

The echinoid genus *Echinogalerus* in the Maastrichtian type area

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Abstract

The Late Cretaceous echinoid genus *Echinogalerus* König, 1825 is remarkably diverse in the Maastrichtian type area (SE Netherlands and adjacent parts of NE Belgium and western Germany). So far, five species have been recognised, namely *E. belgicus* (Lambert, 1898), *E. minutus* (Smiser, 1935), *E. muelleri* (Schlüter, 1902), *E. pusillus* Lambert, 1911 and *E. vetschauensis* (Schlüter, 1902), which occur from the base of the Lower Maastrichtian (*E. belgicus*, *E. pusillus*, *E. muelleri*) up to the K/T boundary (*E. minutus*). *Echinogalerus muelleri*, which has the longest stratigraphical range, is the most diverse, while *E. pusillus* is the smallest echinoid in the area, reaching maximum lengths of 4.5 mm. Comparisons with other species of *Echinogalerus* described in the literature have now led to the recognition of three tentative infrageneric alliances. It is argued that the ordinal position of *Echinogalerus* (Holectypoda or Cassiduloida) cannot be evaluated as long as many species are still insufficiently known and two genera, from the Maastrichtian of northern Germany and Denmark, intermediate between the two orders, remain undescribed.

Keywords: Maastrichtian, echinoids, taxonomy

Introduction

The genus *Echinogalerus* comprises small irregular echinoids known from Cenomanian to Maastrichtian strata in NW Europe. Lambert & Thiéry (1921) listed twenty-one species, and since then, three more have been described (Smiser, 1935; Kongiel, 1950). A number of regional revisions were published during the last decades (Ernst, 1973; Kutscher, 1979; Van der Ham et al., 1987; Smith et al., 1988, 1999; Smith & Wright, 1999; Neumann et al., 2002), but the genus has never been comprehensively monographed. The aim of the present paper is to revise, as a prelude to a more inclusive study, the species from the Maastrichtian type area.

History

Müller (1846) was the first to record a species of *Echinogalerus* from the Maastrichtian type area (Vetschau, see Fig. 1). That author, and later also Binkhorst van den Binkhorst (1859) and Bosquet (1860, 1868, 1879) referred to it as *Caratomus gehrdensis*, a species described by Roemer (1841) from the Santonian of Hannover (northern Germany). However, Schlüter (1902) recognised it as a new species, *C. muelleri*, and in the same paper erected *C. vetschauensis*, also from Vetschau. Lambert (1911) introduced as new *Echinogalerus belgicus* and *E. pusillus*, both from Slenaken. The former had earlier been described by Lambert (1898) from southern Belgium as var. *belgica* of *Caratomus peltiformis*.

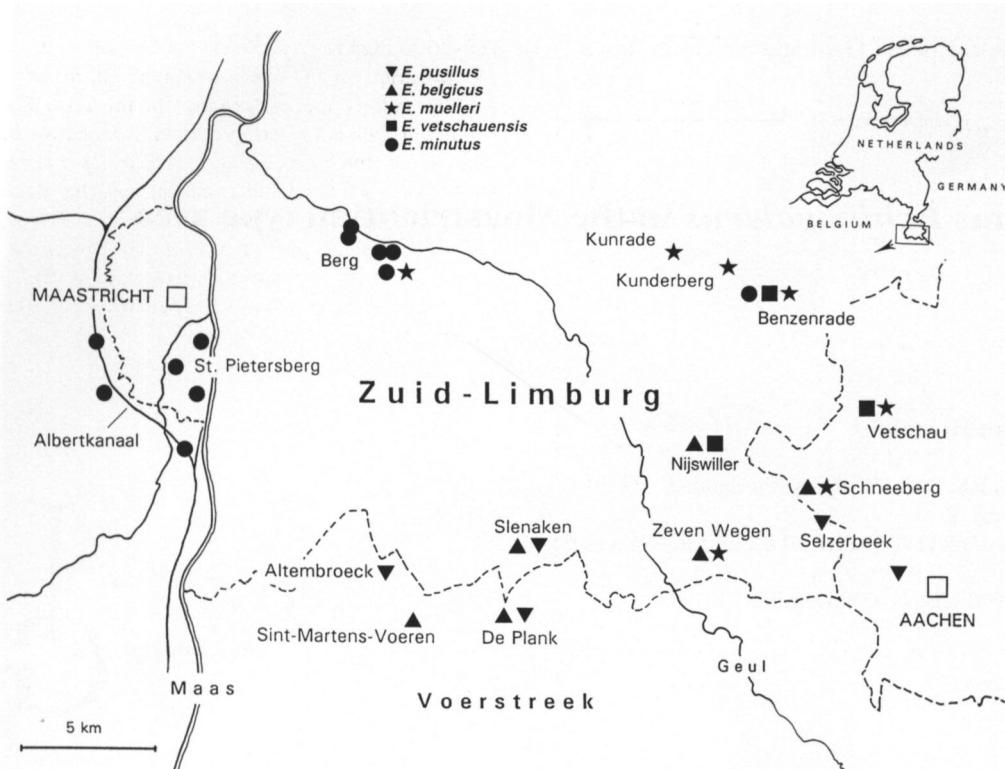


Fig. 1. Map of the Maastrichtian type area, showing localities from which species of *Echinogalerus* have been collected.

Wahlenberg, 1821, a species from the Lower Campanian of southern Sweden. Although Lambert (1898) pointed out that the genus name *Echinogalerus* König, 1825 predated *Caratomus* Desor, 1842, he did not use that genus name until 1911. Smiser (1935) described two new species from the St Pietersberg near Maastricht, viz. *Faujasia?* *transversa* and *Pseudopyrina minuta*. Both were transferred to *Echinogalerus* by Meijer (1956). Although Meijer (1965) covered the entire Maastrichtian type area, he listed only two species of *Echinogalerus*, namely *E. belgicus* and *E. transversus*. Van der Ham et al. (1987) briefly discussed five species (*E. belgicus*, *E. minutus*, *E. muelleri*, *E. transversus* and *E. veschauensis*), while the then single known specimen of *E. pusillus* was considered a possible juvenile of *E. belgicus*. Van der Ham & Van Birgelen (1992) recorded numerous specimens of *E. belgicus* and a few of *E. muelleri* from the Schneeberg near Vaals. Abundant new material has subsequently been collected of the poorly known *E. pusillus* and *E. transversus*. This triggered a preliminary revision of *Echinogalerus* in the Maastrichtian type area. Van Birgelen & Van der Ham (1999) dealt with material from the Gulpen Formation, listing three species, viz. *E. belgicus*, *E. pusillus* and *Echinogalerus* sp. 1, while Van der Ham & Van Birgelen (2000) listed material from the Maastricht Formation (*E. minutus* [= *E. transversus*], *E. muelleri*, *E. veschauensis* and *Echinogalerus* sp. 2). A new species from the Gulpen Formation was referred to as *Echinogalerus* sp. 3 by Van Birgelen & Van der Ham (2000). In the present revi-

sion, *Echinogalerus* sp. 1 and *Echinogalerus* sp. 2 are considered to be variants of *E. muelleri*, and *Echinogalerus* sp. 3 a slightly deviating form of *E. veschauensis*, so that at present the following five *Echinogalerus* species are distinguished in the Maastrichtian type area: *E. belgicus*, *E. minutus*, *E. muelleri*, *E. pusillus* and *E. veschauensis*. Two of these are restricted to the Gulpen Formation, one to the Maastricht Formation, while the other two species occur in both the Gulpen and Maastricht formations (Fig. 2).

Systematic descriptions

Repositories – The following abbreviations are used in the text to denote the repositories of specimens referred to and/or illustrated:

IRScNB Institut royal des Sciences naturelles de Belgiques, Brussels;
 NHMM Natuurhistorisch Museum Maastricht, Maastricht (BL - L. Blezer Colln, JJ - J.W.M. Jagt Colln, GK - W.M. Felder Colln (Gulpen Formation), K - M.M.M. Kuyper Colln, MK - W.M. Felder Colln (Maastricht Formation), MM - M. Meijer Colln, RH - R.W.J.M. van der Ham Colln).

Measurements are given as: minimum (mean) maximum.

