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# Ecology and evolution of Pliocene bivalves from the Antwerp Basin

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## Abstract

The dock construction works in the port of Antwerp at Doel and Kallo (prov. Oost-Vlaanderen, Belgium) have allowed the collection of a rich and diverse Pliocene bivalve fauna. It contains 182 taxa, 178 species and four subspecies. 90 species out of 178 (51%) are extinct. The rate of extinction does not significantly vary between the recognised strata, ranging from Lower to Upper Pliocene. The average longevity of the species is calculated at 10.7 Ma. This long range makes most of these bivalve species unfit for use in Neogene stratigraphy. The bathymetry of the different levels of the Pliocene is assessed, using the species still occurring in the Recent fauna (49% of the total number): it decreases towards the end of the Pliocene.

**Key words:** Stratigraphic range - Bathymetry - Pliocene - Bivalves.

## Résumé

Les travaux de construction des docks dans le port d'Anvers à Doel et à Kallo (prov. Oost-Vlaanderen, Belgique) ont permis de récolter une faune de bivalves pliocènes riche et diverse. Elle contient 182 taxa, 178 espèces et quatre sous-espèces dont 90 espèces (51%) sont éteintes. Le pourcentage d'extinction ne varie pas de façon significative entre les différents niveaux reconnus, qui datent du Pliocène inférieur au Pliocène supérieur. La longévité moyenne des espèces est de10,7 millions d'années. Cette longue distribution dans le temps rend impossible d'utiliser la plupart des espèces de bivalves pour la biostratigraphie du Néogène. La bathymétrie des niveaux pliocènes est calculée, en utilisant les taxa encore présents dans la faune Recente (49% du nombre total): elle diminue vers la fin du Pliocène.

**Mots-clefs:** Durée stratigraphique - Bathymétrie - Pliocène - Bivalves.

## Introduction

The dock construction works in the Antwerp port area at Kallo and Doel (Oost-Vlaanderen, Belgium) started in 1970 and still continue today. During the construction several sections were exposed, ranging in age from the Oligocene to Late Pleistocene. The Pliocene in the area discussed contains two formations with five members: the Kattendijk Fm. (Lower Pliocene) with the Kattendijk Sand Member and the Lillo Fm. (Middle and Upper Pliocene) with the Luchtbal, Oorderen, Kruisschans and Merksem Sand Members. Within the Oorderen Sand Member, several levels can be recognised: a basal crag and the *Atrina*, *Cultellus* and *Angulus benedeni* levels (see Table 1). In general, the Pliocene yielded an extensive, well-preserved and diverse mollusc fauna. The only exception is the Merksem Sand Member, which contains a very poor and partially derived association. In this paper the Bivalvia from the different Pliocene levels will be considered, but not those from the basal crag of the Oorderen Sand Member, because it contains a large number of derived specimens.

Table 1 — Stratigraphy of the Pliocene in the Antwerp Basin, and correlation with the international stratigraphic scale; modified after VANDENBERGHE *et al.*, 1998. I.S.U. = International Stratigraphic Units, BM = benthic molluscs, BF = benthic Foraminifera, PF = planktonic Foraminifera, O = otoliths.

| I.s.u. | Formations | Members | Levels | BM | BF | PF | 0 |
|---|---|---|---|---|---|---|---|
| Gelasian | Lillo | Zandvliet | | BM 22C | | | 19 |
| | | Merksem | | | B 12 | | |
| | | Kruisschans | | | | | |
| Piacenzian | | Oorderen | *Angulus benedeni* | BM 22B | | | |
| | | | *Cultellus* | | | | |
| | | | *Atrina* | | | | |
| | | | basal crag | | | | |
| Zanclean | | Luchtbal | | BM 22A | B 11 | NPF 16 | 18 |
| | Kattendijk | Kattendijk | *Glycymeris-Ditrupa* | BM 21C | B 10 | | 17 |
| | | | *Petaloconchus* | | | | |
| | | | basal bed | | | | |

## Stratigraphic range of the bivalve species

The Pliocene Bivalvia from Doel and Kallo are currently being taxonomically revised by MARQUET (2002, 2004 in press). It consists of 178 nominal species and four subspecies. Of these species 90 (51%) are extinct, whereas 88 (49%) still occur in the Recent fauna (Table 2). Only the latter will be used for the palaeoecological analysis. Although the number of species decreases after the Lower and Middle Pliocene (Kattendijk and Luchtbal Sand Members respectively), the rate of extinction remains more or less the same. This implies that the extinction of Pliocene species occurred at the onset of or during the Pleistocene.

