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Revision of Pliocene representatives of *Cyclocardia* (Bivalvia, Carditidae) from the North Sea Basin

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Pliocene representatives of the genus *Cyclocardia* from the North Sea Basin are revised, two species being recognised, namely *C. chamaeformis* (J. de C. Sowerby, 1825) and *C. scalaris* (J. de C. Sowerby, 1825). *Cyclocardia orbicularis* (J. de C. Sowerby, 1825) is considered synonymous with *C. chamaeformis*. Lectotypes of all three are designated and illustrated.

Key words: Bivalvia, Carditidae, *Cyclocardia*, systematics, lectotype designation, Pliocene, North Sea Basin.

INTRODUCTION

In 1825, James de Carle Sowerby erected three species of *Venericardia* from the Pliocene 'Suffolk and Norfolk Crag', viz. *Venericardia chamaeformis, V. orbicularis* and *V. scalaris*. At present, these taxa are attributed to the genus *Cyclocardia* Conrad, 1867. Shells belonging to this genus are fairly common in the fossil (predominantly Pliocene) shell material washed ashore on beaches or dredged from estuaries in the province of Zeeland, the Netherlands. Such specimens show a wide range of shell shape and other characteristics, which makes identification hazardous; differing interpretations of Pliocene *Cyclocardia* material by subsequent authors add to the confusion.

In order to elucidate the classificatory status of these fossil representatives of *Cyclocardia,* one of us (AWJ) studied in 1970-71 a considerable number of specimens of Pliocene *Cyclocardia* from the North Sea Basin (Coralline and Red Crag formations, as well as various Pliocene strata in the Netherlands and Belgium). Amongst these were also the type series of the three taxa described by J. de C. Sowerby. It was then concluded (Janssen & van der Slik, 1972: 172) that only two species could be recognised in Pliocene material from the North Sea Basin. However, lectotypes have not yet been designated and in order to stabilise the nomenclature we wish to do so here. In addition, the most important distinguishing features are listed and discussed.

METHODS

In the 1970-71 study, the following parameters were used (see fig. 1): shell length, shell height, parameter X, parameter Y, semidiameter (= convexity), the number of ribs.

Parameters X and Y were additionally defined, as positioning of *Cyclocardia* valves to measure height and length sometimes is questionable. Because of the umbonal curvature of the shells it is possible to position all specimens in a similar way on a rule by two points: the umbo and the upper anterior margin. Parameters X and Y were thus measured perpendicular to each other (see fig. 1).

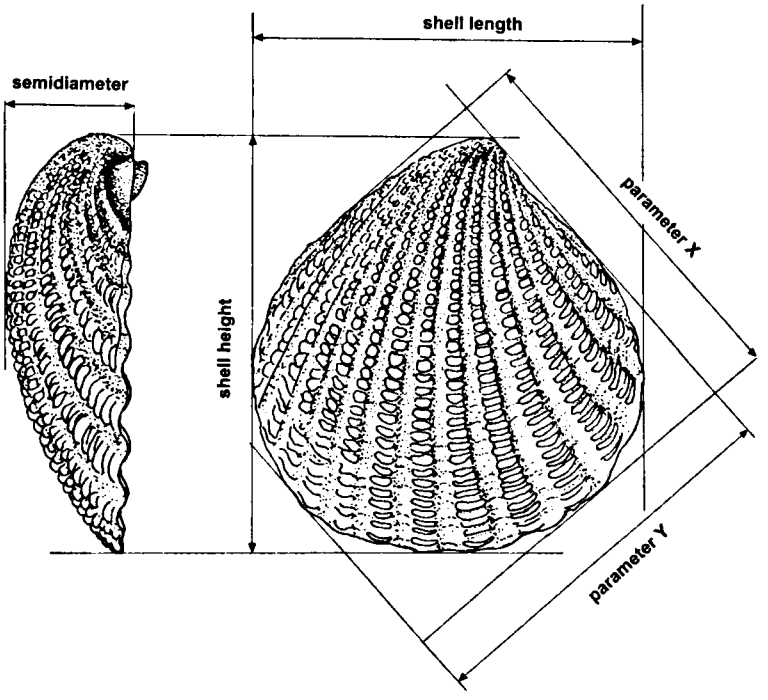


Fig. 1. Quantitative parameters measured in *Cyclocardia*.

