

A new *Pseudogibbaster* Moskvín, 1983 (Echinoidea, Spatangoida) from the mid Danian (Paleocene) deep-shelf chalk of Denmark

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ABSTRACT:

Neumann, C. 2026. A new *Pseudogibbaster* Moskvín, 1983 (Echinoidea, Spatangoida) from the mid Danian (Paleocene) deep-shelf chalk of Denmark. *Acta Geologica Polonica*, **76** (2), e82.

During the mid Danian, deep-water chalk accumulated in the central parts of the Danish Basin, which harboured a markedly impoverished macrobenthos fauna. Among the seven echinoid taxa recorded so far, five are atelostomates belonging to the deposit feeder guild. Here, a new species of the micrasterid echinoid genus *Pseudogibbaster* Moskvín, 1983, *P. herkstroeteri*, is erected to accommodate a single, moderately large-sized, fairly well-preserved test from Dalbyover, in northern Jutland, the only locality where mid-Danian deep-water chalk from the central part of the Danish Basin can be accessed. This is the first record of the genus from the Paleocene of NW Europe. Features that distinguish the new taxon from its congeners are the relatively large size, rectangular test profile and conspicuously large and countersunk phylloidal pores. The latter corresponded with large penicillate podia and are interpreted as an adaptation to the nutrient-deficient bottom conditions by optimizing the ability of bulk sediment feeding.

Key words: Echinoidea; Spatangoida; Danish Basin; Danian; Chalk; New species; *Pseudogibbaster herkstroeteri* sp. nov.

INTRODUCTION

During the Cretaceous-Paleogene transition, the Danish Basin was a cool-water epicontinental marine basin in what is now Denmark, extending into adjacent parts of the North Sea and Southern Scandinavia. Following a regressive phase across the K/Pg boundary, an early Danian transgression initiated a long overall highstand through the Danian until a marked change at the Danian–Selandian transition. In the mid Danian, bryozoan mounds and cold-water coral reefs flourished in some places along the basin margin and hosted diverse macrobenthos communities (Surlyk 1997; Lauridsen and Bjerager 2014). In the deeper parts of the basin centre, however, pelagic nannoplankton ooze accu-

mulated, which harboured an impoverished macrobenthos fauna (Lauridsen *et al.* 2019). Those distally located successions of deep-water chalk have received little attention, all workers focusing on the lowermost Danian (Johansen 1989; Håkansson and Thomsen 1999; Kjaer and Thomsen 1999). Therefore, it is not surprising that neither Ravn (1927) nor Asgaard (1979) mentioned echinoids from the central Danish Basin. The chalk quarry at Dalbyover, 20 km to the north-east of Randers in the north of the Danish Jutland Peninsula, is the only place where mid-Danian deposits of the basin centre are accessible for study. Based on bulk samples, Lauridsen *et al.* (2019) analysed the macrobenthos fauna of the Dalbyover section. They found only 22 taxa and among these, only two echinoids, the



salenid *Salenia pygmaea* (v. Hagenow, 1840) and the very common holasteroid *Echinocorys sulcata* (Goldfuss, 1829–31), the latter being also the most abundant macrofossil. Furthermore, they mentioned indeterminable fragments and spines of regular echinoids. It is thanks to the active collecting efforts of amateur palaeontologists in recent times that the list of echinoids found in Dalbyover has been extended. Ladwig (2009, 2012) reported five additional taxa: the phymosomatoid *Phymosoma* sp., the hemiasterid *Bolbaster* sp. [most likely *B. stella* (Morton, 1830)], the schizasterid *Linthia* sp. and two micrasterids, i.e., *Cyclaster suecicus* (Schlüter, 1897) and *Diplodetus coloniae* (Cotteau, 1877), now presenting the picture of a moderately diverse echinoid community. It is likely that more echinoid taxa, previously unknown from Dalbyover, could be found in various private collections scattered throughout the region. Within one of these, the Ingo Herkstroeter collection, a spatangoid has attracted attention, which turned out to be a new species of the micrasterid genus *Pseudogibbaster* Moskvina, 1983 and is described herein as *Pseudogibbaster herkstroeteri* sp. nov.

GEOLOGICAL SETTING

The Danish Basin belongs to the eastern part of the extensive epicontinental Chalk Sea, covering most of NW Europe during the Late Cretaceous–Danian transition. The WNW–ESE-trending Danish Basin is bounded to the north and north-east by the inverted Sorgenfrei-Tornquist Zone, and to the east and south-east by the Ringkøbing-Fyn High (Surlyk *et al.* 2013). Westward, the basin graded into more strongly subsiding sub-basins in the Danish Central Graben and adjacent North Sea depocenters, with Late Cretaceous–Danian chalk successions extending across these offshore areas. To the south and southeast, the basin connected to other North European shelf seas, with its extent constrained by regional structural highs (Jakobsen 2014; Ineson *et al.* 2022). Palynological and sedimentological data indicate a sea-level fall and a hiatus at the K/Pg boundary, limiting chalk deposition to the central axis of the Danish Basin, the Central Graben of the greater North Sea Basin and the eastern parts of the German-Polish Basin to the NE (Thomsen 1995; Surlyk 1997; Lauridsen *et al.* 2019). The lowstand was followed by renewed onlap and a Danian transgression. Sequence-stratigraphic syntheses of the Danian–Selandian interval identify an early to mid



Text-fig. 1. General map of Denmark showing the location of Dalbyover quarry in northern Jutland.

