

Upper Cretaceous *Liopistha* species in North Western Europe

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Abstract

Liopistha aequivalvis (Poromyidae, Anomalodesmata, Bivalvia) from Upper Cretaceous European strata is redescribed. Hinge elements, not previously described, are illustrated. The presence of a second *Liopistha* species from Maastrichtian white chalks at Hallembaye (Liège, Belgium) is shown.

Key-words: Mollusca, Bivalvia, Cretaceous, Taxonomy, Palaeobiogeography.

Résumé

L'espèce *Liopistha aequivalvis* (Poromuidés, Anomalodesmata, Bivalves) connue des dépôts du Crétacé Supérieur européen, est redécrite. L'illustration de la charnière démontre la présence d'éléments pas encore décrits. Une deuxième espèce de *Liopistha* a été retrouvée dans la craie blanche d'âge maastrichtien à Hallembaye (province de Liège, Belgique).

Mots-clefs: Mollusques, Bivalves, Crétacé, Taxonomie, Paléobiogéographie.

Introduction

In European Upper Cretaceous strata fossil Bivalves occur frequently but their state of preservation is often poor. Calcitic shell parts generally fossilize, but aragonitic elements have almost always been dissolved. As a result species belonging to the subclass Pteriomorphis and especially to the order Pterioidea have been found in most strata. On the other hand specifically recognisable Heterodonta (i.e. with hinge elements preserved) are very rare. The species belonging to the subclass Anomalodesmata, characterised by very thin shells and strong commarginal and radial ornamentation, such as Pholadomyids and *Liopistha* species, are not uncommonly preserved as specifically identifiable composite moulds. *Liopistha* specimens are present in the collections of the Institut Royal des Sciences Naturelles de Belgique in Brussels from the Campanian-Maastrichtian strata of eastern Belgium (provinces of Liège and Limburg), southern Netherlands (province of Limburg), western Germany (area around Aachen). They occur:

— as silicified shells (near Vaals, Zuid-Limburg, Lower Campanian);

— as composite moulds (near Kunrade, Zuid-Limburg, Upper Maastrichtian, and possibly near Aachen, GFR, ? Upper Campanian);

— as internal moulds (near Eisden and Voort, Limburg, Lower Campanian, and in the Maastrichtian stratotypical calcarenites, Sint-Pietersberg, near Maastricht, Zuid-Limburg, upper Upper Maastrichtian).

The main purposes of the present paper are:

— the redescription of *Liopistha aequivalvis* (GOLDFUSS, 1841) with attention to its hinge, to the variability which is artificially induced by different preservations, and an indication of its complete geographic and stratigraphic distribution;

— a brief discussion of the systematic position of the genus *Liopistha*;

— the content of the genus *Liopistha*.

Taxonomy

Classis *Bivalvia*
Subclassis *Anomalodesmata*
Ordo *Pholadomyoidea*
Superfamilia *Poromyacea*
Familia *Poromyidae*
Genus *Liopistha* MEEK, 1864

[Type species: *Cardium elegantulum* F. ROEMER, 1852
(non *C. elegantulum* BECK, 1842)
= *Liopistha elegantulata* VOKES, 1956]

DISCUSSION OF THE GENUS

The type species selected by MEEK, 1864 has only rarely been recorded and is only known from the Santonian of Texas. Among the characteristics of the genus the *radial ornamentation* is very clearly visible on the figures of the type species. Its *hinge*, however, has not been described and remains unknown.

In 1871 STOLICZKA discussed the species group to which *Cardium elegantulum* ROEMER non BECK belonged. His understanding was based mainly on *Pholadomya caudata*

ROEMER [= *Liopistha aequivalvis* (GOLDFUSS)]. He stated (pp. 70, 208) that the hinge was identical with that of a *Pholadomya* ("with one small elongated tooth in each valve" - p. 70). This description of the genus *Pholadomya* is in contradiction with what is generally accepted today (MOORE, 1969, p. N827 "hinge edentulous").

MEEK (1876) discussed the genus *Liopistha* and gave the first description of its hinge, based on *L. protexta* (CONRAD, 1853). He also described, figured and discussed the closely related genus *Cymella*. For both taxa he indicated the presence of two cardinal teeth, but on the left valve he called one of these "rudimentary".

HOLZAPFEL (1884, 1889) described and figured specimens of *L. aequivalvis* from Vaals with preserved shells. For the right valve he mentioned two cardinal teeth, for the left valve one large and one very small cardinal tooth. This agrees entirely with the descriptions given by MEEK. The specimens of *L. aequivalvis* from Vaals, available in the collections of the IRScNB agree with the descriptions given by HOLZAPFEL, except for the fact that both valves have two cardinal teeth and one thin tooth-like partition to the posterior side of the upper cardinal tooth. (Pl. 1, Fig. 7a, Pl. 2, Figs. 1a, b, c). The *L. aequivalvis* specimens from Vaals have near the umbo a commarginal ornamentation which is very close to that which covers the complete valves of *Cymella* as exemplified by its type species *C. undata* (MEEK & HAYDEN). Therefore, we are not entirely convinced that *Cymella* and *Liopistha* are sufficiently different to be considered as two separate genera. Further material would be necessary to draw definite conclusions on this point. *Psilomya* WHITE, 1874 seems to be characterised by a less developed radial ornamentation than that known for *Liopistha*.

