

NEOGENE SPECIES OF *PSEUDAMUSSIUM* (MOLLUSCA, BIVALVIA, PECTINIDAE) FROM BELGIUM

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The status of the pectinid genus *Pseudamussium* Mörch, 1853 is discussed, and differences between this taxon and *Palliolium* Monterosato, 1884 are outlined. Five species from the Neogene of Belgium are assigned to *Pseudamussium*, viz. *P. princeps* (J. de C. Sowerby, 1826), *P. edegemense* (Glibert, 1945), *P. lilli* (Pusch, 1837), *P. sulcatum* (Müller, 1776), and *P. clavatum* (Poli, 1795). All of these are described and illustrated, and their stratigraphic ranges and palaeoecology discussed. *Pseudamussium sulcatum* is here recorded from the Belgian Pliocene for the first time, as is *P. lilli*. The latter species' wide range of variation is discussed and *Pecten scissus* Favre, 1869 is considered to be a junior synonym. The stratigraphic distribution of *P. lilli* suggests a connection between the North Sea Basin and the Paratethys during the Miocene. In addition, the ontogeny of *P. princeps* is described, and the left valve of *P. edegemense* is here illustrated for the first time.

Key words — Bivalvia, Pectinidae, Neogene, North Sea Basin, taxonomy.

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INTRODUCTION

Many new data on Neogene faunas from northwest Belgium have been assembled during the past thirty years, and numerous molluscan species have been recorded for the first time for the North Sea Basin. In addition, certain species identifications could be amended, since the new collections comprised much more and better-preserved material.

Miocene faunas have been extensively collected during construction works of the Kleine Ring (E3) motorway around Antwerp, at the Kennedy Tunnel ex-

cavations, at the construction of a water purification plant near Schijnpoort, Antwerp, at the Antwerp underground construction pits, at Schijnpoort and Schoolplein, at building sites in the Ploegstraat, Antwerp, as well as during temporary excavations at Zonderschot (Heist-op-den-Berg, southeast of Antwerp) by the Belgische Vereniging voor Paleontologie (BVP). Papers on (temporary) sections and their biostratigraphic interpretation include those by De Meuter *et al.* (1967, 1976), Janssen & Van der Mark (1969), Marquet (1991) and Hooyberghs (1996a, b), but the molluscan faunas collected at these localities have not yet been studied in detail. Pliocene gastropod faunas collected at the harbour works at Kallo (west of Antwerp, Oost-Vlaanderen) have recently been described by Marquet (1984, 1993, 1995a, 1996, 1997a-c) and monographed by Marquet (1998).

The present paper is the third in a series of contributions revising Neogene bivalves collected at Kallo and at other recent temporary outcrops, the first being those by Dijkstra & Janssen (1988) and Marquet (1995b).

SYSTEMATIC DESCRIPTIONS

Abbreviations — To denote the repositories of specimens mentioned in the text, the following abbreviations are used: HD - H.H. Dijkstra Collection, IRScNB - Institut royal des Sciences naturelles de Belgique, Brussels (Belgium), RGM - Nationaal Natuurhistorisch Museum/Naturalis, Leiden (the Netherlands, formerly Rijksmuseum van Geologie en Mineralogie), RM - R. Marquet Collection.

Order	Ostreoida Férussac, 1822 (emend. Waller, 1978)
Suborder	Pectinina Waller, 1978
Superfamily	Pectinoidea Wilkes, 1810 (emend. Waller, 1978)
Family	Pectinidae Wilkes, 1810 (emend. Waller, 1978)
Subfamily	Palliolinae Korobkov in Eberzin, 1960
Tribe	Palliolini Waller, 1993 (= <i>Palliolum</i> group, Waller in Shumway, 1991)
Genus	<i>Pseudamussium</i> Mörch, 1853

Type species — *Pecten septemradiatus* Müller, 1776 (= *Ostrea peslutrae* Linné, 1771; see Dijkstra, 1999, p. 427) under the plenary powers (ICNZ Opinion 714).

Stratigraphic distribution — Early Miocene to Recent.

Synonyms — The following taxa are considered to be synonymous with *Pseudamussium*:

- Pseudamusium* Klein, 1753, p. 134 (pre-Linnaean);
- Pseudamussium* Herrmannsen, 1847, p. 340 (*nomen nudum*);
- Pseudamussium* H. & A. Adams, 1853, p. 553 (subgenus of *Pecten*), type species, by subsequent designation of Dall, 1898 (p. 751), is *Ostrea hybrida* Gmelin, 1791 (= *Ostrea exotica* Dillwyn, 1817);
- Pseudamusium* Verrill, 1897, p. 60 (emendation of *Pseudamussium* H. & A. Adams);
- Peplum* Bucquoy *et al.*, 1889, pp. 62, 67 (subgenus of *Pecten*), type species, by original designation, (= *Ostrea clavata* Poli, 1795);
- Platipecten* Monterosato, 1889, p. 191 (subgenus of *Chlamys*), type species by original designation, is *Pecten subclavatus* Cantraine, 1835 (= *Pecten septemradiatus* Müller, 1776);
- Porosichlamys* Barsotti in Lucas, 1979, p. 9 (invalid, ICNZ art. 11e);
- Karnekampia* Wagner, 1988, p. 41, type species, by original designation, is *Pecten bruei* Payraudeau, 1826 (= *Pecten sulcatus* Müller, 1776).

