A new Danian echinoid assemblage from the Greensand in the Kazimierz Dolny area, central Poland: taxonomy, taphonomy and sedimentological implications

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ABSTRACT:

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We describe a new echinoid assemblage, composed of specimens of *Bolbaster* sp., *Cyclaster danicus* (Schlüter, 1897), *Diplodetus vistulensis* (Kongiel, 1950) and *Linthia*? sp. in a distinctive phosphatic preservation, from the so-called Greensand, a marly glauconitic sandstone horizon at the base of the Danian succession in the Kazimierz Dolny area (central Poland). This assemblage presumably is of early Danian age, with *Cyclaster danicus* occurring in the lower Danian of Denmark and southern Sweden. The specimens are preserved as internal moulds, composed of phosphatised glauconitic sandstone, occasionally with some test material adhering. The genesis of these moulds involved the following steps: (1) infilling of tests of dead echinoids with glauconitic sand; (2) penetration of the infills by coelobiotic deposit-feeding organisms that produced burrows along the inner test surface; (3) early-diagenetic cementation of infills by calcium phosphate; and (4) exhumation and intraformational reworking of specimens, leading to abrasion, fragmentation and loss of test material in some individuals. Co-occurring are unphosphatised moulds of *Echinocorys* ex gr. *depressa* (von Eichwald, 1866) and *Pseudogibbaster* cf. *depressus* (Kongiel in Kongiel and Matwiejewówna, 1937), which may represent a younger (middle to late Danian) assemblage. Additionally, the presence of derived late Maastrichtian echinoids, e.g., *Temnocidaris* (*Stereocidaris*) ex gr. *herthae* (Schlüter, 1892), *Pleurosalenia bonissenti* (Cotteau, 1866) and *Hemicara pomeranum* Schlüter, 1902, is confirmed for the Greensand, based on new material and re-examination of previously recorded specimens. In summary, members of three echinoid assemblages of different age and preservation occur together in the Greensand. Our results are compatible with former interpretations of this unit as a condensed, transgressive lag with mixed faunas of different age and provenance. However, they are incompatible with the hypothesis that phosphatised Danian fossils preserved in the Greensand are derived from a facies equivalent, now gone, of the lower Danian Cerithium Limestone in eastern Denmark, because all moulds are composed of phosphatised glauconitic sandstone that is utterly different from the calcareous dinocyst-dominated, fine crystalline matrix of the Cerithium Limestone.

Key words: Echinodermata; Preservation; Ichnology; *Arachnostega*; *Planolites*; Paleocene; Middle Vistula River section; Central Europe.
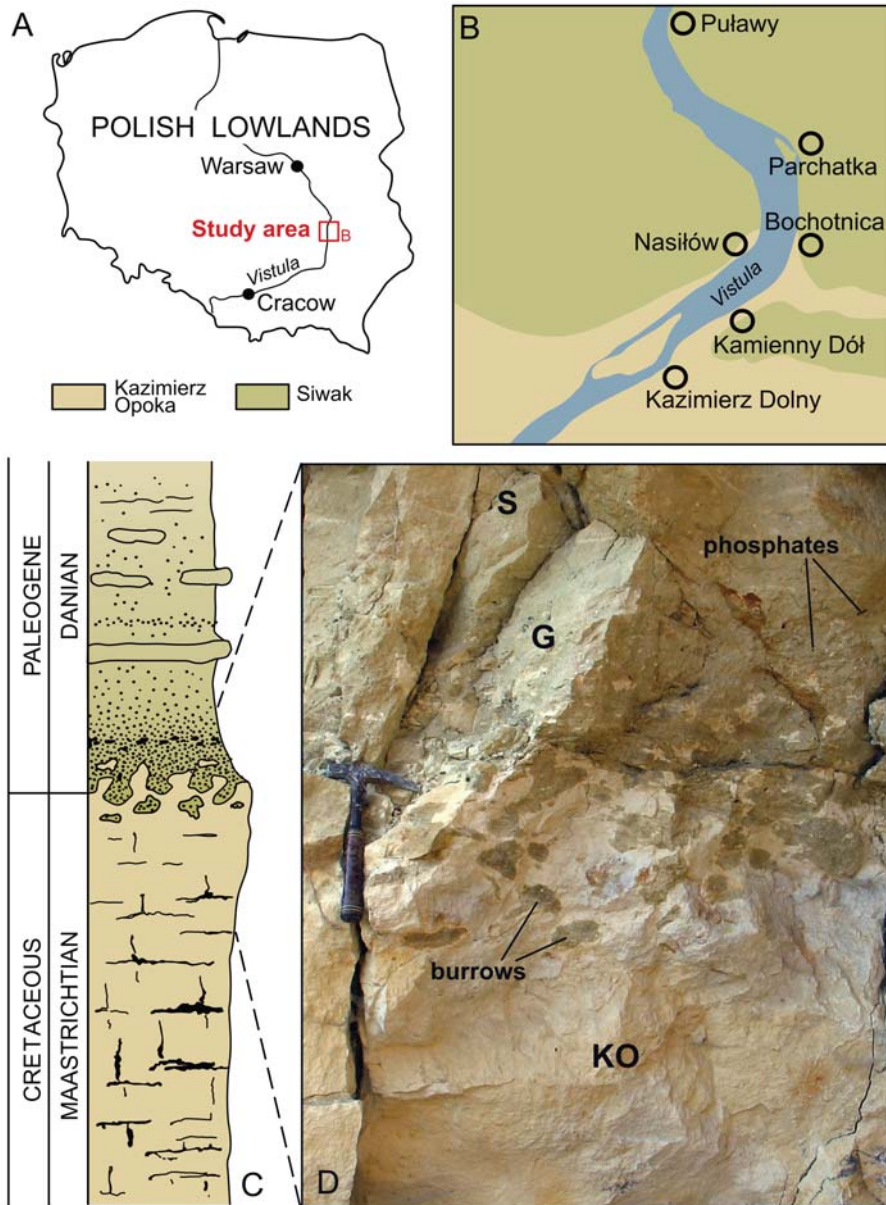
Text-fig. 1. Geological setting of the echinoid assemblages studied. A – Location of the Kazimierz Dolny area (rectangled) in Poland. B – Study area, with localities referred to in the text and distribution of the Kazimierz Opoka and Siwak units. C – Log and stratigraphy of the K/Pg interval in the Kazimierz Dolny area (modified from Machalski and Walaszczyk 1987, pl. 1). D – The Cretaceous–Paleogene (K/Pg) boundary interval as exposed at Bochotnica (section behind the old watermill), showing the uppermost Kazimierz Opoka (KO), the Greensand (G) and the lowermost Siwak (S) (field photograph by M. Machalski 2005)

INTRODUCTION

Echinoid assemblages from upper Maastrichtian (Upper Cretaceous) to Danian (lower Paleocene, Lower Paleogene) strata exposed in the Kazimierz Dolny area, Middle Vistula River section, central Poland (Text-fig. 1A, B) have been receiving attention since the 1930s (Kongiel 1935, 1936, 1939, 1949, 1950;

Kongiel and Matwiejewówna 1937; Mączyńska 1972, 1989; Geys and Machalski 1992). In recent years, additional echinoid material has been recovered from various levels within the upper Maastrichtian and Danian of the Kazimierz Dolny area.

In the present paper, we describe a new assemblage of Danian echinoids (hemiasterids, micrasterids and ?schizasterids), in a distinctive preservation, from the

Kazimierz Dolny area. This material comes from the so-called Greensand at the base of the Danian succession in the study area. It represents a taxonomic composition and style of preservation (i.e., phosphatic glauconitic sandstone internal moulds) which have not yet been identified amongst Danian echinoids from the area. As such, it adds new taxonomic and taphonomic data to our knowledge of the regional echinoid succession across the Cretaceous–Paleogene (K/Pg) boundary. Additionally, it yields some novel clues to our understanding of the depositional history of the echinoid-bearing Greensand.

This contribution commemorates Professor Andrzej Radwański (1935–2016), who authored or co-authored a series of insightful papers on the palaeontology and sedimentology of the K/Pg interval in the Kazimierz Dolny area (Hansen *et al.* 1989; Radwańska and Radwański 1994; Marcinowski and Radwański 1996; Radwański 1996; Machalski *et al.* 2003; Jagt *et al.* 2005). Additionally, this note is concerned with echinoid taphonomy, which was another of Professor Radwański's scientific interests, as demonstrated by his papers on spectacular accumulations of middle Miocene echinoids from Poland and the Ukraine (Radwański and Wysocka 2001, 2004).

GEOLOGICAL BACKGROUND

The present study is based on echinoid material from the Middle Vistula River section. This section consists of a series of exposures along the banks of the River Vistula (Wisła), between the towns of Zawichost and Puławy, central Poland (Pożaryski 1938; Walaszczyk *et al.* 2016). In a northerly direction, the river exposes successively younger strata, with the Maastrichtian–Danian boundary interval accessible near the town of Kazimierz Dolny (Text-fig. 1A, B). No formal lithostratigraphical subdivision of K/Pg strata in this area is available to date, which explains why we here use the traditional, informal lithostratigraphical names for the units discussed, i.e., Kazimierz Opoka, Greensand and Siwak (for a review, see Machalski 1998).

In all, the K/Pg succession in the Kazimierz Dolny area comprises two main units. The lower portion of the succession is formed by the so-called Kazimierz Opoka, a c. 50-m-thick unit of siliceous chalk ("opoka" of Polish workers) with marly and limestone intercalations. The Kazimierz Opoka is of late, but not latest, Maastrichtian age (Błaszkiewicz 1980; Hansen *et al.* 1989; Machalski 1996, 2005a, b; Dubicka and Peryt 2012). The upper portion of the succession is formed by the so-called Siwak, also some 50 m in thickness, and composed of gaizes with intercalations of nodular limestone beds (Pożaryska 1952). Earlier age assignments of the Siwak have varied, but the currently accepted view is that it is of early (but not earliest) to middle Danian age (Hansen *et al.* 1989; Machalski 1998; Żarski *et al.* 1998).

The echinoids studied have been recovered from the basal part of the Danian succession, from a distinctive, thin (c. 50 cm) horizon of marly glauconitic sandstone with phosphatic nodules, referred to in the literature as the "glauconitic sandstone" or "Greensand". This unit rests with a sharp contact on top of the Kazimierz Opoka and passes gradually upwards into the Siwak (Text-fig. 1C, D). The age of the Greensand and the position of the K/Pg boundary in the Kazimierz Dolny area have been disputed for years, mostly due to the mixing of late Maastrichtian and Paleocene fossils in this unit (Kongiel 1935, 1958; Pożaryski 1938; Putzer 1942; Pożaryska 1965; Krach 1974, 1981; Abdel-Gawad 1986; Machalski and Walaszczyk 1987; Hansen *et al.* 1989; Radwański 1996; Machalski 1998, 2005a; Żarski *et al.* 1998; Świerczewska-Gładysz and Olszewska-Nejbert 2006; Keutgen *et al.* 2017). The currently accepted view is that the Greensand is of Danian age (Machalski 1998, 2005a; Żarski *et al.* 1998; Świerczewska-Gładysz and Olszewska-Nejbert 2006; Keutgen *et al.* 2017).

THE GREENSAND AND ITS FOSSILS

A brief presentation of the anatomy of the Greensand and a summary of our views on its development and taphonomy are called for so as to put the present echinoid material in a proper stratigraphical and sedimentological context. At present, the Greensand is most easily accessible at Bochotnica, in a quarry behind the old watermill (51º20'18.953" N, 22º0'13.785" E) in the eastern part of the village (Text-figs 1D; 2A, B), but the lithological development of this unit is uniform across the study area (Krach 1974; Machalski 1998).

