

Rare Campanian Echinoids from Höver and Misburg (Hannover Area, Lower Saxony, Germany)

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With 3 figures and 3 plates

Abstract

Amongst the rich and fairly diverse echinoid faunas from the Campanian marl/marly limestone facies as exposed at the large quarries of the cement industry near Höver and Misburg (east of Hannover, northern Germany), there are a few rare taxa, most of which have not been recorded previously from the Lower Saxony Basin. These include *Echinogalerus peltiformis* (Wahlenberg, 1821), *Conulus* (*C.*) *matesovi* Poslavskaia & Moskvina in Moskvina 1959, *Hagenowia blackmorei* Wright & Wright, 1949, *Diplodetus* sp., and *Peroniaster cotteai* Gauthier in Peron 1887. New material of another rare species, *Hemiaster* gr. *aquisgranensis* Schlüter, 1899, is here described. The palaeoecological significance of the rarity of these is briefly discussed. Of particular note, in a palaeobiogeographic context, are *E. peltiformis* and *C. matesovi*. The former is well known from Lower and Upper Campanian arenitic facies in southern Sweden, while the latter was held to be confined to the Lower Campanian of the Caucasus and Kazakhstan. These two species may have immigrated into the Lower Saxony Basin following transgressive pulses or within transgressive systems tracts.

Key words: Echinoidea, Campanian, Höver, Misburg, new records, palaeoecology, palaeobiogeography, immigration.

Zusammenfassung

Die reiche und vergleichsweise diverse Echinidenfauna der Mergel/Mergelkalk-Rhythmite des Campans von Misburg und Höver bei Hannover enthält einige seltene Taxa, die bisher aus dem Niedersächsischen Becken nicht bekannt waren. Dazu gehören *Echinogalerus peltiformis* (Wahlenberg, 1821), *Conulus* (*C.*) *matesovi* Poslavskaia & Moskvina in Moskvina 1959, *Hagenowia blackmorei* Wright & Wright, 1949, *Diplodetus* sp. und *Peroniaster cotteai* Gauthier in Peron 1887. Für eine weitere Art, *Hemiaster* gr. *aquisgranensis* Schlüter, 1899, werden neue Funde beschrieben. Die paläoökologische Bedeutung der Seltenheit der vorliegenden Taxa wird diskutiert. Als besonders bedeutsam erweisen sich dabei die Vorkommen von *E. peltiformis* und *C. matesovi*. Ersterer war bisher ausschließlich aus den küstennahen Kalkareniten Südschwedens bekannt, letzterer wurde bisher nur im Untercampan des Kaukasus und von Aserbaidschan und Kasachstan nachgewiesen. Beide Arten sind wahrscheinlich im Rahmen transgressiver Schübe dritter Ordnung in das Niedersächsische Becken eingewandert.

Schlüsselwörter: Echinoidea, Campan, Höver, Misburg, Erstnachweise, Paläoökologie, Paläobiogeographie, Faunen-Migrationen.

Introduction

In the Lehrte West syncline (central Lower Saxony Basin), an undisturbed succession of marls and marly limestones of Campanian age is well exposed in several large quarries of the cement industry (Fig. 1, and compare Khosrovshahian [1972], Ernst [1975], Ernst et al. [1979, 1997a–c], and Volkmann [1998]). In particular, the “Alemannia” (Höver) and “Teutonia” (Misburg)

quarries, east of Hannover, are famous for their well-preserved and fairly diverse echinoid faunas. More than twenty taxa within the cohort Irregularia are now known (see Appendix 1). Extensive study of museum and private collections as well as new finds have led to the recognition of five echinoid taxa not previously recorded from the area. Of the sixth rare species, *Hemiaster* gr. *aquisgranensis*, recently collected material is here described and illustrated.

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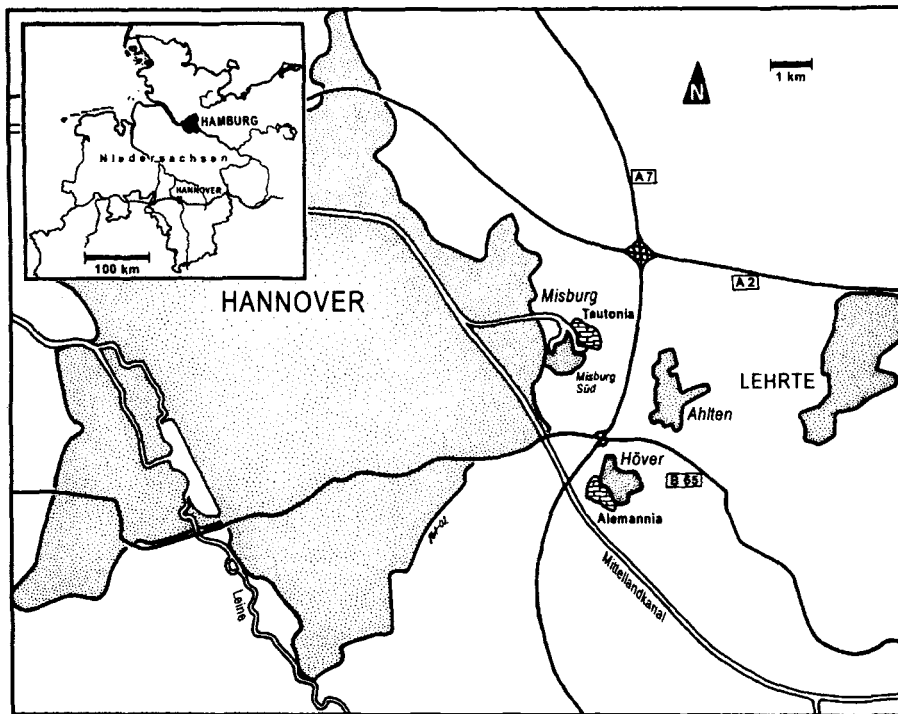


Fig. 1. Map of the Hannover area showing the location of the Teutonia (Misburg) and Alemannia (Höver) quarries.

Campanian echinoid faunas of the Hannover area have been the subject of numerous studies during more than thirty years, and these studies focused either on palaeoecological aspects (Ernst 1970a), particular echinoid lineages (Ernst 1970b, 1971, 1972, Ernst et al. 1971, Frerichs 1989) or their biostratigraphical potential (Ernst 1970c, Ernst & Seibertz 1977, Schulz 1985). The aim of the present paper is to document differences between rare and common taxa and to attempt to reconstruct the various processes behind them. In recent years, the signals in macrofossil groups within sequence-stratigraphic schemes have received some attention (Ernst & Wood 1996). Amongst echinoids, immigration of certain species into the area may be linked directly to transgressive surfaces or transgressive systems tracts. At least one of the rare echinoid species discussed in the present paper (*C. matesovi*) testifies to such events across northern and eastern Europe, as far southeast as the Caucasus.

Institutional Abbreviations

To denote the repositories of material referred to in the text the following abbreviations are used:

BGR	Bundesanstalt für Geowissenschaften und Rohstoffe, Hannover;
MB.E	Museum für Naturkunde, Humboldt Universität Berlin;
NHMM	Natuurhistorisch Museum Maastricht, Maastricht; and
RFWUIP	Rheinische Friedrich-Wilhelms-Universität, Institut für Paläontologie, Bonn (C. Schlüter Colln).