Diagnosis — Radially undulated to smooth Palliolini with antimarginal micro-ornament on anterior and posterior side of disc, absent or rarely intercostal on central portion, and on auricles of left valve. Radial and commarginal macro-ornament in early ontogeny. In later growth stages solid or more or less hollow primary and

secondary radial macro-ornament, rarely intercostal commarginal ornament. Internal surface smooth or lyrate, not carinate. Auricles unequal in size. Ctenolium delicate with closely spaced teeth; byssal notch moderately shallow throughout ontogeny, and byssal fasciole rather broad.

Distribution — Early Miocene to Recent, Europe; Middle Miocene, Iran; Recent, eastern Pacific (see Hertlein in Moore, 1969, p. N354).

Remarks — Numerous previous references to *Pseudamussium* may be found in Grau (1959), who followed mainly North (1951a, b). Hertlein in Moore (1969, p. N354) placed *Pseudamussium* in the *Eburneopecten* group, together with *Cyclopecten* Verrill, 1897, *Hemipecten* Adams & Reeve, 1849 and *Palliolum* Monterosato, 1884 and a number of subgenera. Subsequently, Vaught in Abbott & Boss (1989, p. 119) in part followed Hertlein and assigned *Pseudamussium* to the tribe Eburneopectini, which also included *Delectopecten* Stewart, 1930. *Cyclopecten*, however, is a propeamussiid genus, not a pectinid, according to Waller (1984, p. 213). The monotypic *Hemipecten* resembles *Pedum* Lamarck, 1799 (see Waller, 1972, p. 256) and is now referred to the tribe Chlamydini von Teppner, 1922 (see Waller, 1993, p. 200). With *Placopecten* Verrill, 1897 and *Pseudamussium*, *Palliolum* belongs to the *Palliolum* group, now referred to as the tribe Palliolini (see Waller, 1993, p. 198). Waller & Marinovich (1992, p. 219) have recently placed *Delectopecten* in the Camptonectinae Habe, 1977. *Peplum* and *Karnekampia* show morphological features identical to those of *Pseudamussium* and thus are here considered to be junior synonyms (see also Hertlein in Moore, 1969, p. N355; Waller in Shumway, 1991, p. 35). Neogene species from the North Sea Basin have formerly been assigned either to *Palliolum* or to *Pseudamussium*; differences between these taxa are briefly outlined in Table 1.

Pseudamussium edegemense (Glibert, 1945)

Pl. 1, figs 3, 4

- * 1945 *Pecten* (*Pallium*) *edegemensis* Glibert, p. 77, pl. 3, fig. 3a-c.

Locus typicus — Former clay pit at Edegem, south of Antwerp, Belgium.

Stratum typicum — Berchem Formation, Edegem Member (Miocene, Hemmoorian, Behrendorfian).

Material studied — IRScNB IST 1943 (holotype), IRScNB IST 1944, IRScNB IST 6384, IRScNB IST 6394, in addition to 1 specimen (RM Colln, temporary outcrop garage Gaumont Cinema, Antwerp, Berchem Formation, Antwerpen Member, *Panopea* level), 12 specimens (RM Colln, Antwerp-Ploegstraat, same stratigraphic level), 16 specimens (RM Colln, Antwerp-Kleine Ring motorway exit at Luitenant Lippenslaan,

same stratigraphic level), 33 specimens (RM Colln, Antwerp-underground Schijnpoot, same stratigraphic level), 11 specimens (RM Colln, Antwerp-Kleine Ring motorway, Berchem, same stratigraphic level), 26 specimens (RM Colln, Heist-op-den-Berg, Berchem Formation, Zonderschot Member), 12 specimens (RM Colln, Antwerp-Kennedy Tunnel, Berchem Formation, Edegem Member), 12 specimens (Antwerp-Kleine Ring [co-ordinates 154.5-155.7, 209.5-211.8], Berchem Formation, Antwerpen Member).

Dimensions — see Table 2.

Description — Rather small, tear-shaped, inequivalve shell, taller than wide, left valve more tumid than right. Auricles on both sides clearly different, posterior auricle only one third the length of anterior. Right valve with about twenty well-developed primary radial ribs, which in young specimens are as wide as the intercostal spaces, but in adults become twice as wide; further from umbo, ribs become obsolete. Ribs are hollow internally and at first comprise 2, later 6-8 secondary ribs, roofed by a thin layer of shell material, which may partially be lost in some specimens (e.g. holotype; see Glibert, 1945, fig. 3c). At the anterior and posterior margins, only densely packed antimarginal striae occur; directly at the margins, these striae are perpendicular to the radial ribs, near the centre of the disc they take an umbonal direction. Intercostal areas between primary ribs have mostly three secondary ribs, crossed by commarginal riblets that do not continue on the primary ribs and form weak scales when crossing the secondary ribs. Growth lines rarely visible. Anterior auricle shows central area with five heavy, close-set tuberculate ribs, with only growth lines above and below, most obvious above; posterior auricle shows antimarginal ornament, continuous with that of disc edges. Pallial line straight, ligament pit shallow, chondrophore rather large but shallow. Ctenolium weak, often virtually absent, with 6-8 denticles. Interior surface fairly glossy, with weak primary ribs visible; muscle impressions large, rounded.

Ornament of left valve shows the same elements as the right one, but with more tumid primary ribs and commarginal striae on a larger portion of the disc, as well as commarginal striae continuing over the primary ribs. Secondary intercostal radial ornament lacking, only scales present, stronger than those on right valve. Anterior auricle with 5-7 tuberculate radial ribs, slightly narrower than intercostal areas. Tubercles appear where radial ribs and weaker commarginal lines cross.