Anatomy of the Greensand

At all outcrops studied, the Greensand is c. 50 cm thick and rests on top of the Kazimierz Opoka. The latter is formed by a bed of indurated limestone which passes gradually upwards into a level of soft opoka. This part of the section is penetrated by *Thalassinoides*-type burrows filled with overlying glauconitic sandstone (Text-figs 1C, D; 2A). The bur-
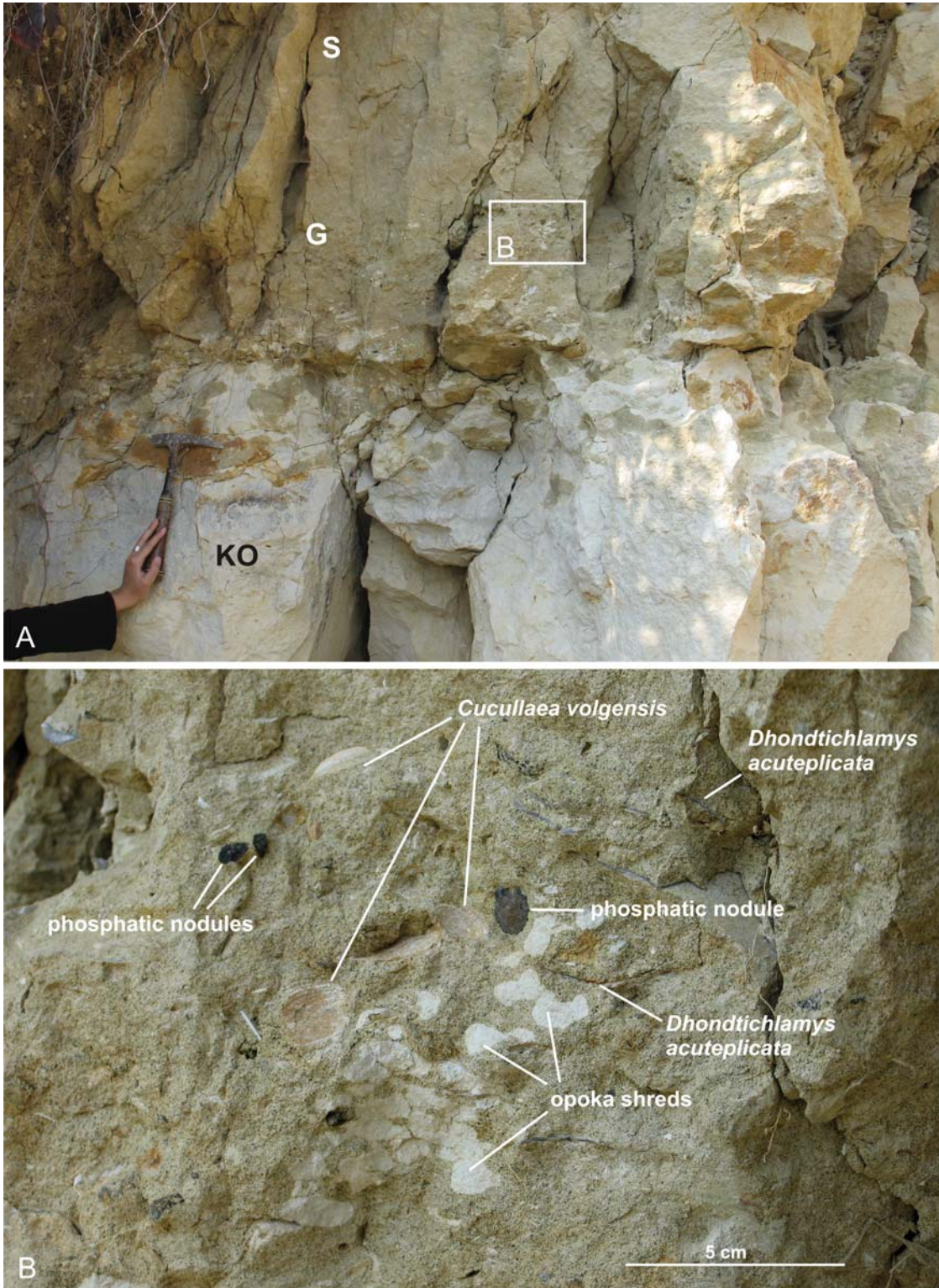
Text-fig. 2. The Cretaceous–Paleogene interval as exposed at the locality behind the old watermill at Bochotnica (see Text-fig. 1B for location). A – General view of the quarry face with the (strongly burrowed) highest levels of Kazimierz Opoka (KO), Greensand (G) and lowermost portion of Siwak (S). Rectangled is the area presented in B. B – Detail of Greensand with phosphatic nodules, floating pieces of soft opoka and two characteristic bivalves, *Cucullaea volgensis* Barbot de Marny, 1874 (a Danian species) and *Dhondtichlamys acuteplicata* (Alth, 1850) (a late Maastrichtian species) (field photographs by M. Machalski, 2005)

row density increases upwards, which results in the brecciated appearance of the uppermost portion of the Kazimierz Opoka, with shreds of soft opoka and abundant opoka-filled fossils 'floating' in a sandy-glauconitic sediment (Text-fig. 2B).

The Greensand itself is composed of angular quartz, glauconite, tiny phosphatic grains and micro-fossil tests set in a marly matrix. At a level c. 20 cm above the top of the limestone, there is a diffuse, intensely bioturbated horizon of nodular phosphates and fossils (the "phosphorite layer" of previous authors) that passes gradually into the overlying gaizes of the Siwak unit (Text-figs 1C, D; 2A). Rare, minute phosphate grains and small phosphatised fossil fragments range up to 1 m above the top of the indurated limestone (Putzer 1942; Machalski 1998; Żarski et al. 1998).

A close examination of the section reveals that the soft opoka shreds range up to the phosphorite level (Text-fig. 2A, B). These shreds are so irregular and filigree in shape (Text-fig. 2B) that they certainly could not have survived any reworking. Consequently, we suggest that the top surface of the Kazimierz Opoka was originally situated approximately at the phosphorite level, having been almost entirely replaced subsequently by sandy-glauconitic sediment that infilled successive burrow generations (Machalski 1998, fig. 7; see analogous interpretation of the mid-Cretaceous Glauconitic Marl/Upper Greensand contact in England by Kennedy and Garrison 1975, fig. 3).

Age and taphonomy of the fossils

The Greensand is crowded with phosphatic nodules and fossils. The latter occur in various states of preservation, ranging from pristine shells, occasionally even with original colour patterns, to barely recognisable, highly abraded phosphatic fragments. In the field, the most conspicuous fossils in the Greensand are sponge fragments, masses of dissociated valves of the scallop *Dhondtichlamys acuteplicata* (Alth, 1850) and rostra of the belemnitellid coleoid group of *Belemnella kazimiroviensis* (Skołozdrówna, 1932). Late Maastrichtian and Danian taxa can be identified amongst these Greensand fossils (Krach 1974; Machalski and Walaszczyk 1987; Machalski 1998; Świerczewska-Gładysz and Olszewska-Nejbert 2006; Keutgen et al. 2017).

The late Maastrichtian fauna is represented by phosphatised and unphosphatised specimens, including sponges, terebratulid brachiopods, belemnites, gastropods and bivalves. Most of these represent taxa with originally calcitic skeletons, those with originally aragonitic shells being preserved exclusively as three-dimensional phosphatic moulds. All late Maastrichtian taxa from the Greensand are here interpreted as remanié material, having been derived from the top of the Kazimierz Opoka or from a glauconitic opoka bed of latest Maastrichtian age that is now gone. The former presence of this "lost" unit in the study area has been inferred from the petrography of fossil infills (Machalski and Walaszczyk 1987; Hansen et al. 1989; Świerczewska-Gładysz and Olszewska-Nejbert 2006). To date, we do not have any late Maastrichtian fossils that can be identified as being indigenous for the Greensand (Machalski 1998). Even the well-preserved belemnitellid rostra that retain the thin alveolar walls have, in our view, been washed out or exhumed by burrowing animals from the soft chalk in the top part of the Kazimierz Opoka. The total absence of unphosphatised late Maastrichtian fossils with originally aragonitic shells in the Greensand fauna supports our views on the *ex situ* nature of the entire assemblage of this age that is preserved in this unit. The originally aragonitic skeletons typically are the first faunal elements to be lost on the sea floor or during early diagenesis, unless transformed into early diagenetic phosphatic steinkerns (Kennedy and Garrison 1975) or, occassionally, bioimmured by oysters (Machalski and Kennedy 2013).

The Danian fauna consists predominantly of small bivalves and gastropods with originally aragonitic shells. These occur as unphosphatised sandstone moulds with a thin powdery film left after shell dissolution. The same taxa and in the same preservation, e.g., the bivalve *Cucullaea volgensis* Barbot de Marny, 1874 (see Text-fig. 2B), also occur in the overlying gaizes of the Siwak unit, and are interpreted as indigenous biota which colonised the sea bed during deposition of the glauconitic sand (Krach 1974, 1981; Machalski and Walaszczyk 1987; Machalski 1998; Żarski et al. 1998). Much less abundant in the Greensand are phosphatised moulds of Danian taxa (Krach 1974; Żarski et al. 1998). These were interpreted by Krach (1974) as remanié material derived from the "first Danian deposits". On the basis of SEM images of fossil infills, Hansen et al. (1989) proposed that an early Danian limestone bed equivalent to the Cerithium Limestone in Denmark had originally been laid down in the Kazimierz Dolny area, having been removed by subsequent erosion. Machalski (1998) regarded this unit, now lost, as the source of all phosphatic Danian fossils that are present in the Greensand.

These late Maastrichtian and Danian phospha-

tised and unphosphatised fossils are randomly mixed in the Greensand sediment. In places, fossils and nodules in different age and preservation classes are aligned more or less horizontally, suggesting hydrodynamic reworking (the 'Aufarbeitungshorizont' of Putzer 1942). In other places, the fossils and nodules occur in 'nests' that are composed of specimens in all possible positions (Text-fig. 2B), which probably is a reflection of intense biogenic reworking of the sediment (Machalski and Walaszczyk 1987).

Genetic interpretation

Based on the characteristics outlined above, we regard the Greensand as the basal transgressive portion of the Danian sedimentary succession, with the phosphorite layer forming a kind of basal conglomerate or lag (compare Pożaryska 1965; Krach 1974; Machalski 1998, 2005a). Analogous, heavily bioturbated admixtures of fossils of variable age, preservation and derivation, are typical of condensed, glauconite- and phosphate-rich transgressive units that are situated at the base of many shallow-marine successions elsewhere (e.g., Kennedy and Garrison 1975; Fürsich *et al.* 1981; Kidwell 1991; Kennedy and Cobban 1996; Wilmsen and Voigt 2006; Wilmsen 2012; Hairapetian *et al.* 2018; Machalski 2018). The renowned Cambridge Greensand Member of the West Melbury Marly Chalk Formation at the base of the Cenomanian succession in eastern England is iconic for this type of deposit, containing an admixture of derived late Albian and derived, plus indigenous, early Cenomanian faunal elements (see a recent review by Machalski 2018). Both the Greensand of the Middle Vistula River section and the Cambridge Greensand in eastern England belong to the lag subtype of early transgressive bioevents as distinguished by Wilmsen (2012, fig. 10).

