

Notes on stratigraphy, taxonomy and nomenclature of a Late Miocene *Pliothyryna* aff. *grandis* (Blumenbach, 1803) (Brachiopoda, Terebratulidae) assemblage from the Westerschelde (The Netherlands)

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The stratigraphy, taxonomy and nomenclature of a Late Miocene assemblage of *Pliothyryna* Van Roy, 1980 shells from the Westerschelde are surveyed. Taxonomical and nomenclatural issues are addressed, with special attention for the work of Lacourt (1983/1984). The Westerschelde shells are provisionally identified as *P. aff. grandis* (Blumenbach, 1803). Further research is needed to elucidate the taxonomical status of the NW European *Pliothyryna* assemblages of Oligocene, Miocene and Pliocene age.

Key words: stratigraphy, taxonomy, nomenclature, *Pliothyryna*, Late Miocene, North Sea Basin, Westerschelde.

Introduction

Since around 1920 shells (mostly molluscs) have been harvested from the Westerschelde (The Netherlands) for the production of lime, shell grit and for other purposes. These faunas were dominated by bleached aragonitic shells of Pliocene age, similar to the fossil content of the Kattendijk and Lillo formations of adjacent northern Belgium. Species from the Pleistocene were common, complemented by small amounts of Eocene, Oligocene, and Miocene species (Moerdijk *et al.*, 2010). The taxonomic composition of the faunas present in the loads landed from the 1920s onwards remained fairly constant until 2006.

In 2006 a large number of reworked but often very well preserved *Pliothyryna* Van Roy, 1980 shells was found among some shiploads of dredged shells from the Westerschelde (Moerdijk, 2007). These shells seemed to be part of a specific Miocene fossil fauna. This paper documents my search for a more exact age of the brachiopod shells and their proper identification.

Material

Westerschelde, dredged offshore between Ellewoutsdijk and Borssele (province of Zeeland) (Fig. 1), 2006, derived from Miocene deposits: 129 mostly incomplete ventral valves, 59 mostly incomplete dorsal valves and 18 mostly incomplete articulated specimens of *Pliothyryna* sp. (RGM coll., ex coll. P.W. Moerdijk).

Of *P. quadratomuscularis* (Lacourt, 1983): one paratype (ventral valve): Westerschelde, sucker dredged by the vessel “Marie”, Oct. 1935, leg. A. Slabber, KZGW collection.

Of *P. zelandica* (Lacourt, 1983): two paratypes (ventral valves): Domburg, 29 Dec. 1930, leg. C. Brakman, KZGW collection.

The numerous specimens examined *c.q.* identified by Lacourt (1983/1984) present in the KZGW collection.

For comparison: Verrebroekdok, Kattendijk Formation (Zanclean): 2 complete specimens, 8 ventral valves and 6 dorsal valves of *Pliothyryna* sp., most damaged (coll. P.W. Moerdijk).

Abbreviations:

KZGW	Koninklijk Zeeuwsch Genootschap der Wetenschappen (KZGW), housed in the Zeeuws Museum (Middelburg, The Netherlands)
RGM	Rijksmuseum van Geologie en Mineralogie, now Naturalis Biodiversity Center, collection Palaeontology (Leiden, The Netherlands).
RMNH.BRA	Rijksmuseum van Natuurlijke Historie, now Naturalis Biodiversity Center, collection Brachiopoda, (Leiden, The Netherlands).
L	Length
H	Height

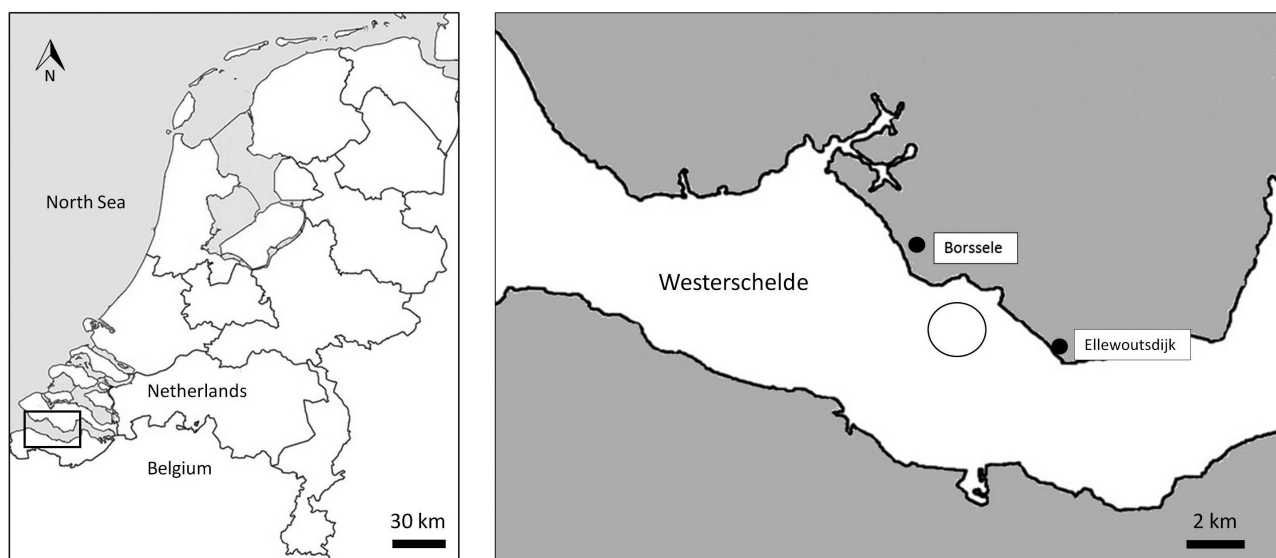


Figure 1. Location of the sucker-dredged Miocene fossils.

Geological context

The shells that were extracted in 2006 and landed in Yerseke derived somewhere offshore between Ellewoutsdijk and Borssele in the Westerschelde (pers. comm. Bram Goetheer). Apart from Pliocene species, also common shells certainly of Miocene age were present in the material: *Mimachlamys angelonii* (De Stefani & Pantanelli, 1878), *Pycnodonte navicularis* (Brocchi, 1814), the brachiopod *Pliothyryna* sp., and in lesser frequency *Hinnites ercolanianus* Cocconi, 1873 and *Pseudamussium clavatum* (Poli, 1795). It concerns well-preserved calcitic shells with generally brownish colours that distinguish them from mostly lighter coloured Pliocene species.

Pliothyryna sp., *Mimachlamys angelonii* and *Pycnodonte navicularis* were not rare in the shell heaps that were dredged before 2006, but these specimens were generally worn. Shells of all the aforementioned brachiopod and mollusc species have been found in the 2006 load in a perfect condition, some of them embedded in the original grey, glauconite-rich and quite coarse sandstone or with adhering sediment. Several articulated *Pliothyryna* shells and even more fragments of posterior parts of these, as well as an articulated specimen of *Pycnodonte navicularis* were found. Lumps of consolidated sediment with Bryozoa and *Ditrupa* Berkeley, 1835 were also present in the load.

Hinnites ercolanianus and *Neopycnodonte cochlear* (Poli, 1795) are species that cement their shells onto hard substrates such as other shells. Moreover, the imprints that are left behind on the shells that have been attached reveal the co-occurrence of other hard-shelled animals. Some specimens were still attached to the inside of a ventral valve of *Pliothyryna*, and shells of *P. navicularis* and *M. angelonii*. *Hinnites ercolanianus* shells show imprints of *P. navicularis*, *M. angelonii*, the inside of the spire of an unknown large gastropod and of echinoids (Moerdijk, 2007). Specimens of *Neopycnodonte cochlear* show imprints of the exterior of *M. angelonii*. This makes the simultaneous ap-

pearance of *H. ercolanianus*, *P. navicularis*, *N. cochlear*, *M. angelonii* and *P. sowerbyana* evident.

The mostly fresh appearance of these fossils, often with adhering sediment indicates that at the locality where these shells were dredged, fossiliferous deposits of Miocene age are being eroded by the tidal currents of the Westerschelde inlet. From the composition of the Miocene fauna a more exact stratigraphical provenance can be inferred.

