

PLIOCENE SPECIES OF *AEQUIPECTEN* (MOLLUSCA, BIVALVIA, PECTINIDAE) FROM THE NORTH SEA BASIN

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Marquet, R. & H.H. Dijkstra. Pliocene species of *Aequipecten* (Mollusca, Bivalvia, Pectinidae) from the North Sea Basin. — Contr. Tert. Quatern. Geol., 37(3-4): 39-55, 6 figs, 2 pls. Leiden, December 2000.

Pliocene deposits in the North Sea Basin have so far yielded three species of the bivalve genus *Aequipecten* P. Fischer, 1886, viz. *A. opercularis* (Linné, 1758), *A. r. radians* (Nyst & Westendorp, 1839) and *A. wagnaari* n. sp. The last-named taxon appears to be restricted to the Early to Middle Pliocene of the North Sea Basin. In the literature, *Aequipecten r. radians* has been recorded from a number of Miocene and Pliocene localities both within and beyond the North Sea Basin; however, these records have proved erroneous. Material from Aquitaine (France) formerly considered to be assignable to *A. r. radians* should be referred to *A. liberatus* (Cossmann & Peyrot, 1914). Material from Touraine and Brittany represents the subspecies, *A. r. assimilatus* (Millet de la Turtaudière, 1866). *Aequipecten opercularis* first occurs in the Lower Miocene of Aquitaine, being represented by the subspecies, *A. o. pinorum* (Cossmann & Peyrot, 1914). Middle Miocene records of *A. opercularis* are known from the Lower Badenian of Romania.

Key words — Bivalvia, Pectinidae, Pliocene, North Sea Basin, taxonomy, new species.

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INTRODUCTION

Newly collected Neogene molluscan material from harbour, underground and motorway works in the Antwerp area (NW Belgium) has allowed an extensive revision of Miocene and Pliocene faunas. In recent years, quite a number of systematic studies on Pliocene gastropods and bivalves have come out (Marquet, 1984, 1993, 1995a, b, 1996, 1997a-c, 1998; Marquet & Dijkstra, 1999), while lithologic logs and maps have been published by Janssen (1974), Hoedemakers & Marquet (1992) and Marquet (1998). The present paper continues the series on Pliocene bivalves from Kallo. At this locality, an un-

described species of pectinid was collected; this had previously been encountered in Dutch beach material, but not yet been formally named because of lack of *in situ* material. It is here described as *Aequipecten wagnaari* n. sp.

SYSTEMATIC DESCRIPTIONS

Abbreviations — In the text the following abbreviations are used: IRScNB IST - 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 Colln; bv - bivalved specimen, v - single valve.

Order	Ostreoida Férussac, 1822
Suborder	Pectinina Waller, 1978
Superfamily	Pectinoidea Wilkes, 1810
Family	Pectinidae Wilkes, 1810
Subfamily	Chlamydinæ von Teppner, 1922

Tribe *Aequipectini* Waller, 1993
 Genus *Aequipecten* P. Fischer, 1886

Type species — *Ostrea opercularis* Linné, 1758, by monotypy (Recent, eastern Atlantic).

New synonyms — *Aequipecten (Perapecten)* Wagner, 1985 (p. 84), type species, by original designation, is *Pecten commutatus* Monterosato, 1875 (= *nom. nov. pro Pecten philippii* Récluz, 1853, *non* Michelotti, 1839); distribution: Recent, eastern Atlantic, from Portugal southwards to Senegal and in the Mediterranean). *Lindapecten* Petuch, 1995 (p. 40), type species, by original designation, is *Pecten muscosus* Wood, 1828; distribution: Recent, (sub)tropical western Atlantic.

Diagnosis — *Aequipectini* with a modified hinge dentition and prominent resilial teeth; shape near-orbicular and equilateral; auricles slightly unequal in size. In early ontogeny with a granulate micro-ornament, lacking reticulation or 'herringbone' structure; in early radial stage, shell generally with ventrally concave commarginal lirae on rib flanks.

Remarks — Wagner (1991, p. 42) raised *Perapecten* to generic level. However, morphological features of this taxon, i.e. macro- and micro-ornament and auricular crura, are similar to those of *Aequipecten*. Petuch (1995, p. 40) considered *Lindapecten* to be different from *Aequipecten* mainly on the basis of the presence of more erect spines on radial costae. This, however, is a very insignificant character, which may also be observed in species of the pectinid bivalve genera *Chlamys* Röding, 1798 and *Mimachlamys* Iredale, 1929. The overall morphological characters of *Lindapecten* and *Aequipecten* are similar, which is why they are here synonymised.

Typical extant species of *Aequipecten* are the following:

- *A. commutatus* (Monterosato, 1875) from the (sub)tropical eastern Atlantic and subtropical West Africa;
- *A. exasperatus* (G.B. Sowerby II, 1842) from the Caribbean region;
- *A. flabellum* (Gmelin, 1791) from the tropical eastern Atlantic;
- *A. muscosus* (Wood, 1828) from the (sub)tropical western Atlantic;
- *A. glyptus* (Verrill, 1882) from the (sub)tropical western Atlantic;
- *A. nicklesi* Dijkstra, 1998 from tropical West Africa;
- *A. opercularis* (Linné, 1758) from the boreal to subtropical eastern Atlantic;
- *A. tehuelchus* (d'Orbigny, 1847) from the (sub)tropical southwestern Atlantic.

***Aequipecten opercularis opercularis* (Linné, 1758)**
 Pl. 1, Figs 1, 2

- * 1758 *Ostrea opercularis* Linné, p. 698.
- 1825 *Pecten gracilis* J. de C. Sowerby, p. 129, pl. 393,

- fig. 2.
- 1827 *Pecten reconditus* J. de C. Sowerby, p. 146, pl. 575, figs 5, 6 (*non* Solander in Brander, 1766).
- 1843 *Pecten opercularis*. Lin. — Nyst, p. 291, pl. 23, fig. 2.
- 1843 *Pecten Sowerbyi* Nyst, p. 293, pl. 22, fig. 3.
- 1856 *Pecten opercularis* Linnaeus — Wood, p. 35, pl. 6, fig. 2.
- 1856 *Pecten gracilis*, J. Sowerby — Wood, p. 37, pl. 6, fig. 5.
- 1874 *Pecten niveus?* Macgillivray — Wood, p. 104, pl. 8, fig. 8.
- 1874 *Pecten opercularis* var. *arcuata* Wood, p. 105, pl. 8, fig. 6.
- 1878 *Pecten opercularis*, L. — Nyst, pl. 15, fig. 1.
- 1878 *Pecten sowerbyi*, Nyst — Nyst, pl. 15, fig. 2.
- 1881 *Pecten opercularis*, Lin. — Nyst, p. 149 (*partim*).
- 1937 *Chlamys opercularis* (Linné 1758) — van Regteren Altena, p. 61 (*partim*).
- 1950a *Pecten (Chlamys) opercularis* (Linné 1758) — Heering, p. 46, pl. 14, figs 3-6 (*partim*).
- 1950b *Pecten (A.) opercularis* (Linné) — Heering, p. 13, pl. 2, fig. 23.
- 1957 *Chlamys (Aequipecten) opercularis* Linné, sp. 1758 — Glibert, p. 28 (*partim*).
- 1969 *Lyropecten (Aequipecten) opercularis* (Linnaeus, 1758) — van Regteren Altena *et al.*, p. 16, pl. 10, fig. 38; pl. 11, fig. 38 (*partim*).
- 1976 *Chlamys (Aequipecten) opercularis* (Linnaeus) — Tebble, p. 60, pl. 5, fig. b, d.
- 1979 *Aequipecten opercularis* (L.) — Lucas, p. 14.
- 1981 *Chlamys (Aequipecten) opercularis* (Linné, 1758) — Lauriat-Rage, p. 44, pl. 4, fig. 7.
- 1991 *Aequipecten opercularis* (L., 1758) — Wagner, p. 40, text-fig. 22, pl. 6, figs 1-5.
- 1992 *Aequipecten (Aequipecten) opercularis* (L., 1758) — Cavallo & Repetto, p. 186, fig. 550.
- 1993 *Chlamys opercularis* (Linnaeus, 1758) — Poppe & Goto, p. 63, pl. 9, fig. 4.
- 1994 *Chlamys (Aequipecten) scabrella* (Lamarck, 1819) — Ben Moussa, p. 83, pl. 3, fig. 12 (*non* Lamarck).
- 1999 *Ostrea opercularis* Linnaeus, 1758 — Dijkstra, p. 421, fig. 7a-d.