Liopistha and its related genera are placed in the Poromyidae by MOORE (1969) as had been done previously by many authors. Nevertheless, it does seem necessary to stress that the Cretaceous taxa *Liopistha*, *Cymella* and *Psilomya* placed in that family do not totally agree with the definition of the family — especially the hinges are more complex, and the average size is much larger. A revision of the placement above might be indicated for the future.

Non-exhaustive list of species assigned to *Liopistha* s.s.:

- *Liopistha subcaudata* (BRIART & CORNET, 1869: p. 84, pl. 5, figs. 19, 20) refigured in MARLIÈRE, 1939 (pl. 4, figs. 12 a-c) from the Albian at Bracquegnies, Hainaut (Belgium).
 - *Liopistha elegantulata* VOKES, 1956, figured in F. ROEMER, 1852, as *Cardium elegantulum*, pl. 6, figs. 5 a-c, from the Austin Chalk, Santonian of Texas (USA).
 - *Liopistha aequivalvis* (GOLDFUSS, 1841) from the ?Turonian to the uppermost Maastrichtian (see below) of Europe and Central Asia.
 - *Liopistha alternata* WELLER, 1907 (p. 527, pl. 57, figs. 7-9, fide GARDNER, 1916) from the Matawan Fm., Lower Campanian of New Jersey (USA).
 - *Liopistha protexta* (CONRAD, 1853) from the Campanian-Maastrichtian strata of the Atlantic and Gulf Coastal Plain deposits, from New Jersey to Texas (USA), figured in MEEK (1876: hinges: p. 227, text-figs. 20-24), in GARDNER (1916: p. 636, pl. 36, fig. 15), in STEPHENSON (1941: p. 162, pl. 26, figs. 27-40; 1955: p. 116, pl. 19, figs. 17-21).
 - *Liopistha formosa* STEPHENSON, 1941 from the Upper Campanian-Maastrichtian strata of Texas and Tennessee (USA) (figured in STEPHENSON, 1941: p. 164, pl. 26, figs. 24-26).
 - *Liopistha inflata* WHITFIELD, 1885 (p. 142, pl. 20, figs. 4, 5) from the Campanian-Maastrichtian of New-Jersey is considered by later authors as a synonym of *L. protexta*.
 - *Liopistha kuemmelii* WELLER, 1907 (p. 529, pl. 58, fig. 3, fide RICHARDS, 1958 — also figured in RICHARDS, pl. 27, fig. 11) from the Merchantville Fm., Lower Campanian in New Jersey (species not mentioned in OWENS *et al.*, 1970).
- Liopistha aequivalvis* (GOLDFUSS, 1841)**
(Pl. 1, Figs. 1-7, Pl. 2, Fig. 1)
- v. 1841 *Corbula aequivalvis nobis* - GOLDFUSS, p. 250, pl. 151, figs. 15 a, b.
 - . 1841 *Pholadomya caudata* N. - F.A. ROEMER, p. 76, pl. 10, fig. 8.
 - . 1843 *Pholadomya caudata* Römer - GEINITZ, p. 11, pl. 1, figs. 28-30.
 - . 1847 *Cardita Goldfussii* Müller - J. MUELLER, p. 20.
 - 1850 *Pholadomya aequivalvis*, d'Orb. - d'ORBIGNY, p. 234.
 - 1850 *Pholadomya caudata* Römer - GEINITZ, p. 148.
 - 1860 ? *Pholadomya aequivalvis* d'Orb. - BOSQUET, n° 332, p. 376.
 - v. 1860 *Poromya ? aequivalvis* Forb. - BOSQUET, n° 332, p. 378.
 - (1861) *Papyridea aequivalvis*, Goldf. - GABB, p. 166.
 - 1863 *Pholadomya caudata* Römer - DRESCHER, p. 342.
 - . 1867 *Pholadomya caudata* Römer - EICHWALD, p. 769.
 - ? 1871 *Pholadomya caudata*, Römer - STOLICZKA, p. 79, pl. 2, figs. 10, 11, pl. 16, fig. 19.
 - . 1873 *Pholadomya aequivalvis* Goldf. sp. - GEINITZ, p. 71, pl. 19, figs. 6, 7.
 - 1875 *Pholadomya caudata* Römer - BRAUNS, p. 360.
 - . 1875 *Pholadomya aequivalvis*, Goldf. sp. - MOESCH, pp. 111-112, pl. 35, fig. 5; pl. 36, figs. 2, 3.
 - ? 1877 *Pholadomya aequivalvis* d'Orb. - FRIC, p. 124, text-fig. 98.
 - . 1884 *Pholadomya aequivalvis* Goldf. sp. - HOLZAPFEL, p. 471, pl. 7, figs. 5a-5b.
 - . 1885 *Liopistha aequivalvis* Gfs. - J. BOEHM, pp. 138-141.
 - 1887 *Liopistha aequivalvis* Goldf. sp. - FRECH, p. 172.
 - . 1889 *Pholadomya caudata* A. Römer - GRIEPENKERL, p. 67.
 - . 1889 *Liopistha aequivalvis* Gldf. sp. - HOLZAPFEL, p. 150, pl. 9, figs. 4-6.
 - . 1895 *Liopistha aequivalvis* Goldf. - VOGEL, pp. 47-48, pl. 3, figs. 11-12.
 - 1897 *Pholadomya aequivalvis*, Golf. - FRIC, p. 60.
 - 1898 *Liopistha aequivalvis* Goldf. sp. - G. MUELLER, p. 76, pl. 10, fig. 9.
 - 1901 *Liopistha aequivalvis* Goldf. sp. - STURM, p. 88.
 - ? 1909 *Liopistha*, sp. - WOODS, p. 258, pl. 43, figs. 5a-c.
 - 1912-1913 - *Liopistha aequivalvis* Goldf. spec. - SCUPIN, p. 143.