Discussion — The left valve of *P. edegemense* is described here for the first time. Hollow radial ribs were held to be the most important character distinguishing the genus *Karnekampia* by Wagner (1988), who mentioned this kind of ornament for the left valve only. The present material shows it to occur on both valves. However, in view of the wide range of intraspecific variation in pectinids, we consider this to be an insufficient character for the erection of a separate genus.

Occurrence — *Pseudamussium edegemense* is rare in the Edegem and Zonderschot members, but fairly common in the *Panopea* bed (Antwerpen Member). According to Hooyberghs (1996a, b), these units of the Berchem Formation are of Early Miocene (Aquitanian-Burdigalian) age, according to Janssen (1998) they however should be included in the Middle Miocene Langhian (Hemmoorian, Behrendorfian in the North Sea basin). The sediment type of these members is a rather coarse, well-sorted glauconitic sand; they have yielded warm, rather deep water faunas, at least partially preserved *in situ* (e.g. *Panopea* level). So far, *P. edegemense* has not been found in the Deurne Member (Diest Formation, Late Miocene). Outside the Antwerp area, the species was found in the Middle Miocene of Haamstede (the Netherlands) (RGM collection, unpublished). *P. edegemense* is endemic for the Miocene North Sea basin.

***Pseudamussium princeps* (J. de C. Sowerby, 1826)**

Pl. 1, figs 1, 2; Pl. 2, fig. 1

- * 1826 *Pecten princeps* J. de C. Sowerby, p. 80, pl. 542, fig. 2.
- 1851 *Pecten Princeps* — Wood, p. 31, pl. 6, fig. 1.
- 1874 *Pecten Princeps*, var. *pseudo-Princeps* Wood, p. 103, pl. 8, fig. 9.
- 1878 *Pecten princeps* — Nyst, pl. 14, fig. 1
- 1881 *Pecten princeps* — Nyst, p. 148.
- 1939 *Chlamys princeps* Sowerby — Roger, p. 170, pl. 24, figs 4, 5; pl. 25, fig. 5; pl. 27, fig. 3.
- 1955 *Chlamys princeps* (Sowerby) — Glibert & de Heinzelin, p. 24.
- 1957 *Chlamys princeps* Sowerby, sp. 1826 — Glibert, p. 25.
- 1969 *Chlamys (Chlamys) princeps* (J. de C. Sowerby, 1826) — van Regteren Altena *et al.*, p. 12, fig. 1, pl. 9, fig. 35.

Locus typicus — Ramsholt, Suffolk (United Kingdom).

Stratum typicum — Coralline Crag (Early Pliocene).

Material studied — IRScNB IST 1811 (material illustrated by Nyst, 1878; Deurne, Diest Formation, Deurne Member), RGM 394 096-097, 17 specimens (RGM Colln, Kallo-Vrasenedok, Kattendijk Formation, *Petalonchus* level), 5 specimens (RM Colln, same locality and stratigraphic level), 14 specimens (RM Colln, Kallo-Verrebroekdok, same stratigraphic level), 5 specimens (RM Colln, Antwerp-Kleine Ring motorway, Borgerhout, Diest Formation, Deurne Member), 12 specimens (RM Colln, Kallo-Vrasenedok, Kattendijk Formation, above *Petalonchus* level), 3 specimens (RM Colln, water purification plant), Antwerp-Schijnpoot, Kattendijk Formation, *Ditrupa* level), 4 specimens (HD Colln, Kallo-'Vierde Havendok', Kattendijk Formation).

Dimensions — see Table 2.

Description — Shell thin, large, up to c. 168 mm tall,

juveniles slightly taller than wide, adults wider than tall, slightly inequivalve, left valve more convex than right. Shell inequilateral, auricles unequal, umbonal angle *c.* 110°. Byssal notch moderately deep, byssal fasciole rather broad. Active ctenolium present in juveniles, consisting of seven tuberos denticles, disappearing in adults. Resilifer triangular. Cardinal crura well developed.

Ornament in left valve of early juveniles with numerous, very fine subequal radial riblets, some of which become stronger gradually. Commarginal growth lines inconspicuous in this portion of shell. Older juveniles with *c.* 22 primary radial costae, up to twice the width of the intercostal areas, but mostly narrower. Ribs consist in central portion of disc of 4-6 secondary radial riblets; in the central intercostal areas, 4 secondary riblets are developed. Near the anterior area, the distinction between primary and secondary ornament disappears, with 6 subequal ribs present. In the intercostal areas of the posterior third and anterior quarter of the disc, delicate antimarginal striae occur, forming angles of 45° in relation to radial ribs. Secondary radial ornament absent in these portions of shell. Posteriorly, these striae already start in early growth stages, being nearly as strong as radial ribs. Late juvenile ornament mostly commences from a clearly visible growth line, gradually developing in other specimens through strengthening of some radial ribs. In adult specimens, primary and secondary ornament equally strong, consisting of up to 80 radial ribs. Antimarginal ornament may cover the disc completely. Scales may be present on intersections of growth lines and radial ribs. Posterior auricle half the length of anterior in juveniles, to three-quarters in adults, with 3-4 strong, spiny antimarginal riblets. Anterior auricle with 5-6 primary antimarginal riblets bearing scales, each occupying about half of intercostal area. Secondary ornament in intercostal area on both anterior and posterior auricles consisting posteriorly of narrow grooves, forming angles of *c.* 30° with primary riblets, and directed to hinge line. Anteriorly, secondary ornament on auricle best developed near hinge line and there consisting of groups of 4-5 narrow furrows, radiating from a common origin on the anterior portion of auricle.