The average longevity of the Bivalvia found at Doel and Kallo is calculated at 10.7 Ma (Fig. 1). This however is an underestimation, because many species still occur and their life span will be longer when they become extinct. A large stratigraphic range consequently may be postulated for most Cenozoic Bivalve species. Nearly 100 species out of 178 have a range of less than 10 Ma, but the remaining species mostly lived between 10 and 20 Ma. Some even ranged from the Upper Eocene to the Recent (e. g. *Corbula gibba* (OLIVI, 1792)). Because of their long stratigraphic range, the aforementioned species cannot be used in a more detailed biostratigraphy of the Neogene. Only the longevity of species (including all subspecies) is considered here. However, it should be noted that the range calculated in this way is taxonomically biased: much depends on the status (subspecies or separate species) that has been accorded to taxa. This for example is also the case for *Corbula gibba*, which according to GLIBERT & VAN DE POEL (1966) consists of four subspecies, two of which have been interpreted as full species by other authors.

MARQUET (1996, 1997, 1998, 2001) revised the taxonomy of a number of gastropod families occurring in the Pliocene of Kallo and the Antwerp region in general: Conidae-Turridae, Cerithiopsidae and Triphoridae. A large number of these gastropod species showed, in contrast to the Bivalvia considered herein, a very short time range, remaining limited to respectively the Lower, Middle or Upper Pliocene. They could be useful in biostratigraphy, but only in a limited geographical area, since they are mainly endemic to the North Sea Basin. It could be concluded that the species turnover is larger and the longevity of the species shorter in gastropods than in bivalves. However, also here a taxonomic bias could be present. Indeed, among the Gastropoda the protoconch is a very fine tool for species identification. It is assumed that all populations differing in number of protoconch whorls and/or protoconch ornament belong to different species. For Bivalvia, a comparable character that fossilizes and allows identification lacks. The hinge is characteristic for species groups at the generic level, family or even higher, but not for individual species.

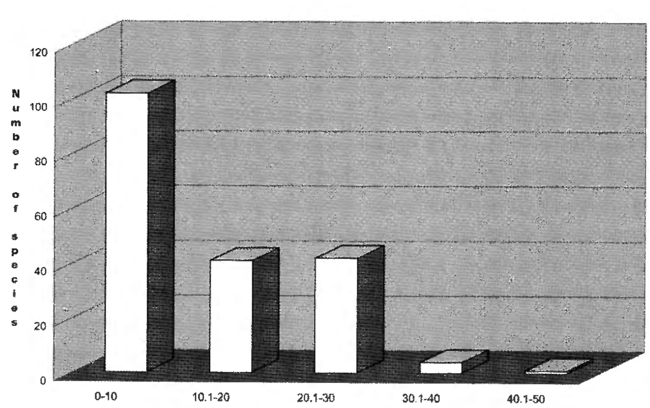


Fig. 1 — Longevity of the bivalve species found in the Doel and Kallo sections.

## Bathymetry of the Kallo and Doel Pliocene deposits

Only the extant species will be considered herein, because accurate data about their ecology are available. We do not accept *a priori* that extinct fossil species have the same ecological requirements as extant congeners. Overlap of ecological habitat and niche would result in heavy interspecific competition, quickly eliminating one of the competing species. However, in the Pliocene fauna of Antwerp it is proven that most species have a long stratigraphic range. In the living fauna too, species from the same genus always show differences in one or several ecological parameters. A disadvantage of this restriction is, that short living species are excluded from the analysis. In the Pliocene fauna of the North Sea Basin this is especially important for the family Astartidae, well represented in species as well as in individuals, but these species mostly have a short stratigraphic range, not reaching to the present.

The water depth ranges of the Recent bivalve species found in the Pliocene sections at Kallo and Doel were taken from the compilation work of POPPE & GOTO (1993), but exceptional occurrences were excluded (see Table 2). Thus only 75 out of the 88 extant species could be taken into consideration. These are listed in table 3 in MARQUET (2004, in press). For each species, the distribution was recorded for the Kattendijk Fm. and the Luchtbal, Oorderen and Kruisschans Sand Members of the Lillo Fm., but not from the Merksem Sand Member, because the data available for this level were too poor. Two different approaches were used:

- In a histogram, the total number of species occurring at each bathymetric interval was counted. Intervals of 10 m were used below 100 m and intervals of 100 m between 100 and 1000 m. This yielded average depth values for each level, for example 50 to 70 m for the Kattendijk Sand Mbr. (see Figs 2 to 5).
- The minimum and maximum bathymetric occurrences of the species for each level were noted and the common overlap area of these species was delimited. This

Table 2 — Bivalve species found in the Kallo and Doel sections. Bat = Bathymetry; e = early; m = middle; l = late; Eo = Eocene; Ol = Oligocene; Mi = Miocene; Pli = Pliocene; Ple = Pleistocene; R = Recent; K = Kattendijk; L = Luchtbal; O*A* = Oorderen *Atrina*; O*C* = Oorderen *Cultellus*; O*Ab* = Oorderen *Angulus benedeni*; Ks = Kruisschans; M = Merksem