Locus typicus — Brittany, France.

Stratum typicum — Recent.

Material studied — In addition to the type material (see Dijkstra, 1999, p. 422), we have studied the following specimens of *A. o. opercularis* (all in RM Colln): Antwerp (Borgerhout Ring, Lt. Lippenslaan, 4 bv/3 v); Antwerp (Ring Rivierenhof and Ring Foorplesin, all from 'Heterocetus level', Diest Formation, Deurne Member, 1 bv/12 v); Kallo (Verrebroekdok, Lillo Formation, Oorderen Member, *Cultellus* level, 108 v); Kallo (Vrasenedok, upper part Kattendijk Formation, 2 bv); Antwerp (Kruisschanssluis, Lillo Formation, Lucht-bal Member, 4 bv); Antwerp (Noordkasteel, Luchtbal Member, 13 bv); Wijnegem (Het Sas, Austruweel Member, 1 v); Ekeren (Schoonbroek, Kruisschans Member, 10 v); Kallo (Verrebroekdok, Kruisschans Member, basal level, 39 v); Kallo (Verrebroekdok, Kruisschans Member, sand lens, 39 v); Antwerp (Ring Borgerhout, mixed derived Pliocene, 1 bv); Antwerp (Berendrecht-Negende Haven-

dok, Merksem Member, 109 v); Kallo (Verrebroekdok, Merksem Member, 21 v); Gedgrave (The Cliff, Coralline Crag, 28 v); Gedgrave (The Broom, Coralline Crag, 21 v); Sutton (Rockhall Wood, Coralline Crag, 50 v); Sutton (Sudbourne Park Pit, Coralline Crag, 50 v); Walton-on-the-Naze (The Naze, Essex, Waltonian Red Crag, 11 v); Alderton (Buckanay Farm Pit, Suffolk, Newbournian Red Crag, 3 v).

Of *Aequipecten o. pinorum* (Cossmann & Peyrot,

1914) we have studied 20 valves from Salles (Ruisseau de Dubern, Gironde, Aquitaine, France; Falun de Salles, Middle Miocene, RM Colln).

Dimensions — Height 67.2 mm, length 70.8 mm, diameter 24.0 mm (bivalved specimen, see Pl. 1, Fig. 1); height 39.2 mm, length 41.7 mm, diameter 12.6 mm (bivalved specimen, see Pl. 1, Fig. 2). For height and length of a sample of 50 specimens see Fig. 1.

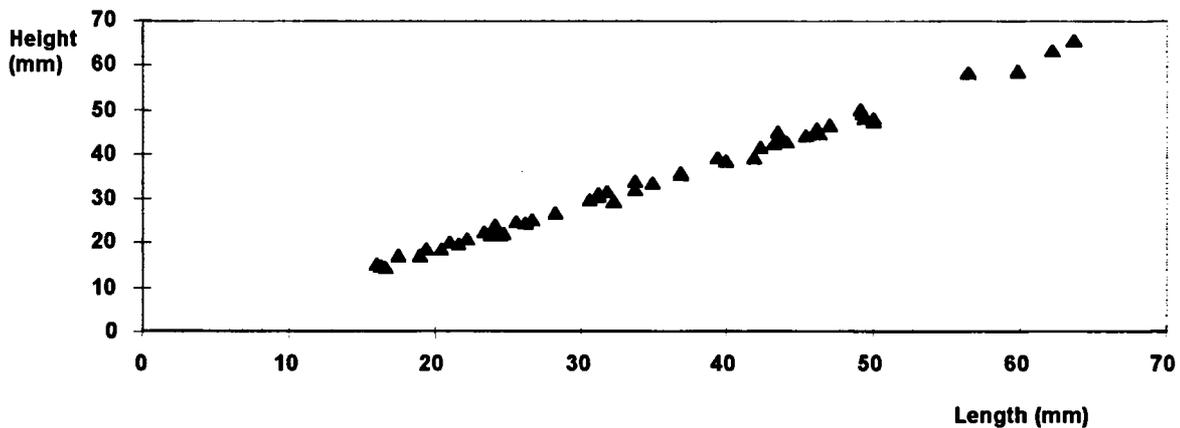


Fig. 1. *Aequipecten o. opercularis* (Linné, 1758), Kallo (Verrebroekdok), Lillo Formation, Oorderen Member, *Cultellus* level and basal level (all RM Colln).

Description — Medium-sized species, reaching heights of less than 40 mm in the Kattendijk Formation, but up to 70 mm in the Oorderen Member (Lillo Formation), while extant specimens may grow to heights of 100 mm. Shell strong, rather tumid, slightly inequilateral and inequivalve with left valve slightly flatter than right one. Ratio of dimensions variable; in Kattendijk Formation, specimen length may surpass height, while in the Oorderen Member mostly the opposite is true. Disc nearly circular, posteriorly slightly oblique. Umbonal angle about 105°. Ornament consisting of 18-25 primary radial ribs (20 in fossil material examined, see Fig. 2), which are about half as wide as the intercostal spaces. On the central part of the disc these ribs mostly comprise three secondary ones; near the anterior and posterior borders the difference between primary and secondary disappears. Intercostally very regular, fine growth lines occur, which may develop into small scales which continue on the radial ribs. Auricles unequal, anterior one clearly larger than posterior. In the narrow border area between disc and auricles, antimarginal ornament is present, especially anteriorly. Ornament of anterior ear consisting of five clear radial ribs, posterior auricle with more, but finer ribs. Length of both auricles together reaching about 50% of total shell length. Byssal notch deep, cte-

nolium well developed. Hinge line usually straight, rarely the auricles form an obtuse angle, so that the umbo lies below the auricles. Edge of hinge line turned inside. Anteriorly, parallel to the hinge line, occurs a plica. Ligament pit shallow and relatively broad. Primary ribs visible inside, muscle insertion vague.

Discussion — The present species is extremely common at Kallo, and ranges from the Kattendijk Formation to the Merksem Member (Lillo Formation). Elsewhere in Belgium, there are Pleistocene (Eemian) beach records.