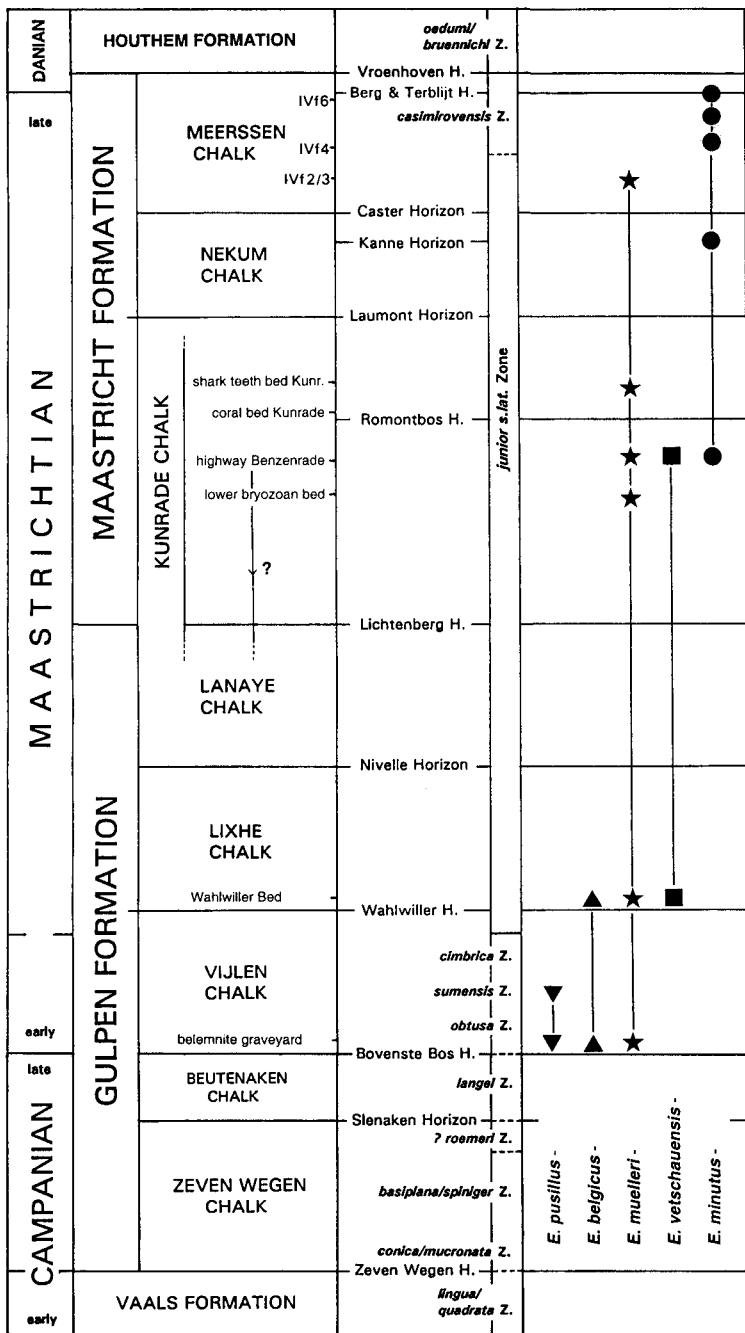


Fig. 2. Stratigraphy of Cretaceous-Danian strata in the Maastrichtian type area, showing the distribution of *Echinogalerus* species collected in the area. The Kunrade Chalk is the easterly facies of strata to the west which (probably) include the upper Lanaye Chalk up to the basal Emael Chalk; note that these westerly strata have not yielded any species of *Echinogalerus*. The relative position of the levels 'Benzenrade highway outcrop' and 'lower bryozoan bed' is uncertain; these levels may actually correlate with the upper Lanaye Chalk.

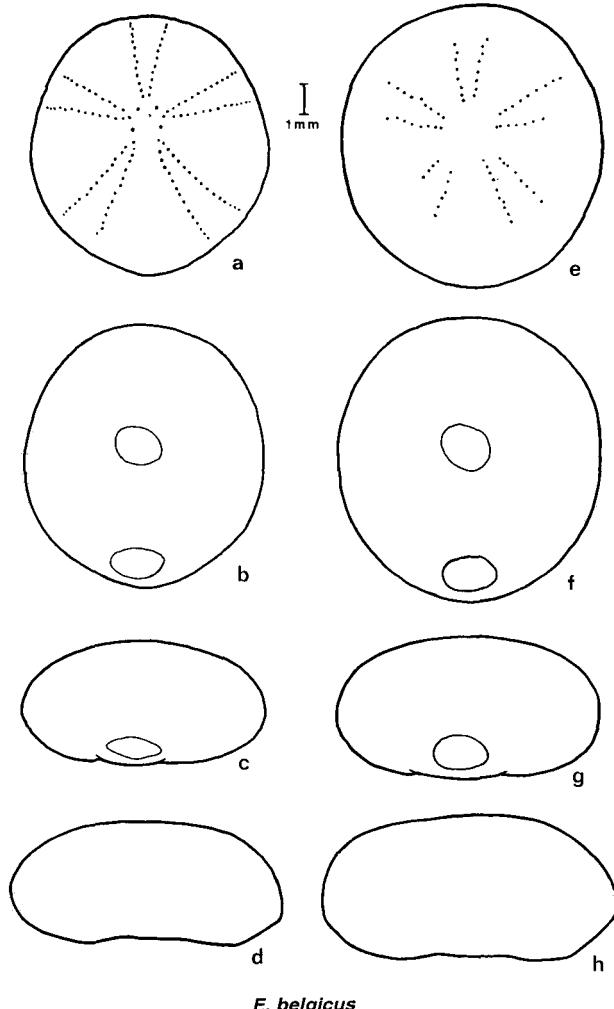
1 - Species from the Gulpen Formation

Echinogalerus belgicus (Lambert, 1898)

Figs 3, 4, 5e-h, 12a

- 1857 *Caratomus sulcato-radiatus* Desor - d'Orbigny, p. 371, pl. 942, figs 7-11.
- 1875 *Caratomus avellana* Agassiz - Cotteau, p. 650.
- 1896 *Caratomus avellana* Cotteau - de Grossouvre, p. 305.
- *1898 *Caratomus peltiformis* Wahlenberg var. *belgica* Lambert, p. 158, pl. 4, figs 11-14.
- 1911 *Echinogalerus belgicus* Lambert, pp. 45, 64, pl. 1, figs 28-35.

- 1921 *Echinogalerus belgicus* Lambert - Lambert & Thiéry, p. 332.
- 1935 *Echinogalerus belgicus* Lambert - Smiser, p. 43.
- 1965 *Echinogalerus belgicus* Lambert - Meijer, p. 23.
- 1987 *Echinogalerus belgicus* Lambert - Van der Ham et al., p. 28, pl. 9, fig. 1.
- 1992 *Echinogalerus belgicus* (Lambert) - Van der Ham & Van Birgelen, p. 149, pl. 3, figs 5, 6.
- 1999 *Echinogalerus belgicus* (Lambert) - Van Birgelen & Van der Ham, p. 215, figs 4e-h, 5a-d.
- 2000 *Echinogalerus belgicus* (Lambert) - Smith & Jeffery, p. 160.
- 2000 *Echinogalerus belgicus* (Lambert) - Jagt, p. 254.



E. belgicus

Fig. 3. Camera-lucida illustrations of *E. belgicus* (a-d: length 8.5 mm, NHMM MM 829, Vijlen Chalk (belemnite graveyard), Slenaken; e-h: length 9.3 mm, NHMM RH 466, Lixhe Chalk, Wahlwiller Bed, Schneeberg). a, e: upper surface; b, f: lower surface; c, g: posterior; d, h: left side.

Types

Holotype is IRScNB 9135, paratype is IRScNB 9136, from the ‘craie phosphatée et poudingue de la Malogne, Ciply’, Belgium.

Material studied

Van Birgelen Colln, nos 477*, 1378; NHMM GK 584, GK 665, GK 1401, GK 1429, GK 1671, GK 1704, NHMM MM 808, MM 829, MM 868, NHMM RH 466*, 607*, 750*; 68 specimens in all (* = measured specimens from the Schneeberg).