| SPECIES | RANGE | BAT. | K | L | O *A* | O *C* | O *Ab* | K S | M |
|---|---|---|---|---|---|---|---|---|---|
| *Nucula (N.) nucleus* | eMi-R | 10-400 | ■ | ■ | ■ | ■ | – | ■ | – |
| *Nucula (N.) trigonula* | eOl-mPli | – | ■ | ■ | ■ | ■ | – | ■ | – |
| *Nucula (Lamellinucula)* cf. *jeffreysi* | eMi-ePle | – | ■ | – | – | – | – | – | – |
| *Leionucula l. laevigata* | uOl-lPli | – | ■ | – | ■ | ■ | ■ | ■ | – |
| *Acula (Truncacila) cobboldiae* | lPli-Ple | – | – | – | – | – | – | – | ? |
| *Yoldiella philippiana wesselinghi* | eMi-R | ? | ■ | – | – | – | – | – | – |
| *Yoldia (Y.) semistriata* | e-mPli | – | ■ | ■ | ■ | ■ | – | – | – |
| *Yoldia (Y.) heeringi* | lPli | – | – | – | – | – | – | ■ | – |
| *Arca (A.) tetragona* | eMi-R | 0-2600 | ■ | ■ | – | – | – | – | – |
| *Barbatia (B.) barbata* | eMi-R | 0-280 | ■ | – | – | – | – | – | – |
| *Barbatia (B.) philippiana* | ePl-R | 150 | ■ | – | – | – | – | – | – |
| *Bathyarca pectunculoides* | eMi-R | 40-1000 | ■ | ■ | – | – | – | – | – |
| *Stiarca scaldensis* | eMi-ePli | – | ■ | – | – | – | – | – | – |
| *Limopsis (L.) aurita* | lOl-R | 100-900 | – | ■ | – | – | – | – | – |
| *Limopsis (Pectunculina) anomala coxi* | lMi-lPli | – | ■ | ■ | – | – | – | – | – |
| *Nucinella ovalis* | eMi-lPli | – | ■ | ■ | – | – | – | ■ | – |
| *Glycymeris (Chevronia) variabilis* | ePli-lPli | – | – | ■ | – | – | ■ | ■ | – |
| *Glycymeris (Chevronia) obovata ringelei* | eOl-ePli | – | ■ | ■ | – | – | – | – | – |
| *Glycymeris (G.) radiolyrata pseudodeshayesi* | | | – | ■ | – | – | – | – | – |
| *Glycymeris (G.) r. radiolyrata* | ePli-mPl | – | – | – | ■ | ■ | ■ | – | – |
| *Mytilus edulis* | ePli-R | 0-40 | ■ | – | ■ | ■ | ■ | ■ | – |
| *Crenella decussata* | lMi-R | 4-200 | ■ | – | – | – | – | – | – |
| *Arcoperna sericea* | lMi-ePle | – | ■ | ■ | ■ | ■ | – | – | – |
| *Gregariella semigranata* | eMi-R | 2-100 | ■ | ■ | – | – | – | – | – |
| *Musculus discors* | ePli-R | ? | ■ | – | – | – | – | – | – |
| *Modiolarca subpictus* | ePli-R | 0-60 | – | ■ | ■ | – | – | – | – |
| *Rhomboidella pridauxi* | eMi-R | ? | ■ | ■ | – | – | – | – | – |
| *Rhomboidella grigisi* | eMi-ePli | – | ■ | – | – | – | – | – | – |
| *Modiolula phaseolina* | eMi-R | 0-160 | ■ | ■ | ■ | – | ■ | – | – |
| *Modiolus modiolus* | lMi-R | 0-150 | – | ■ | – | – | – | – | – |
| *Atrina fragilis kalloensis* | ePli-R? | 150-600 | ■ | ■ | ■ | ■ | ■ | ■ | – |
| *Pteria phalaenacea* | eMi-ePli | ? | – | ■ | – | – | – | – | – |
| *Pecten grandis* | lMi-mPli | – | ■ | ■ | – | – | – | – | – |
| *Pecten complanatus* | m-lPli | – | – | – | – | ■ | ■ | ■ | – |
| *Pseudamussium princeps* | lMi-ePli | – | ■ | – | – | – | – | – | – |
| *Pseudamussium lilli* | eMi-ePli | – | ■ | ■ | – | – | – | – | – |
| *Pseudamussium sulcatum* | mMi-R | – | ■ | – | – | – | – | – | – |
| *Pseudamussium clavatum* | lMi-R | 0-2500 | ■ | – | – | – | – | – | – |
| *Palliolum tigerinum* | eMio-R | 5-1400 | ■ | ■ | ■ | ■ | – | – | – |
| *Palliolum gerardi* | lMi-ePli | 0-400 | ■ | ■ | – | – | – | – | – |
| *Delectopecten vitreus* | ePli-R | – | ■ | – | – | – | – | – | – |
| *Similipecten similis* | eMi-R | 30-600 | ■ | ■ | – | ■ | – | – | – |
| *Aequipecten o. opercularis* | eMi-R | 4-250 | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *Aequipecten radians* | eMi-mPli | 0-400 | ■ | ■ | – | – | – | – | – |
| *Aequipecten wagenaari* | e-mPli | – | – | ■ | ■ | ■ | ■ | – | – |
| *Crassodoma m. multistriata* | | – | ■ | ■ | – | – | – | – | – |
| *Crassodoma multistriata harmeri* | eMi-R | | – | – | ■ | ■ | – | – | – |
| *Monia patelliformis* | mPli-R | 10-180 | ? | ■ | ■ | ■ | ■ | ■ | – |
| *Heteranomia squamula* | mOl-R | 0-50 | ■ | – | ■ | ■ | ■ | ■ | ■ |
| *Lima lima* | eMi-R | 5-110 | – | ■ | – | – | – | – | – |
| *Limatula sulcata* | eMi-R | 3-100 | ■ | ■ | ■ | ■ | – | – | – |
| *Limatula ovata* | ePli | 18-2000 | – | ■ | – | – | – | – | – |
| *Limatula subovata* | ePli-R | – | ■ | – | – | – | – | – | – |
| *Limaria tuberculata* | eMi-R | 28-3500 | ■ | ■ | ■ | – | – | – | – |
| *Limaria hians* | lMi-R | ? | – | ■ | – | – | – | – | – |
| *Limaria loscombei* | mMi-R | 0-100 | – | – | – | ■ | – | – | – |
| *Neopycnodonte cochlear* | ePli-R | 35-100 | ■ | – | – | – | – | – | – |
| *Ostrea edulis* | mMi-R | 27-1500 | – | – | ■ | ■ | ■ | ■ | – |
| *Lucinoma (L.) b. borealis* | lOl-R | 0-90 | ■ | ■ | ■ | ■ | ■ | ■ | – |
| *Parvilucina (Cavilinga) scaldensis* | e-lPli | 0-500 | ■ | ■ | ■ | ■ | ■ | ■ | – |

