

Late Maastrichtian and earliest Danian scaphitid ammonites from central Europe: Taxonomy, evolution, and extinction

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Late Maastrichtian and earliest Danian scaphitid ammonites from key sections in the Maastricht area in the Netherlands and Belgium, Hemmoor in Germany, Stevns Klint (Sjælland) and Jylland in Denmark, the Lublin Upland in Poland and Lviv in the Ukraine, are studied. In total, thirteen scaphitid taxa are recognised: *Hoploscaphites constrictus livivensis* subsp. nov., *H. c. crassus*, *H. c. johnjagti* subsp. nov., *H. tenuistriatus*, *H. pungens*, *H. schmidi*, *H. sp. ex gr. pungens-schmidi*, *H. felderi*, *H. sp. ex gr. waagei-angmartussutensis*, *Acanthoscaphites (Euroscaphites) varians varians*, *A. (E.) varians blaszkiewiczzi*, *A. (E.?) verneuilianus* and *A. (E.?) sp. aff. verneuilianus*. Sexual dimorphism is demonstrated for several species. Additionally, developmental polymorphism of males is proposed to explain a size-dependent variation of ornament in microconchs of *H. c. crassus*. The extinction pattern of European scaphitids is difficult to assess for methodological reasons. The available data indicate, however, that the *Hoploscaphites constrictus* lineage survived unaffected until the very end of the Cretaceous and even crossed the Cretaceous–Paleogene (K–Pg) boundary. The latest Maastrichtian populations of this lineage, assigned to *H. c. johnjagti* subsp. nov., are dominated by individuals with pronounced ribbing and tuberculation of the body chamber. This may reflect increased predation pressure, indirectly related to the late Maastrichtian regression. The successive members of the *Hoploscaphites constrictus* lineage, i.e., *Hoploscaphites constrictus livivensis* subsp. nov., *H. c. crassus*, and *H. c. johnjagti* subsp. nov. are useful for subdivision of upper Maastrichtian deposits.

Key words: Ammonoidea, Scaphitidae, dimorphism, polymorphism, evolution, extinction, Maastrichtian, Danian, central Europe.

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Introduction

Members of the family Scaphitidae Gill, 1871 form a distinctive group of heteromorph ammonites, which first appeared in the Albian (Wiedmann 1965; Wiedmann and Marcinowski 1985; Cooper 1994; Monks 2000). These ammonites were widely distributed in late Maastrichtian epicontinental seas of the Boreal Realm across Europe (e.g., Błaszczewicz 1980; Kennedy 1987; Birkelund 1993; Jagt 2002; Machalski 2005) and one lineage even survived into the earliest Danian (Jagt et al. 2003; Machalski and Heinberg in press).

The main goal of the present paper is to study the taxonomy of late Maastrichtian and earliest Danian scaphitid ammonites from central Europe. Results of this study also have implications for the following topics of ammonite palaeontology: sexual dimorphism (Makowski 1962; Cobban 1969; Matyja 1986), evolutionary relationships (Cooper 1994; Monks 2000), extinction patterns (Wiedmann 1988; Kennedy 1989; Ward 1990), the relationship between shell morphology and environment (Landman and Waage 1993b), the influence of predators on evolution (Ward 1996; Radwański 1996), possible trans-Atlantic links (Jagt and Kennedy 1994) and biostratigraphic potential (Keutgen 1996; Machalski 2005).

The present paper is based mainly on scaphitid material from several upper Maastrichtian and Danian key sections in

central Europe, namely the Maastricht area in the southeast Netherlands (plus adjoining northeast Belgium), Hemmoor in northern Germany, Stevns Klint (Sjælland) and northern Jylland in Denmark, the Lublin Upland in eastern Poland and Lviv in western Ukraine (Fig. 1A, B; see Fig. 1C for palaeogeography of the study area). Material from Poland was collected mostly by the author; some specimens were kindly donated by or received on loan from other people, both private collectors and professionals. Collections from the Netherlands, Belgium, Germany, Denmark and the Ukraine were assembled by scientists from these countries; most of the latter material has been described and/or referred to by previous workers.

Institutional abbreviations.—BMNH, Natural History Museum, London (formerly British Museum, Natural History); EM, École des Mines collections, Université Claud Bernard, Lyon; GPIUH, Geologisch-paläontologisches Institut der Universität Hamburg; DPM NANU, State Museum of Natural History, National Academy of Sciences of Ukraine, Lviv (formerly Muzeum Dzieduszyckich); MGUH, Geological Museum of Copenhagen University, Copenhagen; NHMM, Naturhistorisch Museum Maastricht (MK = Felder collection, JJ = Jagt collection); MKD/MP, Natural History Museum, Department of the Muzeum Nadwiślańskie, Kazimierz

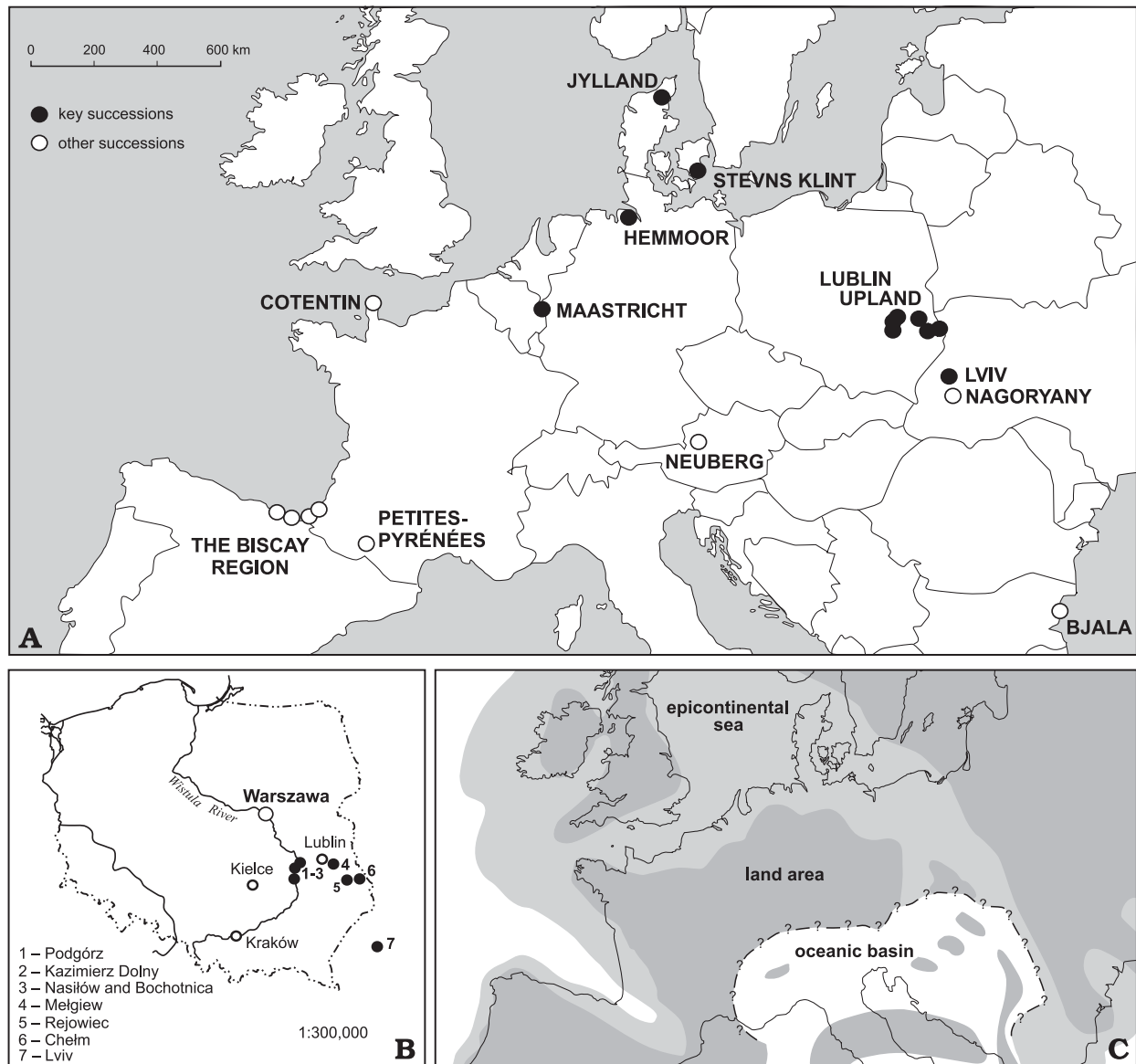


Fig. 1. Location of Maastrichtian and Danian successions which have yielded scaphitids. **A.** Europe. **B.** Poland. **C.** Palaeogeographic map of Europe during the late Maastrichtian (based on Bilotte et al. 2001: fig. 6, modified).

Dolny, Poland; MNB, Museum für Naturkunde, Berlin; MWGUW, Museum of the Geology Department of Warsaw University; NLfB, Niedersächsisches Landesamt für Bodenforschung, Hannover; RGM, Nationaal Natuurhistorisch Museum (Naturalis), Leiden (formerly Rijksmuseum van Geologie en Mineralogie); ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw.

Definition and subdivisions of the Maastrichtian

The traditional subdivision of the Boreal Maastrichtian in central Europe is used in the present paper (Fig. 2). This scheme is based mainly on belemnites and microbrachio-

pods, with the notable recent addition of inoceramid biozones for the lower Maastrichtian by Ireneusz Walaszczyk (Fig. 2; references in caption). In the traditional belemnite zonal scheme, the base of the Boreal Maastrichtian is defined by the first appearance of *Belemnella lanceolata* and the lower boundary of the upper Maastrichtian equates with the first appearance of *Belemnitella junior* (e.g., Jeletzky 1951; Birkelund 1957; Schulz 1979; Christensen 1996). It should be noted, however, that Keutgen (1996) questioned the latter definition, on the basis of his record of *Bt. junior* in the upper lower Maastrichtian *Belemnella sumensis*, *Bn. cimbrica*, and *Bn. fastigata* zones in the Maastricht-Aachen-Liège area (Keutgen 1996; Norbert Keutgen and John W.M. Jagt, unpublished data). Christensen et al. (2004) confirmed Keutgen's (1996) identification of *Bt. junior* in the lower Maastrichtian (*Bn. sumensis* Zone). Thus, the lower/upper

| Chrono- stratigraphy | 1) Faunal zones, NW Germany | 2) Belemnite zones, NW Germany | 3) Conventional belemnite zones | Brachiopod zones, NW Europe | | 6) Inoceramid zones | |
|-------------------------|--------------------------------------|-----------------------------------------|-------------------------------------------------|--------------------------------------------------------|------------------------|---------------------------|---------------------------------------------|
| | | | | 4) | 5) | | |
| MAASTRICHTIAN | U | | <i>Belemnella kazimiroviensis</i> | <i>A. stevensis</i> – <i>M. chitoniformis</i> | 10 | | |
| | | | | | | | <i>Ty. baltica</i> – <i>Ox. danica</i> |
| | L | <i>Belemnitella junior</i> | <i>Belemnitella junior</i> | <i>Me. semiglobularis</i> – <i>R. humboldtii</i> | 8 | | |
| | | | | | | | <i>Ox. danica</i> – <i>T. argentea</i> |
| | | | | | | | <i>T. argentea</i> – <i>Bt. junior</i> |
| | U | <i>Belemnella</i> | <i>fastigata</i> | <i>Ru. tenuicostata</i> – <i>Me. semiglobularis</i> | 7 | | |
| | | | | | | | <i>Sp. tegulatus</i> – <i>Bt. junior</i> |
| | L | <i>Belemnella</i> | <i>cimbrica</i> | <i>Tri. pulchellus</i> – <i>Ru. tenuicostata</i> | 6 | | |
| | | | | | | | <i>Bn. fastigata</i> |
| | L | <i>Belemnella</i> | <i>sumensis</i> | <i>Tri. pulchellus</i> – <i>Tri. pulchellus</i> | 5 | | |
| <i>Bn. cimbrica</i> | | | | | | | |
| L | <i>Belemnella</i> | <i>obtusa</i> | <i>Te. subtilis</i> – <i>Tri. pulchellus</i> | 4 | | | |
| | | | | | <i>Bn. sumensis</i> | | |
| L | <i>Belemnella</i> | <i>pseudobtusa</i> | <i>Ru. spinosa</i> – <i>Te. subtilis</i> | 3 | | | |
| | | | | | <i>Bn. obtusa</i> | | |
| L | <i>Belemnella</i> | <i>lanceolata</i> | <i>Ru. acutirostris</i> – <i>Ru. spinosa</i> | 2 | | | |
| | | | | | <i>Bn. pseudobtusa</i> | | |
| | | | <i>Gi. jasmundi</i> – <i>Ru. acutirostris</i> | 1 | | | |

Fig. 2. Stratigraphical correlation diagram of the European Maastrichtian to show macrofaunal (including belemnite) zones in northwest Germany, conventional belemnite zonation, brachiopod zones for NW Europe and inoceramid zones for the lower Maastrichtian (columns 1–5 adopted from Christensen 1996: fig. 3). Sources: column 1: Schulz and Schmid (1983); column 2: Schulz (1979), Schulz and Schmid (1983); column 3: Jeletzky (1951), Birkelund (1957); column 4: Surlyk (1984); column 5 (Surlyk 1970); column 6 (Ireneusz Walaszczyk, personal communication 2005). T, position of GSSP for the base of the Maastrichtian Stage as accepted in 2001; Z, proposed position of the lower/upper Maastrichtian boundary, based on the first appearance of *Menuites fresvillensis* (see text). Abbreviations: L, lower; U, upper; A., *Argyrotheca*; Bn., *Belemnella*; Bt., *Belemnitella*; Gi., *Gisilinia*; M., *Magas*; Me., *Meonia*; Ox., *Oxytoma*; R., *Ruegenella*; Ru., *Rugia*; Sp., *Spyridoceras*; T., *Tenuipteria*; Te., *Terebratulina*; Tri., *Trigonosemus*; Ty., *Tylocidaris*.

Maastrichtian boundary should be redefined in terms of belemnites.

The Global Stratotype Section and Point (GSSP) for the base of the Maastrichtian Stage was defined at the level 115.2 m on platform IV in the quarry at Tercis near Dax, southwest France (Odin 2001; Odin and Lamaurelle 2001). The correlation of the GSSP with the Boreal base of the Maastrichtian as defined on belemnites in central Europe is still not clear. Recent correlations, based on inoceramids, suggest that the base of the Maastrichtian as defined at Tercis lies much higher than that of the traditional Boreal subdivision of the stage (Walaszczyk et al. 2002; Walaszczyk 2004 and unpublished data; Fig. 2). This is confirmed by the author's re-interpretation of the record of "*Pachydiscus perfidus/neubergicus*" from level 98.2 m at Tercis (internal mould illustrated by Courville and Odin 2001: pl. 6: 45 plus unpublished external cast) as *P. neubergicus*. This species has never been demonstrated to occur below the entry level of *Belemnella lanceolata* anywhere.

A proposal to define the lower/upper Maastrichtian boundary by the first appearance of the pachydiscid ammonite *Menuites fresvillensis* at Zumaya (Bay of Biscay region, Spain) has been put forward (Odin 1996; Fatmi and Kennedy 1999; Klinger et al. 2001). If accepted, this would result in placement of this boundary at a level distinctly lower than that in the Boreal scheme (Fig. 2), which follows from the fact that the entry level of *M. fresvillensis* is significantly lower than the level of last occurrence of non-tegulated ("true") inoceramids in the Bay of Biscay sections (Ward and Kennedy 1993; MacLeod 1994a). The latter level is approximately coeval to the extinction datum of non-tegulated inoceramids on a global scale (MacLeod and Ward 1990; MacLeod 1994a, b). The extinction level of non-tegulated inoceramids lies very close to the traditional Boreal base of the upper Maastrichtian as defined by belemnites (Ireneusz Walaszczyk, personal communication 2005). In view of this, the presence versus absence of non-tegulated inoceramids is used herein as an important criterion for the recognition of

the lower/upper Maastrichtian boundary, especially in view of recent doubts over the traditional belemnite definition of this boundary (see above).

The lower/upper Maastrichtian boundary was dated at “slightly younger than 69.42 ± 0.37 myr” by Jagt and Kennedy (1994: 240), based on the assumption that the Vijlen Member (Interval 6) at the CPL SA-Haccourt (Hallembaye) quarry (Liège, NE Belgium), which had yielded the North American scaphitid time-marker species *Jeletzkytes dorfi* Landman and Waage, 1993a, represented the lowermost portion of the upper Maastrichtian. A slight re-positioning of this part of the Vijlen Member to the uppermost lower Maastrichtian (Keutgen 1996), apparently does not have a significant effect on the original figure by Jagt and Kennedy (1994), taking into account a possible error interval. The maximum age for Danian scaphitid survivors from the *Cerithium* Limestone at Stevns Klint, Denmark, has recently been estimated to be around 0.2 Ma following the K–Pg boundary event (Machalski and Heinberg in press). Assuming the Cretaceous–Paleogene boundary at 65.4 ± 0.1 Ma (Jagt and Kennedy 1994), the present study covers more than 4 Ma of the final stages in scaphitid evolution.

Provenance of material and previous work

The bulk of the scaphitid material studied comes from key sections of the upper Maastrichtian and lowermost Danian in the southeast Netherlands and northeast Belgium (Maastricht area), northern Germany (Hemmoor), Denmark (Stevns Klint at Sjælland, plus northern Jylland), eastern Poland (Lublin Upland) and western Ukraine (Lviv) (Figs. 1A, B, 3). Sections in the Netherlands, Germany and Denmark are widely known and thus are commented on only briefly. In contrast, Polish and Ukrainian sections are usually poorly known outside of these countries and for that reason need to be described in more detail.

The Netherlands and Belgium.—The upper Maastrichtian to lowermost Danian strata in the type area of the Maastrichtian Stage in the Maastricht area (southeast Netherlands and northeast Belgium; Fig. 1A), are developed in a “tuffaceous chalk” facies. The geological and biostratigraphical framework of this succession was outlined by Kennedy (1987, 1993) and Jagt (1999), and the ammonites were described by Kennedy (1987), van der Tuuk (1987), Kennedy and Jagt (1998) and summarised by Jagt (2002). Jagt et al. (1996) reviewed the bio- and lithostratigraphy of the region from a historical point of view. Scaphitids studied come from indurated horizons within the Nekum and Meerssen members of the Maastricht Formation (*Belemnites junior* and *Belemnites kazimiroviensis* zones) as well as from the Kunrade Limestone facies (Felder and Bless 1989), the latter representing exclusively the *Bt. junior* Zone (Jagt 2002).

Scaphitid material from subunit IVf-7 at the very top of the Meerssen Member is also included in the present work, pending full description elsewhere. This subunit, traditionally regarded to be uppermost Maastrichtian, has recently been reassigned to the lowermost Danian, based on microfossil and strontium isotope evidence (Smit and Brinkhuis 1996). According to Jagt et al. (2003), the scaphitid and baculitid ammonites preserved in subunit IVf-7 are early Danian survivors.

Northern Germany.—Upper, but not uppermost, Maastrichtian at the now flooded Hemmoor chalk pit, Lower Saxony (Fig. 1A) is developed as white chalk with flint layers. The Hemmoor section ranges from the *Bn. sumensis* to the *Bt. junior* zones; it was described in detail by Schmid (1982), Schulz and Schmid (1983), Schönfeld et al. (1996) and Christensen et al. (2004), while ammonites were recorded by Schmid (1965), Birkelund (1982) and discussed by Kennedy (1993). Not all individuals available are well localised within the succession; however, most of the specimens with no precise provenance data are at least roughly localised with respect to marl bed M 900 *sensu* Schulz and Schmid (1983), which marks the lower/upper Maastrichtian boundary at Hemmoor. In earlier papers, this bed was referred to as “Tonband”, “T 100” or “M 100”.

Denmark.—The Maastrichtian scaphitid-bearing deposits in Denmark occur in two areas, northern Jylland and eastern Sjælland (Fig. 1A), and are developed in white chalk facies with flints (Surlyk and Birkelund 1977; Surlyk 1984, 1997). The Danish white chalk ammonites were described by Birkelund (1979, 1993) and summarised by Kennedy (1993); the stratigraphic significance of the *Hoploscaphites* succession from Denmark was discussed by Machalski (1996, 2005).

The succession at Jylland starts in the lower Maastrichtian and in some places spans the Cretaceous–Paleogene boundary (Håkansson and Hansen 1979). Many scaphitids from outcrops in Jylland that span the lower/upper Maastrichtian boundary lack precise provenance data and thus may have come from either side of this boundary. In contrast, scaphitid records from the famous K–Pg cliff section at Stevns Klint, Sjælland, 60 km south of Copenhagen (Fig. 1A), are usually better constrained in terms of local litho- and biostratigraphy (see Surlyk 1997; Hart et al. 2004; Hart et al. 2005 for detailed descriptions of the Stevns Klint succession). A microbrachiopod-based correlation of the Danish localities is given by Surlyk (1984: fig. 3).

The highest Maastrichtian ammonites at Stevns Klint come from indurated portions of the so-called Grey Chalk (Gråkridd) at the top of the Maastrichtian succession (Birkelund 1993; Surlyk 1997). The Maastrichtian part of the section represents the *Bn. kazimiroviensis* Zone (Birkelund 1957). There is no detectable gap at the top of Maastrichtian chalk at Stevns Klint (Hultberg and Malmgren 1987; Schmitz et al. 1992). Rare moulds of scaphitid and baculitid ammonites occur also in the *Cerithium* Limestone, which is the lowest Danian carbonate unit at Stevns Klint. According to Machal-

ski and Heinberg (in press) these are the remains of Danian ammonite survivors.

The scaphitid-bearing Maastrichtian part of the succession exposed at Limhamn, southern Sweden, was described by Holland and Gabrielson (1979).

Poland.—The bulk of the scaphitid material available comes from the Lublin Upland (Figs. 1A, B, 3), where the upper Maastrichtian succession is composed of opoka (= siliceous limestone), marls and white chalk (Pożaryski 1956). This succession is traditionally subdivided into two belemnite zones; those of *Bt. junior* and *Bn. kazimiroviensis* (Cieśliński and Wyrwicka 1970; Abdel-Gawad 1986). The late Maastrichtian ammonites from the Lublin Upland were described by Błaszkiwicz (1980), Machalski (1996), Machalski and Jagt (1998), Jagt et al. (1999) and Machalski (2005); the reader is referred to the last-named paper for a more complete overview of earlier work on regional biostratigraphy and ammonite faunas. The scaphitid-bearing exposures of the Lublin Upland are grouped into three areas:

Western part of the Lublin Upland (Middle Vistula River section).—The upper Maastrichtian portion of the classic mid-Cretaceous to lowermost Paleocene succession exposed along the Middle Vistula River (Walaszczyk 2004) comprises a unit of unnamed marls overlain by the so-called Kazimierz Opoka (Błaszkiwicz 1980; Machalski 1996). Scaphitids studied come from the top of the marl unit as exposed in the river escarpment at Podgórz (locality 1 in Figs. 1B, 3), from the lower part of the so-called Kazimierz Opoka as exposed at the town quarry south of Kazimierz Dolny (locality 2 in Figs. 1B, 3) and from the upper part of the Kazimierz Opoka as exposed at the Bochothnica and Nasiłów quarries (localities 3 in Figs. 1B, 3). No material is available from the middle and lower portions of the marl unit, which are covered by deposits of the Vistula and Chodel rivers.

The Nasiłów quarry exposes a dozen or so metres of opoka (Abdel-Gawad 1986: fig. 6; Machalski 2005: fig. 3). The town quarry south of Kazimierz Dolny exposes c. 30 metres of opoka with hard limestone and marly intercalations (Pożaryski 1956; Abdel-Gawad 1986: fig. 5). Numerous specimens from these quarries were collected from scree slopes and thus are not precisely localised. However, two scaphitid collections from the Kazimierz Opoka have more precise provenance data. One of them comes from a hard limestone layer, maximum 1 metre thick, at the top of the Kazimierz Opoka at Nasiłów (“hardground” of earlier authors, see Machalski 1998, 2005); the other lot is from a horizon of marly opoka, c. 2 metres thick, at the base of the upper third of the town quarry succession (“the lower marl bed” of Pożaryski 1956; base of unit C in Abdel-Gawad 1986: fig. 5).

The marls exposed at Podgórz are assigned to the *Bt. junior* Zone (Błaszkiwicz 1980). According to Abdel-Gawad (1986: 147), the Podgórz outcrop yielded the tegulated inoceramid *Spyridoceramus tegulatus*, which allows the section exposed there to be assigned to the (top of the) *Spyridoceramus tegulatus*–*Belemnitella junior* Zone of the Hem-

moor-based zonation of Schulz and Schmid (1983). Belemnite data, reported by Kongiel (1962), indicate that sections at Nasiłów, Bochothnica and the town quarry represent the *Bn. kazimiroviensis* Zone. The highest tegulated inoceramid zonal index, *Tenuipteria argentea*, occurs throughout the Kazimierz Opoka (Abdel-Gawad 1986).

Sections at Nasiłów and Bochothnica span the K–Pg boundary (Machalski and Walaszczyk 1987; Hansen et al. 1989; Radwański 1996; Machalski 1998), and show a rather large hiatus at the top of the Maastrichtian part of the Middle Vistula River succession, documented on scaphitid ammonite and dinoflagellate evidence (Machalski 1996, 2005).

Central part of the Lublin Upland (the Lublin area).—The upper upper Maastrichtian succession, usually rich in scaphitids, is accessible in several outcrops south and east of Lublin (Machalski 2005: fig. 1B). The uppermost metre of the Maastrichtian part of the K–Pg succession at Melgiew (locality 4 in Figs. 1B, 3) has yielded a distinctive, scaphitid-dominated ammonite assemblage, previously unknown from Poland (Machalski 2005). Scaphitid evidence suggests that the hiatus at the top of the Maastrichtian at Melgiew is of a smaller extent than that in the Middle Vistula River sections (Machalski 2005: fig. 15). Other scaphitid-bearing sections in the central part of the Lublin Upland, i.e., Klimusin, Prawiedniki and Mętów, which are all correlatable with the upper part of the Kazimierz Opoka as exposed at the Nasiłów and Bochothnica quarries, were described by Machalski (2005).

Eastern part of the Lublin Upland.—Two large quarries (adjacent to cement plants) expose upper Maastrichtian scaphitid-bearing successions near the towns of Chełm and Rejowiec (localities 5 and 6 in Figs. 1B, 3). Preliminary data on these sections were given by Wyrwicka (1970a, b), Alexandrowicz and Tchórzewska (1975), Alexandrowicz (1977), and Harasiemiuk (1984).

The white chalk succession at Chełm, c. 40 metres thick, is exposed along four exploitation levels, each exposing c. 10 metres of chalk, labelled here levels V to II, in ascending order (level I has now been entirely excavated). Most of the scaphitids studied come from levels III and IV. In addition to ammonites, the chalk has yielded irregular echinoids, brachiopods, cirripedes and rare belemnite guards, the latter including *Bt. junior* (identified by the late Walter K. Christensen). Bivalves are not uncommon, with *Spyridoceramus tegulatus* documented from levels III and IV (Abdel-Gawad 1986; Ireneusz Walaszczyk, personal communication 2005).

On the basis of foraminifera, a “mid-late Maastrichtian age” was suggested for the Chełm succession (Alexandrowicz 1977). A detailed description of the section exposed and of the biostratigraphic significance of selected micro- and macrofossil groups will be presented elsewhere. However, the presence of *Sp. tegulatus* as the sole inoceramid taxon, plus the presence of *Bt. junior*, suggest correlation with the lower upper Maastrichtian *Sp. tegulatus*–*Bt. junior* Zone of the Hemmoor subdivision (Fig. 3).

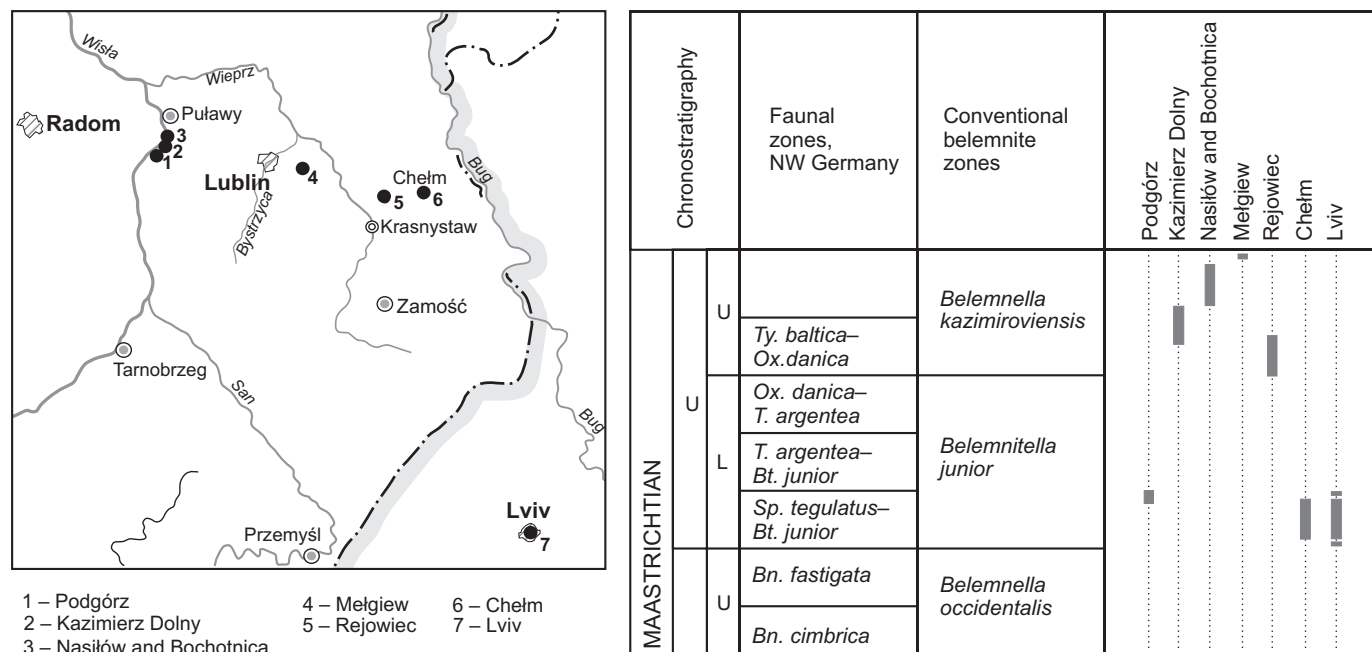


Fig. 3. Correlation of main scaphitid-bearing sections in eastern Poland and western Ukraine (Lviv area). Sources: Kongiel (1962), Błaszkiwicz (1980), Pasternak et al. (1987), Machalski (2005), and unpublished data (M. Machalski, W.K. Christensen, I. Walaszczyk). Abbreviations: L, lower; U, upper; *Bn.*, *Belemnella*; *Bt.*, *Belemnitella*; *Ox.*, *Oxytoma*; *Sp.*, *Spyridoceramus*; *T.*, *Tenuipteria*; *Ty.*, *Tylocidaris*.

The succession at Rejowiec, c. 26 metres thick, comprises opoka and marls, exposed along four exploitation levels, labelled IV to I, in ascending order. Three distinctive horizons of correlative value can be distinguished in this section. The first of these is a laminated marl bed, c. 20 cm thick, situated at the base of the section and probably related to a submarine dissolution event. The two remaining horizons are beds of soft, easily disintegrating marls, each up to 2.5 metres thick, well visible in the middle part of the section. Belemnites and burrows with pyrite-impregnated walls are common in the lower marl bed (“the belemnite bed”), whereas the upper one is replete with current-aligned baculitids (“the baculitid bed”). Most of the scaphitid material studied comes from a 5 m-thick interval of hard, yellow opoka sandwiched between the belemnite and baculitid beds. A detailed description of the Rejowiec section and discussion of its fauna will be given elsewhere.

Foraminifera diagnostic of the middle part of the upper Maastrichtian were reported to occur throughout the Rejowiec succession (Alexandrowicz and Tchórzewska 1975), which would suggest this to be coeval with the Chełm succession. However, the macrofauna indicates a distinctly higher, upper upper Maastrichtian position for the Rejowiec section (Fig. 3). This is evident from the presence of *Bn. kazimiroviensis* in the lower marl bed and of the tegulated inoceramid *Tenuipteria argentea* throughout the section.

Ukraine.—The upper Maastrichtian strata occurring in the environs of the town of Lviv (Lemberg, Lwów or Lvov in older literature), western Ukraine, are developed as marls of the so-called “Lvovskaya svita” (Gavrilishin et al. 1991).

These deposits contain numerous invertebrate fossils (Pasternak et al. 1987). The marls of the “Lvovskaya svita” were formerly referred to as the “Lviv opoka” or the “Lviv marls” (Kner 1848, 1852; Favre 1869; Nowak 1913, 1917; Mikhailov 1951 and references therein). The maximum thickness of the “Lvovskaya svita” is 80 metres, based on borehole data (Gavrilishin et al. 1991).

At present, there are no good exposures of this unit. However, it was accessible in several outcrops situated in and around the town of Lviv, during the nineteenth and early twentieth centuries (Rogala 1911; Syniewska 1923). In the old Polish literature, the most frequently quoted localities exposing the “Lvovskaya svita” at Lviv are Snopków brickyard, Cytadela, Podzamcze and the Dekabrystów, Pełczyńska and Jabłonowskich streets. Many scaphitids studied come from these places; however, many others are labelled merely “Lviv”. The best known localities outside Lviv are Griboviczi (Grzybowice), Zaszkiw (Zaszków), and Lypnyki (Lipniki).

In terms of biostratigraphy, the marls of the “Lvovskaya svita” represent the *Bt. junior* Zone (Pasternak et al. 1987; see Fig. 3). The unit represents the type horizon of the index taxon of this zone; an individual from Zaszkiw illustrated by Nowak (1913: pl. 42: 18) as “*Belemnitella mucronata* Schloth. sp. mut. *junior*” was designated lectotype by Jeletzky (1951).

Nowak (1913: pl. 42: 24) also illustrated another belemnite from the “Lvovskaya svita” of Lypnyki near Lviv, referred to as “*Belemnitella lanceolata* Schl. sp. mut. *junior*”. Nowak (1913: 406) reported this taxon also from Snopków and from Jabłonowskich Street in Lviv. That particular specimen was reassigned to *Bn. sumensis* by Schulz (1979: 118). If this interpretation is correct, the presence of *Bn. sumensis* in the “Lvov-

skaja svita' would indicate the upper lower Maastrichtian *Bn. sumensis* Zone as defined in northern Germany. However, similar specimens of *Belemnella* occur sporadically in the lower part of the upper Maastrichtian in Europe, e.g., in Denmark (recorded as *Belemnella* cf. *cimbrica*, see Christensen 1996: fig. 3). Thus, the stratigraphic importance of "*Belemnella lanceolata* Schl. sp. mut. *junior*" of Nowak (1913) is open to discussion until the original material can be revised.

Pasternak et al. (1987) regarded the *Bt. junior* Zone as an indicator of the lower upper Maastrichtian position of the "Lvovskaja svita". This view cannot be upheld any longer in view of the occurrence of this species in the upper part of the lower Maastrichtian in the Maastricht-Aachen-Liège area (see above). However, the composition of the inoceramid fauna does suggest a late Maastrichtian date for the "Lvovskaya svita". Solely *Spyridoceramus tegulatus* was described by Kociubinskyj (1968: 148, pl. 28: 3; pl. 29: 8) and by Syniewska (1923: fig. 3) from Lviv, the latter as "*Inoceramus* sp. (cf. *tuberculatus* Woods)" (Ireneusz Walaszczyk, personal communication 2005). In view of the apparent absence of non-tegulated inoceramids, *Sp. tegulatus* would indicate the *Sp. tegulatus*-*Bt. junior* Zone of the subdivision by Schulz and Schmid (1983) (Fig. 3).