Systematic palaeontology

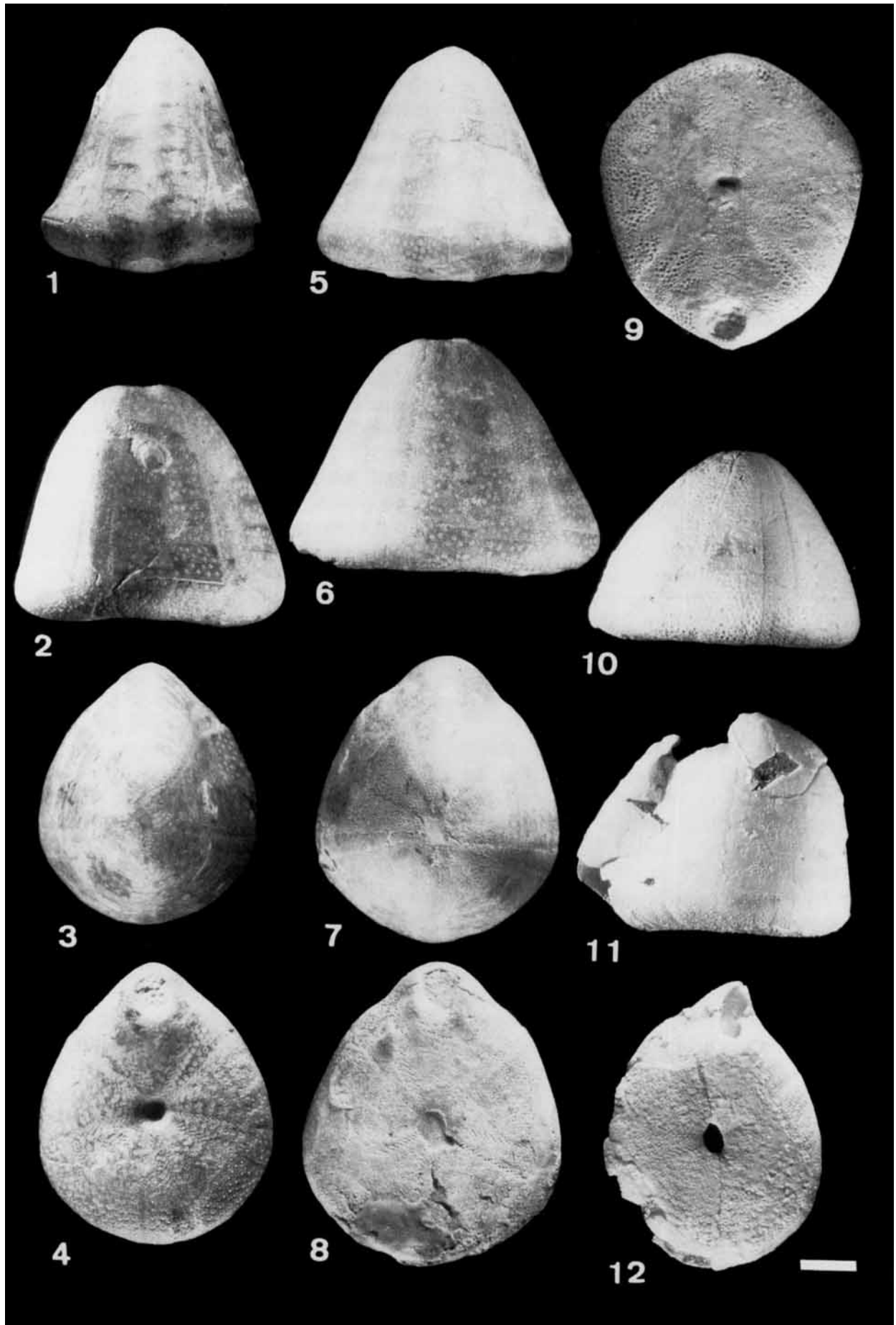
Order **Echinoneoidea** H.L. Clark, 1925

Family **Conulidae** Lambert, 1911

Genus and subgenus **Conulus** (*Conulus*) Leske, 1778

Type species: *Conulus albogalerus* Leske 1778, by monotypy.

Plate 1. *Conulus matesovi* and *Conulus haugi*. 1–4. *Conulus* (*Conulus*) *matesovi* Poslavskaja & Moskvina in Moskvina, 1959, MB.E 3593 in four aspects (1. posterior; 2. lateral; 3. aboral; 4. oral). Alemannia quarry (Höver), upper *papillosa*/lower *conical/papillosa* Zone interval (Lower Campanian). 5–8. *Conulus* (*Conulus*) *matesovi* Poslavskaja & Moskvina in Moskvina, 1959, MB.E 3592 in various aspects (5. posterior; 6. lateral; 7. aboral; 8. oral); Alemannia quarry (Höver), *gracilis/mucronata* Zone (upper Lower Campanian). 9–10. *Conulus haugi* Lambert, 1935, MB.E 3597 (cast; original in W. Judenhagen Colln) in various aspects (9. oral; 10. lateral); from temporary motorway outcrop at Sarasate (Barranca, northeast Spain), Lower Campanian. 11–12. *Conulus* (*Conulus*) *matesovi* Poslavskaja & Moskvina in Moskvina 1959, MB.E 3594 in two aspects (11. lateral; 12. oral); Heidestrasse quarry (Lägerdorf); *gracilis/mucronata* Zone, level F62–1.15 m (upper Lower Campanian; see Schulz & Weitschat 1998). Scale bar for all figures equals 10 mm.



***Conulus (Conulus) matesovi* Poslavskaia & Moskvin in Moskvin, 1959**

Pl. 1: 1–8 and 11–12

*1959 *Conulus matesovi* – Poslavskaia & Moskvin in Moskvin, p. 251, pl. 3, fig. 2.

?1988 *Conulus matesovae* [sic] Moskvin – Ali-Zade et al., p. 188, pl. 2, fig. 1; text-fig. 7.

Material: Two fairly well-preserved specimens (MB.E 3592 and 3593), from the upper *papillosa*/lower *conica/gracilis* Zone interval and *gracilis/mucronata* Zone, respectively, at Höver (Alemania), and a single fragmentary, poorly preserved specimen (MB.E 3594, ex M.-G. Schulz Colln) from the Upper Campanian (*gracilis/mucronata* Zone) at Lägerdorf (quarry 'Heidestrasse').

Measurements (in mm):

	1	2	3	4
Width	41.4	49.9	36.4*	40.0
Length	49.0	58.2	46.6*	45.0
Height	43.1	43.0	37.3*	40.0
L peristome	5.9	6.0	–	–
W periproct	6.6	6.9	–	–

1 = MB.E 3592 (ex J. van den Essen Colln)

2 = MB.E 3593 (cast; original in D. Licht Colln)

3 = MB.E 3594 (ex M.-G. Schulz Colln)

4 = holotype of *C. matesovi* (see Poslavskaia & Moskvin in Moskvin 1959, p. 251).

* = approximate

Description: Both specimens from Höver have suffered slightly from compaction and are abraded in places; in addition, the larger one shows partial recrystallisation, in particular apically. Both are distinctly longer than wide (L/W ratio 1.2 and 1.2 vs 1.1 in the holotype), their outline being subcircular to subpentagonal, with the posterior end more or less constricted. In profile, both specimens are tall with straight anterior/posterior and slightly concave lateral flanks, and have anterior and posterior elevations bordering the apical disc. Test height corresponds to 88 and 74% of test length, respectively (vs 89% in the holotype). The ambitus is situated very low on the test, around 10% of test height above the base. The oral surface forms a flat to slightly concave and broad base, with the posterior interambulacrum slightly elevated around the periproct. As preserved in MB.E 3592 (Pl. 1: 1–4), the apical disc has an enlarged genital plate 2 which does not contact the posterior ocular plates and separate the posterior two genital plates. Ambulacra are comparatively narrow (width ratio A/IA directly above ambitus 0.3 and 0.3), with simple, undifferentiated oblique

pore pairs adapically; pyrinoid plating developing at mid-flank and continuing adorally, occurring in oblique triads on the oral surface. Adapically, every second or third plate with single perforate tubercle close to pore pair, in centre of ring-shaped depression. Interambulacra wide with scattered tubercles of comparable size, as well as much smaller bead-like secondary spines and granules. The peristome is subcentral, subcircular to slightly elongate along axis 3-I. The periproct is oval, widest in posterior half, corresponding to 14.1 and 11.9% of test length, respectively. Periproct position inframarginal, nearly oral on account of low position of ambitus, just partially visible in posterior profile.

Although fragmentary and much more poorly preserved, MB.E 3594 (Pl. 1: 11–12) from Lägerdorf corresponds in all details of ambulacral plating and tuberculation. It is laterally compressed, which accounts for the fact that test measurements (length, width, height) cannot be but approximate. Moreover, it is impossible to measure peristome length and periproct width. Although having less concave lateral flanks, this test is otherwise closely comparable to the specimens from Höver and is here considered to be conspecific.

Discussion: The closest resemblance of the present specimens is to *Conulus matesovi*, originally recorded from the Lower Campanian of the Caucasus (Poslavskaia & Moskvin in Moskvin 1959). Subsequently, Moskvin & Endel'man (1972: 7, table) showed it to range from the upper Lower into possibly lower Upper Campanian of Mangyshlak. Identification of MB.E 3592 from Höver and of MB.E 3594 from Lägerdorf as *C. matesovi* was favoured by the late M.-G. Schulz (pers. comm., July 1985); we concur.

As pointed out by Smith & Wright (1999: 374), species of *Conulus* have been distinguished previously almost exclusively on test shape and lateral profile. Although characteristic shapes occur at different stratigraphic levels, it appears that there are no clear-cut differences as far as plating, tuberculation and ambulacral structure are concerned. Smith & Wright (1999) accepted as valid: *C. castanea* (Brongniart, 1822) (p. 336, pl. 9, fig. 14), ranging from the mid-Albian to the early Late Cenomanian, *C. subrotundus* Mantell, 1822 (p. 191, pl. 17, figs 15, 18), from the Turonian-Santonian and *C. albogalerus* Leske, 1778 (p. 162, pl. 13a, b), which ranges from the Late Coniacian to Early Campanian, but which is best known from the Santonian (see also Malinowska

1989). Interestingly, Smith & Wright (1999) synonymised *C. matesovi* with *C. albogalerus*, noting that specimens referred to the latter species occurred in the Lower Campanian of Rottingdean (Sussex) and Winchester (Hampshire), England. However, these authors remarked (p. 382) that in *C. albogalerus* tests were slightly wider than long, subcircular to subpentagonal in outline, with width 87–98% of length (mean 92%), and had a tall domal to conical profile, with height 65–100% of test length (mean 82%), as well as an oval periproct, 10–13% of test length.