In temporary outcrops of the Late Miocene (Tortonian) Deurne Member of the Diest Formation in nearby northern Belgium *Pliothyryna* sp. and the mollusc species *Mimachlamys angelonii* (de Stefani & Pantanelli, 1878), *Pseudamussium clavatum* (Poli, 1795) and *Pycnodonte navicularis* occur commonly (De Meuter & Laga 1976, Bosselaers *et al.*, 2004, Goolaerts *et al.*, 2020). These sediments are locally very rich in bryozoan, brachiopod and “*Ditrupa*” (Annelida) assemblages (De Meuter & Laga, 1976).

Until now, the occurrence of *Neopycnodonte cochlear* (Poli, 1795) has only been reported from the Early Pliocene Kattendijk Member. However, as *Pycnodonte navicularis* (Brocchi, 1814) is often synonymised with it (e.g. Glibert, 1945, Glibert, 1958), the stratigraphic occurrence data are unreliable. *Hinnites ercolanianus* has not been reported from the Deurne Member and according to Glibert (1958) the species is typical for the Miocene Langhian/Serravallian Antwerpen Member (“Sables d’Anvers à *Glycymeris deshayesi* et à *Chlamys ercolaniana*”). Nevertheless, within the discussed fauna no other species typical for the Miocene Antwerpen Member have been found. In contrast, according to Glibert (1958) *Pseudamussium clavatum* (Poli, 1795) is typical for the Late Miocene Tortonian (“Sables de Deurne à *Peplum clavatum* et à *Terebratula maxima*”), where it apparently has its first occurrence. In fact, nowhere in this area *Hinnites ercolanianus* and *Pseudamussium clavatum* are known to co-occur, so they are good stratigraphic indicators. As *H. ercolanianus* is a quite rare species its occurrence within Deurne Member deposits probably remained unnoticed.

Epoch/age	Stage	Lithostratigraphic units
Pliocene 2,58 – 5,3 Ma	Piazzencian	Lillo Formation
	Zanclean	Kattendijk Formation
Miocene 5,3 – 23 Ma	Messinian	Diest Formation, Deurne Mbr
	Tortonian 7 – 11 Ma	
	Serravallian	
	Langhian	
	Burdigalian	
	Aquitainian	
Oligocene 23 – 34 Ma	Chattian	Boom Formation
	Rupelian	

Figure 2. Simplified stratigraphical framework for the Westerschelde Delta area. Names of the Belgian lithostratigraphic units are used.

From the composition of the fossil assemblage an age of the Westerschelde deposits comparable to that of the Late Miocene Deurne Member of the Diest Formation can be deduced (Fig. 2).

Observations on the *Pliothyryna* shells (Plates 1- 3)

The large number of specimens provides an excellent opportunity for more comprehensive observations. This has some limitations such as the near absence of the possibility to examine the brachidium, the damaged condition of

most of the valves and the fact that only a limited number of specimens are still articulated. An advantage for examination of the lot is the non-eroded condition and the possibility to examine the interior of the valves.

Dimensions of the two largest ventral valves: Length x width = 73.6 x 52 mm and 69 x 55.2 mm. Largest width of a damaged specimen > 60 mm. Length x width of largest dorsal valve = 64.5 x 59.5 mm.

Relatively firm, many of the valves are quite thick and heavy. The shell is principally smooth, growth lines are present and sometimes faint, irregular fine radial lines can be observed. With some magnification the endopunctated micropattern becomes visible. The colour of the shells is a dark grey-brown to yellowish brown. The outline of the valves is very variable with respect to length vs. width as well as to the amount of protrusion of the posterior part of the ventral valve and the position of the broadest part of the shells. There is a considerable disproportional ontogenetic growth, with variable development; some specimens remain rounded, others become oval, some already at an early growth stage. Convexity of the valves varies to a considerable amount.

Most ventral valves are oval or elliptical, others are slightly subpentagonal in outline. The posterior part of the ventral valve can be somewhat shouldered due to the protrusion of the posterior part. The anterior part is more or less extended, so the lateral commissure of the ventral valve becomes concave. The anterior commissure of some specimens is rectimarginate or can be slightly sulcate.

Full grown and gerontic ventral shells can be considerably thickened and heavy especially at the hinge part of the shell. The hinge teeth in such thickened shells are placed further towards the centre. The hinge teeth are broken in most of the isolated ventral valves.

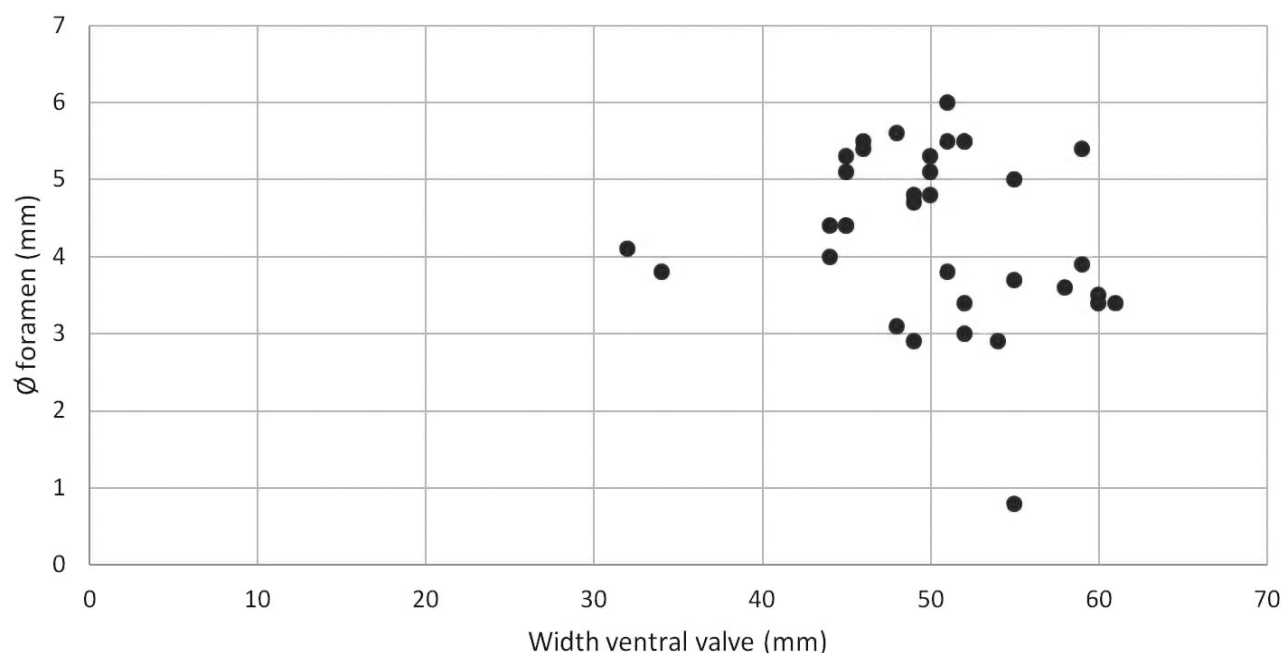


Figure 3. Width ventral valve vs. Ø foramen (n=35).

The foramen is submesothyrid to mesothyrid, not to clearly labiated. On average, the diameters of the foramina are relatively small, but highly variable. In one of the specimens from the Westerschelde this is 1.2 mm, whereas the width of this shell is 56 mm. Another shell of 53 mm wide has a foramen that measures externally 11 mm and internally 5.8 mm. Every kind of dimension in between can be found within the studied material (Fig. 3). Internally, the foramen is bordered by a collar. The umbo is often incurved, symphytium in most specimens exposed. The narrower the foramen, the more incurved the umbo and the longer the collar at the inside of the umbo.

Specimens with an extremely small foramen were described by Lacourt (1984) as *Terebratula* (*Cererithyris*) *distinguenda* Lacourt, 1984. However, as holotype for this species he designated a specimen from an erratic boulder of Jurassic or Cretaceous age found in England, illustrated in Davidson (1874). Thus, this name cannot be used for these forms.

Adductor and diductor muscle scars are often well visible. Their outline varies from specimen to specimen.

In most specimens the outline of the dorsal valves is orbicular, slightly subpentagonal, elliptical to oval. Dorsal valves can be vaguely uniplicate at early growth stages and full-grown specimens can be slightly sulcinate. The angle of the hinge part at the posterior of the dorsal valves varies from c. 122° to 135°.