Other successions.—Scaphitid material from other upper Maastrichtian successions (Fig. 1) is also included in the present paper, as based on published and/or studied collections. These include material from: 1, the Bay of Biscay region, France and Spain (Ward and Kennedy 1993); 2, Petites-Pyrénées, southern France (Kennedy et al. 1986); 3, Bjala, Bulgaria (Ivanov and Stoykova 1994; Ivanov 1995); and 4, Crimea (Ukraine) and Mangyshlak in Kazakhstan (both regions situated outside the range of map in Fig. 1A). Material from the latter region was described by e.g., Mikhailov (1951), Naidin (1974), Naidin et al. (1990) and Jolkichev and Naidin (2000).

The classic ammonite fauna from the "Calcaire à *Baculites*" of Cotentin (Manche, France; Fig. 1) includes several scaphitids (Kennedy 1986, 1993). This fauna was considered to be late Maastrichtian in age by Kennedy (1986), based on ammonite, belemnite, echinoid and foraminiferal evidence. This view was followed by Machalski (1996). However, abundant non-tegulated inoceramids, defining the "*Inoceramus*" *morgani* Zone, are also on record from the "Calcaire à *Baculites*", which suggests that it is late early Maastrichtian in age instead (Walaszczyk et al. 1996; Ireneusz Walaszczyk and William James Kennedy, unpublished data). In spite of this, scaphitids from Cotentin are repeatedly discussed in the present paper as containing type specimens of taxa which cross the lower/upper Maastrichtian boundary. Following de Grossouvre (1901) (*vide* Kennedy 1986: 27), the "Calcaire à *Baculites*" of Cotentin is estimated 4–5 metres in total thickness.

Scaphitids from another classic European ammonite locality, Neuberg (Austria) (Kennedy and Summesberger 1986; Kennedy 1993; see Fig. 1A) are also discussed. The ammonite evidence points to an early Maastrichtian age for this fauna

(Kennedy and Summesberger 1986). In contrast, nannofossils suggest a late Maastrichtian date (Wagreich et al. 2003).

Methodology

Morphological terms used in the present paper for describing scaphitid conchs are explained in Fig. 4A. All specimens studied are preserved as internal, external or composite moulds; in view of the fact that the material commonly is distorted *post-mortem*, only the maximum diameter of the better-preserved specimens has been measured. Because suture lines are poorly preserved in most of the specimens, this feature has not received any attention.

Whenever possible, dimorphic pairs have been identified in the samples studied. Following Makowski (1962), macroconchs (M) are interpreted as females, while microconchs (m) are considered to be males (Fig. 4B). These dimorphs are separated not only by size, but also by other features, e.g., differences in the height of the body chamber. For example, the umbilical wall of the shaft in *Hoploscaphites* is convex in macroconchs and concave in microconchs (Makowski 1962; Kennedy 1989; Landman and Waage 1993a). A distinct umbilical bulge, or swell, is present on the umbilical wall of the shaft in members of the *Hoploscaphites constrictus* lineage (Fig. 4B).

In the present paper, species and subspecies are defined, whenever a sufficient number of specimens was available, on the basis of a population (horizontal) rather than by a typological (vertical) approach (Callomon 1985; Dzik 1985, 1990; see Fig. 4C). It should be noted, however, that the available scaphitid "populations" never fulfil the criteria set for neontologic populations, being averaged from rather thick rock intervals. This results from the fact that many specimens studied are imprecisely located within sections, having been collected from quarry scree.

The concept of temporal subspecies allows for a convenient subdivision of fossil lineages into smaller evolutionary units (Newell 1947, 1956; Sylvester-Bradley 1951; Dzik and Trammer 1980); it is followed here. Dzik and Trammer (1980) proposed that a lack of overlap in ranges of standard deviations of the diagnostic features should be taken as the minimum difference allowing chronosubspecies to be recognised. In neontology, the so-called 75% rule is in common use for the discrimination of geographic subspecies (Amadon 1949; Mayr et al. 1953; Newell 1956). However, no statistical processing of the material has been carried out in view of common *post-mortem* deformation of specimens and significant time-averaging of the available samples. A given sample has been assigned to a particular subspecies when it is dominated by individuals possessing the diagnostic features of that subspecies (Fig. 4C).

Diagnoses of new taxa are differential in character, as recommended by Cifelli and Kielan-Jaworowska (2005). These definitions are based on macroconchs as these predominate in the material studied and seem to be more distinctive than the microconchs (Riccardi 1983; Landman and Waage 1993a).

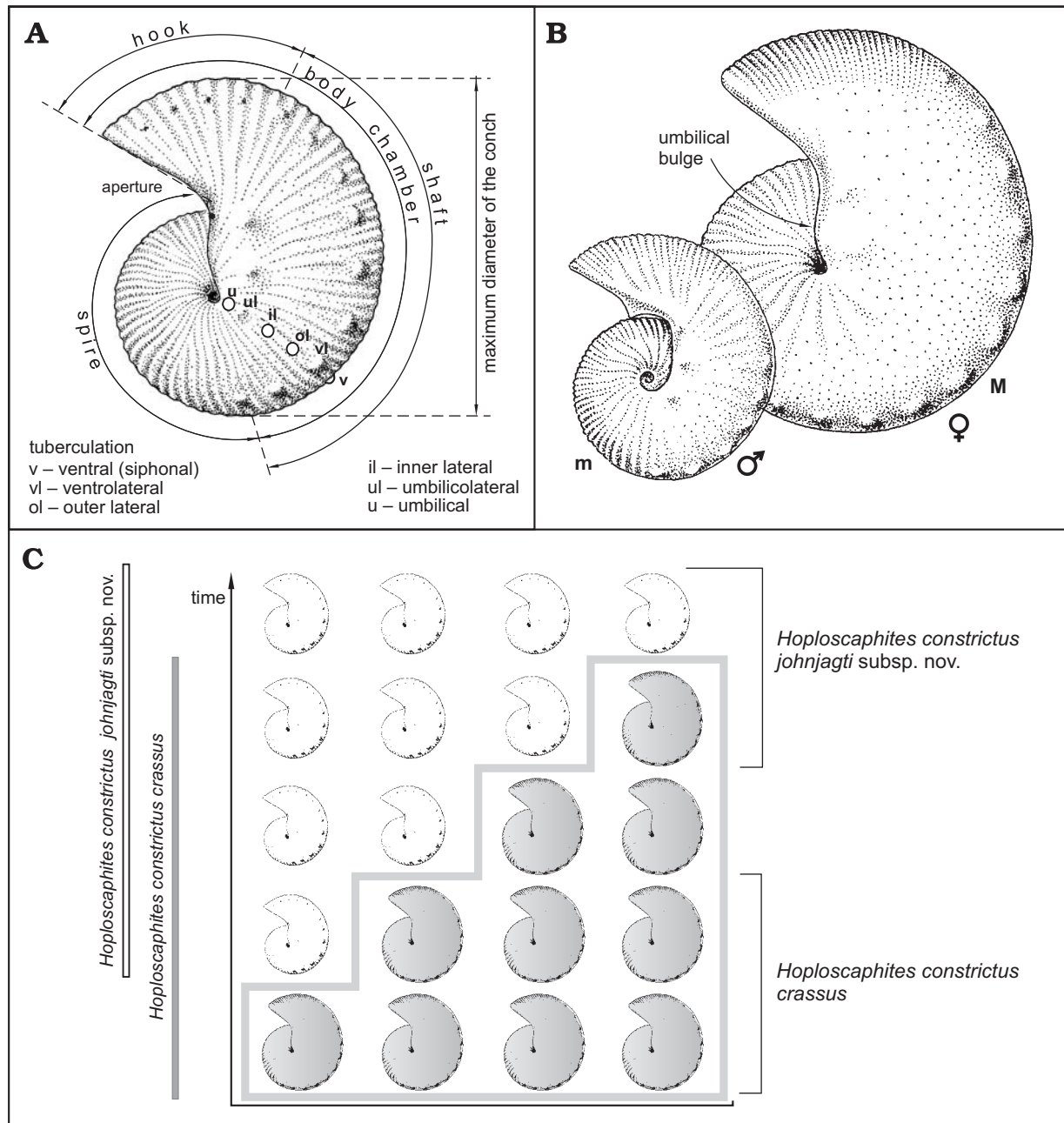


Fig. 4. **A.** Morphologic terms used to describe scaphitid conchs, presented on a reconstruction of an adult macroconch of *Hoploscaphites constrictus johnjagti* subsp. nov.; note the difference between actual and imaginative tubercles (regular circles) introduced to show all possible positions of tuberculation in the scaphitids studied. **B.** Dimorphic pair of *Hoploscaphites constrictus crassus* (Łopuski, 1911): m, microconch; M, macroconch. **C.** The vertical versus horizontal method of defining chronospecies, as exemplified by the evolutionary transition between *Hoploscaphites constrictus crassus* and *H. c. johnjagti* subsp. nov. An idealised succession of populations may be divided in two ways; according to the vertical method all specimens with smooth body chamber represent *H. c. crassus* whereas all specimens with ribbed body chamber belong to *H. c. johnjagti* subsp. nov.; note that the vertical method leads to an artificial overlap of ranges of the subspecies (cf. Dzik 1985). In the horizontal method, accepted herein, all populations dominated by the smooth morphotype are assigned to *H. c. crassus* and populations dominated by the ribbed morphotype, to *H. c. johnjagti* subsp. nov.

Systematic palaeontology

Family Scaphitidae Gill, 1871

Genus *Hoploscaphites* Nowak, 1911

Type species: *Ammonites constrictus* J. Sowerby, 1817, by original designation.

Remarks.—Diagnosis of the genus as given by Landman and Waage (1993a: 73) is followed herein.

Hoploscaphites constrictus (J. Sowerby, 1817)

Type material: Specimen BMNH C36733, a macroconch, from the upper lower Maastrichtain, Ste Colombe, Cotentin (Manche, France) was designated lectotype by Kennedy (1986: pl. 13: 20–22).

Hoploscaphites constrictus lvivensis subsp. nov.

Figs. 5, 6, 7B, E, F.

Holotype: ZPAL Am. 12/1051 (Fig. 5C).

Type horizon: Lower upper Maastrichtian (*Spyridoceras tegulatus*–*Belemnitella junior* Zone).

Type locality: Level III, Chelm chalk pit, Poland.

Derivation of the name: From the town of Lviv, western Ukraine.

Diagnosis.— A temporal subspecies in the *Hoploscaphites constrictus* lineage, intermediate between *H. c. constrictus* and *H. c. crassus* (Łopuski, 1911), defined by an adapertural decrease in distance between ventrolateral tubercles in adult macroconchs.

Material.—From Poland: 227 specimens from Chelm (ZPAL Am. 12/163, 166, 167, 177, 178, 180, 181, 183, 187, 193, 195, 196–205, 207–210, 213, 215, 216, 219–221, 225–227, 241, 364–367, 373–379, 381–396, 405–414, 416, 419–422, 425–436, 438–453, 455, 457, 467–472, 474, 478, 480–488, 491–494, 496–499, 501–508, 510–515, 518, 519–523, 525–542, 550–561, 565, 566, 584–597, 599–606, 608–620, 622, 623, 629, 678, 680, 1051, 1053). From Ukraine: nine specimens from Lviv (DPM NANU PZ-N9262, 9266, 9267, 9275a–c, 9314, 9839, 9840).

Discussion.—There are 116 adult macroconchs and 5 adult microconchs in the sample from level III at Chelm (referred to as “Chelm III sample” below). The maximum diameter has been measured in 32 well-preserved adults, including 28 macro- and 4 microconchs. Macroconchs range between 39 and 63 mm, while microconchs are between 28 and 36 mm (Fig. 9A).

Adult macroconchs from the Chelm III sample and those of *Hoploscaphites constrictus constrictus* (J. Sowerby, 1817) from the “Calcaire à *Baculites*” of Cotentin (Sowerby 1817: pl. A: 1; Kennedy 1986: pl. 13: 1–13, 16–24; pl. 14: 1–38; pl. 15; text-figs. 9, 11A–H) show a similar style of ribbing of the body chamber. In both cases, the ribs are typically slightly effaced and swollen near the base of the body chamber, and become stronger and more accentuated adaperturally. The rib density increases adaperturally, so that the hook usually shows distinct and fairly closely spaced ribs.

A significant difference between the Chelm III and Cotentin samples involves the spacing between the ventrolateral tubercles near the aperture. As judged from illustrations in Kennedy (1986), distances between consecutive tubercles do not change towards the aperture in adult macroconchs from Cotentin, including the lectotype, while they decrease adaperturally in most macroconchs in the Chelm III sample (Figs. 5, 8). As a result, the adapertural portions of the tubercle rows resemble a “string of beads” (e.g., Fig. 5A). Only a few adult macroconchs from the Chelm III sample lack this feature, and are thus indistinguishable from *H. c. constrictus* as defined on material from Cotentin. However, they match the remainder of the material from Chelm in size variation and style of ribbing and are best interpreted as con(sub)specific with other conchs from there.

In addition to the Chelm III sample, 101 macroconchs

and 6 microconchs of *H. constrictus* from levels II, IV and V at Chelm (the latter sample consisting only of a few individuals) have been studied. No differences have been noted between the dominant macroconch morphology in the Chelm III sample and that in other samples.

The adapertural decrease in spacing of ventrolateral tubercles is a distinctive feature which distinguishes the Chelm material from that from Cotentin and from both older and younger samples of *H. constrictus* from the Lublin Upland (Fig. 8). This is why the material from Chelm is here treated as a new subspecies, *H. constrictus lvivensis* subsp. nov. Stratigraphically, this new subspecies is characteristic of the early part of the late Maastrichtian. It constitutes an intermediate stage in the evolution of the *Hoploscaphites constrictus* lineage between late early Maastrichtian *H. c. constrictus* and late late Maastrichtian *H. c. crassus* (Fig. 8).

Another, potentially distinctive, feature of *H. c. lvivensis* subsp. nov. is the degree of extension of ventrolateral tubercles onto the spire. In many specimens from Chelm, including the holotype (Fig. 5C₁), the tubercles extend onto the entire exposed part of the phragmocone. None of the adult macroconchs from Cotentin illustrated by Kennedy (1986) shows this feature. However, tubercles occasionally are present on the whole of the exposed portion of the phragmocone in some specimens of *Hoploscaphites constrictus* from other levels of the European Maastrichtian. This is exemplified by specimen MGUH 20175 from the upper upper Maastrichtian of Denmark (Birkelund 1993: pl. 15: 8a), referred to *H. constrictus johnjagti* subsp. nov. herein. Ventrolateral tubercles are also present on the whole exposed part of the spire in some scaphitid species from the Maastrichtian strata of the U.S. Western Interior (Landman and Waage 1993a), including *Hoploscaphites birkelundae* Landman and Waage 1993a (see also Landman and Cobban 2003). An overall similarity of the latter species to some members of the European *Hoploscaphites constrictus* lineage was pointed out by Landman and Waage (1993a: 126). However, the Western Interior form differs from its European counterparts in its larger overall size, very fine ribbing of the body chamber and in the presence of a distinct adapertural inflexion of ventral ribs near aperture (Landman and Waage 1993a).

The limited number of microconchs from Chelm (Fig. 7B, E, F), eleven in total, does not allow for a precise morphological definition. They seem to share the same style of ribbing with the macroconchs (compare Figs. 5 and 7B, E, F; see also Fig. 8). In almost all specimens studied, ventrolateral tubercles are delicate and barely visible (e.g., Fig. 7B and E). None of the specimens shows the increase in tubercle density towards the aperture, distinctive for macroconchs. The largest microconch from Chelm is ZPAL Am. 12/705 from level IV, with an estimated maximum diameter of 40 mm and strong ventrolateral tuberculation (Fig. 7F).

Material from the “Lvovskaja svita” of Lviv and its environs comprises nine adult macroconchs which match the above diagnosis of *Hoploscaphites constrictus lvivensis* subsp. nov. (Fig. 6). Seeing that there are no data available on

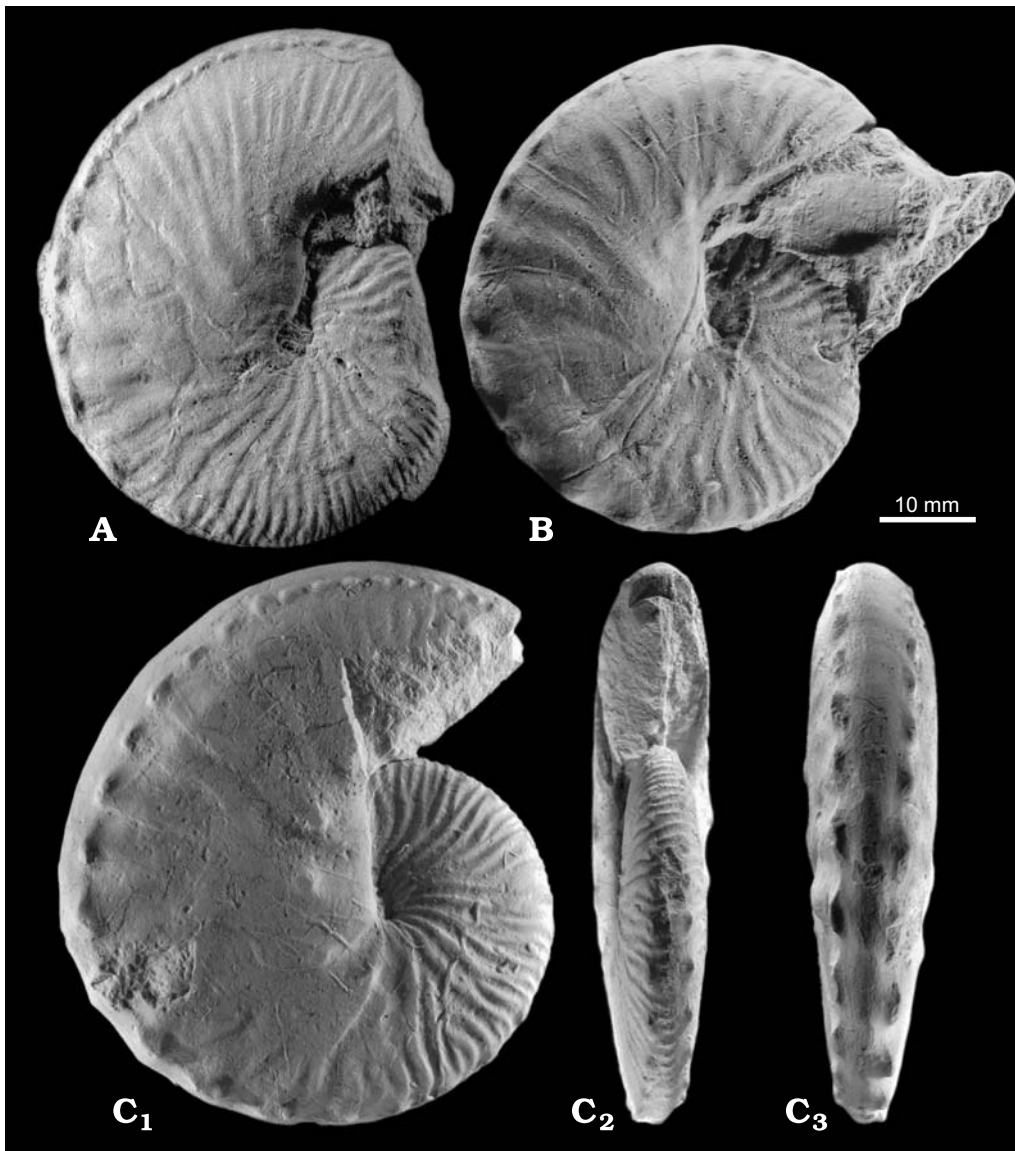


Fig. 5. *Hoploscaphites constrictus livensis* subsp. nov., adult macroconchs, *Spyridoceramus tegulatus*–*Belemnitella junior* Zone, level III at Chelm, Poland. A. ZPAL Am. 12/608 in lateral view. B. ZPAL Am. 12/408 in lateral view. C. Holotype, ZPAL Am. 12/1051 in lateral (C₁), apertural (C₂), and ventral (C₃) views.

ammonite distribution within the “Lvovskaja svita”, their assignment to the present subspecies is rather intuitive and based on typological rather than on population criteria. Surprisingly, no specimens from Lviv showing the diagnostic features of *H. c. livensis* subsp. nov. were illustrated by Nowak (1911), who presented only figures of the *H. constrictus crassus* morphotype. No microconchs are present in the material studied from the “Lvovskaja svita”.

To date, there are no records of *H. c. livensis* subsp. nov. from outside eastern Poland and western Ukraine. This may result from a preservational bias. Records of *Hoploscaphites constrictus* from the *Sp. tegulatus*–*Bt. junior* Zone at Hemmoor (northern Germany) are based on a few, poorly preserved specimens with no tuberculation visible on the apertural portion of the body chamber (e.g., Birkelund 1982: pl. 3: 13, 14 [non 12 = microconch of *H. schmidi*]). The Danish record of *H. constrictus* from the lower part of the upper Maastrichtian is also poor in quantity and quality and precludes identification at the subspecies level. In the Maas-

trichtian type area, *H. constrictus* is recorded from the whole of the upper lower Maastrichtian Vijlen Member, as well as from the upper third of the Nekum Member and from the overlying Meerssen Member (upper upper Maastrichtian) (van der Tuuk 1987; Jagt 1995), although Jagt (2002: fig. 3) erroneously showed the species to range throughout the upper upper Maastrichtian succession in that area. Thus, in the type area of the Maastrichtian Stage there is no record of *H. constrictus livensis* subsp. nov. in Poland and the Ukraine.

Stratigraphic and geographic range.—Lower upper Maastrichtian (*Spyridoceramus tegulatus*–*Belemnitella junior* Zone) of Poland and Ukraine.

Hoploscaphites constrictus crassus (Łopuski, 1911)

Figs. 7A, D, G, H, 10.

1911 *Scaphites constrictus* Sowerby var. *crassus* var. nov.; Łopuski 1911: 115, pl. 2: 4–6; pl. 3: 1, 2.

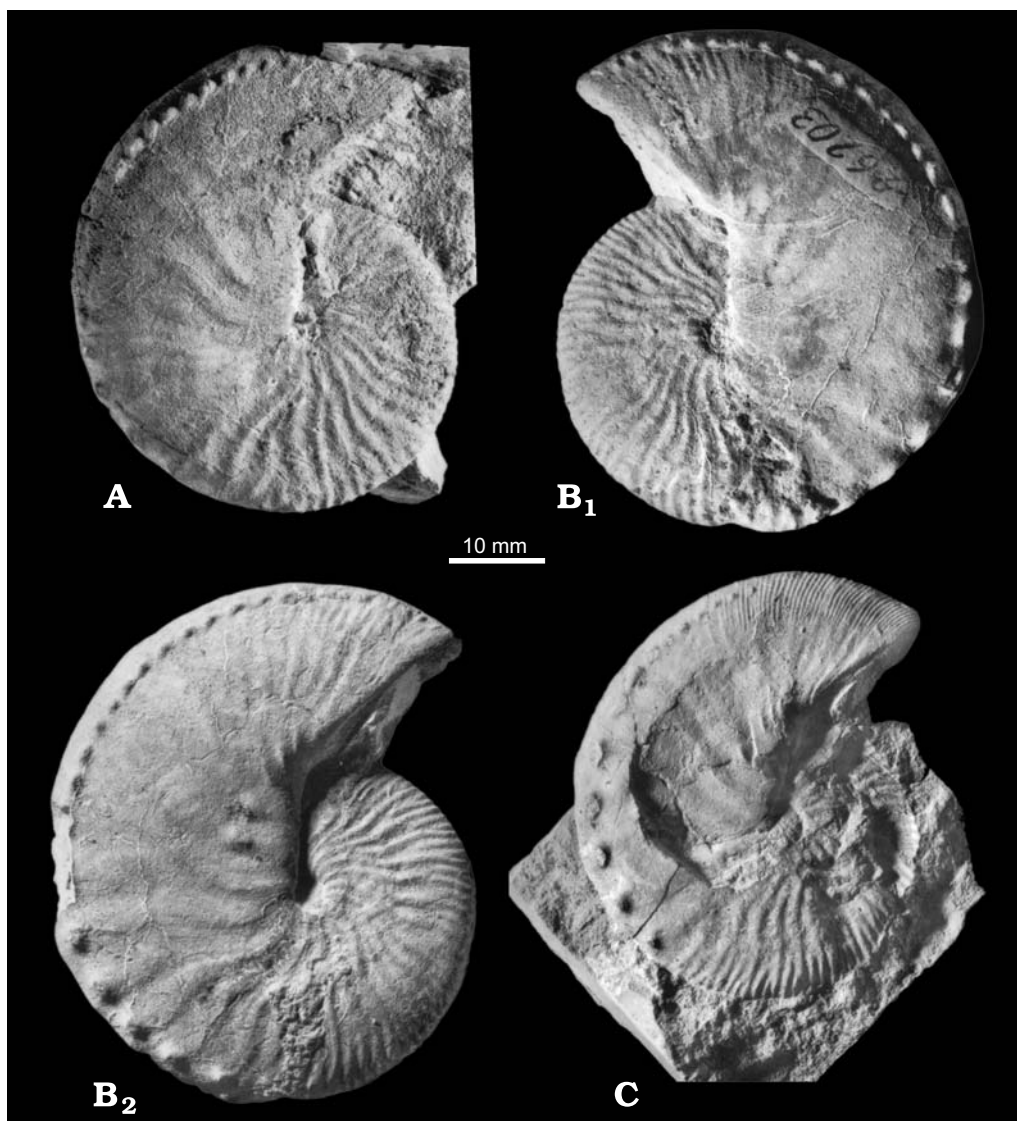


Fig. 6. *Hoploscaphites constrictus lvi-venensis* subsp. nov., adult macroconchs, *Spyridoceramus tegulatus*–*Belemnitebella junior* Zone, Lviv, the Ukraine. A. DPM NANU PZ-K-N9314 in lateral view. B. DPM NANU PZ-K-N9267 in lateral views (B₁, B₂). C. DPM NANU PZ-K-N9839 in lateral view.

1911 *Scaphites constrictus* Sow.; Łopuski 1911: 113, pl. 2: 3, 4.

1911 *Scaphites* sp.; Łopuski 1911: 117, 118, pl. 3: 3–6.

?1911 *Hoploscaphites constrictus* Sowerby *vulgaris*; Nowak 1911: 583 (partim), pl. 33: 8–10 (non pl. 33: 11, 12 = *Hoploscaphites tenuistriatus*).

1962 *Scaphites constrictus* (Sow.); Makowski 1962: 31, text-pl. 4: 3.

1962 *Scaphites constrictus* var. *niedzwiedzki* (Uhlig); Makowski 1962: text-plate 4: 4.

1980 *Hoploscaphites constrictus crassus* (Łopuski, 1911); Błaszkiwicz 1980: 37, pl. 18, 1–3, 11–14.

1993 *Hoploscaphites constrictus* (J. Sowerby, 1817); Birkelund 1993: 57 (partim), pl. 14: 5; pl. 17: 10 (non pl. 14: 1–4, 6, 7, 12; pl. 15, 1–14; pl. 16: 6–16; pl. 17: 5–9, 11–23 = *Hoploscaphites constrictus johnjagti* subsp. nov.).

1996 *Hoploscaphites constrictus* (J. Sowerby, 1817); Radwański 1996: pl. 2: 1, 2; figs. 1–11.

1996 *Hoploscaphites constrictus* (J. Sowerby, 1817); Machalski 1996: figs. 2A–G, 3A–C.

2005 *Hoploscaphites constrictus* subsp. A; Machalski 2005: figs. 8A–E, 10A, B; 11A–D.

Type material: A specimen from the upper upper Maastrichtian at Kazi-

mierz Dolny, illustrated by Łopuski (1911: 115, pl. 2: 4, 5, pl. 3: 1, 2), presumably lost, was designated lectotype by Błaszkiwicz (1980: 37).

Emended diagnosis.—A temporal subspecies in the *Hoploscaphites constrictus* lineage, transitional between *H. c. lvi-venensis* subsp. nov. and *H. c. johnjagti* subsp. nov., defined by the absence of ribbing on a large sector of body chamber in adult macroconchs.

Material.—From Poland: 88 specimens from Rejowiec (ZPAL Am. 12/92, 242, 364, 848–850, 853, 860–863, 866, 869, 875, 941, 943, 944, 947, 949, 950, 952, 954–963, 965–968, 970, 972–978, 980–984, 987, 989, 991–996, 998–1002, 1004–1010, 1012, 1015–1027, 1029–1032); 14 specimens from Podgórz (ZPAL Am. 12/246–248, 250, 251, 675, 676, 732, 735, 737, 739, 753, 757, 798); three specimens from Albrychtówka (ZPAL Am. 12/98 a, b, 728); 117 specimens from the town quarry south of Kazimierz Dolny (ZPAL Am. 12/30, 92–96, 101–105, 109–112, 115, 116, 119–121, 126, 127, 129–134, 137–147, 149–151, 153–156, 157–160, 624–632, 634–640, 643, 650–655, 657, 659–661, 664,

667–670, 677, 679, 681–685, 687, 689–691, 693, 694, 696–699, 725–727, 729–731, 746–751, 754, 810, 811, 813, 931, 1062); 123 from Nasiłów (ZPAL Am. 12/1–10, 12–16, 18–57, 59–63, 65, 67, 69, 71–77, 79, 82–87, 90, 91, 125, 161, 162, 308–315, 318, 320–322, 346, 363, 644–647, 806–809, 1217, 1218, 1220–1239); four specimens from Bochothnica (ZPAL Am. 12/311, 319, 324, 745); twenty-one from Klimusin (ZPAL Am. 12/327–343, 352, 357–359); seven from Prawiedniki (ZPAL Am. 12/350, 351, 353–355, 404, 424); six from Mętów (ZPAL Am. 12/344–349). From Denmark: three specimens from Bjerre (MGUH 1965.588, 1954.634, unregistered); 10 from Hov (MGUH 20156, 27743, 1965.568, 1965.569, 1965.575, 1965.577, 1965.578, 1965.585, 1973.399, 1973.400); 21 from Stevns Klint (MGUH 20206 and 20 unregistered specimens in the private collection of Alice Rasmussen, Fakse). From the Ukraine: one specimen from Lviv (DPM NANU PZ-K-N9282); five from Griboviczi (formerly Grzybowice) (DPM NANU PZ-K-N9204, 9206, 9843–9845).

Discussion.—Łopuski (1911: 116) differentiated his *Scaphites constrictus* Sowerby var. *crassus* from the nominal species only by the “enormous thickness of the conch”. The lectotype, an adult macroconch, is a thick-set individual indeed (Łopuski 1911: 115, pl. 2: 4, 5, pl. 3: 1, 2), but its inflation is exaggerated by strong *post-mortem* deformation. According to Łopuski (1911), this specimen came from “Kazimierz”. Thus, it could have been collected from either the lower part of the Kazimierz Opoka as exposed at the town quarry south of Kazimierz Dolny or from the upper part of that unit, occasionally accessible during construction works in the town.

Material from the Kazimierz Opoka studied comprises 118 adult macroconchs (Fig. 10B, F, G) and 33 adult microconchs (Fig. 7D, G, H). Two subsamples from relatively narrow intervals have been measured; one is from a marly opoka, 2 metres thick, at the bottom of the upper third of the town quarry (referred to as the “Kazimierz Dolny sample” below), the other is from a hard limestone layer, up to one metre thick, which forms the top of the Kazimierz Opoka succession at Nasiłów (the “Nasiłów sample” below).

The Kazimierz Dolny sample comprises 65 adult macro- and 15 adult microconchs; the former range between 29 and 66 mm, while the latter range between 22 and 38 mm in maximum diameter (Fig. 9C). The Nasiłów sample includes 28 adult macro- and 8 microconchs, measuring between 38 and 73 mm and between 24 and 35 mm in maximum diameter, respectively (Fig. 9D). There is thus some overlap of size between dimorphs of *H. c. crassus* in these samples (contrary to Makowski 1962, who claimed that there was no overlap in the material from the Kazimierz Dolny area).

The material of *H. c. crassus* from the Kazimierz Dolny area shows a wide range of variation in conch proportions and ornament, which is best appreciated in illustrations supplied by Łopuski (1911), Błaszkiwicz (1980) and Machalski (1996, 2005). The development of ornament in adult macroconchs does not depend on the size of the conchs as the smaller specimens reveal essentially the same ornament as the larger individuals (Fig. 11A–C).

In general, the Kazimierz Opoka material differs from that of *H. c. constrictus* from Cotentin in the ornament of the body chamber (Fig. 8). Flanks of the shaft are covered with ribs in most adult macroconchs from Cotentin (Kennedy 1986). In contrast, ribbing is absent from a large sector of the body chamber, including the shaft and a considerable region of the hook, in almost all adult macroconchs from the Kazimierz Opoka. Only faint striae or growth lines are visible on the flanks in better-preserved specimens, including those preserved as xenomorphic imprints and replicas on oyster shells (Lehmann and Wippich 1995: fig. 1).

The lack of ribs on the body chamber in macroconchs from the Kazimierz Dolny area *versus* their presence in material from Cotentin was the main criterion used by Błaszkiwicz (1980) to distinguish *H. c. crassus* from the nominal subspecies. This view is accepted herein, and all samples of *H. c. constrictus* in which smooth adult macroconchs predominate, are assigned to *H. c. crassus*. The subspecies is interpreted as part of the *H. c. constrictus* lineage intermediate between the earlier *H. c. lvivensis* subsp. nov. and the later *H. c. johnjagti* subsp. nov. (Fig. 8). The gradual character of the transition from *H. c. crassus* to *H. c. johnjagti* subsp. nov. is documented by the occasional occurrence of the ribbed morphotype in populations of *H. c. crassus* from the upper part of the Kazimierz Opoka, as exposed at Nasiłów and Bochothnica (e.g., Machalski 1996: fig. 2E, 2005: fig. 10A, B), and in populations from the white chalk succession at Sigerslev quarry (Stevns Klint). This is further substantiated by smooth specimens in a sample of *H. c. constrictus johnjagti* subsp. nov. from the Grey Chalk of Stevns Klint (Machalski 2005; see also below) and by the presence of “transitional” specimens with weak ribbing, both from the Kazimierz Dolny area and from the “Dania” quarry (Machalski 2005).

As pointed out by Machalski (2005), the name *crassus* was informally used by Birkelund (1979, 1993), Kennedy (1986, 1987), Jagt (1995), Machalski (1996) and other authors to denote specimens of *Hoploscaphites constrictus* with the body chamber entirely covered by ribs and with ventrolateral tuberculation extending to the aperture. Thus, the “*crassus*” concept of these authors was different from that of Błaszkiwicz (1980); his views are accepted in the present paper.

In addition to the Middle Vistula River valley sections, the best material of *H. c. crassus* comes from a sample from the opoka layer between the belemnite and baculite marls at Rejowiec. This comprises 73 adult macro- and 15 adult microconchs, with the former ranging between 28 and 49 mm, the latter between 22 and 33 mm in maximum diameter, respectively (Fig. 9B). All macroconchs of this sample represent the smooth morphotype (e.g., Fig. 10D), and do not reach the size of the largest specimens from the Kazimierz Dolny and Nasiłów samples (Fig. 10B–D). This difference may be ascribed to some ecophenotypic factors as proposed by Landman et al. (2003) for a similar size variation amongst samples of the North American scaphitid *Hoploscaphites nicolletii* (Morton, 1842).

