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Ammonites of the *Pachydiscus neubergicus* group from the mid-Maastrichtian chalk of Denmark: alternative taxonomic interpretations

MARCIN MACHALSKI[1], KRZYSZTOF OWOCKI[1], JAN AUDUN RASMUSSEN[2] and HENRIK MADSEN[2]

[1] *Institute of Paleobiology, Polish Academy of Sciences, Twarda 51/55, 00-818 Warszawa, Poland; e-mail:mach@twarda.pan.pl*
[2] *Fossil and Mo-Clay Museum, Museum Mors, Skarrehagevej 8, DK-7900 Nykøbing Mors, Denmark*

ABSTRACT:

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Despite their rarity, ammonites of the *Pachydiscus neubergicus* group rank amongst the stratigraphically most important macrofossils in the Maastrichtian of Europe. Here, their taxonomy is studied on the basis of material from mid-Maastrichtian chalk exposed at Hillerslev in Denmark. The studied sample consists of ten specimens in mouldic preservation, collected from a c. 10 m thick chalk interval. Their taxonomic identification is based on comparison with 'type populations' of known members of the *P. neubergicus* group, primarily with the roughly coeval material of *P. neubergicus* (v. Hauer, 1858) from Neuberg in Austria. To date, only *P. neubergicus* has been identified from this group in the Danish chalk. Based largely on differences in ribbing density, the Hillerslev material has conventionally been subdivided into several taxa, namely *P. neubergicus*, *P.* sp. cf. *neubergicus*, *P. jacquoti* (Seunes, 1890), *P.* sp. cf. *jacquoti*, *P.* sp. aff. *armenicus* Atabekian and Akopian, 1969, and *Pachydiscus* sp. Results of the Principal Component Analysis (PCA) and one-sample *t* test for the studied material are compatible with such identifications of the Hillerslev specimens. However, an alternative taxonomic interpretation is possible that the identified morphospecies, with the potential exception of *P.* sp. aff. *armenicus*, are members of a single, highly-variable biospecies, dominated by a sparsicostate morphotype closer to *P. jacquoti* than *P. neubergicus*. Additional material from the mid-Maastrichtian levels of Danish chalk is needed to test the latter hypothesis.

Key words: Cephalopoda; Ammonoidea; Cretaceous; white chalk.

INTRODUCTION

A series of morphologically similar – and probably closely allied – Maastrichtian species of the ammonite family Pachydiscidae Spath, 1922, grouped around *Pachydicus neubergicus* (v. Hauer, 1858), have been referred to as the *P. neubergicus* group (Kennedy and Summesberger 1986). The group is typified by the presence of prominent umbilical bullae and abundant ventral ribs, which weaken or are even effaced on the mid-flank of the whorls. These generally rare species are largely defined by different proportions of the number of umbilical to ventral ribs on the last whorl (Atabekian and Akopian 1969; Kennedy and Summesberger 1986; Ward and Kennedy 1993). These ratios seem to have considerable intra-population variability, which has led to different interpretations of individual species by various workers.

Pachydiscus neubergicus (v. Hauer, 1858), the type species of the genus *Pachydiscus* von Zittel, 1884, is the core species of this group. Given its importance for defining the base of the Maastrichtian, it is among the most intensively studied Maastrichtian ammonite species (Hancock and Kennedy 1993; Odin 1996, 2001a, b; Christensen *et al.* 2000; Odin *et al.* 2001; Odin and Lamaurelle 2001; Jagt and Felder 2003; Niebuhr 2003; Jagt *et al.* 2012; Machalski 2012a, b). According to Wagreich *et al.* (2003), *P. neubergicus* has a considerable stratigraphic range across Europe, from the UC16 to the UC20b nannofossil zones in the Upper Cretaceous calcareous nannofossil zonation of Burnett (1998).

The aim of the present paper is to describe a relatively rich collection (10 specimens) of the *P. neubergicus* group from the mid-Maastrichtian white chalk exposed at Hillerslev, northwest Jutland, Denmark. *Pachydiscus neubergicus* is the only species of this group that has been recorded from Denmark (Birkelund 1979, 1993). Therefore, the Hillerslev material is primarily compared – by a conventional examination supported by some statistical methods – with the roughly coeval material of this species from Neuberg, Austria, and with the material of other species of this group from other locations.

These results provide new data on the ammonite faunas of the Danish White Chalk. On a broader scale, this study illustrates methodological issues in the identification ammonite species in samples composed of specimens whose number and/or preservation are inadequate for effective population analysis (Callomon 1985; Dzik 1986, 1990; De Baets *et al.* 2015).

GEOLOGICAL SETTING AND BIOSTRATIGRAPHY

The studied material comes from the Hillerslev chalk pit in northwestern Jutland, Denmark (Text-fig. 1A). The pit is located north of the western part of Limfjorden Sound, 5 km north of Thisted (57.008° N, 8.72° E). Structurally, the exposure is located in the Danish Basin immediately south of the Tornquist Zone, atop the salt diapir-influenced Thisted Dome (Hansen and Håkansson 1980). The Hillerslev outcrop covers approximately 600 × 700 m, and while the quarry walls can range up to 10 m high, they are commonly lower (Schnetler *et al.* 2025). The Hillerslev chalk belongs to the Møns Klint Formation with respect to lithostratigraphy (see Surlyk *et al.* 2013).

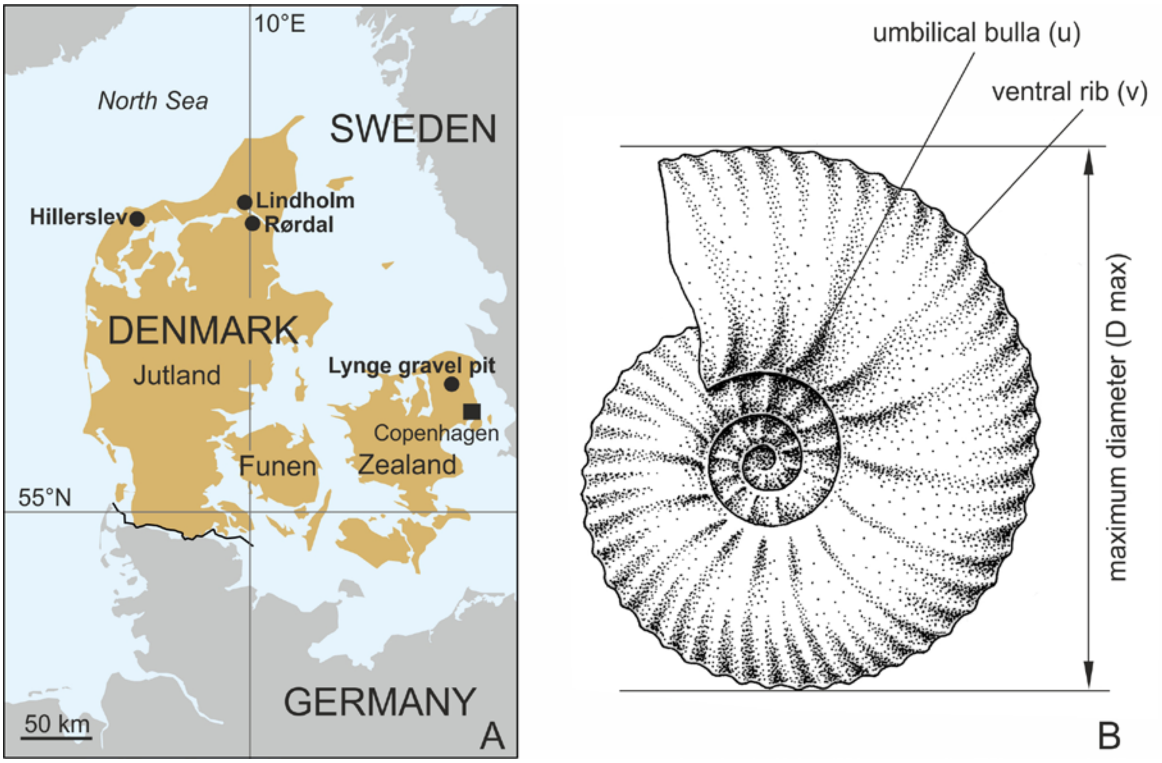
The Hillerslev chalk yields relatively common macrofossils, dominated by siliceous sponges, brachiopods, and bivalves (mainly calcitic epibyssate taxa). Ammonites (mainly scaphitids and their aptychi), belemnites, and echinoderms (mainly echinoids and asteroids) are not uncommon. However, only a few selected fossil groups have been examined in considerable detail, including brachiopods (Surlyk 1984, 2025), ammonites (Birkelund 1993, Machalski 2005b), xenophorid gastropods (Schnetler *et al.* 2025), and trace fossils (Vallon *et al.* 2020).