| SPECIES | RANGE | BAT. | K | L | O *A* | O *C* | O *Ab* | K S | M |
|---|---|---|---|---|---|---|---|---|---|
| *Ctena (C.) decorata* | mPli | – | – | ■ | ■ | ■ | – | – | – |
| *Thyasira (T.) flexuosa* | mOl-R | – | ■ | – | – | – | – | – | – |
| *Leptaxinus (L.) ferruginosum* | ePli-R | 10-2000 | ■ | – | – | – | – | – | – |
| *Diplodonta (D.) rotundata* | lOl-R | 20-1100 | ■ | ■ | – | – | – | – | – |
| *Diplodonta (Zemysina) brocchii* | e-mPli | 0-100 | ■ | ■ | ■ | ■ | ■ | – | – |
| *Felaniella (F.) astartea* | ePli-ePle | – | – | – | ■ | ■ | ■ | ■ | – |
| *Scacchia (S.) elliptica* | mMi-R | ? | – | – | ■ | ■ | – | – | – |
| *Semierycina (S.) kautskyi* | e-lPli | – | ■ | ■ | ■ | ■ | ■ | ■ | – |
| *Semierycina (S.) nitida* | ePli-R | ? | – | ■ | ■ | ■ | – | – | – |
| *Erycina (E.) depressa* | ePli | – | ■ | ■ | – | – | – | – | – |
| *Kellia suborbicularis* | eMi-R | 0-120 | ■ | ■ | – | – | – | – | – |
| *Aligena (A.) orbicularis* | ePli | – | ■ | – | – | – | – | – | – |
| *Bornia deltoidea* | eMi-mPli | – | – | – | ■ | ■ | – | – | – |
| *Montacuta substriata* | eMi-R | 0-600 | – | ■ | ■ | ■ | – | – | – |
| *Mioerycina (Phascoliophila) coarctata* | eMi-lPli | – | ■ | ■ | ■ | ■ | – | ■ | – |
| *Mysella (M.) bidentata* | eMi-R | 0-2500 | ■ | ■ | ■ | ■ | – | – | – |
| *Tellimya ferruginosa* | ePli-R | ? | ■ | ■ | – | – | – | – | – |
| *Laseina ambigua* | ePli-ePle | – | ■ | ■ | ■ | ■ | – | – | – |
| *Laseina* cf. *farnesiniana* | ePli-ePle | – | – | ■ | – | ■ | – | – | – |
| *Glans (Centrocardita) ampla* | lMi-ePli | – | ■ | ■ | – | – | – | – | – |
| *Glans (Centrocardita) scaldensis* | ePli | – | – | ■ | – | – | – | – | – |
| *Cyclocardia (C.) o. orbicularis* | | | ■ | ■ | – | – | – | – | – |
| *Cyclocardia (C.) o. chamaeformis* | eMi-ePle | – | – | ■ | ■ | ■ | – | – | – |
| *Cyclocardia (Scalaricardita) scalaris* | mMi-lPli | – | – | ■ | ■ | ■ | ■ | ■ | – |
| *Pteromeris (Coripia) corbis* | mMi-R | ? | – | ■ | – | – | – | – | – |
| *Glibertia prosperi* | e-mPli | – | – | ■ | ■ | ■ | – | – | – |
| *Erycinella pygmaea* | lMi-mPli | – | ■ | ■ | – | – | – | – | – |
| *Isocrassina basteroti* | e-lPli | – | ■ | ■ | ■ | ■ | ■ | – | – |
| *Isocrassina omalii* | e-mPli | – | ■ | ■ | – | – | – | – | – |
| *Isocrassina bipartita* | e-mPli | – | – | ■ | – | – | – | – | – |
| *Isocrassina fusca ariejansseni* | lMi-ePli | – | ■ | ■ | – | – | – | – | – |