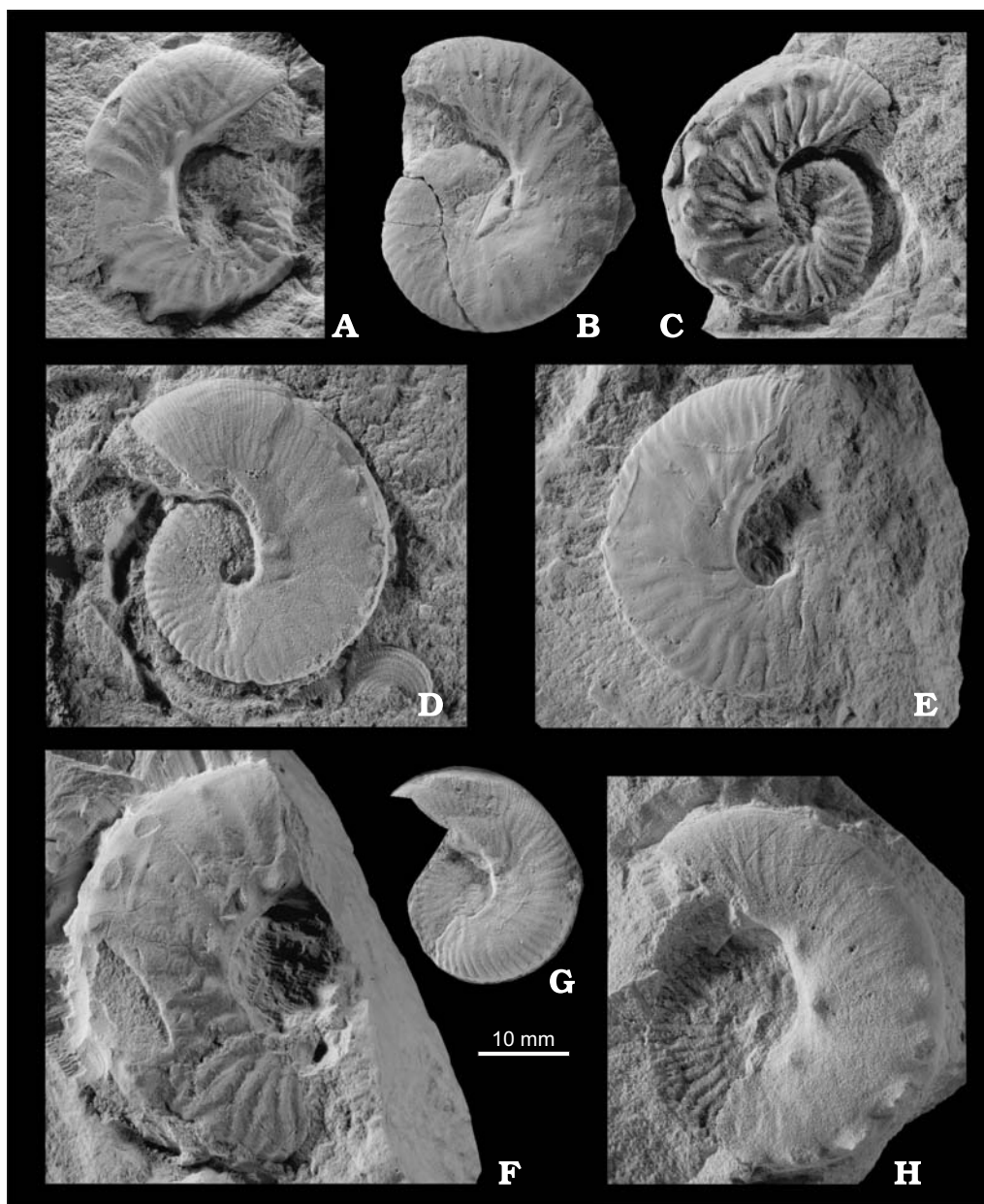


Fig. 7. Adult microconchs of *Hoploscaphites constrictus crassus* (Łopuski, 1911) (A, D, G, H), *H. c. johnjagti* subsp. nov. (C), and *H. c. lvivensis* subsp. nov. (B, E, F), all from Poland. A. ZPAL Am. 12/1005, *Belemnella kazimiroviensis* Zone, Rejowiec. B. ZPAL Am. 12/1053, *Spyridoceras tegulatus–Belemnitella junior* Zone, level III at Chełm. C. ZPAL Am. 12/266, *Bn. kazimiroviensis* Zone, Mełgiew. D. ZPAL Am. 12/685, *Bn. kazimiroviensis* Zone, town quarry south of Kazimierz Dolny. E. ZPAL Am. 12/678, *Sp. tegulatus–Bt. junior* Zone, level IV at Chełm. F. ZPAL Am. 12/705, *Sp. tegulatus–Bt. junior* Zone, level IV at Chełm. G, H. ZPAL Am. 12/679 (G) and ZPAL Am. 12/137 (H), *Bn. kazimiroviensis* Zone, town quarry south of Kazimierz Dolny. All specimens in lateral views.

The remaining samples studied (see synonymy and material) are assigned to the subspecies based on population criteria, i.e., the predominance of macroconchs with smooth flanks of the shaft. These include samples from the opoka successions at Klimusin, Mętów, and Prawiedniki in the Lublin area and from the white chalk succession as exposed at Sigerslev quarry (Stevns Klint), described in more detail by Machalski (2005). Only specimen DPM NANU PZ-K-N9282 (Fig. 10C) from the “Lvovskaja svita” at Lviv was assigned to this subspecies on a purely typological basis be-

cause provenance data are lacking (see above). Alternatively, DPM NANU PZ-K-N9282 might represent an end-member of the population of *H. c. lvivensis* subsp. nov.

Material from the upper, but not uppermost, Maastrichtian of the Bay of Biscay region, referred to as *Hoploscaphites constrictus* (J. Sowerby, 1817) by Ward and Kennedy (1993: figs. 43.1, 43.2, 45.3) is too poorly preserved for subspecific assignment. The same concerns approximately coeval material of the species reported from Bjala (Bulgaria), by Ivanov and Stoykova (1994: pl. 3A, B).

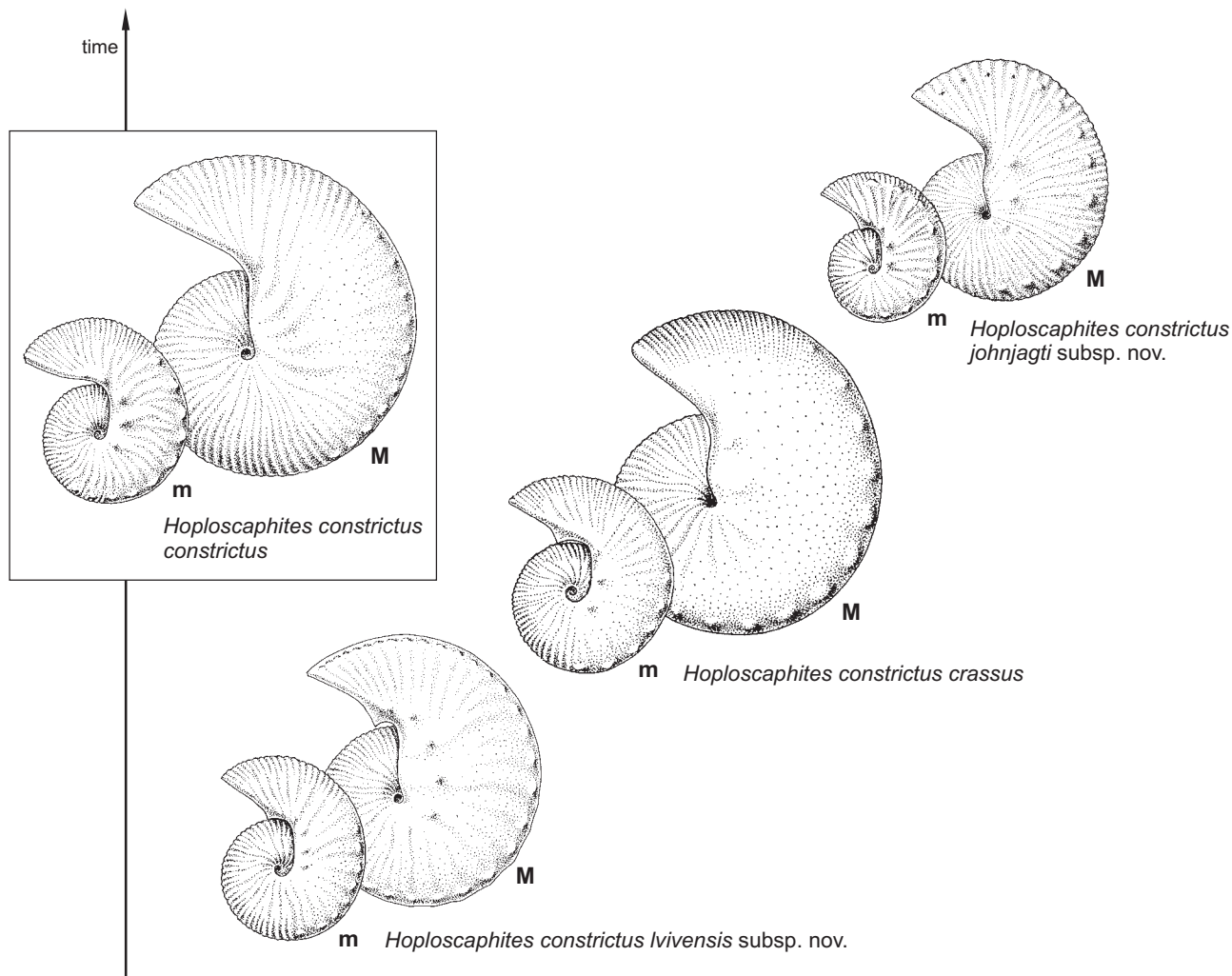


Fig. 8. Reconstructions of the successive members of the late Maastrichtian–earliest Danian part of the *Hoploscaphites constrictus* lineage, represented by adult microconchs (m) and macroconchs (M). A population from the upper lower Maastrichtian of Cotentin, exemplified by a dimorphic pair reconstructed in the box (based on illustrations in Kennedy 1986), forms the standard for the nominal subspecies, *Hoploscaphites c. constrictus* (J. Sowerby, 1817).

Adult microconchs of the subspecies show a remarkable, size-dependent variability in the ornament on the body chamber (Fig. 11). It seems as if the ornament was most complete in the largest individuals, encompassing a long interval of rather diffuse ribbing followed adaperturally by an interval of densely spaced ribs (Fig. 11F). The interval with diffuse ribbing seems to decrease in length in smaller-sized individuals (Fig. 11E), and is entirely lacking in the smallest specimens, where the adapertural stage of dense ribbing contacts directly with the regular ribbing typical of the phragmocone (Fig. 11D). The observed variation may be related to differential onset of maturation in specimens, with small individuals reaching adulthood earlier than large ones. This would concern only microconchs, interpreted as males (Makowski 1962). The macroconchs, thought to be females, do not show such size-dependent variability in ornament (Fig. 11A–C). Such an explanation, if correct, would lead to a rather unexpected merging of the hypothesis of sexual dimorphism in ammonites (Makowski 1962; Callomon 1963) with the developmental polymorphism theory

as advocated by Matyja (1986). Unfortunately, neither whorls nor septa can be counted in the specimens studied, for preservational reasons.

Stratigraphic and geographic range.—Upper, but not uppermost, Maastrichtian of Poland (*Spyridoceramus tegulatus*–*Belemnella junior* Zone and *Belemnella kazimiroviensis* Zone), Denmark (*Argyrotheca stevensis*–*Magas chitoniformis* Zone, *Ruegenella humboldtii*–*Argyrotheca stevensis* Zone and the equivalent *Belemnella kazimiroviensis* Zone) and the Ukraine (*Spyridoceramus tegulatus*–*Belemnella junior* Zone).

Hoploscaphites constrictus johnjagti subsp. nov.

Figs. 7C, 12.

1861 *Scaphites constrictus* d'Orbigny; Binkhorst 1861: 38, pl. 5d: 6a–h.

1986 *Hoploscaphites constrictus* (J. Sowerby 1817); Kennedy et al. 1986: 1019, pl. 3: 1, 9–12; pl. 4: 1–19; pl. 5: 1–17, 21–26.

1987 *Hoploscaphites constrictus* (J. Sowerby, 1817); Kennedy 1987: 197, pl. 31: 1, 8–26; pl. 32, 1–12, 18–21.

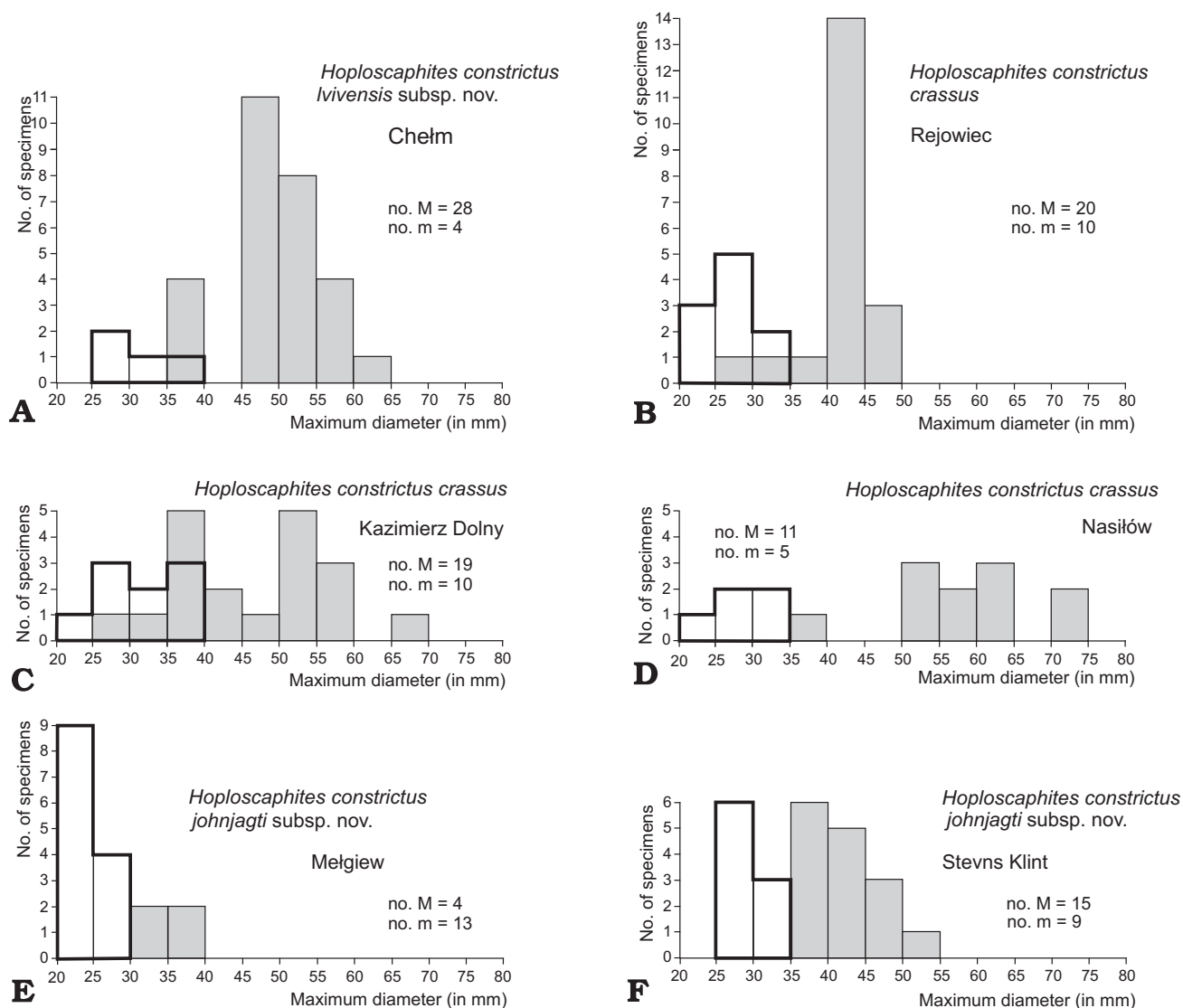


Fig. 9. Size-frequency distributions of microconchs (white columns) and macroconchs (shaded columns) in various samples of *Hoploscaphites constrictus* from Poland and Denmark (based on maximum diameter of measured conchs; see text for further data).

1987 *Hoploscaphites constrictus constrictus* (Sowerby, 1818) [sic]; van der Tuuk 1987: 73, figs. 5–7, 11, 20–23.

1987 *Hoploscaphites constrictus niedzwiedzki* (Uhlig, 1894); van der Tuuk 1987: 76, figs. 9, 10, 24.

1987 *Hoploscaphites constrictus* spp. indet.; van der Tuuk 1987: 77, figs. 8, 25.

1993 *Hoploscaphites constrictus* (J. Sowerby, 1817); Birkelund 1993: 57 (partim), pl. 14: 1–4, 6, 7, 12; pl. 15, 1–14; pl. 16: 6–16; pl. 17: 5–9, 11–23 (non pl. 14: 5; pl. 17: 10 = *Hoploscaphites constrictus crassus*).

1995 *Hoploscaphites constrictus* (J. Sowerby, 1817); Jagt 1995: 30 (partim), pl. 5: 15, 16; pl. 7: 13–19 (non pl. 7: 7 = *Hoploscaphites constrictus* subsp. indet.).

?2000 *Hoploscaphites constrictus crassus*; Jolkichev and Naidin 2000: fig. 4: 11.

2005 *Hoploscaphites constrictus* subsp. B; Machalski 2005: fig. 9A–H.

Holotype: MGUH 20220 (Fig. 12D; see also Birkelund 1993: pl. 17: 23a, b) from the indurated part of the Grey Chalk at Stevns Klint.

Type horizon: Top of the upper upper Maastrichtian *Belemnella kazimiroviensis* and the equivalent *Argyrotheca stevensi*–*Magas chitoniiformis* zones.

Type locality: Stevns Klint, Denmark.

Derivation of the name: in honour of John W.M. Jagt, a prominent student of Late Cretaceous faunas, and a friend.

Diagnosis.—Terminal subspecies in the *Hoploscaphites constrictus* lineage successive to *H. c. crassus*, defined by the presence of ribbing throughout the body chamber in macroconchs.

Upper Maastrichtian material.—From Denmark: 86 specimens from Stevns Klint (MGUH 20202–20220, 59 unregistered or provisionally registered MGUH specimens and 8 unregistered specimens in the private collection of Alice Rasmussen, Fakse), 24 specimens from “Dania” quarry (MGUH 20168–20181, 20187–20193, 20195–197). From Poland: 54 specimens from Melgiew (ZPAL Am. 12/252–305). From

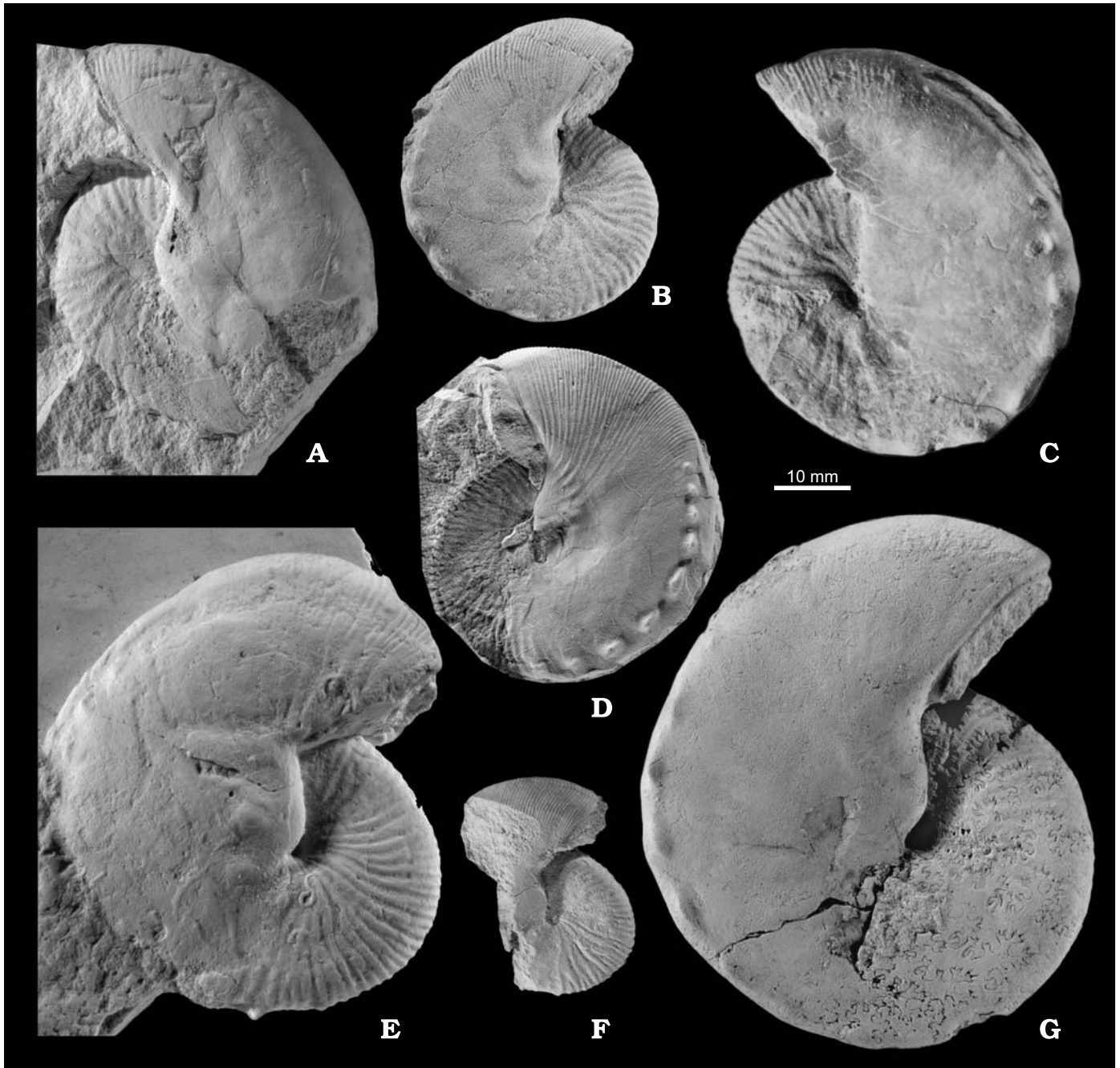


Fig. 10. *Hoploscaphites constrictus crassus* (Łopuski, 1911), adult macroconchs. **A**. ZPAL Am. 12/765, *Spyridoceras tegulatus*–*Belemnitella junior* Zone, Podgórz, Poland. **B**. ZPAL Am. 12/116, *Belemnella kazimiroviensis* Zone, town quarry south of Kazimierz Dolny, Poland. **C**. DPM NANU PZ-K-N9282, *Sp. tegulatus*–*Bt. junior* Zone, Lviv, the Ukraine. **D**. ZPAL Am. 12/1007, *Bn. kazimiroviensis* Zone, Rejowiec, Poland. **E**. MGUH 27743, Hov, Denmark. **F**, **G**. ZPAL Am. 12/681 (**F**) and ZPAL Am. 12/94 (**G**), *Bn. kazimiroviensis* Zone, town quarry south of Kazimierz Dolny, Poland. All specimens in lateral views.

Belgium: a single specimen from the former Albertkanaal outcrops (RGM P. 254, Jongmans collection). From the Netherlands: a single specimen from the former Blom quarry (NHMM JJ 11151), two from Vroenhoven (Albertkanaal section) (NHMM JJ 403, JJ 430), six from the Ankerpoort-Curfs quarry, Geulhem (NHMM JJ 5551, JJ 12456, JJ 12735, JJ 12847, JJ 12848, JJ 12903), three from the ENCI quarry, Maastricht (NHMM MK 3585, JJ 11115, JJ 11114).

From Sweden: seven specimens from Limhamn (MGUH 20152–20155, 20157–20159).

Lower Danian material.—A single specimen from Stevns Klint (MGUH 27366).

Discussion.—The holotype comes from the indurated portion of the Grey Chalk, c. 30 cm thick, at the top of the upper Maastrichtian in the Stevns Klint succession. A sample of 80

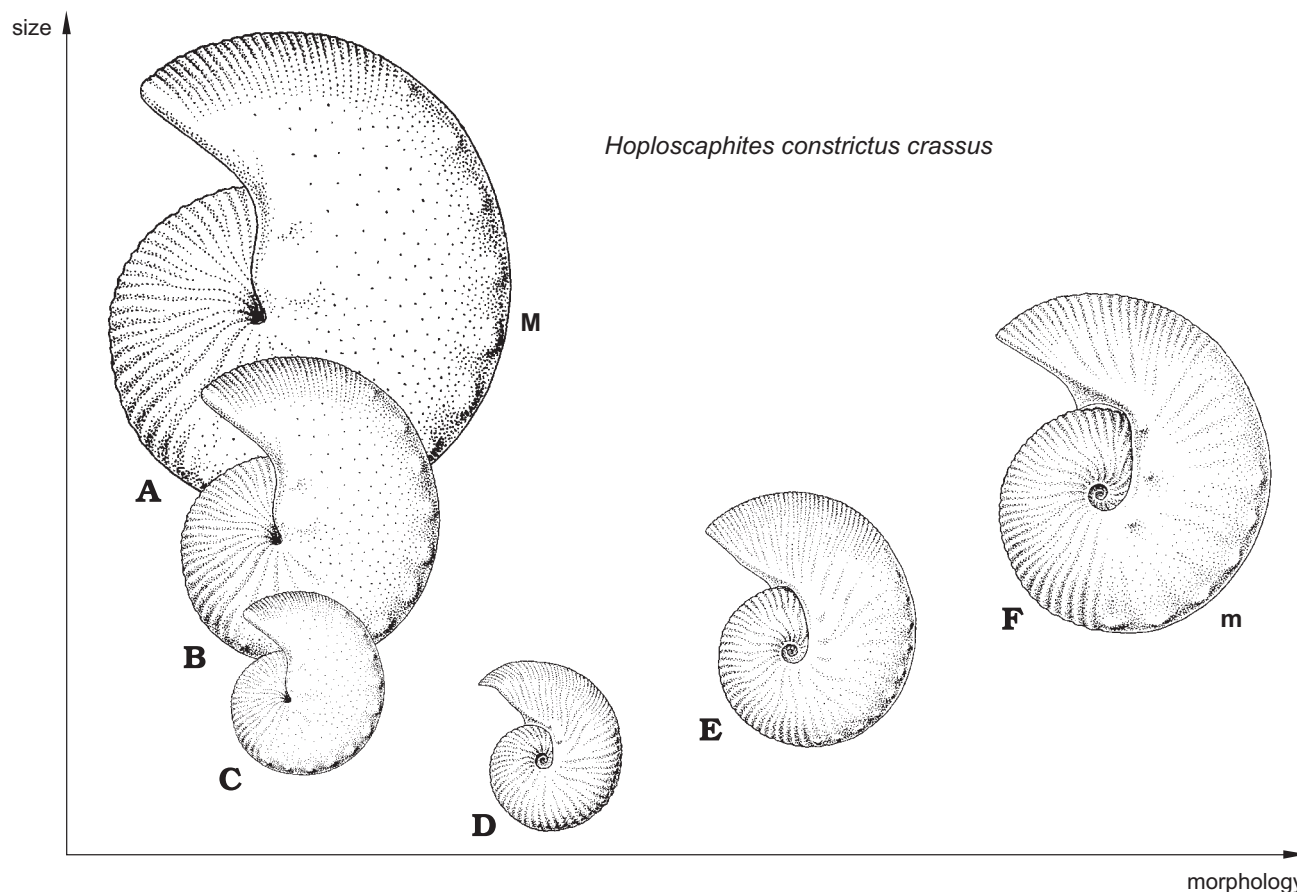


Fig. 11. Size-dependent variation in ornament of adult microconchs (D–F) and lack of such variation in adult macroconchs (A–C) in *Hoploscaphites constrictus crassus* (Łopuski, 1911). D based on Fig. 7G; E based on Fig. 7D; F based on Fig. 7H.

individuals (61 adult macro- and 19 microconchs) from that horizon was studied (see also Machalski 2005). Macroconchs (Fig. 12D) range between 36 and 51 mm and microconchs between 27 and 33 mm in maximum length (Fig. 9F). Body chambers are covered by relatively strong ribs in all adult macroconchs studied; ventrolateral tubercles extend to right up to the aperture in many of these (Birkelund 1993; Machalski 2005).

The differences between *H. c. johnjagti* subsp. nov. and *H. c. constrictus* are rather subtle (Fig. 8). Ribbing is present on the body chamber in most of the Cotentin macroconchs but is usually weaker in comparison to that seen in material from the indurated Grey Chalk. In addition, the extension of ventrolateral tuberculation to the aperture occurs much more rarely in material from Cotentin than in that from the indurated chalk at Stevns Klint. Nevertheless, some specimens from Cotentin, e.g., macroconchs assigned to the “*crassus*” variety by Kennedy (1986: pl. 15: 18–20; 29–31), are virtually indistinguishable from those occurring at the indurated top of the Grey Chalk at Stevns Klint. On this basis, both Kennedy (1986) and Machalski (1996) interpreted the fauna from Cotentin to range very high into the *Belemnella kazimiroviensis* Zone, a view proved incorrect by recent studies of inoceramid bivalves from that area (Ireneusz Walaszczyk, personal communication 2005).

The sample from the Grey Chalk below the indurated zone, maximum 4 metres thick (Hart et al. 2004, 2005), comprises six adult macroconchs (Machalski 2005). Four of them belong to the ribbed morphotype, whereas two represent the smooth morphotype which is typical of samples of *H. c. crassus*. Still lower in the Stevns Klint section, in the pure white chalk, the smooth morphotype prevails. Consequently, the white chalk sample is assigned to *H. c. crassus* (Machalski 2005; see above).

The sample from the “Dania” quarry in Jylland (for location, see Birkelund 1993: fig. 1) comprises 21 adult macro- and 3 adult microconchs (Machalski 2005). None of these is precisely located within the section exposed, which was a maximum of 16 metres thick (Håkansson and Hansen 1979). Specimens measured range between 35 and 53 mm in maximum diameter. Most of the adult macroconchs from “Dania” represent the ribbed morphotype; only a few specimens have smooth sectors on their body chambers (Birkelund 1993; Machalski 2005). Of special importance are specimens showing a morphology intermediate between the ribbed and smooth morphotypes (e.g., Birkelund 1993: pl. 15: 10, 12). Because ribbed macroconchs predominate, the entire sample from “Dania” is assigned to *H. c. johnjagti* subsp. nov. (= *Hoploscaphites constrictus* subsp. B of Machalski 2005). The morphologically transitional individuals between the smooth

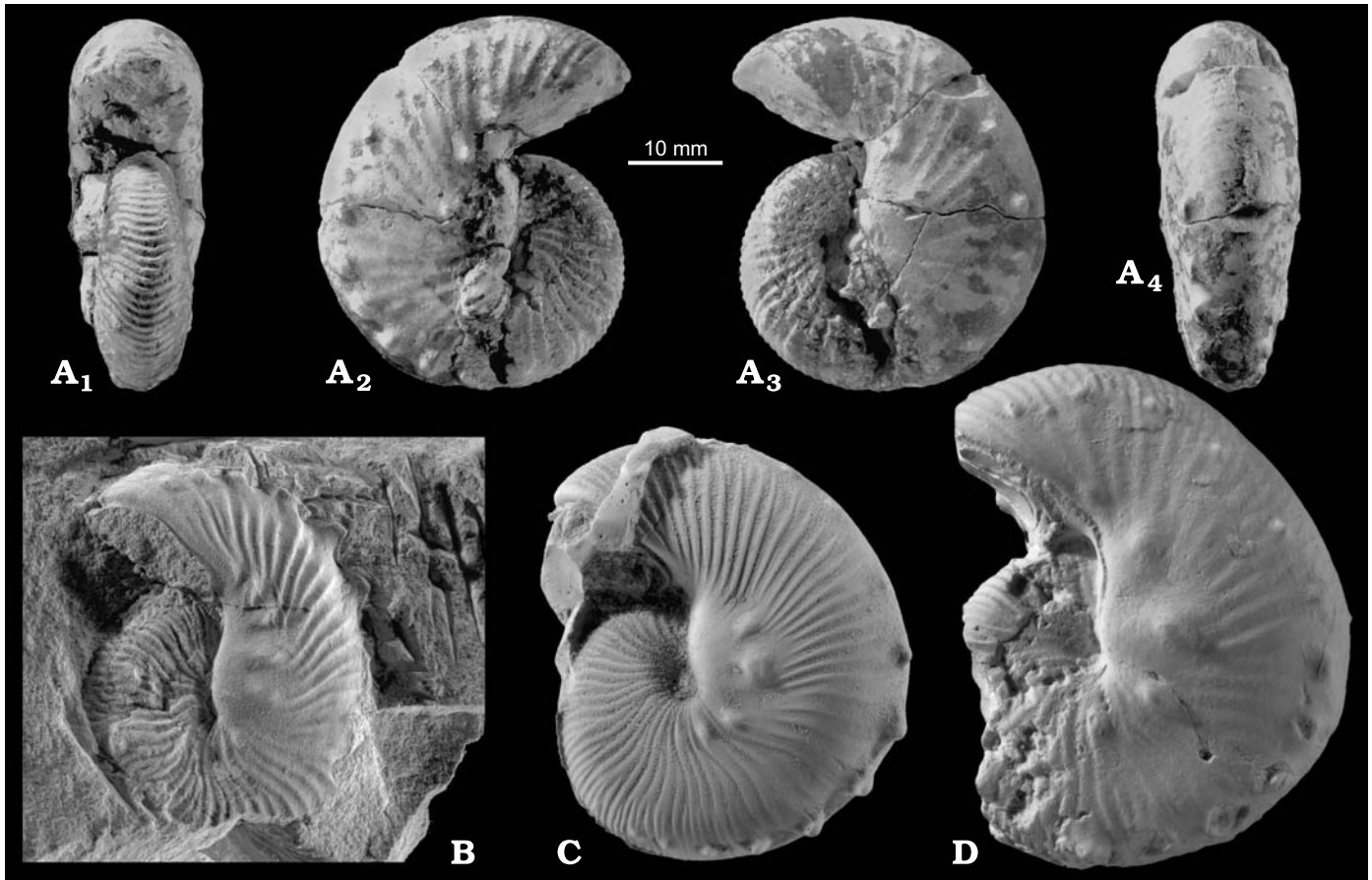


Fig. 12. *Hoploscaphites constrictus johnjagti* subsp. nov., adult macroconchs. A. MGUH 27366, lowermost Danian, Stevns Klint, Denmark, in apertural (A₁), lateral (A₂, A₃), and ventral (A₄) views. B. ZPAL Am. 12/252, *Belemnella kazimiroviensis* Zone, Melgiew, Poland, in lateral view. C. Silicone rubber cast of RGM P. 245, *Bn. kazimiroviensis* Zone, Albert Kanaal outcrop, km mark 23.800, Vroenhoven-Riemst, Belgium, in lateral view. D. Plaster cast of holotype MGUH 20220, *Bn. kazimiroviensis* Zone and the equivalent *Argyrotheca stevensis*–*Magas chitoniformis* Zone, Stevns Klint, Denmark, in lateral view.

and ribbed morphotypes attest to the *in situ* evolution of the subspecies from its precursor *H. c. crassus* (= *Hoploscaphites constrictus* subsp. A of Machalski 2005). In summary, the Danish record allows to interpret *H. c. johnjagti* subsp. nov. as the terminal stage in the evolution of the lineage in Europe.