- 1930 *Liopistha aequivalvis* Goldfuss - HÄGG, p. 55.
 1934 *Liopistha aequivalvis* Goldf. - ANDERT, p. 335, pl. 15, fig. 9, text-fig. 88.
 1935 *Liopistha aequivalvis* (Goldfuss) - HÄGG, p. 51.
 1937 *Liopistha aequivalvis* (Goldf.) - BEYENBURG, p. 316.
 1937 *Liopistha aequivalvis* (Goldfuss, 1840) - LEHNER, p. 161, pl. 25, fig. 30.
 (1938) *Liopistha aequivalvis* Goldf. - POZARYSKI, p. 23.
 (1942) *Liopistha aequivalvis* Goldf. - PUTZER, p. 371.
 1943 *Liopistha aequivalvis* (Goldfuss) - VAN DER WEIJDEN, p. 76, pl. 6, figs. 7, 8.
 1947 *Liopistha aequivalvis* (Goldfuss) - HÄGG, p. 92.
 1954 *Liopistha aequivalvis* (Goldfuss) - HÄGG, p. 53.
 1961 *Liopistha* cf. *aequivalvis* (Goldfuss, 1834) - BOBKOVA, p. 146, pl. 14, fig. 3.
 1977 *Liopistha aequivalvis* (Goldfuss, 1834) - SOBETSKI, p. 218, pl. 17, fig. 13, pl. 18, fig. 1.
 1981 *Liopistha* (*Liopistha*) *aequivalvis* (Goldfuss, 1834) - TZANKOV *et al.*, p. 147, pl. 71, figs. 4 - 6.
 1986 *Liopistha* (*Liopistha*) *aequivalvis* (Goldfuss, 1834) - ABDEL-GAWAD, p. 184, pl. 43, figs. 1, 2.

TYPE SPECIMENS

"*Corbula*" *aequivalvis*: lectotype, designated here: specimen 954a of the Paläontologische Sammlung from the Rheinische Friedrich-Wilhelms Universität, Bonn (FRG). Paralectotypes: 954b (1 to 4), 954d. Specimen 954a is the original of GOLDFUSS (pl. 151, fig. 15 a).

Pholadomya caudata: should be in the Roemer-Pelizaeus Museum in Hildesheim.

LOCUS TYPICUS

Liopistha aequivalvis and *Pholadomya caudata*: Aachen (FRG), (designated here).

STRATUM TYPICUM

Liopistha aequivalvis: "Grünsand": the greensand from Aachen is generally considered as being Lower Campanian (ALBERS & FELDER, 1979, p. 72). However, the type specimens from the GOLDFUSS coll. are preserved in a hard limestone which is closer to the preservation generally found in the Kunrade Limestone which is of Late Maastrichtian age (ROBASZYNSKI *et al.*, 1985). It could be that outcrops extant in 1830 contained levels unknown to us today, or that the specimens came from the Aachen area s.l. *Pholadomya caudata*: "Oberer Kreidemergel": Campanian-Maastrichtian.

MATERIAL STUDIED

Type specimens from the Institut für Paläontologie of the Rheinische Friedrich-Wilhelms Universität in Bonn, FRG. (GOLDFUSS Coll. 954a-d).

Collections of the Institut Royal des Sciences Naturelles de Belgique (IRScNB):

- Coll. BOSQUET (IG 4285) from Vaals (Zuid-Limburg, The Netherlands), from the Hervian (= Lower Campanian): 28 specimens (mainly incomplete), with silicified shell preservation;

- from Kunrade (Zuid-Limburg, The Netherlands) from the Kunrade Limestone (Upper Maastrichtian): Coll. BOSQUET (IG 4285), 14 composite moulds; Coll. PIRLET (IG 6039): 3 composite moulds; Coll. UBAGHS (IG 5185 & IG 6521), 16 composite moulds; Coll. DE JAER (IG 8261), 2 composite moulds;
- from the Sint-Petersberg near Maastricht, from the Maastricht Fm. (Upper Maastrichtian): Coll. BOSQUET (IG 4285), 10 specimens; Coll. UBAGHS (IG 6521), 2 specimens: "Coll. Ancien-nes" (IG 10511), 3 specimens, all in steinkern preservatons;
- IG 8748 (Expl. Institut) from Voort, Colliery Zolder, Pit 1: depth 579.5 to 582 m, Greensand, Campanian: 18 specimens (steinkern preservation) - depth 582-584.3 m: 9 specimens (steinkern preservation); IG 9434 same locality: depth 575.8 m to 579.5 m: 4 specimens (steinkern preservation);
- IG 8831 (Expl. Institut) from Voort, colliery Zolder, Pit 2: depth 581.45 m, Greensand, Campanian: 14 specimens (steinkern preservation); depth 588 m: 8 specimens (steinkern preservation); depth 588 m: 8 specimens (steinkern preservation).