| *Isocrassina mutabilis* | ePli | – | ■ | – | – | – | – | – | – |
| *Isocrassina altenai* | ?eMi-mPli | – | – | ■ | ■ | – | – | – | – |
| *Carinastarte trigonata* | lMi-ePli | – | ■ | – | – | – | – | – | – |
| *Astarte (A.) incerta* | m-lPli | – | – | ■ | ■ | ■ | ■ | ■ | – |
| *Astarte (A.) c. corbuloides* | ePli | – | ■ | ■ | – | – | – | – | – |
| *Astarte (A.) galeotti* | lMi-ePli | – | ■ | – | – | – | – | – | – |
| *Astarte (Digitariopsis) o. obliquata* | | – | – | ■ | ■ | ■ | ■ | ■ | – |
| *Astarte (Digitariopsis) o. burtinea* | lMi-lPli | – | ■ | – | – | – | – | – | – |
| *Digitaria e. excurrens* | eMi-ePli | – | ■ | ■ | – | – | – | – | – |
| *Digitaria digitaria* | lMi-R | 15-250 | ■ | ■ | ■ | ■ | ■ | ■ | – |
| *Digitaria forbesi* | lMi-mPli | – | ■ | ■ | – | ■ | – | – | – |
| *Goodallia (G.) triangularis* | mMi-R | ? | ■ | ■ | ■ | ■ | – | – | – |
| *Goodallia (G.) parvula* | lMi-ePli | – | – | ■ | – | – | – | – | – |
| *Goodallia (G.) pseudopygmaea* | mMi-ePli | – | – | ■ | – | – | – | – | – |
| *Parvicardium exiguum* | lMi-R | 0-55 | ■ | – | – | – | – | – | – |
| *Plagiocardium scabrum* | ePli-R | ? | ■ | ■ | ■ | ■ | – | – | – |
| *Plagiocardium papillosum* | eMi-R | 1-600 | ■ | – | – | – | – | – | – |
| *Nemocardium (Microcardium) doelensis* | ePli | – | – | ■ | – | – | – | – | – |
| *Laevicardium (L.) decorticatum* | e-lPli | – | ■ | ■ | ■ | ■ | ■ | ■ | – |
| *Laevicardium (Dinocardium) parkinsoni* | lPli-ePle | – | – | – | – | – | – | ■ | – |
| *Cerastoderma edule hostiei* | mPli-R | 0-10 | – | – | ■ | ■ | ■ | – | – |
| *Mactra (M.) glauca* | lMi-R | 0-44 | – | – | ■ | – | – | ■ | – |
| *Spisula (S.) arcuata* | e-lPli | – | – | ■ | ■ | ■ | ■ | ■ | – |
| *Spisula (S.) obtruncata* | e-lPli | – | ■ | ■ | ■ | ■ | ■ | ■ | – |
| *Spisula (S.) inaequilatera* | m-lPli | – | – | – | ■ | – | – | – | – |
| *Spisula (S.) albertantonorum* | mPli | – | – | – | – | ■ | – | – | – |
| *Lutraria (L.) scaldensis* | e-lPli | – | ■ | ■ | ■ | ■ | – | ■ | – |
| *Cultellus (C.) cultellatus* | eMi-lPli | – | ■ | – | ■ | ■ | ■ | ■ | – |
| *Ensis complanatus* | m-lPli | – | – | – | ■ | ■ | – | ■ | – |
| *Ensis hausmanni* | lOl-lPli | – | ■ | ■ | ■ | ■ | ■ | – | – |
| *Angulus (Moerella) donacinus* | eMi-R | 0-200 | – | ■ | ■ | ■ | ■ | ■ | ■ |
| *Angulus (Peronaea) b. benedeni* | lOl-lPli | – | – | – | ■ | ■ | ■ | ■ | ■ |
| *Arcopagia (A.) c. crassa* | mMi-R | 0-155 | – | ■ | ■ | ■ | – | – | – |

