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A new Late Maastrichtian species of *Cyranoia* (Terebratulida, Brachiopoda) from Belgium and The Netherlands

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Abstract

Representatives of a new Late Maastrichtian species of the terebratulid brachiopod *Cyranoia* COOPER, 1983 are described from the Meerssen Member (Maastricht Formation) of the Maastricht area (southern Limburg, The Netherlands) and from Vroenhoven (province of Limburg, Belgium). This new taxon is amongst the largest brachiopods ever recorded from Upper Cretaceous strata. The structure of its loop is illustrated by transverse serial sections and by preparation of one specimen. The assignment of this species to the genus *Cyranoia* COOPER, 1983 is discussed in detail.

Key words: Brachiopods, Rectithyridinae, Cretaceous, Upper Maastrichtian, Maastricht, new species.

Résumé

Cet article présente une nouvelle espèce de brachiopode térébratulide appartenant au genre *Cyranoia* COOPER, 1983. Elle est datée du Maastrichtien Supérieur et elle fut collectée dans la Craie de Meerssen (Formation de Maastricht) de la région de Maastricht (Pays-Bas) et de Vroenhoven (province du Limbourg, Belgique). Ce nouveau taxon compte parmi les plus grands brachiopodes découverts dans les terrains du Crétacé Supérieur. La structure du brachidium est établie par la réalisation de sections transversales sériées. L'appartenance de cette espèce nouvelle au genre *Cyranoia* est discutée en détail.

Mots-clefs: Brachiopodes, Rectithyridinae, Crétacé, Maastrichtien Supérieur, Maastricht, espèce nouvelle.

Introduction

FAUJAS DE SAINT-FOND (1803?) was the first author to briefly describe and illustrate Late Maastrichtian brachiopods from the Maastricht area. Subsequently, VON SCHLOTHEIM (1813) discussed and named these, referring to FAUJAS's illustrations. The most important contributions to our knowledge of Maastrichtian brachiopods from the type area, however, are BOSQUET's papers, published in 1854 and 1859. In 1860 appeared an exhaustive list by the same author of all taxa (flora and fauna) known then from the Maastrichtian chalk. Although very rich brachiopod collections from the Maastrichtian type area are housed in the Natuurhistorisch Museum Maastricht (NHMM) and in the Institut royal des Sciences naturelles de Belgique in Brussels (IRScNB), only a handful of studies on this subject have appeared during recent years. This material is in urgent need of revision and would greatly add to our current knowledge of temperate Cretaceous brachiopod faunas.

Within this framework, several specimens of a terebratulid brachiopod are singled out here, collected (Fig. 1) from the Meerssen Member (Maastricht Formation) in the Maastricht area (southern Limburg, The Netherlands) and from Vroenhoven (province of Limburg, Belgium). The biozonation of the Meerssen Member has recently been described by JAGT (1999) who noted the co-occurrence of coleoids of the *Belemnitella junior* group and *Belemnella (Neobelemnella) kazimiroviensis* sensu JELETZKY, 1951. This association assigns a Late Maastrichtian age to this unit.

The terebratulid brachiopod species described was not listed by BOSQUET, although in the Maastricht area it is not exceptionally rare, and mostly well preserved (articulated). Three specimens, studied for internal structures, reveal an intact brachidium.

In his 1860 list, BOSQUET referred to just four species of large terebratulide brachiopods, namely *Terebratula carnea* J. SOWERBY, 1812 (= *Carneithyris carnea* in current nomenclature), *Terebratula fittoni* VON HAGENOW, 1842 (= *Neoliothyrina fittoni*), *Terebratula sowerbyi* VON HAGENOW, 1842 (= *Neoliothyrina obesa* SAHNI, 1925) and *Terebratula scaphula* VON SCHLOTHEIM, 1813. The last-named species is a member of the Rectithyridinae, represented by a ventral valve illustrated by FAUJAS DE SAINT-FOND (1803, pl. 26, fig. 8). It may be that BOSQUET (1860, item number 582) attributed the species described in the present paper to *T. scaphula*, based on the poor illustration given by FAUJAS DE SAINT-FOND. It should be noted, however, that features visible in this illustration preclude assignment of the new terebratulid to *T. scaphula* as interpreted here (see below).