Ornament of right valve largely corresponding to that of left, but primary ribs on central portion of disc clearly wider and flatter; in rare specimens only secondary riblets are present. Scales on radial ribs invariably absent. Antimarginal striae weaker, often restricted to posterior portion of shell. Ribs on anterior portion becoming gradually more equal by thickening of secondary ornament; ribs then as wide as intercostal areas. Posterior auricle half the length of anterior, with 4 prominent, narrow antimarginal riblets, which become weaker near the posterior margin; may be ornamented with up to 6 well-developed or weaker spines. Secondary ornament lacking. Anterior auricle with a variable

number of strong growth lines and about 7 antimarginal riblets on the central/umbonal portion. These riblets are weaker and more closely spaced than those on posterior auricle. Highest quarter and lower half of auricle show prominent growth lines. Secondary ornament mostly present, but weaker than on left valve. Hinge line straight.

Discussion — Juvenile specimens have been collected from the *Petalococonchus* level, a portion of the Kattendijk Formation until now sampled extensively *in situ* at Kallo only. This level is characterised by dense colonies of the bivalve *Petalococonchus glomeratus* (Linné, 1758) and has yielded highly interesting molluscan faunas, amongst which numerous representatives of the Emarginulidae and Polyplacophora are of particular note. The *Petalococonchus* colonies probably provided sufficiently hard substrates for those molluscs to settle. Juveniles of *P. princeps* have a well-developed ctenolium, which suggests that they were probably attached to the substrate by their byssus. The active ctenolium is lost in adults, and these were probably free living; adult shells are absent from the *Petalococonchus* level, but do occur scattered in the overlying beds, where juveniles are absent. The *Petalococonchus* level sand is well sorted, contains large amounts of glauconite, and in the uppermost part yields a number fossils probably preserved in life position, *e.g.* crustacean burrows of the *Ophiomorpha* type, which suggests deposition in calm waters. However, *P. princeps* is also known from the Late Miocene 'Heterocetus Sand' (Diest Formation), which is a coarse sand unit, with gravel and large blocks of sandstone, suggesting deposition in a turbulent setting.

In *P. princeps*, there usually is a clear difference between the ornament of juvenile, subadult and adult specimens; juveniles have far more numerous radial ribs than subadults, which also are subequal. In adults, the distinction between primary and secondary ribs disappears and the number of radials increases. In some specimens, the onset of subadult ornament is gradual, in others it is sudden. The development of spines on auricle ribs is highly variable, the ornament of the remainder of shell however showing little variation, mainly in strength of striae on juvenile portion of shell and in size of area covered in striae instead of secondary radial ornament.

Pseudamussium princeps differs markedly from *P. edegemense* in lacking hollow radial ribs, and in the relative size of the posterior auricles (*i.e.* in excess of 50% of length of anterior auricles in the former, and barely a third in the latter species). *Pseudamussium princeps* also grows to a much larger size than *P. edegemense*.

Wood (1851) considered *Pecten sublaevigatus* Nyst, 1843 to be a synonym of *Pseudamussium princeps*. However, Nyst's species is much smaller than *P. princeps*, has an utterly different adult ornament, and occurs in the Wemmel Member (Late Eocene) at Laeken, near Brussels.

***Pseudamussium lilli* (Pusch, 1837)**

Pl. 2, fig. 2

- * 1837 *Pecten lilli* Pusch, p. 40, pl. 5, fig. 5.
- 1843 *Pecten Lamalii* Nyst, p. 305, pl. 22, fig. 5b, d; pl. 24, fig. 5.
- 1869 *Pecten scissus* Favre, p. 151, pl. 13, fig. 9.
- 1936 *Chlamys (Flexopecten) scissa* Favre — Friedberg, p. 236, pl. 39, figs 16-20; pl. 40, figs 1, 2.
- 1936 *Chlamys (Flexopecten) Lilli* Pusch — Friedberg, p. 241, pl. 40, figs 7-13.
- 1939 *Chlamys scissa* Favre — Roger, p. 187, pl. 19, figs 7-16.
- 1939 *Chlamys lilli* Pusch — Roger, p. 187, pl. 19, figs 17-20.
- 1945 *Pecten (Pallium) lilli* Pusch, 1837 — Glibert, p. 73, pl. 5, fig. 1.
- 1964 *Chlamys (Pallium) tigerina* (O.F. Müller, 1776) — Anderson p. 142 (non Müller)
- 1984 *Pseudamussium lilli* (Pusch, 1837) — Janssen, p. 54, pl. 25, figs 1-5.
- 1986 *Chlamys (Flexopecten) scissus* (Favre, 1869) — Studencka, p. 40, pl. 4, figs 8, 9; pl. 5, figs 1-10; pl. 6, figs 1, 2, 5, 6, 9, 10.
- 1998 *Flexopecten lilli* (Pusch, 1837) — Studencka *et al.*, p. 314.
- 1998 *Flexopecten scissus* (Favre, 1869) — Studencka *et al.*, p. 314.

Locus typicus — Wieliczka, Poland.

Stratum typicum — Badenian (Miocene).

Material studied — IRScNB IST 1756 (Houthalen, Belgian province of Limburg, Berchem Formation, Houthalen Member), IRScNB IST 1935, 1942, 3816 (Antwerp, Berchem Formation, Antwerpen Member), IRScNB IST 1939-1940 (Edegem, Berchem Formation, Edegem Member), 1 specimen (RM Colln, Kallo-Vrasenedok, Kattendijk Formation, *Petalocochus* level), 140 specimens (RM Colln, Antwerp-underground Schoolplein, Berchem Formation, Antwerpen Member, *Glycymeris* level).