| SPECIES | RANGE | BAT. | K | L | O *A* | O *C* | O *Ab* | K S | M |
|---|---|---|---|---|---|---|---|---|---|
| *Arcopagia (Arcopagiopsis) b. tenuilamellosa* | ePli-R | 0-750 | ■ | ■ | – | – | – | – | – |
| *Gastrana laminosa* | mMi-Pli | – | ■ | ■ | ■ | ■ | ■ | ■ | – |
| *Macoma (M.) obliqua* | ePli-mPle | – | ■ | ■ | ■ | ■ | ■ | ■ | – |
| *Macoma (M.) praetenuis* | lPli-lPle | – | – | – | – | – | – | – | ■ |
| *Donax (Capsella) variegatus* | mPli-R | 0-10 | – | – | – | ■ | – | – | – |
| *Gari (Psammobella) costulata* | mMi-R | 0-460 | – | ■ | – | – | – | – | – |
| *Gari (Psammobia) fervensis* | eMi-R | 0-110 | – | ■ | ■ | ■ | ■ | ■ | – |
| *Gari (Gobraeus) depressa* | ePli-R | 0-50 | – | ■ | ■ | ■ | – | – | – |
| *Abra (A.) prismatica* | lMi-R | 0-40 | ■ | ■ | ■ | ■ | – | – | – |
| *Abra (Syndosmya) a. alba* | mMi-R | 0-60 | – | – | ■ | ■ | – | ■ | – |
| *Solecurtus scopulus* | mMi-R | 0-110 | – | ■ | ■ | ■ | – | – | – |
| *Arctica i. islandica* | eOl-R | 0-500 | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *Pygocardia rustica* | lMi-lPli | – | ■ | ■ | ■ | ■ | ■ | ■ | – |
| *Coralliophaga (C.) lithophagella* | mMi-R | 30-200 | ■ | ■ | – | – | – | – | – |
| *Glossus (G.) humanus* | mMi-R | 7-250 | ■ | ■ | – | – | – | – | – |
| *Venus (Dosina) casina* | lMi-R | 5-200 | – | ■ | ■ | ■ | ■ | – | – |
| *Venus (Ventricoloidea) pseudoturgida* | ePli | – | ■ | ■ | – | – | – | – | – |
| *Gouldia (G.) minima* | eMi-R | 0-200 | ■ | ■ | – | – | – | – | – |
| *Pitar (P.) r. rudis* | eMi-R | 0-80 | ■ | ■ | ■ | ■ | – | – | – |
| *Callista (C.) chione* | eMi-R | 0-180 | – | ■ | – | – | – | – | – |
| *Dosinia (Asa) lupines lincta* | mMi-R | 0-200 | – | ■ | ■ | ■ | ■ | ■ | – |
| *Dosinia (Pectunculus)* cf. *exoleta* | ePli-R | 0-70 | ■ | – | – | – | – | – | – |
| *Paphia rhomboides* | ePli-R | 0-180 | – | ■ | ■ | ■ | ■ | ■ | – |
| *Clausinella imbricata* | lMi-mPli | – | – | ■ | ■ | ■ | – | – | – |
| *Timoclea (T.) ovata* | mMi-R | 4-200 | ■ | ■ | ■ | ■ | ■ | ■ | – |
| *Lajonkairea rupestris lupinoides* | l-mPli | – | ■ | ■ | ■ | ■ | – | – | – |
| *Mya (M.) truncata gudmunduri* | ePli-R | 0-75 | – | – | ■ | ■ | ■ | ■ | – |
| *Mya (Arenomya) arenaria lata* | lPli-R | 0-75 | – | – | – | – | – | ■ | – |
| *Sphenia binghami* | lMi-R | 1-60 | – | – | – | ■ | – | – | – |
| *Corbula (Varicorbula) gibba gibba* | lEo-R | 0-250 | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *Lentidium (L.) complanatum* | m-lPli | – | – | – | – | ■ | – | ■ | – |
| *Spheniopsis jugosa* | ePli | – | – | ■ | – | – | – | – | – |
| *Gastrochoena (G.) dubia* | eMi-R | 5-60 | ■ | – | ■ | – | – | – | – |
| *Hiatella (H.) arctica* | mOl-R | 0-1400 | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *Cyrtodaria angusta* | eMi-lPli | – | ■ | ■ | ■ | ■ | ■ | ■ | – |
| *Panomya trapezoides* | mMi-ePle | – | – | – | – | ■ | – | ■ | – |
| *Panopea (P.) glycimeris* | lMi-R | 2-80 | ■ | ■ | ■ | ■ | ■ | ■ | – |
| *Turneria cylindrica* | e-mPli | – | ■ | – | – | ■ | – | – | – |
| *Turneria angulata* | e-mPli | – | ■ | – | – | ■ | – | – | – |
| *Barnea (B.) cylindrica* | e-lPli | – | – | – | – | – | – | ■ | – |
| *Zirfaea crispata* | ePli-R | 0-7 | – | – | – | ■ | – | ■ | – |
| *Xylophaga* sp. | – | ? | – | – | – | – | – | ■ | – |
| Teredinidae | – | ? | ■ | – | – | ■ | – | ■ | – |
| *Pholadomya (P.) hesterna* | lMi-mPli | – | ■ | ■ | – | ■ | – | – | – |
| *Pandora (P.) pinna* | ePli-R | 27-80 | ■ | ■ | ■ | ■ | – | – | – |
| *Lyonsia (L.) mermuysi* | eMi-mPli | – | ■ | ■ | ■ | ■ | – | – | – |
| *Cochlodesma (Bontaea) complanatum* | e-mPli | – | ■ | ■ | – | ■ | – | – | – |
| *Thracia (T.) altenai* | e-mPli | – | – | ■ | ■ | ■ | – | – | – |
| *Thracia (T.) i. inflata* | eMi-mPli | – | ■ | – | ■ | – | – | – | – |
| *Thracia (T.) convexa* | ePli-R | 0-800 | – | – | ■ | – | – | – | – |
| *Thracia (T.) detruncata* | e-mPli | – | ■ | ■ | – | ■ | – | – | – |
| *Thracia (T.)* cf. *villosiuscula* | ePli-R | ? | – | ■ | – | – | – | – | – |
| *Poromya granulata* | lMi-R | 30-600 | ■ | ■ | – | – | – | – | – |
| *Cuspidaria (C.) rostrata* | ePli-R | ? | ■ | – | – | – | – | – | – |
| *Cuspidaria (C.) cuspidata* | eMi-R | 20-250 | ■ | – | – | – | – | – | – |
| *Cuspidaria (C.)* cf. *obesa* | ePli-R | ? | – | ■ | – | – | – | – | – |
| *Cardiomya costellata* | eMi-R | 18-200 | ■ | – | – | – | – | – | – |
| *Verticordia (V.) cardiiformis* | lMi-lPli | – | ■ | ■ | – | – | – | – | – |
| Total number of species | | | 110 | 117 | 82 | 90 | 44 | 53 | 8-9 |
| Number of extinct species | | | 54 | 57 | 38 | 45 | 21 | 29 | 2-3 |
| % of extinct species | | | 49 | 49 | 46 | 50 | 48 | 55 | 34 |