The adductor muscle scars lay relatively close to the posterior of the shell, from the anterior border from the cardinal process at c. 0.4 x of the length of the shell.

In some specimens the inner hinge plates are close to one another, in most of the specimens there is considerable distance between these inner hinge plates. As in the case with the ventral valves, the dorsal valves can be thickened internally. A remarkable phenomenon is that in many of the larger specimens the crura tends to mineralise and in some of these thickened specimens the internal parts of the hinge plates seem to be absorbed or overgrown. This is of note, because the presence of the internal parts of the cardinal plates constitutes the main distinguishing feature of genus *Pliothyryna* compared to *Terebratula*.

In none of the isolated dorsal valves the brachidium is conserved, but F.A.D. van Nieulande managed to expose the brachidium of a complete specimen from the Goetheer collection. In another specimen a slightly damaged brachidium can be observed. The general features of the brachidia are in accordance with published descriptions and illustrations of brachidia in *Pliothyryna*.

Part of the variability can be explained by the allometric growth of *Pliothyryna*: when the animal grows, the shell becomes relatively longer and more convex.

An explanation of another part of the variability lies in environmental factors: limited growth caused by damage of the shell by predators at early growth stages, availability of food, dynamics of the surrounding water or availability of space for growth.

An explanation of the outstanding variability of the dimensions of the foramen can be found in Sulser *et al.* (2010). Besides regular specimens of *Carneithyris subregularis* (Münster, 1828) from the Eocene (Lutetian) of

Fäneren (N.E. Switzerland), they found shells with comparably small foramina. They assumed a connection with the absence of sufficient suitable substrates. Probably not many substrates were available in the southeastern part of the Miocene North Sea. There the animals supposedly lived loose on the sea floor, so the pedicle and foramen became inert. In Cretaceous brachiopods with such an inert pedicle Surlyk (1972) found a strong thickening of the posterior part of the ventral valve. Apparently the function of this is that of a tumbler; due to the thickened rear, the centre of gravity of the shell shifts to the posterior, so the anterior of the animal is orientated upwards. Such a position guarantees the influx of water with food and reduces the likelihood of sediment particles entering.

Overview of the different *Pliothyryna* species

To decide to which species these Westerschelde *Pliothyryna* shells can be ascribed an overview is given of the different Oligocene and Neogene species that have been described from the North Sea Basin. The different forms are briefly described and nomenclature is discussed.

Phylum Brachiopoda Duméril, 1805

Class Rhynchonellata Williams, Carlson, Brunton, Holmer & Popov, 1996

Order Terebratulida Waagen, 1883

Family Terebratulidae Gray, 1840

Genus *Pliothyryna* Van Roy, 1980 (syn. *Apletosia* Cooper, 1983)

Type species – *Terebratula sowerbyana* Nyst, 1845 [*nomen novum* pro *Terebratula variabilis* J. de C. Sowerby, 1827, *non* Schlotheim, 1813]

In 1980 Van Roy established the genus *Pliothyryna*, with type species *Terebratula sowerbyana* Nyst, 1845. Prior to the introduction of this new generic name the species was incorporated in the genus *Terebratula* Müller, 1776. *Apletosia* Cooper, 1983 is considered a junior synonym of *Pliothyryna* (Williams *et al.*, 2006, Lee & Smirnova, 2006).

Shells are smooth, ornamented only by growth lines, sometimes fine and weak radial lines can be observed. The main characteristic that differentiates *Pliothyryna* from *Terebratula* is the presence of well-developed inner hinge plates in the dorsal valve. According to García Ramos (2006) all large terebratulide brachiopods from the Oligocene to the Plio-/Pleistocene of NW Europe belong to the genus *Pliothyryna*.

Pliothyryna grandis (Blumenbach, 1803) appears to be the only Oligocene representative of the genus in NW Europe. Pliocene and Miocene *Pliothyryna*-shells are quite common in most Pliocene marine deposits. Several names have been introduced, with nomenclatural and taxonomical confusion as a result.

According to Muir-Wood (1938) six different species of *Terebratula* (= *Pliothyryna*) have been described from

the Pliocene of Great Britain, viz. *Terebratula spondylodes* W. Smith, 1817, *T. maxima* Charlesworth, 1837, *T. orfordensis* Muir-Wood, 1938, *T. perforata* Desnoyers, 1825, *T. variabilis* J. de C. Sowerby, 1827 and *T. harmeri* Bell, 1921.

Besides these six she mentions a *Terebratula* cf. *maxima*, but this alleged species remains in open nomenclature as the two valves of *T.* cf. *maxima* have so far not been found articulated and the ventral valve is unknown. In the opinion of Muir-Wood (1938), the description without a figure of *T. spondylodes* Smith is insufficient to define any particular Crag species.

Glibert & Vandercammen (1957) mention *Terebratula maxima* and *T. orfordensis* from the Miocene and *T. variabilis* from the Pliocene Kattendijk Formation of Belgium.

Lacourt (1983/1984) recognised the Pliocene species *maxima*, *orfordensis*, *variabilis*, *harmeri*, *perforata* and *sowerbyana* (sensu Van Roy, 1980), but did not succeed in recognising the Oligocene *P. grandis*. Besides that he described two new species: *Terebratula quadratomuscularis* Lacourt, 1983 and *T. zelandica* Lacourt, 1983.

Some notes have to be made in reference to the publication of Lacourt (1983/1984). He treated the representatives of *Pliothyris* that were reworked from Tertiary deposits and had been found on the coast of Walcheren and around the Westerschelde, and among shells that were sucker-dredged from the bottom of the Westerschelde in the province of Zeeland, the Netherlands. Lacourt 'recognised' no less than 30 species. It might be tempting not to take the publication of Lacourt seriously. In my opinion, however, this work deserves serious evaluation. Lacourt based his work among others on the *Pliothyris*-shells in the KZGW collection. Some paratypes of the newly described *Terebratula quadratomuscularis* and *T. zelandica* Lacourt, 1983 are present in this collection, as well as some of the specimens illustrated in the original publication, and specimens identified by Lacourt of almost every treated species.

The fossil mollusc shells that accompany these brachiopod shells are mainly Pliocene in age, and Oligocene, Miocene and Pleistocene fossils are locally common (Wesselingh *et al.* in Moerdijk *et al.*, 2010). Lacourt (1983/1984) 'recognised' 19 species of Carboniferous, Jurassic or Cretaceous age, viz. *Terebratula insignis* Schübler, 1820 [in Von Zieten, 1832], *T. stephani* Davidson, 1877 [1878], *T. (Carneithyris) carnea* J. de C. Sowerby, 1812, *T. (Cerrethyris) intermedia* J. de C. Sowerby, 1812, *T. (Cyrtothyris) dallasii* Walker, 1867, *T. (Cyrtothyris) omalogastyr* Hehl in Von Zieten, 1832, *T. (Cyrtothyris) ovoides* J. de C. Sowerby, 1815, *T. (Cyrtothyris) sphaeroidalis* J. de C. Sowerby, 1825, *T. (Cyrtothyris) trilineata* Young & Bird, 1828, *T. (Dielasma) aff. ficus* McCoy, 1855, *T. (Dielasma) aff. hastata* J. de C. Sowerby, 1824, *T. (Dielasma) praelonga* J. de C. Sowerby, 1836 [= Fitton, 1836!], *T. (Gibbithyris) semiglobosa* J. de C. Sowerby, 1813, *T. (Loboidothyris) decipiens* Deslongchamps, 1873, *T. (Loboidothyris) perovalis* J. de C. Sowerby, 1825, *T. (Praelongithyris) praelongiforma* Middlemiss, 1959, *T. (Rectithyris) depressa* Lamarck, 1819 and *T. (Rectithyris) obesa* J. de C. Sowerby,

1825. A brachiopod specimen originating from the 'Drift of North Pickenham' and found in an erratic boulder of Jurassic or Cretaceous age is illustrated and discussed by Davidson (1874, pl. I, fig. 17) in open nomenclature. For this specimen Lacourt (1984) introduced the name *Terebratula distinguenda*.