Occurrence

Lower and Upper Maastrichtian (GULPEN FORMATION), Vijlen Chalk (basal belemnite graveyard) of

Sint-Martens-Voeren, De Plank, Slenaken, Zeven Wegen; Lixhe Chalk (Wahlwiller Bed) of Nijswiller, Schneeberg (Figs 1, 2). Also known from southern Belgium (Mons Basin), Craie phosphatée de Ciply (Lower Maastrichtian) and Poudingue de la Malogne (basal Danian, including reworked elements from underlying Maastrichtian strata). Records for northern Spain (e.g. Lambert, 1927; Gallemi, 1977) have subsequently been referred to *E. muelleri* (Smith et al., 1999).

Description

Test length 4.1 (8.4) 12.3 mm, width 0.85 (0.89) 0.93% of length, height 0.42 (0.50) 0.61% of length. Outline usually elliptical, widest at or occasionally posterior of midlength. Profile depressed. Lower surface relatively flat. Ambulacra nonpetaloid; pores single aborally. Peristome obliquely elliptical. Periproct inframarginal, slightly larger than peristome, transversely elliptical to obtusely triangular. Tubercles distinct, slightly more pronounced at anterior, inconspicuous above periproct.

Remarks

Echinogalerus belgicus may be recognised by its elliptical, depressed shape and the single-pored aboral ambulacral plates. The type material has not been studied. Therefore, conspecificity of the material from southern Belgium and that from the Maastrichtian type area relies entirely on Lambert (1911). In both areas, species occur (although more rarely) which might be confused with *E. belgicus*, but which can be distinguished by their double aboral pores, viz. *E. ruottii* (Lambert, 1898) in southern Belgium and *E. muelleri* (Schlüter, 1902) in the Maastrichtian type area. If single aboral ambulacral pores in the Belgian specimens of *E. belgicus* could be demonstrated (a fact not explicitly described, nor illustrated by Lambert), this would confirm conspecificity with populations from the Maastrichtian type area.

Echinogalerus pusillus Lambert, 1911

Figs 4, 5a-d, 12b

- *1911 *Echinogalerus pusillus* Lambert, p. 65, pl. 1, figs 10-14.
- 1921 *Echinogalerus pusillus* Lambert - Lambert & Thiéry, p. 332.
- 1935 *Echinogalerus pusillus* Lambert - Smiser, p. 43.
- 1956 *Echinogalerus pusillus* Lambert - Meijer, p. 42.
- 1987 *Echinogalerus pusillus* Lambert - Van der Ham et al., p. 28.

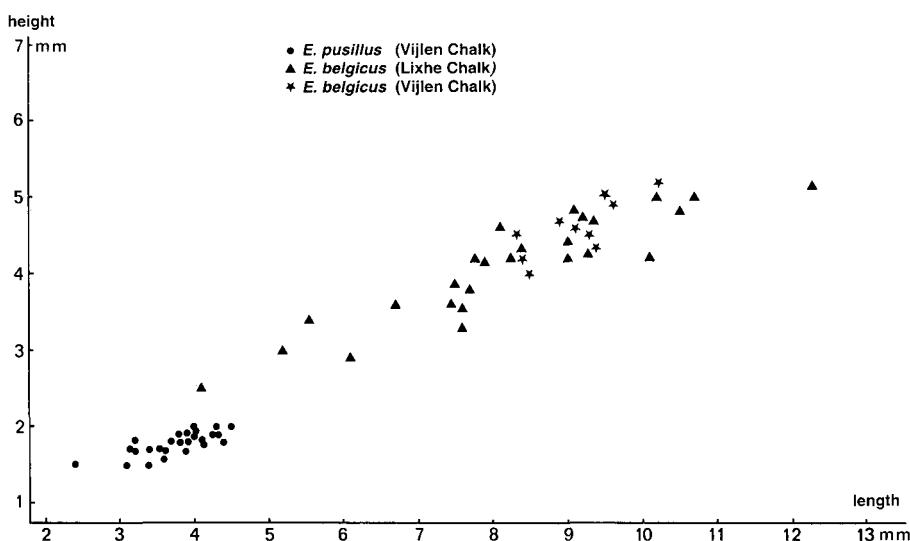


Fig. 4. Graph showing height/length values of a number of well-preserved specimens of *E. belgicus* (Lixhe Chalk, Wahlwiller Bed), Schneeberg ($n = 26$); Vijlen Chalk (belemnite graveyard), Slenaken and Zeven Wegen ($n = 10$) and *E. pusillus* (Vijlen Chalk, *sumensis* Zone), Selzerbeek ($n = 26$).

- 1995 *Echinogalerus belgicus* (Lambert) - Jagt et al., p. 12.
 1999 *Echinogalerus pusillus* Lambert - Van Birgelen & Van der Ham, p. 215, fig. 4a-d.
 2000 ?*Echinogalerus belgicus* (Lambert) - Smith & Jeffery, p. 160.
 2000 *Echinogalerus pusillus* Lambert - Jagt, p. 254.

Types

Holotype is IRSNB 9137, from the 'Craie marneuse de Slenaken', the Netherlands.

Material studied

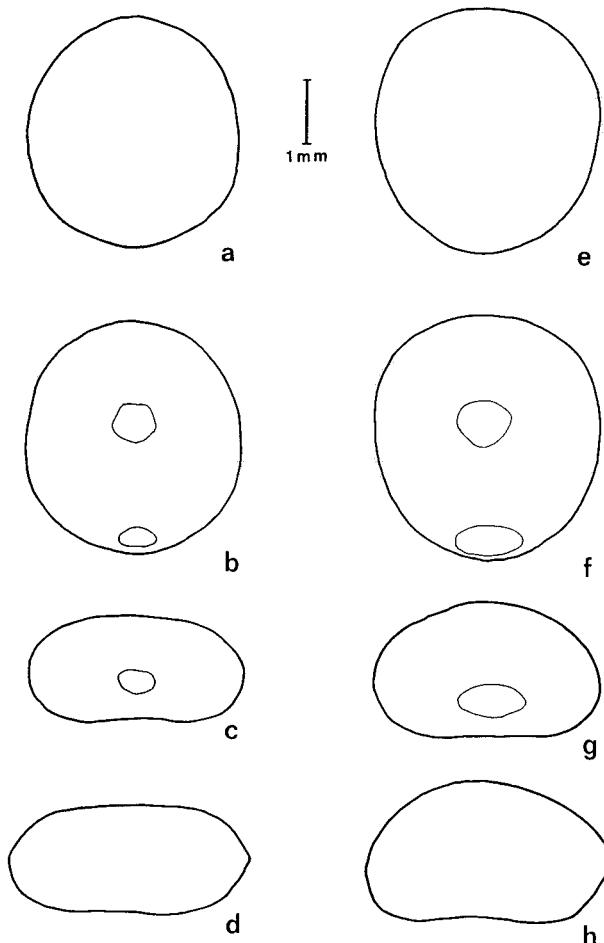
NHMM RH 658*; Van Birgelen Colln, nos 522, 1205, 1239*; Halter Colln, unnumbered; Walschot Colln, unnumbered (* = measured specimens, $n = 26$); in all some 100 specimens.

Occurrence

Lower Maastrichtian (Gulpin Formation), Vijlen Chalk (basal belemnite graveyard and *sumensis* Zone) of Altembroeck, De Plank, Slenaken (type material), Selzerbeek, Aachen-Steppenberglallee (Fig. 2). Not known outside the Maastrichtian type area.

Description

Test diminutive, length 2.4 (3.8) 4.5 mm, width 0.87 (0.91) 0.97% of length, height 0.41 (0.48) 0.62% of length. Outline elliptical, widest at or slightly posterior of midlength. Profile depressed. Lower surface relatively flat. Ambulacra nonpetaloid; pores single aborally. Peristome obtusely pentagonal. Periproct infra-



E. pusillus *E. belgicus*

Fig. 5. Camera-lucida illustrations of *E. pusillus* (a-d: length 3.9 mm, NHMM RH 658, Vijlen Chalk (*sumensis* Zone), Selzerbeek), and a more or less equal-sized specimen of *E. belgicus* (e-h: length 4.1 mm, NHMM RH 466, Lixhe Chalk (Wahlwiller Bed), Schneeberg. a, e: upper surface; b, f: lower surface; c, g: posterior; d, h: left side.

marginal, relatively small, transversely elliptical to indistinctly triangular. Tuberles relatively few and large, slightly more pronounced at anterior side, inconspicuous above periproct.