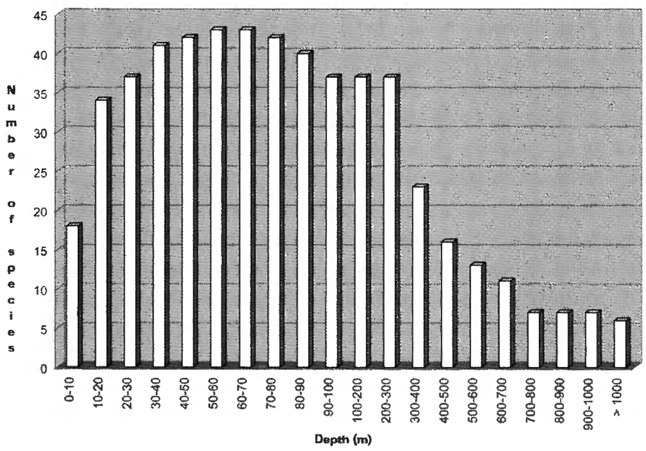


Fig. 2 — Bathymetric distribution of the bivalve species in the Kattendijk Fm. in the Kallo and Doel sections.

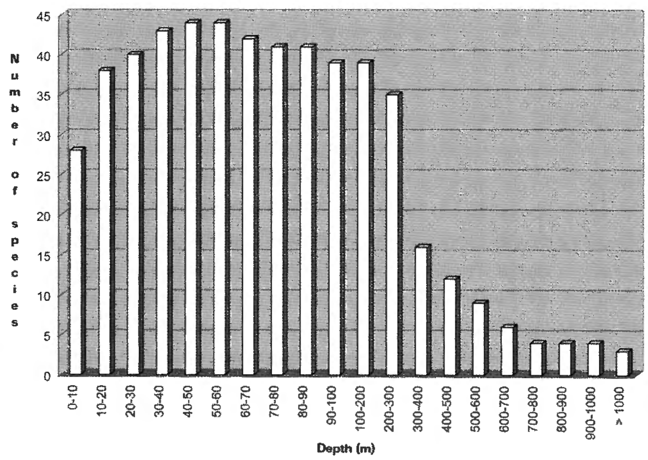


Fig. 3 — Bathymetric distribution of the bivalve species in the Luchtbal Sand Mbr. in the Kallo and Doel sections.

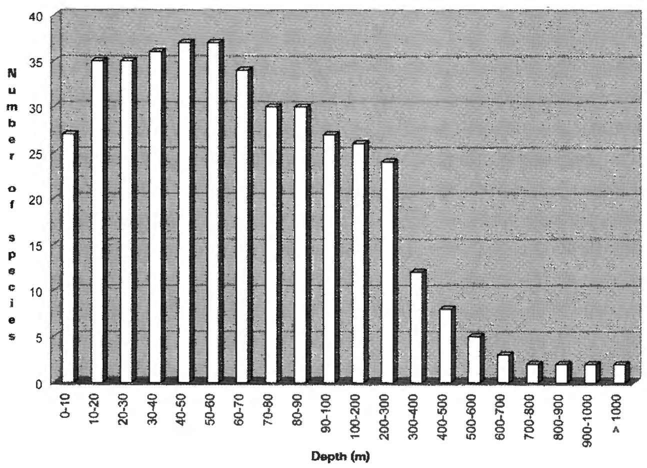


Fig. 4 — Bathymetric distribution of the bivalve species in the Oorderen Sand Mbr. in the Kallo and Doel sections.