The sample from Melgiew comes from the topmost metre of the upper Maastrichtian succession there and includes 11 adult macroconchs (Fig. 12B; see also Machalski 2005: fig. 9G) and 23 adult microconchs (Fig. 7C; see also Machalski 2005: fig. 9F); the remainder of the specimens are spires and fragments of adults, which cannot be classified in terms of the dimorphism (Machalski 2005). The maximum length of macro- and microconchs ranges between 31 and 36 mm and between 21 and 27 mm, respectively (Fig. 9E). All macroconchs from Melgiew belong to the ribbed morphotype which allows them to be considered con(sub)specific with the sample from the indurated portion of the Grey Chalk at Stevns Klint. This would then provide a time correlation of scaphitid-bearing levels at Stevns Klint and Melgiew (Machalski 2005).

The sample studied from the Limhamn quarry, southern Sweden, is composed of seven adult macroconchs of the ribbed type (Birkelund 1993: pl. 14: 1–4, 6–7, 12).

The sample from the Maastricht area studied comprises six adult macroconchs (Fig. 12C; see also Jagt 1995: pl. 5: 15, 16) and six microconchs. These specimens come from the ENCI, Ankerpoort-Curfs and Blom quarries, and all stem from the upper part of the Meerssen Member of the Maastricht Formation, from subunits IVf-4 to -6 in local terminology (Jagt et al. 1996). These subunits represent the last 5–10 metres of the upper Maastrichtian succession in the area, depending on the locality (Jagt et al. 1996). Adult macroconchs from the Maastricht area range between 32 and 51 mm in maximum length, whereas adult microconchs reach between 31 and 35 mm. Of the five better-preserved adult macroconchs in this lot there are three ribbed individuals: two from the top of IVf-6 and a single one from IVf-4. Body chambers in the two other specimens from subunits IVf-4 and IVf-5/6 are smooth.

Although the number of well-localised specimens available from the Maastricht area is rather limited, it appears likely that the distribution of *Hoploscaphites constrictus* in the upper part of the Meerssen Member is similar to that in the Grey Chalk of the Stevns Klint succession. Populations from lower levels within the upper part of this unit are characterised by the co-occurrence of smooth and ribbed specimens. In contrast,

those from its top seem to be composed exclusively of the ribbed variant. The latter assumption finds support in Jagt (2002: 519), who stated that: “Stout specimens with coarse ornament and ventrolateral tubercles extending to (near) the aperture (forma *crassus* of authors) are best known from the top of the unit (IVf-6)”. In the present paper, the whole sample from the upper part of the Meerssen Member is provisionally attributed to *H. constrictus johnjagti* subsp. nov. However, it cannot be excluded that additional bed-by-bed collecting may show that material from levels below the top of the subunit IVf-6 should actually be assigned to *H. c. crassus*.

All adult macroconchs of *Hoploscaphites constrictus* illustrated by Kennedy et al. (1986: pl. 3: 1, 9–12; pl. 5: 1–17, 21–26) from the upper Maastrichtian of Petites-Pyrénées (France) bear distinct ribs on the flanks and, consequently, are here assigned to *H. c. johnjagti* subsp. nov. The subspecies seems to occur also in the uppermost Maastrichtian, just below the boundary clays, in Mangyshlak, Kazakhstan (reported as *Hoploscaphites constrictus crassus* by Naidin et al. 1990; see also Jolkichev and Naidin 2000: fig. 4: 11), although this needs to be checked during further study.

A single, well-preserved mould of *Hoploscaphites constrictus* from the lowermost Danian *Cerithium* Limestone at Stevns Klint (Machalski and Heinberg in press: figs. 3, 4, 6; Fig. 12A₁–A₄), interpreted as the earliest Danian survivor by Machalski and Heinberg (in press), reveals distinct ribs on the body chamber and is assigned herein to *H. c. johnjagti* subsp. nov. This conclusion is based on the assumption that even a single individual can be assigned to a horizontally defined taxon as it is most probable that it represents the predominant morphology in its population (Dzik 1985). More well-preserved specimens are needed to substantiate this assumption.

Other specimens reported by Machalski and Heinberg (in press) from the *Cerithium* Limestone at Stevns Klint (MGUH 27368, 27359, 27360) are too fragmentary for the style of ribbing on their flanks to be clearly established. The same concerns four specimens of *Hoploscaphites constrictus* from the lowest Danian (Meerssen Member, subunit IVf-7) at the Ankerpoort-Curfs quarry. These (NHMM 2001 180/1, 2, 2002 006, 2002 053A–D, 2002 057), regarded as earliest Danian survivors by Jagt et al. (2003), are preserved as spires retaining small portions of body chamber; these cannot be ascribed to either of the dimorphs.

According to Machalski (2005), the smaller size of adult macroconchs is an additional character which distinguishes populations of *H. c. johnjagti* subsp. nov. from those of *H. c. crassus* in Poland and Denmark (Machalski 2005; compare Fig. 9C, D and Fig. 9E, F). This may still hold true in a more general geographic perspective as adult macroconchs of the subspecies from the Netherlands and France are of a size comparable to specimens from the top of the Maastrichtian succession at Stevns Klint and Melgiew. However, samples of *H. c. crassus* from lower levels in the upper Maastrichtian, e.g., from Rejowiec (Fig. 9B), do not differ significantly from samples of *H. c. johnjagti* subsp. nov., as far as size is concerned.

Microconchs in all samples of *H. c. johnjagti* subsp. nov. studied generally match the style of ribbing of macroconchs (compare Figs. 7C and 12B; see also Fig. 8). Microconchs seem to dominate the record of the subspecies in the Maastricht area (Kennedy 1987; John W.M. Jagt, personal communication 2005) and at Melgiew (Machalski 2005; Fig. 9E). It is not clear whether this results from ecological or preservational bias.

Stratigraphic and geographic range.—Top of the upper upper Maastrichtian in Denmark (top of the *Belemnella kazimiroviensis* Zone and its equivalent *Argyrotheca stevensis*–*Magas chitoniformis* Zone), Sweden (top of *Belemnella kazimiroviensis* Zone), Poland (top of *Belemnella kazimiroviensis* Zone), the Netherlands and Belgium (top of *Belemnella kazimiroviensis* Zone), France, and possibly Kazakhstan (top of *Belemnella kazimiroviensis* Zone). Possibly lowermost Danian at Stevns Klint, Denmark.

Hoploscaphites tenuistriatus (Kner, 1848)

Fig. 13.

- 1848 *Scaphites tenuistriatus* sp. nov.; Kner 1848: 10, pl. 1:5.
 1869 *Scaphites tenuistriatus* Kner; Favre 1869: 21, pl. 5: 6, 7.
 1911 *Hoploscaphites constrictus-tenuistriatus* Kner; Nowak 1911: 585, pl. 33: 13, 14.
 1911 *Hoploscaphites constrictus* Sow. *vulgaris* n. var.; Nowak 1911: 586 (partim), pl. 33: 11, 12 (non pl. 33: 8–10 = *Hoploscaphites constrictus crassus*).
 ?1911 *Hoploscaphites constrictus* Sow. *vulgaris* n. var.; Nowak 1911: 586 (partim), pl. 33: 17, 18, 20 (non 15, 16 = *Hoploscaphites constrictus*, non 19 = *Hoploscaphites* sp. juv.).
 ?1911 *Hoploscaphites constrictus* Sow. *tenuistriatus* Kner; Nowak 1911: 586 (partim), pl. 33: 21 (non 22 = *H. constrictus*).
 1932 *Hoploscaphites constrictus* Sow; Wolansky 1932: 10 (partim), pl. 1: 6 (*Hoploscaphites constrictus* var. *tenuistriata* in figure caption) (non 10 = *Hoploscaphites* sp. ex gr. *pungens-schmidi*; non 11 = *Hoploscaphites schmidi*, non 12 = *Hoploscaphites constrictus*).
 1974 *Hoploscaphites constrictus tenuistriatus* (Kner, 1848); Naidin 1974: 173, pl. 58: 12, pl. 60: 5, 6.
 1974 *Hoploscaphites constrictus constrictus* (Sowerby); Naidin 1974: 173 (partim), pl. 58: 9 (non 7, 8 = *Hoploscaphites constrictus*).
 1974 *Hoploscaphites constrictus nicolletii* (Meek); Naidin 1974: 174, pl. 58: 13.
 1982 *Hoploscaphites tenuistriatus* (Kner, 1848); Birkelund 1982: 21, pl. 2: 8–10.
 1987 *Hoploscaphites tenuistriatus* (Kner, 1848); Kennedy 1987: 201 (partim), pl. 31, 2–3, 7 (non 4–6 = *Hoploscaphites* sp. indet).
 1987 *Hoploscaphites tenuistriatus* (Kner, 1848); Kennedy and Summesberger 1987: 35, pl. 11: 3.
 1987 *Hoploscaphites constrictus tenuistriatus* (Kner, 1848); van der Tuuk 1987: 72, fig. 19.
 1993 *Hoploscaphites tenuistriatus* (Kner, 1848); Birkelund 1993: 59 (partim), pl. 14: 8–11, 15, 16 (non 13 = *Hoploscaphites* sp. and non 14 = *Hoploscaphites felderi* Kennedy, 1987).

Type material: The specimen from the lower upper Maastrichtian “Kreidemergel” of Kiselka, north of Lviv, illustrated by Kner (1848: pl. 1: 5) should be designated lectotype if still in existence (Kennedy 1987: 201).

Material.—From Germany: three specimens from Hemmoor (NLfB kma 190–192) and two from Rügen (MGUH 20163,

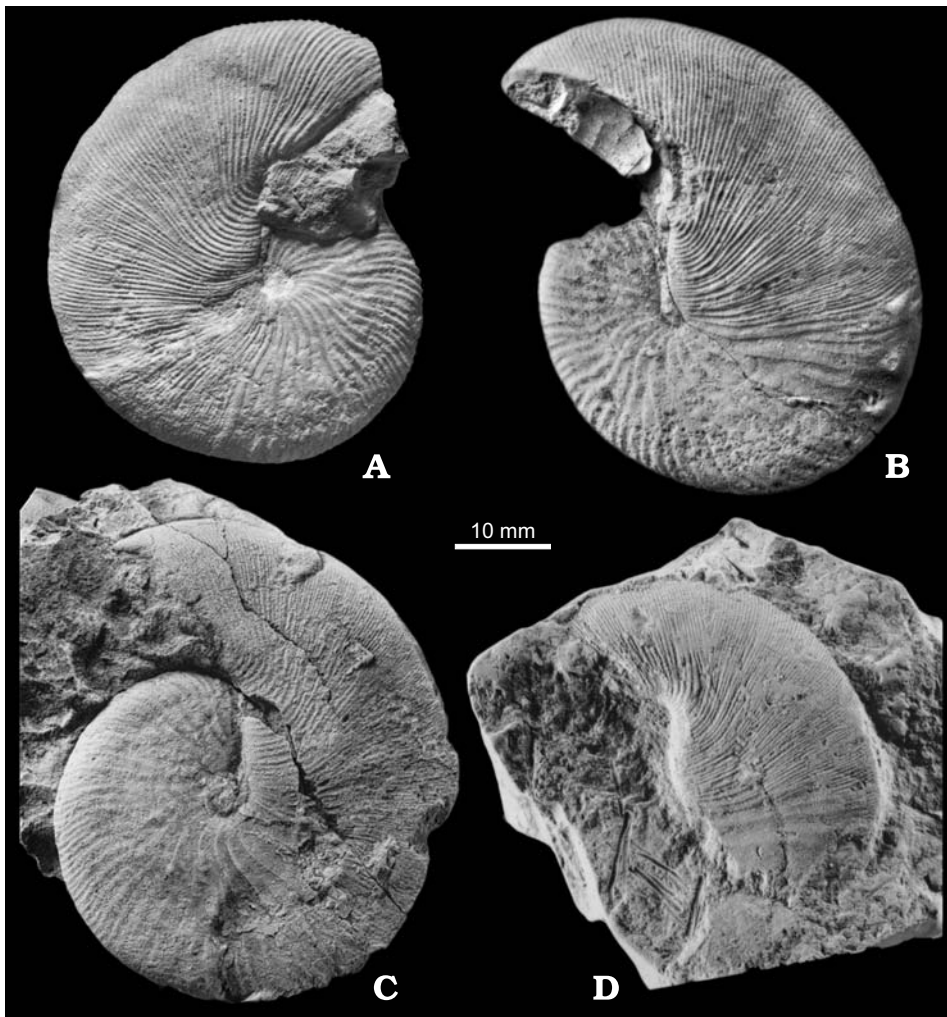


Fig. 13. *Hoploscaphites tenuistriatus* (Kner, 1848), adult macroconchs. A–C. From *Spyridoceramus tegulatus*–*Belemnitella junior* Zone, Lviv, the Ukraine, DPM NANU PZ-K-N9841 (A), DPM NANU PZ-K-N9342 (B), DPM NANU PZ-K-N9340 (C). D. ZPAL Am. 12/206, *Sp. tegulatus*–*Bt. junior* Zone, level II at Chełm, Poland (collected by A. Pisera and M.A. Bitner). All specimens in lateral views.

20166). From the Ukraine: 16 specimens from Lviv (DPN NANU PZ-K-N5606, 9841a–c, 9842a–h, 9290, 9340–9342). From Denmark: four specimens from Ålborg, Jylland (MGUH 20160–20162, 20167). From Poland: a single specimen from Chełm (ZPAL Am. 12/206).

Discussion.—Some confusion surrounds the type horizon and locality of this species. According to Kennedy and Summesberger (1987), Kner's specimen came from the lower lower Maastrichtian sandy opoka of Nagoryany, the Ukraine (*Belemnella lanceolata* and/or *Bn. obtusa* zones, see Christensen 1987). In fact, this specimen is from locality Kiselka (Kner 1848), now being a part of Lviv near Wysoki Zamek (Julia Didenko, personal communication 2005), where the only Maastrichtian strata outcropping are the marls of the "Lvovskaja svita". The type specimen of *Hoploscaphites tenuistriatus* is thus much younger than reported by Kennedy and Summesberger (1987), coming from strata correlating with the *Spyridoceramus tegulatus*–*Belemnitella junior* Zone as defined at Hemmoor.

A sample of 24 adult macroconchs from the "Lvovskaja svita" of Lviv is available for the present study. Most of these are fragmentary or crushed. Thus, reliable measurements of maximum diameter could only be obtained from DPM

NANU PZ-K-N9841a (47 mm) and DPM NANU PZ-K-N9340 (51 mm).

The most distinctive feature of *H. tenuistriatus* is the ribbing of the body chamber, which consists of fine, crowded, flexuous striae or riblets. The ribbing is dense although it varies rather widely. For example, the number of ribs on the last centimetre of the body chamber varies between 11 and 20 in a suite of six measurable specimens from Snopków brickyard at Lviv, the Ukraine (DPM NANU PZ-K-N3182a–f). In contrast, the ribbing of the spire is coarse and does not differ from that seen in *H. constrictus*.

Although some earlier authors (Nowak 1911; Birkelund 1979) mentioned specimens of *H. tenuistriatus* with tubercles, only non-tuberculate individuals (like those in Fig. 13A, C), have conventionally been assigned to this species by subsequent authors (Birkelund 1982, 1993; Kennedy 1987). There are three tuberculate specimens in the sample studied from Lviv: DPM NANU PZ-K-N5606, 9842a, and 9342 (the first specimen being the original of Nowak 1911: pl. 33: 14). These specimens are characterised by the presence of a rather narrow sector of diffused ribbing with three or four ventrolateral tubercles near the base of the body chamber (e.g., Fig. 13B). A similar sector, with a faint trace of at least one tuber-

cle visible, is present near the base of the otherwise densely ribbed and non-tuberculate body chamber in ZPAL Am. 12/206 from level II at Chelm (Fig. 13D).

Tuberculate individuals of *Hoploscaphites* with fine ribbing on the body chamber were illustrated by Naidin (1974, pl. 58: 9) from the lower Maastrichtian of Crimea and by Nowak (1911: pl. 33: 11, 12, 14, 22) from the lower upper Maastrichtian of Lviv. The latter material was tentatively assigned by Jeletzky (1962) to the North American *Hoploscaphites nicolletii* (Morton, 1842) (see Landman and Waage 1993a, for a revision). Jeletzky's view was followed by Naidin (1974) for specimen DPM NANU PZ-K-N5606, which bears a strong resemblance to *H. nicolletii* as seen in the photograph presented by Nowak (1911: pl. 33: 14; refigured by Naidin 1974: pl. 58: 13). Contrary to Jeletzky (1962) and Naidin (1974), Landman and Waage (1993a: 100) did not accept the occurrence of *H. nicolletii* in the Old World, arguing that the smaller umbilicus and the lack of a strong adapertural projection of the ribs and growth lines on the venter in the European specimens precluded their conspecificity with *H. nicolletii*. This view is supported here as a re-examination of the surviving fragment of specimen DPM NANU PZ-K-N5606 (Nowak 1911: pl. 33: 14) reveals that its ribbing, if corrected for *post-mortem* deformation, does not differ from that of other individuals of *H. tenuistriatus* from Lviv.

In conclusion, the tuberculate specimens with dense, *tenuistriatus*-like ribbing on the body chamber are best interpreted as indigenous European scaphitids, morphologically intermediate between *H. constrictus* and *H. tenuistriatus*. The latter species is best regarded as a short-ranging offshoot of the *H. constrictus* lineage. This is contra Birkelund (1967) and Cooper (1994), who proposed a transition from *H. greenlandicus* Donovan, 1953 through *H. tenuistriatus* to *H. constrictus*.

It is tempting to interpret "transitional" specimens as members of truly transitional populations between *H. constrictus* and *H. tenuistriatus*. However, the specimens from Lviv are late Maastrichtian in age and thus significantly postdate the first populations of *H. tenuistriatus* from Hemmoor (see Birkelund 1982: fig. 1), Denmark and the Isle of Rügen (Birkelund 1993) which are of early Maastrichtian age. Moreover, tuberculate specimens with dense ribbing on the body chamber are separated by a distinct morphological gap from co-occurring *H. constrictus lvivensis* subsp. nov., at Lviv as well as at Chelm. Accordingly, tuberculate specimens from these locations are interpreted as atypical end-members of *H. tenuistriatus* populations. The tuberculation preserved in these specimens is thought to be an atavistic feature, attesting to their evolutionary origin. The populations of *Hoploscaphites constrictus* truly ancestral to *H. tenuistriatus* should be sought in the upper lower Maastrichtian. The presence of a very finely ribbed, small individual of *H. constrictus* in the *Belemnella sumensis* Zone of Neuberg, Austria (Kennedy and Summesberger 1986: pl. 16: 13) is worth mentioning in this respect.

According to Radwański (1996: 125), *Hoploscaphites tenuistriatus* "is very similar, if not identical" to *H. melloi* Landman and Waage, 1993a from the lower upper Maas-

trichtian of the Western Interior, North America (see Kennedy et al. 1998: fig. 1 for a correlation of Western Interior ammonite zones with the standard subdivision of the Maastrichtian). Both taxa are indeed similar in ornament. However, *H. tenuistriatus* is characterised by a smaller umbilicus and taller body chamber than *H. melloi*. Moreover, it lacks the strong adapertural projection of the ventral ribs and growth lines, which is regarded to be a distinctive feature of the Western Interior *Hoploscaphites* lineage (Landman and Waage 1993a).

Only macroconchs are present in the material studied and in most collections illustrated by other authors. A small individual from Hemmoor (NLFb kma 187) figured by Birkelund (1982: pl. 2: 5), interpreted by her as a microconch of *Hoploscaphites constrictus* or *H. tenuistriatus*, reveals numerous minute tubercles on the ventrolateral shoulder and is here assigned to *H. constrictus*. The only possible microconchs of the present species are the "Zwergexemplare" (dwarf specimens) of *Hoploscaphites* from the "Lvovskaja svita" at Lviv, illustrated by Nowak (1911: pl. 33: 17, 18, 20, 21). As far as it can be discerned from the photographs in Nowak (1911), these specimens are non-tuberculate and finely ribbed on the near-apertural portions of their body chambers.

Stratigraphic and geographic range.—Upper lower Maastrichtian and/or lower upper Maastrichtian of the Netherlands and Belgium ("Inoceramus" *morgani* Zone, Ireneusz Walaszczyk and John W.M. Jagt, unpublished data), Germany (*Belemnella sumensis* to *Spyridoceramus tegulatus*–*Belemnella junior* zones), Denmark (*Rugia tenuicostata*–*Meonia semiglobularis* to *Meonia semiglobularis*–*Ruegenella humboldtii* zones), Poland (*Spyridoceramus tegulatus*–*Belemnella junior* Zone) and the Ukraine (*Spyridoceramus tegulatus*–*Belemnella junior* Zone). Less well-constrained records are from the lower Maastrichtian of Isle of Rügen, the Czech Republic and southern Russia.

Hoploscaphites pungens (Binkhorst, 1861)

Figs. 14B, D, 17A, B.

1861 *Ammonites pungens* sp. nov.; Binkhorst van den Binkhorst 1861: 32, pl. 5a3: 1a–d.

?1982 *Discoscaphites acutituberculatus* sp. n.; Tzankov 1982: 25, pl. 7: 9, 10.

1987 *Hoploscaphites pungens* (Binkhorst, 1861); Kennedy 1987: 202, pl. 23: 3, 4; pl. 32: 22–25; pl. 34: 2–6, 10, 11, 18, 19; pl. 35: 1–11.

1987 *Hoploscaphites pungens* (van Binckhorst [sic] 1861); van der Tuuk 1987: 62, figs. 12, 18a–c.

1994 *Hoploscaphites pungens* (Binckhorst [sic], 1861); Jagt and Kuypers 1994: fig. 3a, b.

1995 *Hoploscaphites pungens* (Binkhorst van den Binkhorst, 1861); Jagt 1995: 31, pl. 5: 5–14.

1998 *Hoploscaphites* sp. nov.; Kennedy and Jagt 1998: 163 (partim), pl. 2: 10, 11 (non pl. 2: 12–15 = *H. sp. ex gr. waagei-angmartus-sutensis*).

Type material: Holotype, by monotypy, is MNB C606a, b, a microconch, the original of Binkhorst (1861: pl. 5a3: 1a–d), refigured by Kennedy (1987: pl. 35: 1–3), from the lower upper Maastrichtian Kunrade Limestone facies of the Maastricht Formation at Kunrade, the Netherlands.

Material.—From Belgium: five specimens from CBR-Romontbos quarry (NHMM 1992062–1992066). From the Netherlands: a single specimen from Kunrade (NHMM 003529) and a silicone cast of a single specimen from the ENCI quarry (NHMM JJ 11883).

Discussion.—Topotypical material of *Hoploscaphites pungens* as described by Kennedy (1987) comes from the upper portion of the Kunrade Limestone facies of the Maastricht Formation (Kennedy 1987; Jagt and Kuypers 1994) as formerly exposed in the Kunrade-Benzenrade area (the Netherlands). Most of these specimens are adult microconchs characterised by a low whorl to the body chamber, trapezoid whorl section, blunt ribs and prominent tuberculation. The tuberculation of the phragmocone consists of lateral tubercles (inner ventrolateral tubercles of Kennedy 1987) and much stronger ventrolateral ones (outer ventrolateral tubercles of Kennedy 1987). The lateral tubercles do not extend onto the body chamber while the ventrolaterals do, but never reach the hook. Quite strong ventral swellings are observed on the body chambers of some specimens, including the holotype.

Kennedy (1987) thought *H. pungens* to be endemic to the Kunrade area. However, subsequent studies have demonstrated this species to occur in the Gronsveld (Jagt and Kuypers 1994), Nekum and basal Meerssen members (van der Tuuk 1987; Jagt 1995, 2002) of the Maastricht Formation. *Hoploscaphites pungens* has never been reported from outside the Maastricht area. However, *Discoscaphites acutituberculatus* Tzankov, 1982 from the upper Maastrichtian of Drandar near Varna, Bulgaria, based on tuberculate spires, seems to be closely related, if not conspecific. One of the specimens figured by Tzankov (1982: pl. 7: 10) appears closely similar to a spire of *H. pungens* studied herein (NHMM 1992063) from the upper Nekum Member at the CBR-Romontbos quarry (Jagt 1995: pl. 5: 9, 10). A direct study of the originals from Bulgaria is needed to clarify the taxonomic position of *D. acutituberculatus*.

Adult microconchs from the upper Maastrichtian Severn Formation of Maryland, identified as *Jeletzkytes nebrascensis* (Owen, 1852) by Landman and Waage (1993a: fig. 133A–C) and Kennedy et al. (1997: pl. 22: A–C, pl. 23: D, E) are similar to *H. pungens*, although associated macroconchs (e.g., Landman and Waage 1993a: pl. 133 D) morphologically resemble typical specimens of *J. nebrascensis* as recorded from the U. S. Western Interior (Landman and Waage 1993a).

Kennedy (1987) was unable to separate his material into macro- and microconchs. According to Jagt (1995: 32), specimens studied by Kennedy represented microconchs, “as they lack an umbilical bulge and body chambers are not markedly inflated”. This view is supported here, except for a single specimen (Kennedy 1987: pl. 34: 10, 11) here regarded to be a macroconch as based on the proportions of the preserved part of the body chamber. Specimens illustrated by Jagt and Kuypers (1994: fig. 3a, b) and Jagt (1995: pl. 5: 5–7) are considered macroconchs for the same reason.

Amongst the specimens studied, NHMM JJ 11883 from the basal metre of the Nekum Member (Maastricht Forma-

tion) is also an adult macroconch c. 85 mm in maximum diameter. Specimen NHMM 1992066 (Jagt 1995: pl. 5: 14) is clearly a microconch. Specimens NHMM 1992063 (Jagt 1995: pl. 5: 9, 10) and NHMM 1992064 (Jagt 1995: pl. 5: 11, 12; Fig. 14B) are too fragmentary to be identified in terms of dimorphism.

All macroconchs share the same style of tuberculation with microconchs of *H. pungens* (Fig. 17A, B) and are held to be conspecific. NHMM JJ 11883 (Figs. 14D, 17B) is the best-preserved adult macroconch known to date. The phragmocone tuberculation consists of four rows; the outermost position is taken by strong ventrolateral tubercles, followed by outer lateral ones, which are less pronounced than the ventrolaterals. The next row is formed by incipient, swollen inner laterals, followed by umbilical bullae. Only fine ventrolaterals and massive umbilical bullae/tubercles are visible on the preserved part of the body chamber. The ribbing of the phragmocone consists of robust and straight primaries, closely resembling those of microconchs (compare Fig. 17A, B) and secondaries, which are more densely spaced than the primaries and originate at the line of the outer lateral tubercles. The preserved part of the body chamber is covered by delicate primaries and secondaries of various lengths.

The largest specimen of *H. pungens* seen is NHMM 003529 (Kennedy 1987: pl. 35: 10, 11), a fragment of a body chamber with a low whorl, thus almost certainly a microconch. The specimen is too fragmentary to be adequately measured. However, it appears larger than the largest macroconch (NHMM JJ 11883). The only other scaphitid species with a similar size relationship between macro- and microconchs is *Hoploscaphites pumilus* (Stephenson, 1941) from the Campanian/Maastrichtian boundary interval of the United States (Kennedy and Cobban 1993) and Europe (Kennedy et al. 1986; Machalski and Odin 2001). The largest microconchs of this species, defined by the concave umbilical wall of the shaft, are larger than the largest known macroconchs, defined by the presence of an umbilical bulge (Machalski and Odin 2001: 491).

Kennedy (1987) considered *H. pungens* to be a short-lived offshoot of the *H. constrictus* lineage. He stressed its overall similarity to *H. schmidi* (Birkelund, 1982), also based on a microconch (see below), but stated that the latter species “never develops the inner ventrolateral tubercles of *pungens* [lateral tubercles in the present paper] and has a very feebly ribbed final section of the body chamber. The siphonal and outer ventrolateral tubercles are also much stronger in *pungens*” (Kennedy 1987: 203). This is not entirely true as a row of incipient lateral tubercles does occur in the phragmocone of the holotype of *H. schmidi* (Figs. 16A₁, 17C). Macroconchs of *H. pungens* and *H. schmidi* show an even closer similarity, the only significant difference being the presence of an additional row of lateral tubercles on the phragmocone and a coarser ribbing of the hook in the former (compare Fig. 17B and D).

Cooper (1994) united *H. pungens* and *H. schmidi* in a new subgenus, *Hoploscaphites (Tovebirkelundites)*, defined on

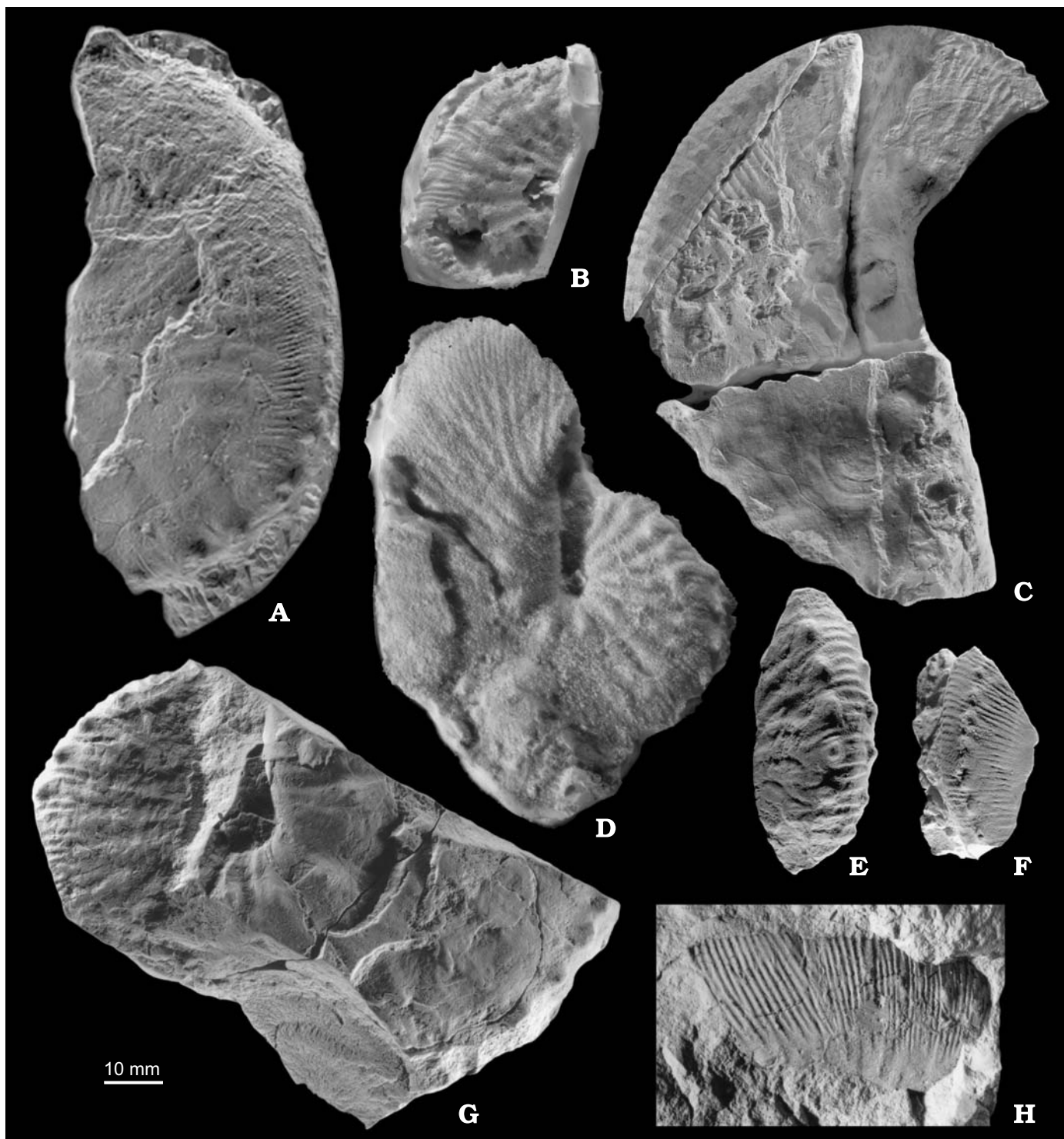


Fig. 14. *Hoploscaphites schmidti* (Birkelund, 1982) (A, C, E–H) and *Hoploscaphites pungens* (Binkhorst, 1861) (B, D). A. NLFb kma 186, *Tenuipteria argentea*–*Belemnitella junior* Zone, Hemmoor, Germany. B. NHMM 1992064 (silicone rubber cast of no. 310788 in the Lux collection), *Bt. junior* Zone, CBR-Romontbos quarry. C. MGUH 27744, *Rugia tenuicostata*–*Meonia semiglobularis* or *Meonia semiglobularis*–*Ruegenella humboldtii* zones, Hillerslev, Denmark. D. Silicone rubber cast of NHMM JJ 11883, *Bt. junior* Zone, ENCI-quarry. E. NLFb Ma 13570, Hemmoor, Germany. F. NLFb Ma 13571, Hemmoor, Germany. G. ZPAL Am. 12/707, *Spyridoceras tegulatus*–*Belemnitella junior* Zone, level III at Chelm, Poland. H. ZPAL Am. 12/703, *Sp. tegulatus*–*Bt. junior* Zone, level III at Chelm, Poland. Specimens A, C, D, G, H are adult macroconchs. All specimens in lateral views, except for E, which is in oblique view.

the basis of conspicuous siphonal swellings on the body chamber (Cooper 1994: 184). However, Kennedy and Jagt (1998) pointed out the presence of siphonal swellings in

Hoploscaphites constrictus and concluded *Tovebirkelundites* to be a junior synonym of *Hoploscaphites* sensu stricto.

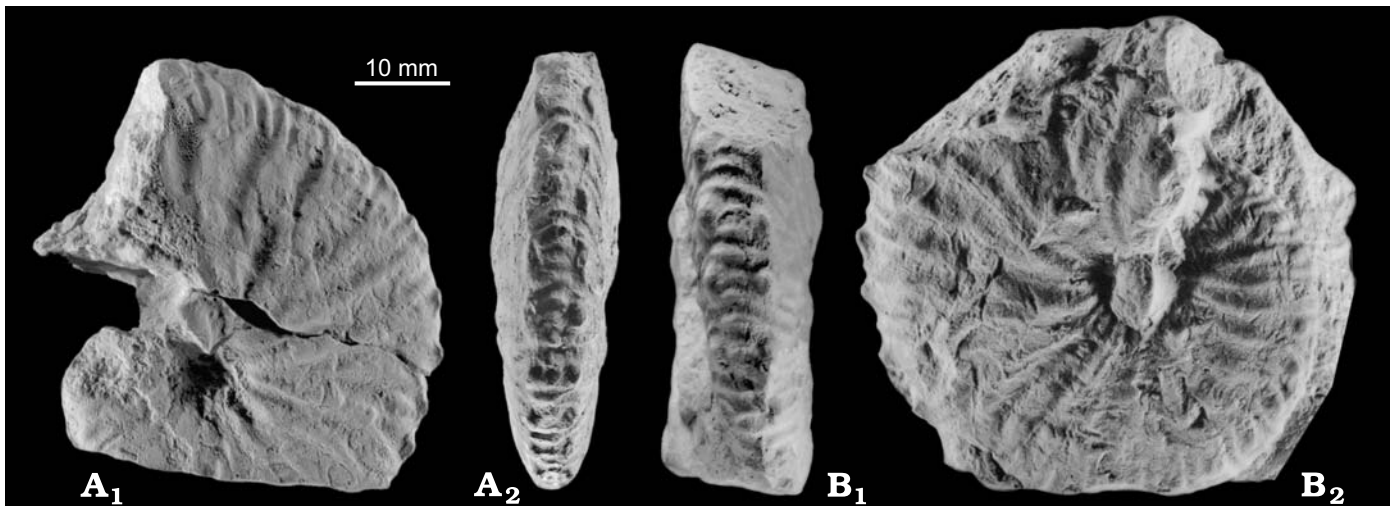


Fig. 15. *Hoploscaphites schmidi* (Birkelund, 1982), macroconch spires. A. NLfB kma 180, *Tenuipteria argentea*–*Belemnitella junior* Zone, Hemmoor, Germany, in lateral (A₁) and ventral (A₂) views. B. ZPAL Am. 12/707, *Spyridoceramus tegulatus*–*Belemnitella junior* Zone, level III at Chełm, Poland, in ventral (B₁) and lateral (B₂) views.