MATERIAL AND METHODS

A suite of phosphatised echinoids from the Greensand, 16 specimens in all, forms the nucleus of the present contribution. They are preserved as more or less complete phosphatic moulds (steinkerns), with occasionally part of the test still adhering. This material comes from two collections. Fourteen specimens are from a lot of Maastrichtian and Danian echinoids from the Kazimierz Dolny area, recovered by one of us (MM) and housed at the Institute of Paleobiology, Polish Academy of Sciences, Warszawa (abbreviated: ZPAL E.12). Three taxa are represented in this material: *Bolbaster* sp. (5 specimens), *Cyclaster danicus* (Schlüter, 1897) (2 specimens) and *Linthia*? sp. (2 specimens). In addition, three indeterminate phymosomatid moulds are contained in this collection; in view of their poor preservation, these are not included in the systematic chapter, nor are they illustrated here. Two additional specimens, here assigned to *Diplodetus vistulensis* (Kongiel, 1950) and *Linthia*? sp., stem from a collection made in the study area by the renowned Polish palaeontologist Roman Kongiel, and now housed at the Museum of the Earth of the Polish Academy of Sciences, Warszawa (abbreviated MZ VIII Ee).

The ZPAL material was collected from the Greensand as exposed in the now abandoned quarry at Nasiłów on the left bank of the River Vistula (see Abdel-Gawad 1986 for a detailed description of the section), as well as from a disused pit in the Kamienny Dół gorge in the northern outskirts of Kazimierz Dolny (for additional data, see Żarski *et al.* 1998). Specimens contained in the MZ collection are from Nasiłów and from a small outcrop at Kazimierz Dolny (Kongiel 1950) that, at present, cannot be more precisely located.

In addition to the phosphatised echinoid material, a number of specimens in other states of preservation from the Greensand and Siwak have been studied. They belong to the ZPAL and MZ collections and are from Nasiłów and Kamienny Dół, from several currently defunct quarries at Bochotnica and from a natural exposure in the Łachów Dół gorge in the southern outskirts of the village of Parchatka, north of Bochotnica. The location of all outcrops mentioned above is indicated in Text-fig. 1B.

The material studied has been examined under a binocular, measured with a caliper and photographed (both in full colour and black and white; in the latter case, specimens were coated with ammonium chloride prior to photography). Additionally, a petrographic thin section was prepared from one of the specimens of *Bolbaster* sp. for examination of its infill.

TAXONOMY

The higher-order classification adopted here follows Kroh and Smith (2010).

Abbreviations: L – test length; W – test width; H – test height; Lap – length of anterior paired petals; Lpp – length of posterior paired petals; app – number of pore pairs in anterior paired petals; ppp – number of pore pairs in posterior paired petals.

Crown group Atelostomata von Zittel, 1879
Order Spatangoida L. Agassiz, 1840
Crown group Spatangoida
Family Hemiasteridae Clark, 1917

Genus *Bolbaster* Pomel, 1869

TYPE SPECIES: *Spatangus prunella* Lamarck, 1816, by original designation (Pomel 1869, p. 15).

REMARKS: We follow Smith and Wright (2008, p. 617) in affording generic status to *Bolbaster* because it differs from the type genus of the family in having a globular outline, a stout and near-rectangular labral plate and paired symmetrical sternal plates with a vertical median suture; where the labral plate abuts the sternal plates a V-shaped suture, rather than a strongly curved suture, is formed.

Bolbaster sp.
(Text-fig. 3A–P)

1987. ?*Micraster vistulensis* (Kongiel); Machalski and Walaszczyk, pl. 1, fig. 8.
partim 2000. *Hemiaster stella* (Morton, 1830); Smith and Jeffery, p. 323, text-fig. 134a, b, f.
2001. *Hemiaster stella* (Morton, 1830); Kroh, p. 410, text-figs 25, 26; pl. 12, figs 1–8.
2006. *Hemiaster* sp. 1; Neumann, p. 242, fig. 9a.
2009. *Bolbaster*; Kahlke *et al.*, p. 99, pls 5–7 (*Bolbaster* sp. in caption).
2009. *Bolbaster* sp. 1; Ladwig, p. 167, pl. 1, figs 1–4.
2009. *Bolbaster* sp. 2; Ladwig, p. 168, pl. 2, figs 1–3.
2012. *Bolbaster* sp.; Ladwig, p. 117, fig. 4.

MATERIAL: Five phosphatic internal moulds (ZPAL E.12/3, 12/4, 12/7, 12/11 and 12/12), one with adherent test fragments, from Nasiłów and Kamienny Dół.

MEASUREMENTS: See Table 1.

DESCRIPTION: ZPAL E.12/3 is an internal mould, without external test material, but in places a deeper-lying, galleried stereom structure is seen. Ambulacrum III is relatively narrow; anterior and posterior ambulacra petaloid and only shallowly sunken; highest point of test posteriorly; anal face near vertical. Periproct relatively large, c. 3.2 mm in height and 2.7 mm in width. ZPAL E.12/4 preserves portions of test, documenting large, non-scrobiculate (non-sunken) tubercles on adoral test surface and part of a narrow (c. 1 mm) peripetalous fasciole (Text-fig. 3G). Ambulacrum III in ZPAL E.12/7 is comparable to that in ZPAL E.12/3; details of pore structure cannot be made out, but in general anterior petals equal at least 1.7 to 2.1 times posterior petals in length; height and width of periproct (c. 3.1 mm and 2.5 mm) comparable to ZPAL E.12/3. Petals in ZPAL E.12/11 rather flush; ambulacrum III narrow; height/width of periproct 2.1 mm and 1.9 mm; burrowed all over. Also burrowed (sub) ambitally is ZPAL E.12/12, with traces of peripetalous fasciole, large gonopores (3 visible, remaining one not preserved); paired ambulacra comparatively more deeply sunken than in other specimens.

DISCUSSION: This material is close to, if not conspecific with, that recorded from the upper Danian Bruderndorf Formation of Austria by Kroh (2001), who followed Smith and Jeffery (2000) in using the specific epiphet *stella* for this form. However, from the synonymy list in the latter paper it is clear that this is quite a heterogeneous lot that is in need of a detailed study. In contrast to the type species of *Bolbaster*, *Spatangus prunella* Lamarck, 1816, of late Maastrichtian age, the Polish material has non-scrobiculate tuberculation (see Smith *et al.* 1999; Jagt 2000; Van der Ham *et al.* 2006). In the Maastrichtian type area (southeast Netherlands

	L	W	H	Lap	Lpp	app	ppp	Text-figs
ZPAL E.12/1	29.3	25.7	17.6	c. 6	c. 5.5	–	–	4A–D, 6B
ZPAL E.12/2	28.1	24.3	18.2	c. 8	c. 6	c. 21	c. 14	4E–H
ZPAL E.12/3	23.3	24.3	18.2	c. 6	c. 3.5	18–22	14–15	3A–D
ZPAL E.12/4	16.7	15.2	11.7	4.2	2.5	12–13	8–9	3G, H
ZPAL E.12/5	>27.2	27.7	19.0	c. 6	–	>24	–	4I, J, 6C
ZPAL E.12/6	19.8	19.8	14.2	c. 8	c. 5.5	c. 20	15–16	4K, L, 6A
ZPAL E.12/7	22.8	23.0	17.3	c. 6.1	c. 3	>15	8–9	3E, F
ZPAL E.12/11	23.3	22.3	17.6	c. 5.5	c. 3.2	13–15	12–13	3I, J, M, N
ZPAL E.12/12	18.0	18.0	14.8	c. 4.5	c. 2.1	>14	c.8	3K, L, O, P
MZ VIII Ee 1553	c. 21.5	c. 21	c. 13.5	–	–	20–21	–	5A–D
MZ VIII Ee 1554	c. 23	c. 23	c. 14	–	–	20–25	–	–

Table 1. Measurements of the echinoids studied (in mm)

Text-fig. 3. Phosphatic specimens of *Bolbaster* sp., coated with ammonium chloride prior to photography. A–D – ZPAL E. 12/3 from Nasiłów, in apical, oral, left lateral and posterior views, respectively. E, F – ZPAL E.12/7 from Kamienny Dół, in apical and oral views, respectively. G, H – ZPAL E.12/4 from Kamienny Dół, in apical and left lateral views (G, H); in G, the peripetalous fasciole (arrow 1) and non-scrobiculate tubercles (arrow 2) are illustrated. I, J, M, N – ZPAL E.12/11 from Nasiłów, in apical, oral, anterior and left lateral views, respectively. K, L, O, P – ZPAL E.12/12 from Nasiłów, in apical, oral, right lateral and anterior views, respectively. Note burrows (*Arachnostega gastrochaenae* Bertling, 1992), best seen in I, J, M and N, and a burrow assigned to *Planolites beverlyensis* (Billings, 1862) in L, O and P

and northeast Belgium), *B. prunella* co-occurs with *B. koninckanus* (d'Orbigny, 1855), which also has scrobiculate tuberculation.

This type of small-sized hemiasterid apparently was widely distributed during the early Paleocene across northern and central Europe, and even further

afield into Central Asia (www.ammonit.ru/text/1227.htm; www.geolsba.dk/echinoids/DKKRAE/DK677.html). Neumann (2006, fig. 9b) recognised a second form, listed as *Hemiaster* sp. 2, with more deeply sunken paired ambulacra and a wide ambulacrum III. It would appear that the oldest representatives of this group are from the Cerithium Limestone Member in eastern Denmark (Sjælland; J.W.M. Jagt, pers. obs., 2012–2014).

Zachos (2017, p. 15, figs. 9.2, 9.4, 10) has recently recorded and illustrated *Hemiaster stella* from the late Paleocene (Thanetian) Vincentown Formation of New Jersey (USA) and the early Paleocene (Danian) Clayton Formation of Alabama (USA). In petal and sternal structure this differs clearly from the material described here.

Hemiaster vistulensis Kongiel, 1936 (Kongiel 1936, p. 5; see also Kongiel 1935, pl. 5 (8), figs 2a–c, 3, as '*Species nova*'), recorded on the basis of two tests from the Siwak at Góra Puławska and Parchatka (Łachów Dół), was listed by Smith and Jeffery (2000, p. 327) as *Hemiaster* sp. indet. 2. In petal structure, this form appears to differ from what is here referred to as *Bolbaster* sp., but a re-examination of Kongiel's material, if still extant, is called for to substantiate this. We failed to locate these tests in the collections studied by ourselves.

OCCURRENCE: In test plating (non-scrobiculate tuberculation), ambulacral structure and test profile, this form is closest to early to late Danian 'populations' from Denmark (Kahlke *et al.* 2009; Ladwig 2009). Material from the upper Danian of Austria appears conspecific as well (Kroh 2001).

Suborder Micrasterina Fischer in Moore, 1966
Family Micrasteridae Lambert, 1920

Genus *Cyclaster* Cotteau in Leymerie and Cotteau, 1856

TYPE SPECIES: *Cyclaster declivus* Cotteau in Leymerie and Cotteau, 1856, by original designation (Cotteau in Leymerie and Cotteau 1856, p. 345).

Cyclaster danicus (Schlüter, 1897)
(Text-figs 4A–H, 6B)

*1897. *Brissopneustes danicus* Schlüter, p. 18, pl. 1, figs 1–4.
*1926. *Cyclaster brünnichi* [sic]; Ødum, p. 163.
 1959. *Cyclaster danicus* Schlüter, 1897; Moskvin and Poslavskaya, p. 291, text-fig. 108a–c, pl. 26, fig. 6a–c.
 1976. *Cyclaster danicus* (Schlüter); Asgaard, p. 363, figs 1–10.
?*partim* 2000. *Cyclaster integer* (Seunes, 1888); Smith and Jeffery, p. 314, text-fig. 130D, F.
 2006. *Cyclaster danicus* (Schlüter, 1897); Neumann, p. 240, fig. 5a, b.
 2009. *Cyclaster*; Kahlke *et al.*, p. 100, pls 9, 10; pl. 15, fig. 4 (as *Cyclaster danicus*).
 2011. *Cyclaster danicus*; Rasmussen *et al.*, p. 81, unnumbered figures.
 2011. *Cyclaster bruennichi*; Rasmussen *et al.*, p. 82 (upper half), unnumbered figures.

MATERIAL: Two specimens, ZPAL E.12/1 and E.12/2, both from the Greensand of Kamienny Dół.