Dimensions — see Table 2.

Description — Rather small, slightly inequivalve, flat shell with near-circular disc and unequal, rather small auricles. No ctenolium. Ligament pit small, triangular, shallow, wider than tall. Muscle insertion rounded. Right valve usually slightly more tumid than left. Ornament extraordinarily variable, at first consisting either of radial ribs divided into primary and secondary ones, or of equal strength; secondly, commarginal ornament develops, but this is much weaker. In both valves, primary ribs may be hollow and composed of several secondary ones. Antimarginal ornament absent on disc. In general, two types of ornament may be distinguished: on right valves of type 1 (commonest in material from the Miocene of Belgium), the number of radial ribs is lower than on left valves, with the right valves having about ten primary ribs, often bifurcating. Intercostal areas are less wide and mostly show secondary radial ornament. Type 2 (rarer in

Miocene strata) has up to 35 radial ribs, mostly occurring in groups of two, and with intercostal areas of the same width as a couple of radial ribs. Secondary ornament may be present, but in some specimens there are commarginal, scale-like striae instead of radial intercostal ribs. In both types, primary ribs consist mostly of up to ten secondary ribs, with very narrow spaces in between. Rarely, weak spines are present on ribs. Left valve with similar ornament, but number of primary ribs mostly higher (18-20), while more valves show type 2 ornament, and ribs rarely bifurcate. Radial as well as commarginal ornament may occur in intercostal areas. Anterior auricle of right valve about twice the length of posterior, with 4 heavy, scaled ribs near upper margin, area bordering disc with growth lines and weak antimarginal ornament. Posterior auricle with 5 faintly delimited, scaled primary ribs over entire height. Between these, wide secondary ribs occur with very narrow intercostal areas, occasionally co-occurring with antimarginal striae. In left valve, a similar but mostly weaker auricle ornament is present.

Discussion — For more complete synonymy lists and illustrations of the present species' range of variation, reference is made to Glibert (1945) and Studencka (1986, *sub C. (F.) scissus*). Roger (1939), Studencka (1986) and Studencka *et al.* (1998) considered *P. lilli* and *P. scissus* to be distinct species, with a lower number of radial ribs in the latter (see Roger, 1939), and the presence in the latter of tubercles where radial and commarginal ornament intersect (see Studencka *et al.*, 1998). Similar tubercles have been observed in material from the Miocene of Belgium, but only very rarely. In *P. lilli*, however, the ornament is extremely variable; we consider a single character to be too small a basis for specific distinction. In addition, in the papers cited both 'species' are recorded from largely the same distribution area, viz. North Sea Basin, Poland and the Paratethys, including the Middle East, but without records from the Mediterranean and Atlantic. This distribution pattern is of note, since it suggests faunal exchange between the North Sea Basin and the Paratethys during the Miocene. The same was proposed amongst others by Janssen & Zorn (1993).

Glibert (1945) also distinguished both types of ornament described here, with type 1 referred to as 'forma *scissus*', and type 2 as 'formae *lilli-kneri*'. The present species is here considered to be assignable to *Pseudamussium* on account of the presence of anti-marginal ornament on the posterior auricle. However, this ornament is less well developed than in its congeners discussed here.

Occurrence — *Pseudamussium lilli* is known to date in the North Sea basin from Belgium (Edegem, Antwerpen and Zonderschot Members), from the Netherlands (Aalten Member, Miste Bed, see Janssen, 1984; Aalten Member, Stemerding Bed, see Janse & Janssen, 1983) and from Germany (Reinbek Schichten, Twistringen

Schichten, Bislicher Schichten, see Anderson, 1964). A single specimen, collected from Pliocene strata at Kallo, subsequently was broken during transport.

Pseudamussium sulcatum (Müller, 1776)

Pl. 2, fig. 3

- * 1776 *Pecten sulcatus* Müller, p. 248.
- 1826 *Pecten Bruei* Payraudeau, p. 78, pl. 2, figs 10-14.
- 1851 *Pecten Bruei*, Payraudeau — Wood, p. 29, pl. 5, fig. 3.
- 1939 *Chlamys bruei* Payraudeau — Roger, p. 201, pl. 21, figs 3-9.
- 1965 *Pseudamussium* (*Zygochlamys*) *bruei* (Payraudeau, 1826) — Glibert & van de Poel, p. 36.
- 1976 *Chlamys* (*Chlamys*) *sulcata* (Müller) — Tebble, p. 59, pl. 6, fig. F.
- 1988 *Karnekampia bruei* (Payraudeau, 1826) — Wagner, p. 42, fig. 1.
- 1988 *Karnekampia sulcata* (Müller, 1776) — Wagner, p. 42, fig. 2.
- 1991 *Chlamys* (*Chlamys*) *bruei* (Payraudeau, 1826) — Rombouts, p. 9, pl. 23, fig. 5.
- 1993 *Chlamys bruei* (Payraudeau, 1826) — Poppe & Goto, p. 60, pl. 7, fig. 4.
- 1995 *Karnekampia* aff. *bruei* (Payraudeau, 1826) — Vera-Peláez *et al.*, p. 100.

Locus typicus — Denmark.

Stratum typicum — Recent.

Material studied — One specimen (RM Colln, off Morano Island, - 200 m, near Venice, Recent), 5 specimens (HD Colln, off Trondheim, Norway, - 120-140 m, Recent), 3 specimens (HD Colln, off South Island, - 460-520 m, Recent), 3 specimens (HD Colln, off Koster Island, western Sweden, - 73-110 m, Recent), 5 specimens (HD Colln, off Capraia Island, Italy, - 120-140 m, Recent), 4 specimens (RM Colln, Kallo-Verrebroekdok, Kattendijk Formation, *Petalo-conchus* level).