Stratigraphic and geographic range.—Lower upper Maastrichtian in the Netherlands and Belgium (*Belemnitella junior* Zone of authors) and, possibly, upper Maastrichtian of Bulgaria.

Hoploscaphites schmidi (Birkelund, 1982)

Figs. 14A, C, E–H, 15, 16A, 17C, D.

1932 cf. *Acanthoscaphites tridens* Kner var. *trinodosus* (Nowak); Wolansky 1932: 10 (partim), pl. 1: 11 (pl. 2: 4 = *Acanthoscaphites* ex gr. *tridens*).

1982 *Acanthoscaphites schmidi* Birkelund 1982: 17, pl. 1: 7–9.

1982 *Acanthoscaphites schmidi* Birkelund 1982: 18, pl. 1: 10; pl. 2: 1–4.

1982 *Hoploscaphites constrictus* (Sowerby, 1818 [sic]); Birkelund 1982: 19 (partim), pl. 3: 12 (non pl. 3: 1–11, 13, 14 = *Hoploscaphites constrictus*).

1982 *Acanthoscaphites varians* (Łopuski, 1911); Birkelund 1982: 16 (partim), pl. 1: 6 (non pl. 1: 4 = *Hoploscaphites* sp. ex gr. *pungens-schmidi*, non pl. 1: 5 = *Acanthoscaphites* (*Euroscaphites*) *variens blaszkiewiczzi*).

Type material: Holotype is NLfB kma 181, a microconch from the lower upper Maastrichtian at Hemmoor, northern Germany (Birkelund 1982: 17, pl. 1: 7–9, refigured here as Fig. 16A₁, A₂).

Material.—From Germany: 13 specimens from Hemmoor (NLfB kma 180–186, 204, 206, NLfB Ma 13570, 13571, plus two unregistered specimens). From Poland: five specimens from Chełm (ZPAL Am. 12/703, 704, 707, 717, 718). From Denmark: a single specimen, in four parts, from Hillelev (MGUH 27744).

Discussion.—Prior to the present study, *Hoploscaphites schmidi* was known exclusively from the Hemmoor section. According to Birkelund (1982), the holotype, an adult microconch 46 mm in maximum diameter (Birkelund 1982: pl. 1: 7–9; Fig. 16A₁, A₂), was collected at 28.4 metres above the lower/upper Maastrichtian boundary clay bed M900 (T100). This level falls within the *Belemnitella junior* Zone (Birkelund 1982) and the lower part of the *Tenuipteria argentea*–*Belem-*

nitella junior Zone (Schulz and Schmid 1983). The holotype was described in detail by Birkelund (1982). Only the presence of two rows of tubercles on the whole of the exposed portion of the phragmocone (Figs. 16A₁, A₂, 17C) needs to be stressed herein, the ventrolaterals being much stronger than the laterals.

Specimen NLfB kma 206 (Birkelund 1982: pl. 3: 12) is reinterpreted as another microconch of the species, because this fragment is indistinguishable from the corresponding part in the holotype (Jagt et al. 1999). This specimen comes from an unknown level above M900 (Birkelund 1982).

The remainder of topotypical material represents macroconchs (Birkelund 1982). This material shares the feeble ventral ribbing on the later part of the body chamber with the microconch holotype and is regarded to be conspecific beyond doubt (Fig. 17C, D). The largest preserved macroconch fragment, NLfB kma 186 (Birkelund 1982: pl. 2: 4; Fig. 14A), suggests an individual c. 100 mm in maximum diameter. The presence of distinct ventral (siphonal) swellings on the early part of the shaft and their absence from the later part should be stressed; see Figs. 14A, 17D).

The macroconch material from Hemmoor comes from the upper *Spyridoceramus tegulatus*–*Belemnitella junior* to lower *Tenuipteria argentea*–*Belemnitella junior* zones of Schulz and Schmid (1993). Amongst four unregistered NLfB specimens studied (e.g., Fig. 14E, F), a single specimen is from the base of the *T. argentea*–*Bt. junior* Zone, while the remaining individuals are either from below or above the lower/upper Maastrichtian boundary and lack additional provenance data. In summary, the material of *H. schmidi* from Hemmoor is averaged from an interval of 30–40 metres in minimum thickness. In spite of this, all specimens studied show a rather uniform style of ornament.

Specimen NLfB kma 180, a spire with the initial part of the body chamber preserved, from the lower part of the *T. argentea*–*Bt. junior* Zone (Birkelund 1982: pl. 1: 6; Fig. 15A₁,

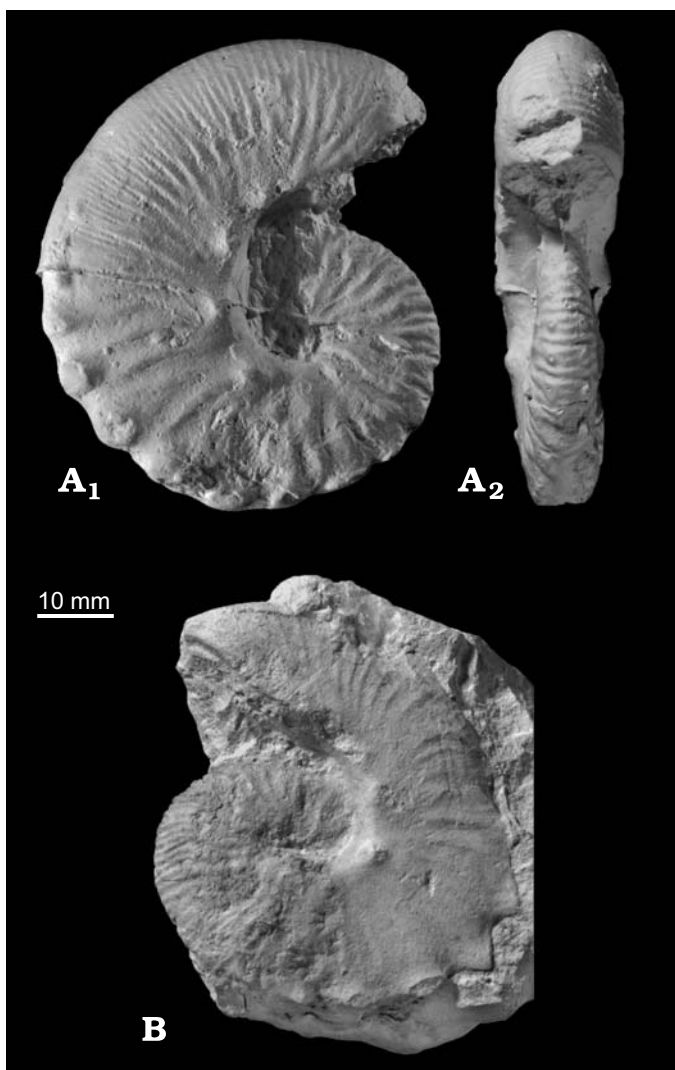


Fig. 16. **A.** Plaster cast of the holotype of *Hoploscaphites schmidi* (Birkelund, 1982), an adult microconch NLfB kma 181, *Tenuipteria argentea*–*Belemnitella junior* Zone, Hemmoor, Germany, in lateral (A_1) and apertural (A_2) views. **B.** *Hoploscaphites schmidi*?, an adult microconch ZPAL AM. 12/97, *Belemnella kazimiroviensis* Zone, Albrychtówka, Poland, in lateral view.

A_2), is not *Acanthoscaphites varians* as claimed by Birkelund (1982). Its ornament is almost identical to that of a spire from Chełm (Fig. 15B₁, B₂) (specimen ZPAL Am. 12/707; see also Fig. 14G) with a morphology typical of *H. schmidi* as defined on Hemmoor material (compare Fig. 15A₁, A₂ and B₁, B₂).

New material of *Hoploscaphites schmidi*, consisting of adult macroconchs, demonstrates the wider geographic range of this species. Five specimens are from the *Spyridoceramus tegulatus*–*Belemnitella junior* Zone at Chełm (levels III and IV) and a single specimen is from Hillerslev, Jylland (exact horizon unknown but the Hillerslev section spans the *Rugia tenuicostata*–*Meonia semiglobularis* to *Meonia semiglobularis*–*Ruegenella humboldtii* zones, see Surlyk 1984: fig. 3).

The most complete specimen from Chełm is ZPAL Am. 12/707 from level III. This is an incomplete spire with a portion of the body chamber preserved (Figs. 14G, 15B₁, B₂). The

ornament of the spire consists of rather coarse ribs which cross the venter and of two rows of tubercles. The ventrolaterals are much stronger than the bullate outer ventral tubercles. The flanks of the preserved portion of the body chamber are essentially smooth with traces of faint ribbing. The tuberculation of the body chamber consists of umbilicolateral and ventrolateral tubercles of similar strength. A less distinct row of ventral tubercles is also visible on the preserved part of the body chamber (Fig. 14G). This thus matches well the corresponding region in specimen NLfB kma 186 (Birkelund 1982: pl. 2: 4; Fig. 14A). The remainder of the body chamber in ZPAL Am. 12/707 is broken off, except for the periumbilical area with well-developed umbilicolateral tubercles and weak ribs. This part of the Chełm specimen corresponds well to the corresponding portion in specimen NLfB kma 184 from Hemmoor (Birkelund 1982: pl. 2: 2).

Other specimens from Chełm are shaft and hook fragments with preserved fine ventrolateral tubercles (but no ventral swellings) and relatively fine ribs crossing the venter (e.g., ZPAL Am. 12/703 in Fig. 14H). Size and style of ornament of these specimens is very similar to corresponding fragments from Hemmoor (Birkelund 1982: pl. 1: 10; pl. 2: 1, 3).

Specimen MGUH 27744 from Hillerslev (Fig. 14C) is an external cast, in four parts, of the body chamber of a macroconch, 90 mm in maximum diameter. An early, smooth part of the body chamber with massive ventrolateral tuberculation is well visible and is similar to those in Polish and German specimens. Most of the flank area in the more adapertural part of the shaft is obliterated. Only the outer flank and venter are better seen. Fine and rather dense ventrolateral tuberculation on this part of the Hillerslev specimen matches well the German and Polish counterparts. However, the ribbing seems to be coarser and more regular (Fig. 14C). Most probably this reflects intrapopulation variation of the species.

Wolansky's specimen (1932: pl. 1: 11) is from an unknown level within the lower Maastrichtian of Rügen, and represents the basal portion of the body chamber of a fairly large specimen with two rows of massive tubercles and is reminiscent of corresponding parts in more complete specimens from Hemmoor and Chełm.

A well-preserved specimen, ZPAL Am. 12/97, from Albrychtówka (a hill between Podgórz and the town quarry near Kazimierz Dolny, Middle Vistula River section) is an adult microconch, 42 mm in maximum diameter (Fig. 16B). Although crushed, it resembles the holotype of *Hoploscaphites schmidi* in style of ornament and even shows incipient ventrolateral tubercles in the early exposed part of the spire. Accordingly, ZPAL Am. 12/97 is referred to as *Hoploscaphites schmidi*?. An alternative interpretation is, however, that this specimen is an atypical end member of the population of *Hoploscaphites constrictus crassus* (Łopuski, 1911). The specimen is from a significantly higher level than the material firmly assigned to *H. schmidi*, having been collected from the lower part of the *Bn. kazimiroviensis* Zone.

According to Kennedy (1987) and Cooper (1994), *H. schmidi* and *H. pungens* are short-lived offshoots of the *H.*

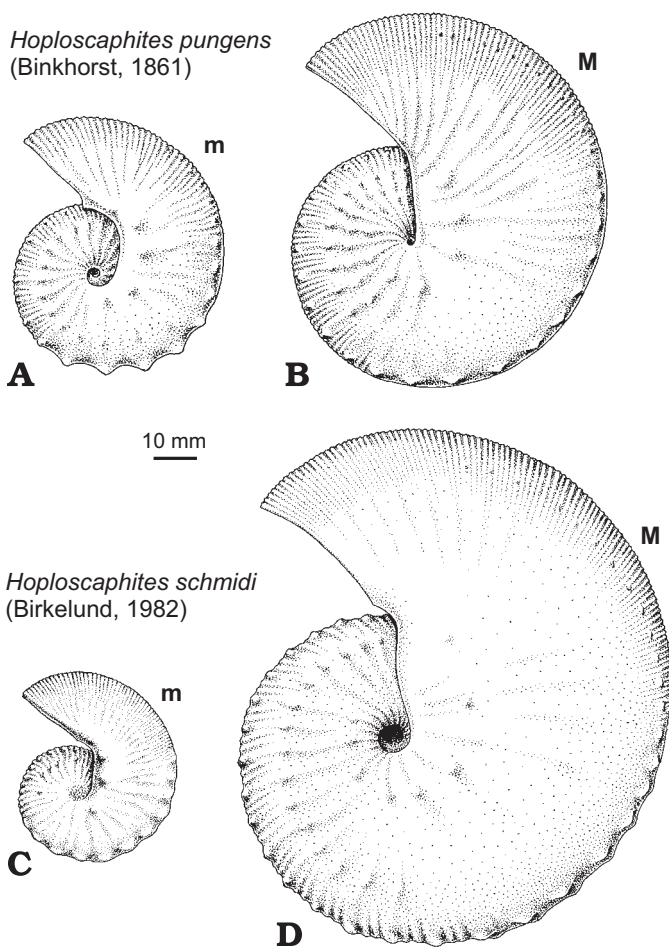


Fig. 17. Dimorphic pairs of *Hoploscaphites pungens* (Binkhorst, 1861) (A, B) and *Hoploscaphites schmidi* (Birkelund, 1982) (C, D), m, microconchs; M, macroconchs. A based on Kennedy (1987: pl. 35), B based on NHMM JJ 11883, C based on NLFb kma 181, D based on ZPAL Am. 12/707, 12/703 and NLFb kma 186.

constrictus lineage. In this context it should be noted that the presence of ventrolateral tuberculation on the entire exposed spire of the holotype of *H. schmidi* recalls an analogous situation in *H. constrictus livivensis* subsp. nov. which occurs in coeval strata at Chełm. Thus, this member of the *H. constrictus* lineage may have been ancestral to *H. schmidi*.

Stratigraphic and geographic range.—Upper lower and/or lower upper Maastrichtian of Germany (*Spyridoceramus tegulatus*–*Belemnitella junior* and *Tenuipteria argentea*–*Belemnitella junior* zones), Denmark (*Rugia tenuicostata*–*Meonia semiglobularis* Zone or *Meonia semiglobularis*–*Ruegenella humboldtii* Zone) and Poland (*Spyridoceramus tegulatus*–*Belemnitella junior* Zone).

Hoploscaphites sp. ex gr. *pungens*–*schmidi*

Fig. 18.

?1932 *Hoploscaphites constrictus* Sow.; Wolansky 1932: 10 (partim), pl. 1: 10 (non pl. 1: 6 = *Hoploscaphites tenuistriatus*, non pl. 1: 12 = *Hoploscaphites constrictus*).

1982 *Acanthoscaphites varians* (Lopuski); Birkelund 1982: 16 (partim),

pl. 1: 4 (non pl. 1: 5 = *Acanthoscaphites varians blaszkiewiczzi*, non pl. 1: 6 = *Hoploscaphites schmidi*).

1987 *Acanthoscaphites* sp.; Kennedy 1987: 208, pl. 32: 15–17.

?1995 ?*Acanthoscaphites* sp. *sensu* Kennedy, 1987; Jagt 1995: 32, pl. 7: 5, 6, 8, 9.

Material.—From Poland: a single specimen from Chełm (ZPAL Am. 12/706). From Denmark: a single specimen from Gudumholm, Jylland (MGUH 27745). From Germany: a single specimen from Hemmoor (NLFb kma 178).

Discussion.—According to Kennedy (1987: 208), his *Acanthoscaphites* sp. “differs from the other *Acanthoscaphites* from the Limburg Maastrichtian in the flexuosity of the flank ribs, presence of only a single order of flank ribs (separating it from *A. verneuilianus*) and no umbilical bullae (separating it from *H. pungens*)”. The specimen described by Kennedy (1987) is from the Kunrade Limestone facies of the Maastricht Formation at Kunrade and consists of half of a whorl, septate for the largest portion (Kennedy 1987: pl. 32: 15–17). Tuberculation consists of distinct ventrolaterals and incipient laterals; no umbilical bullae are visible. Primary ribs are flexuous and prorsiradiate on the flanks; secondaries originate at the junction of flank and ventrolateral shoulder.

All specimens assigned herein share the rib flexuosity with *Acanthoscaphites* sp. of Kennedy (1987). Specimen ZPAL Am. 12/706 (Fig. 18C) comes from level III at Chełm. It is a fragment of a spire plus the early part of the body chamber, 54 mm in maximum preserved diameter. Specimen ZPAL Am. 12/706 shares the presence of distinct ventrolateral tubercles and incipient lateral tubercles with that from Kunrade. In addition, it has umbilical bullae, which are present in *H. pungens* and absent from the Kunrade individual.

Specimen MGUH 27745 (Fig. 18B₁, B₂) is from the Gudumholm section, northern Jylland (*Meonia semiglobularis*–*Ruegenella humboldtii* Zone of Surlyk 1984: fig. 3). It is a fragment of phragmocone with part of the body chamber preserved, 48 mm in maximum preserved diameter. The specimen is probably a macroconch which can be inferred from a convexity of the preserved part of the umbilical wall of the shaft. The tuberculation in MGUH 27745 follows the pattern seen in the Kunrade specimen but the lateral tubercles strengthen markedly adaperturally. There are no umbilical bullae on the specimen, a feature shared with the Kunrade individual.

Specimen NLFb kma 178 (Fig. 18A) is from 20.1 metres above the lower/upper Maastrichtian boundary clay M900 (T100) at Hemmoor, thus from the *Sp. tegulatus*–*Bt. junior* Zone of Schulz and Schmid (1983). It is a part of the phragmocone with the basal portion of the body chamber. An umbilical swelling is seen, which indicates this to be a macroconch. The original photograph of the specimen (Birkelund 1982: pl. 1: 4) is inadequate and the specimen is refigured herein. The latter shows ribbing similar to that in other specimens in the lot discussed here: no umbilical bullae, incipient lateral tubercles and much stronger ventrolaterals.

A specimen from Rügen illustrated by Wolansky (1932) differs from *Hoploscaphites constrictus* and shares a similar

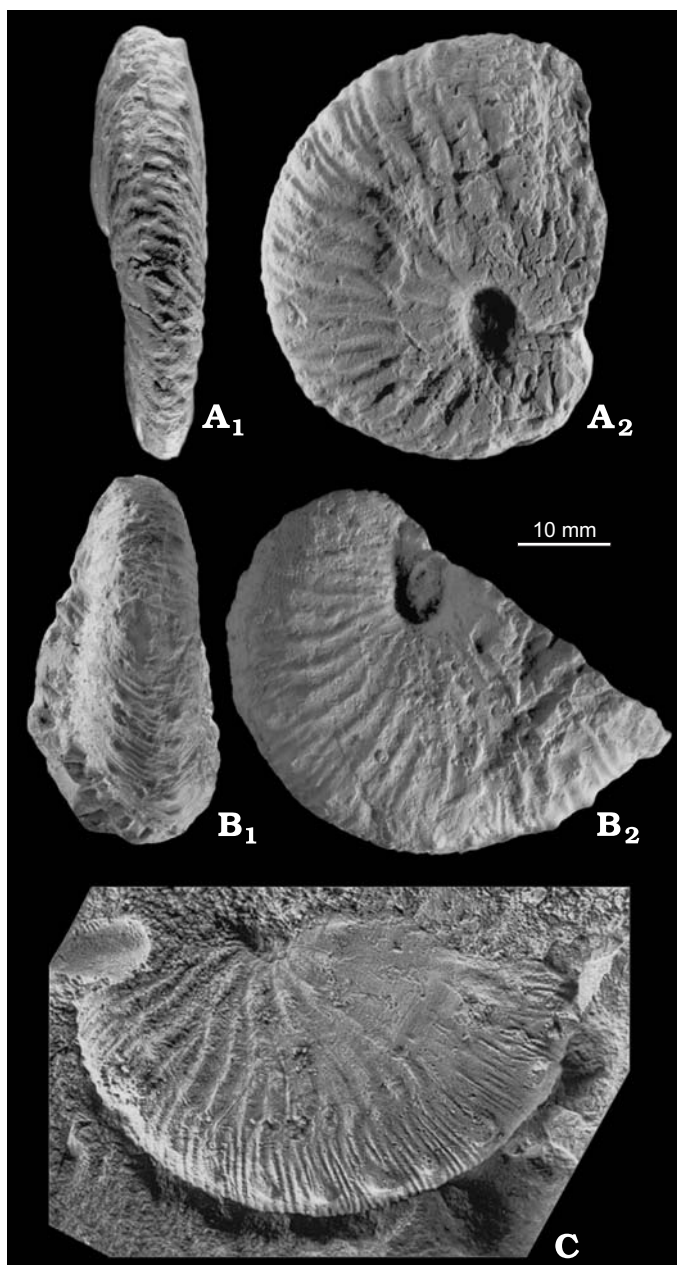


Fig. 18. *Hoploscaphites* sp. ex gr. *pungens-schmidi*. A. NLFB kma 178, *Spyridoceramus tegulatus-Belemnitella junior* Zone, Hemmoor, Germany, in ventral (A₁) and lateral (A₂) views. B. Plaster cast of MGUH 27745, *Meonia semiglobularis-Ruegenella humboldtii* Zone, Gudumholm, Denmark, in ventral (B₁) and lateral (B₂) views. C. ZPAL Am. 12/706, *Spyridoceramus tegulatus-Belemnitella junior* Zone, level III at Chełm, Poland, in lateral view.

ornament with the present group, although the quality of the photograph does not allow to establish its tuberculation pattern.

?*Acanthoscaphites* sp. *sensu* Kennedy, 1987 in Jagt (1995) from the upper Nekum Member (Maastricht Formation) at the CBR-Romontbos quarry, Belgium, is represented by spires of a small diameter which may or may not belong here.

In summary, the present specimens recall both *H. pungens* and *H. schmidi* in tuberculation, but differ in showing flexuous primary ribs on the phragmocone and early part of

the body chamber. This material probably represents a new species of the *H. pungens-schmidi* group, but poor preservation precludes a formal description. Alternatively, these specimens could be end members of *H. pungens* and *H. schmidi* populations.

Stratigraphic and geographic range.—Upper lower Maastrichtian and/or lower upper Maastrichtian of Denmark (*Meonia semiglobularis-Ruegenella humboldtii* Zone), Germany (*Spyridoceramus tegulatus-Belemnitella junior* Zone), Poland (*Spyridoceramus tegulatus-Belemnitella junior* Zone) and, possibly, of Belgium (*Belemnitella junior* Zone of authors).

Hoploscaphites felderi Kennedy, 1987

Fig. 19.

1861 *Ammonites Decheni* sp. nov.; Binkhorst 1861: 30, pl. 5a: 15a–e. 1908 *Scaphites* cf. *roemeri* d’Orbigny; de Grossouvre 1908: 35, pl. 10: 1–3.

1987 *Hoploscaphites felderi* sp. nov.; Kennedy 1987: 203, pl. 27: 1, pl. 33: 1–15; pl. 34: 7–11, 13–17; text-fig. 13c.

1993 *Hoploscaphites tenuistriatus* (Kner, 1848); Birkelund 1993: 59 (partim), pl. 14: 14 (non pl. 14: 8–11, 15, 16 = *Hoploscaphites tenuistriatus*, non pl. 14: 13 = *Hoploscaphites* sp.).

1995 *Hoploscaphites felderi* Kennedy, 1987; Jagt 1995: 30, pl. 6: 3–6; pl. 7: 3, 4, 10–12.

Type material: Holotype is IRScNB 9483, the original of de Grossouvre (1908: pl. 10: 1a–c) from the upper Maastrichtian Kunrade Limestone facies of the Maastricht Formation, Limburg, the Netherlands (refigured in Kennedy 1987: pl. 27: 1).

Material.—From the Netherlands: three specimens, one from quarry ‘t Rooth, Bemelen (NHMM MK 463), another from the ENCI quarry (NHMM JJ 11862a, b) and one from the former Blom quarry (NHMM JJ 7386a, b). From Belgium: two specimens from CBR-Romontbos quarry, Liège (a silicone cast NHMM 1992074 of specimen no. 2015 in the Indeherberge collection and an unnumbered silicone cast of another specimen). From Poland: two specimens, one from Chełm chalk pit (ZPAL Am. 12/710) and one from the town quarry south of Kazimierz Dolny (ZPAL AM. 12/709). From Denmark: two specimens, one from “Danmark” quarry, Jylland (MGUH 20165), another a silicone cast of a specimen from Rørdal quarry, Ålborg (MGUH 27746).

Discussion.—No body chambers are yet known of this species, which is characterised by a compressed whorl section, flattened flanks, distinctive ornament and intricately subdivided suture (Kennedy 1987; Jagt 1995). Topotypes from the Kunrade Limestone facies (Kennedy 1987: pl. 33: 1–8, 10; pl. 34: 7–9, 12–17) do not differ in any respect of their morphology from the holotype. The same concerns other material from the Maastricht area, which is from the Emael and Nekum members of the Maastricht Formation (Jagt 1995: 31; Jagt 2002).

Prior to the present study, *Hoploscaphites felderi* was known exclusively from Belgium and the Netherlands. New finds from Poland and a reinterpretation of some specimens from Denmark have now demonstrated a wider geographic range of this species. All this material consists of incomplete

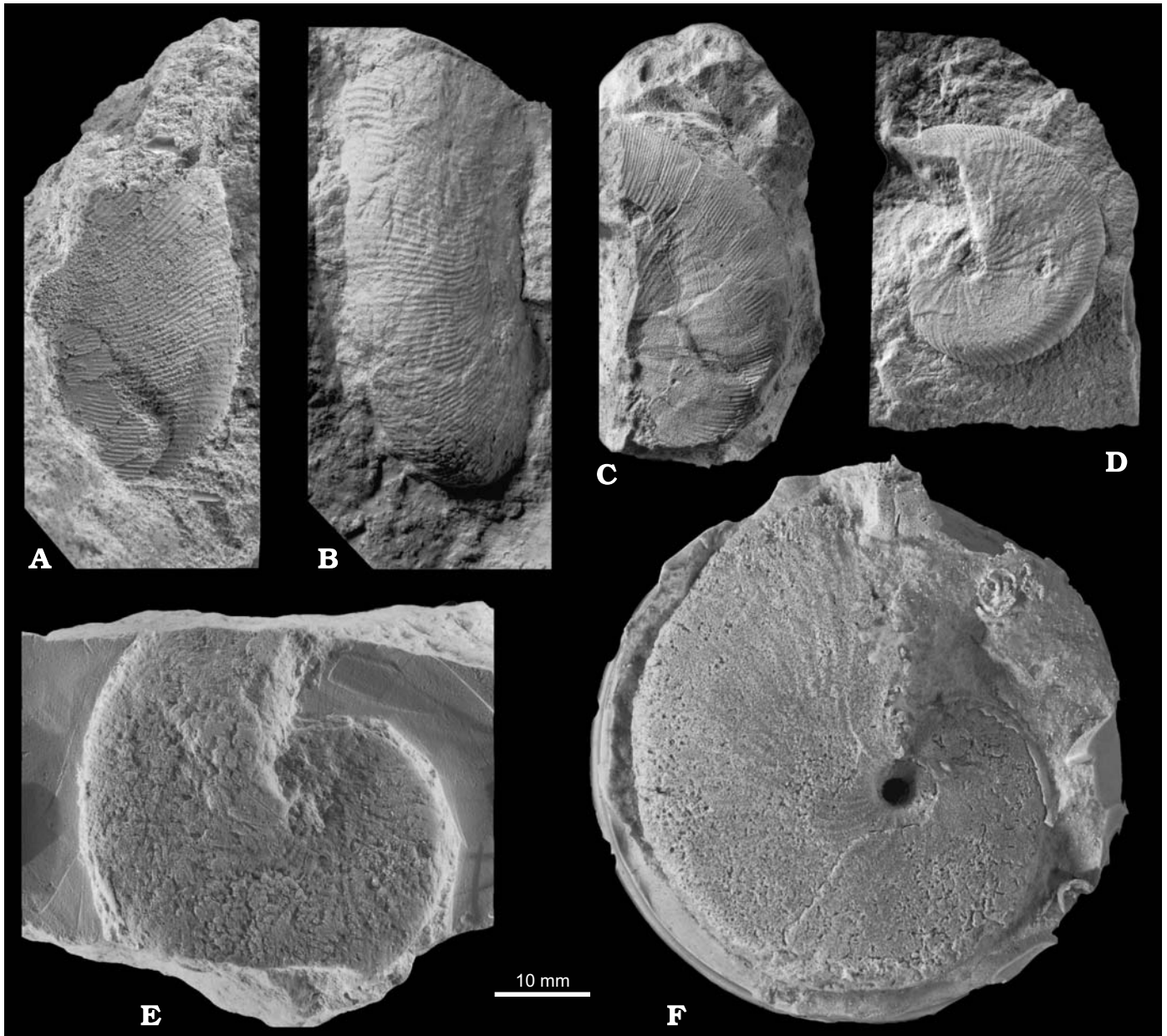


Fig. 19. *Hoploscaphites felderi* Kennedy, 1987. **A.** NHMM JJ 11862a, b, *Belemnitella junior* Zone, ENCI quarry. **B.** Silicone rubber cast of MGUH 27746, *Rugia tenuicostata*–*Meonia semiglobularis* or *Meonia semiglobularis*–*Ruegenella humboldtii* zones, Rørdal, Denmark. **C.** ZPAL Am. 12/709, *Belemnella kazimiroviensis* Zone, town quarry south of Kazimierz Dolny, Poland. **D.** ZPAL Am. 12/710, *Spyridoceramus tegulatus*–*Belemnitella junior* Zone, level III at Chełm, Poland. **E.** MGUH 20165, *Meonia semiglobularis*–*Ruegenella humboldtii* Zone, “Danmark” quarry. **F.** Silicone rubber cast of an unregistered specimen, *Bt. junior* Zone, CBR-Romontbos quarry. All specimens in lateral views, except for B, which is in oblique view.

phragmocones, like the original material from the Maastricht area. This allows to speculate that the body chamber of *H. felderi* was either very thin or weakly calcified and thus prone to destruction shortly after the death of its inhabitant.

Specimen ZPAL Am. 12/709 represents half a whorl, 33 mm in maximum preserved diameter (Fig. 19C). It comes from the lower part of the Kazimierz Opoka (*Bn. kazimiroviensis* Zone) as exposed at the town quarry at Kazimierz Dolny, and shows distinctive ribbing, indistinguishable from that visible on external moulds of *H. felderi* from the Kunrade Limestone (Kennedy 1987: pl. 33: 2, 3) and on

conspecific external moulds NHMM JJ 11862a, b (Fig. 19A) and NHMM JJ 7386a, b from the Nekum Member. In all these specimens, the primary ribs are concave on the inner flank, sweep forwards across mid-flank, and are concave on the outer flank. Secondaries arise on the inner flank, either by insertion or by subdivision of the primaries. In result, the outer flanks, ventrolateral shoulder and venter are covered by dense, sharp ribs.

Another Polish specimen, ZPAL Am. 12/710 (Fig. 19D), is from level III at the Chełm chalk pit, from the *Spyridoceramus tegulatus*–*Belemnitella junior* Zone. It is an incom-

plete spire, 25 mm in maximum preserved diameter, with the same ribbing pattern as described above and flattened flanks characteristic of the species.

Specimen MGUH 20165 (Fig. 19E) from “Danmark” quarry, Jylland, is from the *Meonia semiglobularis*–*Ruegenella humboldtii* Zone (Surlyk 1984: fig. 3). It is 44 mm in maximum preserved diameter. The specimen is not *H. tenuistriatus* as claimed by Birkelund (1993: pl. 14: 14) as it is septate throughout and its ornament consists of fine, dense ribs on the ventrolateral shoulder and outer flank and rarer, stronger ribs on the mid- and inner flanks. Phragmocones of *H. tenuistriatus* tend to be smaller and are additionally covered with rather coarse ribs. Specimen MGUH 20165 is closely similar in proportions and ribbing to an unnumbered silicone cast of *H. felderi* from the CBR-Romontbos quarry (Fig. 19F). In addition, MGUH 20165 has flattened flanks with a marked ventrolateral shoulder, typical of *H. felderi*.

Another specimen from Denmark, MGUH 27746, is from Rørdal quarry, Ålborg, Jylland, from either the upper part of the *Rugia tenuicostata*–*Meonia semiglobularis* Zone or from the lower part of the *Meonia semiglobularis*–*Ruegenella humboldtii* Zone (see Surlyk 1984: fig. 3). It is a contorted fragment of a phragmocone whorl (Fig. 19B). Venter, ventrolateral shoulder and outer flank are visible, and are covered with sharp ribs typical of the species; only few primaries are visible on mid-flank, which, however, is poorly preserved. Parts of a deeply incised suture line are also seen. The size of MGUH 27746 suggests a much larger individual than the majority of other specimens of the species known to date. However, fragments NHMM JJ 11862a, b (Fig. 19A) and NHMM JJ 7386a, b from the Nekum Member, must also have belonged to fairly large individuals. Perhaps, two species or dimorphs are involved. This cannot be clarified until better-preserved specimens with body chambers are found.

Stratigraphic and geographic range.—Upper lower and/or lower upper Maastrichtian of Belgium and the Netherlands (*Belemnella junior* Zone of authors), Denmark (*Meonia semiglobularis*–*Ruegenella humboldtii* Zone and possibly *Rugia tenuicostata*–*Meonia semiglobularis* Zone), and Poland (*Spyridoceramus tegulatus*–*Belemnella junior* Zone and *Belemnella kazimiroviensis* Zone).

Hoploscaphites sp. ex gr.
waagei–*angmartussutensis*

Fig. 20.

1998 *Hoploscaphites* sp. nov.; Kennedy and Jagt: 1998: 163 (partim), pl. 2: 12–15 (non pl. 2: 10, 11 = *Hoploscaphites pungens*).

Material.—From the Netherlands: a silicone cast of a single specimen from the Ankerport-Curfs quarry (NHMM 1994644, ex Dortangs collection). From Poland: a single specimen from Nasiłów (ZPAL Am. 12/1278 ex Małysiak collection). From Denmark: a silicone cast of a single specimen from the “Danmark” quarry, Ålborg, Jylland (MGUH 27747).

Discussion.—Kennedy and Jagt (1998) described two specimens from the Maastricht area under the heading *Hoplo-*

scaphites sp. nov. One of these, from the base of the Maastricht Formation as exposed at Blankenberg quarry (Kennedy and Jagt 1998: pl. 2: 10, 11) is here reinterpreted as part of a macroconch of *Hoploscaphites pungens* (Binkhorst, 1861). Another specimen, NHMM 1994644 (Kennedy and Jagt 1998: pl. 2: 12–15; see Fig. 20C₁, C₂), comes from the uppermost part (subunit IVf-6) of the Meerssen Member of the Maastricht Formation, as exposed at the Ankerpoort-Curfs quarry. It is part of a phragmocone, estimated 55 mm in maximum diameter (Kennedy and Jagt 1998) with relatively distant, wiry ribs on the adapical 90° sector of the outer whorl (Fig. 20C₂). This ornament is replaced by dense, flexuous prorsiradiate ribs on the remainder of the phragmocone (Fig. 20C₂).