Although test height/length and periproct width/length ratios of the present specimens and of *C. albogalerus* (sensu Smith & Wright 1999) overlap, the German material is distinctly longer than wide, has concave lateral flanks, a more or less constricted posterior test surface (around periproct), is flattened apically (highest points just anterior and posterior of apical disc), and has a more longitudinal periproct. Although some specimens of *C. albogalerus* (e.g., pl. 123, figs 1–4, Santonian of Kent, England, in Smith & Wright 1999) are more or less comparable in profile, their ambulacra appear to be wider and their lateral flanks are not concave. Remarkable is, that the holotype of *C. matesovi* and both specimens from Höver (in the Lägerdorf specimen this is much less clearly marked) have concave lateral flanks, and suggests that this may be a feature typical of that species. This assumption becomes even more convincing when another species, *Conulus campaniformis* Melikov & Endel'man, 1963 (p. 136, fig. 1), from the Lower Maastrichtian of the Caucasus, is considered. This has even more concave flanks, is of comparable size to *C. matesovi* (length/width ratios 1.04–1.10; test height 76.5–89.3% of test length), and appears to be a direct descendant of that species. The 'lineage' is characterised by an increase in lateral flank concavity, and may be an offshoot of the main *albogalerus* lineage, more or less confined to the Campanian-Maastrichtian of the southeastern part of the Russian Platform, with the exception of the present records. In order to test this hypothesis more material is needed from the type areas of both forms. For the time being, we here consider the taxa to be distinct species that may be differentiated from congeners (see below) on test profile mainly; ambulacral structure and width is another feature that warrants closer inspection.

The specimen of *C. matesovae* [sic] illustrated by Ali-Zade et al. (1988: pl. 2a, fig. 1) differs

from the material described here in lacking the concave lateral flanks and in having less regular ambulacral plating; it may be more closely related to specimens referred to *C. albogalerus* from the Lower Campanian of England by Smith & Wright (1999).

Other European Campanian-Maastrichtian species of *Conulus*, recorded in the literature (Radig 1973; Kutscher 1986; Jeffery 1997; Smith et al. 1999; Smith & Jeffery 2000) are:

Conulus douvillei (Cotteau & Gauthier, 1895: 70, pl. 11, figs 9–13) (see Smith & Jeffery 2000: 144, fig. 60g–k), from the Campanian of Saudi Arabia and the Maastrichtian of Libya, Oman/United Arab Emirates border regions, Baluchistan, India and Tibet. This clearly differs from *C. matesovi* in having a large, strongly oblique peristome, a submarginal periproct; in addition, test width is between 80 and 95% of test length.

Conulus gigas (Cotteau in Leymerie & Cotteau 1856: 330) (see Smith & Jeffery 2000, fig. 60a, b) from the Maastrichtian of France and northern Spain (see Wilmsen et al. 1996), Libya and Cuba, differs from *C. matesovi* in having an inflated test with rounded margins, a tumid oral surface with a slightly sunken, relatively small peristome as well as a submarginal periproct.

Conulus magnificus (d'Orbigny, 1854: 540, pl. 1004), a late Early to Late Maastrichtian species from Mangyshlak (Kazakhstan), Crimea, northern Caucasus, Bulgaria, ?Kopet Dag, ?Azerbaijan, northern Germany and Denmark, differs from *C. matesovi* in having a transversely oval periproct, fine aboral tuberculation and aboral pore pairs that are strongly oblique and well separated.

Conulus? placentula (Stoliczka, 1873: 36, pl. 6, fig. 4), from the Campanian-Maastrichtian of India (see Smith & Jeffery 2000: 146, fig. 60e, f) is easily distinguished by its depressed profile, a small peristome and a submarginal, longitudinally oval periproct.

Moskvin et al. (1980) listed a few other 'species' from the Maastrichtian of the Caucasus and Mangyshlak, but as Smith & Jeffery (2000: 147) have recently pointed out, these cannot be properly compared due to lack of illustrations and/or descriptions.

Gallemlí et al. (1995: 268, table 1) recorded *Conulus haugi* Lambert 1935 from the Upper Campanian (Unit 3) of the Internal Prebetic (southeast Spain), also known from Navarra and the Pyrenees. According to these authors, *Conulus matesovae* [sic], from the Caucasus and Mangyshlak, is a synonym of *C. haugi*. We do not

subscribe to this view, pending a revision of *C. haugi*. A single specimen (MB.E 3597), of Campanian age, from a temporary motorway outcrop at Sarasate (Barranca, northeast Spain; Pl. 1: 9–10), which may be assigned to *C. haugi* (? = *Conulus* sp. of K uchler 2000: 453, fig. 4) has a less elongate periproct, a comparatively smaller peristome, lacks the concave lateral flanks of *C. matesovi*, and the ambital A/IA ratio differs, with more regular plating. In addition, the L/W ratio is 1.1, and test height corresponds to 70.1% of test length.

Occurrence: Campanian of the Caucasus region, Kazakhstan and Germany.

Order **Cassiduloida** Claus, 1880

Family **Pygaulidae** Lambert, 1905

Genus ***Echinogalerus*** K onig, 1825

Type species: *Echinites peltiformis* Wahlenberg, 1821, by subsequent designation of Lambert (1898).

***Echinogalerus peltiformis* (Wahlenberg, 1821)**

Pl. 2: 1–3

*1821 *Echinites peltiformis* – Wahlenberg, p. 50, pl. 3, fig. 1.
1976 *Echinogalerus peltiformis* (Wahlenberg) – Reyment, p. 5, fig. 15
1995 *Echinogalerus* sp. – Frerichs, p. 14, fig. 10 (*partim*).

Material: A single specimen (MB.E 3595 cast; original in U. Frerichs Colln, Hannover, number F1) from the upper Lower Campanian (*senonensis* or *papillosa*-Zone) of the Alemannia quarry (H over). The tests in the I. Krause Colln, Hannover (numbers K1, K2; see Frerichs 1995: fig. 11) have not been restudied, but may be conspecific.

Description: Medium-sized test (length 18.2 mm, width 16.1 mm, height 12.3 mm), outline elliptical, greatest test width at mid-length; profile rather high. Oral side pulvinate, apical side domed; apex slightly anterior to mid-length. Ambulacra nonpetaloid, with double pores aborally; pore pairs small, each in a shallow pit. Peristome oblique, periproct inframarginal, 4 mm wide, transversely elliptical to triangular. Tubercles relatively small but distinct, also above periproct, slightly more pronounced anteriorly.

Discussion: Van der Ham & van Birgelen (2002) tentatively distinguish three infrageneric ‘groupings’, as well as a number of more or less

isolated species within the genus *Echinogalerus*. ‘Group 1’ includes species with an elliptical outline, subpetaloid ambulacra with distinct double pores aborally, an oblique peristome and a relatively large periproct, *viz.* *Echinogalerus faba* (Desor, 1842) from the Cenomanian of western France and south-west England, *E. goslariensis* (Schl uter, 1902) [Santonian of northern Germany], *E. muelleri* (Schl uter, 1902) [Maastrichtian of the southeast Netherlands and northern Spain], and *E. rutoti* (Lambert, 1898) [Maastrichtian of southern Belgium].

‘Group 2’ comprises species with an elliptical outline, nonpetaloid ambulacra with small pore pairs in shallow pits, an oblique peristome and a relatively large periproct, *viz.* *Echinogalerus bueltenensis* (Schl uter, 1902) (Santonian of northern Germany) and *E. peltiformis* (Campanian of southern Sweden).

‘Group 3’ includes species with a circular outline, nonpetaloid ambulacra with small pore pairs in shallow pits, a near-circular peristome and a relatively small, vaguely triangular to circular periproct, *viz.* *Echinogalerus circularis* (Schl uter, 1902) [Turonian of north-west Germany], *E. tenuiporus* (Schl uter, 1902) [Maastrichtian of northern Germany], *E. vetschauensis* (Schl uter, 1902) [Maastrichtian of the southeast Netherlands and northern Spain], and possibly also *E. dolfussi* (Lambert 1898) and *E. truncatus* (d’Orbigny, 1857) [both Maastrichtian of western France].

Other species of *Echinogalerus* are difficult to tie in with the above groupings. *Echinogalerus belgicus* (Lambert, 1898) and *E. pusillus* Lambert, 1911 both from the Maastrichtian of the southeast Netherlands have simple pores, while *E. minutus* (Smiser, 1935) [Maastrichtian of the southeast Netherlands] resembles *E. gehrdensis* (Roemer, 1841) [Santonian of north-west Germany] in having a concave oral side and a symmetrical peristome. *Echinogalerus rostratus* (Desor, 1842) [Cenomanian of western France and south-west England] is similar to these two species, but has a flat oral side, whereas *E. althi* (Zarczny, 1878) [?Turonian of Poland], *E. laubei* (Nov ak, 1887) [Turonian of Bohemia], and *E. orbicularis* (Desor, 1842) [Cenomanian of western France] are poorly known.