Remarks

Echinogalerus pusillus may be recognised by its small size, depressed shape and obtusely pentagonal peristome. The single aboral ambulacral pores are mostly very difficult to observe.

Previously but a single specimen was known, and Van der Ham et al. (1987) considered *E. pusillus* to be a possible juvenile of *E. belgicus*. However, on the basis of abundant material collected subsequently, Van Birgelen & Van der Ham (1999) argued that *E. pusillus* is a 'good' species, differing clearly from small specimens of *E. belgicus* (Figs 4, 5). Three specimens of *E. pusillus* (3.9, 3.9, 4.3 mm in length) show four gonopores.

The present species is the smallest echinoid known to date from the Maastrichtian type area, and may be found in numbers only by intensive sieving.

As far known, *E. pusillus* is endemic to the Maastrichtian type area, and does not resemble any of the other *Echinogalerus* species.

2 - Species from the Gulpen and Maastricht formations

Echinogalerus muelleri (Schlüter, 1902)

Figs 6-8, 12c

- 1846 *Caratomus gehrdensis* Roemer - Müller, p. 8.
- 1859 *Caratomus gehrdensis* Roemer - Binkhorst van den Binkhorst, pp. 65, 120.
- 1860 *Caratomus gehrdensis* Roemer - Bosquet, p. 406.
- 1868 *Caratomus gehrdensis* Roemer - Bosquet, p. 379.
- 1879 *Caratomus gehrdensis* Roemer - Bosquet, p. 227.
- *1902 *Caratomus Mülleri* Schüter, 1902, p. 316, pl. 11, figs 14-17; pl. 12, fig. 30.
- 1921 *Echinogalerus muelleri* Schüter - Lambert & Thiéry, p. 332.
- 1980 *Echinogalerus* sp. [sic] - Felder, p. 47, pl. 7, fig. 3.
- 1987 *Echinogalerus muelleri* (Smiser) - Van der Ham et al., p. 28, pl. 9, fig. 3.
- 1992 *Echinogalerus muelleri* (Schüter) - Van der Ham & Van Birgelen, p. 149, pl. 3, fig. 7.
- 1999 *Echinogalerus* sp. - Van Birgelen & Van der Ham, p. 217, fig. 5e-h.

- 1999 *Echinogalerus muelleri* (Schüter) - Smith et al., p. 100, pl. 2, figs 17-20.
- 2000 *Echinogalerus muelleri* (Schüter) - Van der Ham & Van Birgelen, p. 37, fig. 5a-d.
- 2000 *Echinogalerus* sp. 2 - Van der Ham & Van Birgelen, p. 39, fig. 6a-l.
- 2000 *Echinogalerus muelleri* (Schüter) - Smith & Jeffery, p. 158, text-fig. 66I-L.
- 2000 *Echinogalerus muelleri* (Schüter) - Jagt, p. 254, pl. 16, figs 6, 7.
- 2000 *Echinogalerus* sp. 1 - Jagt, p. 255.
- 2000 *Echinogalerus* sp. 2 - Jagt, p. 256.

Types

Schüter (1902) based his description on a specimen in the Joseph Müller Colln (Aachen), from the 'obere Kreide von Vetschau bei Aachen', Germany; accord-

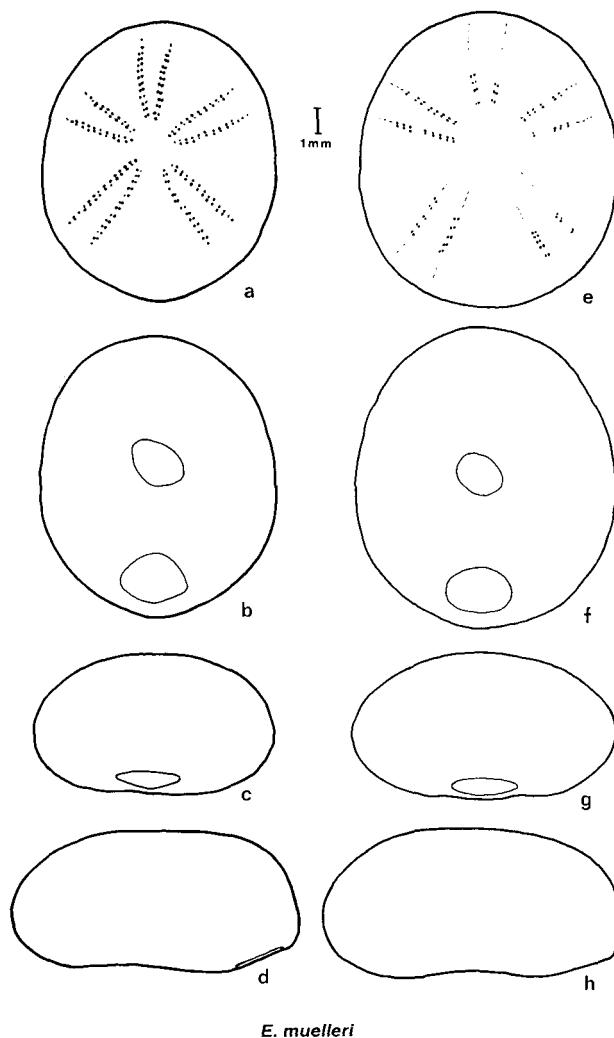


Fig. 6. Camera-lucida illustrations of *E. muelleri* (a-d: length 11.6 mm, NHMM RH 108), Kunrade Chalk, Benzenrade highway outcrop; e-h: length 12.2 mm, NHMM GK 1440, Vijlen Chalk (belemnite graveyard), Zeven Wegen). a, e: upper surface; b, f: lower surface; c, g: posterior; d, h: left side.

ing to W.M. Felder (pers. comm., November 1983), this specimen is lost.

Material studied

Van Birgelen Colln, nos 25, 377, 413, 414, 477, 506, 655, 1301; NHMM BL 0822, NHMM GK 1440, NHMM MM 817 (Orp-le-Petit), NHMM RH 108, RH 253, RH 258, RH 540, RH 566; Nillesen Colln, unnumbered; Vlieks Colln, unnumbered*; Zuidema Colln, no. E265; in all 199 specimens (* = measured specimens from Benzenrade, n = 49).

Occurrence

Lower and Upper Maastrichtian (GULPEN FORMATION), Vijlen Chalk (basal belemnite graveyard) of

Zeven Wegen; Lixhe Chalk (Wahlwiller Bed) of Schneeberg; (MAASTRICHT FORMATION), Kunrade Chalk of Kunrade (shark teeth bed), Kunderberg (lower bryozoan bed), Benzenrade (highway outcrop), Vetschau (type material), and Meerssen Chalk (IVf2/3) of Blom quarry, Berg (Figs 1, 2). Also known from the base of the Maastrichtian at Orp-le-Petit (Belgium), and the Maastrichtian of northern Spain (Smith et al., 1999).

Description

Test length 7.6 (11.2) 18.4 mm, width 0.75 (0.85) 0.91% of length, height 0.39 (0.51) 0.60% of length. Specimens from the Blom quarry are considerably smaller (see Remarks below). Outline elliptical to ovate, widest at or slightly posterior of midlength.