The occurrence of these species from Mesozoic or even Palaeozoic age is [translated from Dutch]: "*The question of the provenance of the Dutch brachiopods cannot be answered with certainty from this reworked (from other layers) material.*" "*An explanation could be that the shells have been reworked, originating from the southern North Sea after the breakthrough of the Strait of Dover.*"

Fossils from rocks from Mesozoic or Palaeozoic age are occasionally found on Dutch beaches, but are scarce. They ended up here embedded in rocks used to reinforce dykes or as flint (chert) from sand from the North Sea used for coastal reinforcement. As far as I know, no Terebratulidae of those ages have been found here. In any case, such fossils would be complete articulated specimens with consolidated matrix, not single valves as in the material studied by Lacourt and myself. No Carboniferous to Cretaceous species are present in the studied material. Likely Lacourt compared the Dutch material with illustrations in the literature, and did this quite scrupulously (for instance, compare fig. 16 in Lacourt, 1983 with the illustrations in Davidson, 1874, pl. III, fig. 1a).

That Lacourt (1983/1984) meant to recognise as much as nineteen pre-Tertiary species illustrates the difficulty of recognising different species of Terebratulidae without data on their provenance; it also highlights the variability of the Dutch material. All specimens identified by Lacourt as pre-Tertiary species can be assigned to species of *Pliothyris* sp.

Lacourt (1983/1984) also 'recognised' three Eocene species, viz. *Terebratula (Cyrtothyris) bartonensis* Muir-Wood, 1933, *T. (Cyrtothyris) hantonensis* Muir-Wood, 1933 and *T. (Gyrothyris) putzeysi* Vincent, 1893. Fossils – mainly mollusc shells and Elasmobranch teeth – from Eocene origin are not uncommon in the area where the brachiopods examined by Lacourt have been found. Especially along the coast of Zeeuws-Vlaanderen and to a lesser extent on the beaches of Walcheren. So, it cannot be *ex ante* excluded that these species are present in the examined material.

In relation to the two last mentioned species Muir-Wood (1938) remarks that "*both species differ from the Pliocene species of Terebratula ... by the internal characters of their brachial valves*". *Terebratula putzeysi* has been described from the late Eocene 'Sables de Wemmel'. It appears to be similar to *T. bartonensis*, *fide* Muir-Wood (1938). These Eocene *Terebratula*-species are quite small and fragile and less inflated than their younger Tertiary relatives. Moreover, they appear to be very rare in Great Britain as well as in Belgium.

Two specimens from the KZGW collection that Lacourt identified as *T. putzeysi* have been examined. The first one is a specimen from a borehole at Ossendrecht (province of Noord-Brabant), from an interval at c. 65 metres below surface. The specimen was accompanied by other

non-eroded *Pliothyryna* specimens, identified by Lacourt as *Terebratula hastata* J. de C. Sowerby, 1824, a species of Carboniferous age, *T. decipiens* Deslongchamps, 1873 (Jurassic) and *T. obesa* J. de C. Sowerby, 1825 (Cretaceous), respectively. The interval where these fossils were found is in fact of Pliocene age, Breda Formation and the specimen is certainly not identical to *T. putzeysi*. The other specimen is a worn, firm ventral valve from the beach of Domburg. The specimen is also much larger and stronger than the specimens described by Vincent and obviously has a Pliocene or Miocene origin.

Lacourt mentions alleged specimens of *Terebratula bartonensis* from the Westerschelde and Ritthem. He provides a picture of one of these ventral valves, that shows some similarity to the illustration in Davidson (1852), but it shows no specific characteristic that could identify this specimen positively as the Eocene species. A ventral valve identified by Lacourt as *T. bartonensis* is present in the KZGW collection and has been examined. This specimen also shows no particular characteristic that discriminates it from other *Pliothyryna*-specimens from the same lot. It has to be mentioned that among the fossil shells from the Westerschelde and Ritthem fossils of Eocene origin are scarce.

According to Lacourt (1983/1984) dr H.C. Brunton, British Museum, Natural History, London identified two dorsal valves from “a quarry at Terneuzen” as belonging to *Terebratula hantonensis*. Lacourt provides no illustration and little detail [translated from Dutch: “The brachial valve is broadly oval, the muscular impressions are long and narrow, pear shaped, quite small.”] of these specimens. Muir-Wood (1938) gives a detailed comparison between the dorsal valves of *T. bartonensis* and *T. hantonensis*, but in the description of Lacourt there is no clue for a positive identification. Lacourt provides no information on where these valves are stored; they could not be retrieved from the RGM collections, the database of the Rotterdam Natural History Museum, nor the collection of the KZGW.

These specimens identified as Eocene species by Lacourt (1983/1984) can also be identified as *Pliothyryna* sp.

The species in *Pliothyryna* Van Roy, 1980

Underneath the different taxa are discussed, so that they can be compared with the *Pliothyryna* from the Westerschelde.

Pliothyryna grandis (Blumenbach, 1803)

Dulai & Von der Hocht (2020) recently gave a comprehensive review of many entries in the literature. Short synonymy and good illustrations of the species:

- *1803 *Terebratulites grandis* Blumenbach, p. 18, pl. 1, fig. 4.
- 1893 *Terebratula grandis* Blumenbach, 1803 – Vincent, p. 57, textfig. without number.

- 1984 *Terebratula grandis* Blumenbach, 1813 [sic!] – Lacourt, p. 46-47, fig. 43 (upper two figs: type-specimen).
- 2006 *Pliothyryna grandis* (Blumenbach, 1803) – García Ramos, p. 32-34, fig. 2.
- 2020 *Pliothyryna grandis* (Blumenbach, 1803) – Dulai & Von Der Hocht, p. 231-234, pl. 2, figs 5-25.

Type – Preserved in the Geologisch-Paleontologisches Institut und Museum der Georg-August Universität in Göttingen and originates from the late Oligocene (Chat-tian) of Osnabrück. It is illustrated in the original publication (Blumenbach, 1803) and in Lacourt (1984, fig. 43).

Vincent (1893) gives a maximum length of 72 mm. Dulai & Von der Hocht (2020) give as largest length 61 mm. They give a brief description of the species. The outline is described as “elongated, oval”. And its lateral commissures as “nearly straight, or curved ventrally at anterior third”. Its anterior commissure becomes sulcinate in adult specimens. The species has a suberect, strongly truncated beak, with a large mesothyrid foramen and a short pedicle collar.

Examination of several photographs and detailed illustrations of *P. grandis* (e.g. Vincent, 1893; Cooper, 1983; Dulai & Von der Hocht, 2020) show a highly variable species with a quite narrow shell, some of them strongly plicated and with less central adductor muscle scars in the dorsal valve.

Muir-Wood (1938) mentions the more incurved umbo of *T. grandis* compared to the Crag shells, concealing the symphitium, the highly convex valves, more circular shell-outline and the shell which is more massive than the Crag-shells.

The more circular shell-outline that Muir-Wood noticed certainly holds true for the type specimen (*vide* Lacourt, 1984, fig. 43), but this is a more rounded example than the average specimens. In fact, most specimens of *grandis* are narrower than the shells of *P. maxima*.

Anomia spondylodes Gmelin, 1791 – *nomen dubium*

- *1791 *Anomia spondylodes* Gmelin, p. 3348 (Ill. Lister, 1685-1692, pl. 211, nr. 45).
- ?1811 *Terebratula spondylodes* Gmelin – Parkinson, p. 137, *non* Gmelin?
- ?1817 *Terebratula spondylodes* – W. Smith, p. 12, *non* Gmelin?

The oldest name associated with NW European *Pliothyryna*-species is *Anomia spondylodes* Gmelin, 1791. Gmelin introduced this name referring to an illustration in Lister (1685-1692, plate 211, nr. 45) and a copy of that illustration in Klein (1753). Parkinson (1811) suggests that this illustration is a *Terebratula*-shell from Essex, because it is “generally found in the mutilated state in which they are here figured by Lister” and “agreeing with the dark colour of the Essex fossil”. The illustrated shell could indeed be a very worn and distorted ventral valve of a *Plio-*

thyrina with the deltidium missing. However, the illustration is of insufficient quality to positively identify it as a Pliocene *Pliothyrina* shell. Furthermore, Lister neither Gmelin provide any information about its origin. Many of the shells illustrated in Lister were from the collection of sir Hans Sloane (1660–1753). But the illustrated shell of *Anomia spondylodes* is not listed by Wilkins (1953) in his paper on the Sloane collection. So, it can be assumed that the whereabouts of the illustrated shell are unknown. As a consequence it is impossible to establish the identity of *Anomia spondylodes* Gmelin, 1791 with any certainty and the name has to be regarded a *nomen dubium*. Buckmann (1908), followed by Vincent (1922) and Muir-Wood (1938) contribute the name *T. spondylodes* erroneously to Smith (1817). Smith (1817) only lists and describes the fossil Crag shell as *Terebratula spondylodes*, without any reference to Gmelin and/or Parkinson.