Danian transgressive-regressive cycle with a major transgression peaking within the Danian around 64.5 Ma; this implies rising and then high relative sea level in early to mid Danian time (Ruban *et al.* 2012). With rising sea level during the mid Danian, the deposition of the pelagic facies of flint-rich, bioturbated calcareous nannofossil chalk continued in the central parts of the Danish Basin (Lauridsen *et al.* 2019). The Dalbyover quarry is located in the central part of the Danish Basin and exposes a succession of mid-Danian chalk belonging to nannofossil Zone 5 (Thomsen 1995). A detailed description of the lithology of succession exposed at the Dalbyover quarry was provided by Lauridsen *et al.* (2019).

MATERIAL AND METHODS

The sole specimen from *Pseudogibbaster herkstroeteri* sp. nov. described herein has been collected by surface-picking in the Dalbyover chalk quarry in north Jutland (Text-fig. 1; 56.613230 N, 10.201556 E). No information about the fossil-bearing bed within the succession exposed in the quarry is available. The adult specimen is largely in excellent preservation, although slightly compressed and with part of the aboral side broken off, also affecting the apical disc. Internally, the echinoid test is filled with flint. Preparation consisted solely of removing adhering

chalk with a soft brush. For photographic work, an OM System OM-1 Mk II camera with a 60 mm macro lens was used. Where focus stacking was applied, images were processed with Helicon Focus Pro. The echinoid was coated with NH_4Cl prior to photography. For the taxonomic description of the echinoid, I followed the scheme of Smith *et al.* (1999) and Kroh *et al.* (2004), respectively.

Repositories

OESM – East Zealand Museums, Faxø, Denmark;
MB.E – Invertebrate Palaeontology collection,
Museum für Naturkunde, Berlin, Germany.

SYSTEMATIC PALAEOLOGY

Order Spatangoida L. Agassiz, 1840
Family Micrasteridae Lambert, 1920
Genus *Pseudogibbaster* Moskvina, 1983

TYPE SPECIES: *Protobrissus akkajensis* Moskvina and Poslavskaya, 1959, p. 290, by original designation.

DIAGNOSIS: Test cordate, with shallow anterior sulcus; inflated, with vertically truncated posterior. Apical disc ethmophract with four gonopores. Anterior ambulacrum sunken with pore-pairs differentiated from those of other ambulacra. Peristome almost non-labiate and downward-facing. Subanal fasciole present (adopted from Smith *et al.* 1999).

Pseudogibbaster herkstroeteri sp. nov.
(Text-figs 2, 4A)

urn:lsid:zoobank.org:act:921BE080-3DCE-47B3-84DD-1A99DE86D201

DIAGNOSIS: A rather large-sized *Pseudogibbaster* with a flat base and rather flat aboral surface, relatively broad petals with anterior petals 1.4 times longer than the posterior pair. Anterior ambulacrum subpetaloid aborally, steeply truncated posterior. Prominent and well-developed phyllodes with deeply countersunk buccal pores.