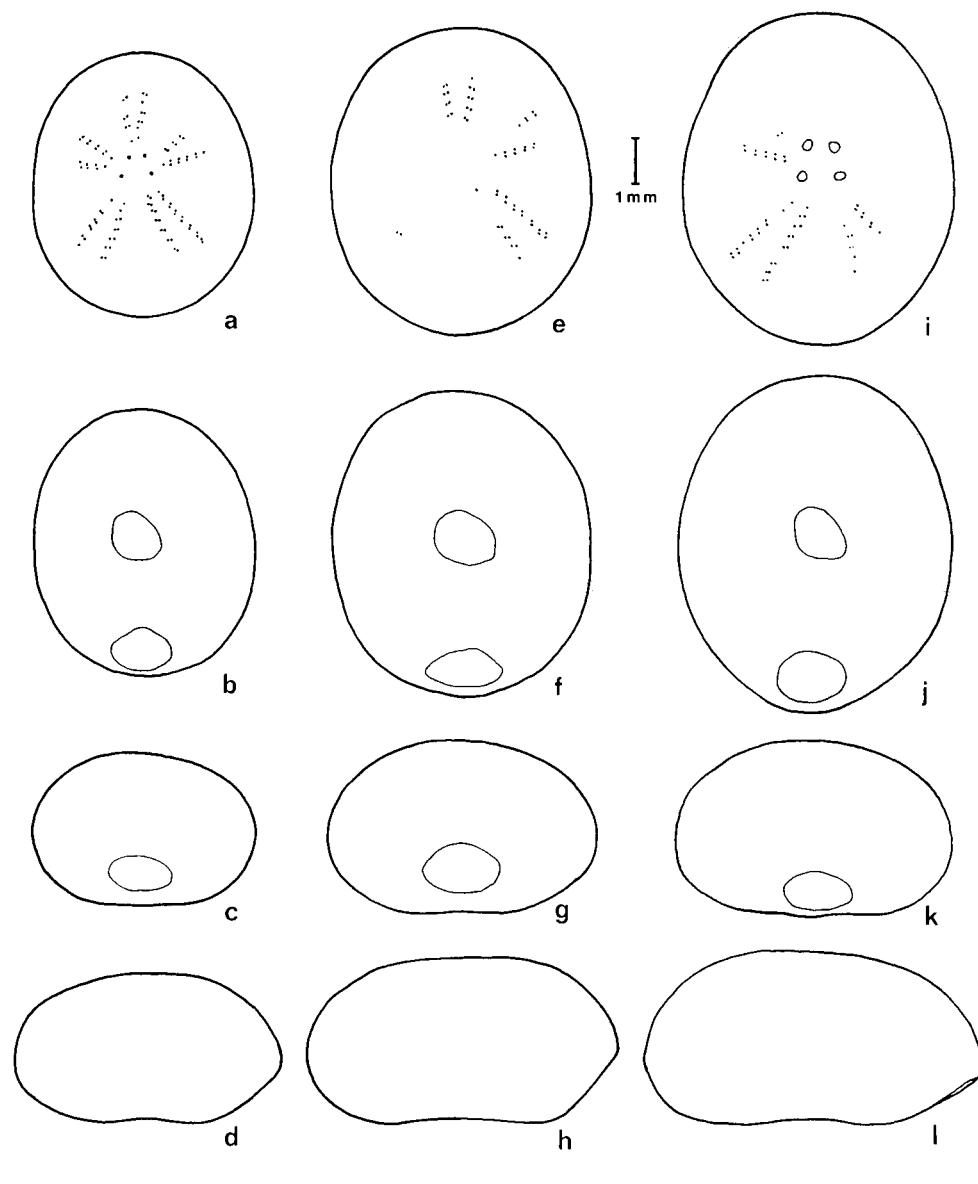


Fig. 7. Camera-lucida illustrations of three small specimens of *E. muelleri* (length 6.0, 6.9, 7.4 mm, Van Birgelen Colln, no. 377, Meerssen Chalk, IVf2/3, Blom quarry, Berg). a, e, i: upper surface; b, f, j: lower surface; c, g, k: posterior; d, h, l: left side.

Profile usually (see Remarks) depressed. Lower surface slightly pulvinate. Ambulacra subpetaloid; pores double aborally. Peristome irregularly triangular to obliquely elliptical. Periproct inframarginal, clearly larger than peristome, transversely elliptical to obtusely triangular. Tubercles distinct, usually more pronounced at anterior side, inconspicuous above periproct.

Remarks

Echinogalerus muelleri may be recognised by its triangular to obliquely elliptical peristome and relatively large periproct. Specimen no. 1301 in the Van Birgelen Colln. deviates slightly from the other specimens from the Kunrade Chalk in being relatively high (height/length: 9.8/15.5) and having a more homogeneous tuberculation. The latter characteristic is also found in specimens from the Gulpen Formation.

Stratigraphically, the present species is the most widely distributed one. Previously, this material was subdivided into three separate taxa, as follows:

Gulpen Formation: *Echinogalerus* sp. 1

Kunrade Chalk: *E. muelleri*

Meerssen Chalk: *Echinogalerus* sp. 2

Material from the Meerssen Chalk (Blom quarry) differs from other specimens in being almost consistently smaller and slightly less depressed (length 3.9 (6.2) 8.7 mm, width/length 0.80 (0.83) 0.87, height/length 0.53 (0.57) 0.63; n = 24). However, constant qualitative differences could not be found. For that reason, the three are here lumped into a single species. There is an additional reason to assign these small specimens to *E. muelleri*: of several other co-occurring echinoid species, e.g. *Procassidulus lapiscancri* (Leske, 1778) and *Pleurosalenia maestrichtensis* (Schlüter, 1892), relatively small specimens occur, which might indicate that environmental factors played a role. In northern Spain, Smith et al. (1999) found horizons with small individuals of *E. muelleri* only.

Echinogalerus muelleri is probably closely related to or even conspecific with *E. rutori* (Lambert, 1898) from the Poudingue de la Malogne in southern Belgium. This species also has a relatively large periproct, and resembles the small specimens of *E. muelleri* from the Meerssen Chalk. One individual of *E. muelleri* from Orp-le-Petit (NHMM MM 817) was initially identified by its collector Max Meijer as *E. rutori*. Remarkably, *E. rutori* was not mentioned by Lambert (1911) in his description of co-occurring *E. belgicus*.

Echinogalerus vetschauensis (Schlüter, 1902)

Figs 9, 10, 12d

- *1902 *Caratomus vetschauensis* Schüter, p. 318, pl. 11, figs 10-13; pl. 12, fig. 29.
- 1921 *Echinogalerus vetschauensis* Schüter - Lambert & Thiéry, p. 332.
- 1987 *Echinogalerus vetschauensis* (Schüter) - Van der Ham et al., p. 28, pl. 9, fig. 5.
- 1999 *Echinogalerus? vetschauensis* (Schüter) - Smith et al., p. 100, pl. 2, figs 13-16.
- 2000 *Echinogalerus vetschauensis* (Schüter) - Van der Ham & Van Birgelen, p. 38, fig. 5e-h.
- 2000 *Echinogalerus? vetschauensis* (Schüter) - Smith & Jeffery, p. 160.
- 2000 *Echinogalerus* sp. 3 - Van Birgelen & Van der Ham, p. 266, fig. 2a-h.
- 2000 *Echinogalerus vetschauensis* (Schüter) - Jagt, p. 255.

Types

Schlüter (1902) based his description on three specimens from the 'unteren Maastricht-Schichten (Kalken von Vetschau) bei Aachen', in the collections of the Museum der Technischen Hochschule (Aachen). According to W.M. Felder (pers. comm., November 1983), the material is probably lost.

Material studied

NHMM RH 758; Van Birgelen Colln, nos 716*, 1378; Van Loo Colln, unnumbered*; Vlieks Colln, unnumbered*; in all 17 specimens (* = measured specimens from Benzenrade, n = 7).

Occurrence

Upper Maastrichtian (Gulpen Formation), Lixhe Chalk (Wahlwiller Bed) of Nijswiller; (Maastricht Formation), Kunrade Chalk of Benzenrade (highway outcrop), Vetschau (type material) (Figs 1, 2). Also known from the Maastrichtian of northern Spain (Smith et al., 1999).

Description

Test length 13.2 (16.2) 18.2 mm, width 0.89 (0.94) 0.96% of length, height 0.46 (0.52) 0.59% of length. Measured specimens from Nijswiller (n = 8) are smaller and more depressed (length 10.9 (12.6) 15.4 mm, height/length 0.41 (0.43) 0.45). Outline broadly elliptical to almost circular, widest at midlength. Profile (much) depressed. Lower surface pulvinate. Am-

bulacra nonpetaloid; pores seemingly single aborally: pores of one pair close set and sunken in a small pit. Peristome slightly obliquely elliptical to almost circular. Periproct inframarginal, relatively small, transversely elliptical to obtusely triangular. Tuberles small, not more pronounced, or hardly so, at anterior side, inconspicuous above periproct.

Remarks

Echinogalerus vetschauensis may be recognised by its almost circular shape and peristome, and the relatively small periproct and tubercles.