Based on these observations, the species of *Echinogalerus* from H over discussed here, belongs to the *bueltenensis-peltiformis* group (‘Group 2’). These two species are morphologically closely related (see Ernst 1973). *Echinogalerus bueltenensis* is well known from the Middle Santonian of the Hannover area; specimens from

Lengede (H.-V. Thiel Colln), Hoheneggelsen and Groß-Bülten (G. Ernst Colln; see Fig. 2B) studied for the present paper closely match Schlüter's (1902) description and illustrations. *Echinogalerus peltiformis* from the Lower Campanian of Skane has been illustrated by Wahlenberg (1821), d'Orbigny (1857), Lambert (1911), Reymont (1976) and Zuidema (1999). The type specimen is present in the Palaeontological Institute in Uppsala (comm. W. Kegel Christensen), but has not been studied. Instead, we have compared the specimen from Höver with other material from southern Sweden, all labelled *E. peltiformis* (see Fig. 2C) and contained in the Swedish Museum of Natural History in Stockholm. According to Schlüter (1902: 308), *E. peltiformis* may reach overall test lengths of 25 mm.

Echinogalerus bueltenensis and *E. peltiformis* are closely similar. The only difference detected so far is the position of the apex, which is clearly anterior to mid-length in the former, and at mid-length or just slightly anterior to it in the latter. On the basis of this character, the Höver specimen is here assigned to *E. peltiformis*; thus extending the geographical distribution of this taxon from southern Sweden to northeast Germany.

To round off this section, a few words on the co-occurring *Echinoconus hannoniensis* Lambert, 1911, are needed. This species was referred to as *Echinogalerus* (?) *hannoniensis* by Schulz (1985) and is known from the upper Lower Campanian of the Hannover area (e.g., Höver). Schulz (1985) discussed its possible assignment to the genus *Echinogalerus*. Based on the original description and illustrations (Roemer 1841, as *Galerites globosus*), this species has a much more spherical test than *E. peltiformis* from Höver: its width and height are 93% and 87% of test length respectively (vs. 88% and 68% in *E. peltiformis*). Schulz (1985) indicated a range between 11.3 and 15.2 mm for eight specimens from Höver, while Ernst (1972) noted lengths between 6 and 16 mm for 58 specimens from Oberg near Peine. *Echinogalerus peltiformis* (MB.E 3595) measures 18.2 mm in length. Additional comparisons, notably of peristome, periproct, and morphology of pores and tuberculation are needed to establish that species' relationship with the genus *Echinogalerus*.

Occurrence: In Sweden, *E. peltiformis* was recorded from the *mammillatus* Zone (uppermost Lower Campanian) and *mucronata* Zone (lowest Upper Campanian) (Christensen 1975, Kennedy & Christensen 1997) of the Kristianstad area in

Scania by Lundgren (1888). It was later recorded from the Malen quarry in the Bastad Basin (Wiman 1916). This locality was placed in the lower Upper Campanian by Christensen (1993).

Order **Holasteroida** Durham & Melville, 1957

Family **Holasteridae** Pictet, 1857

Genus **Hagenowia** Duncan, 1889

Type species: *Cardiaster rostratus* Forbes, 1852, by original designation.

***Hagenowia blackmorei* Wright & Wright, 1949**

Pl. 2: 4–8

*1949 *Hagenowia blackmorei* – Wright & Wright, p. 467, figs 14–16.

1982 *Hagenowia blackmorei* Wright & Wright – Gale & Smith, p. 21, pl. 3, figs 7–8; pl. 4, fig. 6; pl. 6, figs 4, 7, 9; text-fig. 6 (with additional synonymy).

Material: Thirteen rostra from the upper *pilula* Zone to *conical/gracilis* Zone (Lower Campanian) of Höver (Alemannia) (M. Jäger Colln, Dotternhausen, unregistered; four of these have been selected for SEM observations). A single test (lacking rostrum) from Höver (Alemannia) (H. Reim Colln, Hannover; based on photographs). In addition, the BGR microfossil collections (Hannover) contain a small number of *Hagenowia* rostra recovered from various boreholes penetrating the Campanian in the Hannover area.

Description: Rostrum long, slender, club-shaped, well demarcated from body; anterior end of rostrum inflated; high-triangular in cross section, with the lateral sides broader than the dorsal and ventral sides; frontal sulcus shallow with a flattened floor; dorsal ridge of rostrum broad and flattened, distinguishing this species from *H. elongata* (see below); rostral surface densely covered with miliaries; primary tubercles restricted to apex. Genitals 2, 3 not separated from oculars II, IV; number and arrangement of madreporic pores variable.

Discussion: According to M. Jäger (pers. comm. 2000), *H. blackmorei* ranges throughout the entire Campanian at Höver and Misburg with the exception of its basal portion (*lingual quadrata* Zone and lower *pilula* Zone) which is characterised by a much higher clay content. For southern England, Gale & Smith (1982) noted the appearance of *H. blackmorei* to be confined to the lower part of the *Goniot euthis quadrata* Zone (equivalent of the *pilula/senonensis* to gra-

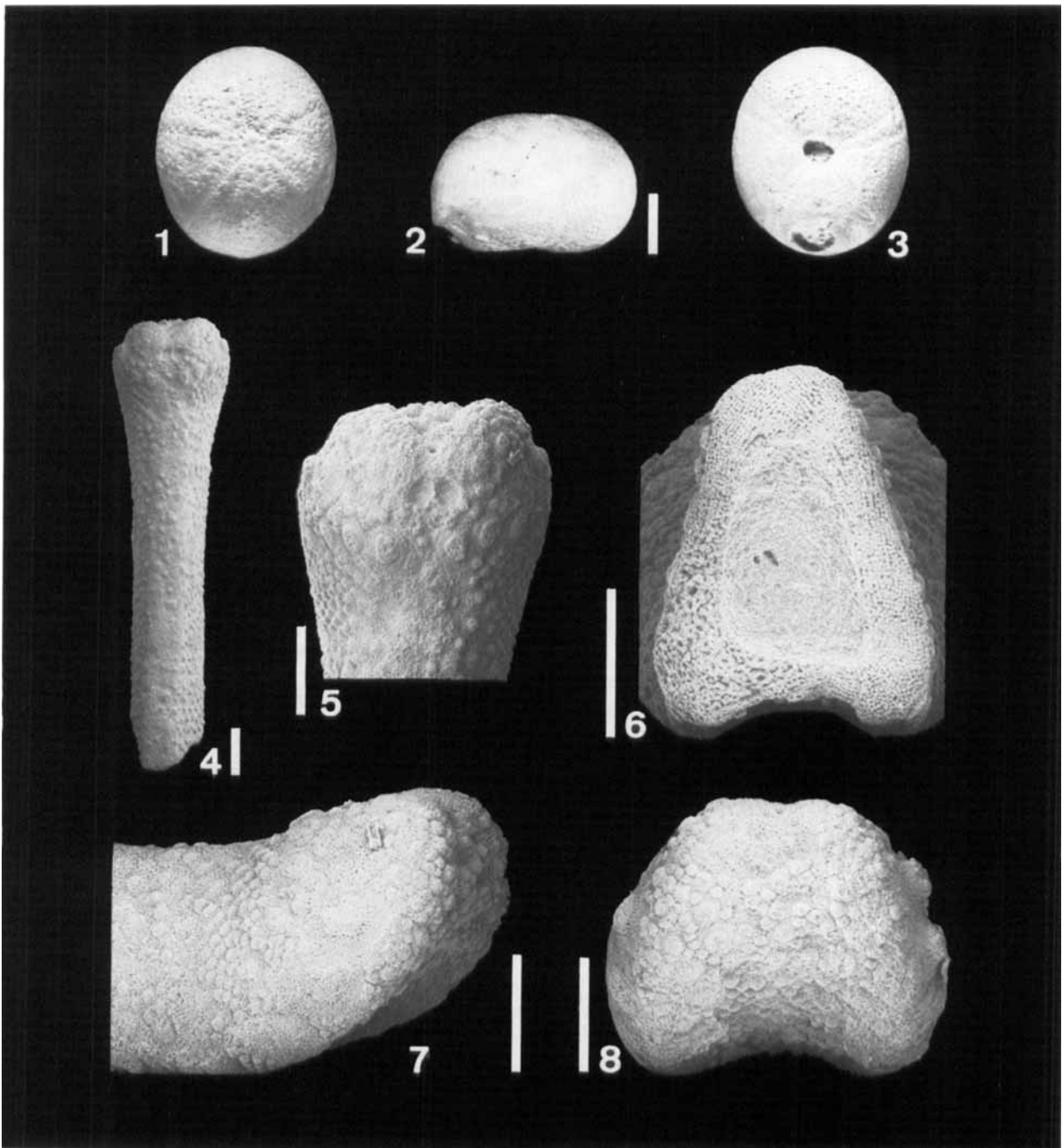


Plate 2. *Echinogalerus peltiformis* and *Hagenowia blackmorei*. 1–3. *Echinogalerus peltiformis* (Wahlenberg, 1821), cast MB.E 3595 in three aspects (1. aboral; 2. lateral; 3. oral). Lower Campanian of Höver (original in U. Frerichs Colln, Hannover, number F1). Scale bar equals 5 mm. 4–8. *Hagenowia blackmorei* Wright & Wright, 1949, rostrum. Lower Campanian of Höver (unregistered, M. Jäger Colln, Dotternhausen). SEM photographs. 4. Rostrum, anterior view; 5. Frontal view of aboral system.; 6. Cross section of rostrum showing well-preserved stereom structure and diagnostic shape; 7. Lateral view of apex; 8. Apical view of apex and frontal furrow. Scale bar for all figures equals 500 μ m.

cilis/mucronata Zones of northern Germany, see Christensen 1991), a range corresponding to the occurrence at Höver recorded in the present paper.