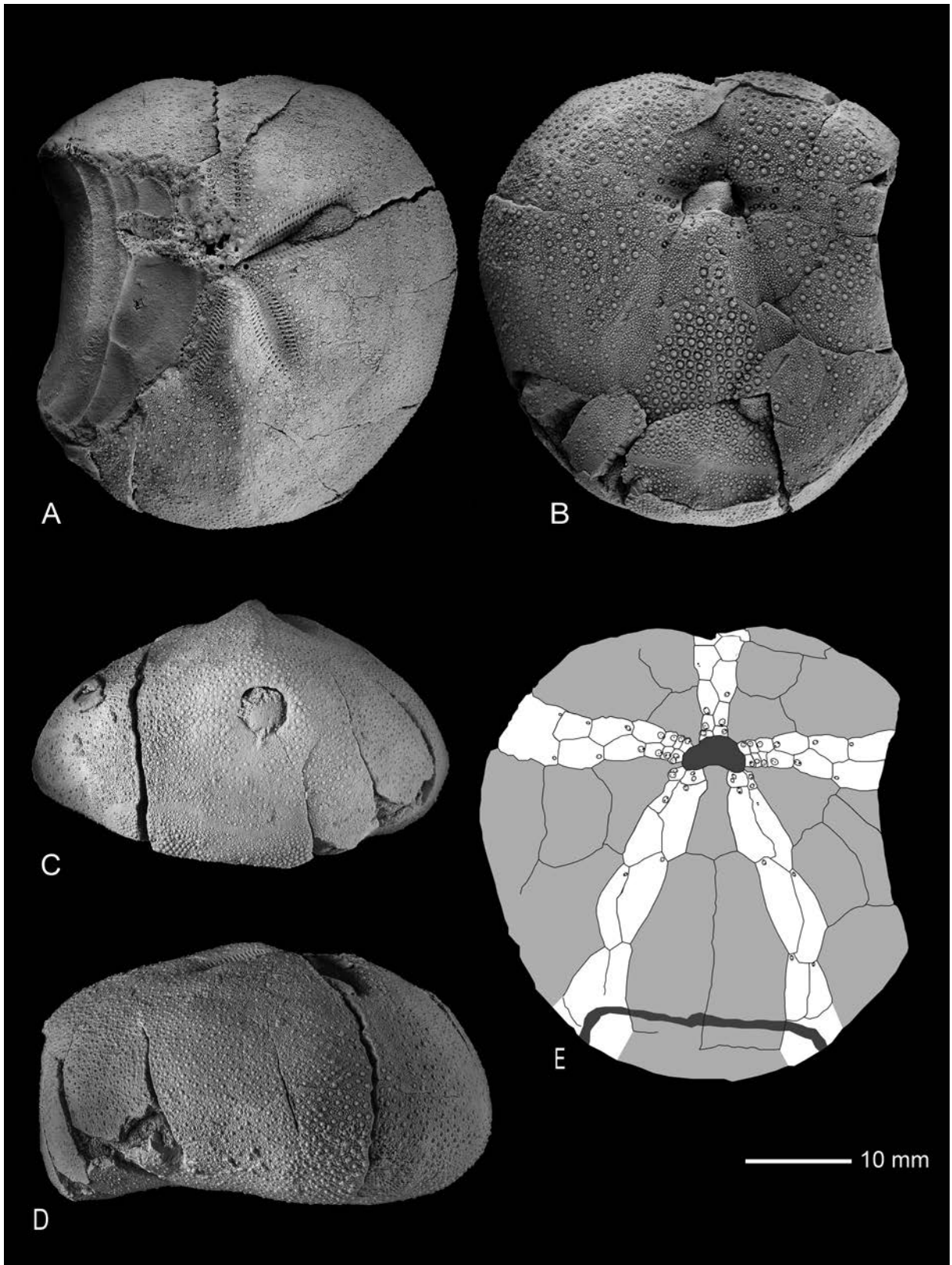
HOLOTYPE: The holotype is a nearly complete and slightly compacted but otherwise well-preserved specimen (OESM 13423).

TYPE HORIZON: Mid Danian (Lower Paleocene), nannofossil Zone 5.

TYPE LOCALITY: Chalk quarry at Dalbyover, Jutland Peninsula, Denmark.

DERIVATION OF NAME: In honour of Ingo Herkstroeter, the collector of the echinoid.

DESCRIPTION: Test relatively large, subcircular in outline, almost as wide as long with a shallow anterior groove and a weakly indented frontal notch (Text-fig. 2A, B). The posterior is rather rounded. The test length is 46.5 mm, test width is 44 mm (94.5% of test length) and test height is 25.2 mm (54.2% of test length). The widest part of the test is almost in the centre (48% of test length from the anterior border). In profile, the test is rectangular with a flat base and a rounded anterior (Text-fig. 2D). The keeled posterior part of the aboral side is gently sloping towards the posterior and abruptly drops to an angle of 90°, forming a vertical anal surface. The highest point of the test is situated on the keel, immediately posterior of the apical disc, which is slightly offset to the anterior (the centre is 42% of test length from the anterior border of the test). The apical disc is partly damaged and genital plate G3 is not preserved. However, G1, G2 and G4 are preserved, exposing moderately large gonopores with G2 separating G1 and G4 but not the posterior oculars, thus representing an ethmophract condition. The paired ambulacra are petaloid aborally and bear elongate anisopores within the petals. The isopores are separated by shallow ridges. The petals are moderately broad, sunken and open distally. The anterior pair is straight whereas the posterior pair is slightly s-curved. The anterior petals are 1.4 times longer than the posterior. The length of the anterior petals is 72% of the corresponding test radius and 47% respectively (posterior) in planar view. The anterior paired petals diverge at an angle of 133°, the posterior ones at 50° (Text-fig. 2A). Aborally, the frontal ambulacrum is semi-petaloid with densely spaced enlarged, partitioned isopores, each separated by a knob-like interporal partition. Halfway to the ambitus, these pores are replaced by tiny and widely spaced simple isopores. The phyllodes are well-developed and consist of rows of up to five countersunk large axially partitioned isopores in each half ambulacrum separated by a large knob-like interporal partition (Text figs 2B and 4A). Adorally the frontal groove leads into the peristome. The plastron is mesamphisternous with both sternal plates equal and separated almost centrally. The labrum is large



Text-fig. 2. *Pseudogibbaster herkstroeteri* sp. nov., holotype, OESM 13423, from the mid Danian of Dalbyover, Denmark, in apical (A), oral (B), posterior (C) and lateral (anterior to the right; D) views; E – oral plating scheme. Specimen coated with ammonium chloride.