In well-preserved specimens, the aboral ambulacrals pores seem to be single (Fig. 9a-d), but in abraded tests (Fig. 9e-h) the pores can be seen lying closely together, being actually double. This fact was not yet fully appreciated by Van Birgelen & Van der Ham (2000), who described the well-preserved ‘single-pored’ specimens as a separate, though closely related species (*Echinogalerus* sp. 3).

Echinogalerus vetschauensis is probably closely related to *E. tenuiporus* (Schlüter, 1902) from the ‘Mucronaten-Kreide’ of Grimme (type material) and the Lower Maastrichtian of Rügen (Kutscher, 1979), both in northern Germany.

3 - Species from the Maastricht Formation

Echinogalerus minutus (Smiser, 1935)

Figs 8, 11, 12e

- *1935 *Pseudopyrina minuta* Smiser, p. 42, pl. 4, fig. 3a-e.
- 1935 *Faujasia? transversus* Smiser, p. 65, pl. 7, fig. 1a-e.
- 1956 *Echinogalerus (Rostrogalerus) transversus* (Smiser) - Meijer, p. 38, text-figs 1-3; pl. 1, figs 1-5.
- 1956 *Echinogalerus minutus* (Smiser) - Meijer, p. 42.
- 1965 *Echinogalerus transversus* (Smiser) - Meijer, p. 23.
- 1987 *Echinogalerus minutus* (Smiser) - Van der Ham et al., p. 28, pl. 9, fig. 2.
- 1987 *Echinogalerus transversus* (Schlüter) – Van der Ham et al., p. 28, pl. 9, fig. 4.
- 2000 *Echinogalerus minutus* (Smiser) - Van der Ham & Van Birgelen, p. 35, fig. 4a-l.
- 2000 *Echinogalerus minutus* (Smiser) - Smith & Jeffrey, p. 161.
- 2000 *Echinogalerus transversus* (Smiser) - Jagt, p. 255, pl. 16, fig. 5.

Types

Holotype of *Pseudopyrina minuta*, from the ‘(upper) Maestrichtian of St. Pierre’, the Netherlands, is IRSNB 9134); holotype of *Faujasia? transversus*, from the ‘Maestrichtian of St. Pierre’ is IRSNB 9185.

Material studied

Van Birgelen Colln, nos 95, 107, 108*, 416, 784*, 1299; NHMM JJ 9521*, NHMM K 750*, NHMM MK 736, MK 1205, NHMM MM 567, MM 847, MM 866, MM 867, NHMM RH 628*; Vlieks Colln, unnumbered; a total of 240 specimens (* = measured specimens from Blom quarry, n = 76).

Occurrence

Upper Maastrichtian (MAASTRICHT FORMATION), Kunrade Chalk of Benzenrade (highway outcrop); Nekum Chalk (slightly above Kanne Horizon) of Vechmaal; Nekum or Meerssen Chalk of Leeraarsgroeve near Berg, St Pietersberg (type material), Albertkanaal-St Pietersberg; Meerssen Chalk (IVf4, IVf6, Berg en Terblijt Horizon) of quarries Barakkenberg, Blom, Curfs, Geulhemmergroeve (all near Berg), St Pietersberg West, ENCI-Maastricht BV, and Albertkanaal near Vroenhoven (N and S of bridge) (Figs 1, 2). Not known from outside the Maastichtian type area.

Description

Test length 3.4 (6.3) 8.8 mm, width 0.80 (0.85) 0.9% of length, height 0.42 (0.51) 0.63% of length. Outline ovate, widest posterior of midlength. Profile depressed. Lower surface slightly concave. Ambulacra subpetaloid; pores double aborally. Peristome lengthwise elliptical. Periproct marginal to inframarginal (slightly supramarginal to marginal in small specimens), slightly larger than peristome, transversely elliptical. Tuberles distinct, more pronounced at anterior side, inconspicuous above periproct.

Remarks

Echinogalerus minutus may be recognised by its ovate, depressed shape and lengthwise elliptical peristome.

Until recently, there was a lot of confusion over *E. minutus*, with the juvenile and adult forms having been described as separate species (*P. minuta* and *F.? transversus*, respectively) by Smiser (1935). Meijer (1956) placed both species in *Echinogalerus*. Van der Ham et al. (1987) referred to the adult form as *E.*

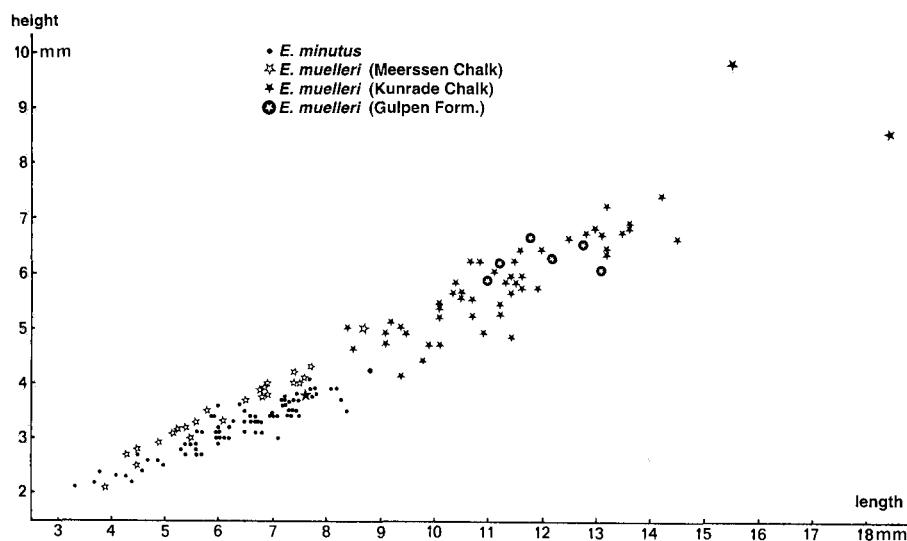


Fig. 8. Graph showing height/length values of a number of well-preserved specimens of *E. minutus* (Meerssen Chalk, IVf4 and IVf6, Blom quarry, Berg, n = 76), and *E. muelleri* (base Maastrichtian, Orp-le-Petit, n = 1; Vijlen Chalk (belemnite graveyard), Zeven Wegen, n = 1; Lixhe Chalk (Wahlwiller Bed), Schneeberg, n = 4; Kunrade Chalk, highway Benzenrade, n = 52; Meerssen Chalk, IVf2/3, Blom quarry, Berg, n = 24).

minutus, while their *E. transversus* appeared to represent small specimens of *E. muelleri*.

Fig. 11 illustrates three specimens of increasing size, demonstrating the shift of the periproct from (supra)marginal (young '*minutus* form') to inframarginal (adult '*transversus* form'), which is common in growing irregular echinoids.

As far we know, *E. minutus* is endemic to the Maastrichtian type area, and bears little resemblance to any of the other *Echinogalerus* species described (see below, under Infrageneric alliances).