In Great Britain, *A. o. opercularis* is recorded from the Coralline, Red and Mammalian crags, while in the Netherlands it is known from boreholes as well as from material washed ashore. Heering's (1950b, pl. 2, fig. 23) specimen clearly belongs to *A. o. opercularis*, which means that his material is possibly younger than Miocene. The oldest occurrence in Belgium is probably in the Late Miocene Deurne Member. *Pecten sowerbyi* Nyst, 1843, a *nom. nov.* for *Pecten reconditus* J. de C. Sowerby, 1825 (*non* Solander in Brander, 1766), is synonymous with *A. o. opercularis*, judging from shell shape and number of radial ribs (22) in Sowerby's figured specimens. Nyst (1878) did still illustrate *P. sowerbyi*, but there is no mention in the text which appeared in 1881.

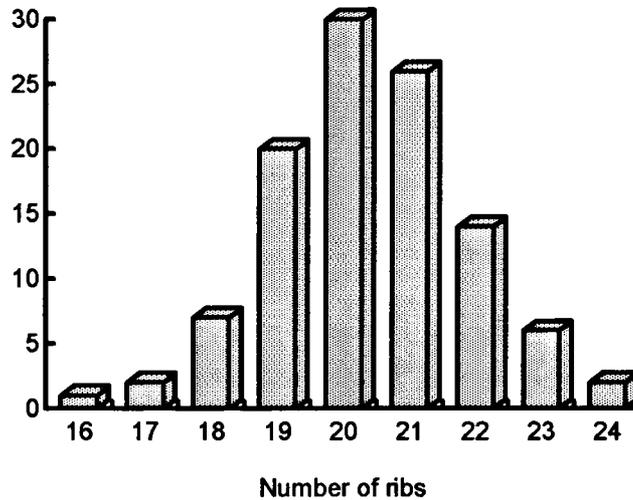


Fig. 2. Histogram of the number of radial ribs in *Aequipecten o. opercularis* (Linné, 1758) from Kallo (Verrebroekdok), Lillo Formation, Oorderen Member, *Cultellus* level (RM Colln).

Pecten gracilis J. de C. Sowerby, 1825 is based on material from the Red Crag of East Anglia. Differences from *A. o. opercularis* mentioned by Wood (1856) include a flatter, thinner shell, slightly different size ratios, and smaller auricles. In showing these features, Sowerby's form is nearly identical with 'var. *lineatus*' (da Costa, 1778) of *A. o. opercularis*.

According to Poppe & Goto (1993), extant *A. o. opercularis* occurs in an area between the Lofoten Islands (Norway) in the north and Madeira, the Canary Islands and the Azores to the south, being also known from the Mediterranean, but not from the Black Sea. The bathymetric range is from low tide level down to 400 m. Like fossil shells, extant specimens characteristically have between 18 and 25 radial ribs.

Aequipecten o. pinorum (Cossmann & Peyrot, 1914) from the Sallomacian (Middle Miocene) of Aquitaine (France) was first described as a distinct species. Here, we follow Glibert & van de Poel (1965) in considering it a subspecies of *A. opercularis*. Indeed, shell shape and size and primary radial ribs (each divided into three secondaries, with two intercostal secondary ribs) are all similar to those of the nominate subspecies, and differences are slight. The number of ribs in *A. o. pinorum* is lower (18-20) and commarginal growth lines form thicker scales when crossing the radial ornament. This subspecies, together with records of *A. opercularis sensu lato* from Lapugiu (Romania) cited by Studencka *et al.* (1998), represent the first occurrence of the taxon to date.

Aequipecten radians radians
(Nyst & Westendorp, 1839)
Pl. 2, Fig. 1

- * 1839 *Pecten radians* Nyst & Westendorp, p. 15, pl. 3, fig. 11.
- 1843 *Pecten radians* Nyst — Nyst, p. 294, pl. 24, fig. 3b.
- 1856 *Pecten dubius*, Brocchi — Wood, p. 38, pl. 6, fig. 3; non pl. 4, fig. 3 (*partim*).
- 1866 *Pecten assimilatus* - Millet de la Turtaudière, p. 30
- 1878 *Pecten radians*, Nyst — Nyst, pl. 15, fig. 3.
- 1881 *Pecten radians*, Nyst — Nyst, p. 151.
- 1939 *Chlamys radians* Nyst — Roger, p. 134, pl. 16, figs 8-12 (*partim*, non pl. 17, fig. 9 = *A. r. assimilatus*).
- 1945 *Pecten (Aequipecten) radians* Nyst — Glibert, p. 65, pl. 3, fig. 5.
- 1950b *Pecten (A.) scabrellus* Lamarck — Heering, p. 13, pl. 2, figs 24, 28 (*non* Lamarck).
- 1957 *Chlamys (Aequipecten) radians* Nyst, sp. 1839 — Glibert, p. 27.
- 1958 *Chlamys scabrella* (Lamarck) var. *sarmentica* Goldfuss — Ertunal-Erentöz, p. 149, pl. 24, fig. 8.
- 1965 *Lyropecten (Aequipecten) radians* (Nyst, 1839) — Glibert & van de Poel, p. 27.
- 1969 *Lyropecten (Aequipecten) opercularis* (Linnaeus, 1758) — van Regteren Altena *et al.*, p. 16 (*partim*).
- 1986 *Chlamys (Aequipecten) zenonis* Cowper-Reed, 1936 — Studencka, p. 40, pl. 4, fig. 11.
- 1995 *Aequipecten radians* (Nyst, 1839) — Lozano-Francisco & Vera-Peláez, p. 26.
- non1920 *Pecten (Aequipecten) seniensis* Lamarck — Dollfus & Dautzenberg, p. 411, pl. 37, figs 8-20 (= *A. r. assimilatus*).
- non1970 *Chlamys radians* Nyst — Bongrain, p. 35, pls a, b (= *A. r. assimilatus*).
- non1970 *Chlamys radians* Nyst var. *assimilis* (Millet) — Bongrain, p. 37, pls c, d (= *A. r. assimilatus*).
- non1981 *Chlamys (Aequipecten) radians* (Nyst, 1839) — Lauriat-Rage, p. 45, pl. 4, fig. 6; pl. 5, fig. 2 (= *A. r. assimilatus*).
- non1987 *Chlamys radians* — Andrés Galache & de Porta Vernet, p. 146, pl. 1, figs 7, 8.
- non1994 *Chlamys (Aequipecten) radians* (Nyst) — Ben

Moussa, p. 79, pl. 3, fig. 6.

Locus typicus — Antwerp (Belgium).

Stratum typicum — Lower Pliocene.

Material studied — In addition to the lectotype (IRScNB IST 4770), we have studied the following material of *A. r. radians*: specimens from Edegem (Edegem Member, Lower Miocene(?), illustrated by Glibert (1945), IRScNB IST 1925, 1926); specimens from Antwerp, 'Scaldisien', as illustrated by Nyst (1878), IRScNB IST 4768, 4799, 4800; IRScNB IST 6403, here illustrated (Pl. 2, Fig. 1), as well as the following specimens (all in RM Colln): Antwerp (dock works at Noordkasteel, Kattendijk Formation, *Ditrupa* level, 15 v); Kallo (Vrasenedok, Kattendijk Formation, *Petalocochnus* level, 123 v); Antwerp (underground Schijn-poort, Kattendijk Formation, *Ditrupa* level, 4 v); Antwerp (parking Gaumont Cinema, Kattendijk Formation, *Ditrupa* level, 21 v); Antwerp (Borgerhout Ring, Lt Lippenslaan, '*Heterocestus* level', Diest Formation, Deurne Member, 1 v); and Estepona (Velerin Conglomerate, province of Malaga, Spain, Zanclean, 2 v).