Recently, the new species was briefly discussed and

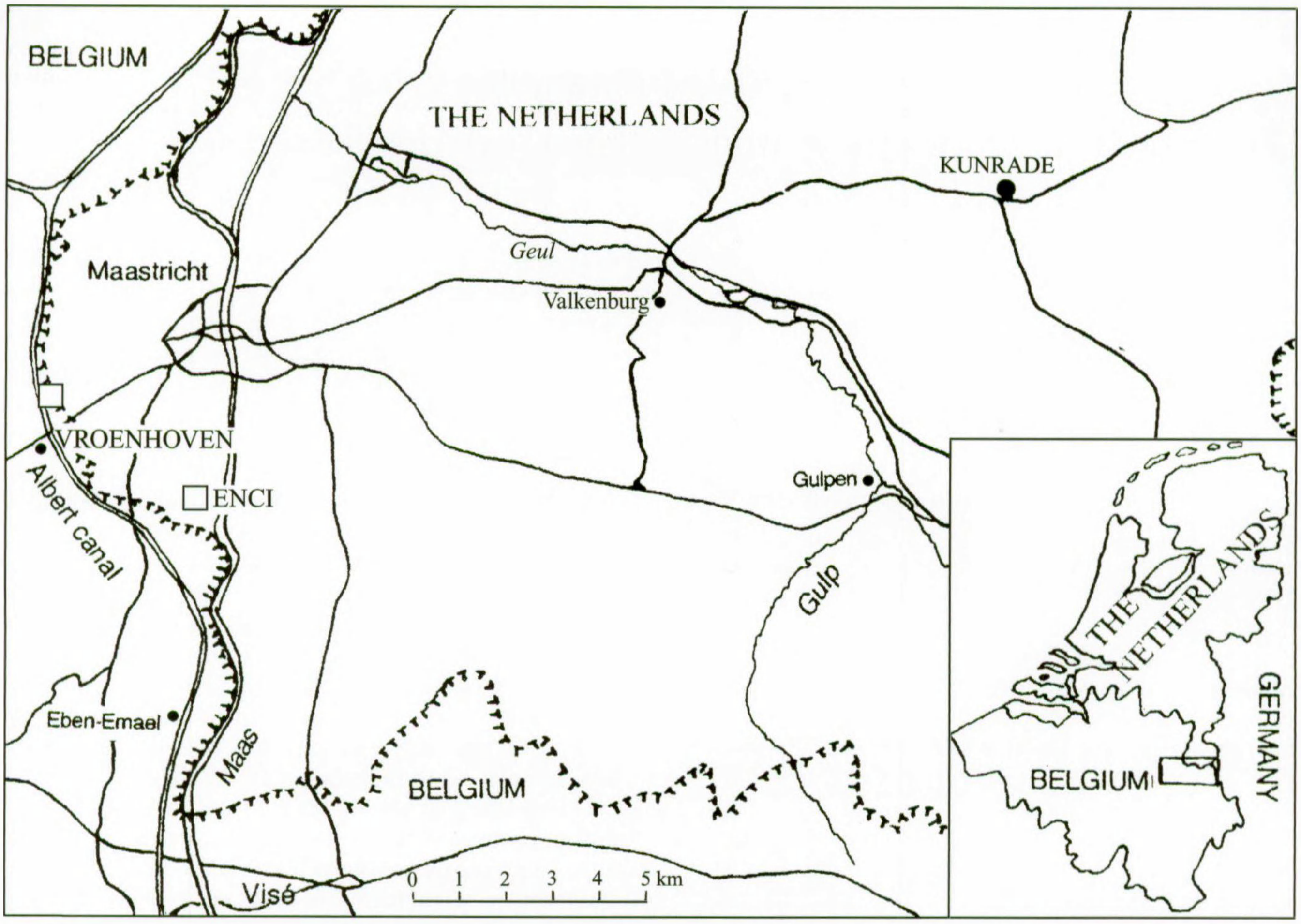

Fig. 1 — Map of the Maastricht area, showing the location of Vroenhoven (province of Limburg, Belgium) and of the ENCI quarry near Maastricht (southern Limburg, The Netherlands). ☐ = Collecting places of specimens of *Cyranoia bosqueti* n. sp.

illustrated by ROBERT (1995, p. 60, fig. 78) under the name of "*Rectithyris*" sp. However, a detailed analysis of the loop shows that this brachiopod cannot be placed in the genus *Rectithyris* SAHNI, 1929.