Dimensions — see Table 2.

Description — Rather small species, fossil specimens studied up to 20 mm in height, extant ones up to 30 mm. Shell very flat, thin and brittle. Disc near-circular to slightly taller than wide, inequivalve with left valve slightly more convex than right. Anterior auricle about three times the length of the posterior, with a prominent byssal notch. Active ctenolium with about 8 denticles.

Right valve with 20-40 weak primary ribs, widely separated or more closely spaced, depending on rib number. Ribs often form clusters, mostly consisting of two ribs, occasionally more. In and on primary ribs, secondary ones occur on the central portion of disc, 2-8 in between ribs, 0-4 on them. Secondary ribs often not much weaker than primary ones, especially near anterior and posterior margins. In intercostal areas between primary ribs, low commarginal scales often occur. On primary ribs, especially anteriorly, higher spiny scales

are mostly present. Growth lines weak. Near umbo, tubercles often are present on and between ribs, effacing on younger portions of shell. Weak anti-marginal ornament on anterior and posterior margins. Anterior auricle with 5-7 radial ribs, lacking on ventral portion. Ribs wider than intercostal areas and covered with strong tubercles. Growth lines strong, ending on hinge line in 8 spines, perpendicular to radial ribs. Posterior auricle with 5-7 tuberculate radial ribs, much weaker than those on anterior auricle. Antimarginal ornament often is well developed.

Ornament of left valve similar, often with stronger commarginal intercostal ornament and heavier rib tubercles; antimarginal ornament also often more pronounced. Primary ribs often hollow, composed of several secondary ones, but this is not always the case.

Discussion — The present species is closely related to *P. lilli* (see above), which is also known from the *Petaloconchus* level (Kattendijk Formation) at Kallo. Both taxa have shell shape and widely variable ornament in common, often with scales in intercostal areas; tubercles can occur in younger growth stages, which holds especially true for 'forma *scissus*' of *P. lilli*. However, in *P. lilli* there is a tendency for radial ribs to form larger clusters; moreover, ribs are hollow in left and right valves. *Pseudamussium lilli* and *P. sulcatum* could well form an evolutionary lineage.

Wood (1851) described and illustrated as *Pecten Bruei* a specimen from the Coralline Crag (Early Pliocene) of Sutton (East Anglia, United Kingdom). There are no records from the Pliocene of the Netherlands. Vera-Peláez *et al.* (1995) recorded *P. sulcatum* from the Early Pliocene (Zanclean) of Malaga (Spain), while Glibert & van de Poel (1965) mentioned Pliocene (Astian) material from Millas, Roussillon (France). Roger (1939) reported its occurrence in the Italian Pliocene, and considered *Chlamys* (*Flexopecten*) *ampferi* Kautsky, 1928 (p. 262, pl. 7, fig. 8) from the Badenian (Middle Miocene) of Steinabrunn (Austria) to be a junior synonym of *P. sulcatum*. However, more material is needed to decide whether this form should be assigned to *P. sulcatum*, or rather to *P. lilli*.

Tebble (1976), Rombouts (1991) and Poppe & Goto (1993) recorded extant *P. sulcatum* from Iceland and Norway to the Cape Verde Islands and from the Mediterranean, in circalittoral settings, and down to depths of 2,500 m, on sand and mud, being rare everywhere.

Pseudamussium clavatum (Poli, 1795)

Pl. 2, figs 4-6

- 1795 *Ostrea inflexa* Poli, p. 160, pl. 28, fig. 5.
- * 1795 *Ostrea clavata* Poli, p. 161, pl. 28, fig. 17.
- 1851 *Pecten Danicus* Chemnitz — Wood, p. 30, pl. 4, fig. 2.
- 1939 *Chlamys clavata* Poli — Roger, p. 208, pl. 28, figs 4, 5, 9-12, 14.

- 1950 *Pecten (Pseudamussium) septemradiatum* (Müller, 1776) — Heering, p. 49, pl. 14, fig. 10.
 1956 *Chlamys (Peplum) clavata* (Poli) — Rasmussen, p. 32, pl. 1, fig. 5.
 1957 *Chlamys (Peplum) clavatum* Poli, sp. 1795 — Glibert, p. 28, pl. 1, fig. 11.
 1968 *Chlamys clavata* (Poli 1795) — Rasmussen, p. 32.
 1969 *Pseudamussium (Pseudamussium) clavatum* (Poli, 1795) — van Regteren Altena *et al.*, p. 17, pl. 11, fig. 40; text-fig. 2a, b.
 1991 *Pseudamussium (Peplum) clavatum* (Poli, 1795) — Rombouts, p. 57, pl. 20, fig. 10.
 1993 *Pseudamussium clavatum* (Poli, 1795) — Poppe & Goto, p. 70, pl. 10, fig. 6.

Locus typicus — Sicily (Italy).

Stratum typicum — Recent.