In addition to Pliocene material, numerous other populations of *Cyclocardia*, varying in age from Eocene to Recent, and from all over Europe and North America, were measured. In search of discriminating characters, Drs B. Kuhry (then Centraal Rekeninstituut, Rijksuniversiteit Leiden, the Netherlands) and M. Freudenthal (then Rijksmuseum van Geologie en Mineralogie, Leiden, the Netherlands) were kind enough to interpret the measurement matrix by means of a multivariate analysis, for which purpose all measurements were transferred to punch cards.

Unfortunately, however, it turned out that multivariate analyses of the quantitative characters did not provide any significant result, which was the main reason why that study was never published.

Therefore, in their interpretation of Pliocene *Cyclocardia*, Janssen & van der Slik (1972) needed to rely on qualitative characteristics only. They concluded that only a two-fold subdivision of the material was possible using features of lunula and ornament.

RESULTS

New well-preserved material from known stratigraphical levels has confirmed earlier findings and yields additional insight into the discrimination of Pliocene North Sea Basin *Cyclocardia* species. Specimens from Pliocene strata in Belgium (c. 100 valves from the Kattendijk Formation, and from the Luchtbal and Oorderen members of the Lillo Formation in the P.W. Moerdijk collection) have demonstrated the development of ornament in particular during early ontogenetic stages to be a consistent and reliable character. Ornament details and lunula development invariably are combined in the same way and thus allow to subdivide specimens into two groups. If the lunula is lanceolate and not impressed, the ornament always shows commarginal grooves developing first during ontogeny. Radial and commarginal rib intervals in young shells are equally strong and give the shell surface a reticulated aspect ('to resemble a ropeladder', J. de C. Sowerby, 1825: 146; see also Janssen & van der Slik, 1972: fig. 79d). This combination of characters is seen in *Cyclocardia scalaris*.

Shells with a cordiform, impressed lunula invariably show ornament starting to develop with radial ribs. Furthermore, the radial rib intervals are always more deeply incised than the intervals between the knobs on the ribs. Such features are found in both *Cyclocardia chamaeformis* and *C. orbicularis*.

Other aspects studied, such as dimensions, height/length-ratio, thickness of the shell, dimensions of the hinge, convexity of the shell, number of ribs etc., have now been shown to be unreliable for subdividing our rich material. Admittedly, some characters may lead to the recognition of forms typical of different populations, but intermediates always occur.

From this it was concluded that *Cyclocardia chamaeformis* and *C. orbicularis* obviously constitute just a single, variable taxon. Janssen & van der Slik (1972) used the name *C. orbicularis* and considered *C. chamaeformis* to be synonymous. However, in view of the fact that J. de C. Sowerby described his '*Venericardia chamaeformis*' first (albeit on the same page), *Cyclocardia chamaeformis* is given priority here. The epithet *orbicularis* could be retained for a forma to refer to comparatively small and convex *C. chamaeformis* which are known from Early and Middle Pliocene assemblages.

Well-preserved specimens of *Cyclocardia chamaeformis* and *C. scalaris* are easily identified and cannot be confused. In heavily abraded specimens the most important feature is the form of the lunula, but a few additional characters are also of importance:

- dimensions: maximum shell length in *C. chamaeformis* is c. 20 mm, in *C. scalaris* c. 16 mm.
- the curvature of the umbo towards the anterior side of the shell: always less pronounced in *C. scalaris*, but this may be difficult to determine.
- the shape, distance and ornament of the ribs in fully-grown specimens: shells with distant, elevated ribs always belong to *C. chamaeformis*. In some forms of this species, however, ribs become close-set and flattened during ontogeny, thus closely resembling those in *C. scalaris*.
- number of ribs: shells with more than 23 ribs always belong to *C. scalaris*. The number of ribs in *C. scalaris*, however, may occasionally be much fewer. With respect to this character there is also overlap.
- convexity: as a rule, specimens of *C. scalaris* are relatively flat.

	Cyclocardia chamaeformis	*Cyclocardia scalaris*
shell width	up to 20.4 mm	up to 16.0 mm
shape of lunula	impressed, heart-shaped	not impressed, lanceolate
development of ornament	distant radial ribs develop first, commarginal ornament is added	commarginal grooves developing first (lower along the anterior margin); radial ribs close-set
umbo	clearly prosogyrate	slightly prosogyrate
radial ribs	16-23, distant to close-set, prominent to flattened	17-27, close-set, flattened (but in some forms the knobs are rather convex)

Table 1. Discriminating features of Pliocene *Cyclocardia chamaeformis* and *C. scalaris*.