The genus *Cyranoia* COOPER, 1983 on the other hand, shows several interesting features which can also be found in the present form. Assignment to this genus is confirmed by the presence of inner hinge plates and the general structure of sockets and cardinalia seen in this new species of brachiopod.

Material and methods

Sixteen articulated specimens have been studied, five of which are from the St-Pietersberg, south of Maastricht, three from the ENCI quarry near Maastricht, five from the Ankerpoort-Marnebel quarry at Eben-Emael (province of Liège, Belgium) from dumped material originally excavated at Vroenhoven (Albert Canal extension works, province of Limburg, Belgium), two relatively small specimens from Maastricht (lacking precise data) preserved in the collection of G. Willems (Berzée, Belgium) and one from the Tuffeau de Saint-Symphorien (Late Maastrichtian) at Ciply (Mons Basin, Province of Hainaut, Belgium).

Transverse serial sections were prepared (see AGER, 1965, pp. 212-218 for procedure) and peels were taken on cellulose acetate following the method described by STERNBERG & BELDING (1942). Peels of the serial sections are in the NHMM collections. One specimen was carefully prepared to expose the brachidium.

Suprafamilial classification follows WILLIAMS et al. (1996). The synonymy list is presented following the recommendations of MATTHEWS (1973).

Taxonomic description

Phylum Brachiopoda DUMÉRIL, 1806
Subphylum Rhynchonelliformea WILLIAMS *et al.*, 1996
Class Rhynchonellata WILLIAMS *et al.*, 1996
Order Terebratulida WAAGEN, 1883
Suborder Terebratulidina WAAGEN, 1883
Superfamily Terebratuloidea GRAY, 1840
Family Terebratulidae GRAY, 1840
Subfamily Rectithyridinae MUIR-WOOD *in* MOORE, 1965

Genus *Cyranoia* COOPER, 1983

Type species: *Terebratula depressa visae* HADDING, 1919

Note: COOPER (1983) used different spellings, namely "*Terebratula depressa vissae* HADDING, 1919" (pp. 185, 214) and "*Cyranoia vissae* (HADDING)" in the caption to his plate 21. However in the caption to plate 54, the trivial name is spelt "*viassae*" . Following HADDING (1919, p. 20), the correct spelling would be "*visae*".

COOPER (1983, p. 185) established his new genus *Cyranoia* on the basis of a few distinctive characters, describing it as a "Terebratulacea with exterior like that of *Rectithyris,* with long beak, round, uncovered symphytium". Four characteristics are then listed, "short outer hinge plates, wide loop, strong development of inner hinge plates, socket ridges not extended laterally".

At first glance, the internal loop characters observed in *C. bosqueti* n. sp. are far removed from this meagre description. The outer hinge plates are rather long, the loop is relatively narrow, and the inner hinge plates are moderately developed. Moreover, in one specimen (exceptional), the socket ridges are moderately extended laterally as in the genus *Rectithyris*. If the diagnosis of *Cyranoia* is strictly applied, a new genus should be erected for *C. bosqueti* n. sp.

A closer analysis of the specimens illustrated by COOPER (1983, pls. 21, 54, 55 and 66) indicates that the characters included in the diagnosis are in fact variable or even subjective.

Specimens in pl. 21, figs. 21, 25 and 26 exhibit relatively long outer hinge plates. They appear much longer than the outer hinge plates of representatives of the genus *Biplicatoria* COOPER, 1983 illustrated in the same plate (pl. 21, figs. 1-6). The outer hinge plates in *Cyranoia* also appear as long as or longer than those observed in representatives of the genus *Rectithyris*. The specimen of *Cyranoia visae* illustrated in COOPER, 1983 pl. 54, fig. 26 shows very long outer hinge plates, indicating that the character of "short outer hinge plates" in the diagnosis is subjective – it should be considered as variable.

The type species *Cyranoia visae* has a "wide loop", which is clearly visible in specimens illustrated by COOPER. In his loop statistics, COOPER (1983, p. 185) gave only a single loop angle value of 47°. Compared with the mean value obtained for *C. bosqueti* n. sp. (35°) it may be said that *C. bosqueti* n. sp. has a narrow brachidium. However, the loop angle value is also very variable. Of specimens of *C. bosqueti* n. sp. studied, one specimen exhibits a loop angle value of 28° whereas two others measure 39°; a difference of 10° among only three investigated specimens.