MEASUREMENTS: See Table 1.

DESCRIPTION: ZPAL E.12/1 has large gonopores suggesting it to be a female individual; labrum narrow, width at base 0.7 mm; sternal suture near-vertical; anterior petals diverging at 115°. ZPAL E.12/2 is comparable; inner test layer (stereom) visible but no remains of external test surface preserved; infill of test heavily burrowed.

DISCUSSION: With test length/width and length/height ratios of 1.14 and 1.66 (ZPAL E.12/1) and 1.16 and 1.54 (ZPAL E.12/2), respectively, these two specimens rank amongst the more depressed individuals, with a more less centrally positioned apical disc that is slightly sunken (see Text-fig. 4C, G). Schlüter's type specimen (1897, pl. 1, figs 1–4; Institut für Paläontologie, Universität Bonn, no. 269a), from the lower Danian of Vixo (Jylland, northern Denmark), is a rather poorly preserved individual; L/W and L/H ratios are 1.30 and 1.82, respectively. For another test in the same lot, the L/W and L/H ratios are 1.20 and 1.56, respectively. However, in all other features (position of apical disc, ambulacral pore structure and position and size of peristome, the Polish material matches early Danian 'populations' from the Cerithium Limestone Member and the overlying bryozoan limestone (Korsnæb Member) in Danish sections (Stevns Klint and elsewhere). There also is a close resemblance to tests from the Korsnæb Member as illustrated by Rasmussen *et al.* (2011, pp. 81, 82) under the names of *Cyclaster danicus* and *C. bruennichi*. The oldest available name for these small representatives is *Brissopneustes danicus*. Schlüter (1897, p. 22) noted that the subanal fasciole was well developed but that there was no trace of a peripetalous fasciole, an observation corroborated by
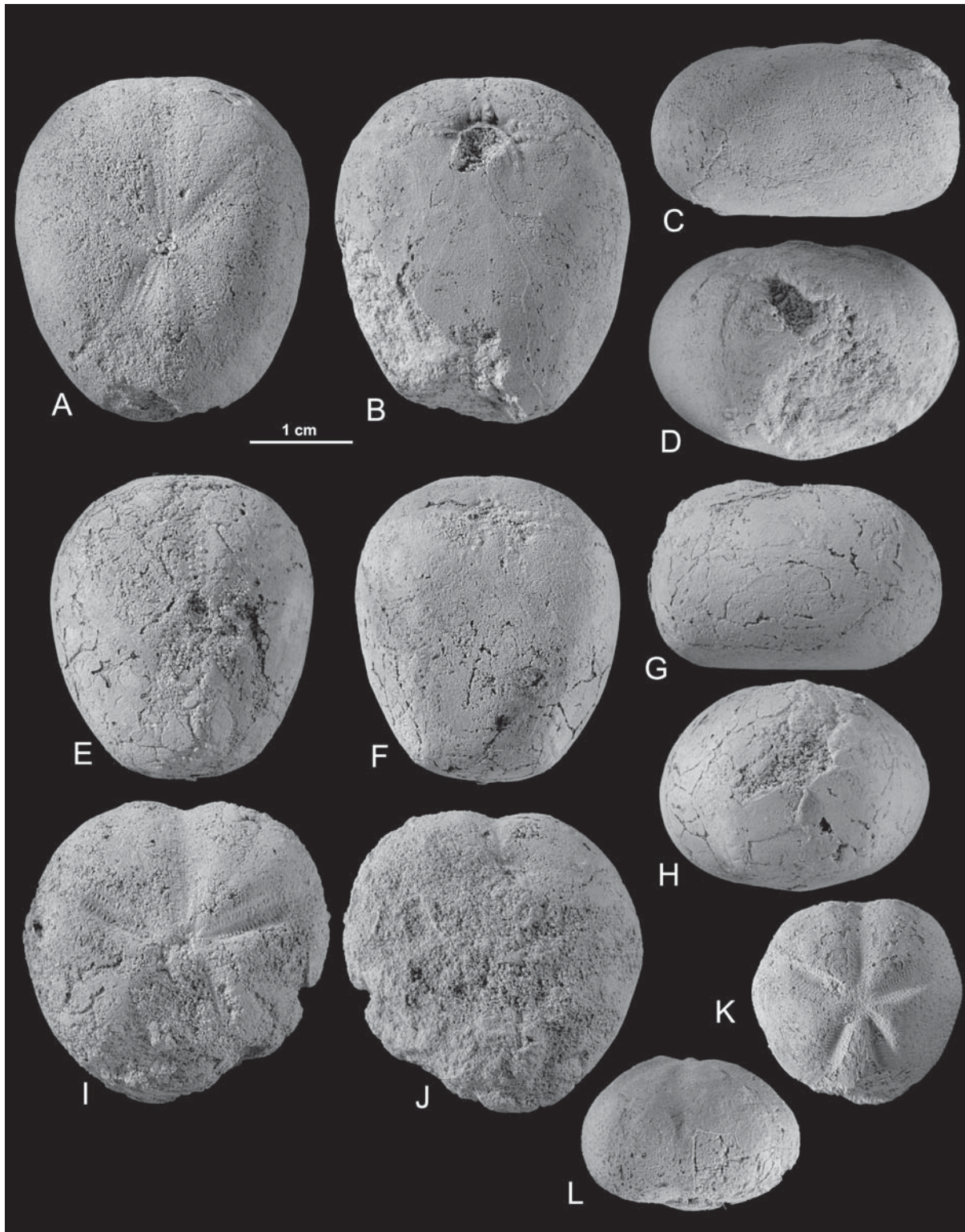
Text-fig. 4. Phosphatic specimens of *Cyclaster danicus* (Schlüter, 1897) (**A-H**) and *Linthia*? sp. (**I-L**), coated with ammonium chloride prior to photography. A-D – ZPAL E.12/1, in apical, oral, left lateral and posterior views, respectively. E-H – ZPAL E.12/2, in apical, oral, right lateral and posterior views, respectively. I, J – ZPAL E.12/5, in apical and oral views, respectively. K, L – ZPAL E.12/6, in apical and anterior views, respectively. All specimens are from Kamienny Dół. Note burrows (*Arachnostega gastrochaenae* Bertling, 1992), best seen in E-I and L

Schneider and Neumann (2013, p. 7) on the basis of a near-pristine individual from Stevns Klint, which has L/W and L/H ratios of 1.16 and 1.61, respectively.

Schneider and Neumann (2013, p. 7) noted that they had reservations about the conspecificity, proposed by Jeffery (1998, table 1), of *Isopneustes integer* Seunes, 1888 and *Brissopneustes danicus* and a few other taxa. In their view, the test of the former was less elongated, much wider anteriorly, had longer petals and a diffuse peripetalous fasciole. Although the Polish specimens lack test material (and any fascioles can therefore not be made out), we concur on the basis of several lots of *C. danicus* from Stevns Klint available to us, as well as a number of erratic flint casts from northern Germany (see e.g., Neumann 2006; Polkowsky 2014). *Cyclaster integer* (see Jeffery 1998, table 1, appendix 2) was stated to have a complete peripetalous fasciole (see also Smith and Jeffery 2000, p. 314), whereas such is, when at all present, very diffuse and restricted to the ends of the posterior petals in *C. danicus*. The original illustrations of *Isopneustes integer* in Seunes (1888) are very schematic; there is much need for good photographs of topotypical material and camera-lucida drawings of test details. In addition, analyses of 'populations' from a wide range of facies types across Europe and into Central Asia are called for. Until such time, we therefore use the specific epithet *danicus* for this type of *Cyclaster* from the Boreal or Temperate Realm of northern Europe.

The only other Boreal congener, *Cyclaster suecicus* (Schlüter, 1897), from the lower to middle Danian of Denmark and southern Sweden, differs from *C. danicus* in having an inflated upper surface, without a posterior carina and virtually flush and distally open petals of equal length (see Ravn 1927, p. 351, pl. 4, fig. 4, as *Brissopneustes suecicus*; see also Neumann 2006, p. 241, fig. 6). Like *C. danicus*, it lacks a peripetalous fasciole.

Jeffery (1998; see also Jeffery 1997) and Smith and Jeffery (2000) also revised other members of *Cyclaster*, most of them Tethyan in distribution (southern Europe, Mediterranean region and into Central Asia), but a number of these (e.g., those from Crimea, the central Caucasus, Kazakhstan and Turkmenistan) appear rather allied to Boreal/Temperate assemblages as a comparison of associated biota (molluscs in particular, and non-echinoid echinoderms) shows. Briefly, these are their conclusions:

Smith and Jeffery (2000, p. 314) characterised *Cyclaster integer* (which they considered to be a senior synonym of both *Brissopneustes danicus* and *Cyclaster bruennichi*) as 'Rectangular to coffin-shaped horizontal outline with broad, shallow frontal groove. Inflated, somewhat carinate upper surface. Short, slightly sunken petals of approximately equal length; anterior petals diverge at 115 degrees; pores in petals round in inner series, elongate in outer series. Labrum long and narrow. Sexual dimorphism in gonopore size. Complete peripetalous fasciole.' Those authors noted *C. integer* to have ranged from the (?lower) upper Maastrichtian to the upper Danian, with records (in their view) from the French Pyrenees, Denmark, Azerbaijan, the northern Caucasus and the Transcaspian region, Georgia, Kazakhstan (Mangyshlak) and northwest Madagascar. For the time being, we prefer to interpret *C. integer* as intended by Seunes (1888) until such time that detailed analyses of 'populations', with all growth stages represented, and link to facies distribution, become available.

Cyclaster vilanovae (Cotteau, 1886), from the Danian of Spain and northwest Turkey, has a coffin-shaped outline, either lacking a frontal notch or having a very faint one; inflated in lateral profile and with a carinate upper surface. Paired ambulacra are of equal length, are slightly sunken and have very well-developed elongate pores. Labrum narrow. Peripetalous fasciole indistinct; crowding of granular tubercles at ends of petals (see Smith and Jeffery 2000, p. 313, text-fig. 130E).

Another form, *Cyclaster gindrei* (Seunes, 1888) (Seunes 1888, p. 795, pl. 28, fig. 2, as *Isopneustes gindrei*), from the Danian of the French Pyrenees, northern Spain, Georgia, the northern Caucasus and the Transcaspian region, has a rectangular to coffin-shaped outline with a shallow frontal groove and a highly inflated upper surface with strongly carinate posterior. Petals are short and slightly sunken, having well-developed, elongate pores; anterior petals longer than posterior ones, diverging at 125–130°. Labrum long and narrow; apical system anterior in position; extent of peripetalous fasciole unknown (see Moskvin and Povlavskaya 1959, p. 292, text-fig. 109a, b; pl. 26, fig. 7a–c; Smith *et al.* 1999, p. 120, text-fig. 31b; pl. 8, figs 1–5). The latter authors also recorded it from the lower Maastrichtian of Tercis-les-Bains, Landes (France; see also Jeffery 1998, fig. 7).