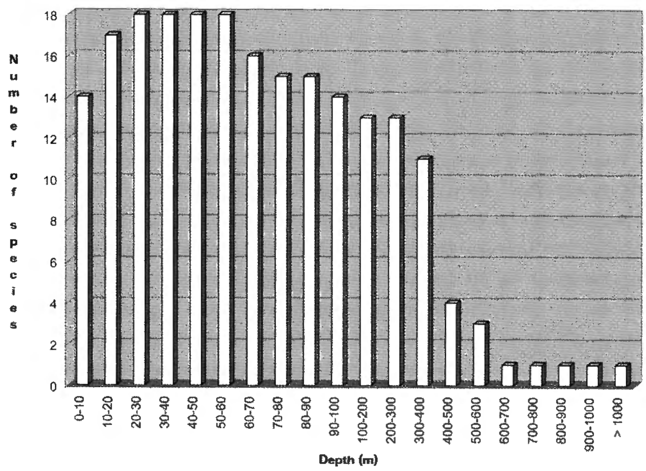


Fig. 5 — Bathymetric distribution of the bivalve species in the Kruisschans Sand Mbr. in the Kallo and Doel sections.

gives shallower depth values: for the Kattendijk Fm. the only common bathymetry for all species is between 45 and 55 m, except for *Bathyarca philippiana* (NYST, 1848), which is found alive only at a depth of 150 m. A possible explanation for the latter fact is the lack of Recent records of this rare species. Moreover in the Oorderen Sand Mbr. an anomaly was discovered: *Donax variegatus* (GMELIN, 1791), which today occurs at a shallower depth than all other bivalve species in the same level. However, this is a very rare species in the sections examined and all specimens were eroded, indicating an allochthonous origin. With the second method, the importance of species with a limited bathymetric range is emphasized, whereas the importance of taxa with an extremely wide range (e.g. from 0 to 2500 meters for *Montacuta bidentata* (MONTAGU, 1803)) is reduced. The resulting values are given in Tables 2 and 3.

Table 3 — Number of bivalve species with known bathymetric range and depth of deposition, according to the distribution of these species, calculated as average value and by common overlap of the species.

| **Stratigraphic unit** | **Number of species** | **Medial depth** | **Common overlap** |
|---|---|---|---|
| Kattendijk Fm. | 46 | 50-70 m | 45-55 m |
| Luchtbal Sand Member | 47 | 40-60 m | 40-50 m |
| Oorderen Sand Member | 39 | 40-50 m | 35-45 m |
| Kruisschans Sand Member | 27 | 20-50 m | 15-55 m |

## Discussion

GAEMERS (1975a, b) discussed the depth of the different members found in the Kallo sections (excluding the Luchtbal Sand Mbr. not found at that time in the research area) based on the occurrence of brachiopods, molluscs, otoliths and sedimentary structures. GAEMERS (1975a) estimated the depth of deposition of the Kattendijk Fm. at minimum 30 to 50 m, but pointed out that some of the otoliths are characteristic of genera, now living deeper than 100 m. He concluded, as is stressed here also, that data on genus level should not be used indiscriminately for the assessment of bathymetry. For the Oorderen Sand Mbr., GAEMERS (1975b) estimated the depth at minimum 10 to 20 m, for the Kruisschans Sand Mbr. less than 10 m. For the two last mentioned deposits, this is shallower than our data indicate, whereas the results for the Kattendijk Fm. are comparable.

NUYTS (1990) investigated the biostratigraphy and lithostratigraphy based on benthic Foraminifera for the deposits at Kallo, except for the Luchtbal Sand Mbr. He concluded that his data were too variable to allow a palaeoecological conclusion and placed the Kattendijk Fm. at a depth of at least a few tens of metres, not very close to the continent. The Oorderen and Kruisschans Sand Mbrs (between which he could not distinguish by means of the foraminiferal content) he classified as near-shore environments.

The data presented here for the bivalve fauna of the Belgian part of the North Sea Basin cannot be easily compared with molluscan data from the British or Dutch coeval deposits. Indeed, first a systematic revision is needed to ascertain that the species under discussion are indeed different from each other and from Recent material. Then, as complete as possible distribution lists should be assembled per locality or member. However, the latest complete reviews from the British Pliocene bivalves are from WOOD (1851-1882), while the gastropods were treated subsequently by HARMER (1914-1925). Especially the last author split up his material excessively, so that the total number of species is highly overestimated and the number of extinct and endemic species is exaggerated. The Dutch material from borings is extensive, but only a small part has been published, the bivalves by HEERING (1950). This author does not divide his samples according to different assemblages or members, so interpretation is difficult; a systematic revision of this material is needed.

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