In a recent study, LEE *et al.* (2001, pp. 56-70) noted the variation in the loops of two Recent species of *Liothyrella* THOMSON, 1916, namely *L. neozelanica* THOMSON, 1918 (Doubtful Sound, New Zealand) and *L. uva* (BRODERIP, 1833) (South Orkney Islands, Antarctica). These authors stressed the fact that some loop measurements are difficult to do correctly and precisely. They also demonstrated that some characters considered as very important by COOPER (1983) are in fact very variable among individuals within the same species. This is the case for the loop angle which may vary within a species to a much greater extent than suggested by COOPER (1983). This indicates that several measurements of the loop angle are required to provide a valid basis for describing a new genus. As a significant statistical analysis of the variation of the loop angle value and other characters within the material available for *C. bosqueti* n. sp. is not possible, the erection of a new genus should be avoided.

In his detailed description of *C. visae*, COOPER (1983, p. 185) insisted that the outer hinge plates are narrow, a character not included in his diagnosis, writing "...outer hinge plates are narrow, a mere connective dorsally welding the high crural bases and socket ridges, the combination producing narrow V-shaped troughs". Specimen USNM 112312b (COOPER, 1983, pl. 21, figs. 25-26) matches this description perfectly because the outer hinge plates are extremely narrow. Such a structure is also visible on the drawing of a loop (COOPER, 1983, pl. 66, fig. 2). In contrast, specimen USNM 550948a (COOPER, 1983, pl. 21, fig. 21) exhibits much wider outer hinge plates, the outer hinge plate on the right side appearing even wider than that on the left. In this specimen, the outer hinge plates are similar to those observed in *C. bosqueti* n. sp. although slightly narrower. Specimen USNM 112312 (COOPER, 1983, pl. 54, figs. 25-26) presents outer hinge plates of intermediate width, suggesting that this character could also be quite variable within representatives of the same species.

When all this material is reconsidered, some features seem more distinctive for distinguishing the genus *Cyranoia* from other rectithyridine Terebratulids. The outline of the cardinal process is identical in all specimens within representatives of this genus. It is a thin half elliptical plate with a depressed surface surrounded by a low ridge. It is larger, more developed, in *C. visae* than in *C. bosqueti* n. sp. but similar in outline. The myophore faces posteroventrally. The crural bases are extremely thin and high, with an acute ventral edge in all representatives of the genus *Cyranoia*. Few terebratulid representatives show such a height for their crural bases. The general architecture of the cardinalia (sockets, outer hinge plates, crural bases) is also a very similar character among all representatives of the genus *Cyranoia*. If a statistical analysis could be made on a larger number of specimens, an emended, and more reliable diagnosis might result for this genus.

Cyranoia bosqueti n. sp.

Text-Figures 2-3, Tables 1-2, Plate 1, Figures 1a-e – 5a-e, Plate 2, Figures 1a-e –5a-e.

non 1813 *Terebratula scaphula* sp. n. – VON SCHLOTHEIM, p. 113.
non 1860 *Terebratula scaphula* v. Schl. Sp. – BOSQUET, number 532.
v 1995 "*Rectithyris*" sp. – ROBERT, p. 60, fig. 78.