Lectotype designations (see below) were accepted by the former curator, Mr C.P. Nuttall, at the British Museum (Natural History), Department of Palaeontology, London (in litt., 10 June 1971).

SYSTEMATIC PALAEONTOLOGY

Cyclocardia chamaeformis (J. de C. Sowerby, 1825) (figs 2a-b, 3a-b)

Venericardia chamaeformis Sowerby, 1825: 145, pl. 490 fig. 1.
Cardita chamaeformis. Sow.; Nyst, 1845: 211, pl. 16 fig. 7 a, b, d.
Cardita chamaeformis, Leathes' MS; Wood, 1853: 167, pl. 15 fig. 3 a, b.
Cardita chamaeformis; Nyst, 1878: pl. 22 fig. 7 a, b.
Cardita chamaeformis, Leathes' MSS; Nyst, 1881: 205.
Cardita chamaeformis (Leathes M.S., J. Sowerby, 1825); van Regteren Altena, 1937: 69, pl. 9 figs 139-143. Heering, 1950a: 83, pl. 13 figs 7-8, 12-13, 14, 17-18.
? *Cardita chamaeformis* (Leathes M.S., J. Sowerby 1825); Heering, 1950a: pl. 13 figs 19-20.
Cardita (Cyclocardia) chamaeformis Sowerby, sp. 1825 - Glibert, 1957b: 16, pl. 2 fig. 11.
Cyclocardia chamaeformis (Sowerby, 1825) – Geys & Marquet, 1979: pl. 18 fig. 4.

Venericardia orbicularis, Sowerby, 1825: 145, pl. 490 fig. 2.
Cardita orbicularis. Leathes' MS - Wood, 1853: 167, pl. 15 fig. 4.
Cardita orbicularis (Leathes M.S., J. Sowerby, 1825); van Regteren Altena, 1937: 70. Heering, 1950a: 85, pl. 13, figs 9, 29, 30, 31.
Cardita (Cyclocardia) orbicularis orbicularis Sowerby, sp. 1825; Glibert, 1957b: 15 (pars).
Cyclocardia (Cyclocardia) orbicularis (Sowerby, 1825); Janssen & van der Slik, 1972: 173, pl. 27 fig. 78a-b; pl. 28 fig. 78c-d.

Material studied. – Red Crag Formation (various locations): 113/2 specimens. Coralline Crag Formation (various locations): 58/2 specimens. Dredged from the Westerschelde off Ellewoutsdijk: 253/2 specimens.

Lectotype designation for *Venericardia chamaeformis*. – We here select the specimen illustrated by J. de C. Sowerby (pl. 490 fig. 1, right), a left valve housed at The Natural

History Museum, Department of Palaeontology, London, registration number LL 18597/2. This specimen is here illustrated in fig. 2a-b. Dimensions: shell height 14.4 mm, length 13.6 mm, semidiameter 4.3 mm, 19 radial ribs.

Original diagnosis: "Convex, orbicular, with rather produced beaks; ribs rugged, distant, about 14; hinge large."

Locus typicus: "Suffolk".

Stratum typicum: "Crag", undoubtedly Red Crag Formation, judging from the dark, rusty colour.

Paralectotypes: 2/2 specimens from the Red Crag Formation of Suffolk in the same collections, registered LL 18597/1 (left valve, possibly the specimen illustrated by J. de C. Sowerby in pl. 490 fig. 1 (specimen in centre), and LL 18597/4, right valve, possibly the original of J. de C. Sowerby, pl. 490 fig. 1 (left specimen).

Lectotype designation for *Venericardia orbicularis*. – We select a specimen from the syntype series in the same collection, registered LL 18598/3, and here illustrated in fig. 3a-b. Right valve, shell height 7.9 mm, length 7.9 mm, semidiameter 2.5 mm, 20 (19) radial ribs (this specimen was not illustrated by J. de C. Sowerby).

Original diagnosis: "Orbicular, rather convex, concentrically striated; ribs about 16, not close, crenated; hinge small."

Locus typicus: Suffolk.