The Hillerslev chalk is placed within the uppermost lower to lower upper Maastrichtian (informally, the 'mid-Maastrichtian'), based on micromorphic brachiopod biozonation (Surlyk 1984, 2025). This author indicated the presence of two microbrachiopod zones at Hillerslev: the upper lower Maastrichtian *tenuicostata–semiglobularis* Zone and the lower upper Maastrichtian *semiglobularis–humboldtii* Zone. These are also referred to as zones 7 and 8, respectively, in the regional microbrachiopod biozonation. The *semiglobularis-humboldtii* Zone captures most of the Hillerslev succession (Surlyk 1984, fig. 3). In terms of Danish belemnite biozonation (Christensen 1996), the Hillerslev succession spans the uppermost *Belemnella occidentalis* Zone to the lower *Belemnitella junior* Zone.

Correlation between the microbrachiopod zones of Surlyk (1984) and nannofossil zones of the Boreal calcareous nannofossil zonation (Thibault *et al.* 2025, fig. 5) indicates that the Hillerslev chalk belongs to the uppermost UC19S2 and UC20S1 nannofossil subzones. This interval is consistent with the uppermost part of the UC19 Zone and the lower part of the UC20 Zone of Burnett (1998). In absolute terms, the Hillerslev chalk is constrained to between 69 and 68 Ma (Thibault *et al.* 2025, fig. 5).

MATERIAL AND METHODS

The material studied comprises 10 specimens in mould (steinkern) preservation from the Hillerslev pit, which are housed at the Fossil and Mo-clay Museum (Museum Mors), Denmark (collection acronym MM). None of these specimens are precisely located within the quarry section. The specimens were photographed, their maximum preserved diameter measured, and the number of umbilical and ventral ribs counted (for terminology see Text-fig. 1B). However, the presented data (Table 1) are somewhat approximate due to imperfect specimen preservation. Comparative material from Denmark includes four specimens from three mid-Maastrichtian sections in Jutland (Lindholm, Rørdal and Hillerslev) and from



Text-fig. 1. Provenance and morphology of the studied ammonites of the *Pachydiscus neubergicus* (v. Hauer, 1858) group. A – Danish outcrops yielding the analysed specimens; B – Measurement and rib terminology.

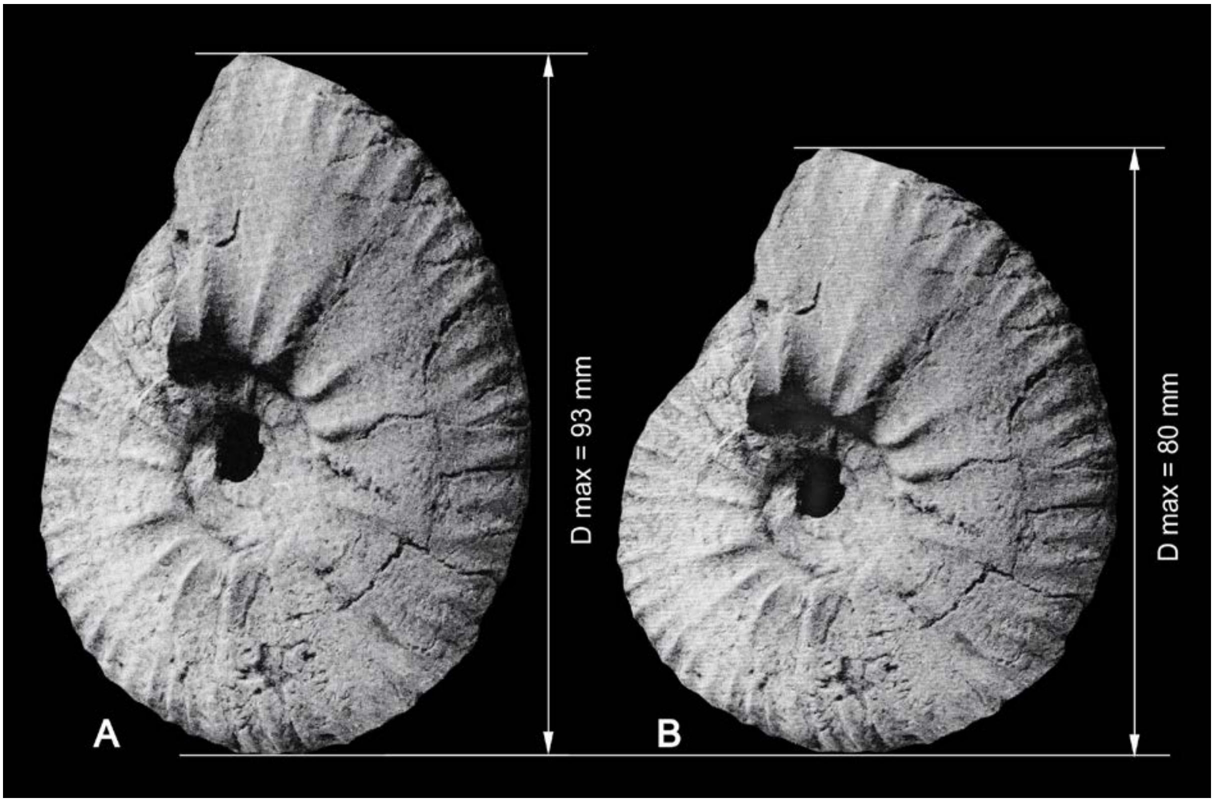
the glacial deposits of the Lynge gravel pit, Zealand (Text-fig. 1A; Birkelund 1993), which are currently housed in the Natural History Museum of Denmark (Copenhagen; collection acronym MGUH).

The Hillerslev material can be primarily compared with the material of *P. neubergicus*, also preserved as steinkerns, from lower upper Maastrichtian sandstones exposed in Neuberg, Styria, Austria. The Neuberg material was described by Kennedy and Summesberger (1986) and is housed in various Viennese institutions. Direct measurements were done on plaster casts of the lectotype GBA.1858.1.6 and the topotypes GIUW 1875.XXX 1 and JOAG 6109 (for acronym explanations see Kennedy and Summesberger 1986). Quantitative data for other specimens were obtained from the natural-size illustrations of Kennedy and Summesberger (1986). As many of these specimens were tectonically distorted, their illustrations were graphically retrodeformed using CorelDRAW v.18 to obtain the original dimensions. This was executed by using the 'modify shapes' option with the suboption 'maintain proportions' disabled, allowing the transformation of the distorted fossil into a regular ammonite shell spiral. This is exemplified by the lectotype, which was originally distorted into an ellipse (Text-fig. 2A, B). Ten specimens from Neuberg were analysed following this approach; the type measurements of other *P. neubergicus* group members were taken from the literature (Table 1).

The Principal Component Analysis (PCA) and a one-sample *t* test, based on PCA scores, were performed on selected specimens to determine their fit into the 'type population' of *P. neubergicus* from Neuberg. Data analysis was performed using palaeontological statistics software package PAST (PAleontological STatistics; Hammer *et al*. 2001).

MATERIAL CHARACTERISTICS

The Hillerslev specimens are presented in Text-figs 3–5, with accompanying morphometric data in Table 1 (specimens H1–H10). The material is dominated by specimens in early and middle growth stages that are typically preserved as incomplete, occasionally laterally crushed phragmocone moulds, rarely with parts of the body chamber retained. Only



Text-fig. 2. Retrodeformation of Neuberg specimens, as exemplified by the lectotype of *Pachydiscus neubergicus* (v. Hauer, 1858) (specimen GBA.1858.1.6). A – original photograph from Kennedy and Summesberger (1986, pl. 3, fig. 2); B – specimen image following graphical retrodeformation.

the largest specimen has most of its body chamber preserved (Text-fig. 4C). The suture lines are barely discernible, hampering precise identification of the last suture in most instances. The maximum diameter of specimens ranges from 24 to 135 mm (Table 1). The umbilical diameter oscillates around 30% of the maximum diameter, except for the largest specimen (c. 34%; Text-fig. 4C). Some specimens appear to be oval in whorl section, with flattened flanks (e.g., Text-figs 3A, C; 4A, B), while others seem to be more inflated (e.g., Text-figs 3B, D, E; 5A). The ribbing consists of prominent umbilical bullae and more numerous ventral ribs in varying proportions. Only umbilical bullae are present in the earliest growth stages (Text-fig. 3D, E); ventral ribs appear later in the ontogenic development. For instance, the ventral ribbing starts at the second half of the whorl in the specimen figured in Text-fig. 3E. The middle growth stages vary in respect to rib density, ranging from a specimen with coarse and distant ribs (12 umbilical and 36 ventral ribs; Text-fig. 5A) to a finely ribbed specimen (estimated 24 umbilical ribs and 54 ventral ones; Text-fig. 4B, see Table 1). The ribs in the middle growth stages are narrow and blunt, but the living chamber of the largest specimen (Text-fig. 4C) is ornamented with comparatively broad ribs.