Kennedy and Jagt (1998) compared their *Hoploscaphites* sp. nov. to *Scaphites* (*Discoscaphites*) *waagei* Birkelund, 1965 and *S. (D.) angmartussutensis* Birkelund, 1965, from the upper Maastrichtian of western Greenland (Birkelund 1965; see also Kennedy et al. 1999). They also considered the material from the Maastricht area to represent a new species, too fragmentary for formal description (Kennedy and Jagt 1998: 164). This view is followed here for specimen NHMM 1994644.

Two additional specimens from Poland and Denmark, well comparable to NHMM 1994644, attest to a wider stratigraphic and geographic range of *Hoploscaphites* sp. ex gr. *waagei*–*angmartussutensis*. Specimens ZPAL Am. 12/1278 (Fig. 20B₁, B₂) comes from the upper part of the Kazimierz Opoka as exposed at Nasiłów quarry. This is half a whorl of a spire with proportions and ornament very similar to those of NHMM 1994644 (compare Fig. 20B₁ and C₂). The only significant difference between these two individuals is that the Meerssen specimen is much more inflated than that from Nasiłów (compare Fig. 20B₂ and C₁). This is arbitrarily interpreted here as the result of intrapopulation variation, taking into account the wide range of this parameter documented for many scaphitids, e.g., in the type material of *Hoploscaphites constrictus* (J. Sowerby, 1817) from Cotentin (Kennedy 1986).

Specimen MGUH 27747 was found loose on the lowest exploitation level at the “Danmark” quarry, which exposes white chalk of the *Meonia semiglobularis*–*Ruegenella humboldtii* Zone (Surlyk 1984: fig. 3). It is a piece of whorl with ribbing similar to that of specimens described above (Fig. 20A).

Stratigraphic and geographic range.—Upper Maastrichtian of the Netherlands (*Belemnella kazimiroviensis* Zone) and Poland (*Belemnella kazimiroviensis* Zone) and Denmark (*Meonia semiglobularis*–*Ruegenella humboldtii* Zone).

Genus *Acanthoscaphites* Nowak, 1911

Type species: *Scaphites tridens* Kner, 1848: 10, pl. 2: 1, by subsequent designation of Diener (1925).

Discussion.—Following Kennedy and Summesberger (1987) and Jagt et al. (1999), the presence of distinct ventral (siphonal) tubercles is accepted here as a diagnostic feature of the genus. It should be noted that ventral swellings, occasionally even prominent, do occur in some representatives of the genus

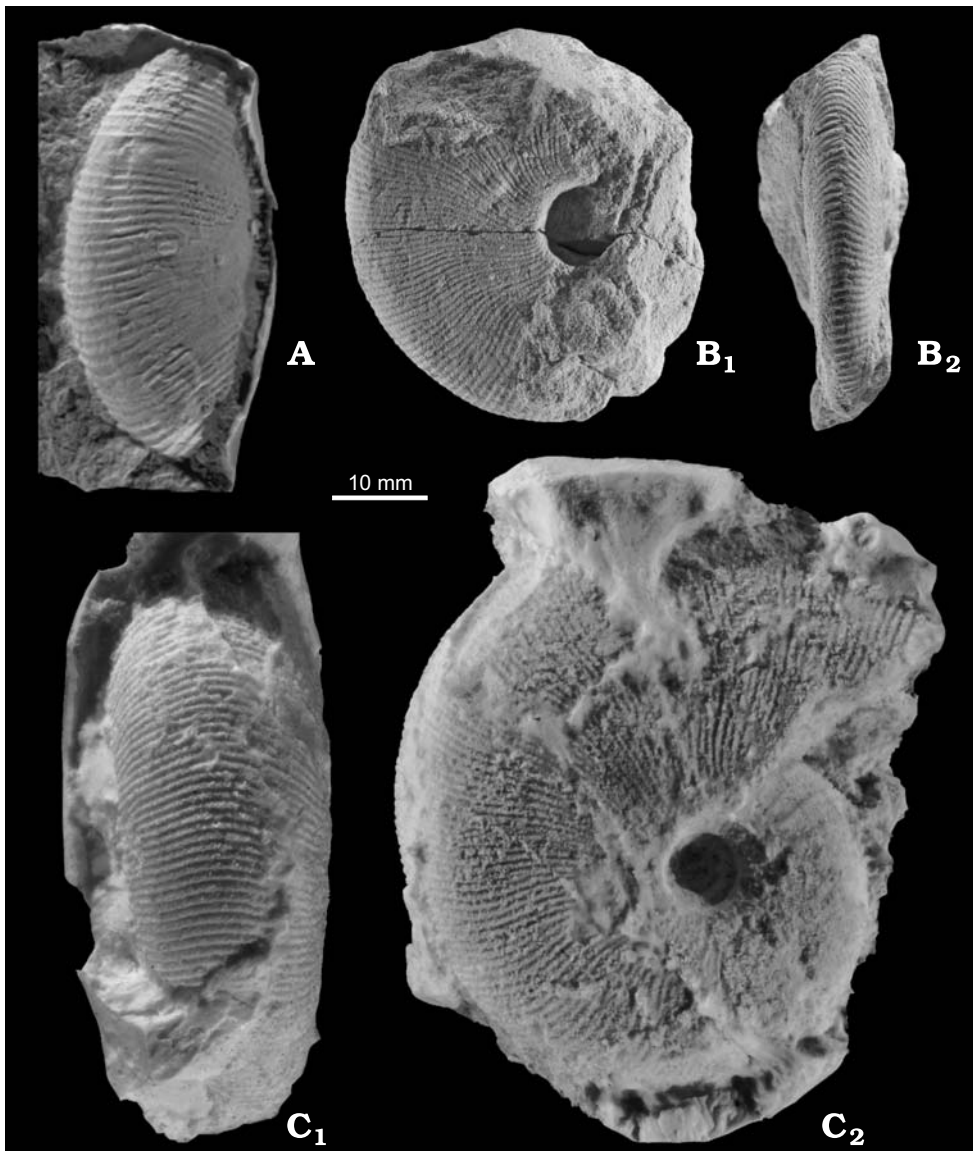


Fig. 20. *Hoploscaphites* sp. ex gr. *waagei-angmartussutensis*. A. Silicone rubber cast of MGUH 27747, *Meonia semiglobularis* Zone, "Danmark" quarry, in oblique view. B. ZPAL Am. 12/1278 (ex Małysiak collection), *Bn. kazimiroviensis* Zone, Nasilów, in lateral (B₁) and ventral (B₂) views. C. Silicone rubber cast of NHMM 1994644 (ex Dortangs collection), Ankerpoort-Curfs quarry, in ventral (C₁) and lateral (C₂) views.

Hoploscaphites, including the lectotype of its type species, *H. constrictus* (see Kennedy 1986), but they never acquire the appearance of "true", regular tubercles.

Subgenus *Acanthoscaphites* (*Euroscaphites*) Jagt, Kennedy, and Machalski, 1999

Type species: *Scaphites varians* Łopuski, 1911: 120, pl. 4: 1–3, by original designation.

Acanthoscaphites (*Euroscaphites*) *variens varians* (Łopuski, 1911)

Figs. 21, 22B.

1911 *Scaphites varians* sp. nov.; Łopuski 1911: 120, pl. 4: 1–3.

1980 *Acanthoscaphites varians* (Łopuski); Błaszkiwicz 1980: 40, pl. 25: 1, 2, 5, 6.

1996 *Acanthoscaphites varians* (Łopuski, 1911); Machalski 1996: 378, fig. 6.

1999 *Acanthoscaphites* (*Euroscaphites*) *variens varians* (Łopuski, 1911); Jagt et al. 1999: 137 (partim), text-figs. 3, 4; pl. 3, pl. 4: 2, 3; pl. 5: 1–4; pl. 6; pl. 7 (non pl. 4: 1).

non 2002 *Acanthoscaphites varians* (Łopuski, 1911); Reich and Frenzel 2002, pl. 23: 1a, b [= *Acanthoscaphites* (*Euroscaphites*?) sp. aff. *verneuilianus*].

Type material: Holotype, by monotypy, is the original of Łopuski (1911: pl. 4: 1–3) from the upper upper Maastrichtian at Kazimierz Dolny, Middle Vistula River section, Poland. The specimen is presumably lost.

Material.—From Poland: five specimens from the town quarry south of Kazimierz Dolny (ZPAL Am. 12/400, 778; MKD/MP-135; unregistered specimen in Marcinowski collection, unregistered specimen in the Praszki and Dembicz collection) and six specimens from the Rejowiec quarry (ZPAL Am. 12/401, 776, 777, 779, 1279, unregistered specimen in the Praszki and Dembicz collection).

Discussion.—The specimens assigned herein to *A. (E.) v. varians* were treated in detail by Łopuski (1911), Błaszkiwicz (1980), Machalski (1996), and Jagt et al. (1999) and there is no need to repeat these descriptions. Newly collected

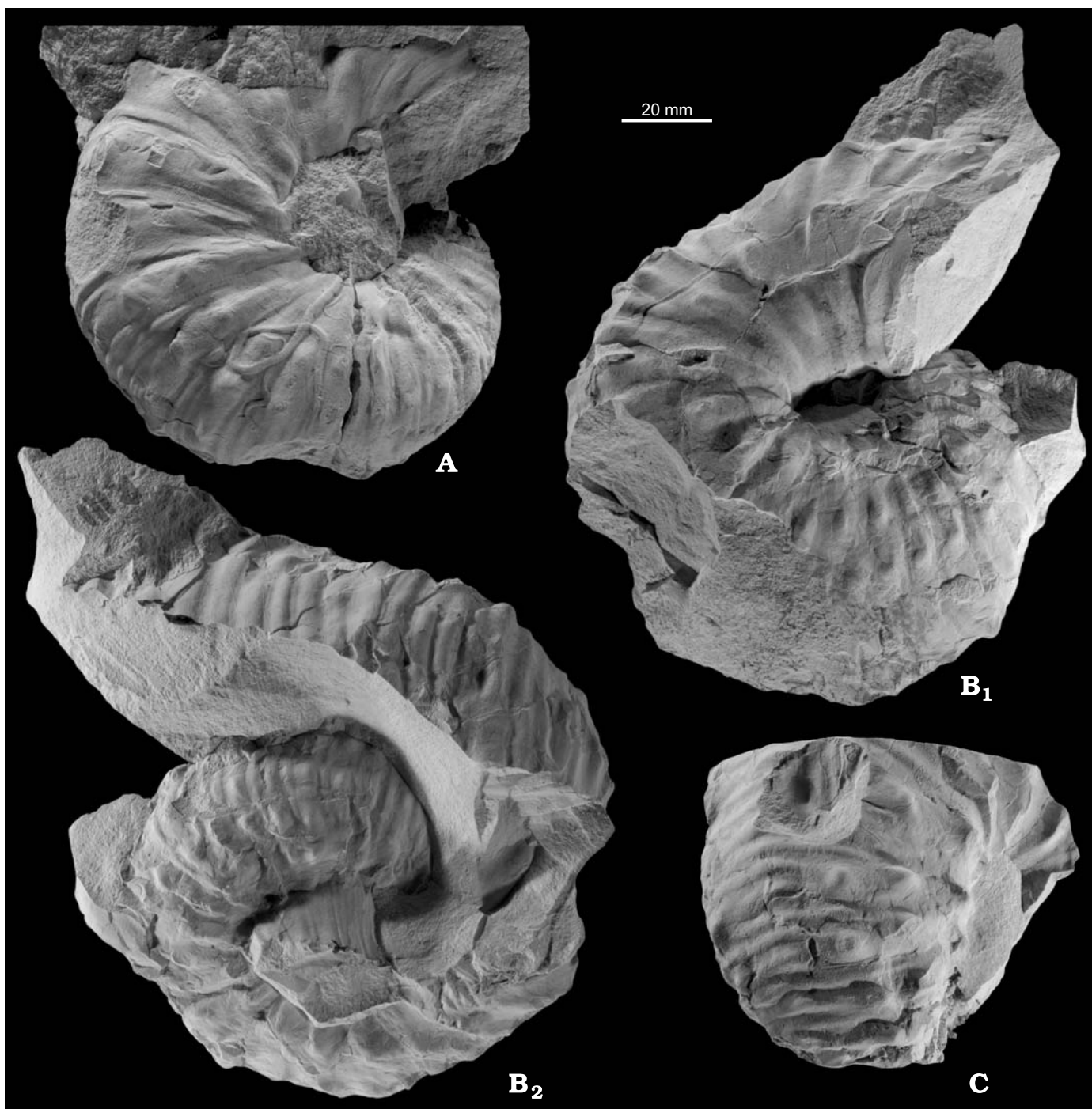


Fig. 21. *Acanthoscaphites (Euroscaphites) varians varians* (Łopuski, 1911) from Poland, possibly macroconchs, *Belemnella kazimiroviensis* Zone. A. ZPAL Am. 12/778, town quarry south of Kazimierz Dolny, in lateral view. B. ZPAL Am. 12/776, Rejowiec, in lateral views (B₁, B₂). C. ZPAL Am. 12/773, in ventral view.

specimens from Rejowiec and Kazimierz Dolny (Fig. 21) match in their ribbing and tuberculation the previously recorded material.

All material studied comes from the lower part of the *Belemnella kazimiroviensis* Zone as exposed at the town quarry south of Kazimierz Dolny and at Rejowiec. The new finds indicate that *A. (E.) v. varians* is not restricted to certain parts of these sections as assumed by Jagt et al. (1999), but

occurs throughout. No records of the subspecies outside Poland are known to date.

Both the holotype and other specimens known are best interpreted as macroconchs, being similar in size and shell proportions to those of *Acanthoscaphites tridens* (Kner, 1848) as described by Kennedy and Summesberger (1987) and Jagt et al. (1999). The largest macroconch of *A. (E.) v. varians* known to date is ZPAL Am. 12/401, a complete specimen

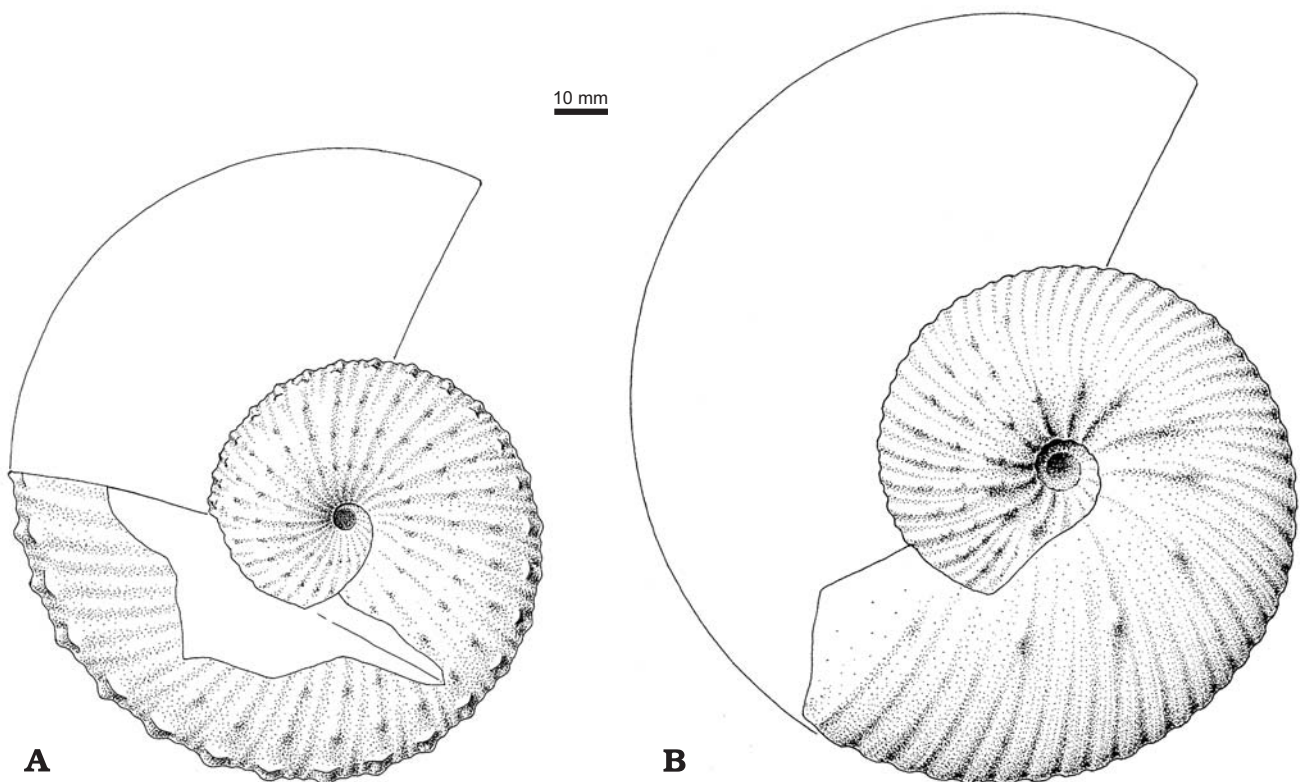


Fig. 22. Partial reconstructions. **A.** The holotype of *Acanthoscaphites (Euroscaphites) varians blaszkiewiczzi* Jagt, Kennedy, and Machalski, 1999, MGUH 20129A, *Rugia tenuicostata*–*Meonia semiglobularis* Zone or *Meonia semiglobularis*–*Ruegenella humboldtii* Zone, Rørdal, Denmark (reversed). **B.** Unregistered specimen of *Acanthoscaphites (Euroscaphites) varians varians* (Łopuski, 1911) in the Marcinowski collection, town quarry south of Kazimierz Dolny, Poland.

with markedly constricted aperture and a maximum diameter of 256 mm (Jagt et al. 1999: fig. 3, pl. 6). This specimen comes from an opoka unit between the baculite and belemnite marls at Rejowiec.

No specimens which could be interpreted as microconchs of *A. (E.) v. varians* are known yet. Specimen ZPAL Am. 12/152 from the town quarry south of Kazimierz Dolny was interpreted as microconch by Jagt et al. (1999). However, it has a smooth venter with indistinct siphonal swellings and is better regarded as unrelated to the present subspecies.

Stratigraphic and geographic range.—Upper upper Maastichtian of Poland (*Belemnella kazimiroviensis* Zone).

Acanthoscaphites (Euroscaphites) varians blaszkiewiczzi Jagt, Kennedy, and Machalski, 1999

Figs. 22A, 23, 24, 25C, E.

1965 *Acanthoscaphites tridens varians* (Łopuski); Schmid 1965: 684, pl. 62: 1; pl. 63: 1–3.

1982 *Acanthoscaphites varians* (Łopuski); Birkelund 1982: 16 (partim), pl. 1: 5 (non pl. 1: 4 = *Hoploscaphites* sp. ex gr. *pungens*–*schmidi*, non pl. 1: 6 = *Hoploscaphites schmidi*).

?1986 *Acanthoscaphites* cf. *verneuillianus* (d'Orbigny, 1841); Kennedy 1986: 74, pl. 16: 20, 21.

1989 *Acanthoscaphites varians* (Łopuski, 1911); Jagt and Kennedy 1989: 238, figs. 1–3.

1993 *Acanthoscaphites varians* (Łopuski, 1911); Birkelund 1993: 56,

pl. 9 (partim), pl. 9: 3, 4, 6, 7; pl. 10: 3 [non pl. 9: 5, pl. 10: 2 = *Acanthoscaphites (Euroscaphites?)* sp. aff. *verneuillianus*].

1999 *Acanthoscaphites (Euroscaphites) varians blaszkiewiczzi* n. subsp.; Jagt et al. 1999: 139 (partim), text-figs. 5, 6; pl. 8: 2–4, 6 [non pl. 8: 1, 5 = *Acanthoscaphites (Euroscaphites?)* sp. aff. *verneuillianus*].

non 2002 *Acanthoscaphites varians* (Łopuski, 1911); Reich and Frenzel 2002, pl. 23: 1a, b [?= *Acanthoscaphites (Euroscaphites?)* sp. aff. *verneuillianus*].

Type material.—The specimen in Birkelund (1993: pl. 10: 3) from the upper lower or lower upper Maastichtian of Rørdal, Jylland, is holotype (see Fig. 22A). It is numbered MGUH 20129A herein to avoid confusion as two specimens referred to *Acanthoscaphites varians* (Łopuski, 1911) by Birkelund (1993) erroneously bear the same number, MGUH 20129 (Birkelund 1993: pl. 9: 7; pl. 10: 3).

Material.—From Germany: four specimens from Hemmoor (GPIUH 821–823, NLfB kma 179). From Denmark: eight specimens from Rørdal (MGUH 20125, 20126, 20128, 20129, 20129A, 27750, MGUH 1973. 841, 844). From Belgium: one specimen from the CPL quarry, Haccourt (NHMM 198840-1–3, ex Jagt collection), and one from the CBR-Lixhe quarry, Lixhe (NHMM MB 1147). From Poland: one specimen from Chełm (ZPAL Am. 12/372). Additionally, a specimen MWGUW ZI/35/147 of unknown provenance (ex Makowski collection).

Discussion.—According to Jagt et al. (1999), the present subspecies differs from the later *Acanthoscaphites (Euro-*

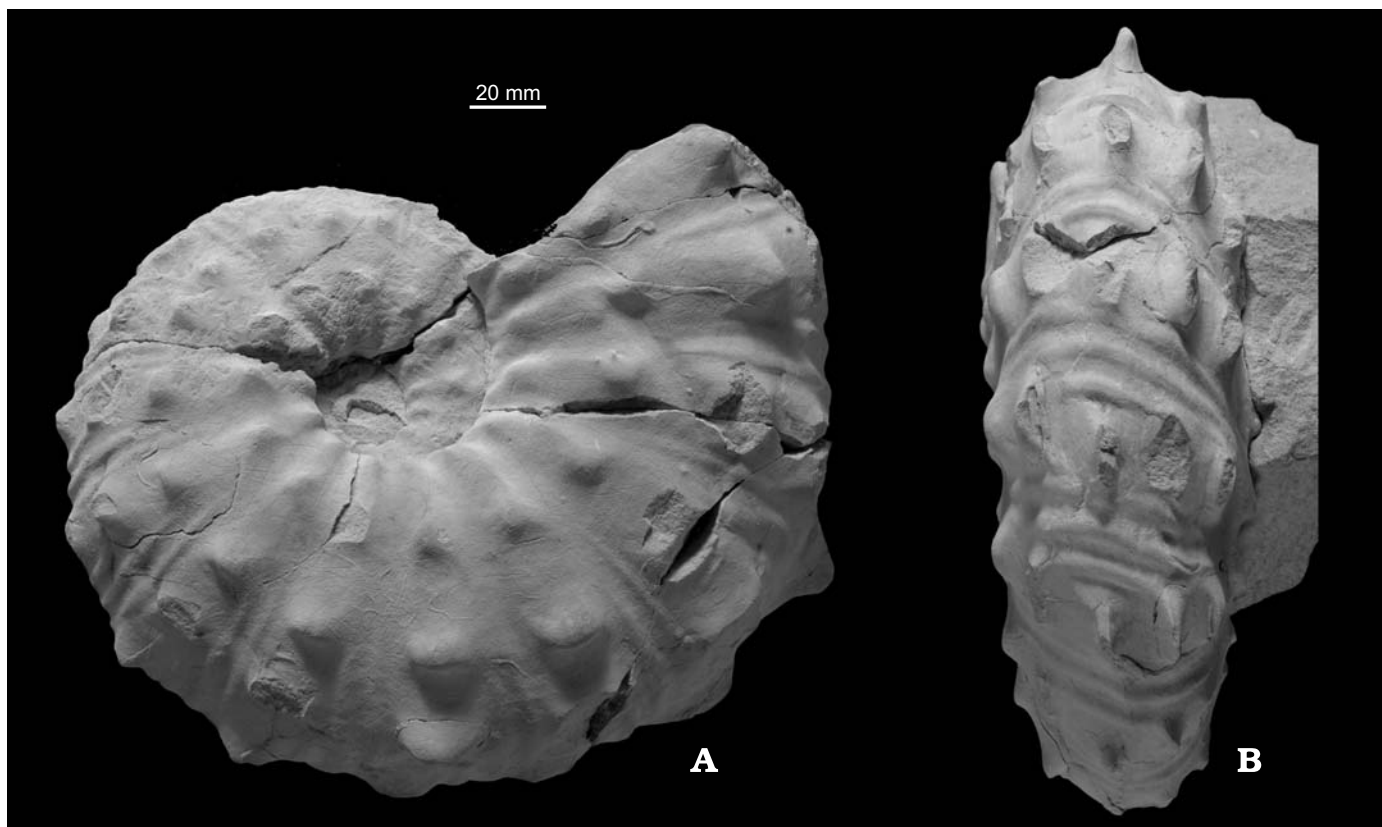


Fig. 23. *Acanthoscaphites varians blaszkiewiczzi*, MWGUW ZI/35/147 of unknown provenance, in lateral (A) and ventral (B) views.

scaphites) varians varians in retaining multiple tuberculation on macroconch body chambers, especially the ventral row and two rows of outer flank tubercles (Fig. 22). Only on the youngest parts of the body chamber in specimens from Denmark has the loss of some rows of tubercles been observed (Birkelund 1993; Jagt et al. 1999; Fig. 22A). However, this process starts with the inner flank tuberculation, in contrast to material of *A. (E.) v. varians* in which the siphonal row is the first to be lost.

The best-preserved specimens of *A. (E.) v. blaszkiewiczzi* come from Rørdal, Jylland, either from the upper lower Maastrichtian *Rugia tenuicostata*–*Meonia semiglobularis* Zone or from the lower upper Maastrichtian *Meonia semiglobularis*–*Ruegenella humboldtii* Zone (Birkelund 1993; Jagt et al. 1999). The remainder of the material studied comes from the upper lower to lower upper Maastrichtian at Hemmoor (Schmid 1965; Birkelund 1982), and in the Haccourt-Lixhe area in Belgium (Jagt and Kennedy 1989; Jagt et al. 1999). The latter records, from units 5–6 of the Vijlen Member (Gulpen Formation) as exposed at the CBR-Lixhe and CPL quarries were assigned to the *Belemnitella junior* Zone of authors by Jagt and Kennedy (1989) and Jagt et al. (1999) and claimed to be of early late Maastrichtian age. However, recent work on inoceramid bivalves places this interval within the upper lower Maastrichtian “*Inoceramus*” *morgani* Zone (Ireneusz Walaszczyk and John W.M. Jagt, unpublished data).

Acanthoscaphites cf. verneuillianus (d’Orbigny, 1841) of Kennedy (1986: 74, pl. 16: 20, 21), from the “Calcaire à *Baculites*” of Cotentin, is also assigned here, albeit with a query. The specimen bears siphonal tubercles and feeble umbilical and lateral bullae, plus strong inner and outer ventrolateral tubercles (Kennedy 1986: 76), being thus very close in its ornament to *A. (E.) varians blaszkiewiczzi*. Also its umbilicus is of comparable diameter to that of *A. (E.) varians blaszkiewiczzi* (compare Kennedy 1986: pl. 16: 20, 21 and Fig. 25C herein).

The only specimen from Chełm assigned to *A. (E.) v. blaszkiewiczzi* is a fragment of body chamber ZPAL Am. 12/372 from level III. It belonged to a large specimen, presumably a macroconch, and shows four distinct tubercles arranged in two rows. Only one row of umbilicolateral tubercles persists to the early part of the body chamber in *A. (E.) v. varians*.

Another specimen, MWGUW ZI/35/147 (Fig. 23A₁, A₂) comes from the former collection of Henryk Makowski at the Geology Department at Warsaw University and lacks provenance data. MWGUW ZI/35/147 is preserved in opoka, typical of Maastrichtian deposits outcropping in the Lublin and Miechów uplands. Two samples of the matrix of the specimen MWGUW ZI/35/147 have been investigated for its nannofossil content by Jackie Lees (personal communication July 2005). Both samples contain *Arkhangelskiella maastrichtiana*. The first occurrence of *A. maastrichtiana* defines the base of Nannofossil Subzone UC20cBP in the lower up-

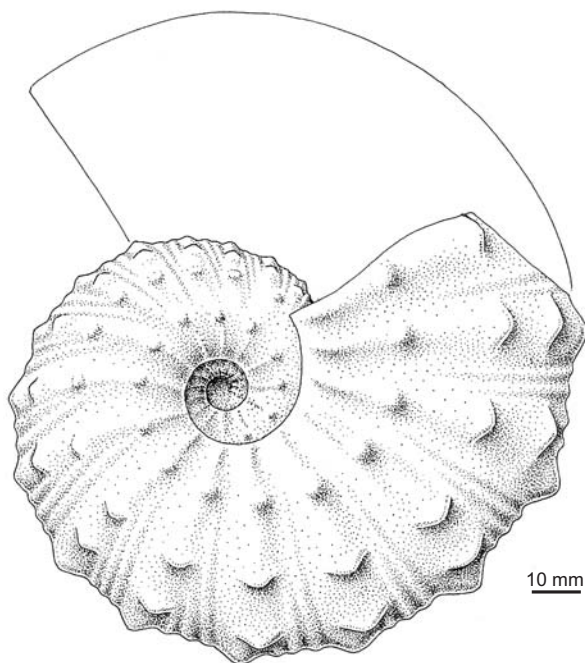


Fig. 24. Partial reconstruction of *Acanthoscaphites (Euroscaphites) varians blaszkiewiczzi*, MWG UW ZI/35/147 of unknown provenance.

per Maastrichtian (Burnett 1998). The samples also contain *Nephrolithus frequens* and *Lithraphidites quadratus*, the first occurrences of which mark the underlying subzones in the lower upper Maastrichtian. In contrast, *Cribrosphaerella daniae*, which marks the base of the younger subzone, UC20dBP in the upper upper Maastrichtian, was missing in both samples studied. In summary, MWG UW ZI/35/147 is no older than early late Maastrichtian, and may be as young as late late Maastrichtian (Jackie Lees, personal communication July 2005).

MWG UW ZI/35/147 is a macroconch with the adapertural part of the shaft and the final hook missing (Fig. 24). The specimen is 165 mm in maximum preserved diameter. The ornament of the preserved part of the shaft and the exposed part of the spire of MWG UW ZI/35/147 consists of seven rows of tubercles: three on the flank and one on the venter. Additionally, umbilical bullae of moderate strength are visible on the umbilical shoulder. The ventrolateral and siphonal tubercles are stronger than the remaining tubercles. There is no sign of fading away of the tubercles at the adapertural part of the preserved part of the shaft. Thus, MWG UW ZI/35/147 matches in its tuberculation the best-preserved individuals of *Acanthoscaphites (E.) v. blaszkiewiczzi* as described by Schmid (1965), Birkelund (1993) and Jagt et al. (1999). However, the tubercles are more robust and more widely spaced in MWG UW ZI/35/147 than in the remainder of the material.

There are also differences in ribbing between specimen MWG UW ZI/35/147 and the remaining material of *A. (E.) v. blaszkiewiczzi* studied. In the latter specimens, the primary tuberculate ribs are separated by one or two, exceptionally three, thin and nontuberculate secondaries. In MWG UW ZI/35/147

the interprimary intervals are much wider and contain three secondaries each (Figs. 23, 24). Moreover, the secondaries are set at an acute angle to the succeeding primary rib, as if they arose from the adapical face of that primary. This recalls the ribbing in the holotype of *A. (E?) verneuillianus* (d'Orbigny, 1841) as described in Kennedy (1986) and below.

The above-mentioned differences in ornament suggest that specimen MWG UW ZI/35/147 is an end-member of the population of *Acanthoscaphites (E.) v. blaszkiewiczzi*. Alternatively, it could be described as a new species. This matter cannot be resolved, however, with only a single specimen of unknown provenance at hand.

Contrary to Birkelund (1993) and Jagt et al. (1999), no microconchs exist which could be convincingly matched with macroconchs of *Acanthoscaphites (E.) v. blaszkiewiczzi* in terms of style of ribbing and number of tubercles. The purported microconchs of this subspecies (Jagt et al. 1999: pl. 8: 1, 5, the latter refigured in Fig. 25B) differ from specimens of *A. (E.) v. blaszkiewiczzi* of similar size (Birkelund 1982: pl. 1: 5, refigured in Fig. 25C; Fig. 25E) and are better assigned to a separate taxon: *Acanthoscaphites (Euroscaphites?)* sp. aff. *verneuillianus* (d'Orbigny, 1841) (see discussion below).

Stratigraphic and geographic range.—Upper lower and/or lower upper Maastrichtian of northern Germany (*Belemnella cimbrica* to *Tenuipteria argentea*–*Belemnella junior* zones), Belgium (“*Inoceramus*” *morgani* Zone), Denmark (*Rugia tenuicostata*–*Meonia semiglobularis* and *Meonia semiglobularis*–*Ruegenella humboldtii* zones), and Poland (*Spyridoceramus tegulatus*–*Belemnella junior* Zone).

Acanthoscaphites (Euroscaphites?) verneuillianus (d'Orbigny, 1841)

1841 *Ammonites Verneuillianus* d'Orbigny 1841: 329, pl. 98: 3–5.
1986 *Acanthoscaphites verneuillianus* (d'Orbigny, 1841); Kennedy 1986: 74, pl. 16: 15–17; text-fig. 10c.

Type material: Holotype, by monotypy, is an unregistered specimen (EMP) from the upper lower Maastrichtian at Fresville, Cotentin, France (Kennedy 1986, pl. 16: 15–17).

Discussion.—The holotype was described in detail by Kennedy (1986: 74). This is an inflated spire c. 47 mm in maximum preserved diameter, with eleven narrow, distant primary ribs on the outer whorl. The primaries are concave at the umbilical shoulder and straight and prorsiradiate on the flanks. Up to six secondary ribs intercalate between each pair of primaries. The secondaries “are set at an acute angle to succeeding primary rib, as though they were secondaries arising from adapical face of that primary” (Kennedy 1986: 74). The tuberculation consists of a maximum of three rows of tubercles: the ventrolaterals, outer laterals (inner ventrolateral tubercles of Kennedy 1986) and siphonal tubercles. The specimen illustrated by d'Orbigny (1841), presumably lost, is very similar to that claimed to be the holotype by Kennedy (1986).