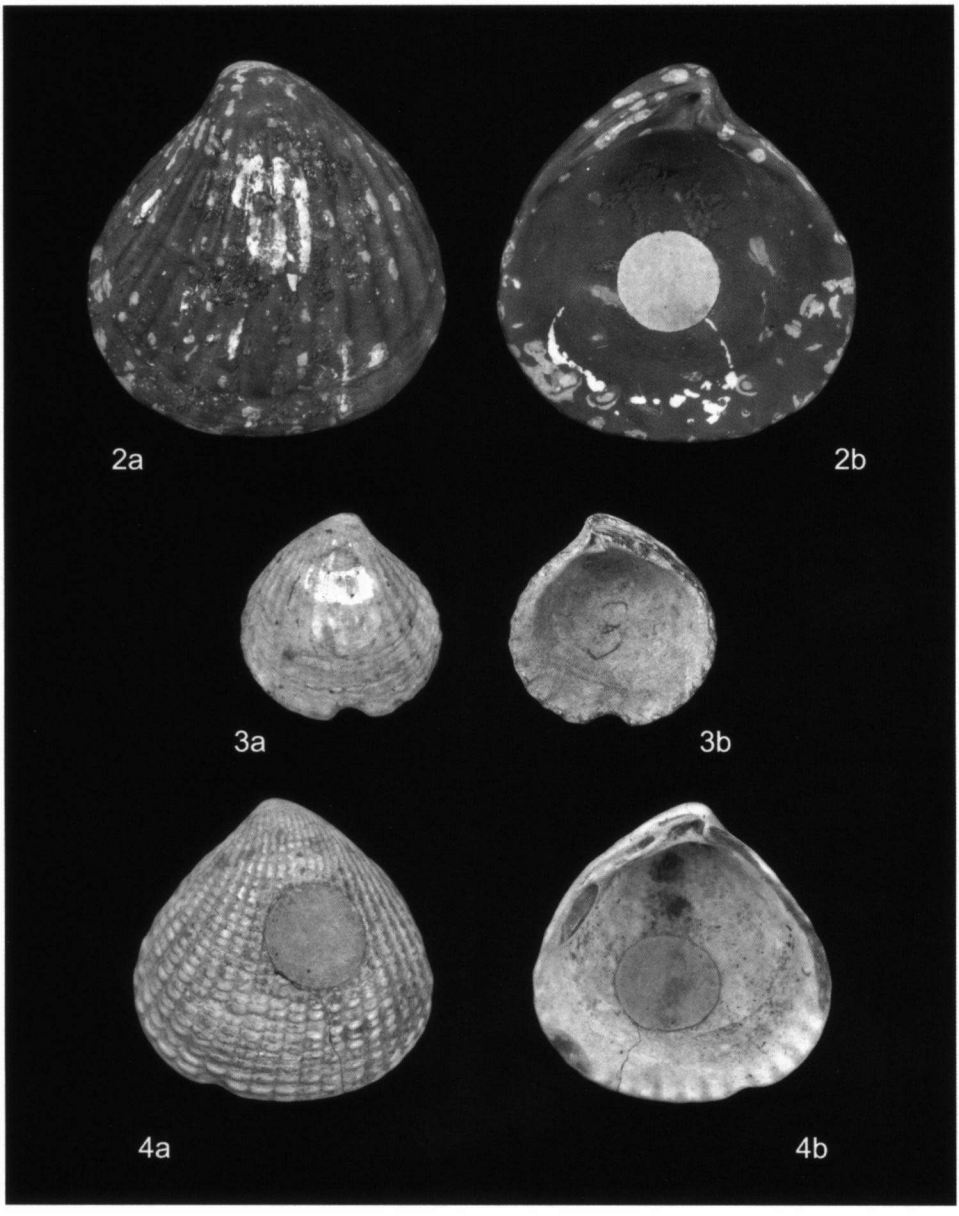
Stratum typicum: "Coralline Crag".

Paralectotypes. – Coralline Crag Formation of Suffolk: registration number LL 18598/1 (left valve, illustrated by J. de C. Sowerby, pl. 490 fig. 2, top); registration number LL18598/2 (right valve, illustrated by Sowerby, pl. 490 fig. 2, bottom), Coralline Crag Formation (?): registration number LL 18598/4 (left valve).

Revised diagnosis of *C. chamaeformis*. – Rounded-triangular to orbicular shell with prosogyrate umbo. Width of radial ribs variable, but as a rule the rib intervals are about as wide as the ribs themselves. Number of radial ribs ranging between 16 and 23. Lunula clearly impressed. Development of ornament during ontogeny starting with distant radial ribs.