The last species, *Cyclaster aturicus* (Seunes, 1888) (Seunes 1888, p. 797, pl. 28, fig. 3, as *Isopneustes aturicus*), from the Danian of the French and Spanish Pyrenees, the lower Danian of Austria, the lower to upper Danian of Georgia, the southern Caucasus, the Transcaspian region and western Kopet-Dagh (Iran), has a coffin-shaped outline with a distinct frontal groove. Its upper surface is highly inflated, carinate; paired petals are long and sunken, with a large num-
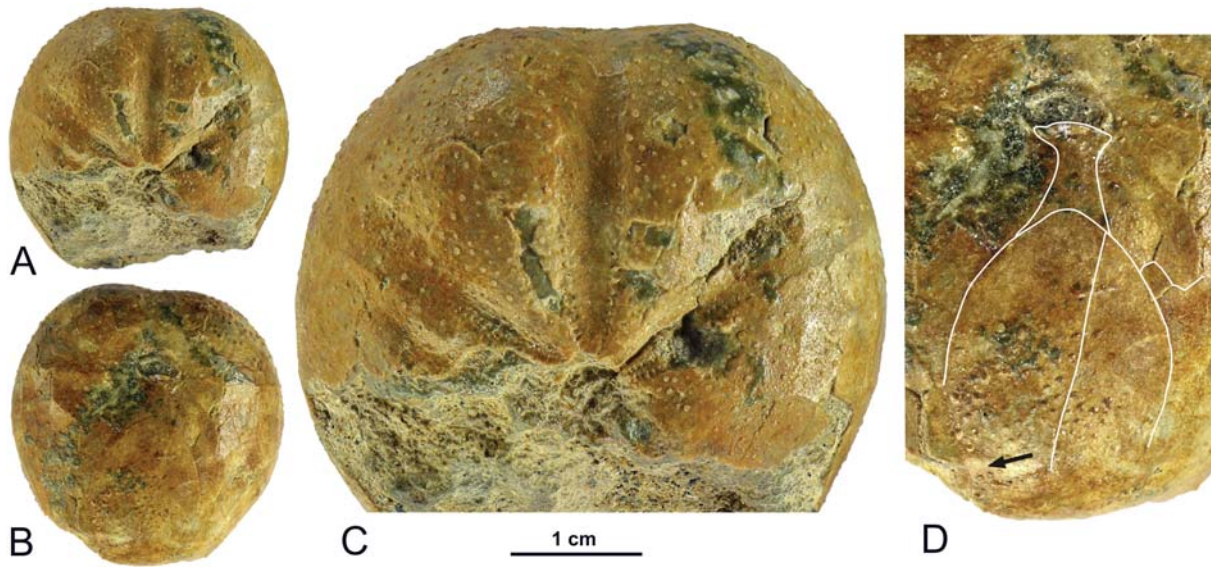
Text-fig. 5. Phosphatic specimen of *Diplodetus vistulensis* (Kongiel, 1950) with well-preserved test material adhering, MZ VIII Ee 1553 from Nasiłów, in apical and oral views (A, B), with detailed views of apical test portion (C), peristome, labral plate and sternum, traces of subanal fasciole (arrowed) and schematic drawing of oral plating (D)

ber of closely spaced, elongate pores; petals of equal length, anterior ones diverging at 125–130°; labrum long and narrow; apical system placed anteriorly, no peripetalous fasciole (Jeffery 1998, fig. 2D–F; Smith *et al.* 1999, p. 124, text-figs 31c, 32; pl. 9, figs 15–17; Smith and Jeffery 2000, p. 312, text-fig. 130A–C; Kroh 2001, p. 404, text-figs 21–23; pl. 9, figs 1–6; pl. 10, figs 1–4).

OCCURRENCE: *Cyclaster danicus*, as here understood, is typical of the lower Danian of eastern and northern Denmark and southern Sweden, where it ranges from the Cerithium Limestone Member into the overlying Korsnæb Member (Ravn 1927; Wienberg Rasmussen 1971; Asgaard 1979; pers. obs.). Erratic material from northern Germany is of the same age and provenance area (Oppenheim 1921; Neumann 2006; Polkowsky 2014). Material from Crimea, the northern Caucasus, Kazakhstan and Turkmenistan (J.W.M. Jagt, pers. obs.) appears to belong here as well, but a revision of specimens assigned in recent years to *C. integer* is awaited.

Genus *Diplodetus* Schlüter, 1900

TYPE SPECIES: *Diplodetus brevistella* Schlüter, 1900, by original designation (Schlüter 1900, p. 364).

Diplodetus vistulensis (Kongiel, 1950)
(Text-fig. 5)

partim *1950. *Micraster vistulensis* Kongiel, pp. 318, 325, pl. 2, figs 5–8 only.
?*partim* 2000. *Diplodetus coloniae* (Cotteau, 1877); Smith and Jeffery, p. 309, text-fig. 129A, B.

MATERIAL: A single specimen, MZ VIII Ee 1553, the holotype of *Micraster vistulensis*, from the Greensand at Nasiłów (leg. R. Kongiel, 1949).

MEASUREMENTS: See Table 1.

DESCRIPTION: MZ VIII Ee 1553 has recently been cleaned, revealing complete phosphatic infill, despite the fact that it preserves half of the test. Ambulacrum III measures 4.2 mm in length, is quite shallow and barely indents ambitus; 18–20 plates to ambitus. Oblique pores with large interporal partition. Anterior petals slightly sunken; inner pores round, outer pores elongate; 20–21 pores; posterior petals and apical system not preserved. Tip of right posterior petal shows traces of diffuse peripetalous fasciole under low-angle light. Peristome rather small, 3.4 mm in width, including rim, with notable lip and rim. Labrum broad based (2 mm), length 3.7 mm, inclusive of lip. Sternum semi-quadrate, suture slightly

oblique, largest tubercles on margins. Traces of sub-anal fasciole, 5–9 miliary tubercles abreast.

DISCUSSION: Petal and sternal structure and the rimmed peristome demonstrate that this form cannot be assigned to *Micraster* Agassiz, 1836. Smith and Jeffery (2000, p. 367) noted that it was 'Most similar in overall appearance to *Diplodetus coloniae*', but that form from the lower Paleocene of the French Pyrenees (Haute Garonne; Cotteau 1877) is much larger, has deeper paired petals and a proportionally much larger peristome (compare Neumann 2006, fig. 7; www.paleotheque.fr/echinodermes/). The Polish form bears a certain resemblance to Smiser's (1935) *Isopneustes eysdenensis* and *I. montensis* from the middle/upper Danian of northeast Belgium, although these have fully-developed peripetalous fascioles, a more elongate test and better-developed paired petals. We doubt that these are synonymous with *D. coloniae*, as proposed by Smith and Jeffery (2000, p. 309). The sternal suture and broad-based labrum, as well as petal structure, distinguish MZ VIII Ee 1553 from species of the genus *Cyclaster*; unfortunately, the apical system (which has 3 gonopores in *Cyclaster* and 4 in *Diplodetus*) is not preserved. For now, we consider this form to be clearly assignable to *Diplodetus*, but the species remains a *nomen dubium*.

OCCURRENCE. Of the various species of late Maastrichtian and early Danian age on record from the type area of the Maastrichtian Stage (Jagt 2000; see also Smith and Jeffery 2000) none is similar. The Polish form, with sparse tuberculation, short and faintly depressed petals and diffuse peripetalous fasciole, may constitute an undescribed species, for which the specific epithet *vistulensis* of Kongiel (1950) is available. For the time being, we consider this to be of Danian age, in view of the fact that it has a complete phosphatic infill similar to that in other specimens from the present material. Preservation of test material in this specimen is remarkable, but some other forms amongst the lot described herein, also retain portions of test, even with tuberculation and traces of fascioles (e.g., Text-figs 3G, H; 4K, L; 6A).

Suborder Paleopneustina Markov and Solovjev, 2001
Family Schizasteridae Lambert in Doncieux, 1905 (?)

Genus *Linthia* Desor, 1853 (?)

TYPE SPECIES: *Linthia insignis* Merian in Desor, 1853, by original designation (Desor 1853, p. 278).

Linthia? sp.
(Text-figs 4I–L; 6A, C)

partim 1950. *Micraster vistulensis* Kongiel, pp. 318, 325 [non pl. 2, figs 5–8 = *Diplodetus vistulensis*, as interpreted herein].
?2009. "*Linthia danica*"; Kahlke *et al*., p. 101, pl. 12 (*nomen nudum*).

MATERIAL: Two specimens (ZPAL E.12/5 and 12/6) from the Greensand of Kamienny Dół and one (MZ VIII Ee 1554) from the same horizon at Kazimierz Dolny, the original of Kongiel (1950, pp. 318, 325; leg. W. Pożaryski, 1949).

MEASUREMENTS: See Table 1.

DESCRIPTION: ZPAL E.12/6 has a wide ambulacrum III forming a shallow sulcus, isopores being flanked by a single large tubercle and up to 20–25 miliaries; anterior and posterior petals diverge at 135º and 50º, respectively; apical system with four gonopores; portions of test preserved and diffuse peripetalous fasciole visible, but no lateroanal one. ZPAL E.12/5 is comparable, but less well preserved (no trace of fasciole). Of MZ VIII Ee 1554, the anterior test portion is well preserved; one primary turbercle per plate and up to 20–25 miliary tubercles; frontal notch very shallow. Peristome and periproct not preserved. Anterior petals have 22–25 pores; no fascioles visible. Posterior petals not preserved. Apical system not preserved.

DISCUSSION: This is a puzzling form that cannot be identified beyond doubt because important features of fasciole(s), test plating and labral and sternal structure are not preserved. Only a single specimen in this lot, ZPAL E.12/6, retains part of the adoral test surface. A rather diffuse peripetalous fasciole can be seen, but there is no trace of any lateroanal one, making placement in *Linthia* questionable. In addition, labral structure cannot be determined. Although not described in detail, there is a match between these Polish specimens and material, of slightly larger size (www.geolsba.dk/echinoids/), from burrow fills inside the Cerithium Limestone Member at the Dania quarry (Mariager Fjord, Jylland, northern Denmark), originating from levels dated as early Danian (*Tylocidaris abildgaardi* Zone) and identified as *Micraster* sp. by Søren Bo Andersen. Of note is that all three illustrated specimens from northern Denmark lack test material and could therefore be representative of some remanié (or lag) assemblage. We do not know of any
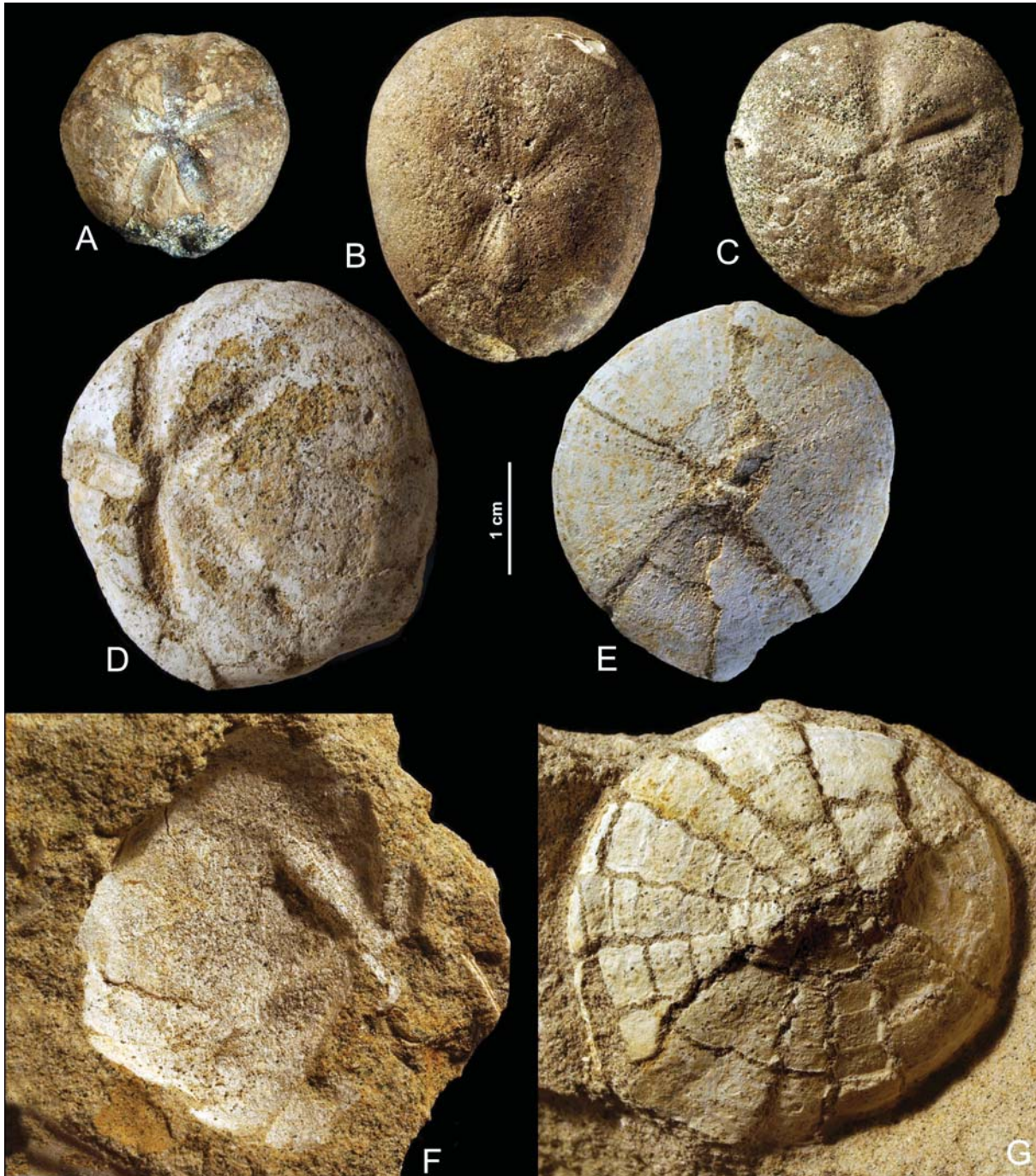
Text-fig. 6. Members of two Danian echinoid assemblages from the Greensand and lowermost Siwak. Phosphatic moulds of *Linthia*? sp. (**A**, **C**) and *Cyclaster danicus* (Schlüter, 1897) (**B**), compared to specimens in 'ghost preservation' of *Pseudogibbaster* cf. *depressus* (Kongiel in Kongiel and Matwiejewówna, 1937) (**D**, **F**) and *Echinocorys* ex gr. *depressa* (von Eichwald, 1866) (**E, G**). A – ZPAL E.12/6 from Kamienny Dół, in apical view (see Text-fig. 4K, L). B – ZPAL E.12/1 from Kamienny Dół, in apical view (see Text-fig. 3A–D). C – ZPAL E.12/5 from Kamienny Dół, in apical view (see Text-fig. 4I, J). D, F – ZPAL E.12/17a, b from Bochotnica, in oblique apical view (part and counterpart). E – ZPAL E.12/16 from Nasiłów. G – ZPAL E.12/19 from Kamienny Dół, 0.2 m above phosphorite layer, E and G both in apical view. All specimens uncoated