Of *A. r. assimilatus* we have studied material from Ferrière Larçon, Pontlevoy and Bossée (Touraine, 'Pontilevian', as illustrated by Dollfus & Dautzenberg, 1920, IRScNB IST 1379-1391), as well as material (all con-

tained in RM Colln) from St. Clément de la Place (Marne-et-Loire, Le Grand Chauvère, 'Redonian', 15 v); Sceaux d'Anjou (Marne-et-Loire, La Presselière, 'Redonian', 21 v) and Brigné (Beugnon, Marne-et-Loire, 'Redonian', 4 v); Ferrière Larçon (pit near D66, Indre-et-Loire, 'Pontilevian', 10 v); Ferrière Larçon (Ferme La Placette, Indre-et-Loire, 'Pontilevian', 59 v); Le Grand Pressigny (Paulmy, Indre-et-Loire, 'Pontilevian', 5 v); Pauvrelay (Carrière Buzelé, Indre-et-Loire, 'Pontilevian', 8 v); Manthelan (quarry near D50, Indre-et-Loire, 'Pontilevian', 3 v); Le Louroux (Le Petit Bray, Indre-et-Loire, 'Pontilevian', 11 v); Amberre (quarry near Moulin Pocha, Vienne, Touraine, 'Pontilevian', 15 v).

Of *A. liberatus* (Cossmann & Peyrot, 1914) we have studied the following material (all in RM Colln): Martillac (Pas de Barreau, Gironde, Burdigalian, Falun de Léognan, 22 v); Saucats (Coquillière, Gironde, Burdigalian, 27 v); Corbleu (Moulin de Carro, Gironde, Falun de St. Avit, Aquitanian-Burdigalian, 7 v); Saint Martin d'Oney (quarry along D365, Landes, Falun de St. Avit, Aquitanian-Burdigalian, 7 v); Roquefort (Palombières Douze valley, Landes, Falun de St. Avit, Aquitanian-Burdigalian, 2 v); Uzeste (Moulin de Gamachot, Gironde, Falun de Bazas, Aquitanian-Burdigalian, 25 v).

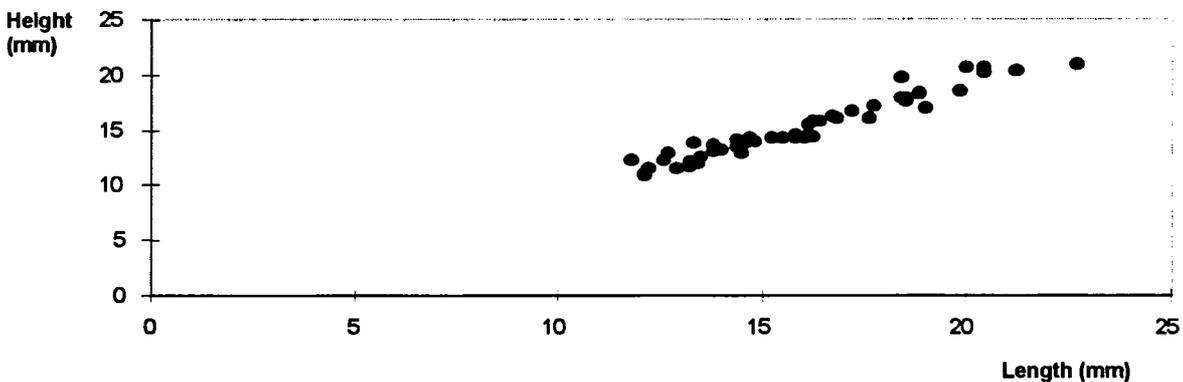


Fig. 3. *Aequipecten r. radians* (Nyst & Westendorp, 1839), Kallo (Vrasenedok), Kattendijk Formation, *Petalocochnus* and *Similipecten* levels (RM Colln).

Dimensions — Height 12.0 mm, length 12.0 mm, diameter 4.2 mm (bivalved specimen, see Pl. 2, Fig. 1). For height and length of a sample of 50 specimens see Fig. 3.

Description — Small species, up to 23 mm in height, with strongly inequivalve, but only slightly inequilateral, fragile shell. Shape of disc near ventral margin circular, but part of anterior and posterior margin closest to the umbo straight instead of curved (from about half height). Both valves strongly flattened. Ornament variable and often markedly different on left and right valves. Right

valves of typical specimens with eighteen very fine, primary radial ribs (see Fig. 4), which are about half the width of intercostal spaces. These spaces show on each side of the primary ribs very fine antimarginal lines. In addition, clear growth lines occur; these become irregular where they cross secondary radials. On the primary ribs, spines are formed at junction of radial and commarginal ornament, on the posterior side occasionally scales occur. Many specimens have in the centre of the disc 4-5 radial ribs which are heavier than the other primary commarginal ones, with better-developed spines.

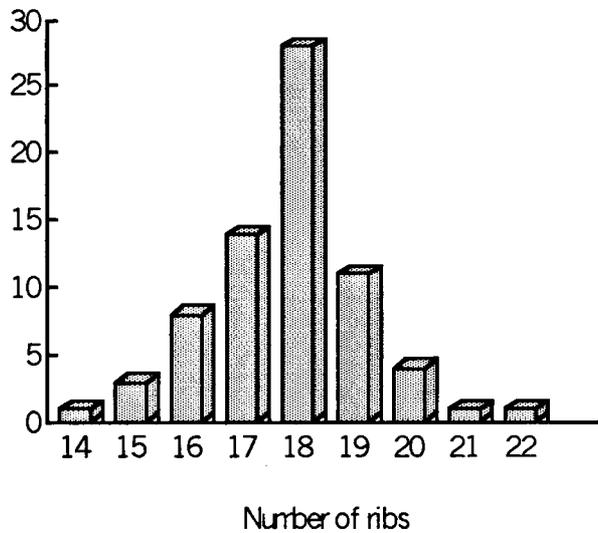


Fig. 4. Histogram of the number of radial ribs in *Aequipecten r. radians* (Nyst & Westendorp, 1839), Kallo (Vrasenedok), Kattendijk Formation, *Petalococonchus* level (RM Colln).

Left valve invariably with finer ornament, usually lacking spines or heavier commarginal growth lines. In some specimens, the ornament of the right valve also is markedly weaker, while all radials are equally well developed. Usually the secondary radials and a few spines remain visible. Hinge line straight, auricles large, taking up about half of total shell length, posterior auricle always clearly smaller than anterior one. Where disc and auricles meet, antimarginal ornament occurs. Auricles with 5-7 (anterior) or 3-5 (posterior) radial ribs, about as wide as interspaces. Inner side of shell with small, obtuse triangular ligament pit and a clearly marked ridge, parallel to hinge line. Ribs visible interiorly only up to half height. Ctenolium internally clearly visible, with 4-5 denticles. Muscle insertion nearly indistinguishable.

Discussion — The present species is abundant throughout the Kattendijk Formation at Kallo and at other localities around Antwerp; is not rare either in the Pliocene (Coralline Crag) of Great Britain and in Dutch material. There are a few records of Miocene material from the North Sea Basin; Glibert (1945) listed specimens from the Early Miocene Houthalen and Edegem members - these appear to constitute the earliest record of the species, which is also found in the Late Miocene 'Heterocetus Sands' (Diest Formation). Heering (1950b) recorded, under the name of *Pecten (A.) scabrellus*, material from Maasbree (Limburg, the Netherlands), which, judging from his illustrations, should be referred to *A. r. radians*.