Material studied — IRScNB IST 4801 (Deurne, Diest Formation, Deurne Member), IRScNB IST 4802 (Berchem, same stratigraphic level), as well as 20 specimens (RM Colln, Borgerhout-Kleine Ring motorway, Diest Formation, 'Heterocetus sand'), 4 specimens (RM Colln, same locality, Diest Formation, Deurne Member), 5 specimens (RM Colln, Deurne, water purification plant at Schijnpoot, same stratigraphic level), 5 specimens (RM Colln, Deurne-Rivierenhof pond, same stratigraphic level), 1 specimen (RM Colln, old clay pit Gram, Denmark, 'Gram Stufe'), 3 specimens (RM Colln, Ohle sandpit, Gross Pampau, Holstein (Germany), 'Langenfeld Stufe'), 1 specimen (RM Colln, Kallo-tunnel, Kattendijk Formation, basal gravel), 6 specimen (RM Colln, Kallo-tunnel, Kattendijk Formation, below *Petalocochus* level), 44 specimens (RM Colln, Kallo-Vrasenedok, Kattendijk Formation), 67 specimens (RM Colln, same locality, Kattendijk Formation, *Similipecten* level), 2 specimens (RM Colln, Antwerp-underground Schijnpoot, Kattendijk Formation).

Dimensions — see Table 2.

Description - Medium-sized (up to 30 mm in height), tear-shaped disc, strongly inequivalve, right valve tumid, left valve flat, with a depression below umbo. Auricles small, unequal, posterior measuring but a third of length of anterior; byssal notch absent. Active ctenolium weak or absent.

Right valve with 4 very wide primary ribs, separated by 3 less wide (1/3-2/3 of width of ribs) intercostal areas. Ribs on disc sharply delimited, anterior and posterior ribs effacing. Primary ribs and intercostal areas covered with secondary radial ornament, which may either be well developed or appear absent. On primary ribs, 7-40 rather wide to very narrow secondary ribs occur, which may cause ribs to appear hollow. In intercostal areas, 7-10 secondary ribs occur; these are fine, much more widely spaced than on primary ribs and covered with small scales. Antimarginal ornament present only on margins. Commarginal ornament mostly absent, growth lines visible only occasionally. Anterior auricle with about 7 irregular ribs, with close-set scales; ribs

becoming weaker ventrally. Posterior auricle with 3-5 faintly delimited ribs, clearly showing antimarginal ornament. Interior of valve glossy, showing primary ribs and in some specimens the largest secondary ones on ventral margin.

Left valve flat, with 3 primary ribs and relatively much wider intercostal areas (1-2 times the width of primary ribs). Secondary radial ornament present. Ten closely spaced ribs on primary radials, 5 more widely spaced ones in between, both showing small scales. Antimarginal ornament on anterior and posterior margins. Ornament on auricles similar to that in right valves, but ribs clearer, finer and more widely separated.

Discussion — The present species is known to date in the North Sea Basin from the Late Miocene to the Early Pliocene, and from the Early Pliocene onwards in the Mediterranean, extending from Algeria to Syria (Roger, 1939). In Belgium, *P. clavatum* is known from the Diest Formation, occurring both in fine sands of the Deurne Member as well as in the overlying gravels of the 'Heterocetus Sand'. In the Kattendijk Formation, it is common in the lower part, especially in the *Similipecten* bed and in the level with *Ophiomorpha*-type crustacean burrows immediately above the *Petalocochus* level. It is absent from the upper *Ditrupa-Glycymeris* beds (Kattendijk Formation), as well as from younger Pliocene strata. In the Netherlands, material has been recorded from beaches and boreholes; in the United Kingdom, the species is rare in the Coralline Crag.

Poppe & Goto (1993) recorded it from the British Isles to Portugal and from the Mediterranean, on muddy bottoms in depths between 5 and 1,400 m.

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Character	<i>Pseudomussium</i> Mörch, 1853 Type species: <i>Pecten septemradiatus</i> Müller, 1776 by SD: ICNZ Op. 714	<i>Palliolium</i> Monterosato, 1884 Type species: <i>Pecten incomparabilis</i> Risso, 1826 by SD: Crosse, 1885
Size	Up to 180 mm high	Up to 30 mm high
Convexity	RV more convex than LV	RV slightly more convex than LV
Shape	Rarely equivalve, mostly inequivalve ; equilateral , seldom inequilateral Rarely smooth, mostly radially undulated Orbicular to slightly elongate (oblong)	Equivalve , rarely inequivalve; equilateral Smooth Orbicular
Microsculpture	Antimarginal on flanks of disc	Antimarginal
Macrosculpture	Primary radial lyrae, secondary radial riblets and secondary commarginal striae in early ontogeny	Absent on disc , present on auricles
Auricles	Anterior larger than posterior	Anterior much larger than posterior
Byssus	Byssal notch moderately shallow, mostly deep; byssal fasciole narrow or absent, ctenolium active present in juveniles, absent in adults to inactive and nearly absent	Notch deep; byssal fasciole broad, active or inactive ctenolium present, well developed

Table 1. Differences between the genera *Pseudamussium* and *Palliolium*. **Bold**: most important characters.

Specimen	Height (mm)	Length (mm)	Diameter (mm)	Posterior auricle length (mm)
<i>P. princeps</i> , right valve juvenile	31.2	27.5	3.3	6.2
<i>P. princeps</i> , left valve juvenile	24.4	21.0	3.4	6*
<i>P. princeps</i> , adult bivalved	137.2	142.7	39.8	39.6
<i>P. edegemensis</i> , left valve	26.3	24.6	4.7	3.2
<i>P. edegemensis</i> , right valve	26.8	23.1	3.0	3.3
<i>P. lilli</i> , right valve	16.2	16.3	2.4	2.3
<i>P. sulcatum</i> , left valve	18.1	19.4	2.7	3.2
<i>P. clavatum</i> , bivalved spec.	26.0	23.3	8.3	4.2
<i>P. clavatum</i> , right valve	28.8	25.4	5.2	*
<i>P. clavatum</i> , right valve	31.8	29.3	7.0	*

Table 2. Measurements of material illustrated in Pls 1, 2; * = auricle damaged, size approximate.