comparable material from the Stevns Klint section. Erratic internal moulds (Kahlke *et al.* 2009) from the Limfjord area (northern Denmark) may also be closely related, if not conspecific.

OCCURRENCE: In the lower Danian of the Maastricht area (southeast Netherlands/northeast Belgium), schizasterids are comparatively common. Van der Ham (1988, p. 155, pl. 9, figs 6–8) recorded *Linthia*(?) *breviuscula* (d'Orbigny, 1855) and *Linthia* sp. (spp.), which Smith and Jeffery (2000) referred, at least in part, to *Paraster sindensis* (Duncan and Sladen, 1882). In Upper Cretaceous strata of northern and eastern Europe, schizasterids are extremely rare, which probably is a facies-controlled issue. Only from the lower Paleocene onwards do representatives of *Linthia* become commoner. Species of *Linthia* have been recorded, albeit rarely, from the upper Danian of Austria (Kroh 2001, 2003, 2004), northeast and southern Belgium (Cotteau 1879; Smiser 1935; pers. obs.) and the Paris Basin (France; Roman 1989). Other schizasterids have been described from the upper Danian of Denmark (Asgaard 1979; Gravesen 1979; Neumann 2006; www.geolspb.dk).

AGE OF THE PHOSPHATIC ASSEMBLAGE

As noted previously, the phosphatic echinoid assemblage described above is new to the Kazimierz Dolny area and is composed of elements that are conspecific or closely affiliated with Danian forms from northern and eastern Europe (Denmark, Crimea, the southern Russian Platform and further afield). In particular, the new assemblage appears to find its best match with that from the Cerithium Limestone Member (Rødvig Formation) and the lower part of the overlying Korsnæb Member (Stevns Klint Formation) in Denmark (see Surlyk *et al.* 2006 for lithostratigraphy). In both units *Cyclaster danicus* predominates, being commonly found in burrows piping down from the lowermost part of the Korsnæb Member into underlying Danian and upper Maastrichtian deposits (Wienberg Rasmussen 1971; Asgaard 1976). With the exception of *Diplodetus vistulensis*, all other taxa in the present material (micrasterids, hemiasterids and ?schizasterids) have counterparts in lower Danian strata in Denmark.

It should be noted that the Korsnæb Member is replete (Gravesen 1993) with remains (spines, tests and test portions) of psychocidarids (*Tylocidaris oedumi* Brünnich Nielsen, 1938 and *T. abildgaardi* Ravn, 1928). In contrast, with the exception of two psychocidarid spines (Gravesen 1979, 1993) and a record of a phymosomatid, *Phymosoma* (Rosenkrantz 1940), no regular echinoids are known from the Cerithium Limestone Member in Denmark. The Greensand in the Kazimierz Dolny area has not yielded any psy-

chocidarids at all. However, this cannot be used for a more precise correlation between Denmark and Poland in view of the fact that psychocidarid remains are totally missing from the entire Danian succession in the Kazimierz Dolny area. In contrast, these are abundant in Danian glauconitic sands penetrated in the Boryszew borehole near Sochaczew, c. 200 km northeast of Kazimierz Dolny (Kongiel 1958; Rosenkrantz 1964). In view of the close facies similarity between the Boryszew sands and the Greensand and Siwak of the Kazimierz Dolny area, the absence of psychocidarids in the latter cannot be satisfactorily explained for now.

TAPHONOMY OF THE PHOSPHATIC ASSEMBLAGE

General characteristics

The material studied is preserved as phosphatic internal moulds (Text-figs 3–5, 6A–C), occasionally with more or less phosphatised test material still adhering to their surface (e.g., Text-figs 5, 6A). Some moulds are entirely devoid of test material (e.g., Text-figs 3, 6B, C). In other specimens partial test plating is preserved; two intergradational types are seen: the first retaining the outer test surface with primary and miliary tubercles (e.g., Text-figs 5A–D, 6A) and the second with abraded external stereom and exposure of the underlying, partially galleried stereom (e.g., Text-fig. 3A). The colour of the moulds ranges from dark brown to black. In cases when test material is well preserved, it is usually lighter than the internal mould, as exemplified by the rich amber hue of *Diplodetus vistulensis* (Text-fig. 5A–D) and the light brown test of *Linthia*? sp. (Text-fig. 6A). These differences presumably reflect weaker phosphatisation of the tests in comparison to their sedimentary infills.

All specimens studied are three-dimensionally preserved, with no evidence of compactional deformation, which suggests that they formed during early stages of diagenesis ('pre-fossilised' moulds *sensu* Kennedy and Garrison 1975). In contrast, many unphosphatised Danian fossils in the Greensand and Siwak, including echinoids (Text-fig. 6D–F), are crushed by compaction. A number of phosphatised specimens in the present lot are worn and/or fragmentary (e.g., Text-fig. 6B, C). The worn and/or broken surfaces do not appear fresh in most cases and are therefore interpreted to be the result of hydrodynamic damage of the specimens on the sea floor. A specimen of *Cyclaster danicus* with fresh damage
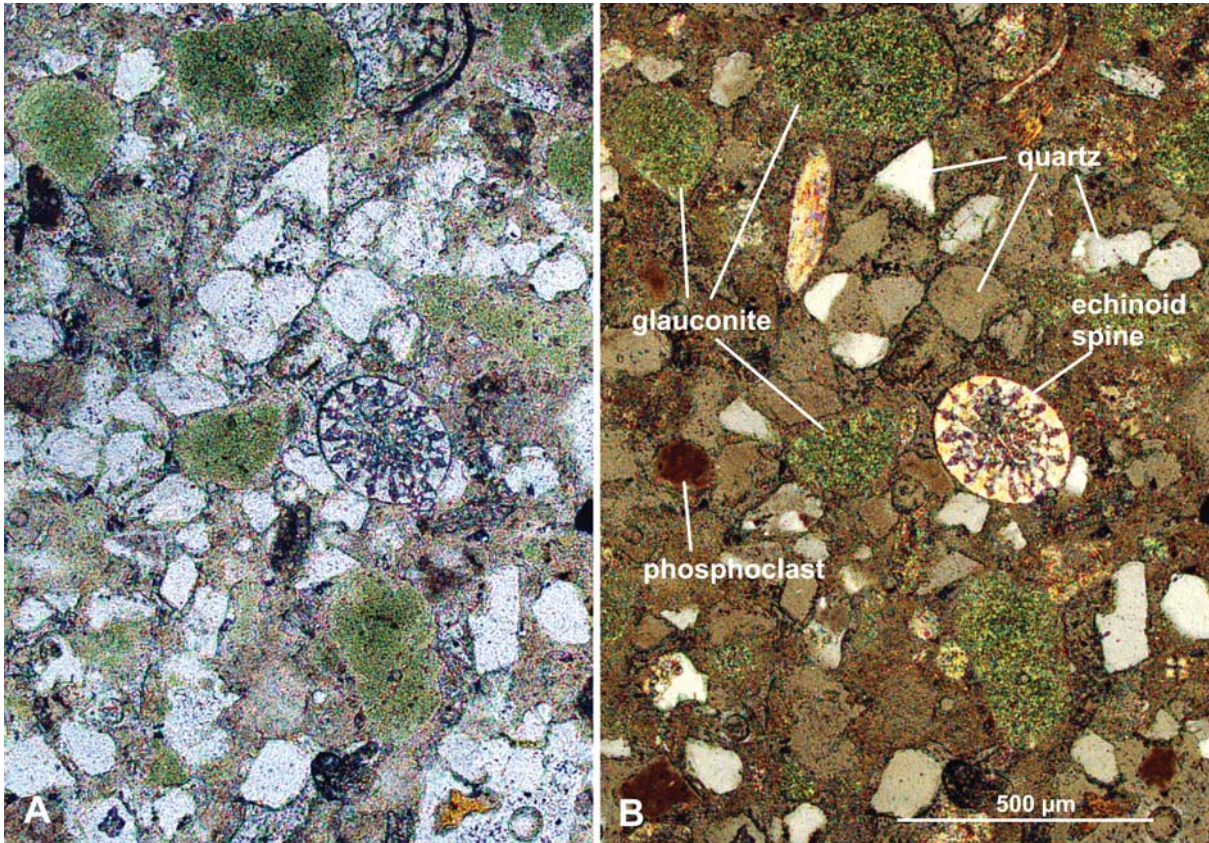
Text-fig. 7. Thin section of the phosphatic infill of a specimen of *Bolbaster* sp. (ZPAL E. 12/8) from Kamienny Dół. A – nicols uncrossed. B – nicols crossed

(Text-fig. 4A–D) is an exception, this having been accidentally hit by hammer during its recovery.

The external surfaces of all available moulds and a thin section of an individual of *Bolbaster* sp. (ZPAL E.12/8), have been examined for infill petrography. It turns out that the internal matrix of all specimens studied consists of phosphatised glauconitic sandstone (Text-fig. 7A, B), which is identical in terms of grain composition and proportions to the matrix of the glauconitic sandstone that the specimens were recovered from. This is a phosphatic quartz-glauconite packstone composed of angular quartz, glauconite, tiny phosphatic intraclasts and skeletal elements, including echinoid spines and tests of foraminifera (Text-fig. 7A, B; for detailed petrographic descriptions and illustrations of the glauconitic sandstone see Pożaryska 1952; Świerczewska-Gładysz and Olszewska-Nejbert 2006).