Hagenowia sp. ?nov. from the lower Upper Campanian of Liège (NE Belgium; see Jagt 2000: 279, pl. 23, figs 1–4) and Norfolk (England) may be transitional between *H. blackmorei* and *H. elongata* (Brünnich Nielsen 1942) (see

Schmid 1972), from the (upper) Lower Maastriichtian of northern Germany (Kutscher 1978a) and Denmark. This form appears to have the gently concave floor of the sulcus, the narrow dorsal ridge on the rostrum, and the number of gonopores and arrangement/number of madreporic pores in common with *H. blackmorei*. However, genitals 2, 3 seem to be separated from culars II, IV, a feature typical of *H. elongata*. The

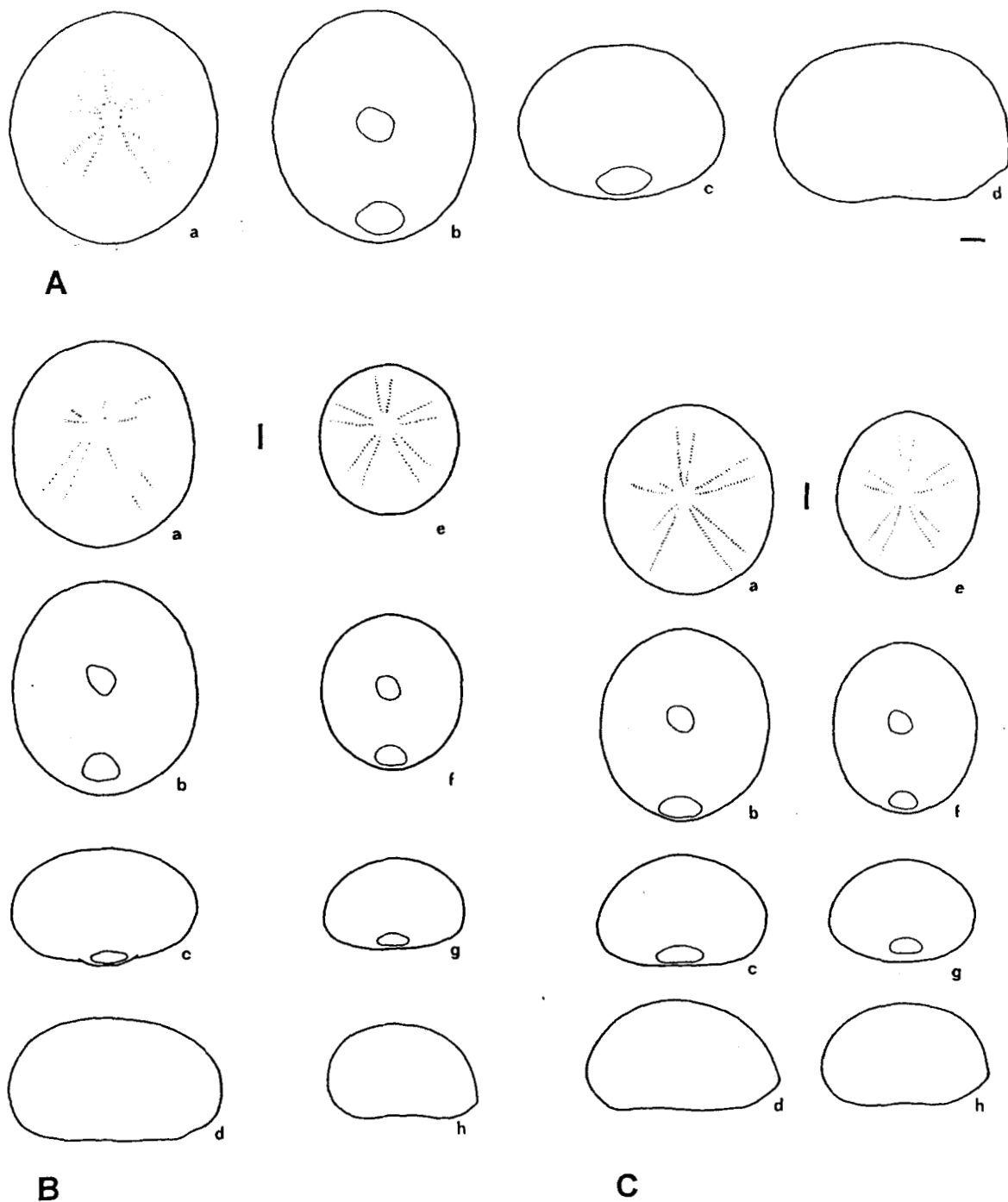


Fig. 2. Camera lucida drawings of *Echinogalerus* species discussed in the text. **A.** *Echinogalerus peltiformis* (Wahlenberg, 1821) in various aspects, MBE 3595 (cast; original in U. Frerichs Colln, no. F1); Alemannia quarry (Höver); Lower Campanian. Scale bar equals 2 mm. **B.** *Echinogalerus bueltenensis* (Schlüter, 1902) in various aspects. a–d = G. Ernst Colln, no. 30 (Berlin) from the Middle Santonian of Groß Bülten; e–f = G. Ernst Colln, no. 71 (Berlin) from the Santonian of Hoheneggelsen. Scale bar equals 2 mm. **C.** *Echinogalerus peltiformis* (Wahlenberg, 1821) in various aspects. a–d: 7584–7643/345 from the Lower Campanian of Kjuge (southern Sweden); e–f: unregistered specimen in the De Geer Colln from the Lower Campanian of Barnakälla (southern Sweden); both specimens in collections of the Swedish Museum of Natural History (Stockholm). Scale bar equals 2 mm.

relationship between *Hagenowia* sp. nov., *H. blackmorei* and *H. elongata* will be discussed in detail elsewhere.

Hagenowia is a highly specialised endofaunal mud dweller previously assumed to have been restricted to the pelagic white chalk facies (e.g.,

Gale & Smith, 1982) where it often ranks among the most common echinoids (H. Ernst 1984). The occurrence of *H. blackmorei* in the marly limestone facies at Höver and Misburg clearly demonstrates that this species had a much wider ecological range than assumed previously. More-

over, *Hagenowia* has a small and fragile tests leading to a limited preservation potential, which makes it more than likely that the isolated rostra are often overlooked by collectors.

Occurrence: *H. blackmorei* is known from the Campanian of Germany and England.

Order **Spatangoida** Claus, 1876

Suborder **Micrasterina** Fischer in Moore, 1966

Family **Micrasteridae** Lambert, 1920

Genus ***Diplodetus*** Schlüter, 1900

Type species: *Diplodetus schlueteri* Lambert in Lambert & Thiéry, 1924 [= *Diplodetus brevistella* (Schlüter, 1870a)], by subsequent designation of Lambert & Thiéry (1924).

***Diplodetus* sp.**

Pl. 3: 4

Material: A single specimen (MB.E 3336) from the upper Lower Campanian (*gracilis/mucronata* Zone, G/K 24 *sensu* Khosrovshahian, 1972) at Misburg (Teutonia). The thin test is crushed and incomplete, lacking most of the aboral surface.