Pliothyrina maxima (Davidson, 1852)

- 1837 *Terebratula variabilis* Charlesworth (non J. de C. Sowerby, 1824?), p. 92, figs 13a, 14.
- *1852 *Terebratula maxima* Charlesworth, 1837 – Davidson, p. 16, 17 (as synonym of *T. grandis sensu* Davidson).
- 1852 *Terebratula grandis* Blumenbach, 1803 – Davidson, pl. 2, figs 1 a-c, 2, 3.
- 1874 *Terebratula grandis* Blumenbach, 1803 – Davidson, pl. II, fig. 1.
- 1874 *Terebratula grandis* Blumenbach, 1803 – S.V. Wood, pl. XI, figs 5 a- d.
- 1938 *Terebratula maxima* Charlesworth, emended Muir-Wood – Muir-Wood, p. 160-165, fig. 4.
- 1983 *Apletosia maxima* (Charlesworth) – Cooper, pl. 5, figs 10, 11.

Lectotype – Charlesworth, 1837, figs 13a, 14 (see Muir-Wood, 1938).

According to Muir-Wood (1938) the shell is large, with an elongate-oval or subcircular outline. The species is about 100 mm long, 75 mm wide, and 52 mm thick. The ventral valve is more convex than the dorsal one. The ventral valve has an erect to suberect umbo, truncated by the large marginate permesothryrid foramen. Its beak-ridges are obscure, the anterior commissure is uniplicate or incipiently sulcinate. Apical angle about 80°. The shells of gerontic specimens can be thickened. Inner hinge-plates separate in adult.

The brachidium is comparatively large and slender (see Davidson, 1874, pl. II, fig. 1; Wood, 1874, pl. XI, fig. 5a; Cooper, 1983, pl. 5, fig. 10, 11).

Vincent (1893) compared the valve of *maxima* illustrated by Davidson (1874, pl. II, fig. 1) with the interior of the dorsal valve of *grandis*. The main difference that Vincent noted was, that the position of the adductor muscle scars in *maxima* is more central than in *grandis*. Other differences with *grandis*: *maxima* specimens are much larger (107 mm) than the largest *grandis* (72 mm); its plicae are

comparatively weak and never reach the development such of that observed in *grandis*; the umbo of the ventral valve is generally longer and more curved and overhangs that of the dorsal valve; the angle of the opening of the deltidium is larger and the brachidium is longer in *maxima*. Illustrations of *grandis* by e.g. Cooper (1983) and Dulai & Von der Hocht (2020) show that the shell of *maxima* is generally wider.

Pliothyrina maxima is distinguished from *P. orfordensis* (Muir-Wood, 1938) by its larger dimensions and greater shell width, by its larger apical angle, less erect umbo, and less advanced folding of the shell, as well as by differences in the internal characteristics of the dorsal valve. Indistinguishable though in early growth-stages, when both are approximately circular in outline and slightly biconvex.

It has been found in the Coralline Crag of Suffolk.

Charlesworth (1837) is the source of the name *Terebratula maxima*. He used this name one time in his discussion on the specimens of ‘*Terebratula*’ he obtained: “*Could Mr. Sowerby have seen this fossil in the state in which it is procured at these localities, I do not think he would have distinguished it by the term variabilis. Máxima would seem a more appropriate designation; particularly too, if, as I have some reason to imagine, the variations in form are principally confined to the early periods of growth.*”

Although the title of his work “... description of a Gigantic Species of *Terebratula*” could suggest otherwise, Charlesworth (1837) apparently had no intention to establish a new species, but considers the shells that he discusses as the full-grown shells of what Sowerby described as *Terebratula variabilis*. Apart from the reference above this is also clear from the following text-fragments: “*This shell cannot, it is true, be looked upon as an entirely new fossil, since Sowerby has, in the Mineral Conchology, figured and described several specimens, which are undoubtedly young specimens of the same species.*” ..., “*Sowerby designated this species by the term variabilis, from observing that many specimens of it were much more orbicular than others; now, this variation in shape, constantly exhibited by immature shells, is shown only in a very slight degree by such as have attained the size of fig. 13.*” ..., “*Terebratula variabilis is, I think, the only Tertiary species yet described as occurring in this country, though three or four are said to exist in the British seas.*”

Charlesworth respects the name *variabilis* and uses the name given by Sowerby consistently (five times) in his text in reference to his specimens. So, Charlesworth had no intention to introduce a new species and uses *variabilis* as the name for the brachiopods he treats in this publication. Available names can be introduced in zoological nomenclature in two manners: by giving a name to a new taxon or by giving a replacement name (*nomen novum*) to an existing taxon. The introduction of the name *maxima* does not fulfil the requirements of the ICZN.

The introduction of the species name *maxima* as a valid name instead of *sowerbyana* can be traced back to Davidson (1852), who wrote on this subject: “*Mr. Nyst (in 1845) rejects Mr. Sowerby's name, on account of a similar de-*

nomination having been given by Schlotheim in 1813 to a plaited Lias Terebratula, and proposes in lieu of that of T. sowerbii. Mr. Charlesworth advocated likewise in 1837, the name of T. maxima as a substitute for variabilis."

As shown, Charlesworth (1837) was not aware of the pre-occupation of the name *Terebratula variabilis* by Von Schlotheim and in fact did not recommend to replace the name *variabilis* by *maxima*. If Charlesworth would have had the intention to replace the name *variabilis* by *maxima*, his motive to reject the name *variabilis* would be that the name *maxima* would seem more appropriate. In that case this act would be invalid: ICZN rule 23.3.7: "An available name ... is not to be rejected ... for a reason such as its inappropriateness ...".

As stated before, the name *maxima* is not available from Charlesworth. The combination *Terebratula maxima* has to be ascribed to Davidson (1852), who listed this name as a synonym of *T. grandis*.

***Pliothyryna orfordensis* (Muir-Wood, 1938)**

- *1938 *Terebratula orfordensis* Muir-Wood, p. 165-169, figs 2, 3A-C.
- 1983 *Pliothyryna orfordi* [sic!] Muir-Wood – Cooper, pl. 5, fig. 9

Holotype – Muir-Wood (1938), figs 3 A- C; paratype; fig. 2. The holotype of *Pliothyryna orfordensis* is preserved in the Walker Collection, British Museum (Nat. list.), BB. 3477. It originates from the Coralline Crag of Park Pit, Sudbourne, near Orford, Suffolk.

According to Muir-Wood the shell of this Coralline Crag (Zanclean) species is about 70 mm long and 50 mm wide, with an apical angle of *c.* 70°. Gerontic specimens are clearly sulcinate. The inner hinge plates in the interior of the dorsal valve are usually fused.

Pliothyryna maxima grows larger and is less plicate than *P. orfordensis*. The inner hinge plates in the brachial valve in *P. maxima* are separated. *Pliothyryna sowerbyana* is smaller and has a thicker shell than *P. orfordensis* and tapers more rapidly towards the umbo and its growth-lines are more marked, more numerous and lamellose.

The dorsal valve of *P. orfordensis* can be identified by its usually fused inner hinge-plates.

***Pliothyryna perforata* (Desnoyers, 1825) sensu Muir-Wood, 1938**

- 1730 *Concha longa Fossilis fasciata* Dale, p. 294, tab. XI, fig. 9.
- *1825 *Terebratula perforata* Desnoyers, p. 239.
- ?1837 *Terebratula perforata* Defr. - Dujardin, p. 272.
- ?1852 *Terebratula perforans* Dujardin, 1837 – d'Orbigny, p. 134, *nomen nudum*
- 1938 *Terebratula perforata* Desnoyers, 1825 - Muir-Wood, p. 170-175, fig. 12.

Type – Dale, 1730, tab. XI, fig. 9

According to Muir-Wood (1938) this is a species that can be discriminated from the other Red Crag species by its large apical angle (75°). It is about 55 mm long, 45 mm wide, and 28 mm thick, "subcircular to elongate-oval in outline, tapering rapidly to the umbo, biconvex, incipiently sulcinate, umbo short, erect, truncated by circular, narrowly marginate foramen, beak-ridges mesothyrid to permesothyrid. Inner hinge-plates separate or incompletely fused."

