 13), all minute macroconchs, belong to this species without doubt.

In Poland, the heterogenic and controversial type material of *H. constrictus anterior* (discussed in Taxonomy) comes from the upper portion of the *E. typica* Zone.

At Volsk (Saratov region, Russian Federation), a rich scaphitid fauna has been documented (Selt’ser & Ivanov, 2010; Selt’ser & Machalski, 2019). This succession includes *H. pumilus* and *H. constrictus*. The first unequivocal records of the latter species stem from equivalents of the upper portion of the *E. typica* Zone (Vladimir Selt’ser, personal communication, 2018; Machalski, 2019).

In summary, the evidence available to date points to the FAD of *Hoploscaphites constrictus* somewhere in the *E. typica* Zone, most probably in its upper part. This zone is the lowermost Maastrichtian inoceramid zone in Europe in the currently accepted subdivision (e.g., Walaszczyk et al., 2002a, 2002b). There is no evidence that J. Sowerby’s species appeared close to the formerly accepted lower boundary of the Maastrichtian, which is near the base of conventional *Belemnella lanceolata* Zone.

A view that *Hoploscaphites constrictus* represents an example of evolutionary stasis (Kennedy, 1989) cannot be upheld in face of subsequent works. Machalski (2005, 2012b) divided the upper part



**Figure 5.** Succession of temporal subspecies, each represented by a dimorphic pair in their presumed life positions, within the main *Hoploscaphites constrictus* lineage in the European Maastrichtian. Restored views of successive subspecies are based on Kennedy & Cobban (1993) for ‘early’ *H. pumilus*, Machalski & Odin (2001) for ‘late’ *H. pumilus*, Błaszkiwicz (1980) for *H. c. anterior*, Kennedy (1986) for *H. c. constrictus*, and Machalski (2005) for *H. c. livvensis*, *H. c. crassus* and *H. c. johnjagti*. The scaphitid succession is presented against the inoceramid-based subdivision of the Maastrichtian stage, modified from Landman et al., (2021, fig. 2, originally compiled from data provided by Abdel-Gawad, 1986; Walaszczyk et al., 2016, fig. 3; Machalski & Malchuk, 2016, fig. 4, Gale et al., 2020, fig. 27.9, and by Ireneusz Walaszczyk, personal communication, 2021). Scaphitid ranges are based on the papers quoted above; the precise positioning of *H. c. anterior* is based on speculative extrapolation of the trend in addition to the data presented by Błaszkiwicz (1980). *H.*, *Hoploscaphites*; *c.*, *constrictus*; *E.*, *Endocostea*; *Tr.*, *Trochoceras*, *I.*, *Inoceramus*; *S.*, *Spyridoceras*; *T.*, *Tenuipteria*; *m* – microconch, *M* – macroconch.

of the *H. constrictus* lineage into a succession of temporal subspecies (chronosubspecies) of biostratigraphical significance based on rich ‘populations’ from various locations and levels in central Europe. These range from *H. constrictus constrictus* as understood based on the Cotentin material to *H. c. johnjagti*, which even passed across the Cretaceous–Paleogene (K–Pg) boundary (Fig. 5). As far as the lower part of the succession in Figure 5 is concerned, it is admittedly speculative in view of uncertainties in precise positioning of the Nahoryany specimens of *H. pumilus* and *H. constrictus* and the controversial status of *H. constrictus anterior* from Poland. What is referred to as ‘early’ *H. pumilus* in Figure 5 refers to the robust and distinctively ‘hump-backed’ specimens known from the upper Campanian of the Saratoga Chalk and the upper Campanian and lowermost Maastrichtian of the Tercis les Bains section, and from the lower Maastrichtian of Nahoryany. What is shown as ‘late’ *H. pumilus* in Figure 5 refers to more slender and less ‘hump-backed’ early Maastrichtian specimens identified at Tercis les Bains and Nahoryany. These ‘late’ forms are morphologically similar to *H. constrictus*, and considered along *H. constrictus anterior*, which seems to be even more closely similar to *H. constrictus constrictus*, suggesting an evolutionary transition from *H. pumilus* to *H. constrictus* as proposed by Machalski &

Odin (2001) and Machalski (2019). However, the chronological succession from ‘late’ *H. pumilus* through *H. c. constrictus anterior* to *H. c. constrictus* presented in Figure 5 is based on arbitrary extrapolation of morphologies and should be tested in future, ideally based on analysis of stratigraphically better-constrained ‘populations’.