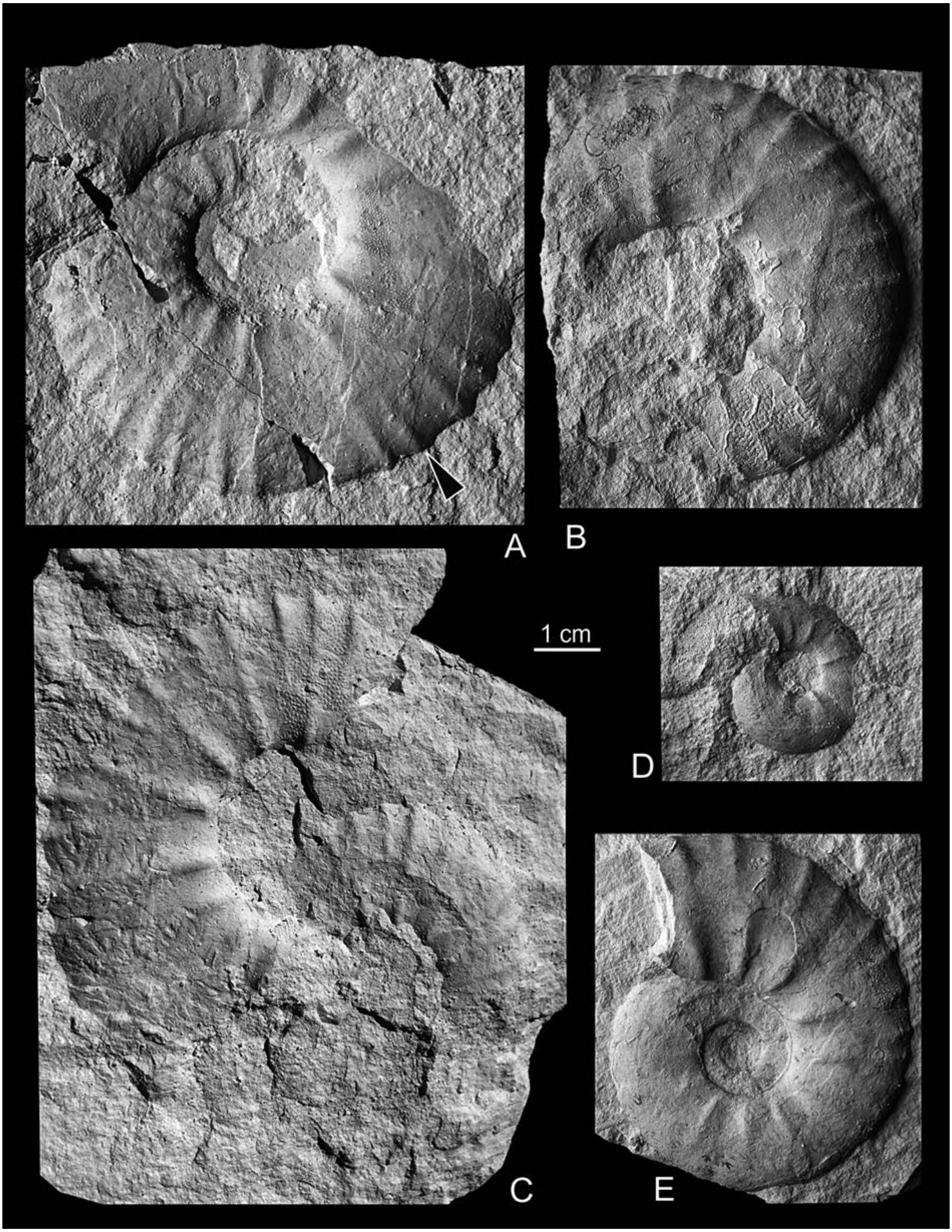
PRINCIPLES OF TAXONOMIC IDENTIFICATION

There are two approaches to palaeontological species identification that are pertinent to ammonite studies (e.g., Callomon 1985; Dzik 1986, 1990; De Baets *et al.* 2015). In both methods, the type material of a species is the primary reference standard for subsequent identification. The morphological (typological) method focuses on direct comparison of the studied specimens with existing holotypes and topotypes; such species are best regarded as morphospecies (*sensu* Callomon 1985, pp. 57, 58). In contrast, the populational method places more emphasis on the intra- and interpopulational distribution of diagnostic characters, which ideally leads to the identification of biospecies (Callomon 1985; Dzik 1986, 1990).

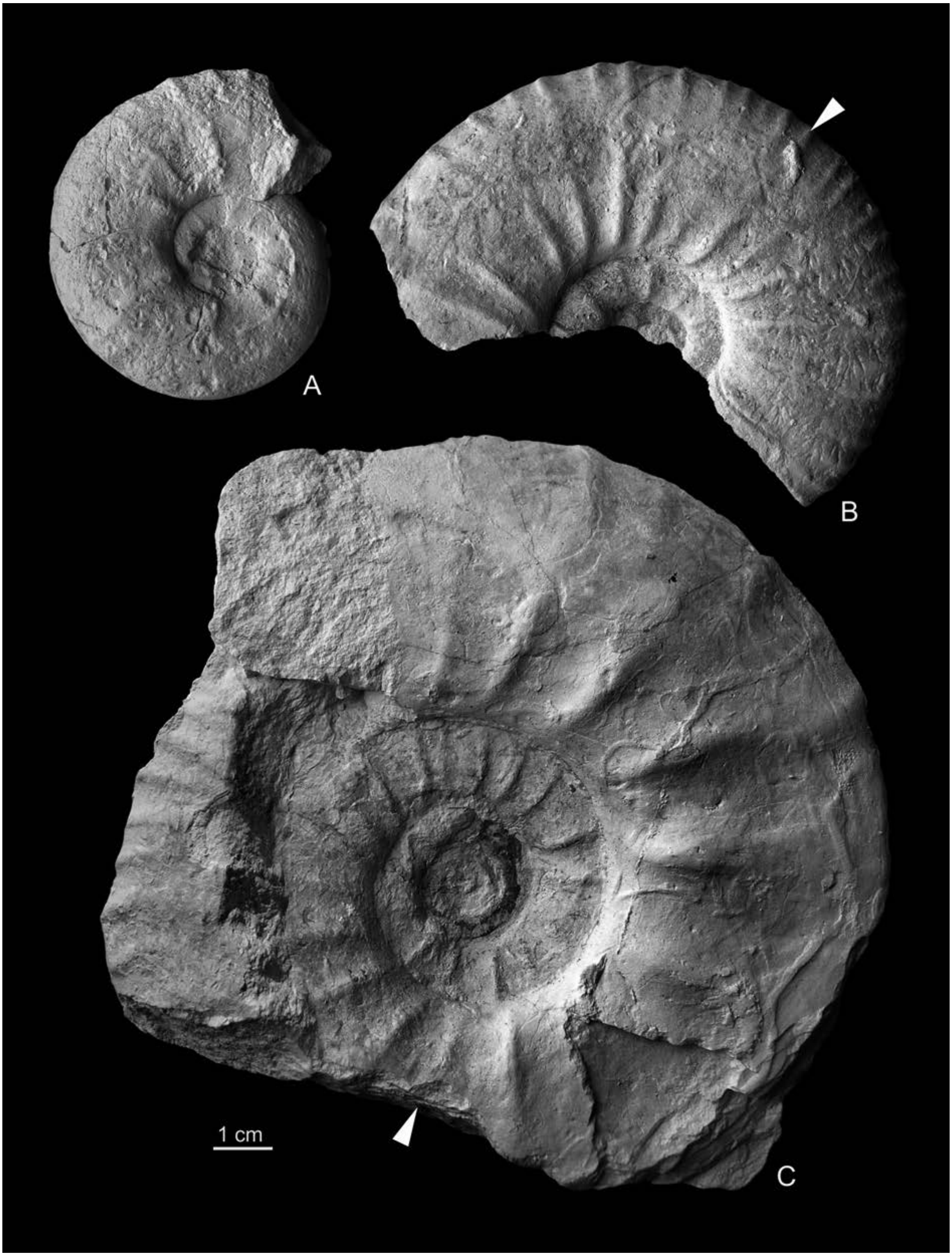
There are numerous issues associated with the practical application of the populational method (De Baets *et al.* 2015). Firstly, the analysed samples may be taphonomically or analytically time-averaged, so they do not represent real biological populations. Secondly, the number of specimens and/or growth stages available for study may be insufficient for reliable statistical analysis. According to De Baets *et al.* (2015), over 30 specimens of each ontogenetic stage should ideally be used for meaningful statistical analysis of material. All these shortcomings apply to the Hillerslev sample (Text-figs 3–5), which is analytically time-averaged – collected indiscriminately from a c. 10 m thick chalk interval – and consists of only a few, fragmentarily preserved specimens. It is therefore impossible to determine whether the original distribution of diagnostic morphological characters was unimodal and normal, suggesting that the assemblage consists of a single species – or multimodal, suggesting that the assemblage consisted of multiple species, or at a minimum multiple discrete morphotypes. In such cases, it appears most reasonable to assign co-occurring specimens to different species based on morphological criteria, even if they potentially belong to a single biospecies (De Baets *et al.* 2015, p. 380). Accordingly, the Hillerslev taxonomic assignments are based primarily on morphological comparisons with the specimens from type localities and strata of known species (hereafter referred to as 'type populations') which allows the avoidance of issues related to often subjective interpretations of these species by authors dealing with material from other locations and stratigraphic levels. The open nomenclature qualifiers cf. and aff. are used to express uncertainty in specimen identification, following Sigovini *et al.* (2016). An alternative populational interpretation is also discussed.