Terebratula perforata Desnoyers, 1825 gives reference to the illustration of the 'Concha longa Fossilis fasciata' by Dale (1730, Pl. XI, fig. 9) in the pre-Linnaean 'The Natural History of the Sea Coast and Country about Harwich'. Muir-Wood (1938) states that this illustrated specimen should be taken as the type-specimen. It is a fossil from the Pliocene Crag of Essex, in the neighbourhood of Harwich. The fossil 'fauna' which it is part of contained among others *Neptunea angulata* Harmer, 1914 and *Mya arenaria* Linnaeus, 1758, so this is an assemblage of definitely Late Pliocene age. The present locality of the specimen is unknown. Of note: Dale could not find "... in Lister ... any shell that resembles this ... fossil".

D'Orbigny (1852) introduced the name *perforans* Dujardin, 1837. However, in this 1837 work of Dujardin only the name *perforata* Desnoyers, 1825 is mentioned. Consequently, the name *perforans* has to be attributed to d'Orbigny (1852) and has to be regarded as a *nomen nudum*.

It is doubtful whether the *Pliothyryna* from the Miocene of NW France is conspecific with the Red Crag form (Muir-Wood, 1938).

***Pliothyryna sowerbyana* (Nyst, 1845)**

- 1827 J. de C. Sowerby, *Terebratula variabilis* non Schlotheim, 1813, p. 14, pl. 576, figs 2, 3, 5.
- *1845 Nyst, *Terebratula sowerbyana*, (*nomen novum* pro *T. variabilis* J. de C. Sowerby), p. 335, pl. XVII, fig. 3, pl. XVIII, fig. 3 (copy after J. de C. Sowerby).
- 1908 *Terebratula variabilis* Sowerby – Buckman, p. 445.
- 1938 *Terebratula variabilis* J. de C. Sowerby – Muir-Wood p. 175, figs 9, 10, 13.
- ?1980 *Pliothyryna sowerbyana* (Nyst, 1843)[sic], *partim?* – Van Roy, p. 1-52.

Lectotype – J. de C. Sowerby, 1827, pl. 576, fig. 2 (Buckman, 1908).

Adapted from Muir-Wood's (1938) description of *P. variabilis* [= *P. sowerbyana*]: A quite thick, elongate oval shell from *c.* 50 mm long and 35 mm wide. The umbo of the ventral valve is massive and has an apical angle of 60°, and the foramen is quite large. It is narrower and less biplicate than *P. orfordensis* and its umbo is more tapering. Often asymmetrical or dwarfed.

The name *Terebratula variabilis* Sowerby, 1827 is based on a specimen from the Red Crag of Suffolk. Lectotype of *variabilis* designated by Buckman (1908) is the ven-

tral valve from fig. 2 on pl. 576 in Sowerby (1827). The specimen is not preserved in the Sowerby collection (*fide* Muir-Wood, 1938).

In the opinion of Nyst (1845) the Belgian Miocene and/or Pliocene fossils are identical with Sowerby's species. He found that the name *Terebratula variabilis* was used prior to Sowerby by Von Schlotheim (1813) for another species and therefore could not be conserved: "*L'on ne peut encore conserver à cette espèce la dénomination spécifique de Variabilis déjà employée précédemment (en 1813) par MM. Schlotheim et Léonhard, par une espèce très-différente ...*"; "*... nous proposons de dédier l'espèce du crag à l'auteur anglais, qui l'a décrit le premier ...*". Consequently, Nyst proposed the name *Terebratula sowerbyana* as *nomen novum* for *Terebratula variabilis*.

Dautzenberg & Dollfuss (1896) thought that the name chosen by Nyst was unfortunate because DeFrance (1828, p. 165) would have used it before, so this name was also preoccupied. DeFrance however, used the name *Terebratula? Sowerbyi*, which is essentially different from *sowerbyana* (see Van Roy, 1980).

The reintroduction of the name *variabilis* by Buckman (1908), followed by Muir-Wood (1938) is incorrect. The motive that Von Schlotheim's species in fact belongs to a totally different genus (*Rhynchonella*) as stated by Davidson (1852) is not valid (see Dautzenberg & Dollfuss, 1896). Nevertheless Glibert & Vandercammen (1957) use the name *variabilis* for specimens from the Belgian Kattendijk Sands.

Van Roy (1980) apparently missed that *sowerbyana* is a *nomen novum* and considers *sowerbyana* a new species described by Nyst. Van Roy thereafter selects a lectotype for *sowerbyana* from the Nyst collection. This specimen is not part of the type-series of Sowerby. Buckman already designated the specimen illustrated in Sowerby (1827) on pl. 576, fig. 2 as the type-specimen for *variabilis*, which is thus the lectotype of *sowerbyana*.

Pliothyryna harmeri (Bell, 1921)

- 1874 *Terebratula grandis* Blumenbach – S.V. Wood, p. 108, Pl. VII, fig. 11 c.
 *1921 *Terebratula harmeri* Bell, p. 2.
 1938 *Terebratula harmeri* A. Bell, emend. Muir-Wood – Muir-Wood, p. 169-170, figs 6, 8.
 1983 *Pliothyryna harmeri* (Bell) – Cooper, pl. 5, figs 7, 8.

Lectotype – S.V. Wood (1874), pl. VII, fig. 11 c (Muir-Wood, 1938).

Terebratula harmeri Bell, 1921 is based on three specimens from the Red Crag of Waldringfield, illustrated in Wood (1874). Muir-Wood designated one of the specimens as the lectotype of the species. She regards the other two specimens as belonging to *T. variabilis*.

In the sense of Muir-Wood (1938) only elongate-elliptical specimens with a narrow ventral valve with a tubular posterior belong to this species. The species is quite small, to about 30 mm long and 19 mm wide.

Pliothyryna quadratomuscularis (Lacourt, 1983) – *nomen dubium*

Plate 4, figs 1 a-d

- *1983 *Terebratula quadratomuscularis* Lacourt, p. 17, 18, figs 6, 7.

Holotype – Lacourt, 1983, fig. 6, ventral valve, Westerschelde near Ellewoutsdijk (Zeeland, The Netherlands), leg. H. Smits 1950-1954, RGM.1383642 (ex RGM.142575).

Paratypes – 2 paratypes (paratype status indicated on original label, not in publication): ventral valves, Westerschelde near Ellewoutsdijk (Zeeland, The Netherlands), leg. unknown, RGM.1383644 (ex RMNH.BRA.592); all material stored in Naturalis Biodiversity Center, Leiden, The Netherlands; one paratype (ventral valve): Westerschelde, sucker dredged by the vessel "Marie", Oct. 1935, leg. A. Slabber, present in the KZGW collection (paratype status indicated on original label, not in publication).

Description (translated from Dutch) – "The ventral valve is large, quite broadly oval, convex, thick; the umbo is low, broad, truncated: the foramen is wide; the teeth are thick; the muscle impression is exceptionally large, quadrate, truncated at the dorsal side, broad at the ventral side, rounded; the growth line is broadly oval trapezoid, slightly rounded. Length 85 mm, width 60 mm.

Pliothyryna quadratomuscularis can be differentiated by the large muscle impressions from *P. maxima*, which has a pear-shaped muscle impression. Above that the shell of that species is slender, thin (sometimes translucent) and has a long umbo. It can be differentiated from *P. zelandica* by its squarish though smaller muscle impressions. The shell of *P. quadratomuscularis* is narrower and very convex, whereas the one of *P. zelandica* is flat and wide."

Pliothyryna quadratomuscularis is based on incomplete, reworked and poorly preserved Tertiary (probably Pliocene and/or Miocene) ventral valves. Lacourt did not illustrate nor describe any dorsal valve. The valves treated by Lacourt probably belong to one or more of the species that have been described from the Pliocene or have a Miocene origin. Due to their poor state of preservation and the absence of the dorsal valves *P. quadratomuscularis* must be considered *nomen dubium*.

Pliothyryna zelandica (Lacourt, 1983) – *nomen dubium*

Plate 4, figs 2 a- d

- *1983 *Terebratula zelandica* Lacourt, p. 18-20, figs 8, 9, 10.