Previous authors who followed Roger (1939) considered two Miocene species to be synonymous with *A. radians*, although they are not. *Aequipecten liberatus*, which occurs in Aquitanian, Burdigalian and 'Salloma-

cian' strata in Aquitaine and in 'Pontilevian' deposits of Touraine, is characterised by a higher number of primary ribs composed of, as in *A. opercularis*, a number of secondary ones. These ribs are as wide as the intercostal spaces; on the radial ribs, scales rather than spines are present, and specimens with heavier primary ribs are absent. Moreover, the shell may grow to larger sizes than that of *A. radians*. The general shape, however, is nearly the same as in *A. radians*, being also flattened. In other features, however, *A. liberatus* is closer to *A. opercularis*.

Another representative of the same group occurs in the 'Redonian' of Brittany and in the 'Pontilevian' of Touraine. Dollfus & Dautzenberg (1920) wrongly identified part of this material as '*Pecten (Aequipecten) seniensis* Lmk', while Roger (1939), Glibert & van de Poel (1965) and Lauriat-Rage (1981) used the specific name *radians* for it. Differences include the higher number of radial ribs (c. 20), narrower intercostal spaces, much finer commarginal ornament, mostly lacking spines or scales on radials, and a more tumid shell. However, specimens with stronger radial ribs do occur; see e.g. Dollfus & Dautzenberg (1920, pl. 37, fig. 20, IRScN IST 1391) and Bongrain (1970, pls c, d). In addition, according to Roger (1939, p. 135), the primary rib number may amount to 18. For that reason, this material is here considered to be closely related to the North Sea Basin species, but assignable to a distinct subspecies which is restricted to the Atlantic 'Redonian' and 'Pontilevian-Savignean' (Miocene). For this type of shell, the name *Pecten assimilatus* Millet de la Turtaudière, 1866 is available. Ben Moussa (1994) identified specimens of Messinian (Late Miocene) age from Morocco as *A. radi-*

ans; the material he illustrated shows only 13 radial ribs and a shell shape completely different from that of *A. radians*. Studencka's (1986, pl. 4, fig. 11, under the name of *Chlamys (Aequipecten) zenonis*) specimen from Rybnica (Poland), of Middle Miocene age, represents genuine *A. r. radians* with its typical ornament. The same probably applies to a Middle Miocene specimen from the Karaman Basin (Turkey) figured by Erünal-Erentöz (1958, pl. 24, fig. 8) with typical *radians* ornament and shell shape. Kojumdgieva & Strachimirov (1960, pl. 22, figs 9-12) illustrated material from the Middle Miocene of Bulgaria, under the name of *Chlamys (Aequipecten) seniensis* (Lamarck), which certainly does not belong to that species, on account of their symmetrical shell shape. Their shape in fact is rather like that of *A. radians*, but illustrations of the ornament are not clear enough to be certain of this; material from the region was not available for study. Studencka's, Erünal-Erentöz's and possibly also Kojumdgieva & Strachimirov's records are younger than the oldest North Sea Basin records of *A. r. radians*, which thus appears to have migrated from the North Sea Basin into the Paratethys. Apparently, *Aequipecten radians* also reached the Atlantic 'Pontilevian' and 'Redonian' localities, where a distinct subspecies developed, probably because of separation from the main distribution area. In the Mediterranean, no authentic Miocene or Recent records appear to exist, while Pliocene specimens are known only from the Iberian Peninsula.

Aequipecten radians cannot be considered a predecessor of *A. o. opercularis*, which rather appears to have evolved from *A. o. pinorum* from the Middle Miocene of the Aquitaine Basin.

Aequipecten wagenaari n. sp.

Pl. 2, Fig. 2

- 1856 *Pecten dubius*, Brocchi — Wood, p. 38, pl. 4, fig. 3 (*partim*).
 1881 *Pecten opercularis*, Lin. — Nyst, p. 149 (*partim*).
 1937 *Chlamys opercularis* (Linné 1758) — van Regteren Altena, p. 61 (*partim*).
 1950a *Pecten (Chlamys) opercularis* (Linné 1758) — Heering, p. 46, pl. 14, figs 7-9, 25 (*partim*).
 1957 *Chlamys (Aequipecten) opercularis* Linné, sp. 1758 — Glibert, p. 28 (*partim*).
 1969 *Lyropecten (Aequipecten) spec ?* — van Regteren Altena *et al.*, p. 16.

Derivatio nominis — In honour of Mr M. Wagenaar, for his valuable help in producing the photographs which illustrate this and previous papers.

Locus typicus — Kallo (Verrebroekdok), province of Oost-Vlaanderen, Belgium.

Stratum typicum — Lillo Formation, Oorderen Member (*Cultellus* level), Middle Pliocene.

Types — Holotype is IRScNB IST 6401, paratypes are IRScNB IST 6402 and RGM 456 050.

Material studied — In addition to the type specimens,

we have studied the following specimens (all in RM Colln): Kallo (Verrebroekdok, Oorderen Member, *Angulus benedeni* level, 2 v); Kallo (Verrebroekdok, Oorderen Member, *Atrina* level, 1 v); Kallo (Verrebroekdok, Oorderen Member, basal level, 14 v); Kallo (Verrebroekdok, Oorderen Member, *Cultellus* level, 66 v); Antwerp (Ring Borgerhout, mixed derived Pliocene, 3 v); Orford (The Broom, Suffolk, Coralline Crag, 2 v); Sutton (Sudbourne Park Pit, Suffolk, Coralline Crag, 1 v); Walton-on-the-Naze (The Naze, Essex, Waltonian Red Crag, 2 v).

Of *A. malvinae* (du Bois de Montpereux, 1831), we have studied one valve from Lychow (Tarnobrzeg, Poland) of Middle Miocene age (RM Colln).

Of *A. elegans* (Andrzejowski, 1820), we have studied material from Weglin (Trzydniczanka valley, Tarnobrzeg, Poland, Middle Miocene, 19 v, RM Colln), of *A. vasconiensis* (Cossmann & Peyrot, 1914), specimens from Mios (Ruisseau de Surgenne, Gironde, Falun de Mios, 'Sallomacian', 6 v, RM Colln), of *A. degrangei* (Cossmann & Peyrot, 1914), eight valves from Salles (Ruisseau de Minoy, Gironde, Falun de Salles, Middle Miocene, RM Colln), of *A. raouli* (Cossmann & Peyrot, 1914), two valves from the same locality and level (RM Colln), and of *A. seniensis* (Lamarck, 1819) material from Antwerp (Ploegstraat 29, Berchem Formation, Antwerp Member, *Panopea* level, 21 v, RM Colln); Antwerp (Schijnpoort, same level, 25 v, RM Colln); Baldichieri (orchard on road to Monale, Asti, Italy, Middle Pliocene, 23 v, RM Colln), and Diolo (calanca on road to Chiavenna, province of Piacenza, Italy, Piacenzian, Middle Pliocene, 37 v and 1 bv, RM Colln).

Dimensions — Height (holotype) 18.6 mm, length 18.4 mm, diameter 4.6 mm; paratype IRScNB IST 6402 (left valve), height 19.3 mm, length 19.5 mm, diameter: 4.0 mm; paratype RGM 456 050 (right valve), height 20.7 mm, length 20.0 mm, diameter 5.6 mm. For height and length of a sample of 50 specimens see Fig. 5.

Diagnosis — Rather small (*c.* 30 mm in height) species with near-circular, strongly tumid disc, with a primary radial rib number of 15, without secondary radial ornament, with rather heavy commarginal ornament, forming scales on junctions with radial ornament, and with auricles which together measure about 3/4 to 2/3 of total shell length.