Symbol	**Species**	**Specimen**	**Dmax** [mm]	**Ru**	**Rv**	**Rv/Ru**
H1	*P.* sp. cf. *jacquoti*	MM-10950	24	8	absent	-
H2	*P.* sp. cf. *jacquoti*	MM-10947	55	7 (½)	14 (½)	2
H3	*P.* sp.	MM-10951	57	10	?	-
H4	*P.* sp. cf. *jacquoti*	MM-10948	64	8 (½)	16 (½)	-
H5	*P.* sp. cf. *neubergicus*	MM-10944	70	16	?	-
H6	*P.* sp. cf. *jacquoti*	MM-10943	74	7 (½)	14 (½)	-
H7	*P.* sp. aff. *armenicus*	MM-10949	92	12(½) 24 (ex)	27 (½) 54 (ex)	2.25
H8	*P. jacquoti*	MM-10945	101	12	36	3
H9	*P. neubergicus*	MM-10970	110	14	44	3.1
H10	*P.* sp. cf. *neubergicus*	MM-10946	135	17	?	-
Lg	*P. neubergicus*	MGUH 20131	95	15	44	2.9
N1	*P. neubergicus*	NHMW1852.XXI.1881	69	7 (½)	26 (½)	3.8
N2	*P. neubergicus*	Kennedy and Summesberger (1986: pl. 6, fig. 5)*	72	16	56 (ex)	3.5
N3	*P. neubergicus*	NHMW 1851.XXI.1880	74	14	60 (ex)	4.3
N4	*P. neubergicus*	GBA.1858.1.6 (lectotype)	80	16	50	3.1
N5	*P. neubergicus*	GIUW 1876.XV.7	80	17	56	3.3
N6	*P. neubergicus*	GBA.1935.01.39	88	16	48	3
N7	*P. neubergicus*	PIUW unregistered	94	17	48	2.8
N8	*P. neubergicus*	JOAG 6109	99	14	48	3.4
N9	*P. neubergicus*	JOAG 6112	117	8 (½)	20 (½)	2.5
N10	*P. neubergicus*	GIUW 1875.XXX.1	126	15	42	2.8
C1	*P. jacquoti*	Seunes (1890, pl. 3, fig. 3)	49	8	absent	-
C2	*P. jacquoti*	Seunes (1890, pl. 3, fig. 2)	64	12	18 (½)	-
C3	*P. jacquoti*	Seunes (1890, pl. 3, fig. 1, suggested lectotype by Kennedy 1986)	108	14	33	2.4
A1	*P. armenicus*	2/101 in Atabekian and Akopian (1969)	98	19	62	3.3
A2	*P. armenicus*	3/101 in Atabekian and Akopian (1969) (holotype)	130	20	73	3.7

Table 1. Morphometric data of specimens from Hillerslev (H) and comparative specimens from Lynge (Lg), Neuberg (N), Cotentin (C), and Azizbek (A), arranged by increasing size in each locality. Explanations: Dmax – maximum preserved diameter (in the case of Neuberg, retrodeformed); Ru – number of umbilical ribs on the last whorl; Rv – number of ventral ribs on the last whorl; (ex) – extrapolations from incomplete specimens; (½) – half whorl numbers; *specimen with missing caption in Kennedy and Summesberger (1986).

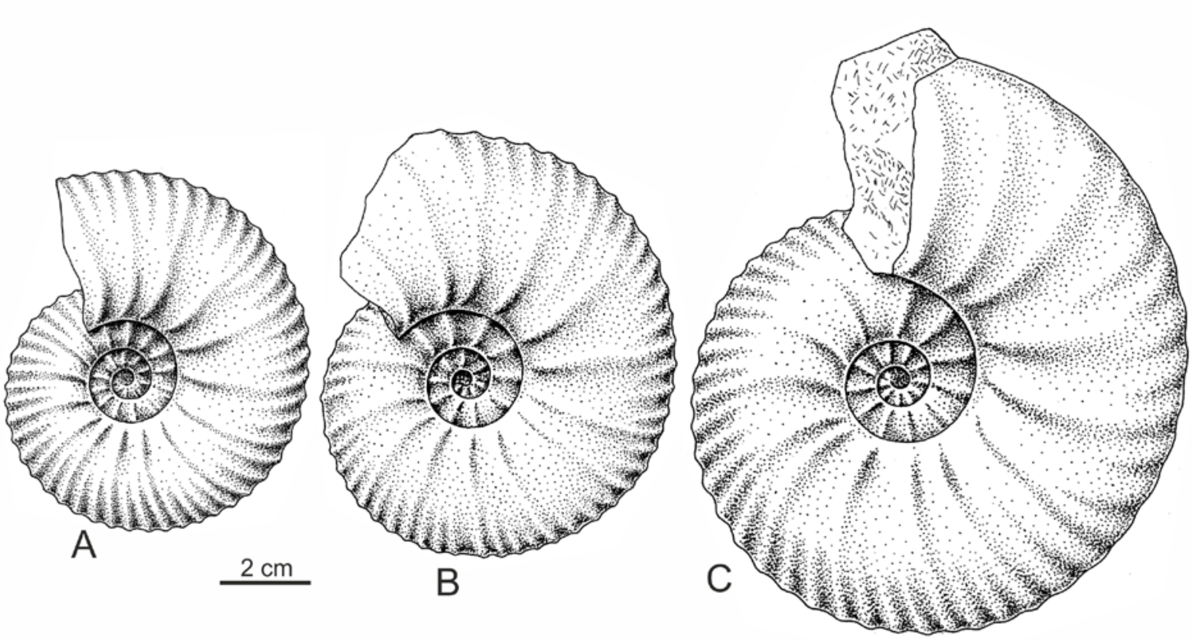


Text-fig. 3. Ammonites of the *P. neubergicus* group from Hillerslev, Denmark. A – *Pachydiscus* sp. cf. *neubergicus* (v. Hauer, 1858), specimen MM-10944 (H5 in Table 1); B–E – *Pachydiscus* sp. cf. *jaquoti* (Seunes, 1890), specimens MM-10948 (B, H4 in Table 1), MM-10943 (C, H6 in Table 1), MM-10950 (D, H1 in Table 1), and MM-10947 (E, H2 in Table 1). In A, the black arrow indicates the approximate position of the last suture.



Text-fig. 4. Ammonites of the *P. neubergicus* group from Hillerslev, Denmark. A – *Pachydiscus* sp., specimen MM-10951 (H3 in Table 1); B – *Pachydiscus* sp. aff. *armenicus* Atabekian and Akopian, 1969, specimen MM-10949 (H7 in Table 1); C – *Pachydiscus* sp. cf. *neubergicus* (v. Hauer, 1858), specimen MM-10946 (H10 in Table 1). In B and C, white arrows indicate the approximate position of the last suture.

Text-fig. 5. Ammonites of the *P. neubergicus* group from Hillerslev, Denmark. A – *Pachydiscus jacquoti* (Seunes, 1890), specimen MM-10945 (H8 in Table 1); B – *Pachydiscus neubergicus* (v. Hauer, 1858), specimen MM-10970 (H9 in Table 1). White arrows indicate the approximate position of the last suture.



Text-fig. 6. Reconstructions of the original, undeformed appearance of *Pachydiscus neubergicus* (v. Hauer, 1858) specimens from the lower upper Maastrichtian of Neuberg, Austria, based on plaster casts. A – lectotype GBA 1858.1.6; B – PIUW unregistered; C – GIUW 1875.XXX.1. Modified from Machalski (2012a, text-fig. 3).