Holotype – Lacourt, 1983, fig. 8, ventral valve, Westerschelde near Ellewoutsdijk (Zeeland, The Netherlands), leg. L.A.W. Lucas, ex Filiaal-collection, RGM.1383645 (ex. RMNH.BRA.292).

Paratypes – 2 paratypes (paratype status indicated on

original label, not in publication): ventral valves, Westerschelde near Ellewoutsdijk (Zeeland, The Netherlands), leg. L.A.W. Lucas, ex Filiaal-collectie, RGM.1383646 (ex. RMNH.BRA.292); 7 paratypes (mentioned in publication): ventral valves, Westerschelde near Ellewoutsdijk (Zeeland, The Netherlands), leg. H. Smits 1950-1954, RGM.142575); 2 paratypes (ventral valves): Domburg, 29 Dec. 1930, leg. C. Brakman, KZGW collection (paratype status indicated on original label, not in publication).

Description (translated from Dutch) – “Shell broad and flat, the ventral valve is strong and thick, convex, with a round outline; the umbo is low and broad, truncated; the foramen is wide: the teeth are thick, hook shaped, bended upwards; the muscle scars are relatively short and broad; the growth lines are round, in larger shells broad-trapezoid. The shell is thicker and as large as *P. maxima*, which is narrower, thinner and more arched and in with the muscle scars are longer, narrower and pear shaped. Can be differentiated from *P. quadratomuscularis* by its larger muscle impression and a more convex shell.”

Also *P. zelandica* is based entirely on incomplete, re-worked and poorly preserved Tertiary (probably Pliocene and/or Miocene) pedicle valves and belongs to one or more of the species that have been described from the Red Crag or have a Miocene origin. As for *P. quadratomuscularis* also *P. zelandica* must be considered a *nomen dubium*.

Valid names

From the above discussion of the different *Pliothyryna* taxa it can be concluded that the names used for NW European *Pliothyryna* species from Oligocene to Pliocene age, *Pliothyryna grandis* (Blumenbach, 1803), *P. perforata* (Desnoyers, 1825), *P. sowerbyana* (Nyst, 1845), *P. harmeri* (Bell, 1921) and *P. orfordensis* Muir-Wood, 1938, seem to be available, and the name *Terebratula maxima* is available from Davidson (1852).

The species *Pliothyryna grandis* was described from the late Oligocene (Chattian) of Germany and is also reported from the early Oligocene of Germany (Bitner & Müller, 2022). Muir-Wood (1938) treated five different Pliocene species, currently placed within *Pliothyryna*. Two of these originated from the Zanclean Coralline Crag, viz. *P. maxima* and *P. orfordensis*, the other three (*sowerbyana*, *perforata* and *harmeri*) are Red Crag (Piacenzian) taxa. No specific names are attached to specimens from the Belgian Pliocene or Miocene.

Discussion

The Miocene Westerschelde *Pliothyryna* specimens show a high degree of variation. Outstanding is the extreme variability with respect to the diameter of the foramen and the development of the inner hinge plates, although no specimen shows fused inner hinge plates. Above that

there appears to be a considerable variability of the outline of the shells, probably caused by several factors like availability of food sources, water dynamics and predation.

This high degree of variation is comparable to that found by García Ramos (2006) within *Pliothyryna* from the Kattendijk Formation (Pliocene, Zanclean). He assessed a high variability with respect to the relative diameter of the foramen, degree of exposure and shape of the symphytium, the degree of labiation of the foramen, the outline and the ontogenetic development of the outline, the anterior commissure that can be rectimarginate, uniplicate or sulcinate, the degree of development of the inner cardinal plates (joint or disjunct). These observations can be acknowledged by my own observations on some specimens and valves from the Kattendijk Formation.

Muir-Wood (1938) states that *P. sowerbyana* (as *variabilis*), *P. perforata* and *P. harmeri* have very similar internal characteristics and belong to the same genus. All three have been found in the Red Crag of Waldringfield, of which at least *sowerbyana* and *harmeri* with articulated valves. Given the variability within the Westerschelde and Kattendijk Member *Pliothyryna* populations, it could be deduced that these three Late Pliocene forms in fact represent not more than one, variable species. It is of note that from the available names for these Late Pliocene species *P. perforata* (Desnoyers, 1825) is the oldest.

The discussed Miocene Westerschelde specimens do not reach dimensions like that of *P. maxima* and have a less slender brachidium. The folding of the shell is less developed in the Miocene specimens than in *Pliothyryna grandis*. They are larger than the Late Pliocene shells, having dimensions comparable to those of *P. grandis* and *P. orfordensis* and in contrast to *P. orfordensis* the Westerschelde specimens have separated inner hinge plates. Whereas within *Pliothyryna* populations the variability is high, a phylogenetical development can be observed from the early to late Oligocene *P. grandis*, leading to its optimal development during the Pliocene Zanclean with the large *P. maxima* and the somewhat smaller *P. orfordensis* with its fused inner hinge plates, further to the even smaller and often irregular *P. sowerbyana* and *P. harmeri* during the Late Pliocene (Piacenzian), and eventually to its extinction around the advance of the Pleistocene.

Conclusions

Differences among *Pliothyryna* shells can be observed at population level, but the main question is whether there are constant characteristics that distinguish species and, consequently, whether all introduced and available names refer to a single, or to two or more different species.

In the opinion of Davidson (1852) all NW European Tertiary large *Terebratula*-species should be considered conspecific with *T. grandis*. Further research on the different populations is needed to elucidate the taxonomic status of these NW European forms. The opinion of Davidson seems to be the best starting point for a thorough evaluation of the NW European representatives of *Pliothyryna*.

The discussed *Pliothyryna* population from the Westerschelde is of Late Miocene (Tortonian) age, at least in part contemporaneous with the Deurne Member in Belgium. The Miocene Westerschelde *Pliothyryna*'s seem closer to the Oligocene *P. grandis* rather than to the Pliocene forms. Although there are no species names available for specifically Miocene *Pliothyryna*'s, it does not seem in the interest of stability of nomenclature to introduce yet another formal name, so it seems best to refer provisionally to these Late Miocene *Pliothyryna* as *P. aff. grandis* (Blumenbach, 1803).

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Plate 1. *Pliothyryna* aff. *grandis* (Blumenbach, 1803) – dredged from the Westerschelde offshore between Ellewoutsdijk and Borssele, 2006. 1, 2, 5: articulated specimens; 1a, 2a, 5: dorsal view; 1b, 2b: lateral view; 2c: anterior view; 3, 4: ventral valves interior; 6: posterior fragment with hinge in connection; 7, 8, 9, 10: foramen of some ventral valves, 7 and 10 being the extremes. 1. RGM.1383682; 2. RGM.1383683; 3. RGM.1383684; 4. RGM.1383685; 5. RGM.1383686; 6. RGM.1383687; 7. RGM.1383688; 8. RGM.1383689; 9. RGM.1383690; 10 RGM.1383691. Photographs by the author.



Plate 2. *Pliothyryna* aff. *grandis* (Blumenbach, 1803) – dredged from the Westerschelde offshore between Ellewoutsdijk and Borssele, 2006. 1-5: ventral valves; 1b, 2, 3, 4b, 5: interior; 1a, 4a: lateral view; 4c: anterior view. 1. RGM.1383692; 2. RGM.1383693; 3. RGM.1383690 (same specimen as Pl. 1, fig. 9); 4. RGM.1383694; 5. RGM.1383695. Photographs by the author.