Description: Medium-sized spatangoid (length: 37.7 mm; width: 30.3 mm), rectangular to coffin-shaped in outline, with a broadly rounded anterior, no frontal sulcus; test truncated posteriorly, anal surface high, overhanging (angle 80°); plastron asymmetrical, sternal suture meets the labrum far to the right; labrum relatively large, triangular, with broad contact to the sternal plates of the plastron; periproct small, circular and situated high on the posterior surface; peristome ovoid, relatively small, surrounded by conspicuous phyllode pores; primary tubercles small, scattered and uniform except anteriorly and on the plastron, where tubercle arrangement is slightly denser, tubercles larger and with areole

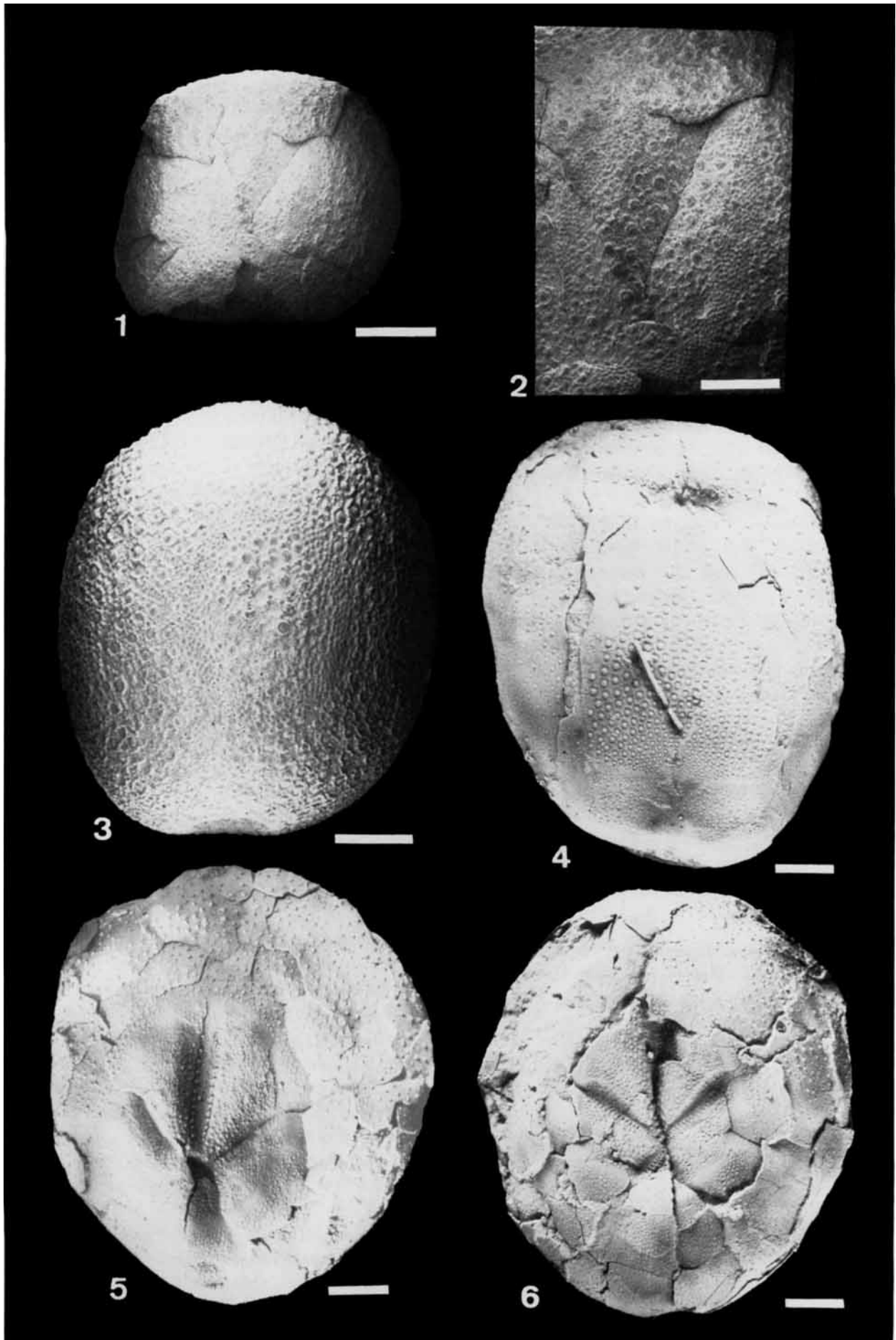
enlargement towards the posterior. A well-defined subanal fasciole is present.

Discussion: Although the aboral surface is missing we assign this specimen to *Diplodetus* on account of test shape, type of tuberculation, plastron/labral structure, in combination with the presence of a subanal fasciole. A number of characters clearly distinguishes this specimen from Campanian *Micraster* species: *Micraster* differs by its thicker test and cordiform outline, and its symmetrical plastron with a narrow and long labrum which protrudes over the peristome and which is only in little contact with the sternal plates. The peristome of *Micraster* is positioned at the frontal margin of the test. Moreover, the tuberculation of *Micraster* is markedly denser and coarser.

The find of *Diplodetus* sp. in the hemipelagic marly limestone facies of Misburg is surprising. As noted by Stokes (1979), the occurrence of members of the genus *Diplodetus* was strongly facies controlled, with most species having been recorded from more marginal, often glauconitic biocalcarenic facies rather than pure, white chalk facies types. Numerous 'species' have been described from the Lower and Upper Campanian of the Münsterland Basin by Schlüter (1870a, b, 1900) but these are in need revision. Hampering such a revision is the general poor preservation of the types and lack of stratigraphically well-documented material. Jagt (2000: 292) noted that too much splitting may have taken place in this genus. For comparison with the Misburg specimen described above, the following taxa of *Diplodetus* (or *Plesiaster*, to which some species have originally been attributed), are considered. However, for a more in-depth comparison more material from the Hannover area is needed, especially specimens preserving aboral test features:

Diplodetus brevistella (Schlüter, 1870a: 132; see also Schlüter 1900: 364, pl. 15, figs 3–5; RFWUIP Schlüter no. 281) was recorded from the 'Untere Mucronaten-Schichten' (= lower

Plate 3. *Peroniaster cotteaui*, *Hemiaster aquisgranensis* and *Diplodetus* sp. 1–2. *Peroniaster cotteaui* Gauthier in Peron, 1887; Lower Campanian of Höver. Specimen MB.E 3532. SEM photographs. 1. Aboral view. Scale bar equals 2 mm. 2. Detail of aboral surface. Note peripetalous fasciole and enlarged primary tubercles bordering ambulacrum III. Scale bar equals 1 mm. 3. *Peroniaster cotteaui* Gauthier in Peron 1887. Juvenile specimen in aboral view, showing a well-developed peripetalous fasciole. Ambulacral pores and gonopores are still lacking. Lowermost Maastrichtian (mB 606, *lanceolata* Zone), white chalk of Kronsmoor. Scale bar equals 1 mm. 4. *Diplodetus* sp. Specimen MB.E 3336. View of the preserved oral surface. Upper Lower Campanian (*gracilis/mucronata* Zone, G/K 24 *sensu* Khosrovshahian, 1972) at Misburg. Scale bar equals 0.5 cm. 5. *Hemiaster aquisgranensis* Schlüter 1899. Specimen MB.E 3337, aboral view. Lower Campanian of Höver. Scale bar equals 5 mm. 6. *Hemiaster aquisgranensis* Schlüter 1899. Specimen MB.E 3789, aboral view. Upper Campanian of Misburg. Scale bar equals 5 mm.



Upper Campanian by inference) at Coesfeld-Sückerhoek and Darup (Münsterland, Germany), i.e. in a glauconitic facies type;

Diplodetus cretaceus (Schlüter, 1870b: 956; see also Schlüter, 1900: 366, pl. 15, fig. 2; RFWUIP Schlüter no. 282a) which is slightly younger, having been described from the 'obere Mucronaten-Kreide, Zone des *Heteroceras polyplacum*' (= upper Upper Campanian) at Haldem (Germany). This species has recently also been recorded from the upper *bipunctatum/roemeri* Zone Zone (upper Upper Campanian) of Ahlten, by Niebuhr et al. (1997); both these occurrences refer to the so-called Opoka (siliceous limestone) facies;

Diplodetus? recklinghausenensis Schlüter, 1900 (p. 368, pl. 15, fig. 1; RFWUIP Schlüter no. 283) is a Late Santonian species from Recklinghausen, also known from the Santonian of Gehrden (Ernst 1973: 99, fig. 6), in a sandy, glauconitic facies type;

Plesiaster minor (Schlüter, 1870a: 132; see also Schlüter 1900: 369, pl. 16, figs 3–5; RFWUIP Schlüter no. 284), now also assigned to *Diplodetus*, is from the upper Lower Campanian ("... in den jüngsten Schichten mit *Actinocamax quadratus* ...") of Lette, Coesfeld and Holtwick (Münsterland), as is *Plesiaster? cavifer* Schlüter 1900 (p. 371, pl. 17, figs 3, 4; RFWUIP Schlüter no. 285a) ("... in der jüngsten Quadraten-Kreide, Zone der *Becksia Soekelandi* ...") of Lette and Coesfeld. Slightly younger is *Plesiaster? cordiformis* Schlüter, 1900 (p. 372, pl. 16, figs 1, 2; RFWUIP Schlüter no. 286), from the "untere Mucronaten-Schichten" near Coesfeld. All these "species" are from glauconitic, comparatively coarse-grained sediments.

Suborder **Hemiasterina** Fischer in Moore, 1966
Family **Hemiasteridae** H. L. Clark, 1917
Genus **Hemiaster** Agassiz in Agassiz & Desor, 1847

Type species: *Spatangus bufo* Brongniart 1822, by subsequent designation of Savin (1903).