PLATE 1

- Figs 1, 2. *Pseudamussium princeps* (J. de C. Sowerby, 1826), juvenile left and right valves, respectively; Kallo-Vrasenedok (Beveren, Oost-Vlaanderen, Belgium), Early Pliocene (Kattendijk Formation, *Petalococonchus* level), RGM 394 096-097, x 3.4 (1a, 2) and x 6 (1b).
- Figs 3, 4. *Pseudamussium edegemense* (Glibert, 1945), right and left valve, respectively; temporary outcrop garage Gaumont Cinema (Antwerp, Belgium), Early Miocene (Berchem Formation, Antwerpen Member, *Panoepa* level), IRScNB IST 6384 and IST 6394, respectively, x 3.4 and x 3.3, respectively.

PLATE 1

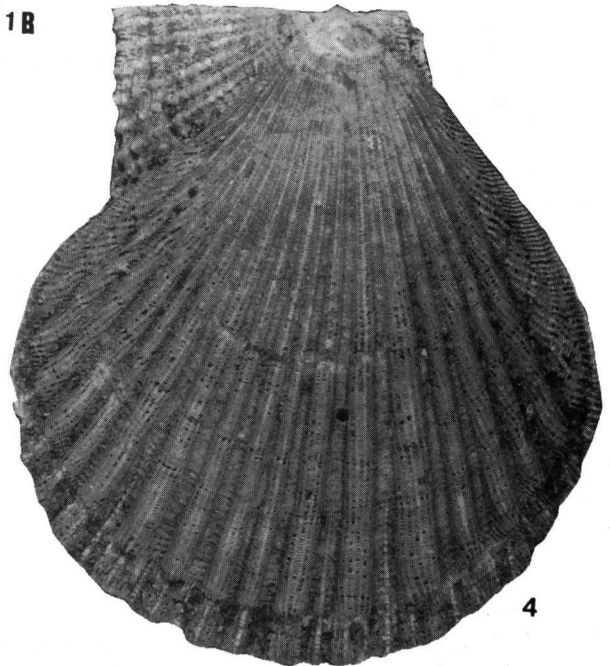
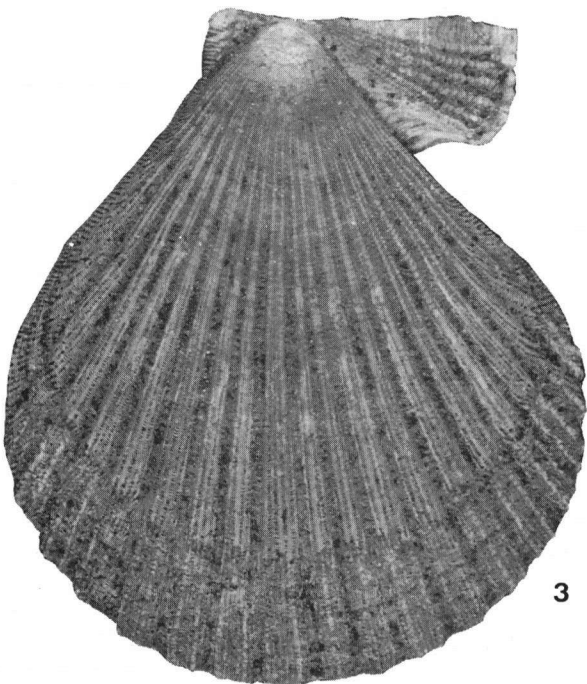
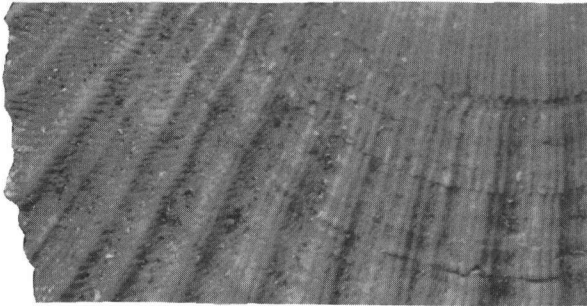


PLATE 2

- Fig. 1. *Pseudamussium lilli* (Pusch, 1837), right valve; Kallo-Vrasenedok (Beveren, Oost-Vlaanderen, Belgium), Early Pliocene (Kattendijk Formation, *Petalococonchus* level), Marquet Colln, x 2.4 (a) and x 3.4 (b).
- Fig. 2. *Pseudamussium sulcatum* (Müller, 1776), left valve; Kallo-Verrebroekdok (Beveren, Oost-Vlaanderen, Belgium), Early Pliocene (Kattendijk Formation, *Petalococonchus* level), x 2.9 (a) and x 4.6 (b).
- Fig. 3. *Pseudamussium princeps* (J. de C. Sowerby, 1826), adult; Kallo-Vrasenedok (Beveren, Oost-Vlaanderen, Belgium), Early Pliocene (Kattendijk Formation, *Petalococonchus* level), Marquet Colln; left valve, x 0.34 (a); right valve, x 0.34 (b); both valves, x 0.45 (c).
- Figs 4, 5. *Pseudamussium clavatum* (Poli, 1795), right valve and articulated specimen, respectively; Kallo-Vrasenedok (Beveren, Oost-Vlaanderen, Belgium), Early Pliocene (Kattendijk Formation, *Similipecten* level, Marquet Colln, x 1.8 (4); left valve, x 2 (5a), right valve, x 2 (5b).

PLATE 2