No data on the original orientation of the specimens within the sediment, a fact that may be of key importance in deciphering the nature of fossil echinoid accumulations (Kudrewicz 1992; Kudrewicz and Olszewska-Nejbert 1997; Olszewska-Nejbert 2005), are available for the present material. Most specimens were collected from naturally weathered Greensand residues on scree slopes at outcrops.

Epibionts, so typical of many echinoid shells or moulds in various settings (e.g., Kudrewicz 1992; Donovan *et al.* 2014) are missing in the present material, except for an adherent benthic foraminifer ('*Bullopora*' sp.) in ZPAL E.12/1 (see Text-figs 4A, 6B, right-hand margin), which attached to the inner surface of the test prior to this being infilled, and became visible only after removal of the test.

Ichnology of echinoid internal moulds

Irregular networks composed of minute meandering and branching tunnels are visible on the surface of several moulds (e.g., Text-figs 3I, M, N, 4E–H). In addition, a single, gently curved tunnel of much larger diameter is visible in one of the moulds (Text-fig. 3L,

O, P). We interpret these structures as trace fossils, notably burrows, produced by vermiform coelobiotic deposit-feeding organisms, possibly polychaetes. The ichnotaxon *Arachnostega gastrochaenae* Bertling, 1992 is available for such networks (Bertling 1992; Vinn *et al.* 2014) and the single burrow of larger diameter may be identified as *Planolites beverleyensis* (Billings, 1862) (compare Donovan *et al.* 2014; Van den Ende and Donovan 2014).

These *Arachnostega* and *Planolites* burrows would have collapsed had they been produced in soft sediment and we interpret them as having been made in a cohesive substrate, at an early stage of progressive hardening of the echinoid infills. Ingress to the sediment inside of the echinoid tests was presumably through the natural openings of the dead test (i.e., peristome, periproct). In accordance to an opportunistic feeding programme (Bertling 1992), the burrow makers were closely following the internal surface of the tests. After test removal by abrasion, the burrows became visible as unroofed half tunnels on the surface of the moulds. Similar tunnels on the surfaces of cephalopod phosphatic steinkerns from the Upper Cretaceous Miria Formation of Western Australia have been interpreted as borings by Henderson and McNamara (1985). However, we favour an interpretation as burrows, at least for our material, given the high detrital quartz content of the moulds studied, which would possibly prohibit any activity of potential borers. In summary, there is no evidence for borings in the material studied, neither on the moulds nor on preserved test surfaces.

Genetic interpretation

In spite of the absence of borings and epibionts into/on the phosphatic moulds studied, their general habitus (phosphatisation, lack of compaction, abrasion, fragmentation of some specimens) suggests that they represent early-diagenetically hardened material ("pre-fossilised moulds"), subsequently disinterred by scour and reworked on the sea floor (compare Kennedy and Garrison 1975; Fürsich *et al.* 1981). The fact that the internal matrix of the moulds is identical to that of the surrounding sediment demonstrates, in turn, that the moulds underwent reworking in the same depositional environment they were formed in. In other words, they represent intraformationally reworked rather than remanié material that was derived from an older substrate of different lithology. Redeposited remanié echinoid moulds and tests have also been described from the Upper Cretaceous of the Kraków area in southern Poland, specifically from the

Turonian of Wielkanoc quarry by Olszewska-Nejbert (2005) and from the Santonian of Korzkiew by Kudrewicz (1992; see also Kudrewicz and Olszewska-Nejbert 1997).

Localised phosphatisation of the sediment infills of the echinoid tests possibly took place prior to their erosional disinterment, some distance below the sediment/water interface under conditions of low net sedimentation (compare Trappe 1998). The phosphatisation of the sediment inside the echinoid tests could have been triggered by decay processes of the echinoid soft tissues (Kudrewicz 1992), which possibly also attracted coelobitic producers of the burrows described above.

In summary, the succession of events which led to the formation of the echinoid moulds may be described as follows: (1) infilling of tests of dead echinoids with glauconitic sand; (2) penetration of infills by coelobiotic deposit-feeding organisms, possibly polychaetes; (3) early-diagenetic cementation of infills by calcium phosphate under conditions of low sedimentation rate; and (4) exhumation and intraformational reworking of specimens by hydrodynamic agents, leading to abrasion, fragmentation and spalling off of test material.

OTHER GREENSAND ASSEMBLAGES AND THEIR TAPHONOMY

The phosphatised Danian specimens which form the focus of our paper, are not the only echinoid fossils known from the Greensand. Generally, echinoids are subordinate elements of the Greensand fauna, except for ubiquitous tiny spines of regular echinoids (chiefly phymosomatids). More or less complete tests in various states of preservation are rare (Kongiel 1950; Machalski and Walaszczyk 1987). Not all specimens seen can be assigned a precise age and provenance, either due to insufficient preservation or problems with taxonomic identification. Moreover, not all specimens from the Greensand and Siwak recorded in the older literature have survived to this day and therefore cannot be assessed in terms of taxonomic position and taphonomic pathways that they were subjected to. This is best exemplified by the holasteroid *Pseudoananchis rydzewski* Kongiel, 1936 (illustrated as *species nova* by Kongiel 1935, pl. 1, fig. 3a–c), which is based on a single specimen from Bochotnica with a poorly preserved test. We did not come across this specimen when screening the MZ collections and, therefore, consider it lost. Its original descriptions and (rather poor) illustrations

do not allow any firm conclusions as to taxonomic attribution, age and taphonomy. In spite of these drawbacks, our collections (partially presented in Machalski and Walaszczyk 1987), combined with a re-examination of previously recorded specimens of Kongiel (1950), still preserved in the MZ collections, allow the identification of two additional assemblages amongst Greensand echinoids, which are characterised below.

Danian unphosphatised assemblage

These are unphosphatised specimens (five in total) of micrasterids (ZPAL E.12/17) and echinocorythids (ZPAL E.12/16, 18, 24), as well a single phymosomatid (ZPAL E.12/15, not illustrated herein). Their distinguishing character is a kind of 'ghost preservation', with yellowish white, powdery and crushed sandstone moulds, with few or no details of tuberculation and/or test plating (Text-fig. 6D–G). The phymosomatid is indeterminate generically, but the micrasterids (Text-fig. 6D, F) may be tentatively identified as *Pseudogibbaster* cf. *depressus* (Kongiel in Kongiel and Matwiejewówna, 1937) and the echinocorythids (Text-fig. 6E, G) as *Echinocorys* ex gr. *depressa* (von Eichwald, 1866). These are middle to late Danian taxa that are known from Poland and some localities further to the east and southeast, into Central Asia (Kongiel 1949; Moskvin and Poslavskaya 1959; Ali-Zade *et al.* 1988). They occur fairly commonly throughout the whole Siwak succession in the Kazimierz Dolny area (Kongiel and Matwiejewówna 1937; Kongiel 1949). Tests of individuals from the Greensand are always lost by dissolution, a preservation typical also of some intervals of the overlying Siwak (e.g., Text-fig. 6G). In other portions of Siwak, however, the same taxa are represented by much better-preserved specimens with intact tests, as exemplified by a suite of complete specimens collected at Parchatka (Text-fig. 8A–D).

Danian echinoids in 'ghost preservation' were first recorded from the Greensand by Machalski and Walaszczyk (1987), their *Diplodetus depressus* (their pl. 3, fig. 5) being here assigned to *Pseudogibbaster* cf. *depressus* (Text-fig. 6D, F). Machalski and Walaszczyk (1987) interpreted these fossils as constituents of a Danian indigenous fauna, post-dating the phosphates, and we here concur with this view. These echinoids, along with other unphosphatised Danian fossils, mostly bivalves and gastropods (Krach 1974, 1981), colonised the sea floor after more continuous sedimentation resumed, heralding the onset of typical gaize deposition of the Siwak.

Late Maastrichtian assemblage

In contrast to the Danian echinoid assemblages, the Maastrichtian assemblage is heterogeneous as far as preservation of specimens is concerned. The commonest elements of the late Maastrichtian association are isolated spines and test plates of cidarids, including *Temnocidaris* (*Stereocidaris*) ex gr. *herthae* (Schlüter, 1892) and spines of phymosomatids that are assignable to *Phymosoma granulosum* (Goldfuss, 1829) *sensu* Schlüter *et al.* (2012); both species are widely distributed in northern and central Europe. The above-mentioned taxa are present in our own collections from the Greensand, and also in the MZ collection. We interpret them as derived late Maastrichtian fossils, a view supported by the fact that they are occasionally entombed in soft opoka shreds that 'float' in the Greensand (see above).

In addition to isolated skeletal elements, four late Maastrichtian specimens in test preservation were available for the present study, all housed in the MZ collections. These are discussed as follows:

(1) Two specimens of the saleniid *Pleurosalenia bonissenti* (Cotteau, 1866) [*sensu* Lambert 1898] (MZ VIII Ee 836; MZ VIII Ee 1575), which were previously recorded by Kongiel (1950) and Mączyńska (1989), respectively. Specimen MZ VIII Ee 1575 is from the Greensand at Nasiłów (illustrated in Kongiel 1950, pl. 1, figs 1–4). It is a well-preserved test, damaged in some spots, with sedimentary infill visible through the peristome. This infill is identified as a yellow, very soft opoka, pointing to its derivation from the top of the Kazimerz Opoka. This is a typical sort of infill of many derived late Maastrichtian fossils from the Greensand (Machalski 1998). Another individual of *Pleurosalenia bonissenti*, MZ VIII Ee 836 (illustrated by Mączyńska 1989, pl. 188, fig. 6a–c), is from the Greensand at Bochotnica. The specimen is in an excellent state of preservation and, at first sight, looks like an indigenous Maastrichtian fossil, an impression supported by the presence of soft glauconitic sand, which is seen through the peristome. However, careful scraping of this sediment along the margin of peristome has revealed the presence of a soft opoka underneath the test surface, which demonstrates that the specimen is derived from the Maastrichtian opoka as well. It was possibly gently washed or excavated by burrowing organisms, its original infill partially removed and replaced with glauconitic sediment, giving a false impression of an *in situ* Maastrichtian fossil in the Greensand. We have frequently observed similar phenomena amongst Greensand fossils from Bochotnica, including articulated individuals of the undoubtedly
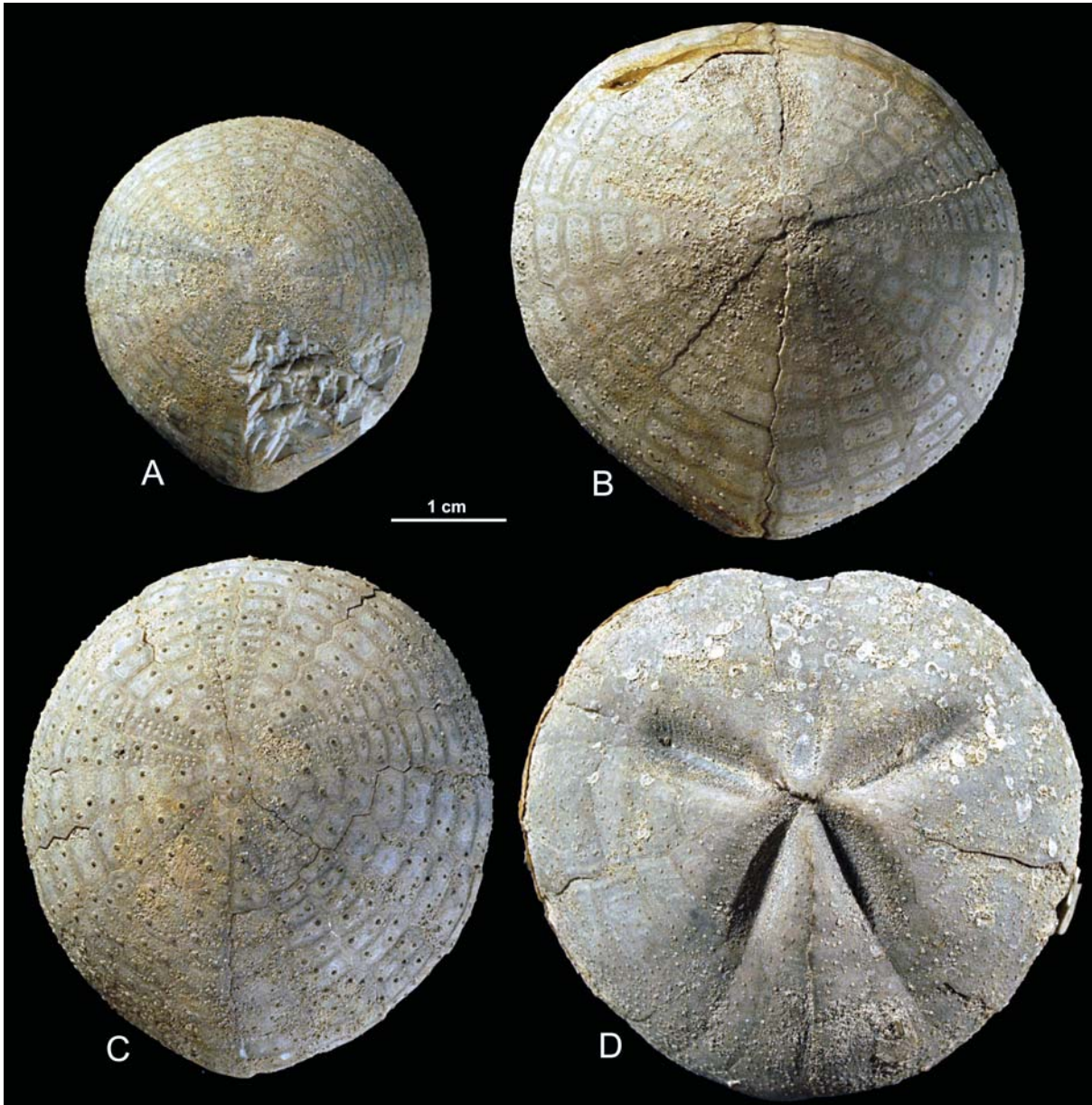
Text-fig. 8. Test preservation of *Echinocorys* ex gr. *depressa* (von Eichwald, 1866) (**A–C**) and *Pseudogibbaster* cf. *depressus* (Kongiel in Kongiel and Matwiejewówna, 1937) (**D**) from the middle/upper Danian Siwak at Parchatka (see Text-fig. 1B for location map), all in apical view. A – ZPAL E.12/23. B – ZPAL E.12/20. C – ZPAL E.12/22. D – ZPAL E.12/21 (note oyster spat on anterior portion of test)

Maastrichtian terebratulid brachiopods *Carneithyris carnea* (J. Sowerby, 1813) and *Neoliothyrina obesa* (Sahni, 1925), which are almost entirely infilled with glauconitic sand, except for a small plug of opoka left in their umbonal cavities. *Pleurosalenia bonissenti* definitely is of (early and late) Maastrichtian age, with records from southern and northeast Belgium, northwest France, east-central Poland, northern Germany and northern Spain (Jagt 2000).

(2) A single specimen of *Gauthieria*(?) *pseudoradiata* (Schlüter, 1883) from Nasiłów was described by Kongiel (1950, p. 314, pl. 1, figs 5–8; *G. pseudoradiata* according to Jeffery 1997); it is now registered as MZ VIII Ee 1576. This is a relatively well-preserved test of a very small (juvenile?) individual, with almost black phosphatic infill, visible through the peristome. However, the petrographic composition of the infill cannot be precisely determined due to small area

which is available for examination. *Gauthieria pseudoradiata* is also a definitively Maastrichtian taxon, recorded from Mangyshlak (Kazakhstan), the Isle of Rügen, Belgium, the Netherlands, and Denmark (Jeffery 1997; Jagt 2000).

(3) The single specimen of *Hemicara pomeranum* Schlüter, 1902, registered as MZ VIII Ee 840, the holotype of *Echinogalerus bochotnicensis* Kongiel, 1950 (Kongiel 1950, pl. 2, figs 1–4), is from the Greensand at Bochotnica (see also Mączyńska 1989, pl. 191, fig. 7a, c, d [b missing]). The specimen is preserved as an incomplete test infilled with a pale brown, slightly phosphatised sandy opoka, comparable to the infills of many *ex situ* Maastrichtian fossils present in the Greensand (Machalski and Walaszczyk 1987; Machalski 1998; Świerczewska-Gładysz and Olszewska-Nejbert 2006), which points to its derived nature. This rare and interesting echinoid species is of an undisputed late Maastrichtian date, with records from northern Germany and east-central Poland (Mączyńska 1972; Neumann 2006). The only other specimen of *H. pomeranum* known from the study area is from the Kazimierz Opoka at Bochotnica and was first described by Kongiel (1935, pl. 2, fig. 7a–c) and subsequently by Mączyńska (1972, text-figs 1–9, pls 1–3; reillustrated by Mączyńska 1989, pl. 193, fig. 3a–e).

In summary, the preservational styles and inferred taphonomic pathways of the late Maastrichtian assemblage from the Greensand are compatible with previous views that the late Maastrichtian fauna from this unit consisted exclusively of derived fossils (Machalski 1998; Świerczewska-Gładysz and Olszewska-Nejbert 2006). No indigenous echinoid specimens of late Maastrichtian age have been identified in the Greensand material during the present study.

SEDIMENTOLOGICAL IMPLICATIONS

Generally speaking, the occurrence of these three echinoid assemblages of different age and preservation/provenance in the Greensand of the Kazimierz Dolny area, documented in the present work, is compatible with previous interpretations of this unit as a condensed basal transgressive deposit of Danian age, which contains an admixture of late Maastrichtian and Danian fossils (Krach 1974; Machalski and Walaszczyk 1987; Hansen *et al*. 1989; Machalski 1998; Świerczewska-Gładysz and Olszewska-Nejbert 2006). These are features typical of transgressive lags in shallow-marine settings (Kidwell 1991; Wilmsen

2012), which form under conditions of low net sedimentation and contain time-averaged assemblages composed of fossils in various states of preservation. The fossils may have been eroded from older highstand strata and/or may represent biota that are indigenous of transgressive environments (Kidwell 1991; Wilmsen 2012).

As discussed earlier in the present paper, the phosphatised Danian echinoid assemblage consists of specimens which underwent *in situ* reworking. According to Asgaard (1976), clearly reworked echinoid specimens, including ubiquitous *Cyclaster danicus*, occurred current swept into open crustacean burrows in the basal Danian hardground that truncates the Cerithium Limestone basins and intervening crests of upper Maastrichtian bioherms at Stevns Klint, Denmark (see Wienberg Rasmussen 1971, fig. 1; Bromley 1975, fig. 18.10, for illustrations depicting the topography of the boundary interval at Stevns Klint). In the Dania quarry at Mariager Fjord (Jylland, northern Denmark), reworked specimens of *Cyclaster danicus*, often preserved as internal moulds with no tests, belong to the commonest fossils just above the K/Pg hardground (Asgaard 1976). Specimens that are comparable to the Polish *Linthia*? sp. (see above), from burrow fills inside the Cerithium Limestone Member at the Dania quarry, are similar in terms of preservation. In both Danish settings, this hardground corresponds to Sequence Boundary 2, marking a significant fall in sea level during the early Danian (Surlyk 1997, fig. 5). According to Machalski *et al*. (2016, fig. 16; see also Racki *et al*. 2011), the above-mentioned hardground and sequence boundary in Denmark may be correlated with the burrowed surface at the top of Kazimierz Opoka in the study area. The lowermost levels of the overlying bryozoan limestones in Denmark (i.e., Korsnæb Member, Stevns Klint Formation) and the Polish Greensand may thus be regarded as roughly coeval. The presence of intraformationally reworked echinoids was therefore typical of the early phases of the Danian sedimentary cycle (Sequence 2 of Surlyk 1997), both in Poland and Denmark.

The echinoid moulds described here are composed of phosphatised glauconitic sandstone, identical to the surrounding Greensand sediment, except for the phosphatisation of the intergranular matrix. This is an important observation within the context of a previously formulated hypothesis that the Danian phosphatised fossils in the Greensand are derived from a limestone unit, now lost, which was the facies equivalent of the Danish Cerithium Limestone (Machalski 1998). This idea was born based on SEM observations of the infill of a belemnitellid alveolus that appeared similar to

the distinctive Cerithium Limestone matrix (Hansen *et al.* 1989, fig. 5). All our moulds are infilled with phosphatised glauconitic sandstone, entirely different from the fine crystalline matrix of the Cerithium Limestone which is dominated by calcareous dinocysts (Machalski and Heinberg 2005). In summary, our results are incompatible with the "Cerithium Limestone in Poland" hypothesis of Hansen *et al.* (1989) and Machalski (1998).

SUMMARY

A new echinoid assemblage, comprising specimens of *Bolbaster* sp., *Cyclaster danicus*, *Diplodetus vistulensis* and *Linthia*? sp. in a phosphatic preservation, is described from the basal Danian Greensand in the Kazimierz Dolny area, central Poland.

The present assemblage is presumably of early Danian age, with *Cyclaster danicus* (= *Brissopneustes danicus*, *C. bruennichi*) being typical of lower Danian strata in Denmark and southern Sweden, and other forms also closely affiliated with echinoid taxa from Denmark.

The echinoids occur as internal moulds, occasionally with some test material adhering. The moulds are composed of phosphatised glauconitic sandstone, identical in grain support to the Greensand sediment which they have been recovered from.

The origin of the moulds involved: (1) infilling of tests of dead echinoids with glauconitic sand; (2) penetration of infills by coelobiotic deposit-feeding organisms, possibly polychaetes, whose burrows (ichnogenera *Arachnostega* and *Planolites*) were produced along the inner surface of tests; (3) early-diagenetic cementation of infills by calcium phosphate under conditions of low sedimentation rates; and (4) disinterment and intraformational reworking of specimens by scour, leading to abrasion, fragmentation and loss of test material in some individuals.

Co-occurring with the phosphatic echinoids are unphosphatised sandstone moulds of *Echinocorys* ex gr. *depressa* and *Pseudogibbaster* cf. *depressus*, which represent another, probably younger (middle to late) Danian echinoid assemblage.

The presence of remanié specimens of late Maastrichtian echinoids, e.g., *Temnocidaris* (*Stereocidaris*) ex gr. *herthae*, *Pleurosalenia bonissenti* and *Hemicara pomeranum*, is also confirmed for the Greensand, based on new material and re-examination of specimens previously recorded in the literature.

This late Maastrichtian assemblage is heterogeneous in terms of preservation. This concerns mainly the infill of tests, which ranges from unphosphatised soft opoka, through slightly phosphatised sandy opoka to black phosphatic deposit rich in glauconite and quartz. This variation in preservational states of late Maastrichtian echinoids reflects variable provenance and taphonomic pathways of particular specimens.

Members of three echinoid assemblages of different age and preservation are now buried together in the Greensand, a situation which is compatible with former interpretations of this unit as a condensed, transgressive lag with mixed faunas of different age and provenance.

The glauconitic sandstone infills of the phosphatic echinoids are incompatible with the previously formulated hypothesis that the phosphatised Danian fossils that occur in the Greensand are derived from a limestone unit, now gone, that was considered to be a facies counterpart of the lower Danian Cerithium Limestone of Denmark.

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