***Hemiaster* gr. *aquisgranensis* Schlüter, 1899**

Pl. 3: 5–6

*1899 *Hemiaster(?) aquisgranensis* – Schlüter, p. 123, pl. 10, figs 1, 2.

*1911 *Hemiaster rutoti* Lambert, p. 52, pl. 3, figs 3–5.

1995 *Hemiaster (Bolbaster) aquisgranensis* Schlüter – Jagt & van Knippenberg, p. 111, figs 1, 2.

1997 *Diplodetus cretaceus* (Schlüter) – Niebuhr et al., pl. 4, fig. 6 only.

2000 *Hemiaster* gr. *aquisgranensis* Schlüter – Jagt, p. 292, pl. 28, figs 1–6.

Material: Two specimens studied: M.B.E. 3337 (ex M. Jäger Colln) from Höver (Alemannia, Lower Campanian) and M.B.E. 3789 (ex G. Ernst Colln) from Misburg (Teutonia, Upper Campanian).

Description: Although crushed and partially damaged, both specimens retain fairly well-preserved aboral test surfaces. Thin-tested, almost as broad as long (M.B.E. 3337 measures 37.7 mm in length and 35.0 mm in width), circular in outline, no frontal sulcus. Apical system slightly anterior. Plastron with nearly symmetrical sternal plates. Labrum, periproct and peristome not preserved, but it appears that the position of the peristome was submarginal. Petals well developed, length of anterior ambulacra is 44% of length of posteriors. Pores in petals slit-like. Frontal ambulacrum narrow and slightly sunken within the peripetalous fasciole. Here, pores are oblique isopores which show a prominent interporal partition. Peripetalous fasciole well-developed, narrow. Primary tubercles on the aboral side are large and scattered, inside the peripetalous fasciole smaller and more densely arranged. On the oral surface, primary tubercles are small and scattered, except on the plastron.

Discussion: For the time being, usage of the name *H. aquisgranensis* is preferred for medium- to large-sized hemiasterids with non-scrobicular tuberculation. The type is a flint-preserved internal mould from strata of undoubted Late Maastrichtian age. Large collections from the upper Gulpen and lower Maastricht formations (inclusive of the Kunrade Limestone facies) of the type area of the Maastrichtian stage are available, and these clearly demonstrate that *H. rutoti* is a junior synonym. Van der Ham (1985) and Jagt (2000), who both referred material of Early Campanian to Late Maastrichtian age to *H. aquisgranensis*, stressed that this was a heterogeneous lot, and that various test morphologies might be separated on the basis of biometric analyses in the future. Pending such a revision, all material is here assigned to *H. aquisgranensis*. From the Hannover-Misburg area, this hemiasterid was first recorded by Jagt & van Knippenberg (1995).

Smith & Jeffery (2000) tentatively synonymised *H. aquisgranensis* and *H. rutoti* with *Hemiaster stella* (Morton, 1830: 245, pl. 3, fig. 11), originally recorded from the Paleocene Vincentown Sand of New Jersey (USA).

Occurrence: *H. aquisgranensis* is well known from the Campanian/Maastrichtian of Limburg, Liège, Aachen and the western Münsterland Basin. In our context, it is interesting, that it was recently found in the upper Upper Campanian (*polyplacum* to *bipunctatum/roemeri* Zones) of the nearby locality Ahlten, where it occurs in the spiculitic chalk of the so-called Opoka facies.

Genus *Peroniaster* Gauthier in Peron, 1887

Type species: *Peroniaster cotteai* Gauthier in Peron 1887, by monotypy.

***Peroniaster cotteai* Gauthier in Peron, 1887**

Pl. 3: 1–3

*1887 *Peroniaster cotteai* – Gauthier in Peron, p. 390, pl. 7, figs 1–7.

1978b *Peroniaster cotteai* Gauthier – Kutscher, p. 1025, pl. 1.

2000 *Hemiaster* sp. indet. 4 – Smith & Jeffery, p. 327.

2001 *Bolbaster cotteai* (Gauthier) – Néraudeau & Odin, p. 624, pl. 3, figs 60–62.

(non) 1974 *Peroniaster* cf. *cotteai* Gauthier – Ernst & Schulz p. 24, fig. 6.

Material: Two specimens (MB.E 3532, 3533) from Höver (Alemannia, upper Lower Campanian).

Description: Test small (in MB.E 3532 length is 8.2 mm and width is 7.1 mm), nearly circular in outline; no frontal sulcus. Oral and aboral surfaces flattened, test highest anterior of centre; anterior surface steep, inclined ca. 85° so that the periproct is just visible from above. Plastron wide, slightly inflated, sternal plates almost symmetrical; peristome submarginal, kidney-shaped with distinct rim, with the labrum forming a prominent lip projecting slightly over peristome; apical disc damaged, but apparently positioned centrally; with the exception of the periplastral area, the test is densely covered with large, perforate scrobicular tubercles; periplastral areas show marked labyrinthic ornamentation. Frontal ambulacrum bordered laterally by single rows of enlarged tubercles; peripetalous fasciole wide and well developed. Aborally, paired ambulacra are non-petaloid, flush with test; pores reduced or altogether lacking. Within the peripetalous fasciole, the frontal ambulacrum is weakly sunken and bears a low number of tiny, circular isopores. Phyllode pores are missing.

Discussion: Although both specimens are crushed and have a slightly abraded test surface, preservation is such that they may be identified at species level with confidence. Previously, the status of the genus *Peroniaster* has often been the subject of controversy. In Gauthier's original illustration of the species, gonopores cannot be made out. Duncan (1889) and Fischer (1966) considered it to be synonymous with *Hemiaster* and Mortensen (1950) opined that *Peroniaster cotteai* might be a juvenile of an unknown *Hemiaster*. Recently, Smith & Jeffery (2000) adopted Mortensen's point of view while Néraudeau & Odin (2001) assigned it to the genus *Bolbaster*, generally considered to be a subgenus of *Hemiaster*. On the other hand, Ernst & Schulz (1974) and Kutscher (1978b) provided illustrations of *Peroniaster* with open and clearly visible gonopores and noted that specimens studied by them were indeed small but without doubt represented adult echinoids.

Peroniaster cotteai appears to be a markedly pedomorphic species with juveniles lacking developed gonopores, albeit similar in overall shape to adult ones (see also Pl. 3: 3). The largest known representative of the genus is *Peroniaster* sp. from the Middle Coniacian of Lägerdorf (maximum test length 17.5 mm); this also has non-petaloid and almost completely reduced aboral ambulacra (Ernst & Schulz 1974).

Peroniaster is distinguished from *Bolbaster* in lacking petaloid ambulacra, in both the juvenile and adult stage. In the latter, petals form at an early stage of postlarval development at which ambulacral pores are already well-developed and slit-like (see Jagt 2000: pl. 29, figs 5–8).

Psephoaster McNamara, 1987, a small globular hemiasterid from the Cainozoic of Australia also has non-petaloid ambulacra with round isopores and a frontal ambulacrum which is flush with the test. It differs from *Peroniaster* in its larger size as well as in features of tuberculation, and in having a narrower peripetalous fasciole and more numerous pores in the paired ambulacra.

Occurrence: Santonian to Maastrichtian of Spain, France and Germany. In Germany, *P. cotteai* occurs sporadically in the chalk facies at Lägerdorf and Krons Moor, ranging from the Santonian to the Lower Maastrichtian. The species is markedly commoner in the Lower Maastrichtian of Rügen (M. Kutscher, pers. comm. 1999; pers. obs.).