If the interpretation of the evolutionary transition from *H. pumilus* to *H. constrictus* is correct, some considerations are possible about its significance in terms of functional morphology and mode of life of these cephalopods. According to Landman et al. (2010) and Landman et al. (2012), scaphitid species with long shaft and hook separated from the spire were poorly designed for active horizontal swimming, relying more on passive vertical scanning of the water column. The long shaft meant that the centres of buoyancy and mass of the adult shell were located relatively far from each other, enhancing the hydrostatic stability of the animal, better suitable for a life as a rather passive ‘vertical scanner’ than an active ‘horizontal swimmer’. The conchs of *H. pumilus*, especially those of the ‘early’ forms of the species (Fig. 5), were robust, heavily ornamented, with the hook well separated from the spire (especially in microconchs), thus representing the category of ‘poor horizontal swimmers’. In contrast, more slender and less



heavily ornamented scaphitids with short shafts and closer contacts of the hook and phragmocone may be interpreted as better swimmers, able to do more efficient horizontal movements (Landman et al., 2012). The recoiled shells of *H. constrictus constrictus* and younger subspecies fall into this category (Figs. 2, 5). In summary, the shortening of the body chamber and associated recoiling of the shell during the transition from *H. pumilus* to *H. constrictus* enhanced the active horizontal swimming ability, and perhaps also the manoeuvrability of these cephalopods.

As pointed out by Wiedmann (1965), Landman et al. (2012), Landman et al. (2017) and Landman et al. (2021), many lineages of Late Cretaceous scaphitid ammonites showed a tendency to recoil the final body chamber during their evolution. A recoiling trend, for instance, was demonstrated for the lineage of giant European scaphitids (Landman et al., 2021, fig. 2) mentioned in Introduction.

### Final remarks

The early Maastrichtian scaphitid fauna from Nahoryany, south of Lviv (western Ukraine), has been described with three species identified: *Hoploscaphites pumilus*, *H. constrictus* and *H. sp.* All specimens studied came from the old museum collections which lack data on their provenance level within the section, so it cannot be determined whether or not they occurred together or formed a succession. Inoceramid data suggest that the section once exposed at Nahoryany encompassed two successive, essentially lower Maastrichtian inoceramid zones. In view of this, and taking into account the better-constrained records of both species from other European sections, it could be assumed that at Nahoryany *H. pumilus* came from layers older than *H. constrictus* (see Fig. 5). In this context, it is intriguing that all specimens identified here as *H. pumilus* come exclusively from the GSA collection, containing specimens collected (probably well) before the publication of Favre's monograph in 1869. As far as I know, the SMNH collections were largely assembled later on, possibly during the last decades of the nineteenth century. Perhaps, different portions of the section were accessible for fossil collecting at different times.

The ancestor–descendant relationship between *H. pumilus* and *H. constrictus* is proposed in the present paper, following Machalski & Odin (2001). The inferred evolutionary transition was towards a less robust, recoiled shell, which in currently accepted interpretations of the scaphitid palaeobiology, would have enhanced the horizontal swimming ability and manoeuvrability of these cephalopods. As mentioned earlier, the recoiling trends have been documented in several lineages of scaphitid ammonites. The conceivable explanations of such trends may involve response to physical factors (e.g., changes in bathymetry) or to biological interactions (e.g., predation, competition), but this is the theme for another study.