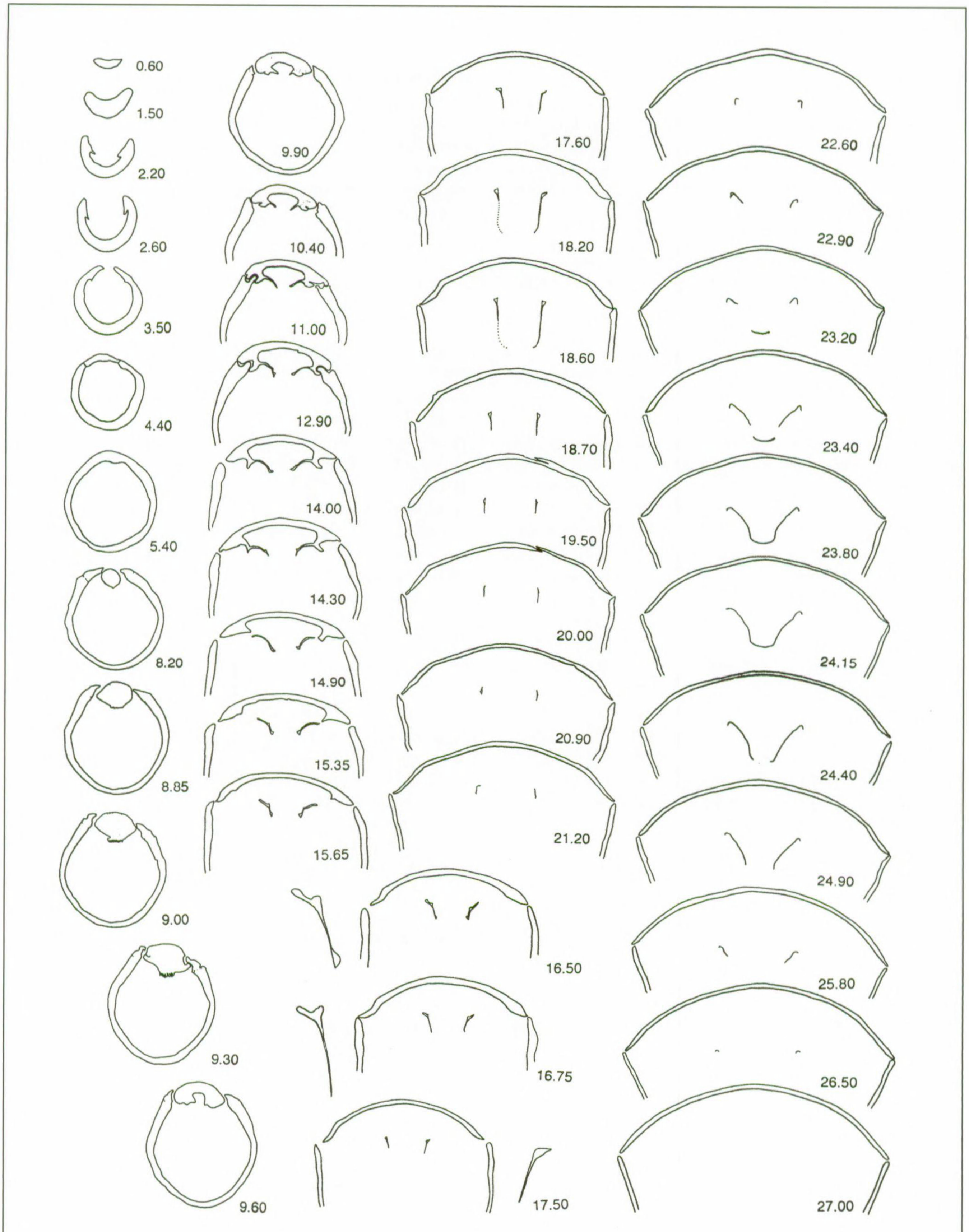

Fig. 2 — Transverse serial sections through the umbonal portion of a medium-sized adult specimen (NHMM 2002 139, ex Senden Coll., paratype) of *Cyranoia bosqueti* n. sp., from the Meerssen Member (Maastricht Formation, Late Maastrichtian) at Vroenhoven, x 1.6.

Table 1 — Measurements (in mm) of type specimens of *Cyranoia bosqueti* n. sp. illustrated in the present paper; all from the Meerssen Member (Maastricht Formation) of the Maastricht area. L - length of shell, LDV - length of dorsal valve, W - width of shell, T - thickness of shell, ØF - diameter of foramen.

Reference number	Type of specimen	Remarks	L mm	LDV mm	W mm	T mm	ØF mm	W/LDV	anterior commissure
NHMM 001388	Fully adult specimen	Holotype	75,0	61,0	51,2	38,6	9,0	0,83	Strongly sulciplicate
NHMM 2002 139	Adult	Paratype sectioned	62,3	53,3	40,5	28,6	5,8	0,75	Slightly sulciplicate
NHMM 2002 140	Small adult	Paratype excavated	42,5	36,5	27,0	18,2	5,2	0,74	Rectimarginate
NHMM 2003 208	Young specimen	Paratype sectioned	26,6	22,8	16,9	11,3	2,7	0,74	Rectimarginate
NHMM 2003 209	Adult	Paratype(bite-marks)	47,0	40,3	31,4	22,1	3,8	0,78	Slightly sulciplicate
NHMM JJ 8323	Gerontic	Paratype	98,6	87,2	69,7	56,6	12,7	0,80	Strongly sulciplicate
NHMM 2003 207	Adult (asymmetrical)	Paratype	56,7	46,9	38,9	25,3	5,5	0,83	Slightly sulciplicate
IRScNB MI n° 10937	Gerontic (Ciply)	Paratype	87,7	75,8	61,1	43,0	10,9	0,81	Strongly sulciplicate