and elongate and has a broad contact with both sternal plates (Text-fig. 2B, E). Tuberculation consists of homogenous small and closely spaced primaries on the aboral site and densely crowded secondary and milliary tubercles in between. Here, primaries do not possess crenulations or enlarged areoles. On the oral side, primaries are larger and more widely spaced, crenulated and with enlarged areoles, especially on the plastron and the basal interambulacra 1 and 4. The periplastral ambulacra are densely covered with secondary tubercles while primary tubercles are absent. The only present fasciole is a well-developed broad and completely closed subanal parafasciole (*sensu* Néraudeau *et al.* 1998). It is ovate in outline and slightly indents below the periproct. The peristome is anterior, its anterior margin is 22% of test length from the anterior margin of the test. It is transversally elongated (D-shaped) in outline and slightly projecting forward. It measures 6.3 vs. 4.8 mm. The labrum hardly projects over the peristome (Text-fig. 2B, E). The almost circular periproct is small with a diameter of 4.8 mm and situated high on the posterior surface (Text-fig. 2C).

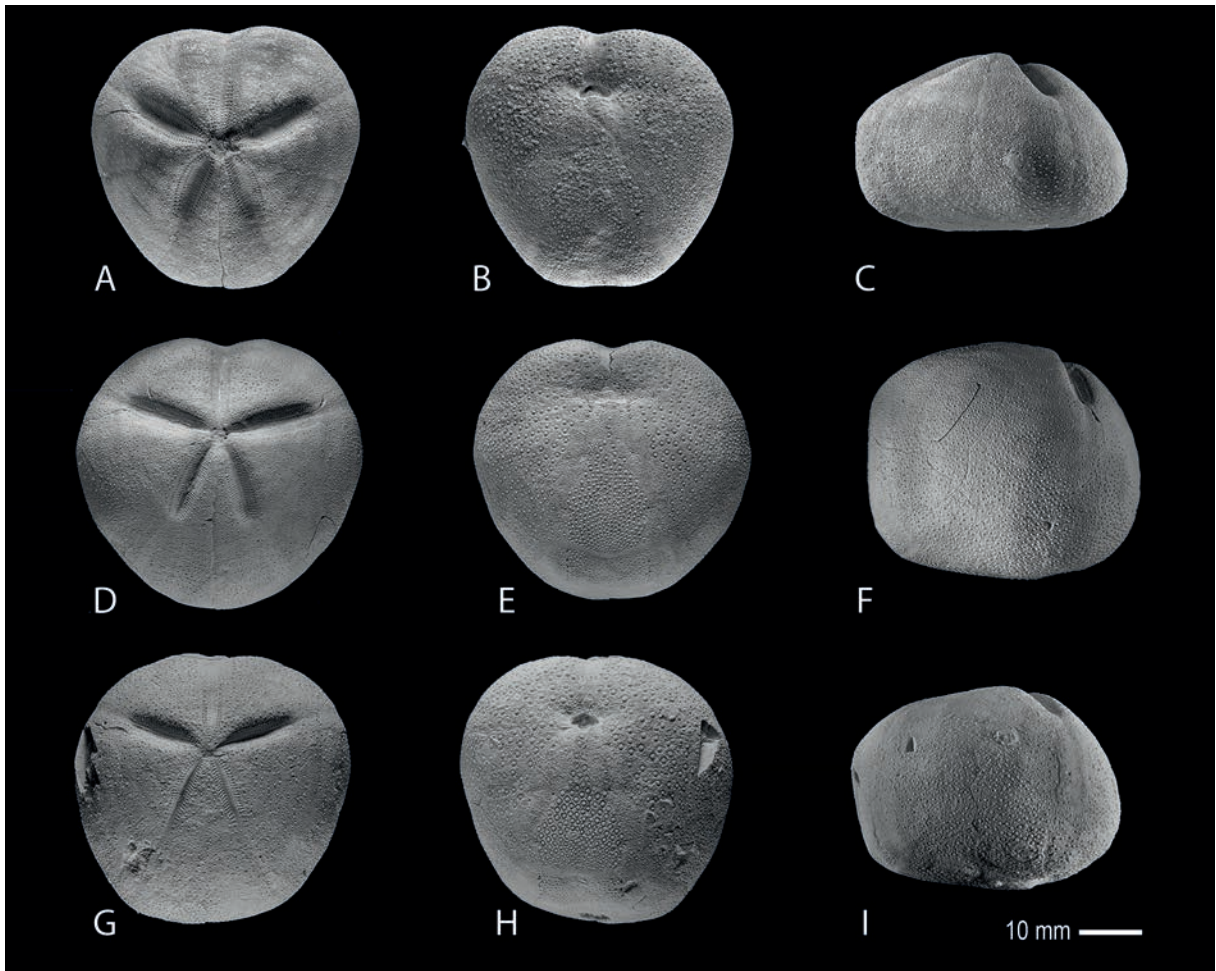
DISCUSSION:

Relationships and comparisons

The subanal fasciole and the absence of further fascioles characterise *Pseudogibbaster herkstroeteri* sp. nov. as belonging to the Micrasteridae. Within this family, the new species can be assigned to *Pseudogibbaster* on the base of the truncated posterior, highest point centrally, subequal petals, semi-petaloid frontal ambulacrum and non-labiate peristome. It cannot be ruled out that *Pseudogibbaster* may have already appeared in the upper Campanian (Kroh *et al.* 2004) whereas all species described so far are of Paleocene age. The genus has been recorded from Crimea, northern Caucasus, the Transcaspien region, Georgia, Bulgaria, Spain and eastern Poland (Smith and Jeffery 2000). *Pseudogibbaster herkstroeteri* sp. nov. thus represents the first record of the genus from the Paleocene of NW Europe. At Dalbyover, the new taxon can easily be distinguished from other co-occurring spatangoids. The micrasterid *Diplodetus coloniae* (Cotteau, 1877) is ovate in outline, has no frontal notch and the paired petals are almost equal in length. Additionally, the plastron is protamphisternous with asymmetric sternal plates and an oblique median suture. The only

other co-occurring micrasterid, *Cyclaster suecicus* (Schlüter, 1897) can be ruled out by its ovate outline, flush petals and only three gonopores. The schizasterid *Linthia* sp. differs markedly by the presence of a peripetalous and a latero-anal fasciole.

The genus *Pseudogibbaster* was described by Moskvina in 1983 who included six species, *P. akkajensis* (Moskvina and Poslavskaya, 1959), *P. canaliculatus* (Cotteau, 1887), *P. depressus* (Kongiel in Kongiel and Matwiejewówna, 1937), *P. tercensis* (Cotteau, 1877), *P. indolensis* (Poslavskaya and Moskvina, 1960), and *P. rionensis* (Moskvina, 1964). Subsequently, Smith and Jeffery (2000) accepted only three species: *P. akkajensis* (including *P. canaliculatus*, early Danian), *P. tercensis* (late Danian to late Thanetian) and *P. depressus* (including *P. indolensis*; early to mid Danian), but did not consider *P. rionensis* from the Thanetian of Georgia and Bulgaria. All of these species have an inflated gibbous test often including a convex base. *Pseudogibbaster herkstroeteri* sp. nov. can be distinguished from its congeners by its rectangular profile, large size and the large and well-developed buccal pores with deeply indented periporal areas, immediately distinguishing it from all other *Pseudogibbaster* species. The new taxon differs from *P. akkajensis* (Text-fig. 3A–C) by its rounded outline, larger size, and greater peristome. Moreover, *P. akkajensis* possesses aborally a dense scrobiculate tuberculation, a character that is lacking in the new taxon. *Pseudogibbaster tercensis* (Text-fig. 3D–F) can immediately be excluded by its gibbous test with inflated lower and upper surfaces and narrow petals. *Pseudogibbaster tercensis* is a large species, reaching up to 65 mm in length (Smith *et al.* 1999). *Pseudogibbaster depressus* (Text-fig. 3G–I) has a protamphisternous plastron, an overhanging posterior face, a small peristome, narrower petals and a lower periproct. Machalski and Jagt (2018, p. 584, fig. 6D–F) mentioned and figured *P. cf. depressus* from the mid to late Danian of the Kazimierz Dolny area, Poland. However, preservation of the figured specimen is too poor for an adequate assessment. *Pseudogibbaster herkstroeteri* sp. nov. shares the character of a flat base with *P. rionensis*, but differs otherwise in its having a pyramidal profile and a non-truncate, well-rounded posterior. Finally, a questionable *Pseudogibbaster* sp. from the upper Campanian of Gschliefgraben, Austria, described by Kroh *et al.* (2004) needs to be considered. This echinoid is more cordate in outline, higher in profile and possesses a protamphisternous plastron structure. Some species of *Pseudogibbaster* exhibit



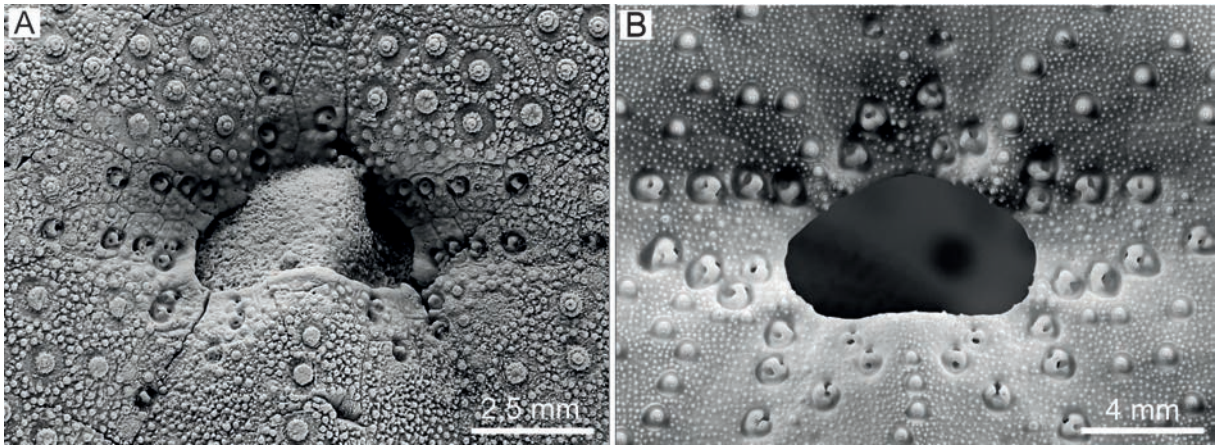
Text-fig. 3. Species of *Pseudogibbaster* Moskvina, 1983. A–C – *Pseudogibbaster akkajensis* (Moskvina and Poslavskaya, 1959), from the lower Danian of Mangyshlak Peninsula, Kazakhstan, MB.E 6923 in apical (A), oral (B) and lateral (anterior to the right, C) views. D–F – *Pseudogibbaster tercensis* (Cotteau, 1877), from the upper Danian of Tercis, France, MB.E 8823 in apical (D), oral (E) and lateral (anterior to the right, F) views. G–I – *Pseudogibbaster depressus* (Kongiel in Kongiel and Matwiejewówna, 1937), from the mid Danian of East Crimea, Ukraine, MB.E15204 in apical (G), oral (H), and lateral (anterior to the right, I) views. Specimens coated with ammonium chloride.