Kennedy (1986) described two other specimens from Cotentin, both incomplete spires, which he regarded to be allied to the holotype of *A. (E?) verneuillianus*. Of these, *Acanthoscaphites* sp. of Kennedy (1986: pl. 16: 7–10) is

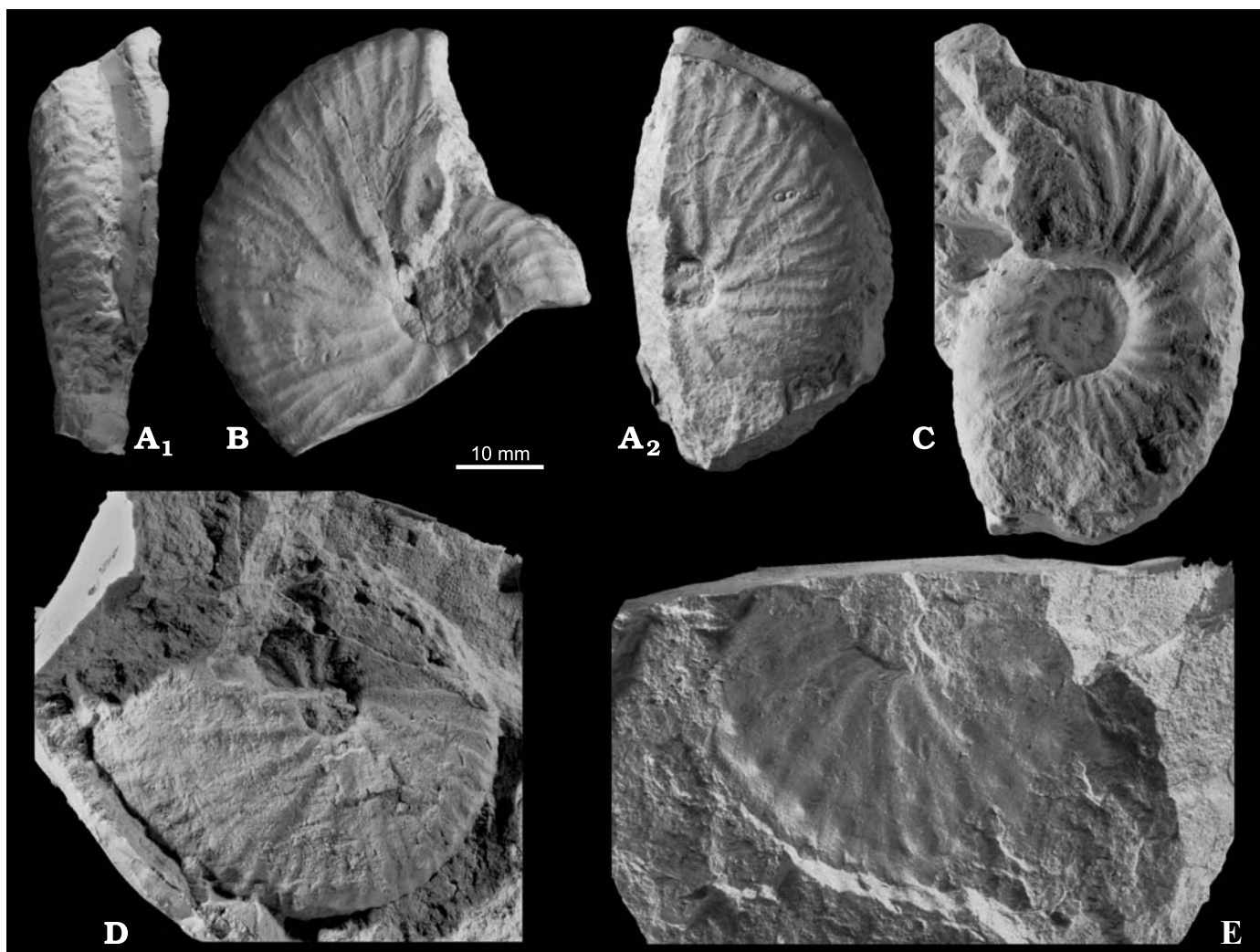


Fig. 25. *Acanthoscaphites* (*Euroscaphites*?) sp. aff. *verneuillianus* (A, B, D) and *Acanthoscaphites* (*Euroscaphites*) *varians blaszkiewiczzi* (C, E). A. Plaster cast of MGUH 27748, *Meonia semiglobularis*–*Ruegenella humboldtii* Zone, Gudumholm, Denmark, in ventral (A₁) and lateral (A₂) views. B. Plaster cast of MGUH 20127, in lateral view. C. NLfB 179, *Spyridoceramus tegulatus*–*Belemnitella junior* Zone, Hemmoor, Germany, in lateral view. D. Silicone rubber cast of MGUH 27749, in lateral view. E. Silicone rubber cast of MGUH 27750, in lateral view. B, D, and E are from *Rugia tenuicostata*–*Meonia semiglobularis* Zone or *Meonia semiglobularis*–*Ruegenella humboldtii* Zone, Rørdal, Denmark.

herein referred to as *Acanthoscaphites* sp. aff. *verneuillianus* and *A.* cf. *verneuillianus* of Kennedy (1986: pl. 16: 20, 21) is thought to be very close to or conspecific with *Acanthoscaphites varians blaszkiewiczzi* (see above).

Acanthoscaphites cf. *verneuillianus* from the Kunrade Limestone facies of the Maastricht Formation (Kennedy 1987: 207, pl. 34: 1) is too poorly preserved for any firm taxonomic placement. Thus, there are no definitive records of the species outside the Cotentin area.

Stratigraphic and geographic range.—Upper lower Maastrichtian of France (“*Inoceramus*” *morgani* Zone).

Acanthoscaphites (*Euroscaphites*?) sp. aff. *verneuillianus* (d’Orbigny, 1841)

Fig. 25A, B, D.

?1951 *Acanthoscaphites tridens* (Kner) var. *varians* (Łopuski); Mikhailov 1951: 104, pl. 16, 72, 73.

1986 *Acanthoscaphites* sp.; Kennedy 1986: 74, pl. 16: 7–10.

1993 *Acanthoscaphites varians* (Łopuski, 1911); Birkelund 1993: 56 (partim), pl. 9: 5; pl. 10: 2 [non pl. 9: 3, 4, 6, 7, pl. 10: 3 = *Acanthoscaphites* (*Euroscaphites*) *varians blaszkiewiczzi*].

1999 *Acanthoscaphites* (*Euroscaphites*) *varians blaszkiewiczzi* subsp. nov.; Jagt et al. 1999: 139 (partim), pl. 8: 1, 5 only.

?2002 *Acanthoscaphites varians* (Łopuski, 1911); Reich and Frenzel 2002: pl. 23: 1a, b.

Material.—From Denmark: Three specimens from Rørdal (MGUH 20127, 20130, 27749) and a single specimen from Gudumholm (MGUH 27748).

Discussion.—A spire from Cotentin referred to as *Acanthoscaphites* sp. by Kennedy (1986: pl. 16: 7–10) closely resembles the holotype of *A.* (*E.*?) *verneuillianus* in ribbing up to diameter of 27 mm, but its later growth stages differ in that the primaries are separated by a single secondary rib only. As virtually nothing can be said on the range of variation of the “type population” of *A.* (*E.*?) *verneuillianus*, Kennedy’s (1986) spec-

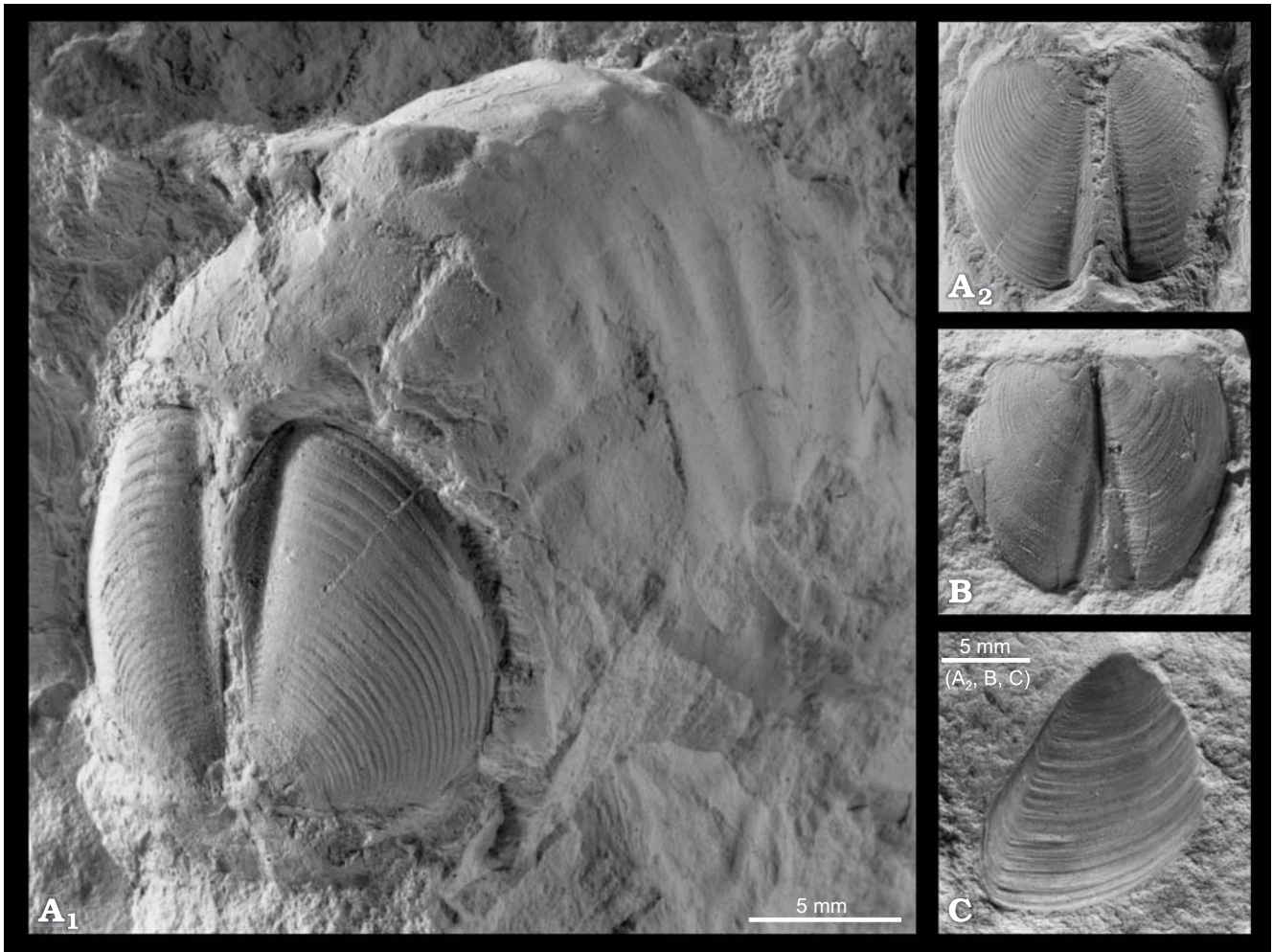


Fig. 26. Aptychi of *Hoploscaphites constrictus* from Poland. A. A double-valved aptychus in the body chamber of *Hoploscaphites constrictus livivensis* subsp. nov., ZPAL Am. 12/796, *Spyridoceramus tegulatus*–*Belemnitella junior* Zone, level IV at Chelm; A₁, general view of the specimen; A₂, in external view of the aptychus. B. Another paired aptychus, ZPAL Am. 12/801, *Sp. tegulatus*–*Bt. junior* Zone, level IV at Chelm, in external view. C. A single valve APAL Am. 12/782, *Belemnella kazimiroviensis* Zone, town quarry south of Kazimierz Dolny, in external view.

imen is best regarded as belonging to a separate taxon, allied to *A. (E.?) verneuillianus*.

Amongst the specimens studied from Denmark, MGUH 20127 (Fig. 25B, also Birkelund 1993: pl. 8: 5; Jagt et al. 1999: pl. 8: 5), MGUH 20130 (Birkelund 1993: pl. 10: 2; Jagt et al. 1999: pl. 8: 1), and MGUH 27749 (Fig. 25D) are from Rørdal, Jylland, from the upper lower Maastrichtian *Rugia tenuicostata*–*Meonia semiglobularis* Zone and/or lower upper Maastrichtian *Meonia semiglobularis*–*Ruegenella humboldtii* Zone (Surlyk 1984: fig. 3). The fourth specimen, MGUH 27748 (Fig. 25A₁, A₂), is from Gudumholm, from the *Meonia semiglobularis*–*Ruegenella humboldtii* Zone (Surlyk 1984: fig. 3). All these specimens are spires that share the presence of narrow primary ribs, concave at the umbilical shoulder and straight or feebly flexuous, but always prorsiradiate on the flanks. Up to four secondaries are intercalated between the primaries in MGUH 20127 (Fig. 25B) and in MGUH 27748 (Fig. 25A₁, A₂), and up to two in MGUH 27749 (Fig. 25D); the secondaries cannot be counted in MGUH 20130 (Birkelund 1993: pl. 10: 2; Jagt et al. 1999:

pl. 8: 1) due to poor preservation of the specimen. Distinct siphonal tubercles are visible in MGUH 27748 (Fig. 25A₁); they are barely visible in MGUH 20127. The well-developed ventrolateral tuberculation is present in three specimens illustrated (Fig. 25A, B, D) but cannot be seen in MGUH 20130 due to the incompleteness of the specimen. In addition, outer ventrolaterals are visible in MGUH 20127 (Fig. 25B).

Specimens MGUH 20127 and 20130 were interpreted by Jagt et al. (1999) as microconchs of *Acanthoscaphites (E.) varians blaszkiewiczzi*. However, they differ significantly in style of ornament and number of tubercles from spires of comparable size attributed to *A. varians blaszkiewiczzi* (Fig. 25C, E) and are better interpreted as a separate taxon. In general, the ornament of the Danish material discussed above, although variably developed, recalls that of the holotype of *A. (E.?) verneuillianus*. However, the differences are such that the material studied is referred to as *Acanthoscaphites (E.?)* sp. aff. *verneuillianus*. Better-preserved specimens from Cotentin and Denmark are needed to clarify its taxonomic position.

Mikhailov's (1951) specimen from the "Maastrichtian" of Emba River and the specimen from the lower Maastrichtian of Rügen figured by Reich and Frenzel (2002) seem to belong here as well, but poor preservation of the Emba specimen and poor quality of the photograph of the Rügen specimen, preclude any firm conclusions.

Acanthoscaphites sp. of Kennedy and Christensen (1997: 124, fig. 40) from the upper Maastrichtian of southern Sweden seems to be unrelated, having a different ribbing which recalls that of *Discoscaphites rossi* Landman and Waage, 1993a from the upper Maastrichtian of the U.S. Western Interior (Landman and Waage 1993a: 231, figs. 181–189). Here too, preservation is inadequate to allow firm conclusions.

Stratigraphic and geographic range.—Upper lower and/or lower upper Maastrichtian of Denmark (*Rugia tenuicostata*–*Meonia semiglobularis* Zone and/or *Meonia semiglobularis*–*Ruegenella humboldtii* Zone) and, possibly, of Germany and Russia.

Scaphitid aptychi

Fig. 26.

Material.—Three specimens from Nasilów (ZPAL Am. 12/787, 788, 790), four specimens from Kazimierz Dolny (ZPAL Am. 12/782–784, 786), 20 specimens from Chełm (ZPAL Am. 12/458, 484, 544–548, 792–804), all from Poland.

Discussion.—Aptychi are paired calcitic coverings of the outer surface of ammonoid lower jaws which could have served additionally as opercula as proposed by Lehmann and Kulicki (1990) and Seilacher (1993), although Landman and Waage (1993a: 63) expressed some doubts in respect to this interpretation). Aptychi attributable to scaphitids were reported for instance from the white chalk successions at Hemmoor (Birkelund 1982: pl. 2: 6–7) and Stevns Klint (Birkelund 1993: pl. 17: 2–4). The Polish material studied (Fig. 26) generally corresponds in morphology to specimens mentioned above and could be assigned to "*Aptychus*" *portlocki* in the parataxonomic classification of aptychi, followed by earlier authors (e.g., Trauth 1928) but abandoned today. The relatively small size of the aptychi studied suggests that they belonged to members of the *Hoploscaphites constrictus* lineage. No aptychi attributable to larger scaphitids have been identified.

The scaphitid aptychi from Kazimierz Opoka in the Middle Vistula River sections are represented exclusively by single valves dissociated from the conchs of their owners (Fig. 26C). In contrast, some specimens from Chełm are double-valved, being found in a "butterfly position" (Seilacher 1993) on the surface of the white chalk slabs (Fig. 26B). An exceptional specimen ZPAL Am. 12/796 from level IV at Chełm represents a double-valved aptychus preserved within the body chamber of *Hoploscaphites constrictus lvivensis* subsp. nov. (Fig. 26A₁, A₂). The generally better preservation of aptychi in the white chalk at Chełm in comparison to those from opoka in other sections suggests instantaneous waterlogging of the conchs in the Chełm area and rapid subsequent burial (Maeda and Seilacher 1996: fig. 5).

Implications

Sexual dimorphism.—In the classic version of the theory of ammonite sexual dimorphism (Makowski 1962; Callomon 1963; see Matyja 1986 and Davis et al. 1996 for updated overviews), growth rate and morphological development were identical during early morphological stages of both microconchs and macroconchs. In later stages, microconchs halted their development and attained maturity earlier than macroconchs did, which underwent further stages of morphological development.

Matyja (1986, see also 1994) opposed the theory of sexual dimorphism, claimed the occurrence of one, two, three or more morphs amongst Jurassic ammonite species and came up with an alternative theory of developmental polymorphism. According to this theory, different populations of the same species could reach maturity at different ages which therefore could appear at a different size and in different morphological classes (polymorphs).

There is no indication for the existence of developmental polymorphism *sensu* Matyja (1986) in the scaphitid material studied. A distinct dimorphism of the type characteristic of many scaphitids (Cobban 1969; Kennedy and Summesberger 1987; Landman and Waage 1993a) can be demonstrated for *Hoploscaphites constrictus lvivensis* subsp. nov., *H. c. crassus*, *H. c. johnjagti* subsp. nov., *H. pungens*, and *H. schmidi*. Microconchs and macroconchs are defined not only by size but also by the shape of the umbilical wall of the shaft. Microconchs usually are smaller than macroconchs; some overlap in size range between dimorphs has been observed in several cases though (Fig. 9).

Dimorphs are not recognisable in the remainder of the taxa studied. However, this is almost surely a function of preservational bias, at least in the case of *Hoploscaphites* sp. ex gr. *pungens*–*schmidi*, *H. felderi*, *H. sp.* ex gr. *waagei*–*angmartussutensis*, *Acanthoscaphites (Euroscaphites?) verneuillianus* and *A. (E.?) sp. aff. verneuillianus*, which all are represented by incomplete individuals only. The absence of demonstrable microconchs in *A. (E.) varians varians* and *A. (E.) varians blaszkiewiczzi* is more intriguing. It cannot be excluded that these taxa were monomorphic in contrast to their possible ancestors of the early Maastrichtian *Acanthoscaphites (A.) tridens* group, in which a clear dimorphism could be demonstrated by Kennedy and Summesberger (1987) and Jagt et al. (1999).

Size-dependent differences in ornament of adult microconchs of *Hoploscaphites constrictus crassus* (Łopuski, 1911) from the Kazimierz Opoka (Fig. 11) may be related to a variable timing of maturity in males. In contrast, the variation in ornament in adult macroconchs of this subspecies seems to be size (and age) independent (Fig. 11). If the above assumptions are correct, populations of *H. c. crassus* demonstrate clear dimorphism, most possibly sexual in nature (cf. Makowski 1962), and additionally, a developmental polymorphism of males (cf. Matyja 1986). This unexpected fusion suggests that

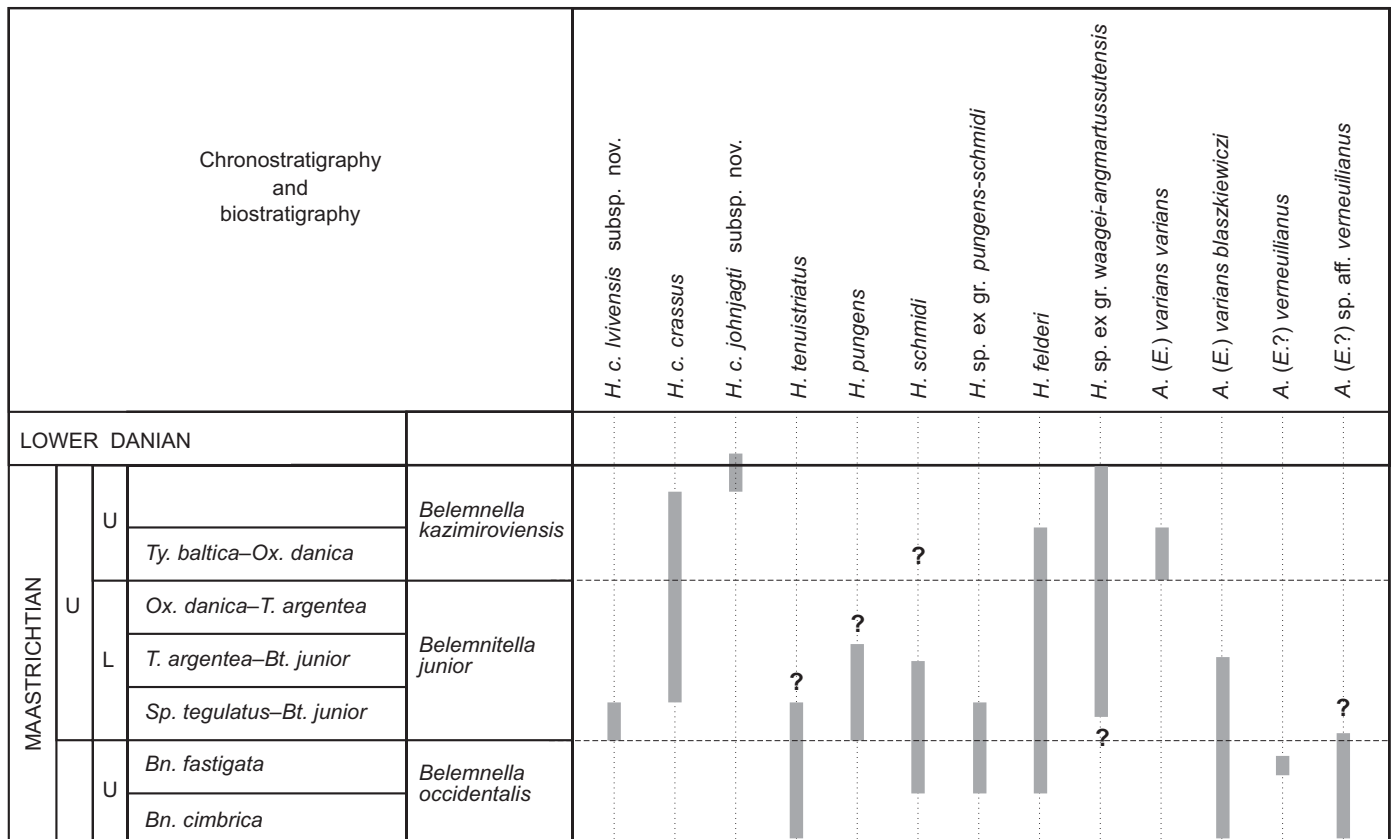


Fig. 27. Vertical ranges of scaphitids studied. The upper Maastrichtian ranges are plotted on the upper Maastrichtian zonation for NW Germany and standard belemnite zones. Abbreviations: L, lower; U, upper; A. (E.), *Acanthoscaphites* (*Euroscaphites*); Bn., *Belemnella*; Bt., *Belemnitella*; H., *Hoploscaphites*; H.c., *Hoploscaphites constrictus*; Ox., *Oxytoma*; Sp., *Spyridoceras*; T., *Tenuipteria*; Ty., *Tylocidaris*.

the developmental polymorphism hypothesis as advocated by Matyja (1986) does not necessarily contradict that of traditional sexual dimorphism. The existence of more than two morphs within a given species, seen by Matyja as an argument against the theory of sexual dimorphism, may simply reflect the variation in time of maturity within one sex. Better material is needed, however, for further exploration of this theme.

Evolutionary relationships.—Scaphitid evolution has recently been discussed by Riccardi (1983), Landman and Waage (1993b), Cooper (1994) and Monks (2000). Two main evolutionary lineages, possibly endemic to Europe, may be distinguished in the upper Maastrichtian and lower Danian material studied. The *Hoploscaphites constrictus* lineage comprises successive members of the main stock: *Hoploscaphites constrictus livensis* subsp. nov., *H. c. crassus*, and *H. c. johnjagti* subsp. nov., and short-lived offshoots: *H. tenuistriatus*, *H. pungens*, *H. schmidi*, and *Hoploscaphites sp. ex gr. pungens-schmidi*. The *Hoploscaphites constrictus* lineage started around the Campanian/Maastrichtian boundary interval, descending possibly from *Hoploscaphites pumilis* (Machalski and Odin 2001). According to Jagt et al. (2003) and Machalski and Heinberg (in press), the lineage survived Maastrichtian–Danian boundary perturbations.

Hoploscaphites pungens and *H. schmidi* were treated as derivatives of the main *H. constrictus* lineage by Kennedy

(1987) and Cooper (1994). Both taxa recall in ornament some species of *Jeletzkytes* from the U.S. Western Interior (Landman and Waage 1993a). However, the presence of ventral swellings in both European taxa, a feature shared with *Hoploscaphites constrictus*, precludes their direct relationship with the North American *Jeletzkytes* lineage.

Another distinctive lineage is represented by successive members of the *Acanthoscaphites* (*Euroscaphites*) main stock: *A. (E.) varians blaszkiewiczzi* and *A. (E.) v. varians*. The remaining *A. (E.?) verneuillianus* and *A. (E.?) sp. aff. verneuillianus* are best interpreted as offshoots. This group of taxa descended from the early Maastrichtian *Acanthoscaphites* (*Acanthoscaphites*) *tridens* group (Kennedy and Summesberger 1987; Jagt et al. 1999). The *Acanthoscaphites* (*Euroscaphites*) lineage did not extend across the Cretaceous–Paleogene boundary.

The affinities of *Hoploscaphites felderi* are entirely unclear (Kennedy 1987). In contrast, *H. sp. ex gr. waagei-angmartussutensis* may be related to a group of scaphitids known from the Maastrichtian of Greenland (Birkelund 1965; Kennedy and Jagt 1998).

The extinction pattern.—The extinction pattern of the last ammonites, including scaphitids, was discussed by Wiedmann (1988), Kennedy (1989) and Ward (1990). The recorded stratigraphic ranges of the scaphitids studied are here summarised in Fig. 27. However, this diagram cannot be literally

translated into an extinction pattern of European scaphitids. Only three taxa amongst the studied set are represented by adequate numbers of individuals needed for a reliable assessment of the extinction pattern (see Hallam and Wignall 1997: 16). These are *Hoploscaphites constrictus livivensis* subsp. nov., *H. c. crassus*, and *H. c. johnjagti* subsp. nov. However, these taxa are arbitrarily defined members of a single phyletic lineage and their upper ranges have nothing to do with true extinction events. Amongst the remaining taxa recorded in Fig. 27, at least some represent real biological units (e.g., *H. felderi*). However, all these taxa are represented by such limited material that their highest occurrences are extremely unlikely to represent the very last individuals of these species.

In spite of the difficulties in interpreting scaphitid ranges, some conclusions as to their extinction are possible. The first is that the last European scaphitids were essentially unaffected by the “mid-Maastrichtian extinction event” which led to the demise of non-tegulated inoceramids (MacLeod 1994a, b; MacLeod and Huber 1996; Barrera 1994). Secondly, the *Hoploscaphites constrictus* lineage, represented by its last subspecies *H. c. johnjagti* subsp. nov., remained unaffected and ranged to the very end of the Maastrichtian. This is documented by abundant material of *H. c. johnjagti* subsp. nov. from just below the Maastrichtian–Danian boundary in the essentially complete K–Pg section at Stevns Klint (Birkelund 1993; Machalski 2005).

Some, possibly decimated, populations of this subspecies crossed the Cretaceous–Paleogene boundary as evidenced by rare finds of this taxon above the K–Pg boundary, considered to be indigenous Danian ammonites by Jagt et al. (2003) and Machalski and Heinberg (in press). Thus, the record of the last scaphitids at the K–Pg boundary seems to contradict views held by others on the gradual decline of ammonites prior to the K–Pg boundary (e.g., Wiedmann 1988) or on linking their ultimate fate with an instant catastrophe related to a bolide impact (e.g., Alvarez et al. 1984).

Form, environment and predators.—Landman and Waage (1993b) provided compelling examples of what they interpreted to be environmentally induced variation amongst some North American scaphitids. Environment-related changes invoked by those authors involve such in shell proportions and strength of ornament. Similar changes in nautiloid shells were interpreted by Tintant and Kabamba (1985) to be an adaptive response to life in shallow environments. Those authors assumed that heavily ornamented shells were more resistant against mechanic destruction in agitated waters. However, a defensive explanation of ornament intensity is more probable (Ward 1981, 1996).

The last populations of the *Hoploscaphites constrictus* lineage, referred to as *H. c. johnjagti* subsp. nov., are dominated by, or composed exclusively of, specimens with a fully ribbed shaft and with ventrolateral tuberculation often extending to the aperture. In contrast, populations of ancestral *H. c. crassus* are dominated by specimens with smooth flanks on the shaft and no tubercles in the adapertural region.

The evolutionary transition from the smooth *Hoploscaphites constrictus crassus* to the ribbed *Hoploscaphites constrictus johnjagti* subsp. nov. paralleled a general trend towards the shallowing of the sea, well documented in Poland and Denmark, except for short-term deepening just prior to the K–Pg boundary in the latter area (Abdel-Gawad 1986; Schmitz et al. 1992; Machalski 1998; Surlyk 1997; Hart et al. 2005). Macrofaunal diversity is reported to generally increase upwards in these regressive sections (Abdel-Gawad 1986; Surlyk 1997). One may intuitively postulate that the number of shell-crushing (durophagous) predators increased concomitantly. In fact, decapod crustaceans and mosasaurid reptiles, listed by Lehmann (1976) as potential predators on ammonoids, occur only in the upper, shallower part of the Kazimierz Opoka (Radwański 1996; Machalski et al. 2003). The appearance of more heavily ribbed and tuberculated shell in populations of *H. c. johnjagti* subsp. nov. may thus reflect increased predation pressure, indirectly related to the late Maastrichtian regression.

Abundant traces of shell-breaking predators, thought to have been benthic crabs, on shells of *Hoploscaphites constrictus crassus* were reported from the hard limestone layer at the top of the Kazimierz Opoka succession at Nasiłów by Radwański (1996). These traces were alternatively interpreted as made by swimming crabs (Fraaye 1996). Whatever their origin, no traces of this kind are present on conchs of *H. c. johnjagti* subsp. nov. in the terminal Maastrichtian horizons at Stevns Klint (personal observation). It is not clear whether this reflects increased resistance of the ribbed shells to the activity of shell-breakers. Anyway, the absence of traces of durophagy on members of the Stevns Klint population contradicts Radwański’s (1996) hypothesis on the direct link between the activity of durophagous predators and the extinction of the last populations of *Hoploscaphites constrictus*.

Possible trans-Atlantic links.—Finds of the essentially North American scaphitid *Jeletzkytes dorfi* in the upper lower Maastrichtian Vijlen Member (Interval 6) of the Gulpen Formation at the CPL quarry, Haccourt, Belgium, have enabled an approximate time-correlation between North American and European sections (Jagt and Kennedy 1994; see also comments on p. 656). Somewhat surprisingly, no definitive North American intruders are known from the study area up to now. Previous assumptions about the presence of *H. nicolletii* in Europe (Jeletzky 1962) can be refuted (see p. 673). A possible exception is *Acanthoscaphites* sp. of Kennedy and Christensen (1997) from the upper Maastrichtian of southern Sweden, which recalls *Discoscaphites rossi* Landman and Waage, 1993a from the upper Maastrichtian of the U.S. Western Interior (see p. 689). There is no reason to assume, however, that finds of trans-Atlantic migrants are not possible in the upper Maastrichtian of Europe, especially at the base of transgressive units in the westerly part of the continent.

Biostratigraphic potential.—In contrast to the largely endemic scaphitid lineages of the U.S. Western Interior, which form the basis of a detailed subdivision of the upper Maas-

trichtian there (Landman and Waage 1993a; Kennedy et al. 1998), coeval scaphitids in Europe were not used for biostratigraphic purposes. The only exception is the *Hoploscaphites constrictus crassus* Zone of Błaszkiwicz (1980), defined by the range of the index taxon in the Middle Vistula River succession, and thought to be the terminal Maastrichtian zone, equivalent of the upper part of the classic *Bt. junior* Zone and to the *Belemnella kazimiroviensis* Zone (Błaszkiwicz 1980; Kennedy 1993). This concept should be modified in view of the fact that *Hoploscaphites constrictus crassus* cannot be regarded anymore as the youngest member of the *H. constrictus* lineage, since it is replaced upwards by *H. c. johnjagti* subsp. nov.

In accordance with the spirit of Błaszkiwicz's (1980) work, the successive members of the *H. constrictus* lineage as defined in the present paper are actually of great potential for correlation and subdivision of European upper Maastrichtian deposits. The last member of the lineage, *H. c. johnjagti* subsp. nov., seems to be particularly useful for identification of top-most Maastrichtian strata (Machalski 2005). Three successive zones defined by the total ranges of their index taxa could be easily distinguished, namely the *Hoploscaphites constrictus lvivensis* subsp. nov. Zone, *H. c. crassus* Zone, and *H. c. johnjagti* subsp. nov. Zone. Their formal definition is, however, hampered by the absence of sections where the lower boundaries of the two lower zones can be indicated.

Other scaphitids studied are of lesser biostratigraphic value, mainly due to their local occurrence or small numbers of specimens available. However, some short-ranging taxa, for example *H. tenuistriatus*, seem to provide good correlation tools throughout the area of their occurrence.

Summary

- In total, thirteen scaphitid taxa are recognised in the upper Maastrichtian and lowermost Danian of central Europe. These are: *Hoploscaphites constrictus lvivensis* subsp. nov., *H. c. crassus*, *H. c. johnjagti* subsp. nov., *H. tenuistriatus*, *H. pungens*, *H. schmidi*, *Hoploscaphites* sp. ex gr. *pungens-schmidi*, *H. felderi*, *H. sp. ex gr. waagei-angmartussutensis*, *Acanthoscaphites (Euroscaphites) varians varians*, *A. (E.) varians blaszkiewiczzi*, *A. (E.?) verneuilianus*, and *A. (E.?) sp. aff. verneuilianus*.
- The more important taxonomic results of the present study involve: subdivision of the *Hoploscaphites constrictus* lineage into three successive chronosubspecies (*Hoploscaphites constrictus lvivensis* subsp. nov., *H. c. crassus*, *H. c. johnjagti* subsp. nov.); modification of definition of *H. tenuistriatus* to accommodate tuberculate specimens, previously assigned to *H. constrictus*; extension of the geographic range of *H. schmidi*, previously known only from Hemmoor in northern Germany, into Poland and Denmark; extension of the geographic range of *H. felderi*, thought for a long time to be endemic to the Maastricht area, to Poland and Denmark; and reinterpretation of the

Acanthoscaphites (Euroscaphites?) verneuilianus group with indication of its occurrence in Denmark.

- Dimorphism may be demonstrated for *Hoploscaphites constrictus lvivensis* subsp. nov., *H. c. crassus*, *H. c. johnjagti* subsp. nov., *H. pungens*, and *H. schmidi*. Developmental polymorphism of males is additionally proposed to explain the size-dependent variation of ornament in microconchs of *H. c. crassus*. Dimorphism could not be demonstrated for remaining species, mainly for preservational reasons.
- Two main evolutionary lineages of late Maastrichtian and earliest Danian scaphitids may be distinguished in Europe, as based on literature data and results of the present study. The *Hoploscaphites constrictus* lineage comprises successive members of the main stock: *Hoploscaphites constrictus lvivensis* subsp. nov., *H. c. crassus*, and *H. c. johnjagti* subsp. nov., and short-lived offshoots: *H. tenuistriatus*, *H. pungens*, *H. schmidi* and *Hoploscaphites* sp. ex gr. *pungens-schmidi*. The *Acanthoscaphites (Euroscaphites)* lineage is represented by successive members of the *Acanthoscaphites (Euroscaphites)* main stock: *A. (E.) varians blaszkiewiczzi* and *A. (E.) v. varians*, with *A. (E.?) verneuilianus* and *A. (E.?) sp. aff. verneuilianus* best treated as offshoots. The affinities of *Hoploscaphites felderi* are entirely unclear whereas *H. sp. ex gr. waagei-angmartussutensis* may be related to a group of scaphitids known from the Maastrichtian of Greenland.
- The extinction pattern of the European scaphitids is difficult to assess for methodological reasons. The available data indicate, however, that the *Hoploscaphites constrictus* lineage survived unaffected until the very end of the Cretaceous and even crossed the Cretaceous–Paleogene (K–Pg) boundary.
- The latest Maastrichtian populations of the *Hoploscaphites constrictus* lineage, assigned here to *H. c. johnjagti* subsp. nov., are dominated by individuals with a fully ribbed shaft and with ventrolateral tuberculation often extending to the aperture. In contrast, populations of ancestral *H. c. crassus* are dominated by specimens with smooth flanks on the shaft and no tubercles in the adapertural region. The appearance of more heavily ribbed and tuberculated shells in populations of *H. c. johnjagti* subsp. nov. may reflect increased predation pressure, indirectly related to the late Maastrichtian regression.
- The successive members of the *Hoploscaphites constrictus* lineage, i.e., *H. c. lvivensis* subsp. nov., *H. c. crassus*, and *H. c. johnjagti* subsp. nov. are useful for subdivision, and temporal correlation, of upper Maastrichtian deposits.