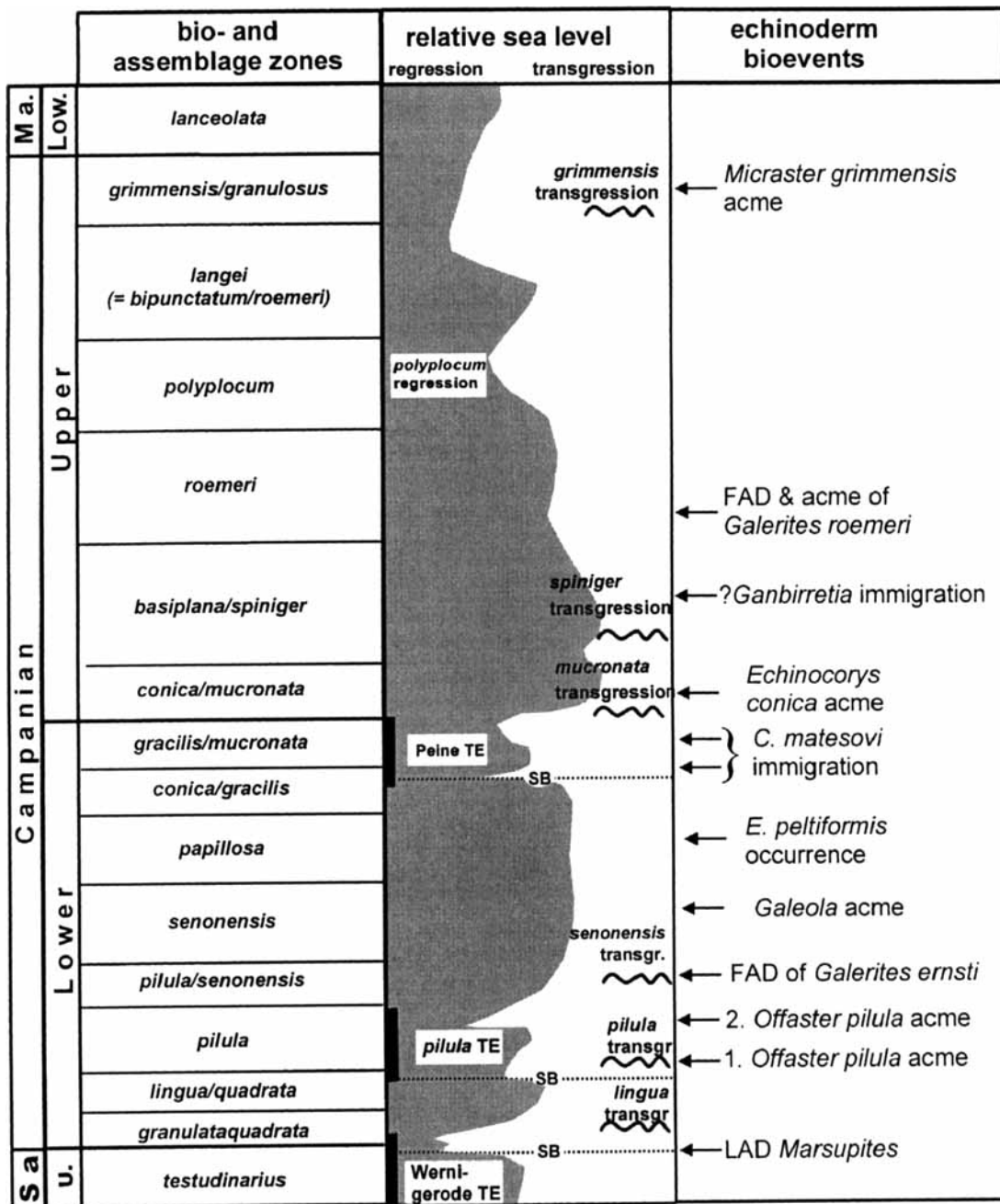


Fig 3. Echinoderm bio-events in the Campanian of northern Germany in relation to eustatics and Subhercynian tectonic phases (sea-level curve and sequence-stratigraphic interpretation compiled after Mortimore et al. [1998], Niebuhr et al. [1997] and unpublished data of G. Ernst). Abbreviations: **FAD**: First appearance datum; **LAD**: Last appearance datum; **SB**: Sequence boundary; **TE**: Tecto-event.

The ecological reasons of rarity in the fossil record

Most of our knowledge of fossil (and extant!) benthic communities comes from the study of common species, but many species are rare. Sea-level driven changes in the relative abundance of common chalk echinoids such as *Echinocorys* and *Micraster* were already recognised by Ernst (1970a) and later by Néraudeau & Villier (1997). However, all the echinoid species discussed in

the present paper are extraordinarily rare in the Campanian strata of the Lower Saxony Basin. How may their rarity be explained? To answer this, we need to address the various ecological and taphonomic processes which may contribute to this picture. Of particular concern is the bias in our knowledge of the structure and ecology of benthic palaeocommunities including biotic interactions, because rare and common species may, and indeed often do, differ in more ways than just their abundance patterns.

Below, we list the four most important processes that may lead to rarity of species in the fossil record, viz. ecological, physical, taphonomic processes as well as sampling biases. These may act together and reinforce each other:

1. Rarity in the fossil record created by the palaeobiology and -ecology of species in a given community (see also Gaston 1996):

Low dispersal abilities

Low reproductive effort

Unfavourable ecological conditions (e.g. low food supply, concurrence/predation pressure)

Patchiness

Temporal persistence (= taxon age)

Endemism

Ranges size.

2. Rarity created by events

Short-term changes of sea level, ocean circulation, climate, food supply may cause short-term invasions of species from neighbouring palaeobiogeographic realms or lead to expansions of distribution ranges. Generally, these 'intruder' species or 'vagrants' are unable to establish populations over a longer period (pulse appearance, Ernst & Wood 1996).

3. Rarity created by taphonomy

Low preservation potential of small or fragile species or species with weakly mineralised hard parts also leads to rarity in the fossil record (this is also the case for early ontogenetic stages as juveniles are markedly under-represented in the fossil record, e.g., Dodd et al. 1985). These are occasionally preserved under sheltered conditions, e.g. in fossil traps (for instance, cephalopod body chambers), or in obrution deposits (*Konservat-Lagerstätten*). This shows that, additionally to taxonomy and ontogeny, preservation potential is strongly controlled by the sedimentary regime which is intimately related to water depth (e.g., Parsons & Brett 1991, Smith et al. 2001).

4. Rarity as a sampling artefact

Sampling methods can also create rarity, e.g. if small or fragmented species are not recognised or overlooked at outcrop or if non-standardised sampling methods are used (non-quantitative sampling methods, in particular).

Applying the above to the irregular echinoids from Höver and Misburg described in the present paper, results in the following interpretation:

Conulus matesovi probably is an intruder (vagrant) from southeast Europe (Caucasus) while the origin of *Echinogalerus peltiformis* remains unknown, since it occurs in younger strata in Southern Sweden. However, we suggest that it

intruded from the northern margin of the North Sea Basin, where it is markedly more abundant in nearshore coarse-grained arenitic limestones. Although ranging throughout the Campanian of the Lower Saxony Basin, *Hagenowia blackmorei* is a rare species; it is much commoner in the pelagic white chalk facies. Its rarity is probably a function of suboptimal ecological conditions (clay content of the substrate?). Isolated rostra are probably also often overlooked by collectors, adding a sampling bias. The genus *Hagenowia* is endemic to the North Sea Basin. Both *Diplodetus* sp. and *Hemiaster aquisgranensis* were probably occasional intruders from more neritic environments elsewhere. Both share the same burrowing and feeding habits (shallow infaunal selective deposit feeders). The latter species is fairly common in neritic sediments (arenitic/spiculitic chalks and limestones) of the western Münsterland Basin, in the Aachen area and in the Liège-Limburg Basin. For *Peroniaster cotteui* we may assume that this small and delicate species had a limited preservation potential in the marly limestone facies where small echinoids are commonly crushed due to compaction and tests surfaces often show signs of dissolution; It is also rare in the pelagic white chalk of the North Sea Basin, but here its preservation is excellent (see Pl. 3: 3). It might be an intruder from southwestern Europe, where it is fairly common in the uppermost Campanian at Tercis les Bains (Landes, France) (see Néraudeau & Odin 2001).

Naturally, the above picture cannot be but preliminary. To explain why some species in the fossil record are rare we need to know much more about their palaeobiology, community interactions, palaeobiogeographic distribution, stratigraphic ranges, facies dependence, taphonomic processes and basin history of any area studied. In addition, proper sampling methods need to be considered and robust data bases developed so as to minimise sampling biases. The echinoid material described in the present paper is the result of more or less random sampling, generally without strict stratigraphic control. Much work still needs to be done for this picture to become more detailed and reliable.

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APPENDIX 1

Irregular echinoid taxa recorded from the Campanian of the Hannover area (Höver, Misburg and Ahlten) (based on Ernst 1975, Niebuhr et al. 1997 and own observations). Asterisks (*) mark species discussed in the present paper.

Holoctypoida

- **Conulus matesovi* Poslavskaja & Moskvina in Moskvina
- Galerites (Peroniaster) ernsti* Schulz
- Galerites roemeri* (Desor)
- Galerites vulgaris* (Leske)
- Galerites sulcatoradiatus* (Goldfuss)

Cassiduloida

- **Echinogalerus peltiformis* (Wahlenberg)
- Echinogalerus? hannoniensis* (Lambert)

Holasteroidea

**Hagenowia blackmorei* Wright & Wright
Offaster pilula (Lamarck)
Offaster aff. *pomeli* Munier-Chalmas
Galeola senonensis d'Orbigny
Galeola papillosa papillosa (Leske)
Galeola papillosa basiplana Ernst
Echinocorys gr. *conica* (Agassiz)
Echinocorys gr. '*gibba/marginata*'
Echinocorys subglobosa (Goldfuss)
Echinocorys pyramidata (Portlock)
Cardiotaxis gr. *lehmanni/heberti*
Cardiaster cordiformis (Woodward)

Spatangoida

**Hemiaster aquisgranensis* Schlüter
**Peroniaster cotteaui* Gauthier in Peron
Micraster fastigatus Gauthier, sensu Stokes
(= *M. gibbus* sensu auct.)
Micraster gr. *schroederi/glyphus*
Micraster stolleyi Lambert
Diplodetus cretaceus Schlüter
**Diplodetus* sp.