traces of a diffuse peripetalous fasciole, but this character may often be poorly developed or even absent as is the case with *P. herkstroeteri* sp. nov.

Notes on paleoecology

The deep shelf of the central Danish Basin represents a habitat with an impoverished macrobenthos community characterised by low diversity and low abundances. In addition to the soft nature of the substrate, nutrient deficiency was probably a great challenge for seafloor-dwelling animals. In order to successfully cope with these conditions, the organisms required special adaptations. As Lauridsen *et al.*

(2019) noted, some inhabitants were survivors of the K/Pg extinction and therefore already well-adapted to the conditions at the chalk sea floor. Others, such as the micrasterid *Pseudogibbaster* only evolved in the Danian (but see Kroh *et al.* 2004). *Pseudogibbaster herkstroeteri* sp. nov. belonged to the mobile deposit feeder guild. Adaptations for a burrowing mode of life include sunken petals associated with respiratory tube feet, a subanal fasciole, a frontal groove associated with large partitioned isopores, indicating the presence of funnel-building podia in order to build a shaft to the sediment surface for respiratory demands and possibly also for gathering food from the sediment surface (Chesher 1968; Smith 1980; De Ridder *et al.* 1987).



Text-fig. 4. Detail of the oral side showing the peribuccal region with the phyllodes. A – *Pseudogibbaster herkstroeteri* sp. nov., OESM 13423, holotype from the mid Danian of Denmark; B – *Corystus relictus* (de Meijere, 1902), from the recent of Siquijor Island, Philippines (author's collection).

In areas where surface sediments are characterised by low organic content, spatangoids derive most of their nutritional intake by processing bulk sediment using the buccal podia around the peristome (Hollertz 2002; Barras 2008). Bulk (i.e., non-selective) deposit feeding is especially common in benthic communities living in organically poor sediments. In nutrient-impoverished environments, bulk deposit feeders that process massive volumes of sediment can still survive, grow, and often dominate the benthic community (Lopez *et al.* 1989; Jumars *et al.* 1990). A remarkable feature of *P. herkstroeteri* sp. nov. are the prominent and countersunk axially partitioned buccal pores found on the phyllodes around the peristome (Text-fig. 4A). This condition is rarely encountered in just a few atelostomates, notably in the holasteroid *Corystus* Pomel, 1883 (Text-fig. 4B, see also Forster and Philip 1978, pl. 86, fig. 3) whose only representative today also lives in deep waters (de Meijere 1902; Smith 2004). These pores corresponded with particularly large podia which terminated in large penicillate discs. The particular expression of this character, which does not occur in any congener, is interpreted here as an adaptation to the nutrient-deficient bottom conditions in the deep-water chalk of the Danish Basin and apparently served to optimise the ability of bulk sediment feeding.

CONCLUSIONS

1. The micrasterid spatangoid *Pseudogibbaster herkstroeteri* sp. nov. is formally described from

the mid-Danian deep-water chalk of Dalbyover, Denmark. Dalbyover was situated in the central part of the Danish Basin and harboured an impoverished macrobenthos fauna during the mid-Danian highstand. The new taxon is the first record of the genus from the Paleocene of NW Europe.

2. The new species is distinguished from all congeners by its considerably large size, rectangular test profile and prominent and well-developed phyllodes with large countersunk buccal pores.

3. The expression of the phyllodes is interpreted as an adaptation to a nutrient-deficient environment, optimizing the ability of bulk-sediment feeding.

4. The list of echinoids occurring at the Dalbyover locality now contains eight taxa. Six of these are atelostomates and belong to the deposit feeder guild.

Acknowledgements

I am indebted to Ingo Herkstroeter (Geesthacht) for the donation of the only known specimen from his collection. I would like to express my sincere thanks to Dave Ware (Berlin) for his assistance in creating the illustrations. I further thank the referees Andreas Kroh (Vienna) and Andy Gale (Portsmouth) for their invaluable comments on an earlier draft of the typescript.