Diagnosis

Large biconvex, sulciplicate species of *Cyranoia*, regularly oval in outline, with a typical capillate ornamented shell surface. Beak strong, often erect in young specimens, suberect in adults and straight in gerontic individuals. Foramen large, circular, mesothyrid. Brachidium relatively long, with high crural bases and weakly developed inner hinge plates. Ventrally directed outer hinge plates form, with inner socket ridges and crural bases, elongated troughs, subcircular in transverse section. Brachidium angle relatively narrow with a median value of 35°. Crural processes clearly anterior to midloop. Transverse band strongly and evenly arched.

Derivatio nominis: after Joseph BOSQUET (1814-1880), amateur-palaeontologist and pharmacist in Maastricht.

Locus typicus: Valkenburg aan de Geul, southern Limburg, The Netherlands.

Stratum typicum: Meerssen Member, Maastricht Formation, Late Maastrichtian.

Holotype: NHMM 001388 (Pl. 1, Figs. 1a-e; Table 1), a medium-sized adult specimen collected, according to the label, in 1925 (leg. CASELLI) from Valkenburg (southern Limburg, The Netherlands).

Paratypes:

NHMM 2002 139 (ex SENDEN colln.), Meerssen Member, Vroenhoven (province of Limburg, Belgium): an adult specimen used for transverse serial sections (Tables 1-2; Text-Fig. 2; Pl. 1, Figs. 2a-e).

NHMM 2002 140 (leg. R. LANGEVELD), Meerssen Member, Vroenhoven (province of Limburg, Belgium): a small adult specimen, prepared to reveal the brachidium (Tables 1-2; Pl. 1, Figs. 3a-e; Pl. 2, Figs. 2a-b).

NHMM 2003 208 (leg. E. SIMON), Meerssen Member, Maastricht, Ankerpoort-Marnebel quarry, Eben-Emael, from dumped material originally excavated at Vroenhoven (province of Limburg, Belgium): a young specimen used for transverse serial sections (Tables 1-2, Text-Fig. 3, Pl. 1, Figs. 4a-e).

NHMM 2003 209 (ex SIMON Colln, leg. H. ROBERT), Meerssen Member, Ankerpoort-Marnebel quarry, Eben-Emael, from dumped material originally excavated at Vroenhoven (Table 1; Pl. 1, Figs. 5a-e).

NHMM JJ 8323, Meerssen Member, ENCI quarry near Maastricht: a gerontic specimen (Table 1; Pl. 2, Figs. 1a-e).

NHMM 2003 207, Meerssen Member, St-Pietersberg (Maastricht): a medium-sized adult specimen with asymmetric outline (Table 1; Pl. 2, Figs. 3a-e).

IRScNB-MI 10937, Base of the Tuffeau de Saint-Symphorien (Late Maastrichtian), Ciply (province of Hainaut, Belgium): a gerontic specimen (Table 1; Pl. 2, Figs. 5a-e).

Description

External characters

Adult specimens may attain large sizes (Table 1). With a total length of 98.6 mm, paratype NHMM JJ 8323 is among the largest terebratulid brachiopods recorded from Upper Cretaceous strata. Large adult shells are biconvex. The greatest depth of the ventral valve is situated in its posterior part, whereas the greatest depth of the dorsal valve is near mid-valve. The shell is oval in outline, lenticular in lateral profile and lenticular to subcircular in anterior view. Its greatest width appears in the middle of the dorsal valve. Numerous faint growth lines are visible on the shell surface and a capillate ornamentation is clearly visible on the shell surface. The capillae are always better developed on the lateral parts of the beak but they are often visible on the dorsal and ventral lateral parts of the shell. The anterior commissure is sulciplicate.