IDENTIFICATION OF THE HILLERSLEV MATERIAL

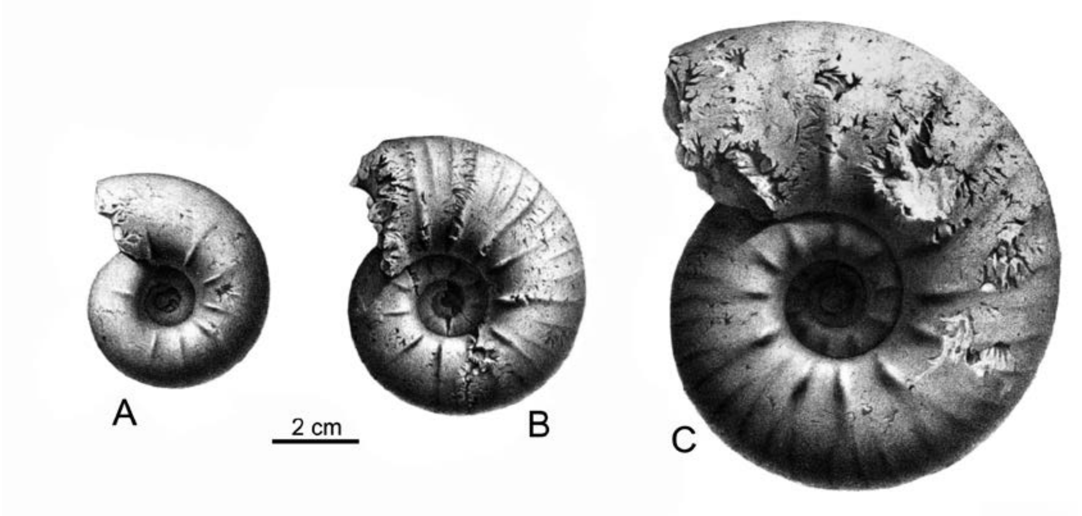
Even a superficial examination of the Hillerslev material (Text-figs 3–5) reveals the presence of morphotypes that are comparable to several members of the *P. neubergicus* group known from the Maastrichtian, namely *Pachydiscus neubergicus*, *P. jacquoti*, and *P. armenicus*. Below, the 'type populations' of these species are reviewed and then used as reference standards for determination of the Hillerslev specimens.

***Pachydiscus neubergicus* (v. Hauer, 1858)**

The primary reference for identification of this species is the 'type population' from the lower upper Maastrichtian of Neuberg, Styria, Austria. According to Wagreich *et al.* (2003), the Neuberg section represents the UC20 nannofossil Zone, and therefore is roughly coeval to the Hillerslev section.

The Neuberg material of *P. neubergicus* encompasses relatively involute and densely ribbed specimens with an oval whorl section, rather flat whorl flanks, 14–17 umbilical bullae, and 48 to almost 60 ventral ribs (Kennedy and Summesberger 1986, pp. 189, 191). The lectotype GBA 1858.1.6 is distorted into an ellipse of 93 mm maximum diameter (see illustrations of v. Hauer 1858, pl. 2, figs 1–3; Kennedy and Summesberger 1986, pl. 3, figs 1–3; and Summesberger and Zorn 2012, fig. 2a–d). The lectotype has 16 umbilical bullae and 50 ventral ribs, with a maximum preserved (retrodeformed) diameter of 80 mm (see Text-figs 2 and 6A; Table 1). Text-fig. 6 presents reconstructions of three representative Neuberg specimens.

Morphometric data from the retrodeformed Neuberg specimens (N1–N10 in Table 1) are consistent with the species descriptions of Kennedy and Summesberger (1986). The sole exception is GIUW 1875.XXX.1 (Text-fig. 6C; Kennedy and Summesberger 1986, pl. 5, figs 4, 5), which has 15 umbilical and only 42 ventral ribs at the preserved diameter of 135 mm. Given its overall similarity to the rest of the material, it is regarded here as a less densely ribbed member of the 'type population'. The earliest ontogenetic stages are missing in the Neuberg material (the smallest available specimen is 69 mm in diameter, see Table 1). However, the lower Maastrichtian specimens from the Piesting Formation



Text-fig. 7. Syntypes of *Pachydiscus jacquoti* (Seunes, 1890) from the lower upper Maastrichtian of Cotentin Peninsula, Manche, France (redrawn from Seunes 1890; B and C are mirror images of the original figures). A – specimen from Seunes (1890, pl. 3, fig. 3a); B – specimen from Seunes (1890, pl. 3, fig. 2a); C – specimen from Seunes (1890, pl. 3, fig. 1a).

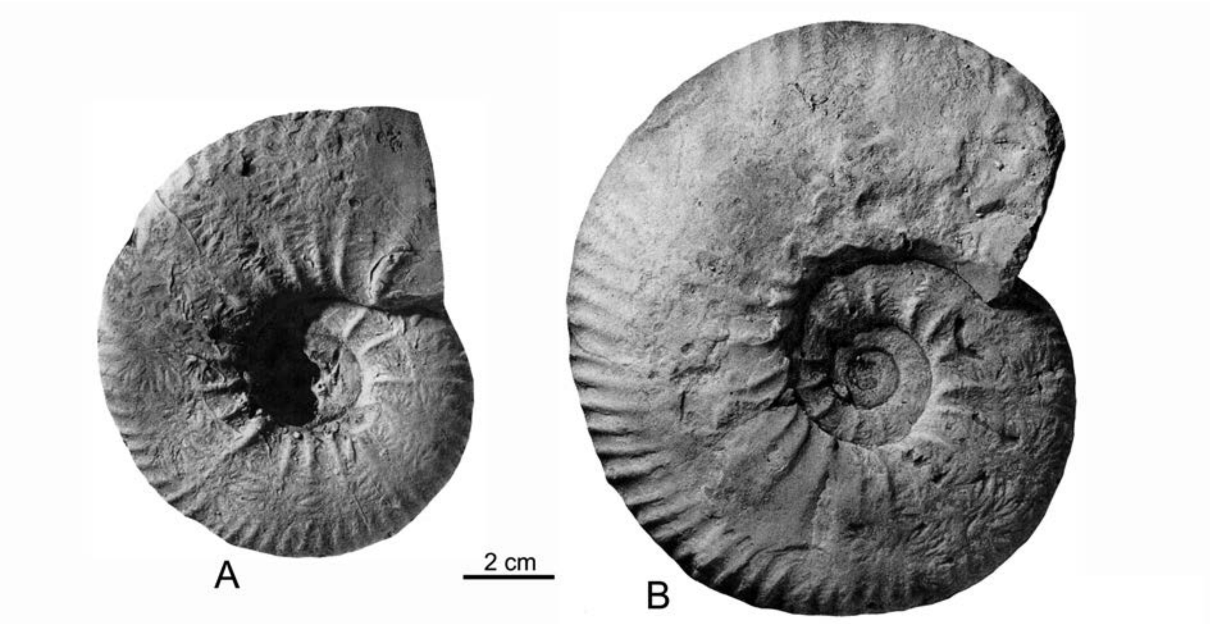
(Austria) include two juvenile specimens (37 and 38 mm in diameter, respectively). Importantly, in these specimens the ribbing style characteristic of subsequent ontogenetic stages began at diameters of 22–25 mm, suggesting that it is already present in the juvenile forms (Summesberger *et al.* 2002, p. 389, pl. 1, figs 2 and 3).

Only a single Hillerslev specimen can be firmly attributed to *P. neubergicus* (Text-fig. 5B). This specimen contains 14 umbilical ribs and 44 ventral ribs at the maximum preserved diameter of 110 mm, and so it is within the variability of the Neuberg material – albeit near the lower end of its range (Table 1). Two additional Hillerslev specimens are referred to *P.* sp. cf. *neubergicus*, due to moderate deviations from the Neuberg assemblage. The largest specimen (Text-fig. 4C) is damaged in the earlier half of the last whorl. While it broadly resembles the largest specimen of the Neuberg material (Text-fig. 6C), the ventral ribs on the preserved sector of the last whorl are more distantly spaced compared to this specimen (compare Text-figs 4C and 6C). Another specimen referred to *P.* sp. cf. *neubergicus* (Text-fig. 3A) is fragmentary. It closely resembles the Neuberg specimens in having flattened flanks and a similar ribbing style – however, the ribbing density, especially the number of ventral ribs, is likely less than in the 'type population' of the species. A third specimen (Text-fig. 4A) is heavily worn and thus assigned to *Pachydiscus* sp. However, the relatively flat flanks of the whorls suggest a tentative affinity with *P. neubergicus*.

***Pachydiscus jacquoti* (Seunes, 1890)**

The type material of this species is from the Calcaire à *Baculites* of the Cotentin Peninsula, Manche, France (Seunes 1890; Kennedy 1986). This unit was regarded as upper upper Maastrichtian by Kennedy (1986), but a lower upper Maastrichtian position was suggested by Walaszczyk and Kennedy (2011) based on the presence of non-tegulated inoceramids. There are three illustrated syntypes from Fresville (Seunes 1890, pl. 3, figs 1a, b, 2a, b, and 3a, b); their morphometric data are presented as C1–C3 in Table 1. Kennedy (1986, p. 36) noted that specimens 1 and 2 were lost, and suggested that the largest specimen (Seunes 1890, pl. 3, figs 1a, b) should be designated the lectotype, if found. While this material is not abundant, it is treated here as a taxonomic reference for this species.