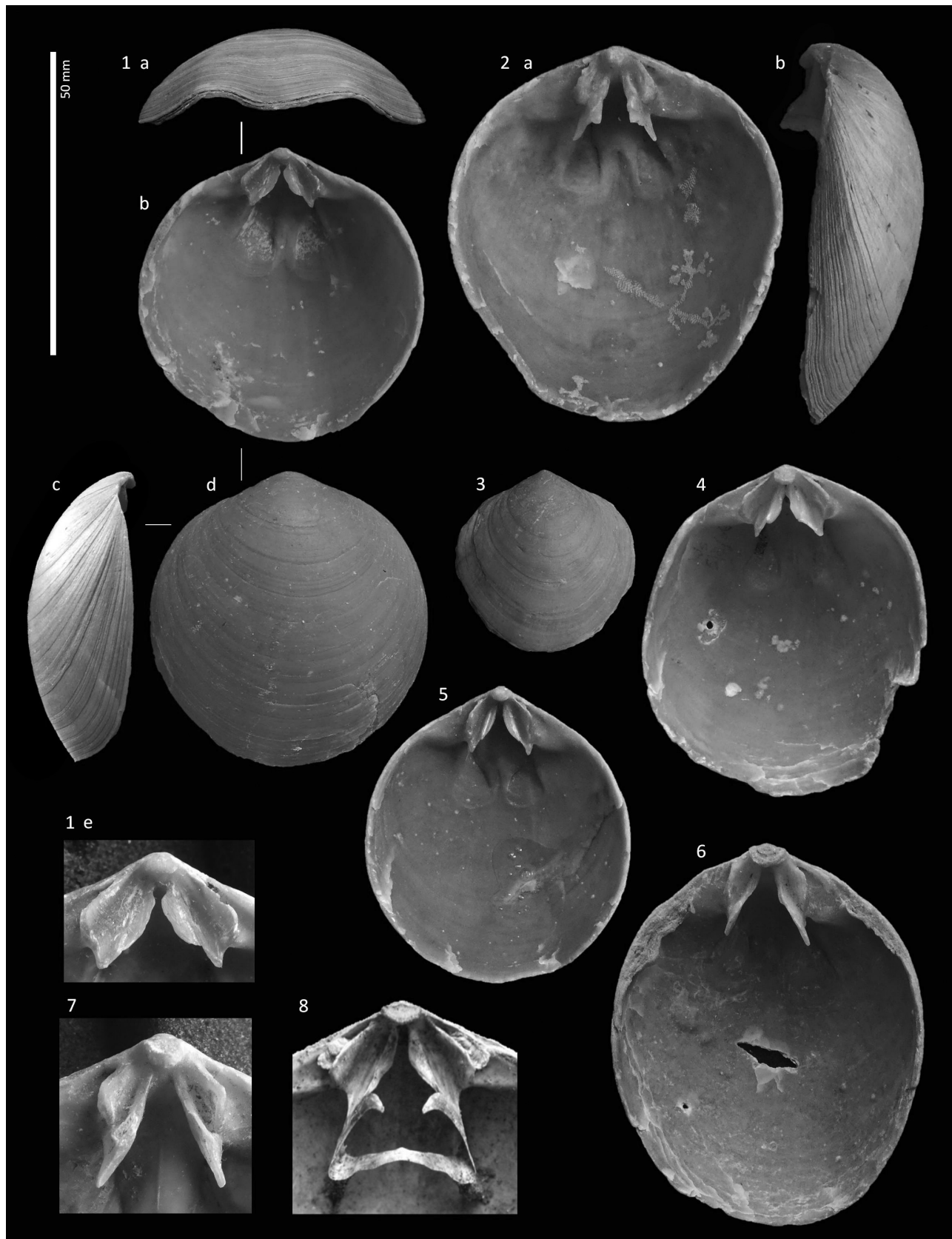


Plate 3. *Pliothyryna* aff. *grandis* (Blumenbach, 1803) – dredged from the Westerschelde offshore between Ellewoutsdijk and Borssele, 2006. 1-6: dorsal valves; 1b, 2a, 4, 5, 6: interior; 1c, 2b: lateral view; 1d, 3: dorsal view; 1a: frontal view; 1e: hinge with developed inner hinge plates; 7: hinge with absorbed (?) hinge plates; 8: hinge with brachidium. 1. RGM.1383696; 2. RGM.1383697; 3. RGM.1383698; 4. RGM.1383699; 5. RGM.1383700; 6. RGM.1383701; 7. RGM.1383702; 8. Bram Goetheer collection. Photograph fig. 8 by F.A.D. van Nieulande, other photographs by the author.

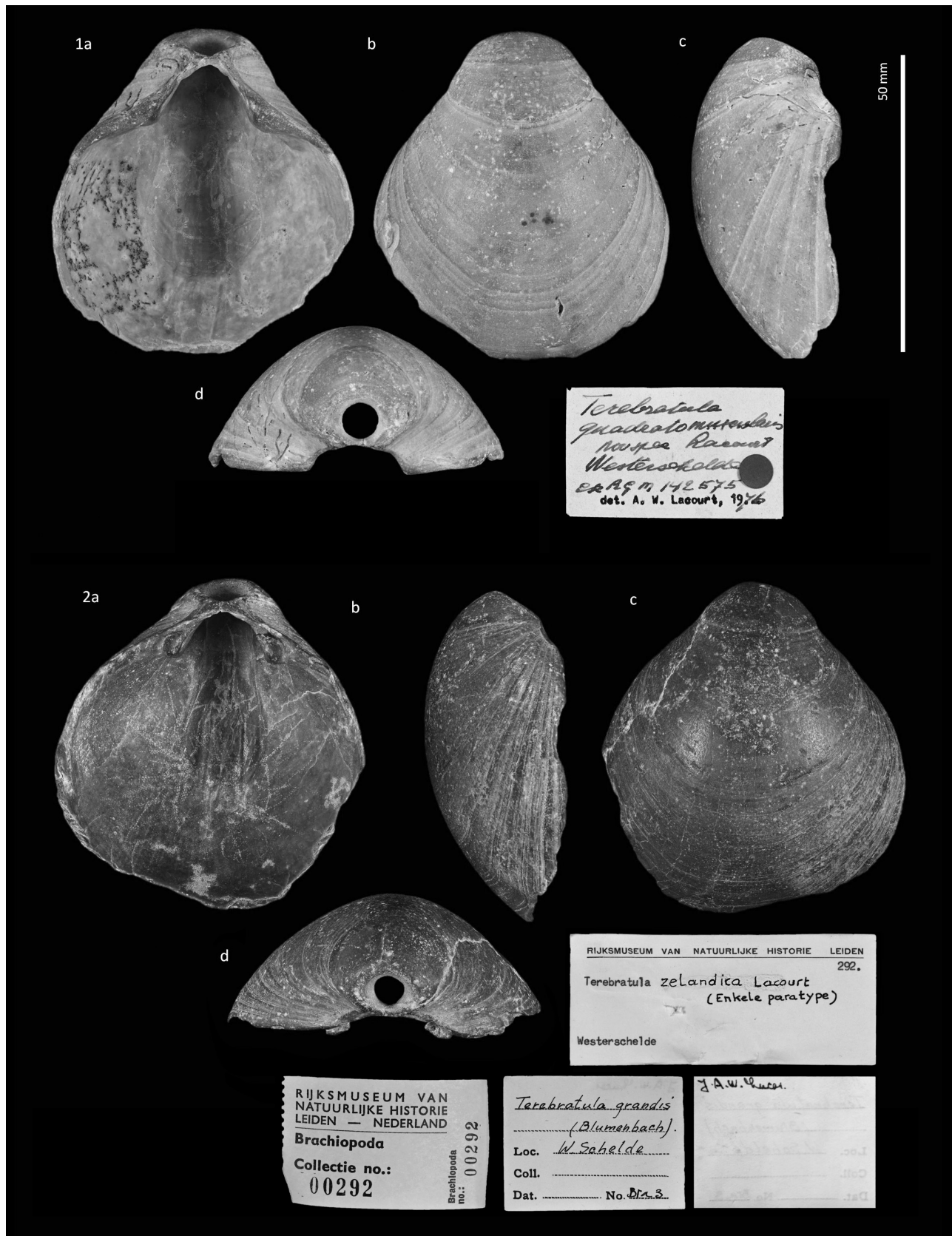


Plate 4. 1. *Pliothyryna quadratomuscularis* (Lacourt, 1983). Holotype, ventral valve, Westerschelde near Ellewoutsdijk (Zeeland, The Netherlands), leg. H. Smits 1950-1954, RGM.1383642 (ex RGM.142575); a. interior; b. lateral view; c. exterior; d. posterior view. 2. *Pliothyryna zelandica* (Lacourt, 1983). Holotype: ventral valve, Westerschelde near Ellewoutsdijk (Zeeland, The Netherlands), leg. L.A.W. Lucas, ex Filiaal-collection, RGM.1383645 (ex. RMNH.BRA.292); a. interior; b. lateral view; c. exterior; d. posterior view. Photographs by R. Pouwer.