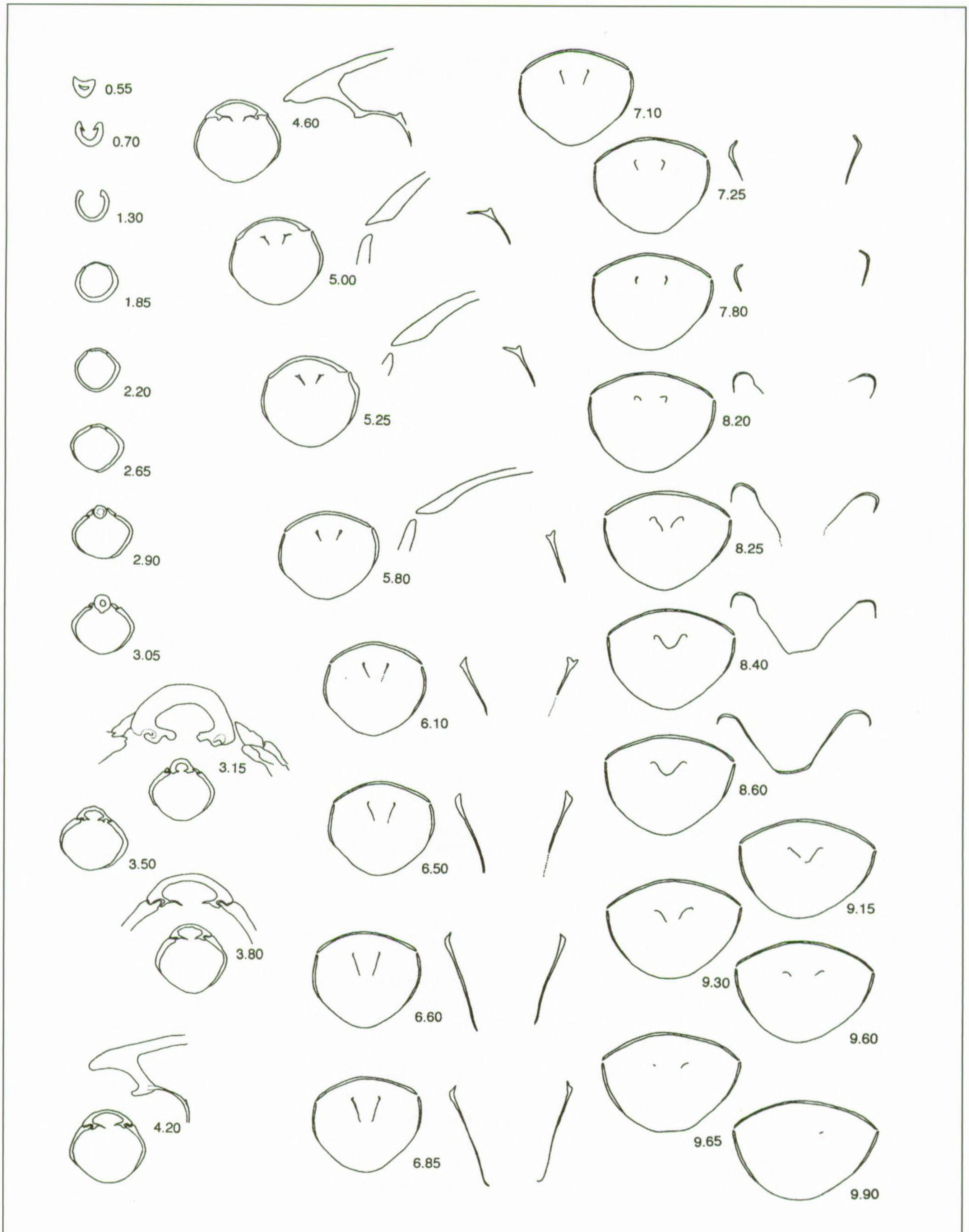

Fig. 3 — Transverse serial sections through the umbonal portion of a young individual (NHMM 2003 208, leg. E. Simon, paratype) of *Cyranoia bosqueti* n. sp. from the Meerssen Member (Maastricht Formation, Late Maastrichtian). Collected from dumped material at the Ankerpoort-Marnebel quarry, originally excavated at Vroenhoven, x 2.1.

Table 2 — Measurements of parts of the loop made on prepared and sectioned paratypes of *Cyranoia bosqueti* n. sp. from the Meerssen Member (Maastricht Formation) of the Maastricht area. Terminology and method of measuring follow COOPER (1983, pp. 14, 15). Calculated ratios; a/LI, b/LI, c/LI, d/LI, e/LI, f/LI, e+f/LI, g/W, g/WI, WI/LI, LI/W and WI/W offer an evaluation of the relationships between loop and shell parameters. These relationships are identical to those outlined extensively by COOPER (1983, p. 15).