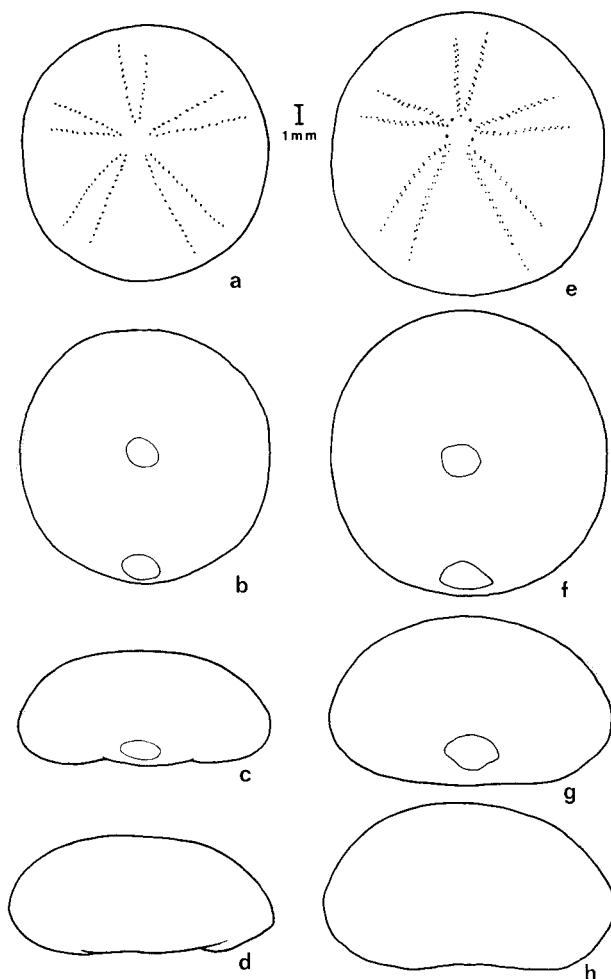
Ordinal position of *Echinogalerus*

Whether *Echinogalerus* should be assigned to the order Holecotypoida or the order Cassiduloida is still a matter of debate. Wagner & Durham (1966) placed this genus, together with *Amblypygus* and *Rhopostoma*, in the order Holecotypoida (suborder uncertain), since these taxa lacked the cassiduloid floscelle and showed some resemblance to representatives of the suborder Echinoneina, i.e. gross morphology and lack of lantern, but ambulacra subpetaloid. Ernst (1973) considered placement with the Cassiduloida improbable, on account of the absence of a floscelle. Rose (1982), who reviewed the post-1966 (Wagner & Durham, 1966) taxonomic history of the Holecotypoida, ascribed *Amblypygus* to the family Echinoneidae (Holecotypoida) and *Rhopostoma* to the Cassiduloida (family Nucleolitidae), but did not change the position of *Echinogalerus* (suborder uncertain). According to Schulz (1985), *Echinogalerus* might belong to the Cassiduloida. Smith et al. (1988) placed the genus in the family Galeritidae (Holecotypoida, suborder Echinoneina), while Smith & Wright (1999) excluded the suborder Echinoneina from the Holecotypoida, raising it to the rank of order (Echinoneoida) as sister group

to the Cassiduloida (and Clypeasteroida). The genus *Echinogalerus* was subdivided, with the subgenus *Rostrogalerus* Lambert, 1911 being placed, as a genus, in the Echinoneoida (family Galeritidae). The other species, including the type *E. faba*, were referred to the Cassiduloida (see also Smith et al., 1999). *Rostrogalerus* was differentiated by Lambert (1911) and Smith & Wright (1999) by its more rostrate posterior, circular peristome and nonpetaloid ambulacra (adapical pore pairs not enlarged). Smith & Wright (1999) considered it to be very close to *Galerites*, differing only in its small size and higher position of the periproct.

The borderline between *Echinogalerus* and *Galerites* has always been somewhat vague. Schulz (1985) treated a number of species of *Galerites*, viz. *G. hanoniensis*, *G. hemisphaericus* and *G. sulcatoradiatus*, as well as a few undescribed related taxa, all differing from the other *Galerites* species in their relatively wide ambulacra around the peristome, as possibly belonging to *Echinogalerus*. Also, *Galerites* was suspected to be a cassiduloid by that author. The species of *Galerites* which were provisionally transferred to *Echinogalerus* differ from true *Galerites* in having circular tests, nonpetaloid ambulacra and, in part, more circular peristomes. However, Smith & Wright (1999) maintain these species in *Galerites*; in their view *Echinogalerus* should be restricted to species with a subtriangular (oblique) peristome and subpetaloid ambulacra, while *Galerites* should contain species with a circular peristome and nonpetaloid ambulacra.

We consider it difficult to evaluate the ordinal position of *Echinogalerus* so long as many species are still insufficiently known. Moreover, Schulz (1985) mentioned the existence of two undescribed, possibly related, genera from the Maastrichtian of northern Germany and Denmark that would be intermediate



E. vetschauensis

Fig. 9. Camera-lucida illustrations of *E. vetschauensis* (a-d: length 13.5 mm, Van Birgelen Colln, no. 1378, Lixhe Chalk, Wahlwiller Bed, Nijswiller; e-h: length 15.0 mm, Van Birgelen Colln, no. 716, Kunrade Chalk, highway Benzenrade). a, e: upper surface; b, f: lower surface; c, g: posterior; d, h: left side.

between *Galerites* and certain cassiduloids. In addition to the poorly known species of *Echinogalerus*, these two genera should be duly considered in a discussion on the subdivision and ordinal position(s) of *Echinogalerus*. Below, our current views on the relationship of *Echinogalerus* species from the Maastrichtian type area and species from elsewhere are presented. This brief overview may stimulate discussions on the ordinal and infrageneric classification of the genus.

Infrageneric relationship of *Echinogalerus*

Within the genus *Echinogalerus*, the five species from the Maastrichtian type area make up a diverse group. However, when some relatively well-known species from other areas are taken into account, this allows to distinguish several groups of more closely related

species. One such group includes the following species, all of which clearly have double pores aborally (ambulacra subpetaloid), an oblique peristome and a relatively large, triangular periproct:

- E. faba* (Desor, 1842) (Cenomanian of southwest England and western France);
- E. goslawiensis* (Schlüter, 1902) (Santonian of northern Germany);
- E. muelleri* (Schlüter, 1902) (Maastrichtian of northern Spain and SE Netherlands).
- E. rutoti* (Lambert, 1898) (Maastrichtian of southern Belgium);

A second group comprises species with small pore pairs, sunken in small pits aborally, and non-petaloid ambulacra, an oblique peristome and a relatively large, triangular periproct:

- E. bueltenensis* (Schlüter, 1902) (Santonian of northern Germany);
- E. peltiformis* (Wahlenberg, 1821) (Campanian of southern Sweden and northern Germany).

A third group consists of species with a circular ambitus, small pore pairs sunken in small pits, non-petaloid ambulacra, a circular peristome and a small, vaguely triangular to circular periproct:

- E. circularis* (Schlüter, 1902) (Turonian of western Germany);
- E. tenuiporus* (Schlüter, 1902) (Maastrichtian of northern Germany);
- E. vetschauensis* (Schlüter, 1902) (Maastrichtian of northern Spain and SE Netherlands).
- Echinogalerus dolfussi* (Lambert, 1898) and *E. truncata*

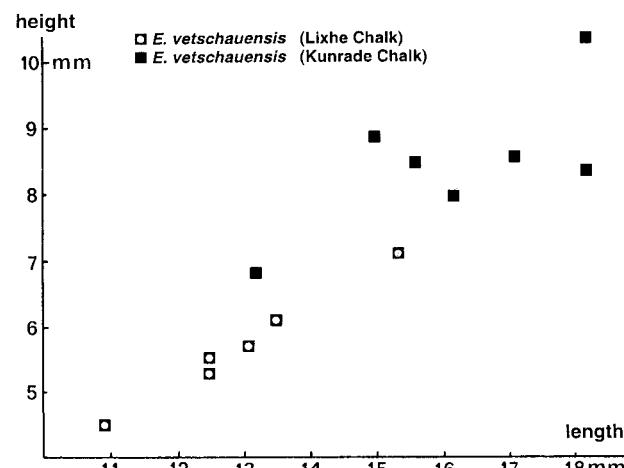
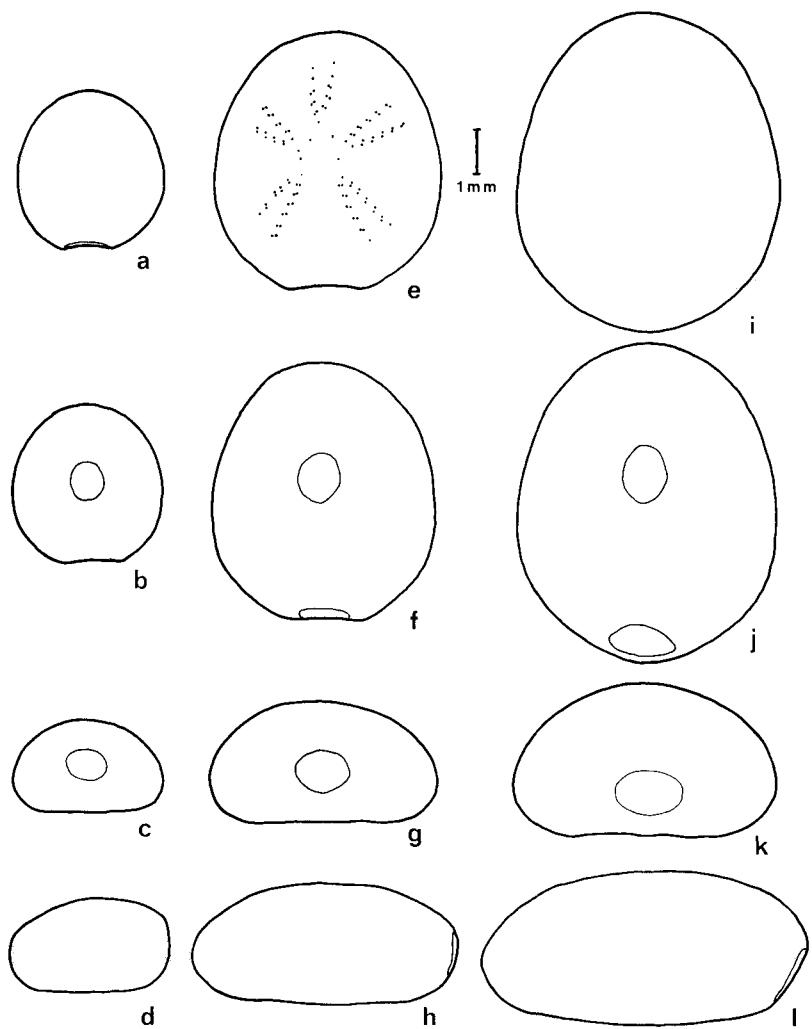