Description — Rather small species, with a maximum height of 32.0 mm (see Fig. 5); shell solid, slightly inequilateral and inequivalve. Disc nearly orbicular, but height mostly exceeding length. Shell rather tumid, left valve flatter than right. Ornament at first consisting of 15 primary radial ribs (see Fig. 6), which in the majority of specimens are not divided into secondary ribs; this occurs only exceptionally in the largest specimens. Width of radial ribs about a third of the intercostal spaces on left valve, to a third on the right valve, which is usually more strongly ornamented than the left one. Growth lines form low scales in intercostal spaces, on the ribs are high, hollow scales. Hinge line nearly always straight.

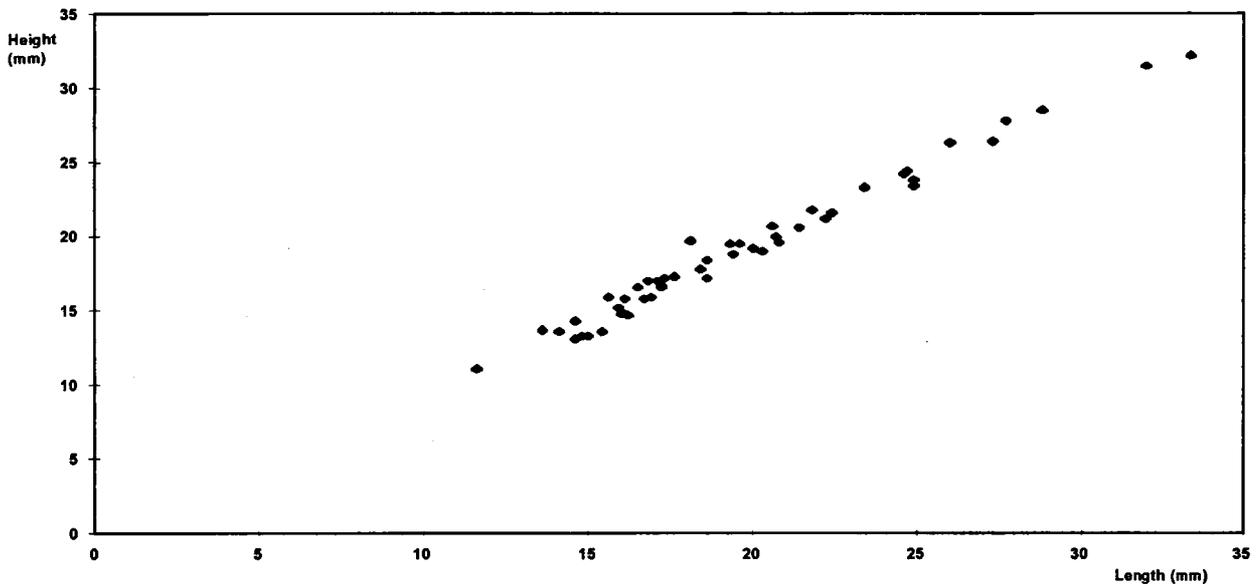


Fig. 5. *Aequipecten wagnaari* n. sp., Kallo (Verrebroekdok), Lillo Formation, Oorderen Member, *Cultellus* level and basal level (RM Colln).

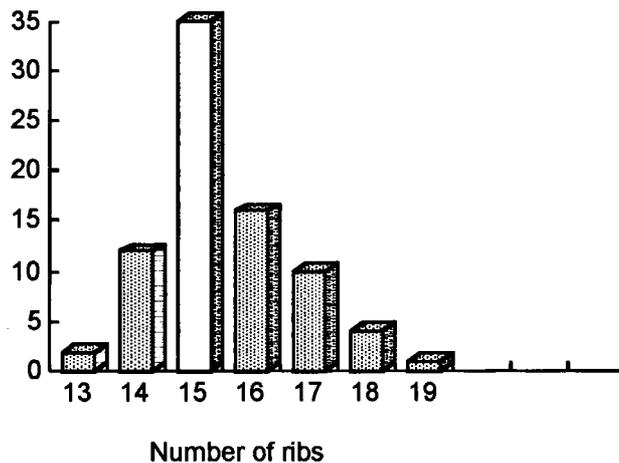


Fig. 6. Histogram of the number of radial ribs in *Aequipecten wagnaari* n. sp., Kallo (Verrebroekdok), Lillo Formation, Oorderen Member, *Cultellus* level and basal level (RM Colln).

Auricles comparatively large, to more than 3/4 of total length in juvenile specimens and 2/3 in adults. Anterior auricle twice as large as posterior, with a deep byssal notch. In the area between disc and auricles occurs anti-marginal ornament, especially anteriorly. Anterior auricle with six radial ribs, posterior one with three. Anteriorly, clear scales are present on the radials. Auricular denticles anteriorly clearly visible, ctenolium well developed, with five teeth visible on the inside of the shell. Ligament pit broadly triangular, shallow. Hinge line with ridges, parallel to margin. Radial ribs clearly visible on the inside of the shell, muscle insertion vague.

Discussion — The present species differs from *A. opercularis* in having a smaller shell (see Figs 1 and 5), in shell length exceeding height, in usually having about fifteen radial ribs instead of twenty, in nearly always having single radial ribs instead of divided into secondary ribs, in showing on the radial ribs heavy scales, in having nearly always a straight hinge line, and in having relatively more tumid valves with wider auricles.

Differences between the new species and *A. r. radicans* also are clear. *Aequipecten wagnaari* has a much more tumid shell, the ornament on left and right valve differs less, radials are thicker and their number is lower

(15 instead of 18), intercostal secondary radial lines are invariably absent, and the radials have scales instead of spines; moreover, the umbonal portions of anterior and posterior margin are straight to a much more limited degree.

In Miocene strata of Belgium, a single species of *Aequipecten* occurs, namely *A. seniensis*. This was well described and illustrated by Glibert (1945, pp. 69, 72, pl. 3, fig. 6; pl. 4, fig. 2). It differs even more clearly from *A. wagnaari* in shell shape (*i.e.* moderately to strongly inequilateral and oval instead of near-circular); its rib number is mostly comparable to that of the new species, but the radials are relatively wider and consist of at least two, but often more secondary ribs. Scales are prominent between as well as on the radial ornament elements. *Aequipecten seniensis* occurs in the Miocene of Touraine, although some of the records of this species are in fact erroneous identifications by Dollfus & Dautzenberg (1920). It is also known from the Paratethys; the youngest records are from the Pliocene of Italy and Spain. By that time, however, the species had gone extinct in the North Sea Basin.

Another Miocene species from Belgium has also been previously considered to belong to the genus *Aequipecten*, *viz.* *Mimachlamys angelonii* (Meneghini, 1859). This differs from *A. wagnaari* in having 20-25 radial ribs, bearing 3-5 rows of strong spines; scales are never present and the intercostal commarginal ornament is relatively weak. The shells grow to much larger sizes, reaching almost 70 mm in height. *Mimachlamys angelonii* is known from the Italian and Austrian Miocene, from where it has been described under the name of *Chlamys glaesneri* Kautsky, 1928. Studencka *et al.* (1998) assigned it to the genus *Amussiopecten* Sacco, 1897.