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### References

- Abdel-Gawad, G.I.**, 1986. Maastrichtian non-cephalopod mollusks (Scaphopoda, Gastropoda and Bivalvia) of the Middle Vistula Valley, Central Poland. *Acta Geologica Polonica* **36**: 69–224.
- Alth, A.**, 1850. Geognostisch-palaeontologische Beschreibung der nächsten Umgebung von Lemberg. Haidingers naturwissenschaftliche Abhandlungen, Bd. III. (Wien): 171–284. Wien.
- Arkhangelsky, A.D.**, 1912. Verkhne-melovye otlozheniya wostoka Evropeiskoi Rossii. *Materialy dlya Geologii Rossii* **25**: 1–631. (In Russian)
- Atabekyan, A.A. & Khakimov F. K.**, 1976. Kampanskiye i maastrikhtskyye ammonity sredney Azii (Dushanbe): 1–146. (in Russian)
- Bakayeva, S.H.**, 2011. Piznokreidovi cherevonohi moliusky Volyno-Podillia. *Naukova Dumka (Kyiv)*: 200 pp. (in Ukrainian)
- Birkelund, T.**, 1982. Maastrichtian Ammonites from Hemmoor, Niederelbe (NW-Germany). *Geologisches Jahrbuch A* **61**: 13–33.
- Birkelund, T., Hancock, J.M., Hart, M.B., Rawson, P.E, Remane, J., Robaszynski, F., Schmid, F. & Surlyk, F.**, 1984. Cretaceous stage boundaries – Proposals. *Bulletin of the Geological Society Denmark* **33**: 3–20.
- Błaszkiwicz, A.**, 1980. Campanian and Maastrichtian ammonites of the Middle Vistula River valley, Poland: a stratigraphic-paleontological study. *Prace Instytutu Geologicznego* **92**: 1–63.
- Christensen, W.K.**, 1987. *Belemnella (Pachybelemnella) inflata* (Arkhangelsky) from Nagoryany, USSR. *Beiträge zur Paläontologie von Österreich* **13**: 79–84.
- Christensen, W.K.**, 1996. A review of the Upper Campanian and Maastrichtian belemnite biostratigraphy of Europe. *Cretaceous Research* **17**: 751–766.
- Cobban, W.A.**, 1974. Ammonites from the Navesink Formation at Atlantic Highlands, New Jersey. *Geological Survey Professional Paper* **845**: 1–21.
- Cobban, W.A.**, 1969. The Late Cretaceous ammonites *Scaphites leei* Reeside and *Scaphites hippocrepis* (DeKay) in the Western Interior of the United States. *U.S. Geological Survey Professional Paper* **619**: 1–27.
- Favre, E.**, 1869. Description des Mollusques fossiles de la craie des environs de Lemberg en Galicie. *H. Georg (Geneve)*: 1–173.
- Gale, A.S., Mutterlose, J., Batenburg, S.** with contributions by Gradstein, F.M., Agteberg, F.P., Ogg, J.G. & Petrizio, M.R., 2020: Chapter 27. The Cretaceous Period. In Gradstein, F.M., Ogg, J.G., Schmitz, M.D. & Ogg, G.M. (eds.): *Geologic Time Scale 2020, 1023–1085*. Elsevier.
- Geinitz, H.B.**, 1849–50. Das Quadersandsteingebirge oder Kreidegebirge in Deutschland. *Freiberg*. 1–229.
- Gill, T.**, 1871. Arrangement of the families of Mollusks. *Smithsonian Miscellaneous Collections* **227**: xvi + 1–49.
- Jagt, J.W.M. & Jagt-Yazykova, E.A.**, 2018. Stratigraphical ranges of tegulated inoceramid bivalves in the type area of the Maastrichtian Stage (Belgium, the Netherlands). *Cretaceous Research* **87**: 385–394.
- Jagt, J.W.M., Kennedy, W.J., & Machalski, M.**, 1999. Giant scaphitid ammonites from the Maastrichtian of Europe. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* **69**: 133–154.
- Jagt, J.W.M. & Kennedy, W.J.**, 1994. *Jeletzkytes dorfi* Landman & Waage 1993, a North American ammonoid marker from the lower Upper Maastrichtian of Belgium, and the numerical age of the Lower/Upper Maastrichtian boundary. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* **4**: 239–245.
- Janiszewska, K., Mazur, M., Machalski, M., & Stolarski, J.**, 2018. From pristine aragonite to blocky calcite: Exceptional preservation and diagenesis of cephalopod nacre in porous Cretaceous limestones. *PLoS ONE* **13**(12): e0208598.
- Jurkowska, A. & Świerczewska-Gładysz, E.**, 2022. Opoka – A mysterious carbonate-siliceous rock: an overview of general concepts. *Geology, Geophysics & Environment* **48**: 257–278.
- Kennedy, W.J.**, 1984a. Systematic palaeontology and stratigraphic distribution of the ammonite faunas of the French Coniacian. *Special Papers in Palaeontology* **31**: 1–159.