Description of the species

ORIGINAL DESCRIPTION

"*Corbula aequivalvis*" in GOLDFUSS:

"*Corbula nucleo subaequalvi ovali fornicato concentric striato, umbonibus antemedianis incurvis cruciatis, lunula magna cordata laevi, dorso costis radiantibus regularibus crebris, latere postico laevi. Ex arena viridi Juliae, Westphaliae et Silesiae. M.B. M.M.*

Der Quere nach verkehrt-eyförmig gewölbt, zart concentrisch gestreift, mit gegenseitig übergreifenden, gekreuzten Wirbeln, welche vor der Mitte liegen. Die beiden Klappen haben eine gleichförmige Wölbung, und die rechte ist nur am hintern Ende etwas länger. Das grosse, herzförmige, flach vertiefte Mondchen nimmt die Hälfte der vorden (sic) Seite ein. Der Rücken ist mit schmalen, zahlreichen ausstrahlenden Rippen bedeckt, die hintere Seite aber glatt. Findet sich im Grünsande bei Aachen, Dülsen und in der Grafschaft Glatz ziemlich häufig als Steinkern und von mässiger Grösse ..., seltener mit der Schale oder in verdoppelter Grösse..."

ADDITIONAL DESCRIPTION

Diagnosis:

Liopistha species with incurved umbones, a fine commarginal ornamentation in the umbonal region and 20 to 39 major radial ribs, smooth extended posterior areas, and a hinge with two large cardinal teeth and one thin tooth-like partition in the right valve, but one large and one small cardinal tooth and one thin tooth-like partition in the left valve.

Dimensions:

(all linear dimensions in mm)

[Abbreviations used: b: bivalved specimen; CM: composite mould preservation; H: height; I: inflation, both valves; I*: inflation, one valve; L: length; l: left valve; P: preservation; r: right valve; Ri: number of ribs; S: side of the shell = valve; SK: steinkern preservation; (dimension): not very accurate because of preservation.]

	H	L	I	Ri	S	P
type-specimens						
lectotype 954a	46.6	>74.4	22.2*	(37)	l	SK
paralectot. 954b-1	29.5	>42	15*	32	r	CM
paralectot. 954b-2	30.5	>41	13*	33	l	CM
paralectot. 954b-3	27.7	>36	11*	30	l	CM
paralectot. 954b-4	19.5	>26	9.5*	(30)	r	CM
paralectot. 954d	18.8	>24	13.5	38	b	CM
Goldfuss specimens (not types)						
from Glatz 954c-1	27.8	39.5	—	27	r	SK
from Glatz 954c-2	—	46.0	—	24	l	SK
— specimens from Vaals (IG 4285) with almost complete shell preservation:						
Hmin 7.2 - Hmax	28.5		Hav. 17.2		(N= 15)	
Lmin 9.0 - Lmax	33.0		Lav. 22.4		(N= 12)	
Imin 6.5 - Imax	21.0		Iav. 10.4		(N= 6)	
Ri min 28 - Ri max	39		Ri av. 34		(N= 15)	
— specimens from Kunrade (IG 4285, 5185, 6039, 6521, 8261), composite mould preservation:						
Hmin 17.7 - Hmax	49.0		Hav. 27.3		(N= 22)	
Lmin 22.5 - Lmax	69.2		Lav. 34.7		(N= 22)	
Imin 16.8 - Imax	25.0		Iav. 21.5		(N= 13)	
Ri min 25 - Ri max	37		Ri av. 29		(N= 25)	
— specimens from the Sint Pietersberg near Maastricht (IG 4285, 6521, 10511) steinkern preservation:						
Hmin 18.3 - Hmax	27.6		Hav. 23.7		(N= 15)	
Lmin 23.0 - Lmax	38.0		Lav. 30.0		(N= 13)	
Imin 14.2 - Imax	22.5		Iav. 18.8		(N= 6)	
Ri min 24 - Ri max	34		Ri av. 29		(N= 15)	
— specimens from Voort, Pit 1 (IG 8748), steinkern preservation in coarse sandy sediments:						
Hmin 23.2 - Hmax	51.0		Hav. 40.8		(N= 25)	
Lmin 33.2 - Lmax	67.0		Lav. 58.4		(N= 12)	
Ri min 19 - Ri max	24		Ri av. 22.4		(N= 18)	
— specimens from Voort, Pit 2 (IG 8831), steinkern preservation in coarse sandy sediments:						
Hmin 36.0 - Hmax	52.0		Hav. 45.8		(N= 13)	
Lmin 52.7 - Lmax	72.0		Lav. 62.2		(N= 12)	
Ri min 21 - Ri max	25		Ri av. 23		(N= 11)	

Description:

Shell-shape: seemingly equivalve, inequilateral, with incurved umbones, no noticeable gape between the posterior lateral extensions.

Hinge: is visible on a few specimens from Vaals: on the left valve: one largish cardinal tooth on a plate under the umbo, with one small cardinal and one thin tooth-like partition above it, directly attached at the hinge margin; between the large and the small teeth a large cavity, under the umbo; on right valve: one upper cardinal tooth narrow and pointed and one thin tooth-like partition attached to the hinge margin, one larger, triangular lower cardinal tooth; between the two a cavity which is wide on the anterior shell side but narrower on the posterior side. The lower tooth and the cavity seem to be situated on a platform-like extension.

The hinge margin posteriorly of the teeth forms a triangular extension which is probably the nymph, and is situated at the beginning of the escutcheon, which is delimited by a

fold (Pl. 1, Fig. 7a, Pl. 2, Fig. 1a). The size of the teeth seems to decrease proportionally with the shell size (allometric growth).