Fig. 10. Graph showing height/length values of 13 well-preserved specimens of *E. vetschauensis* (Lixhe Chalk, Wahlwiller Bed, Nijswiller, n = 6; Kunrade Chalk, highway Benzenrade, n = 7).



E. minutus

tus (d'Orbigny, 1857), both from the Maastrichtian of western France (the latter possibly also occurring in the Campanian of western Germany; see Schlüter, 1902), might also belong to this group.

It is difficult to ally other species of *Echinogalerus* to the species groups listed above. *Echinogalerus belgicus* and *E. pusillus*, both from the Maastrichtian of SE Netherlands, have simple pores, but in all other respects they are clearly different (see above). *Echinogalerus minutus*, from the Maastrichtian of SE Netherlands, resembles *E. gehrdensis* (Roemer, 1841) from the Santonian of northern Germany. Both have clearly double pores aborally and a symmetrical peristome. However, the latter differs by its more anterior apex, clearly rostrate posterior and more inframarginal periproct. The clearly inframarginal periproct separates *E. gehrdensis* also from the rostrate *E. rostratus* (Desor, 1842) from the Cenomanian of southwest England and western France.

The following species are poorly known: *E. (Rostro-*

Fig. 11. Camera-lucida illustrations of *E. minutus* (a-d: length 3.7 mm, NHMM JJ 9521, 4e-l: length 5.9, 7.4 mm, Van Birgelen Colln, no. 784, Meerssen Chalk, IVf4, Blom quarry, Berg). a, e, i: upper surface; b, f, j: lower surface; c, g, k: posterior; d, h, l: left side.

galerus) orbicularis (Desor, 1842) from the Cenomanian of western France, *E. (R.) althi* (Zareczny, 1878) from the Turonian(?) of Poland, and *E. laubei* (Novák, 1887) from the Turonian of Bohemia (Czech Republic). *Echinogalerus bohotnicensis* Kongiel, 1950, from the Maastrichtian of Poland, is not an *Echinogalerus*, but closely resembles *Hemicara pomeranum* Schlüter, 1902, whereas *E. avellana* (Dubois, 1840) and *E. globosus* (Roemer, 1841) belong to *Galerites* (see Lambert & Thiéry, 1925 and Schulz, 1985, respectively).

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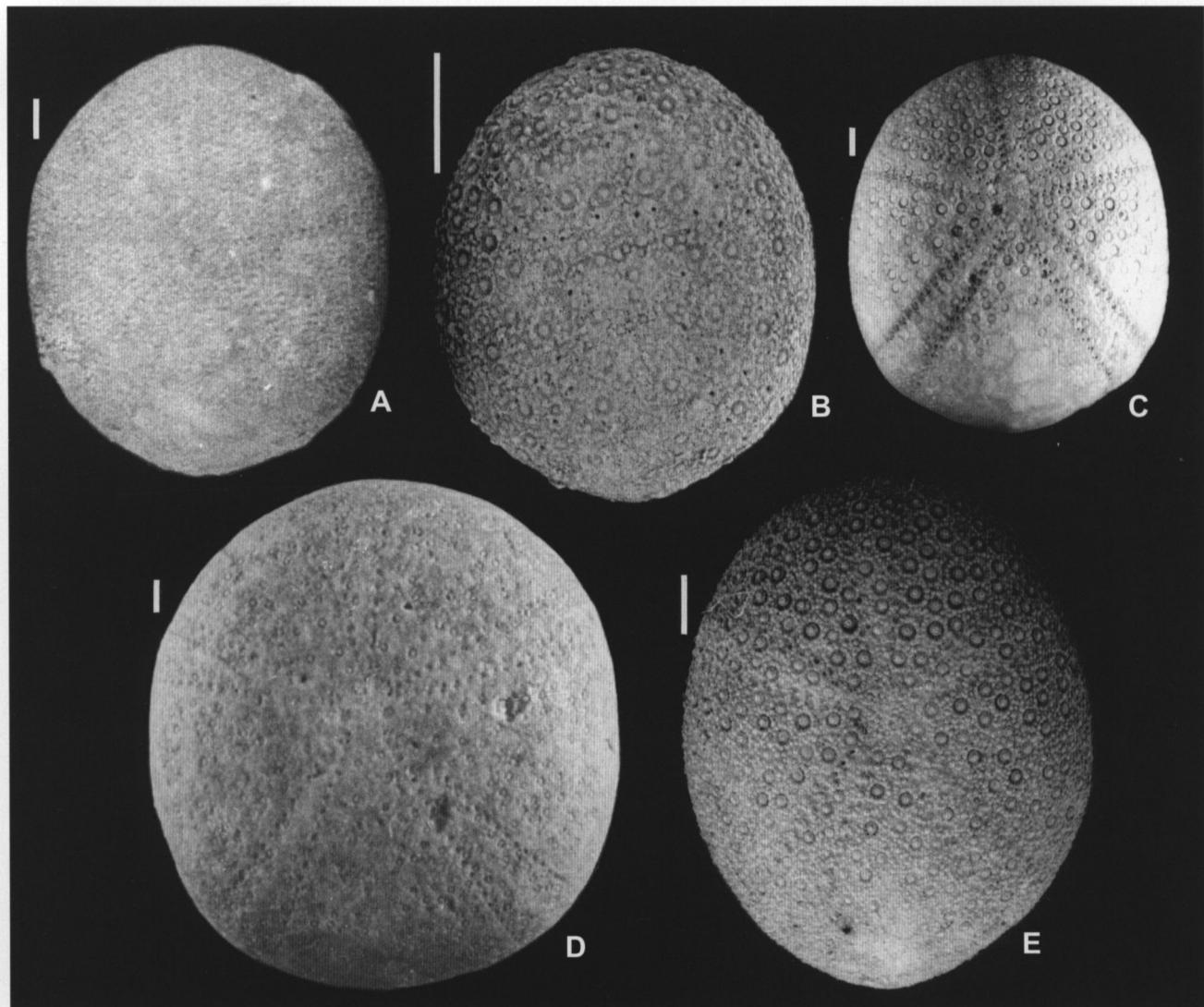


Fig. 12. Photo (a, c, d) and scanning (b, e) electron micrographs of upper surfaces, showing aboral ambulacrals pores and details of tuberculation (scale bar = 1 mm). a: *E. belgicus*, length 10.7 mm, Van Birgelen Colln, no. 477, Lixhe Chalk, Wahlwiller Bed, Schneeberg; b: *E. pusillus*, length 3.7 mm, Halter Colln, unnumbered, Vijlen Chalk, Aachen; c: *E. muelleri*, length 12.8 mm, NHMM BL 0822, Kunrade Chalk, Kunrade area; d: *E. vetschauensis*, length 16.2 mm, Vlieks Colln, unnumbered, Kunrade Chalk, highway Benzenrade; e: *E. minutus*, length 8.8 mm, NHMM K 750, Meerssen Chalk, IVf4, Blom quarry, Berg.

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