- Kennedy, W.J.**, 1984b. Ammonite faunas and the “standard zones” of the Cenomanian to Maastrichtian Stages in their type areas, with some proposals for the definition of the stage boundaries by ammonites. *Bulletin of the Geological Society of Denmark* **33**: 147–161.
- Kennedy, W.J.**, 1986. The ammonite fauna of the Calcaire à *Baculites* (Upper Maastrichtian) of the Cotentin Peninsula (Manche, France). *Palaeontology* **29**: 25–83.
- Kennedy, W.J.**, 1989. Thoughts on the evolution and extinction of Cretaceous ammonites. *Proceedings of the Geologists' Association* **100**: 251–279.
- Kennedy, W.J.**, 1993. Ammonite faunas of the European Maastrichtian; diversity and extinction. In: House, M.R. (ed.), *The Ammonoidea: Environment, Ecology, and Evolutionary Change*. Systematics Association Special Volume **47**: 285–326.
- Kennedy, W.J., Bilotte, M., Lepicard, B., & Segura, F.**, 1986. Upper Campanian and Maastrichtian ammonites from the Petites-Pyrénées, southern France. *Eclogae Geologicae Helveticae* **79**: 1001–1037.
- Kennedy, W.J. & Cobban, W.A.**, 1993. Ammonites from the Saratoga Chalk (Upper Cretaceous), Arkansas. *Journal of Paleontology* **67**: 404–434.
- Kennedy, W. J. & Summesberger, H.**, 1986. Lower Maastrichtian ammonites from Neuberg, Steiermark, Austria. *Beiträge zur Paläontologie von Österreich* **12**: 181–242.
- Kennedy, W. J. & Summesberger, H.**, 1987. Lower Maastrichtian ammonites from Nagoryany (Ukrainian SSR). *Beiträge zur Paläontologie von Österreich* **13**: 25–78.
- Klug, C., Zatoń, N.M., Parent, H., Hostettler, B. & Tajika, A.**, 2015. Mature modifications and sexual dimorphism. In: Kug, C., Korn, D., De Baets, K., Kruta, I. and Mapes, R. H. (eds). *Ammonoid Paleobiology: From Anatomy to Ecology*. *Topics in Geobiology*, **43**. Springer: 253–320. Springer.
- Kner, R.**, 1848. Versteinerungen des Kreidemergels von Lemberg und seiner Umgebung. *Haidingers naturwissenschaftliche Abhandlungen*, Bd II. Wien: 1–42. Wien.
- Kner, R.**, 1852. Neue Beiträge zur Kenntniss der Kreideversteinerungen von Ost-Galizien. *Denkschriften der Kaiserlichen Akademie der Wissenschaften* **3**: 293–334.
- Kotsiubynskiy, S.P.**, 1958. Inotseramy kreidovykh vidkladiv Volyno-Podilskoi plyty. *Akademia Nauk Ukrainkoi SSR, Kyiv*, 1–49. (In Ukrainian)
- Kotsiubynskiy, S.P.**, 1968. Inoceramidae. In: Pasternak, S.I., Havrylyshyn, V.I., Hynda, V.A., Kotsiubynskiy, S.P. & Senkovskiy, J.M. (eds.) *Stratyhrافیa i fauna kreidovykh vidkladiv zakhodu Ukrainy*. *Naukova Dumka*, 115–148. (In Ukrainian)
- Kronenthal**, 1843. Kamieniomy w Nagórzanach pod względem geologicznym. *Gazeta Lwowska* **48**: 317–318.
- Landman, N.H., Cobban, W. A. & Larson, N. L.**, 2012. Mode of life and habitat of scaphitid ammonites. *Geobios* **45**: 87–98.