REFERENCES

Agassiz, L. 1838–1842. Monographies d'échinodermes vivants et fossiles, 316 pp. Petitpierre; Neuchâtel.

- Asgaard, U. 1979. The irregular echinoids and the boundary in Denmark. In: Birkelund, T. and Bromley, R.G. (Eds), Cretaceous–Tertiary Boundary Events, I. The Maastrichtian and Danian of Denmark, pp. 74–77. University of Copenhagen; Copenhagen.
- Barras, C.G. 2008. Morphological innovation associated with the expansion of atelostomate irregular echinoids into fine-grained sediments during the Jurassic. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **263**, 44–57.
- Chesher, R.H. 1968. The systematics of sympatric species in West Indian spatangoids, 168 pp. University of Miami Press; Miami.
- Cotteau, G. 1877. Description des Echinides. In: Locard, A. (Ed.), Description des Faunes des terrains Tertiaires moyens de la Corse: *Annales de la Société d'Agriculture, Histoire Naturelle et Arts Utiles de Lyon*, ser. 4, **9**, 1–374.
- De Ridder, C., Jangoux, M. and De Vos, L. 1987. Frontal ambulacral and peribuccal areas of the spatangoid echinoid *Echinocardium cordatum* (Echinodermata): a functional entity in feeding mechanism. *Marine Biology*, **94**, 613–624.
- Foster, R.J. and Philip, G.M. 1978. Tertiary holasteroid echinoids from Australia and New Zealand. *Palaeontology*, **21**, 85–93.
- Goldfuss, G.A. 1829–1831. Petrefacta Germaniae tam ea quae in Museo Universitatis Regiae Bourssicae Fridericiae Rhenanae servantur quam alia quaecumque in Museis Hoeninghusiano aliisque extant Iconibus et Descriptionibus illustrata Arnz and Co.; Düsseldorf.
- Hagenow, F. v. 1840. Monographie der Rügen'schen Kreideversteinerungen, II. Abtheilung: Radiarien und Annulaten nebst Nachträgen zur ersten Abtheilung. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefaktenkunde*, **7**, 630–672.
- Håkansson, E. and Thomsen, E. 1999. Benthic extinction and recovery patterns at the K/T boundary in shallow water carbonates, Denmark. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **154**, 67–85.
- Hollertz, K. 2002. Feeding biology and carbon budget of the sediment-burrowing heart urchin *Brissopsis lyrifera* (Echinoidea: Spatangoida). *Marine Biology*, **140**, 959–969.
- Ineson, J.R., Petersen, H.I., Andersen, C., Bjerager, M., Jakobsen, F.C., Kristensen, L., Mork, F. and Sheldon, E. 2022. Early Cretaceous stratigraphic and basinal evolution of the Danish Central Graben: a review. *Bulletin of the Geological Society of Denmark*, **71**, 75–98.
- Jakobsen, F. 2014. Late Cretaceous stratigraphy and basin development in the Danish Central Graben. *Danmarks og Grønlands Geologiske Undersøgelse Rapport*, **2014/41**, 1–49.
- Johansen, M.B. 1989. Background extinction and mass extinction of the brachiopods from the chalk of Northwest Europe. *Palaiois*, **4**, 243–250.
- Jumars, P.A., Mayer, L.M., Deming, J.W., Baross, J.A. and Wheatcroft, R.A. 1990. Deep-sea deposit-feeding strategies suggested by environmental and feeding constraints. *Philosophical Transactions of the Royal Society of London. Series A*, **331(1616)**, 85–101.
- Kjaer, C.R. and Thomsen, E. 1999. Heterochrony in bourguetiacrinid sea-lilies at the Cretaceous/Tertiary boundary. *Paleobiology*, **25**, 29–40.
- Kongiel, R. and Matwiejewówna, L. 1937. Matériaux fauniques de la Craie supérieure des environs de Puławy. *Prace Towarzystwa Przyjaciół Nauk w Wilnie, Wydział Nauk Matematycznych i Przyrodniczych*, **11**, 1–34. [In Polish with French summary]
- Kroh, A., Jagt, J.W.M. and Wagneich, M. 2004. Additional records of Late Cretaceous and Early Palaeogene echinoids from the Gschliefgraben (Ultrahelvetic, Upper Austria). *Acta Geologica Polonica*, **54**, 551–571.
- Ladwig, J. 2009. Anmerkungen zur Seeigel-Gattung *Bolbaster* aus dem Danium von Dänemark. *Der Geschiebesammler*, **42**, 165–173.
- Ladwig, J. 2012. Der Fund eines Seeigels *Diplodetus coloniae* (COTTEAU, 1877) aus dem mittleren Danium von Dalbyover in Dänemark. *Arbeitskreis Paläontologie Hannover*, **40**, 115–120.
- Lambert, J. 1920. Étude sur quelques formes primitives des Spatangidés. *Bulletin de la Société des Sciences d'Histoire naturelle de l'Yonne*, **73**, 1–41.
- Lauridsen, B.W. and Bjerager, M. 2014. Danian cold-water corals from the Baunekule facies, Faxø Formation, Denmark: a rare taphonomic window of a coral mound flank habitat. *Lethaia*, **47**, 437–455.
- Lauridsen, B.W., Edvardsen, T., Blinkenberg, K.H. and Stemmerik, L. 2019. Palaeoecology and survival strategies of an impoverished benthic chalk community in a mid-Danian deep shelf setting. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **514**, 474–486.
- Lopez, G.R., Taghon, G.L. and Levinton, J.S. 1989. Ecology of marine deposit feeders, 322 pp. Springer; Berlin.
- Machalski, M. and Jagt, J.W.M. 2018. A new Danian echinoid assemblage from the Greensand in the Kazimierz Dolny area, central Poland: taxonomy, taphonomy and sedimentological implications. *Acta Geologica Polonica*, **68**, 571–596.
- Meijere, J.C.H. de 1902. Vorläufige Beschreibung der neuen, durch die Siboga-Expedition gesammelten Echiniden. *Tijdschrift der Nederlandsche Dierkundige Vereeniging*, 2^{de} serie, **8**, 1–16.
- Morton, S.G. 1830. Synopsis of the organic remains of the ferruginous sand formation of the United States, with geological remarks. Part 2. *American Journal of Science*, **18**, 243–250.
- Moskvin, M.M. 1964. The echinoid *Protobrissus* in the Danian and Paleocene deposits in the USSR, 185–202. Publication in honour of Academician Y.S. Yovchev, Sofia. [In Russian]