Ornamentation: both radial and commarginal elements can be seen on the shell. (1) Near the umbo radial and commarginal elements are equally developed. The shell is covered by a trellis-like ornamentation of a certain thickness which reminds one of the ornamentation of *Cymella*. (2) Further away from the umbo, towards the ventral margin, only radial ornamentation remains: these radial ribs are not distributed evenly over the shell and are not equal. (2a) Near the anterior dorsal margin the shell appears granular or smooth. Without sharp delimitation, riblets (or filae) appear, more clearly visible near the ventral margin: they vary in number (up to 6). (2b) Beyond the riblets appear ribs with fairly sharp summits and intercostal intervals of about the same width as the ribs. Towards the posterior part of the shell the ribs are somewhat stronger and the intervals are wider than the ribs. (2c) Abruptly the ribs end, two to three filae can sometimes be seen beyond the ribs, otherwise the dorsal area is smooth, except for fine commarginal lines. (3) Along the dorsal posterior margin a relatively strong radial fold delimits a narrow, elongated area (the escutcheon) which is covered by stronger commarginal ornamentation. On the radial ribs small spines can be seen (and felt) at regular intervals. The rib number varies from 20 to 39 depending on the preservation. (See below).

Discussion:

Variability: hinge: the hinge can only be seen on specimens which are preserved either completely (i.e. with the shell) or on some composite moulds. In the material before us this means that only specimens from Vaals and a few from Kunrade give hinge information. Many authors have discussed the hinge of *L. aequivalvis* and related species, generally with the purpose of the generic attribution. Very rarely have they had specimens with properly preserved hinges. The hinge seems to be smaller on larger valves than on smaller ones: probably due to allometric growth. **ribs:** *L. aequivalvis* is a relatively "well-known" species and has been recorded from Turonian to Maastrichtian strata. Authors have agreed on characteristics such as shell-shape, the hinge and the presence of radial ribs. Yet, where it concerns the **number** of these radial ribs literature has quoted figures which vary very widely (19 to 40). The origin of this variation is probably a combination of biological and preservational facts:

— biological (ecological): in some Bivalve species from Upper Cretaceous strata the rib-characteristics seem to be influenced/related to the nature of the sediment: in coarser sediments such as sands, greensands, and "tourtia" ribs are fewer, stronger, and more subdivided than they are on specimens of the same species from fine grained sediments such as chalks or marls [ex. *Mimachlamys cretosa* (DEFrance, 1822 figured in Woods, 1902, pl. 32 & 33), which generally has lower, less sharp, always undivided and more numerous ribs in

white chalks, but fewer, unequal, heavier ribs in the Maastrichtian stratotypical calcarenites]. Applied to *L. aequivalvis* this would mean that specimens from fine sediments, such as the Kunrade Chalks, would have a higher number of ribs than those from the Hervian greensands: Kunrade average: 29, Vaals greensands average 34, but Hervian greensands from Voort: average 22-23. A different factor from the strictly environmental seems to have influenced the number of ribs.

— preservational: if we consider the specimens for which the varying rib figures have been quoted in the literature and by us, it becomes obvious that the preservation differs from locality to locality. Generally the specimens are internal moulds or steinkerns, more rarely are they composite moulds, and in Eurasia only in Vaals is the (silicified) shell preserved. Because the shell is very thin, almost all the ribs can be seen on the moulds. However, the riblets which appear on the posterior and anterior areas can only be seen on shell-specimens or on some composite moulds; these riblets are included in the rib count. Thus shell specimens or composite moulds should have up to 9 ribs more than the steinkern specimens: this allows explain most of the difference between Vaals and Voort: rib-average for Vaals 34. $34 - 9 = 25$ which is only a few entities above the Voort average of 22-23.

— ontogenetic changes: as stated above the hinge teeth size changes allometrically with growth; the number of ribs increases with size according to some authors, because new ribs originate occasionally by intercalation. This is rare, but does occur.

— whether there is an evolutionary change in rib number (i.e. whether in older strata the rib number is lower or higher) is impossible to check because all the older specimens of *L. aequivalvis* are preserved as steinkerns.

shell shape: GOLDFUSS (and others) mentioned that the umbones are not placed opposite of one another but alongside each other: on the specimens we studied this is not confirmed. The beaks are definitely incurved but remain opposite on well preserved specimens. Since the shell of *Liopistha* is very thin it is quite possible that deformation during fossilization (pelomorphosis) occurs commonly in the shell. Under such circumstances the beaks might no longer be opposite. On the specimens studied we found no proof of a gape. As stated by VAN DER WEIJDEN (1943) the shape of the valves varies considerably and especially the posterior extensions differ.

Synonymy: for *Corbula aequivalvis* GOLDFUSS, most authors have given a publication year anterior to the one used here. We have preferred to follow QUENSTEDT 1963 (p. 18) for *Petrefacta Germaniae* "7. Lieferung = Teil II, 4: S.I-III, 225-312, Taf. CXLVII-CLXV: 1841 (1. Jahreshälfte)". To our knowledge this is the only bibliographic research done recently on this topic.

Pholadomya caudata ROEMER, according to the same bibliographic research (ibid., p. 24), was also published in the first half of 1841. For stability of nomenclature and possibly also because GOLDFUSS's figures and description

are more complete than those by ROEMER, there seems to be no valid reason to change the established usage.