- Landman, N. H., Kennedy, W.J & Larson, N. L.**, 2015. A new species of scaphitid ammonite from the Lower Maastrichtian of the Western Interior of North America, with close affinities to *Hoploscaphites constrictus* Sowerby, 1817 [sic]. *American Museum Novitates* **3833**: 1–40.
- Landman, N.H., Machalski, M., & Whalen, C.D.**, 2021. The concept of ‘heteromorph ammonoids’. *Lethaia* **54**: 595–602.
- Landman, N.H., Plint, A.G. & Walaszczyk, I.**, 2017. Scaphitid ammonites from the Upper Cretaceous (Coniacian–Santonian) Western Canada Foreland Basin. *Bulletin of the American Museum of Natural History* **414**: 105–172.
- Landman, N.H., Kennedy, W.J., Cobban, W.A. & Larson, N.L.**, 2010. Scaphites of the ‘Nodosus Group’ from the Upper Cretaceous (Campanian) of the Western Interior of North America. *Bulletin of the American Museum of Natural History* **342**: 1–242.
- Landman, N.H., Kennedy, W. J., Larson, N. L., Grier, J. C., Grier, J. W. & Linn, T.**, 2019. Description of two species of *Hoploscaphites* (Ammonoidea: Ancyloceratina) from the Upper Cretaceous (Lower Maastrichtian) of the U. S. Western Interior. *Bulletin of the American Museum of Natural History* **427**: 1–72.
- Lomnicki M.**, 1897. Atlas geologiczny Galicji. Tekst do zeszytu dziesiątego, cz. I. Kraków: 1–208. Wydawnictwo Komisji Fizyograficznej Akademii Umiejętności, Kraków.
- Łopuski, C.**, 1911. Przyczynki do znajomości fauny kredowej guberni Lubelskiej. *Sprawozdania Towarzystwa Naukowego Warszawskiego* **4**: 104–140.
- Machalski, M.**, 1996. Scaphitid ammonite correlation of the Late Maastrichtian deposits in Poland and Denmark. *Acta Palaeontologica Polonica* **41**: 369–383.
- Machalski, M.**, 2005. Late Maastrichtian and earliest Danian scaphitid ammonites in central Europe: taxonomy, evolution, and extinction. *Acta Palaeontologica Polonica* **50**: 653–696.
- Machalski, M.**, 2012a. Stratigraphically important ammonites from the Campanian–Maastrichtian boundary interval of the Middle Vistula River section, central Poland. *Acta Geologica Polonica* **62**: 91–116.
- Machalski, M.**, 2012b. A new ammonite zonation for the Maastrichtian Stage in Poland. In: J.W.M. Jagt & E.A. Jagt-Yazykova (eds.), *The Maastrichtian Stage; the Current Concept*. *Natuurhistorisch Museum Maastricht (The Netherlands)*: 40–44.
- Machalski, M.**, 2019. Scaphitid ammonites in the Maastrichtian of Europe: evolution and stratigraphical implications. In: Bogdanova, T. H., *et al.* (eds.) *Morfologischeskaya evolucija i stratigraficheskoje problemy*. Materials to the LXV Session of the Palaeontological Society, RAN (1–5 April 2019 r., Sankt-Petersburg: 99–101, Kartfabrika VSEGEI. (in Russian)