Variation. – As stated above, the multivariate analysis of quantitative data did not yield any significant result, nor could the observed differences be correlated with the stratigraphical age of the populations. In the measured Pliocene material, shell height may exceed width, height and width may be equal, or width may exceed height. Radial ribs strongly vary in number and may be either narrower or wider than their interspaces. When the ribs are relatively wide they tend to be rather flat. The rib ornament consists principally of rounded knobs, but when the ribs are flatter and wider the knobs will be elongated longitudinally. Occasionally knobs are evident, in other cases they are less clearly separated. According to the original description, the relative height of the hinge could be of importance in separating *C. chamaeformis* and *C. orbicularis*. This character, however, is very variable even within a single population and could thus not be applied.

Discussion. – Specimens from the Early Pliocene Kattendijk Formation in Belgium are smaller and the ribs tend to flatten out, becoming also wider compared to the rib intervals. In addition, the knob ornament of the ribs becomes more longitudinal. In early growth stages, however, there are no differences between these and Middle-Late Pliocene specimens. All kinds of intermediate forms occur among the material washed ashore and dredged in the province of Zeeland and it seems best, for the time being, to consider material from the Kattendijk Formation to represent a stratigraphical forma. This can only be decided after having gained a better knowledge of the phylogeny of *Cyclocardia*, especially during the Oligocene and Miocene. A first attempt at this was made by Glibert (1957b: 15), who considered the Early Oligocene *C. tuberculata* (Goldfuss, 1837) to be the ancestral



Figs **2-4** [a, exterior; b, interior]. Lectotypes for species of *Cyclocardia*, erected by J. de C. Sowerby (1825), × 3.5. **2a-b**, Lectotype of *Venericardia chamaeformis* (= *Cyclocardia chamaeformis*) (BMNH LL 18597/2), illustrated by J. de C. Sowerby (1825: pl. 490 fig. 1, right), left valve, shell height 14.4 mm; 'Crag of Suffolk'. **3a-b**, Lectotype of *Venericardia orbicularis* (= *Cyclocardia chamaeformis*) (BMNH LL 18598/3), not illustrated in J. de C. Sowerby (1825), right valve, shell height 7.9 mm; 'Coralline Crag'. **4a-b**, Lectotype of *Venericardia scalaris* (= *Cyclocardia scalaris*) (BMNH LL 18599/1), illustrated by J. de C. Sowerby (1825: pl.490 fig. 3, top), left valve, shell height 11.4 mm; 'Coralline Crag', Suffolk.

form.

Both names, *Cyclocardia chamaeformis* and *C. orbicularis*, are frequently used (e.g.: Heering, 1944, 1950b; Glibert, 1945, 1957a, b; Anderson, 1964; Nordsieck, 1972; Neuffer, 1973) in reference to Oligocene and Miocene populations of *Cyclocardia*. Doubts over such identifications was expressed by Janssen (1972), and both Janssen (1984) and Wienrich (1999) listed populations of Miocene *Cyclocardia* in open nomenclature. Here we recommend that J. de C. Sowerby's names be restricted to Pliocene material.

Cyclocardia scalaris (J. de C. Sowerby, 1825) (fig. 4a-b)

**Venericardia scalaris* Sowerby, 1825: 146, pl. 490 fig. 3.
Cardita scalaris. Sow.; Nyst, 1845: 213, pl. 16 fig. 9a, b, d.
Cardita scalaris Leathes' MSS; Wood, 1853: 166, pl. 15 fig. 5.
Cardita scalaris Leathes; Wood, 1874: 131.
Cardita scalaris; Nyst, 1878: pl. 22, fig. 8 a, b.
Cardita scalaris Leathes' MSS; Nyst, 1881: 204.
Cardita scalaris (Leathes M.S., J. Sowerby, 1825); van Regteren Altena, 1937: 70.
Cardita (Cyclocardia) scalaris Sowerby, 1825; Glibert, 1945: 130, pl. 8 fig. 9.
Cardita scalaris (Leathes M.S., J. Sowerby 1825); Heering, 1950a: 86, pl. 13 figs 5-6, 10-11, 15-16.
Cardita (Cyclocardia) scalaris Sowerby, sp. 1825; Glibert, 1957b: 16.
Cyclocardia (Cyclocardia) scalaris (Sowerby, 1825); Janssen & van der Slik, 1972: 174, pl. 27 fig. 79a-b, pl. 28 fig. 79c-d.
Cyclocardia (Cyclocardia) scalaris (Sowerby, 1825) subspec.; Janssen & van der Slik, 1972: 174, pl. 27 fig. 80a-b, pl. 28 fig. 80c.
Cyclocardia scalaris (Sowerby, 1825); Geys & Marquet, 1979: pl. 18 fig. 6.