Differentiation: As already stated by previous authors *Liopistha aequivalvis* is similar in shape, ornamentation and hinge to the North-American species *L. protexta* (CONRAD, 1853) from the Campanian-Maastrichtian Atlantic and Gulf Coastal Plain deposits. The differences seem to be in the rib form and in the continuation of the ribs towards the anterior dorsal margin.

Because American specimens are frequently preserved with the shell they are somewhat difficult to compare with steinkern material. An exception is *L. kuemmelii* WELLER, 1907 from Lower Campanian strata in New Jersey and Delaware, probably only known in steinkern preservation. *L. kuemmelii* seems to be very similar to those specimens which are found in strata of the same age in the Belgian collieries.

Indian specimens were considered by STOLICZKA as being synonymous with *L. aequivalvis*. KOSSMAT, 1897, disagreed and again considered the Indian taxon [*L. lucerna* (FORBES, 1846)] as specifically different. The specimens on which FORBES erected the taxon are today in the B.M. (Nat. Hist.) in London. Some of these have been studied by us (LL 31923 - 31931). Their preservation is different from that of the European material and most have some original shell material preserved. At first glance the Indian and the European specimens appear to be almost identical in shape and in ornamentation. The number of ribs is comparable (on the 9 Indian specimens studied it varies from 28 to 38). The ribs themselves appear more rounded, the intervals narrower and the commarginal ornamentation somewhat more strongly developed and regular on the Indian specimens than on the best preserved European specimens from Vaals. Undoubtedly both series of specimens belong to closely related taxa, but the slight differences do not seem to be due to preservation only. Whether these differences allow distinction at the specific or at the subspecific level remains to be decided in the light of a larger assemblage of Indian specimens.

Generic attribution:

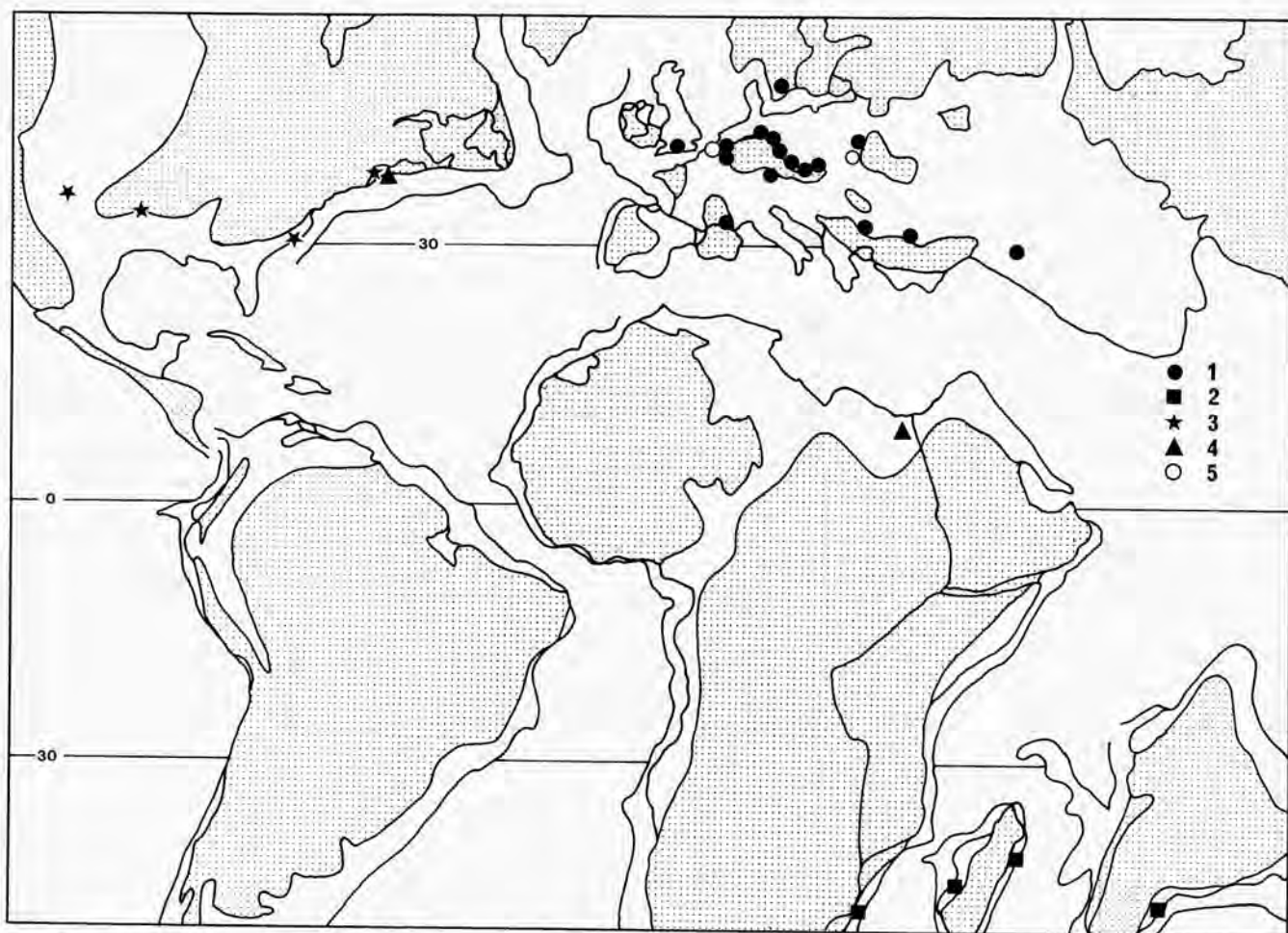
Liopistha aequivalvis (GOLDFUSS, 1841) is very similar to the type species of the genus *Liopistha* MEEK, 1864 (*Cardium elegantulum* ROEMER, 1852 non BECK, 1842) and hence there can be no doubt as to its generic attribution.