- Machalski, M.**, 2021. Correlation of shell and apertural growth provides insights into the palaeobiology of a scaphitid ammonite. *Palaeontology* **64**: 225–247.
- Machalski, M., & Heinberg, C.**, 2005. Evidence for ammonite survival into the Danian (Paleogene) from the Cerithium Limestone at Stevns Klint, Denmark. *Bulletin of the Geological Society of Denmark* **52**: 97–111.
- Machalski, M., Jagt, J.W.M., Landman, N.H., & Motchurova-Dekova, N.**, 2007. The highest records of North American scaphitid ammonites in the European Maastrichtian (Upper Cretaceous) and their stratigraphic implications. *Acta Geologica Polonica* **57**: 169–185.
- Machalski, M., & Malchuk, O.**, 2016. Klasyficyjne stanoviska paleontologiczne górnej kredy zachodniej Ukrainy: historia badań oraz biostratygrafia. *Przegląd Geologiczny* **64**: 570–576. (in Polish with English abstract).
- Machalski, M. & Malchuk, O.**, 2019. Relative bathymetric position of opoka and chalk in the Late Cretaceous European Basin. *Cretaceous Research* **102**: 30–36.
- Machalski, M. & Odin, G.S.**, 2001. Scaphitid ammonites of the Campanian–Maastrichtian at Tercis-les-Bains (Landes, France). In: Odin, G.S. (ed.): *The Campanian–Maastrichtian boundary*. Elsevier Science B.V: 515–527. Elsevier.
- Makowski, H.**, 1962. Problem of sexual dimorphism in ammonites. *Palaeontologia Polonica* **12**: 1–92.
- Malchuk, O., Machalski, M., Waksmundzki, B. & Duda, M.**, 2017. Shell ornament, systematic position and hatching size of *Epicymatoceras vaelsense* (Nautilida): new insights based on specimens in mould preservation from the Upper Cretaceous of Poland. *Cretaceous Research* **80**: 1–12.
- Mikhailov, N.P.**, 1951. Verkhnemelovye ammonity ijuga evropejskoj tschasti SSSR i ikh znachenye dlja zonalnoy stratigrafii. *Trudy Instituta Geologicheskikh Nauk, Akademia Nauk SSSR* **129** (geology series 50): 1–143. (in Russian).
- Niebuhr, B.**, 2003. Late Campanian and Early Maastrichtian ammonites from white chalk of Krons Moor (northern Germany) – taxonomy and stratigraphy. *Acta Geologica Polonica* **53**: 257–281.
- Niebuhr, B., Hampton, M.J., Gallagher, L.T. & Remin, Z.**, 2011. Integrated stratigraphy of the Krons Moor section (northern Germany), a reference point for the base of the Maastrichtian in the Boreal Realm. *Acta Geologica Polonica* **61**: 193–214.
- Nowak, J.**, 1911. Untersuchungen über die Cephalopoden der oberen Kreide in Polen. II Teil. Die Skaphiten. *Bulletin international de l'Académie des Sciences de Cracovie, Série B* **1911**: 547–589.
- Odin, G.S., Courville, Ph., Machalski, M. & Cobban, W.A.**, 2001. The Campanian–Maastrichtian ammonite fauna from Tercis (Landes, France); a synthetic view. In: Odin, G.S. (ed.): *The Campanian–Maastrichtian Boundary*. Elsevier Science B.V: 579–595. Elsevier.