The Middle-Late Miocene *A. r. assimilatus* of Touraine and Brittany differs from *A. wagnaari* in having more radial ribs (*c.* 18), finer commarginal ornament without scales or spines and relatively wider auricles. The tumid, near-circular and nearly equilateral shell shape, however, is quite similar and these species may be closely related. *Aequipecten liberatus* has more (20) and wider ribs than *A. wagnaari*, and these are composed of secondary ribs. Its shell is flattened and grows to twice the size of that of *A. wagnaari*.

Aequipecten macrotis (G.B. Sowerby, 1847) was originally described from Miocene (Tortonian) strata near Lisbon (Portugal). Material from the type area was illustrated by Roger (1939, p. 114, pl. 14, figs. 7-10; pl. 15, figs 7, 8; text-fig. 58), who considered *Chlamys (Aequipecten) multiscabrella* Sacco, 1897, *Ch. plubienensis* Ugolini, 1906, *Ch. (A.) vasconiensis*, *Ch. (A.) raulini*, *Ch. (A.) raouli*, *Ch. (A.) degrangei* and *Ch. (A.) liberata* to be subjective junior synonyms. With the exception of the second, these taxa are here considered to be valid. Portuguese material of *A. macrotis* differs from *A. wagnaari* in having 18-24 radial ribs with small squamae, but without spines, while its disc shape comes close to that of *A. opercularis*.

The Miocene of western Paratethys has yielded, according to Studencka *et al.* (1998), eight species which possibly belong to the genus *Aequipecten*: *A. opercularis*, *A. macrotis*, *A. r. radians* and *A. seniensis* (= *scabrellus*), all of which have been discussed above, as well as *A. elegans*, *A. malvinae*, *A. diaphanus* (du Bois de Montpéreux, 1831) and *A. lapugyensis* (Nicorici, 1977). *Aequipecten malvinae* clearly differs in having a much higher number of radial ribs (29-40; see Studencka, 1986, p. 35, pl. 4, figs 5, 7, 10). Material of *A. elegans* contained in the RM Colln has only 10-13 radial ribs, which are mostly smooth, but which may be divided into fine secondary ribs. The commarginal ornament is very weak and occurs only intercostally, while spines or scales on the radial ribs are absent. Its shape is oval rather than circular, so it more closely resembles *A. seniensis*. *Aequipecten diaphanus*, figured by Friedberg (1936, p. 230, pl. 39, figs 1-3) and Roger (1939, p. 147, pl. 18, fig. 11) differs markedly from *A. wagnaari* in having radial ornament near the shell margins only, while the centre of the disc remains smooth.

In Miocene strata of the Aquitaine occur a large number of species of *Aequipecten*. Unlike *A. wagnaari*, *A. vasconiensis* (see Cossmann & Peyrot, 1914, p. 123, pl. 14, figs 22-25; pl. 16, figs. 1-6) from the Middle Miocene has an oval, strongly inequilateral shell, with 18 wide radial ribs, rounded in cross section; in the central part of the disc these radials are not composed of secondaries. They are, however, near the anterior and posterior margins. The commarginal ornament in *A. vasconiensis* is highly variable; in some specimens it is nearly absent, in others developed into clear scales on the ribs and intercostally. This might represent but a forma of sympatric *A. seniensis*, which has the same shell shape, but a different ornament.

Another species from the same area and level is *A. degrangei* (see Cossmann & Peyrot, 1914, p. 132, pl. 20, figs 5-8), which is larger and much flatter than *A. wagnaari*, has wider auricles and more numerous radial ribs (25-28); secondary ornament is absent; commarginal lines and scales are present on and between the radials, but are weak. This species is not unlike *A. r. assimilatus*, but grows larger; the shell is markedly flatter and has more radial ribs. *Aequipecten raouli* (see Cossmann & Peyrot, 1914, p. 124, pl. 16 [not 14 as indicated in the text], figs 40-42) has flat valves, very wide auricles, 18-20 radial ribs, wider than intercostal spaces, is near-equilateral but height exceeds length; the commarginal ornament is like that of the preceding species, from which this taxon mainly differs in shell shape and in number of ribs. *Aequipecten raulini* (see Cossmann & Peyrot, 1914, p. 128, pl. 17, figs 1, 2, 22, 23), which also occurs in Middle Miocene deposits, is near-equilateral, with wide auricles and a high rib number (24-25); the commarginal ornament is heavy, with prominent scales intercostally as well as on the radials; it is much smaller than *A. wagnaari*.

Pecten haveri Michelotti, 1847 was also considered by Cossmann & Peyrot (1914, p. 134, pl. 17, figs 6-9) to

belong to *Aequipecten*; however, this is incorrect. Both valves are too inequilateral and the ornament resembles that of *Chlamys spinulosus* (von Münster in Goldfuss, 1833) more closely than it does that of any representative of *Aequipecten*.

Sacco (1897) discussed a lot of Neogene species which he considered to be assignable to *Aequipecten*. Amongst these are *A. opercularis*, '*A. haveri*', *A. malvinae*, and *A. seniensis*; all of these have been discussed above. In the Miocene of Torino occurs *A. northamptoni* (Michelotti, 1839); this is more than three times larger than *A. wagnaari*, and has, judging from Sacco's (1897, pl. 4, figs 1-16; pl. 5, figs 1-11) figures fifteen radial ribs (18-20 according to the text on p. 16), which are most often composed of several secondaries and bear clear spines in typical specimens. *Aequipecten bicknelli* Sacco, 1897 (p. 21, pl. 6, figs 14-17) is found in the Piemonte Pliocene; it has 25-28 strongly spinose, narrow radial ribs, and its shell is rather flattened and round, being more than twice the size of that of *A. wagnaari*. *Aequipecten spinovatus* Sacco, 1897 (p. 21, pl. 6, figs 21-25), from the Pliocene of Italy, is close in shell shape to *A. bicknelli* and also has a large number of radial ribs (22-25). These are a little wider than those of the previous species and show in the centre of the disc a tendency to split into three secondaries.

Of the Miocene *A. mioalternans* Sacco, 1897 (p. 23, pl. 7, figs 11, 12) only fragments are known; these are large, with 16-17 primary radial ribs and secondary ones in the intercostal spaces. Commarginal ornament is lacking. *Aequipecten multiscabrellus* Sacco, 1897 (p. 29, pl. 8, figs 38-41) from Miocene strata in Italy is higher than long, tumid, with 19-22 radials and long auricles; centrally, commarginal ornament and spines on the ribs are absent, but near the anterior and posterior margins these may be present. The species is not unlike the Aquitaine Miocene *A. raulini*. *Aequipecten scabriusculus* (Mathéron, 1842), from the Miocene of the Rhône Valley (France) and from Italy was illustrated by Sacco (1897, p. 30, pl. 9, figs 1-4); it is a very large species, with 14-17 radial ribs composed of secondaries; the shell is wider than high. The Early Miocene '*A. oblitaquensis*' Sacco, 1897 (p. 18, pl. 5, figs 12-14) probably belongs to another genus, on account of the shape of its left valve.

Van Regteren Altena (1937) was the first to mention the occurrence of *A. wagnaari* in Dutch beach material, but did not name it. Heering (1950a) recorded specimens of '*Pecten (Chlamys) opercularis*' from boreholes sunk at Vlissingen, Beers and Oss with sixteen ribs, all of which probably belong to the new species. However, he considered these to belong to the var. *sowerbyi* Nyst of *A. opercularis*. As outlined above, this variety was based on specimens with 22 radial ribs. *Aequipecten wagnaari* also occurs in the British Pliocene, since Wood's (1856, pl. 4, fig. 3) specimen indeed has 16 ribs; the shell shape of that specimen differs from that of the new species, but the number of ribs is here considered of more importance.