As defined by Seunes (1890) and Kennedy (1986), *P. jacquoti* is characterised by a moderately involute shell with rounded whorl flanks. The whorl section is depressed and semi-circular, unlike *P. neubergicus* in which it is compressed and oval. Syntypes of *P. jacquoti* document successive stages of shell ornamentation (Text-fig. 7). Only umbilical bullae appear in the earliest growth stages, with eight present at a diameter of 49 mm (Text-fig. 7A; Seunes 1890, pl. 3, fig. 3b). Secondary ventral ribs appear on the later half whorl of the larger syntype, which is 64 mm in diameter (Text-fig. 7B; Seunes 1890, pl. 3, fig. 2a). There are c. 14 umbilical bullae and c. 33 ventral ribs



Text-fig. 8. Plaster casts of the type specimens of *Pachydiscus armenicus* Atabekian and Akopian, 1969, from the upper Maastrichtian of Azizbek region, Armenia. A – specimen 2/101 in Atabekian and Akopian (1969); B – the holotype specimen 3/101 in Atabekian and Akopian (1969).

on the last whorl of the largest syntype, which is still septate at the maximum preserved diameter of 108 mm (Text-fig. 7C; Seunes 1890, pl. 3, fig. 1a; C3 in Table 1). Another phragmocone from Cotentin has 13–14 umbilical bullae and c. 28 ventral ribs at a diameter of 70 mm (Kennedy 1986, p. 36). Secondary ribs disappear in the later ontogenetic stages of the largest illustrated specimen (122 mm in diameter; Kennedy 1986, pl. 6, figs 1–3), which is only ornamented with distant primary ribs on the last part of the whorl. In summary, there is minimal overlap in the number of umbilical ribs in the middle growth stages between the topotype materials of *P. jacquoti* (12–14) and *P. neubergicus* (14–17), and there is no overlap in the number of ventral ribs (28–34 *vs.* 42–60, respectively). Correspondingly, *P. jacquoti* is more distantly and sparsely ribbed than *P. neubergicus.*

Five Hillerslev specimens resemble *P. jacquoti*. The best-preserved specimen (Text-fig. 5A; H8 in Table 1) has inflated flanks, 12 umbilical bullae, and 36 ventral ribs at a diameter of 101 mm; that is, slightly fewer umbilical bullae and slightly more ventral ribs than a very similar specimen from Cotentin (Text-fig. 7C). This difference is insignificant, given the limited Cotentin reference material, and this specimen is assigned to *P. jacquoti*. Other Hillerslev specimens (Text-fig. 3B–E) look like those of comparable size from Cotentin, but given their incompleteness they are assigned with some reservation to *P.* sp. cf. *jacquoti*. A particularly remarkable similarity is noted between the smallest Hillerslev specimens and the juvenile *P. jacquoti* specimens from Cotentin (compare Text-fig. 3D and 3E with Text-fig. 7A and 7B, respectively).

***Pachydiscus armenicus* Atabekian and Akopian, 1969**

This species was originally established as *Pachydiscus gollevillensis armenicus* by Atabekian and Akopian (1969, p. 8, pl. 1, fig. 2, pl. 3, figs 1 [the holotype] and 2). The type specimens are from upper Maastrichtian deposits exposed 1.5 km west of Bartsruni in the Azizbek region of the former Armenian Soviet Socialist Republic (present-day Armenia). Their plaster casts were illustrated by Ward and Kennedy (1993, fig. 34.1-6, re-illustrated here as Text-fig. 8A, B), who raised the taxonomic rank of these specimens to species level based on their clear morphologic distinction from *P. gollevillensis* (d’Orbigny, 1850).

As defined by Atabekian and Akopian (1969), *P. armenicus* is typified by a moderately involute conch with compressed whorls, and it can be easily distinguished from other members of the *P. neubergicus* group by the presence of very dense ribbing, which consists of 16 to 20 umbilical bullae and 62–73 ventral ribs per whorl. More specifically, these figures are 20 and c. 73, respectively, at a diameter of 130 mm in the holotype specimen (3/101; Atabekian and Akopian 1969, p. 8; Text-fig. 8B; A2 in Table 1), and 19 *vs.* 63 at a diameter of 98 mm in another specimen (their 2/101; Text-fig. 8A; A1 in Table 1). In contrast, *P. gollevillensis* is characterised by 9–11 umbilical bullae and up to 80 ventral ribs per whorl (Kennedy 1986).

Only a single incomplete (half-preserved), densely ribbed specimen from Hillerslev is comparable to the *P. armenicus* type specimens (Text-fig. 4B, H7 in Table 1), in having a distinctly compressed shell form and fine ribbing. It has 12 umbilical and as many as 27 ventral ribs at a diameter of 92 mm (Table 1). The Armenian type specimens do not show any substantial change in ribbing density at this size, so it may be assumed that the ribbing pattern of the Hillerslev specimen was uniform throughout the entirety of the last whorl. If so, the complete individual would have 24 umbilical and 54 ventral ribs (Table 1). The Hillerslev specimen therefore has more umbilical and fewer ventral ribs than the smaller Armenian specimen (Text-fig. 8A), leading to its assignment as *P.* sp. aff. *armenicus*.

PRINCIPAL COMPONENT ANALYSIS AND *T* TEST

Although meaningful and decisive statistical analysis of the discussed ammonite material is impossible given the small number of specimens at hand, Principal Component Analysis (PCA) and subsequent one-sample *t* test, based on PCA scores, were performed on selected specimens to determine if they fit into the 'type population' of *Pachydiscus neubergicus* from Neuberg (Text-fig. 9, Table 2). Four parameters were included in the PCA analysis (Text-fig. 9) to compare specimens from selected locations with the type material of *P. neubergicus*: maximum preserved diameter (Dmax); number of umbilical ribs on the last whorl (Ru); number of ventral ribs on the last whorl (Rv) and the Rv/Ru ratio. Because the input data include different measures (distance, number and ratio), a correlation matrix was selected instead of a variance-covariance matrix.

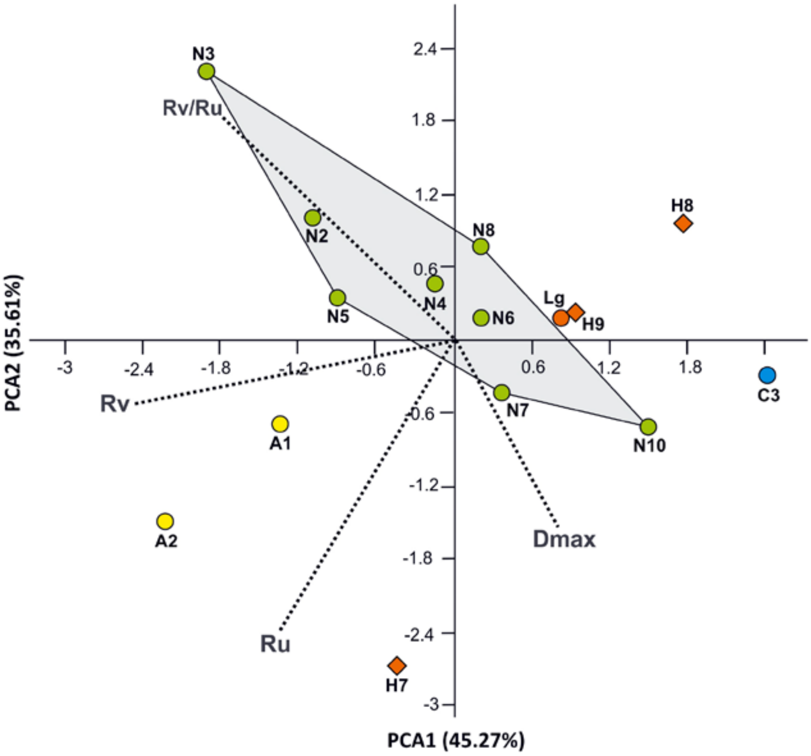
Specimens Lg (from Lynge) and H9 (from Hillerslev), both conventionally attributed to *P. neubergicus*, occupy a very similar plot area adjacent to the Neuberg specimens in a two-dimensional plot including the two axes representing most of the variation, that is the PCA1 and PCA2 axes (Text-fig. 9). In contrast, specimens H8 (*P. jacquoti* from Hillerslev) and C3 (one of the syntypes of *P. jaquoti* from Cotentin) differ from the Neuberg group with significantly higher PCA1 and PCA2 scores. Specimens A1 and A2 (types of *P. armenicus* from Armenia) and H7 (from Hillerslev, identified here as *P.* sp. aff. *armenicus*) varied from the Neuberg group in having more negative PCA2 and PCA1 scores, respectively.