Geographic and stratigraphic distribution (Text-Figure 1): Recorded from Turonian (?) - Coniacian to Maastrichtian deposits from England to Crimea, possibly into Central Asia.

Liopistha sp. cf. *L. alternata* WELLER, 1907.

? 1986 *Liopistha* (? *Psilomya*) sp. - ABDEL-GAWAD, p. 184, pl. 47, figs. 3-5.

From the Vijlen Chalk (lower Upper Maastrichtian) at Hallembaye (Liège, Belgium) one of us (JWJ) has col-



Text-Figure 1. — Palaeogeographic distribution of *Liopistha* species: (1) *L. aequivalvis* (GOLDFUSS, 1841), (2) *L. lucerna* (FORBES, 1846), (3) *L. protexta* (CONRAD, 1853), (4) *L. alternata* WELLER, 1907, (5) *Liopistha* sp. cf. *L. alternata*. Data out of literature and personal research. Palaeogeographic reconstruction at 80 million years from BARRON et al., 1981.

lected two *Liopistha* specimens (3655 and 3656) in steinkern preservation which are close to *L. alternata* WELLER, 1907 (p. 527, pl. 58, figs. 7-9, fide RICHARDS, 1958, p. 168) from the Merchantville Fm., i.e. Lower Campanian (OWENS et al., 1970).

Dimensions (mm):	H	L	S	P
3655	22.8	27.2	1	SK
3656	13.8	19.2	1	SK, deformed

The two specimens are somewhat deformed but certain features can be observed:

- the ornamentation: numerous (between 50 and 60) radial ribs of varying development, bearing remnants of spines, and showing traces of commarginal lines. This ornamentation reaches the anterior dorsal margin.
- near the posterior margin lies a smooth area. The umbones are squashed and the hinges are not visible. The radial ribs do not alternate as regularly as has been described for *L. alternata*, but more strongly developed ribs alternate irregularly with 1, 2, 3 or even 4 weaker ribs. The total number of ribs is higher than has been

reported for *L. alternata*, but otherwise the specimens are closer to that taxon than they are to any other *Liopistha* species known to us. ABDEL-GAWAD (1986, pl. 47, figs. 3-5) illustrated from Maastrichtian strata in the Middle Vistula Valley (Poland) specimens of *Liopistha* (? *Psilomya*) sp. which could be very close to the specimens from the Vijlen Chalk, but the illustrations are not good enough to draw definite conclusions.

QUAAS (1902, p. 227, pl. 25, figs. 7a, b) described and figured "*Pholadomya* cf. *lucerna* FORBES" from Maastrichtian strata of the western desert in Egypt. The Egyptian specimen does not seem to be identical with those described from S. India by FORBES and STOLICZKA. It is undoubtedly close to *L. alternata*, has a similar rib number and pattern, but shows commarginal ornamentation which is barely visible on *L. alternata*, or on the two specimens from the Vijlen Chalk.

The preservation of the two specimens from the Vijlen Chalk is not good enough to describe it as a new species, but if further and better specimens were found it might be possible to do so.

In the literature we have not found references to any species identical (except perhaps those from Poland) with these specimens from Hallembaye. It is possible that such specimens have not been collected previously because the preservation in the white chalks is not always very satisfactory.