- Odin, G.S. & Lamaurelle, M.A.**, 2001. The global Campanian–Maastrichtian stage boundary at Tercis les Bains, Landes, SW France. *Episodes* **4**: 229–238.
- Pasternak, S.I., Havrylyshyn, V.I., Hynda, V.A., Kotsiubynskyi, S.P. & Senkovskiy, Y.M.**, 1968. Stratyhrafia i fauna kreidovykh vidkladiv zakhodu Ukrainy. *Naukova Dumka* (Kyiv): 472 pp. (In Ukrainian)
- Pasternak, S.I., Senkovskiy, Y.M. & Havrylyshyn, V.I.**, 1987. Volyno-Podillya u kreidovomu periodi. *Naukova Dumka* (Kyiv): 258 pp. (In Ukrainian)
- Remin, Z.**, 2012. The *Belemnella* stratigraphy of the Campanian–Maastrichtian boundary; a new methodological and taxonomic approach. *Acta Geologica Polonica* **62**: 495–533.
- Riccardi, A.C.**, 1983. Scaphitids from the Upper Campanian–Lower Maastrichtian Bearpaw Formation of the Western Interior of Canada. *Geological Survey of Canada Bulletin* **354**: 1–51.
- Schmid, F.**, 1955. Biostratigraphie der Grenzsichten Maastricht/Campan in Lüneburg und in der Bohrung Brunhilde. 1. Teil: Megafauna und Schichtenfolge. *Geologisches Jahrbuch* **70**: 339–356.
- Schulz, M.-G.**, 1979. Morphometrisch-variationsstatistische Untersuchungen zur Phylogenie der Belemniten-Gattung *Belemnella* im Untermaastricht NW-Europas. *Geologisches Jahrbuch A* **47**: 3–157.
- Schulz, M.-G., Ernst, G., Ernst, H. & Schmid, F.**, 1984. Coniacian to Maastrichtian stage boundaries in the standard section for the Upper Cretaceous white chalk of NW Germany (Lägerdorf-Kronsmoor-Hemmoor): Definitions and proposals. *Bulletin of the Geological Society of Denmark* **33**: 203–215.
- Self'ser, V.B. & Ivanov, A.V.**, 2010. Atlas pozdnemelovykh ammonitov Saratovskogo Povolsha. Monograf [sic]. University Press (Moscow), 152 pp. [in Russian]
- Self'ser, V.B. & Machalski, M.**, 2019. Sukcesya skaphitidnykh ammonitov v mastrichtskikh othloshenyah Saratovskogo Povolsha. In T. H. Bogdanova, *et al.* (eds.) *Morfologicheskaya evolyuciya i stratigraficheskoye problemy. Materials to the LXV Session of the Palaeontological Society, RAN* (1–5 April 2019 r., Sankt-Petersburg: 138–140, Kartfabrika VSEGEI. (in Russian)
- Siemiradzki, J.**, 1905. O utworach górnokreidowych w Polsce (Note sur les dépôts crétacés supérieurs en Pologne). *Kosmos* **30**: 471–492.
- Sowerby, J.**, 1817. *The Mineral Conchology of Great Britain*, vol. 2. London: The author. [7 vols.]
- Stephenson, L.W.**, 1941. The Larger Invertebrate Fauna of the Navarro Group of Texas. *The University of Texas Publication* **4101**: 1–641.
- Syniewska, J.**, 1923. Kilka nowych skamieniałości z kredy okolic Lwowa. *Kosmos* **48**: 276–302.
- Walaszczyk, I.**, 2004. Inoceramids and inoceramid biostratigraphy of the Upper Campanian to basal Maastrichtian of the Middle Vistula River section, central Poland. *Acta Geologica Polonica* **54**: 95–168.
- Walaszczyk, I., Jagt, J.W.M. & Keutgen, N.**, 2010. The youngest Maastrichtian “true” inoceramids from the Vijlen Member (Gulpen Formation) in northeast Belgium and the Aachen area (Germany). *Netherlands Journal of Geosciences* **89**: 147–167.
- Walaszczyk, I. & Kennedy, W.J.**, 2011. The inoceramid fauna and inoceramid-based correlations of the Calcaire à *Baculites* (Maastrichtian) of the Cotentin Peninsula, Manche, France. *Freiberger Forschungshefte C540*: 103–118.
- Walaszczyk, I., Cobban, W.A. & Odin, G.S.**, 2002a. The inoceramid succession across the Campanian–Maastrichtian boundary. *Bulletin of the Geological Society of Denmark* **49**: 53–60.
- Walaszczyk, I., Odin, G.S. & Dhondt, A.V.**, 2002b. Inoceramids from the Upper Campanian and Lower Maastrichtian of the Tercis section (SW France), the Global Stratotype Section and Point for the Campanian–Maastrichtian boundary; taxonomy, biostratigraphy and correlation potential. *Acta Geologica Polonica* **52**: 269–305.
- Walaszczyk, I., Dubicka, Z., Olszewska-Nejbert, D. & Remin, Z.**, 2016. Integrated biostratigraphy of the Santonian through Maastrichtian (Upper Cretaceous) of extra-Carpathian Poland. *Acta Geologica Polonica* **66**: 313–350.
- Wiedmann, J.**, 1965. Origin, limits, and systematic position of *Scaphites*. *Palaeontology* **8**: 397–453.
- Wilmsen, M., Engelke, J., Linnert, Ch., Mutterlose, J. & Niebuhr, B.** 2018. A Boreal reference section revisited (Kronsmoor, northern Germany): high-resolution stratigraphic calibration of the Campanian–Maastrichtian boundary interval. *Newsletter on Stratigraphy*, **52**: 155–172.