Subsequently, one-sample tests were performed to test whether selected single specimens are statistically similar to the *P. neubergicus* 'type population' from the type area (eight specimens N2–N8, N10). More precisely, the mean value of the PCA scores from the *P. neubergicus* 'population' from each of the PCA axes that represent more than 5% of the variation (i.e., PCA axes 1, 2 and 3) was compared with the scores of the selected specimens on the same three axes. A Shapiro-Wilk normality test revealed that the *P. neubergicus* locations on each of the three axes are normally distributed, and thus allow us to use the relatively strong parametric one-sample *t* test for a given mean value.

The one-sample *t* test demonstrates that specimen H7 represents a morphotype which is most different from the Neuberg material with regard to the PCA2 and PCA3 scores at $p \leq 0.001$ (Table 2). In contrast, specimen Lg represents a morphology which is most similar to the Neuberg material and only exhibits a statistically significant difference in PCA1 at slightly below $p<0.05$ (more precisely $p=0.03$). Specimens H8 and H9 are less similar to the Neuberg specimens than specimen Lg showing significant or near significant statistical differences with regard to PCA1 and PCA3. In summary, the null-hypothesis (H0) that specimens H7, H8 and H9 are similar to the

Specimen	Results	PCA1	PCA2	PCA3
H7	*t*	0.58	9.9	5.35
	p	0.58	2.27E-05	0.001
H8	*t*	-5.33	-1.46	-1.94
	p	0.001	0.19	0.09
H9	*t*	-3.16	0.78	-3.67
	p	0.02	0.46	0.008
Lg	*t*	-2.80	0.94	0.14
	p	0.03	0.38	0.89

Table 2. Results of the one-sample *t* test comparing the material of *Pachydiscus neubergicus* from Neuberg with selected specimens from the mid-Maastrichtian of Hillerslev (H7–H9) and Lynge (Lg), identified in the present paper as *P.* sp. aff. *armenicus* (H7), *P. jacquoti* (H8), and *P. neubergicus* (H9 and Lg). The test gives a value for the *t* statistic and a probability for equality. If $p<0.05$, the sample is significantly different from the mean of the *P. neubergicus* 'type population' along the selected PCA axis.



Text-fig. 9. Principal Component Analysis plot based on the correlation matrix which compares selected ammonite specimens with a morphospace of Neuberg material (grey-coloured) using four selected variables: maximum preserved diameter (Dmax); number of umbilical ribs on the last whorl (Ru); number of ventral ribs on the last whorl (Rv) and Rv/Ru ratio. Dotted lines show significant correlations of the analyzed parameters along PCA axes 1 and 2. Explanations: N2–N8, N10 – *P. neubergicus*; H7 – *P.* sp. aff. *armenicus*; H8 – *P. jacquoti*; H9 and Lg – *P. neubergicus*; C3 – *P. jacquoti*; A1 and A2 – *P. armenicus*.

mean values of the *P. neubergicus* type material is rejected. Overall, the results of PCA and one-sample *t* tests are compatible with the conventional identification of the Hillerslev specimens proposed earlier.

PREVIOUS RECORDS FROM DENMARK

Four Danish specimens of the *P. neubergicus* group were described by Birkelund (1993). Of these, three came from mid-Maastrichtian sections in Jutland, e.g., Lindholm, Rørdal, and Hillerslev, and one from glacial deposits exposed at Lynge, Zealand (Text-fig. 1A). Birkelund (1993) identified her specimens as sparsicostate individuals of *P. neubergicus*, but the present material suggests that these identifications should be reassessed.

The specimen from Rørdal (Birkelund 1993, pl. 4, fig. 1) comes from either the *tenuicostata–semiglobularis* or the *semiglobularis–humboldtii* microbrachiopod zones, and is quite worn. However, the widely spaced, distant ventral ribs on the better-preserved part of the last whorl suggest assignment to *P.* sp. cf. *jaquoti*.

The specimen from Lindholm (Birkelund 1993, pl. 8, fig. 1) is from the *semiglobularis-humboldtii* Zone, and is likewise poorly preserved. It is here considered to represent *Anapachydiscus* Yabe and Shimizu, 1926, based on the rib bifurcation point which is situated low in the inner flank of the whorl, immediately from the umbilical bullae or tubercles. A comparable specimen of *A. terminus* Ward and Kennedy, 1993 from the upper upper Maastrichtian chalk in the ‘Dania’ quarry, Jutland, was illustrated by Birkelund (1993, pl. 6, fig. 3) as *A.* aff. *fresvillensis* (Seunes, 1890).

The specimen from Hillerslev (Birkelund 1993, pl. 4, fig. 2), recovered from either the *tenuicostata–semiglobularis* or the *semiglobularis–humboldtii* zones, resembles the more complete specimen discussed below and may be classified as a sparsicostate individual of *P. neubergicus*.

The undated, but probably mid-Maastrichtian, specimen from Lynge (Birkelund 1993, pl. 10, fig. 1) is the best preserved among Birkelund's (1993) material. It has 15 umbilical and 44 ventral ribs at a diameter of 95 mm matching the lower range of variation within the Neuberg material (Table 1). As such, the identification of the Lynge specimen as a sparsicostate individual of *P. neubergicus* is supported here. As noted by Birkelund (1993), the specimen is extremely close to the lower Maastrichtian specimen from Lüneberg (Germany) figured as *P. neubergicus* by Schlüter (1872, pl. 18, figs 1–3).