- Moskvin, M.M. 1983. *Pseudogibbaster*, a new genus of Danian and Paleocene echinoids. *Paleontologicheskii Zhurnal*, **1983/3**, 112–115. [In Russian]
- Moskvin, M.M. and Poslavskaya, N.A. 1959. Echinodermata. In: Moskvin, M.M. (Ed.), Atlas verkhnemelovoy fauny severnogo Kavkaza i Kryma, 237–304. Gostoptechisdat; Moskva. [In Russian]
- Néraudeau, D., David, B. and Madon, C. 1998. Tuberculation in spatangoid fascioles: Delineating plausible homologies. *Lethaia*, **31**, 323–334.
- Pomel, N.A. 1883. Classification méthodique et genera des Échinides vivants et fossils, 133 pp. A. Jourdan; Alger.
- Poslavskaya, N.A. and Moskvin, M.M. 1960. Echinoids of the order Spatangoida in Danian and adjacent deposits of Crimea, Caucasus and Transcaspian region, 42–82. In: Reports of Soviet geologists. International Geological Congress, XXI session, Problem 5 (The Cretaceous–Tertiary Boundary). Publishing House of the Academy of Sciences of the USSR; Moscow. [In Russian]
- Ravn, J.P.J. 1927. De irregulære Echinider i Danmarks Kridtaflejringer. *Det Kongelige Danske Videnskabernes Selskab Skrifter, naturvidenskabelige og matematiske Række, ser. 8*, **11**, 307–354.
- Ruban, D.A., Zorina, S.O., Conrad, C.P. and Afanasieva, N.I. 2012. In quest of Paleocene global-scale transgressions and regressions: constraints from a synthesis of regional trends. *Proceedings of the Geologists' Association*, **123**, 7–18.
- Schlüter, C. 1897. Über einige exocyclische Echiniden der baltischen Kreide und deren Bett. *Zeitschrift der deutschen geologischen Gesellschaft*, **49**, 18–50.
- Smith, A.B. 1980. The structure, function and evolution of tube feet and ambulacral pores in irregular echinoids. *Palaeontology*, **23**, 39–83.
- Smith, A.B. 2004. Phylogeny and systematics of holasteroid echinoids and their migration into the deep-sea. *Palaeontology*, **47**, 123–150.
- Smith, A.B., Gallemí, J., Jeffery, C.H., Ernst, G. and Ward, P.D. 1999. Late Cretaceous–early Tertiary echinoids from northern Spain: implications for the Cretaceous–Tertiary extinction event. *Bulletin of the Natural History Museum of London. Geology series*, **55**, 81–137.
- Smith, A.B. and Jeffery, C.H. 2000. Maastrichtian and Palaeocene echinoids: A key to world faunas. *Special papers in Palaeontology*, **63**, 1–406.
- Surlyk, F. 1997. A cool-water carbonates ramp with bryozoan mounds: Late Cretaceous – Danian of the Danish Basin. In: James, N.P., Clarke, J.D.A. (Eds), Cool-Water Carbonates. *SEPM Special Publication*, **56**, 293–307.
- Surlyk, F., Rasmussen, S.L., Boussaha, M., Schiøler, P., Schovsbo, N.H., Sheldon, E., Stemmerik, L. and Thibault, N. 2013. Upper Campanian–Maastrichtian holostratigraphy of the eastern Danish Basin. *Cretaceous Research*, **46**, 232–256.
- Thomsen, E., 1995. Kalk og kridt i den danske undergrund. In: Nielsen, O.B. (Ed), Aarhus Geokompender, **1**, 31–67. Aarhus Universitet; Aarhus.

Manuscript submitted: 12th February 2026

Revised version accepted: 18th March 2026