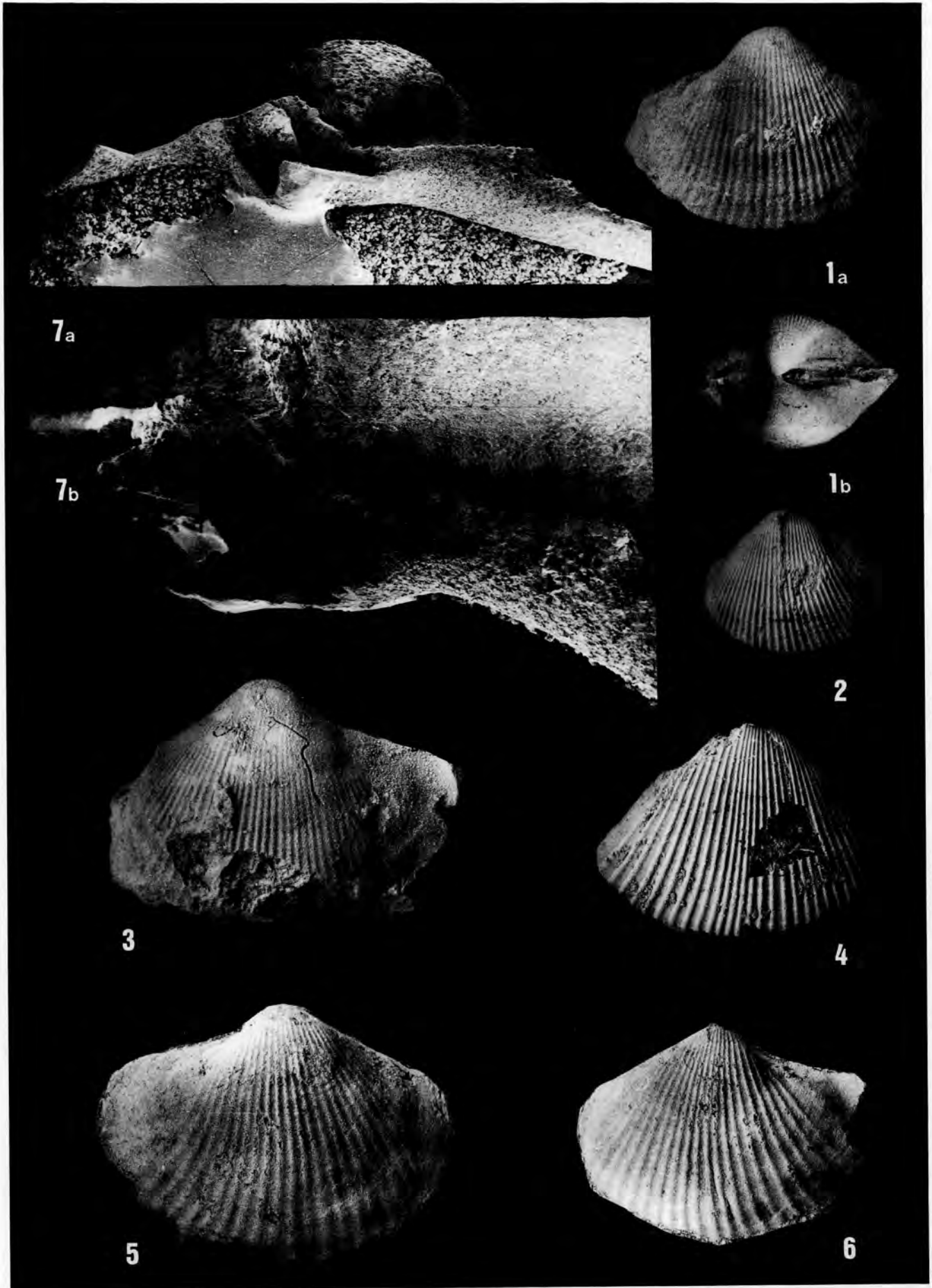
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Explanation of the plates

Figured specimens are preserved in the Institut royal des Sciences naturelles de Belgique - Koninklijk Belgisch Instituut voor Natuurwetenschappen, except when indicated otherwise.

PLATE 1

- Fig. 1a. – *Liopistha aequivalvis* (GOLDFUSS): right valve, steinkern, from the Kunrade "Limestone" (Maastrichtian), from Kunrade, Zuid-Limburg, The Netherlands; Bosquet Coll., IST MI 10481; $\times 1.5$.
- Fig. 1b. – Same specimen as Fig. 1a, view on the umbones.
- Fig. 2. – *Liopistha aequivalvis* (GOLDFUSS): left valve, composite mould, from "Aachener Grünsand" (?) (Campanian), from Aachen, F.R.G.; Goldfuss Coll. 954d, Palaeontologisches Institut, Bonn University. $\times 1.5$.
- Fig. 3. – *Liopistha aequivalvis* (GOLDFUSS): lectotype, left valve, steinkern, from "Kreide" (?) (? Campanian), from Aachen, F.R.G.; Goldfuss Coll. 954a, Palaeontologisches Institut, Bonn University. $\times 1$.
- Fig. 4. – *Liopistha aequivalvis* (GOLDFUSS): incomplete right valve, silicified shell, from the "Vaalser Grünsand" (Lower Campanian), from Vaals, Zuid-Limburg, The Netherlands; Bosquet Coll., IST MI 10479; $\times 2$.
- Fig. 5. – *Liopistha aequivalvis* (GOLDFUSS): right valve, steinkern, from the "Hervian" (Lower Campanian), from Voort (Zolder colliery, Pit 2, Depth 582.50 m), Limburg, Belgium; IST MI 10480; $\times 1$.
- Fig. 6. – *Liopistha aequivalvis* (GOLDFUSS): left valve, steinkern, from the "Hervian" (Lower Campanian), from Voort (Zolder colliery, Pit 2, Depth 581.45 m), Limburg, Belgium; IST MI 10482; $\times 1$.
- Fig. 7a. – *Liopistha aequivalvis* (GOLDFUSS): silicified shell, hinge region of right valve showing upper and lower cardinal teeth and thin toothlike partition to the right of upper cardinal tooth; from the "Vaalser Grünsand" (Lower Campanian), from Vaals, Zuid-Limburg, The Netherlands; Bosquet Coll., IST MI 10477; $\times 12$.
- Fig. 7b. – Same specimen seen from the dorsal side, showing the upper and lower cardinal teeth; $\times 20$.

PLATE 2

- Fig. 1. – *Liopistha aequivalvis* (GOLDFUSS): silicified shell, hinge region of left valve; from the "Vaalser Grünsand" (Lower Campanian), from Vaals, Zuid-Limburg, The Netherlands; Bosquet Coll., IST MI 10478.
- Fig. 1a. – Hinge, almost complete, $\times 12$.
- Fig. 1b. – Close-up of Fig. 1a, showing teeth and thin tooth-like partition, $\times 24$.
- Fig. 1c. – Same hinge, seen from the dorsal side, showing teeth and tooth-like partition, $\times 24$.
- Fig. 1d. – Same hinge, seen from the anterior side, showing large lower tooth, $\times 24$.
- Fig. 1e. – Same hinge, seen from the ventral side, $\times 10$.