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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.
- Alexandrowicz, S.W. 1977. Sclerites of octocorals from the Upper Cretaceous of eastern Poland. *Journal of Paleontology* 51: 687–692.
- Alexandrowicz, S.W. and Tchórzewska, D. 1975. The Cretaceous marls and opokas from Rejowiec. *Geologia* 1: 5–14.
- Alvarez, W., Kauffman, E.G., Surlyk, F., Alvarez, L.W., Asaro, F., and Michel, H.V. 1984. Impact theory of mass extinctions and the invertebrate fossil record. *Science* 223: 1135–1141.
- Amadon, D. 1949. The seventy-five per cent rule for subspecies. *The Condor* 51: 250–258.
- Barrera, E. 1994. Global environmental changes preceding the Cretaceous–Tertiary boundary: Early–late Maastrichtian transition. *Geology* 22: 877–880.
- Bilotte, M., Odin, G.S., and Vrielynck, B. 2001. Geology and Late Cretaceous palaeogeography of the geological site at Tercis les Bains (Landes, France). In: G.S. Odin (ed.), *The Campanian–Maastrichtian Stage Boundary: Characterisation at Tercis les Bains (France) and Correlation with Europe and Other Continents*. *Developments in Palaeontology and Stratigraphy* 19: 47–59.
- Binkhorst van den Binkhorst, J.T. 1861. *Monographie des Gastéropodes et des Céphalopodes de la Craie Supérieure du Duché de Limbourg*. 83 + 44 pp. Muquardt, Brussels; Muller Frères, Maastricht.
- Birkelund, T. 1957. Upper Cretaceous belemnites from Denmark. *Biologiske Skrifter, Kongelige Danske Videnskaberne Selskab* 9: 1–69.
- Birkelund, T. 1965. Ammonites from the Upper Cretaceous of West Greenland. *Grønlands Geologiske Undersøgelse* 56: 1–192.
- Birkelund, T. 1967. Die Entwicklung der jüngsten Scaphiten und ihre stratigraphische Bedeutung im baltischen Gebiet. *Berichte der deutschen Gesellschaft für geologische Wissenschaften, A: Geologie und Paläontologie* 11: 737–744.
- Birkelund, T. 1979. The last Maastrichtian ammonites. In: T. Birkelund and R.G. Bromley (eds.), *Cretaceous–Tertiary Boundary Events. I. The Maastrichtian and Danian of Denmark*, 51–57. University of Copenhagen, Copenhagen.
- Birkelund, T. 1982. Maastrichtian ammonites from Hemmoor, Niederelbe (NW-Germany). *Geologisches Jahrbuch A* 61: 13–33.
- Birkelund, T. 1993. Ammonites from the Maastrichtian White Chalk of Denmark. *Bulletin of the Geological Society of Denmark* 40: 33–81.
- Błaskiewicz, A. 1980. Campanian and Maastrichtian ammonites of the Middle Vistula River Valley, Poland: a stratigraphic-paleontological study. *Prace Instytutu Geologicznego* 92: 3–63.
- Burnett, J.A. (with contributions from L.T. Gallagher and M.J. Hampton) 1998. Upper Cretaceous. In: P.R. Bown (ed.), *Calcareous Nannofossil Biostratigraphy*, 132–199. British Micropalaeontological Society Series, Chapman & Hall/Kluwer Academic Publishers, London.
- Callomon, J.H. 1963. Sexual dimorphism in Jurassic ammonites. *Transactions of the Leicester Literary and Philosophical Society* 57: 1–36.
- Callomon, J.H. 1985. The evolution of the Jurassic ammonite family Cardioceratidae. In: J.C.W. Cope and P.W. Skelton (eds.), *Evolutionary Case Histories from the Fossil Record. Special Papers in Palaeontology* 33: 49–90.
- 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.
- Christensen, W.K., Schmid, F., and Schulz, M.-G. 2004. *Belemnitella* from the Upper Maastrichtian of Hemmoor, Northwest Germany. *Geologisches Jahrbuch A* 157: 23–67.
- Cieśliński, S. and Wyrwicka, K. 1970. Kreda obszaru lubelskiego. In: *Przewodnik XLII Zjazdu Polskiego Towarzystwa Geologicznego, Lublin 3–5 września 1970*, 56–74. Wydawnictwa Geologiczne, Warszawa.
- Cifelli, R.L. and Kielan-Jaworowska, Z. 2005. Diagnosis: differing interpretations of the ICZN. *Acta Palaeontologica Polonica* 50: 650–652.
- Cobban, W.A. 1969. The Late Cretaceous ammonites *Scaphites leei* Reeside and *Scaphites hippocrepis* (DeKay) in the Western Interior of the United States. *United States Geological Survey, Professional Paper* 619: 1–29.
- Cooper, M.R. 1994. Towards a phylogenetic classification of the Cretaceous ammonites. III. Scaphitaceae. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 193: 165–193.
- Courville, P. and Odin, G.S. 2001. Les ammonites spirales du Campanien et du Maastrichtien de Tercis les Bains (Landes, France). In: G.S. Odin (ed.), *The Campanian–Maastrichtian Stage Boundary: Characterisation at Tercis les Bains (France) and Correlation with Europe and Other Continents*. *Developments in Palaeontology and Stratigraphy* 19: 529–549.
- Davis, R.A., Landman, N.H., Dommergues, J.-L., Marchand, D., and Bucher, H. 1996. Mature modifications and dimorphism in ammonoid cephalopods. In: N.H. Landman, K. Tanabe, and R.A. Davis (eds.), *Ammonoid Paleobiology. Topics in Geobiology* 13: 463–539.
- Diener, C. 1925. *Ammonoidea neocretacea*. In: *Fossilium Catalogus (I: Animalia)* 29, 1–244 pp. W. Junk, Berlin.
- Donovan, T. 1953. The Jurassic and Cretaceous stratigraphy and paleontology of Trail Ø, east Greenland. *Meddelelser om Grønland* 111: 1–150.
- Dzik, J. 1985. Typologic versus population concepts of chronospecies: implications for ammonite biostratigraphy. *Acta Palaeontologica Polonica* 30: 71–91.
- Dzik, J. 1990. The concept of chronospecies in ammonites. In: G. Pallini, F. Fecca, S. Cresta, and M. Santantonio (eds.), *Atti del Secondo Convegno Internazionale Fossili, Evoluzione, Ambiente, Pergola 25–30 ottobre 1987*, 273–289. Comitato Centenario Raffaele Piccinini, Pergola.

- Dzik, J. and Trammer, J. 1980. Gradual evolution of conodontophorids in the Polish Triassic. *Acta Palaeontologica Polonica* 25: 55–89.
- Fatmi, A.N. and Kennedy, W.J. 1999. Maastrichtian ammonites from Balochistan, Pakistan. *Journal of Paleontology* 73: 641–662.
- Favre, E. 1869. *Description des Mollusques fossiles de la Craie des environs de Lemberg en Galicie*. 187 pp. H. Georg, Genève.
- Felder, P.J. and Bless, M.J.M. 1989. Biostratigraphy and ecostratigraphy of Late Cretaceous deposits in the Kunrade area (South-Limburg, SE Netherlands). *Annales de la Société géologique de Belgique* 112: 31–45.
- Fraaye, R.H.B. 1996. Late Cretaceous swimming crabs: radiation, migration, competition, and extinction. *Acta Geologica Polonica* 46: 269–278.
- Gavriliškin, V.I. [Gavrilišin, V.I.], Pasternak, S.I., and Rozumiejko, S.V. 1991. *Stratigrafičeskie podrazdelenija melovyh otloženiij platformennoj časti zapada Ukrainy*. 536 pp. Akademiya Nauk Ukrainskoj SSR, Instytut geologii i geohimii gorūčih iskopaemyh. Lviv.
- Gill, T. 1871. Arrangement of the families of mollusks. *Smithsonian Miscellaneous Collections* 227: 1–49.
- Grossouvre, A. de 1894. Recherches de la craie supérieure, 2, Paléontologie. Les ammonites de la craie supérieure. *Mémoires du Service de la Carte géologique détaillée de France*. 264 pp. (misdated 1893). Imprimerie nationale, Paris.
- Grossouvre, A. de 1908. Description des ammonites du Crétacé Supérieur du Limburg Belge et Hollandais et du Hainaut. *Mémoires du Musée royal d'histoire naturelle de Belgique* 4: 1–39.
- Hallam, A. and Wignall, P.B. 1997. *Mass Extinctions and Their Aftermath*. 309 pp. Oxford University Press, Oxford.
- Håkansson, E. and Hansen, J.M. 1979. Guide to Maastrichtian and Danian boundary strata in Jylland. In: T. Birkelund and R.G. Bromley (eds.), *Cretaceous–Tertiary Boundary Events. I. The Maastrichtian and Danian of Denmark*, 171–188. University of Copenhagen, Copenhagen.
- Hansen, H.J., Rasmussen, K.L., Gwozdz, R., Hansen, J.M., and Radwański, A. 1989. The Cretaceous/Tertiary boundary in Central Poland. *Acta Geologica Polonica* 39: 1–12.
- Harasimiuk, M. 1984. Kamieniołom margli i opok górnego mastrychtu w Rejowcu. In: *Przewodnik LVI Zjazdu Polskiego Towarzystwa Geologicznego, Lublin 6–8 września 1984 roku*, 149–152. Wydawnictwa Geologiczne, Warszawa.
- Hart, M.B., Feist, S.E., Price, G.D., and Leng, M.J. 2004. Reappraisal of the K–T boundary succession at Stevns Klint, Denmark. *Journal of the Geological Society, London* 161: 885–892.
- Hart, M.B., Feist, S.E., Håkansson, E., Heinberg, C., Price, G.D., Leng, M.J., and Watkinson, M.P. 2005. The Cretaceous–Palaeogene boundary succession at Stevns Klint, Denmark: foraminifers and stable isotope stratigraphy. *Palaeogeography, Palaeoclimatology, Palaeoecology* 224: 6–26.
- Holland, B. and Gabrielson, B. 1979. Guide to Limhamn quarry. In: T. Birkelund and R.G. Bromley (eds.), *Cretaceous–Tertiary Boundary Events. I. The Maastrichtian and Danian of Denmark*, 142–151. University of Copenhagen, Copenhagen.
- Hultberg, S.U. and Malmgren, B.A. 1987. Quantitative biostratigraphy based on Late Maastrichtian dinoflagellates and planktonic foraminifera from Southern Scandinavia. *Cretaceous Research* 8: 211–228.
- Ivanov, M. 1995. Upper Maastrichtian ammonites from the sections around the town of Bjala (eastern Bulgaria) [in Bulgarian]. *Review of the Bulgarian Geological Society* 56: 57–73.
- Ivanov, M.I. and Stoykova, K.H. [Stojkova, K.H.]. 1994. Cretaceous/Tertiary boundary in the area of Bjala, eastern Bulgaria—biostratigraphical results. *Geologia Balcanica* 24: 3–22.
- Jagt, J.W.M., 1995. A late Maastrichtian ammonite faunule in flint preservation from northeastern Belgium. *Mededelingen van de Rijks Geologische Dienst* 53: 21–47.
- Jagt, J.W.M. 1999. Late Cretaceous–Early Palaeogene echinoderms and the K–T boundary in southeast Netherlands and northeast Belgium. Part 1: Introduction and stratigraphy. *Scripta Geologica* 116: 1–57.
- Jagt, J.W.M., 2002. Late Cretaceous ammonite faunas of the Maastrichtian type area. In: H. Summesberger, K. Histon, and A. Daurer (eds.), *Cephalopods—Present and Past. Abhandlungen der Geologischen Bundesanstalt Wien* 57: 509–522.
- Jagt, J.W.M. and Kennedy, W.J. 1989. *Acanthoscaphites varians* (Lopuski, 1911) (Ammonoidea) from the Upper Maastrichtian of Haccourt, NE Belgium. *Geologie en Mijnbouw* 68: 237–240.
- Jagt, J.W.M. and 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* 1994 (4): 239–245.
- Jagt, J.W.M. and Kuypers, M.M.M. 1994. A note on *Hoploscaphites pungens* (Binckhorst, 1861) (Cretaceous Ammonoidea). *Cretaceous Research* 15: 765–770.
- Jagt, J.W.M., Felder, W.M., Dortangs, R.W., and Severijns, J. 1996. The Cretaceous/Tertiary boundary in the Maastrichtian type area (SE Netherlands, NE Belgium); a historical account. In: H. Brinkhuis and J. Smit (eds.), *The Geulhemmerberg Cretaceous/Tertiary boundary section (Maastrichtian type area, SE Netherlands)*. *Geologie en Mijnbouw* 75: 107–118.
- Jagt, W.J.M., Kennedy, W.J., and 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., Smit, J., and Schulp, A. 2003. ?Early Paleocene ammonites and other molluscan taxa from the Ankerpoort-Curfs quarry (Geulhem, southern Limburg, the Netherlands). In: M.A. Lamolda (ed.), *Bioevents: Their Stratigraphic Records, Patterns and Causes, Caravaca, 3rd–8th June 2003*, p. 113. Ayuntamiento de Caravaca de la Cruz.
- Jeletzky, J.A. 1951. Die Stratigraphie und Belemnitenfauna des Obercampan und Maastricht Westfalens, Nordwestdeutschlands und Dänemarks, sowie einige allgemeine Gliederungs-Probleme der jüngeren borealen Oberkreide Eurasiens. *Beihefte zum Geologischen Jahrbuch* 1: 1–142.
- Jeletzky, J.A. 1962. The allegedly Danian dinosaur-bearing rocks of the globe and the problem of the Mesozoic–Cenozoic boundary. *Journal of Paleontology* 36: 1005–1018.
- Jolkichev, N.A. [Jolkičev, N.A.] and Naidin, D.P. 2000. Upper Cretaceous of North Bulgaria, Crimea and Mangyshlak. 3. Upper Cretaceous stratigraphy of western Mountain Mangyshlak [in Russian]. *Bulletin Moskovskogo Obščestva Ispytatelej Prirody, Otdel geologičeskij* 75: 62–75.
- 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. 1987. The ammonite fauna of the type Maastrichtian with a revision of *Ammonites colligatus* Binckhorst, 1861. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 56 (1986): 151–267.
- 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: M.R. House (ed.), *The Ammonoidea: Environment, Ecology, and Evolutionary Change. Systematics Association Special Volume* 47: 285–326.
- Kennedy, W.J., Bilotte, M., Lepicard, B., and Segura, F. 1986. Upper Campanian and Maastrichtian ammonites from the Petites-Pyrénées, southern France. *Eclogae Geologicae Helveticae* 79: 1001–1037.
- Kennedy, W.J. and Christensen, W.K. 1997. Santonian to Maastrichtian ammonites from Scania, southern Sweden. *Fossils and Strata* 44: 75–128.
- Kennedy, W.J. and Cobban, W.A. 1993. Ammonites from the Saratoga Chalk (Upper Cretaceous), Arkansas. *Journal of Paleontology* 67: 404–434.
- Kennedy, W.J., Cobban, W.A., and Landman, N.H. 1997. Maastrichtian ammonites from the Severn Formation of Maryland. *American Museum Novitates* 3210: 1–30.
- Kennedy, W.J. and Jagt, J.W.M. 1998. Additional Late Cretaceous ammonite records from the Maastrichtian type area. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 68: 155–174.
- Kennedy, W.J., Nøhr-Hansen, H., and Dam G. 1999. The youngest Maastrichtian ammonite faunas from Nugsuaq, West Greenland. *Geological Survey of Greenland Bulletin* 184: 13–17.
- Kennedy, W.J. and Summesberger, H. 1986. Lower Maastrichtian ammonites from Neuberg, Steiermark, Austria. *Beiträge zur Paläontologie von Österreich* 12: 181–242.
- Kennedy, W.J. and Summesberger, H. 1987. Lower Maastrichtian ammonites from Nagoryany (Ukrainian SSR). *Beiträge zur Paläontologie von Österreich* 13: 25–78.

- Kennedy, W.J., Landman, N.H., Christensen, W.K., Cobban, W.A., and Hancock, J.M. 1998. Marine connections in North America during the late Maastrichtian: palaeogeographic and palaeobiogeographic significance of *Jeletzkytes nebrascensis* Zone cephalopod fauna from the Elk Butte Member of the Pierre Shale, SE South Dakota and NE Nebraska. *Cretaceous Research* 19: 745–775.
- Keutgen, N. 1996. *Biostratigraphie, Paläoökologie und Invertebratenfauna des Untermaastricht von Aachen (Westdeutschland) und angrenzenden Gebieten (Südostniederlande, Nordostbelgien)*. 213 pp. Shaker Verlag, Aachen.
- Klinger, H.C., Kennedy, W.J., Lees, J.A., and Kitto, S. 2001. Upper Maastrichtian ammonites and nannofossils and a Palaeocene nautiloid from Richards Bay, Kwa Zulu, South Africa. *Acta Geologica Polonica* 51: 273–291.
- Kner, R. 1848. Versteinerungen des Kreidemergels von Lemberg und seiner Umgebung. *Haidingers naturwissenschaftliche Abhandlungen* 2: 1–42.
- Kner, R. 1852. Neue Beiträge zur Kenntniss der Kreideversteinerungen von Ost-galizien. *Denkschriften der Akademie der Wissenschaften in Wien* 3: 293–334.
- Kociubynskij, S.P. [Kociubins'kij, S.P.] 1968. Inoceramidae [in Ukrainian]. In: S.I. Pasternak, V.I. Gavrilišin, V.A. Ginda, S.P. Kociubins'kij, and Ū.N. Sen'kows'kij, *Stratigrafiâ i fauna krejdovoyh vidkladiv zahodu Ukrainy*, 115–148. Naukovaâ Dumka, Kyiv.
- Kongiel, R. 1962. On belemnites on Maastrichtian, Campanian and Santonian sediments in the Middle Vistula Valley (central Poland). *Prace Muzeum Ziemi* 5: 1–148.
- Landman, N.H. and Waage, K.M. 1993a. Scaphitid ammonites of the Upper Cretaceous (Maastrichtian) Fox Hills formation in South Dakota and Wyoming. *Bulletin of the American Museum of Natural History* 215: 1–257.
- Landman, N.H. and Waage, K.M. 1993b. Morphology and environment of Upper Cretaceous (Maastrichtian) *Scaphites*. *Geobios, Mémoire spéciale* 15: 257–265.
- Landman, N.H. and Cobban, W.A. 2003. Ammonites from the upper part of the Pierre Shale and Fox Hills Formation of Colorado. *American Museum Novitates* 3388: 1–45.
- Landman, N.H., Klofak, S.M., and Sarg, K.B. 2003. Variation in adult size of scaphitid ammonites from Upper Cretaceous Pierre Shale and Fox Hills Formation. In: P.J. Harries (ed.), *Approaches in High-resolution Stratigraphic Paleontology*, 150–194. Kluwer Academic Publishers, Dordrecht.
- Lehmann, U. 1976. *Ammoniten: Ihr Leben und ihre Umwelt*. 171 pp. Ferdinand Enke Verlag, Stuttgart.
- Lehmann, U. and Kulicki, C. 1990. Double function of aptychi (Ammonoidea) as jaw elements and opercula. *Lethaia* 23: 325–331.
- Lehmann, J. and Wippich, M.G.E. 1995. Oyster attachment scar preservation of the late Maastrichtian ammonite *Hoploscaphites constrictus*. *Acta Palaeontologica Polonica* 40: 437–440.
- Łopuski, C. 1911. Przyczynki do znajomości fauny kredowej guberni Lubelskiej. *Sprawy 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. 1998. Granica kreda-trzeciorzęd w przełomie Wisły. *Przegląd Geologiczny* 46: 1153–1161.
- Machalski, M. 2005. The youngest Maastrichtian ammonite faunas in Poland and their scaphitid dating. *Cretaceous Research* 26: 813–836.
- Machalski, M. and Heinberg, C. (in press). Evidence for ammonite survival into the Danian (Paleogene) from the Cerithium Limestone at Stevns Klint, Denmark. *Bulletin of the Geological Society of Denmark* 52.
- Machalski, M. and Jagt, J.W.M. 1998. Latest Maastrichtian pachydiscid ammonites from the Netherlands and Poland. *Acta Geologica Polonica* 48: 121–133.
- Machalski, M., Jagt, J.W.M., Dortangs, R., Mulder, E.W.A., and Radwański, A. 2003. Campanian and Maastrichtian mosasaurid reptiles from central Poland. *Acta Palaeontologica Polonica* 48: 397–408.
- Machalski, M. and Odin, G.S. 2001. Scaphitid ammonites of the Campanian–Maastrichtian at Tercis les Bains (Landes, France). In: G.S. Odin (ed.), *The Campanian–Maastrichtian Stage Boundary: Characterisation at Tercis les Bains (France) and Correlation with Europe and Other Continents*. *Developments in Palaeontology and Stratigraphy* 19: 487–499.
- Machalski, M. and Walaszczyk, I. 1987. Faunal condensation and mixing in the uppermost Maastrichtian/Danian Greensand (Middle Vistula Valley, Central Poland). *Acta Geologica Polonica* 37: 75–91.
- MacLeod, K.G. 1994a. Extinction of inoceramid bivalves in Maastrichtian strata of the Bay of Biscay region of France and Spain. *Journal of Paleontology* 68: 1048–1066.
- MacLeod, K.G. 1994b. Bioturbation, inoceramid extinction, and mid-Maastrichtian ecological change. *Geology* 22: 139–142.
- MacLeod, K.G. and Huber, B.T. 1996. Reorganization of deep ocean circulation accompanying a Late Cretaceous extinction event. *Nature* 6573: 422–425.
- MacLeod, K.G. and Ward, P.D. 1990. Extinction pattern of *Inoceramus* (Bivalvia) based on shell fragment biostratigraphy. In: V.L. Sharpton and P.D. Ward (eds.), *Global Catastrophes in Earth History. An Interdisciplinary Conference on Impacts, Volcanism, and Mass Mortality*. *Geological Society of America, Special Paper* 247: 509–518.
- Maeda, H. and Seilacher, A. 1996. Ammonoid taphonomy. In: N.H. Landmanet, K. Tanabe, and R.A. Davis (eds.), *Ammonoid Paleobiology. Topics in Geobiology* 13: 543–578.
- Makowski, H. 1962. Problem of sexual dimorphism in ammonites. *Palaeontologia Polonica* 12: 1–92.
- Matyja, B.A. 1986. Developmental polymorphism in Oxfordian ammonites. *Acta Geologica Polonica* 36: 37–68.
- Matyja, B.A. 1994. Developmental polymorphism in the Oxfordian ammonite subfamily Peltoceratinae. *Paleopelagos, special publication* 1: 277–286.
- Mayr, E., Linsley, E.G., and Usinger, R.L. 1953. *Methods and Principles of Systematic Zoology*. 328 pp. McGraw Hill, New York.
- Mikhailov, N.P. [Mihailov, N.P.] 1951. Upper Cretaceous Ammonites from the southern part of European Russia and their importance for zonal stratigraphy (Campanian, Maastrichtian) [in Russian]. *Trudy Instituta Geologičeskikh Nauk, Akademia Nauk SSSR* 129 (seriâ geologičeskaâ 50): 1–143.
- Monks, N. 2000. Functional morphology, ecology, and evolution of the Scaphitaceae Gill, 1871 (Cephalopoda). *Journal of Molluscan Studies* 66: 205–216.
- Morton, S.G. 1842. Description of some new species of organic remains of the Cretaceous Group of the United States with a tabular view of the fossils hitherto discovered in this formation. *Journal of Academy of National Sciences of Philadelphia* 8 (2): 207–227.
- Naidin, D.P. 1974. Ammonoidea [in Russian]. In: G.Á. Krymgolc (ed.), *Atlas verhnemelovoj fauny Donbassa*, 158–195. Nedra, Moskva.
- Naidin, D.P., Kopaevich, L.F. [Kopaevič, L.F.], Moskvina, M.M., Schimanskaya, N.V. [Šimanskaâ, N.V.], Kalnichenko, G.P. [Kalničenko, G.P.], and Andreev, Yu.N. [Andreev, Ū.N.], 1990. Macropaleontological data on the Maastrichtian/Danian boundary from continuous sections in Mangyshlak [in Russian]. *Izvestiâ Akademii Nauk SSSR, Serâ Geologičeskaâ* 11: 17–25.
- Newell, N.D. 1947. Intraspecific categories in invertebrate paleontology. *Evolution* 1: 163–171.
- Newell, A.D. 1956. Fossil populations. In: P.C. Sylvester-Bradley (ed.), *The Species Concept in Palaeontology*. *The Systematics Association* 2: 63–82.
- 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.
- Nowak, J. 1913. Untersuchungen über die Cephalopoden der oberen Kreide in Polen. III Teil. *Bulletin international de l'Académie des Sciences de Cracovie. Classe des Sciences Mathématiques et naturelles, Série B, Sciences Naturelles* 1913: 335–415.
- Nowak, J. 1917. Die Verbreitung der Cephalopoden im Polnischen Senon. *Bulletin international de l'Académie des Sciences de Cracovie, Série A* 1917: 129–152.
- Odin, G.S. (compiler). 1996. Definition of a Global Boundary Stratotype Section and Point for the Campanian/Maastrichtian boundary. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre* 66 (Supplement): 111–117.
- Odin, G.S. 2001. The Campanian–Maastrichtian boundary: definition at Ter-

- cis (Landes, SW France) principle, procedure, and proposal. In: G.S. Odin (ed.), *The Campanian–Maastrichtian Stage Boundary: Characterisation at Tercis les Bains (France) and Correlation with Europe and Other Continents. Developments in Palaeontology and Stratigraphy* 19: 820–833.
- Odin, G.S. and Lamaurelle, M.A. 2001. The global Campanian–Maastrichtian stage boundary at Tercis les Bains, Landes, SW France. *Episodes* 4: 229–238.
- Orbigny, A. d' 1842. *Paléontologie française: terrains crétacés. I. Céphalopodes*, 121–430. Masson, Paris.
- Owen, D.D. 1852. Description of new and imperfectly known genera and species of organic remains, collected during the geological surveys of Wisconsin, Iowa, and Minnesota. In: *Report of a Geological Survey of Wisconsin, Iowa, and Minnesota; and Incidentally of a Portion of Nebraska Territory*, 573–587. Lippincott, Philadelphia.
- Pasternak, S.I., Senkovskiy, Yu.N. [Sen'kows'kij, Ū.N.], and Gavrilishyn, V.I. [Gavrilišyn, V.I.] 1987. *Wolino-Podillâ u krejdovomu periodi*. 258 pp. Naukovaâ Dumka, Kyiv.
- Požaryski, W. 1956. Kreda. In: M. Książkiewicz and S. Dźułyński (eds.), *Regionalna geologia Polski, Tom II. Region Lubelski*, 14–56. Państwowe Wydawnictwo Naukowe, Kraków.
- Radwański, A. 1996. The predation upon, and the extinction of, the latest Maastrichtian populations of the ammonite species *Hoploscaphites constrictus* (J. Sowerby, 1817) from the Middle Vistula Valley, Central Poland. *Acta Geologica Polonica* 46: 117–136.
- 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.
- Reich, M. and Frenzel, P. 2002. Die Fauna und Flora der Rügener Schreibkreide (Maastrichtium, Ostsee). *Archiv für Geschichtskunde* 3: 74–284.
- Rogała, W. 1911. Przyczynek do znajomości mukronatowej kredy okolicy Lwowa. *Kosmos* 36: 487–499.
- Schmid, F. 1965. *Acanthoscaphites tridens varians* (Lopuski 1911) aus dem Maastricht von Hemmoor (Niederelbe) in Nordwest-Deutschland. *Geologisches Jahrbuch* 83: 681–692.
- Schmitz, B., Keller, G., and Stenvall, O. 1992. Stable isotope and foraminiferal changes across the Cretaceous/Tertiary boundary at Stevns Klint, Denmark: arguments for long-term oceanic instability before and after bolide impact. *Palaeogeography, Palaeoecology, Palaeoclimatology* 96: 233–260.
- Schönfeld, J., Schulz, M.-G., McArthur J.M., Burnett, J., Gale, A., Hambach, U., Hansen, H.J., Kennedy, W.J., Rasmussen, K.L., Thirwall, M.F., and Wray, D.S. 1996. New results on biostratigraphy, paleomagnetism, geochemistry and correlation from the standard section for the Upper Cretaceous white chalk of northern Germany (Lägerdorf-Kronsmoor-Hemmoor). *Mitteilungen aus dem Geologisch-Paläontologischen Institut der Universität Hamburg* 77: 545–575.
- Schmid, F. 1982. Das erweiterte Unter-/Ober-Maastricht-Grenzprofil von Hemmoor, Niederelbe (NW-Deutschland). *Geologisches Jahrbuch* A 61: 7–12.
- 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. and Schmid, F. 1983. Das Ober-Maastricht von Hemmoor (N-Deutschland): Faunenzonen-Gliederung und Korrelation mit dem Ober-Maastricht von Dänemark und Limburg. *Newsletter of Stratigraphy* 13: 21–39.
- Seilacher, A. 1993. Ammonite aptychi: how to transform a jaw into an operculum? In: P. Dodson and P. Gingerich (eds.), *Functional Morphology and Evolution. American Journal of Science* A 293: 2–32.
- Smit, J. and Brinkhuis, H. 1996. The Geulhemmerberg Cretaceous/Tertiary boundary section (Maastrichtian type area, SE Netherlands); summary of results and a scenario of events. In: H. Brinkhuis and J. Smit (eds.), *The Geulhemmerberg Cretaceous/Tertiary Boundary Section (Maastrichtian Type Area, SE Netherlands). Geologie en Mijnbouw* 75: 283–293.
- Sowerby, J. 1817. *The Mineral Conchology of Great Britain*, 2, pls. 151–184, A, 185, 186, The Author, London.
- Stephenson, L.W. 1941. The larger invertebrate fossils of the Navarro Group of Texas (Exclusive of corals and crustaceans and exclusive of the fauna of the Escondido Formation). *University of Texas Publications* 4101: 1–641.
- Surlyk, F. 1970. Die Stratigraphie des Maastricht von Dänemark und Norddeutschland aufgrund von Brachiopoden. *Newsletter of Stratigraphy* 1: 7–16.
- Surlyk, F. 1984. The Maastrichtian Stage in NW Europe, and its brachiopod zonation. *Bulletin of the Geological Society of Denmark* 33: 217–223.
- Surlyk, F. 1997. A cool-water carbonate ramp with Bryozoan mounds: Late Cretaceous–Danian of the Danish Basin. In: N.P. James and J.D.A. Clarke (eds.), *Cool-water Carbonates. SEPM Special Publication* 56: 293–307.
- Surlyk, F. and Birkelund, T. 1977. An integrated stratigraphical study of fossil assemblages from the Maastrichtian White Chalk of northwestern Europe. In: E.G. Kauffmann and J.E. Hazel (eds.), *Concepts and Methods in Biostratigraphy*, 257–281. Dowden, Hutchinson and Ross, Stroudsburg.
- Sylvester-Bradley, P.C. 1951. The subspecies in palaeontology. *Geological Magazine* 88: 88–102.
- Syniewska, J. 1923. Kilka nowych skamieniałości z kredy okolicy Lwowa. *Kosmos* 48: 276–302.
- Tintant, H. and Kabamba, M. 1985. The role of the environment in the Nautilaceae. In: U. Bayer and A. Seilacher (eds.), *Sedimentary and Evolutionary Cycles. Lecture Notes in Earth Sciences* 1: 58–66.
- Trauth, F. 1928. Aptychenstudien II. Die Aptychen der Oberkreide. *Annalen des Naturhistorischen Museums in Wien* 42: 121–193.
- Tuuk, L.A. van der 1987. Scaphitidae (Ammonoidea) from the Upper Cretaceous of Limburg, the Netherlands. *Paläontologische Zeitschrift* 61: 57–79.
- Tzankov, V. [Cankov, V.] 1982. *Cephalopoda (Nautiloidea, Ammonoidea) et Echinodermata (Echinoidea). Les fossiles de Bulgarie. Va. Crétacé supérieur*. 126 pp. Editions de l'Académie Bulgarie des Sciences, Sofia.
- Wagreich, M., Küchler, T., and Summesberger, H. 2003. Correlation of calcareous nannofossil zones of the local first occurrences of *Pachydiscus neubergicus* (von Hauer, 1858) (Ammonoidea) in European Upper Cretaceous sections. *Netherlands Journal of Geosciences* 82: 283–288.
- Walaszczyk, I., Smirnov, J.P., and Tröger, K.-A. 1996. Trochoceramid bivalves (Inoceramidae) from the Lower Maastrichtian of Daghestan (Aimaki section, NE Caucasus) and south-central Poland. *Acta Geologica Polonica* 46: 141–164.
- Walaszczyk, I., Cobban, W.A., and Odin, G.S. 2002. The inoceramid succession across the Campanian–Maastrichtian boundary. *Bulletin of the Geological Society of Denmark* 49: 53–60.
- Walaszczyk, I. 2004. Inoceramids and inoceramid biostratigraphy of the Upper Campanian to basal Maastrichtian of the Middle Vistula Valley, central Poland. *Acta Geologica Polonica* 54: 95–168.
- Ward, P.D. 1981. Shell sculpture as a defensive adaptation in ammonoids. *Paleobiology* 7: 96–100.
- Ward, P.D. 1990. A review of Maastrichtian ammonite ranges. In: V.L. Sharpton and P.D. Ward (eds.), *Global Catastrophes in Earth History; An Interdisciplinary Conference on Impacts, Volcanism, and Mass Mortality. Geological Society of America, Special Paper* 247: 519–530.
- Ward, P.D. 1996. Ammonoid Extinction. In: N.H. Landman, K. Tanabe, and R.A. Davis (eds.), *Ammonoid Paleobiology. Topics in Geobiology* 13: 815–824.
- Ward, P.D. and Kennedy, W.J., 1993. Maastrichtian Ammonites from the Biscay region (France, Spain). *Paleontological Society Memoir* 34: 1–56.
- Wiedmann, J. 1965. Origin, limits, and systematic position of *Scaphites*. *Palaeontology* 8: 397–453.
- Wiedmann, J. 1988. Ammonoid extinction and the “Cretaceous–Tertiary boundary event”. In: J. Wiedmann and J. Kullmann (eds.), *Cephalopods—Present and Past*, 117–140. Schweizerbart, Stuttgart.
- Wiedmann, J. and Marcinowski, R. 1985. *Scaphamites passendorferi* n. gen. n. sp. (Ammonoidea, Cretaceous)—ancestor of Scaphitaceae Meek? *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1985 (8): 449–463.
- Wolansky, D. 1932. Die Cephalopoden und Lamellibranchiaten der Oberkreide Pommerns. *Abhandlungen aus dem geologisch-palaeontologischen Institut der Universität Greifswald* 9: 1–72.
- Wyrwicka, K. 1970a. Utwory kredowe okolic Chełma. In: *Przewodnik XLII Zjazdu Polskiego Towarzystwa Geologicznego, Lublin 3–5 września 1970*, 148–154. Wydawnictwa Geologiczne, Warszawa.
- Wyrwicka, K. 1970b. Odkrywka w Rejowcu. In: *Przewodnik XLII Zjazdu Polskiego Towarzystwa Geologicznego, Lublin 3–5 września 1970*, 161–164. Wydawnictwa Geologiczne, Warszawa.