Aequipecten wagnaari is fairly common in the Oor-

deren Member (Lillo Formation) in the Antwerp area and appears to be common also in Dutch borehole and beach material. However, it is never as common as *A. o. opercularis*, and would seem to constitute a species endemic to the Pliocene of the North Sea Basin.

CONCLUSIONS

Species of *Aequipecten* are difficult to identify on account of a wide range of variation in ornament, which often differs between both valves. Therefore, no single feature may be considered diagnostic for any of its species, but a set of characters in a population rather than in a single individual shell are needed to define taxa. As the histograms of Figs 2, 4 and 6 show, the number of ribs however forms a Gauss curve in the three sympatric species of *Aequipecten* from the Pliocene of the North Sea Basin. A summation of the three frequency distributions would never give a normal curve with a clear primary value. Thus this character appears to be of real importance. In addition, variability in itself could be considered a character. This is notably the case in *A. radians*, where the occurrence of specimens with stronger primary ornament is a feature of populations of this species, even if not every individual shows it. When this feature is altogether absent, the population can never be considered to represent *A. radians*. In other forms under study, e.g. *A. liberatus*, more differentiating features might reveal themselves upon careful examination.

The genus *Aequipecten* appears to have spread from different centres of speciation in the European Neogene. The Miocene North Sea Basin, from which *A. radians* seems to have migrated into the Paratethys and the Atlantic and the Aquitaine (France), whence the *A. opercularis* stock appears to originate, spreading into the North Sea Basin in the latest Miocene. In addition, several endemic species evolved in the Atlantic, Mediterranean and Paratethys basins during the Miocene and Pliocene, the youngest of which was *A. wagnaari*, which was confined to the Middle Pliocene of the North Sea Basin.

ACKNOWLEDGEMENTS

For allowing us to study material contained in the IRScNB and RGM collections, and to use IRScNB research facilities, we wish to thank A.V. Dhondt, A.W. Janssen, F. Wesselingh and K. Wouters. M. Wagnaar, L. Cilis (IRScNB) and W. Miseur (IRScNB) assisted with the photography, for which we are grateful.

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Manuscript received 26 March 2000, revised version accepted 4 October 2000.

PLATE 1

- Fig. 1. *Aequipecten o. opercularis* (Linné, 1758), bivalved specimen (RM Colln), Kallo (Verrebroekdok), Lillo Formation, Oorderen Member, *Atrina* level); A - right valve, x 1.1; B - left valve, x 1.1; C - both valves, x 1.4.
- Fig. 2. *Aequipecten o. opercularis* (Linné, 1758), bivalved specimen (RM Colln), Kallo (Vrasenedok), Kattendijk Formation, top level; micro-ornament, A - x 2.5; B - x 6.8.

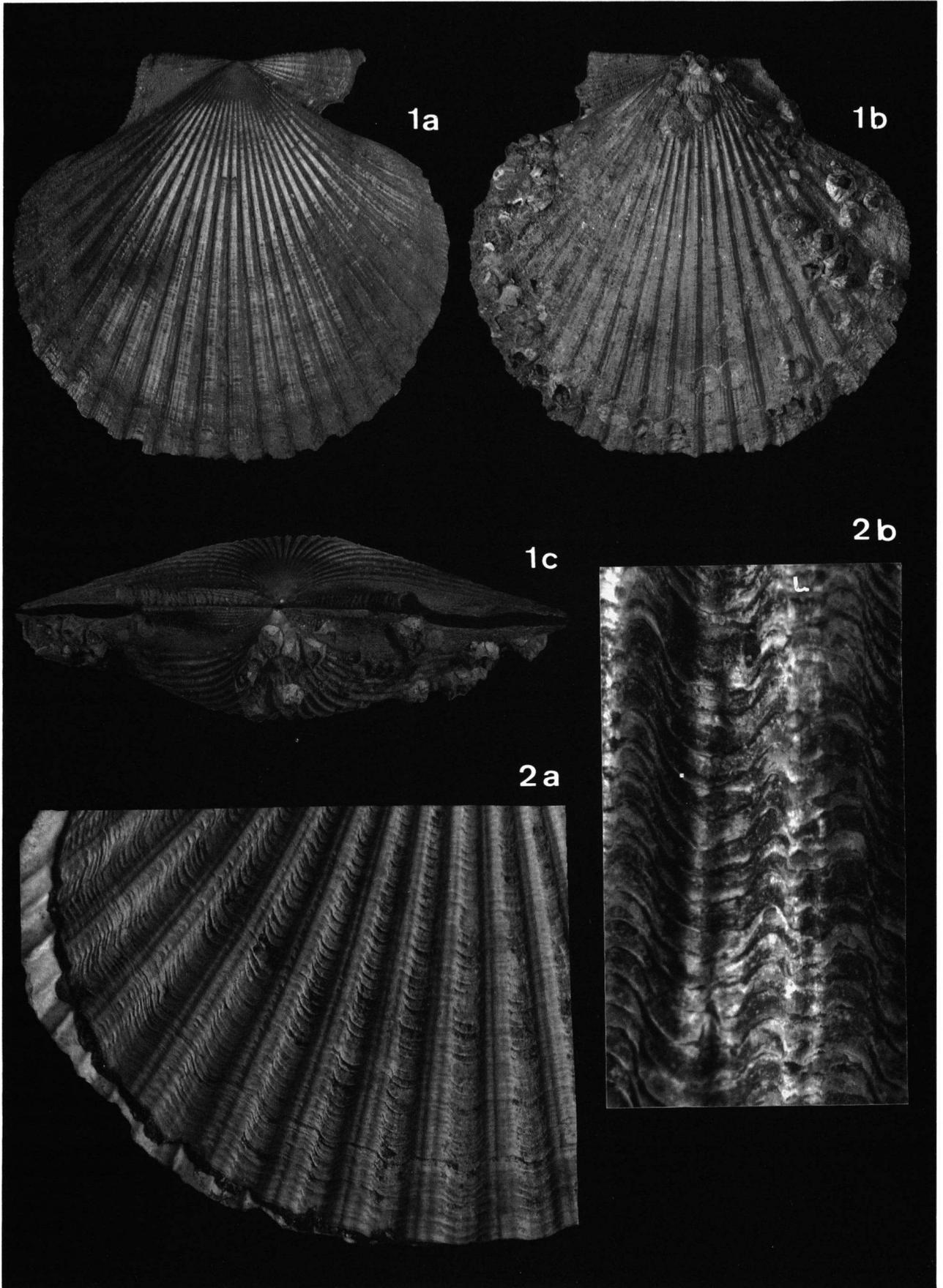


PLATE 2

- Fig. 1. *Aequipecten r. radians* (Nyst & Westendorp, 1839), bivalved specimen (IRScNB IST 6403), Kallo (Vrasenedok), Kattendijk Formation, *Petaloconchus* level; A - right valve, x 3.6; B - left valve, x 3.7; C - micro-ornament of left valve, x 11.4 (SEM images).
- Fig. 2. *Aequipecten wagnaari* n. sp., Kallo (Verrebroekdok), Lillo Formation, Oorderen Member, *Cutellus* level; A-C - holotype (IRScNB IST 6401), left valve, x 2.5, x 2.4, and x 5.6, respectively; D - paratype (IRScNB IST 6402), left valve, x 3.8.

PLATE 2