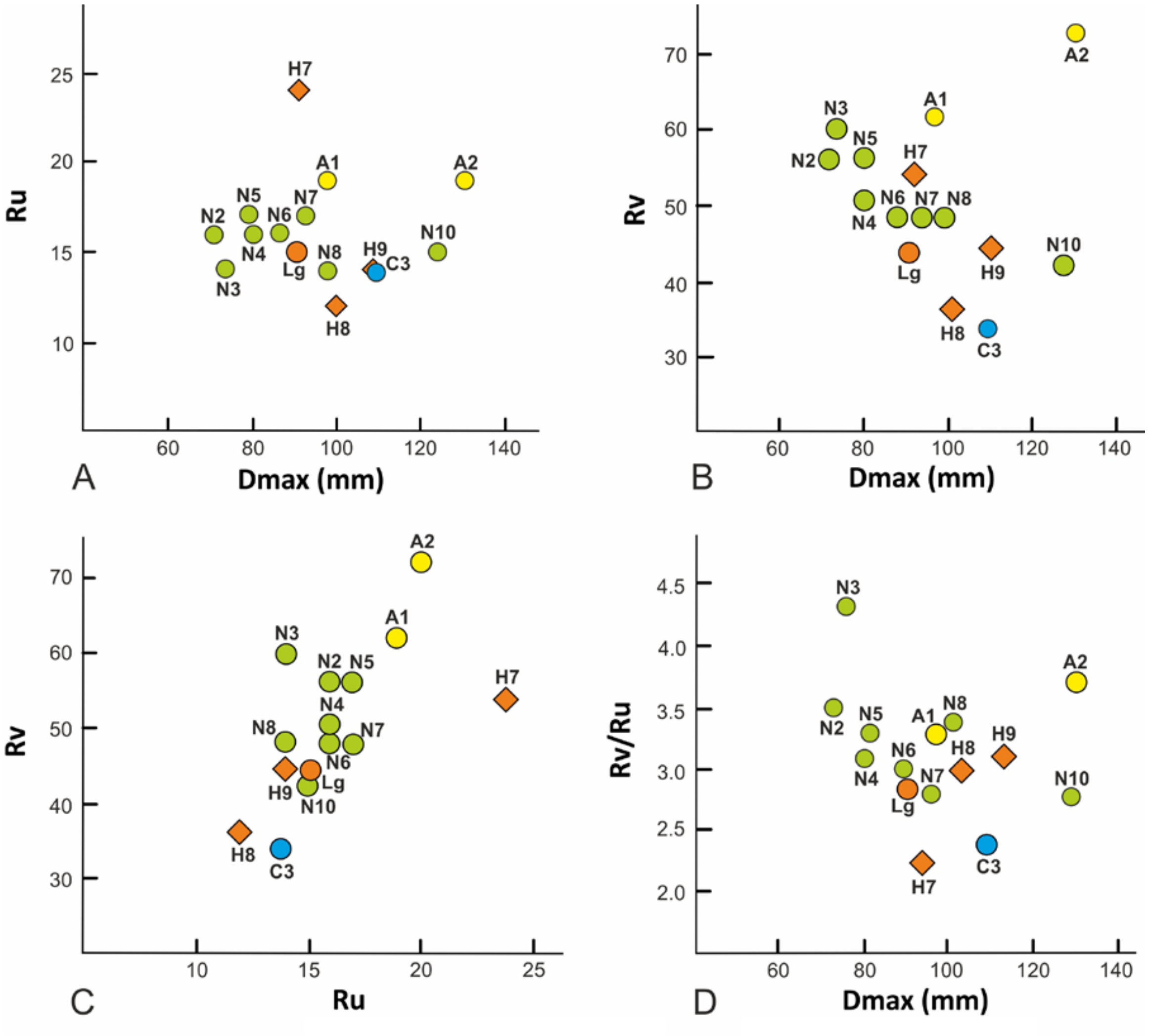
DISCUSSION

A wide range of intra-population (intra-species) morphological variation within ammonite conchs has been previously documented (De Baets *et al.* 2015). For Mesozoic ammonites, impressive cases were described by Dagys and Weitschat (1993) for the Triassic, Callomon (1985), Zatoń (2008), and Jain *et al.* (2023) for the Jurassic, and by Wilmsen and Mosavinia (2011) and Kennedy (2013) for the Cretaceous. For example, Dagys and Weitschat (1993) analysed the variation present within 700 adult specimens of a Triassic ceratitid ammonite packed within a concretion from Siberia. These specimens ranged from smooth suboxycones, to feebly ribbed platycones, to strongly ornamented subcadicones. Importantly, morphological variation was continuous, and so Dagys and Weitschat (1993) concluded that these morphotypes – which were often described individually under different generic or specific names – belonged to a single genetically linked population and constituted a single biospecies. This, and many other studies demonstrate that intra-populational variation in ammonites can be expressed through both conch proportions and ornamentation style, and that these characters can be correlated (Buckman's rules of covariation; see Monnet *et al.* 2015).

In the present paper, several morphospecies have been identified in the Hillerslev material based on comparisons with the 'type populations' of the species of the *P. neubergicus* group. These are: *Pachydiscus neubergicus*, *P.* sp. cf. *neubergicus*, *P. jacquoti*, *P.* sp. cf. *jacquoti*, *P.* sp. aff. *armenicus*, and *Pachydiscus* sp. However, in the light of the above presented data, it is reasonable to anticipate that the members of the group experienced rather wide morphological variability, both in terms of rib density and whorl inflation. If so, it is quite possible that the identified Hillerslev morphospecies actually belonged to a single, morphologically variable biospecies (*sensu* Callomon 1985). Unfortunately, the small number of specimens at hand prevents rigorous statistical testing of the single-biospecies hypothesis. More better-preserved specimens are needed to reach a definite conclusion. However, some preliminary remarks on this subject are possible (see below), illustrated by scatterplots presenting the distribution of ribbing indices plotted against conch diameter in selected specimens (Text-fig. 10).

A densely ribbed specimen that has the highest number of umbilical ribs in the present material (Text-fig. 4B; H7 in Text-fig. 8A) fits least well with the single-biospecies hypothesis. This specimen resembles *P. armenicus* in shell ribbing and proportions, but is identified here as *P.* aff. *armenicus* as the number of umbilical ribs exceeds that of the Armenian types (A1 and A2 in Text-fig. 10C). Consequently, H7 stands out from the rest of the *P. neubergicus* group in terms of the Rv/Ru ratio as well (Text-fig. 10C). However, it does not deviate from the Neuberg specimens in terms of ventral ribbing density (Text-fig. 10B).

The majority of the Hillerslev material (Text-figs 3–5) consists of specimens that are much less densely ribbed than H7, although only the data from the two best preserved and unequivocally determinable specimens (H8 and H9) are plotted in Text-fig. 10. Specimen H9, identified here as *P. neubergicus* (Text-fig. 5B), falls within the umbilical rib distribution range of the *P. neubergicus* 'type population', as does the Lynge specimen (Lg; Text-fig. 10A). However, both specimens are situated in the lower portion of the 'type population' ventral ribbing range (Text-fig. 10B), being clearly sparsicostate in comparison with the Neuberg material. The more distantly ribbed specimen H8, assigned to *P. jacquoti* (Text-fig. 5A), is situated close to the proposed lectotype of this species from Cotentin (C3 in Text-fig. 10B and C). In terms of ribbing density, *P. jacquoti* is quite close to the sparsicostate individuals of *P. neubergicus*, which is probably why de Grossouvre (1894) regarded both species as synonymous. However, the distinctiveness of *P. jacquoti* from *P. neubergicus* is clear from the occurrence of morphometrically-typical *P. jacquoti* specimens in locations and stratigraphic intervals where typical *P. neubergicus* specimens are absent; for instance, in the lower upper Maastrichtian of Cotentin (Kennedy 1986) or the upper upper Maastrichtian of Poland (Machalski 2005a). It is probable that in some cases, the *P. jacquoti* style ribbing may appear in raricostate end-members of the *P. neubergicus* range, while in other cases it characterises populations of *P. jacquoti* understood as a separate biospecies. As a further complication, sparsicostate specimens are occasionally referred to the subspecies *P. neubergicus raricostatus* Błaszkiewicz, 1980 (e.g., Ivanov 1995,



Text-fig. 10. Distribution of ribbing density indices in the *P. neubergicus* group from Hillerslev (H7–H9) and Lynge (Lg) compared to specimens from Neuberg (N2–N8, N10), Cotentin (C3), and Azizbek (A1, A2). Only the best preserved specimens in middle growth stages (70 to 130 mm in diameter) are plotted, as species diagnoses are typically based on this size range. Specimens of this size typically display no significant changes in ribbing density on the last whorl, enabling extrapolation of rib numbers from the better preserved portions of the incomplete specimens, if necessary (Table 1). Explanations: Dmax – maximum diameter; Ru – number of umbilical ribs; Rv – number of ventral ribs; N2–N8, N10 – *P. neubergicus*; H7 – *P.* sp. aff. *armenicus*; H8 – *P. jacquoti*; H9 and Lg – *P. neubergicus*; C3 – *P. jacquoti*; A1 and A2 – *P. armenicus*.

misspelled as *rarecostatus*). The reader is referred to Kennedy (1986) and Machalski (2012a) for arguments against the validity of this subspecies.

In summary, the Hillerslev material is dominated by specimens which may be identified as conspecific or closely related to *P. jacquoti* (five specimens) and to a sparsicostate 'variety' of *P. neubergicus* (three specimens). It is quite possible that these specimens were actually members of a widely variable population (or rather a series of populations, considering the time-averaging of the Hillerslev assemblage) of a single biological species. It is somewhat less probable – although still possible – that the densely ribbed specimen assigned to *P.* aff. *armenicus* is also an extreme end-member of the variability of the same species. The morphotype dominating this hypothetical Hillerslev 'population' would be possibly closer to *P. jacquoti* rather than typical *P. neubergicus*, at least in terms of ribbing density.

The Hillerslev and Neuberg samples are approximately synchronous according to calcareous nannofossil correlation, so the differences between these materials may be of a biogeographical nature. However, the data at hand are too sparse to reach any conclusions. Additional material from the mid-Maastrichtian chalk of Denmark, preferably collected from more narrowly defined stratigraphic intervals to avoid extensive time-averaging, is required to test the single-biospecies hypothesis. The Hillerslev Quarry seems to be the most promising in this respect due to continued fossil collector activity.

CONCLUSIONS

- The taxonomy of *Pachydiscus neubergicus* group ammonites is studied based on material from the mid-Maastrichtian chalk at Hillerslev, Jutland, Denmark.
- This material comes from an interval encompassing the upper lower Maastrichtian *tenuicostata-semiglobularis* Zone and the lower upper Maastrichtian *semiglobularis–humboldtii* Zone in the regional microbrachiopod biozonation.
- The ammonite-bearing interval at Hillerslev correlates with the uppermost UC19 and the lower UC20 zones in terms of standard calcareous nannofossil biozonation.
- The studied material from Hillerslev consists of ten specimens and is heterogenous with regards to ribbing density and whorl inflation, which are both diagnostic species characteristics within the *P. neubergicus* group.
- Taxonomy of the Hillerslev specimens is based on direct comparison with ‘type populations’ of known *Pachydiscus* species, primarily with the approximately coeval *P. neubergicus* type material from Neuberg, Austria, which comes from the UC20 Zone.
- Several taxa are distinguished in the Hillerslev material, primarily based on differences in ribbing density: *Pachydiscus neubergicus* (one specimen), *P.* sp. cf. *neubergicus* (two specimens), *P. jacquoti* (one specimen), *P.* sp. cf. *jacquoti* (four specimens), *P.* sp. aff. *armenicus* (one specimen), and *Pachydiscus* sp. (one specimen).
- Principal Component Analysis and one-sample *t* tests performed on the studied specimens support the conventional identification of Hillerslev specimens proposed in this paper.
- Given the typically wide intra-populational variability of ammonite conchs, an alternative interpretation is considered possible – that these morphospecies, with the potential exception of *P.* sp. aff. *armenicus*, are members of a single, variable biospecies, probably dominated by a sparsicostate morphotype closer to *P. jacquoti* than to *P. neubergicus*.
- While more specimens from the mid-Maastrichtian Danish chalk are needed to test the single-species hypothesis, the Hillerslev section may be an ideal target for further studies.

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