? *Cardita orbicularis*. Sow.; Nyst, 1845: 214, pl. 16 fig. 10a, b, d (non Sowerby ?).
Cardita orbicularis; Nyst, 1878: pl. 22 fig. 9 a-c (non Sowerby).
Cardita orbicularis Leath.; Nyst, 1881: 206 (non Sowerby).
Cardita (Cyclocardia) orbicularis Sowerby, sp. 1825; Glibert, 1945: 123, pl. 6 fig. 14 b–d (non Sowerby).
Cardita (Cyclocardia) orbicularis orbicularis Sowerby, sp. 1825; Glibert, 1957b : 15 (pars, non Sowerby).
Cyclocardia orbicularis orbicularis (Sowerby, 1825); Geys & Marquet, 1979: pl. 18 fig. 5 (non Sowerby).

Material studied. – Red Crag Formation (various localities): 91/2 specimens. Coralline Crag Formation (various localities): 287/2 specimens. Dredged from Westerschelde off Ellewoutsdijk: 21/2 specimens.

Original diagnosis: "Orbicular, subtriangular, depressed; longitudinal sulci about 20, linear; concentrically striated, hinge teeth long and thin".

Revised diagnosis. – Subtriangular, umbo slightly prosogyrate. About 20 radial ribs, almost touching each other. Lunula not impressed and convex. During ontogeny, commarginal ornament develops first, and is anteriorly lower in relation to margin and growth lines, radial ornament develops later.

Lectotype designation. – The left valve illustrated by J. de C. Sowerby [1825, pl. 490 fig. 3 (top)] is here designated lectotype (see fig. 4a-b), contained in The Natural History Museum (Department of Palaeontology), London, registration number LL 18599/1. Shell height 11.7 mm, shell length 11.4 mm, semidiameter 3.5 mm, 24 radial ribs.

Locus typicus: Suffolk

Stratum typicum: Coralline Crag Formation.

Paralectotypes: 4 left valves, registration numbers LL 18599/2-3, 6-7; one right valve,

registration number LL 18599/8, all from the Coralline Crag Formation, Suffolk.

Variation. – Dimensions, height/length ratio, length/semidiameter ratio, number of ribs, width of ribs, amplitude of ribs, and rib ornament are all subject to considerable variation. Most remarks as given above for *Cyclocardia chaemaeformis* also apply to the present species, albeit that the ribs are always wider than their interspaces.

Discussion. – Nyst (1845, 1878, 1881) considered the inflated form of *C. scalaris* to be J. de C. Sowerby's *C. orbicularis*. This can be concluded from the remarks "lunule ... peu enfoncé" (= lunula hardly impressed) (1845: 215) and "côtes ... séparées par un sillon etroit" (= ribs divided by a narrow groove) (1881: 206) and from the illustration (1878: pl. 22 fig. 9a-c), clearly showing a lanceolate lunule instead of a cordiform one and the umbones being just slightly prosogyrate. This confusion of the inflated form of *C. scalaris* with *C. orbicularis* was continued by Glibert (1945, 1957 a, b) and Geys & Marquet (1979).

Specimens of '*C. orbicularis*' illustrated by Glibert (1945: pl. 6 fig. 14b-d) clearly represent the inflated form of *C. scalaris*. It is very improbable that these specimens originate from the Miocene of Edegem and Antwerp, respectively, as Glibert stated, but this is also the case for various other Pliocene species dealt with in his 1945 work (see Janssen & van der Mark, 1969).

Specimens undoubtedly related to *C. scalaris* do occur in Miocene deposits of the North Sea Basin, e.g. material from Houthaelen, illustrated by Glibert (1945: pl. 6 fig. 14a) sub nomen *Cardita (Cyclocardia) orbicularis* (Sowerby) f. *tuberculata*. Very similar forms are also known from Miocene deposits in the Netherlands and northern Germany. Whether or not such material is really assignable to *C. scalaris* needs to be determined.

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