Loop parameters measured	**Measurements** mm		
	NHMM 2003 208	NHMM 2002 140	NHMM 2002 139
Length of the loop (LI)	6.9	12.8	17.7
Width of the loop (WI)	3.9	6.1	11.1
Length to the tip of the crural process (a)	3.8	7.5	9.2
Length from tip of the crural process till terminal points (b)	3.1	5.3	8.7
Measure of outer hinge plates length (c)	2.1	4.4	5.6
Measure of crus from end of outer hinge plates to tip of the crural process (d)	1.6	3.1	3.7
Distance from crural process to bridge (e)	1.6	3.3	5.4
Length from posterior limit of transverse band to terminal points (f)	1.5	2.4	2.4
Width of hinge (g)	3.9	6.9	10.5
Length of transverse band at its apex (h)	0.8	1.3	1.2
Length of the dorsal valve (LDV)	22.8	36.5	53.3
Width of the shell and dorsal valve (W)	16.9	27.0	40.5
Loop Angle (in degree)	38.5°	28.0°	39.0°
Calculated ratios	**Values observed**		
	NHMM 2003 208	NHMM 2002 140	NHMM 2002 139
WI/LI	0.57	0.48	0.63
LI/W	0.30	0.47	0.44
WI/W	0.23	0.23	0.27
LI/LDV	0.30	0.35	0.33
a/LI	0.55	0.59	0.52
b/LI	0.45	0.42	0.49
c/LI	0.31	0.34	0.32
d/LI	0.23	0.24	0.21
e/LI	0.23	0.26	0.31
f/LI	0.22	0.19	0.13
e+f/LI	0.45	0.45	0.44
g/WI	1.00	1.13	0.94
g/W	0.23	0.25	0.26

The beak is strong and slightly suberect. The mesothyrid foramen is fairly large, circular, slightly attrite, but never labiate. An uncovered, trapezoidal, wide and slightly convex symphytium is bounded by a straight and relatively deep ridge along its lateral edge. The outer surface of this symphytium is faintly and irregularly striated.

A very young specimen (Table 1) with a length of 23.4 mm exhibits a shell outline that differs from that of larger adults. At this ontogenetic stage, the shell is clearly ventribiconvex and the dorsal valve shows its greatest depth near the umbo. The anterior commissure is rectimarginate. The beak appears relatively shorter and is more erect than in adult shells. Such a small specimen is already capillate on both valves and on the lateral parts of the beak. Another specimen (length 26.6 mm) exhibits a similar aspect. Specimens which are respectively 38.8 mm and 42.0 mm long are still ventribiconvex. Only in older adult and gerontic specimens, does the shell become equally biconvex. The beak of younger individuals already has the pattern found in adult specimens but the anterior commissure of these shells remains rectimarginate. A slightly sulciplicate shell is observed for a 50.0 mm-long specimen but this character is very variable. A larger specimen of 62.3 mm exhibits a weaker sulciplication than smaller individuals (Table 1).

Amongst 16 specimens studied, three are variously asymmetric to varying degrees. In such shells, it should be noted that the largest width is mid-dorsal valve or more posteriorly.

Internal characters

In the ventral valve, an excavate, extremely short pedicle collar is present. The teeth are short and narrow.

In the dorsal valve, a relatively weak cardinal process appears as a transverse half elliptical plate with a depressed surface, surrounded by a low ridge. In specimen NHMM 2002 140 the myophore faces postero-ventrally.

Sockets are quite long and narrow. The socket ridges are long and stout, with inner socket ridges higher than outer socket ridges. Socket ridges are laterally inclined resulting in quite narrow sockets. In their posterior part the sockets are roofed. Exceptionally, as in NHMM 2002 140, a discrete plate appears on the free edge of the socket ridge and extends over the posterior part of the socket. This peculiar character has not been observed in the other specimens studied. This is a typical feature in members of the genus *Rectithyris* SAHNI, 1929. It is not surprising to find this special character in a species of *Cyranoia*, which is also included in the subfamily Rectithyridinae MUIR-WOOD, 1965. However, it is not considered to be of specific value.

The outer hinge plates are quite long. In their posterior part, these are ventrally directed. The outer hinge plates are tapered by sharp crural bases and the inner socket ridges. Inner socket ridges, outer hinge plates and crural bases together form a pair of troughs which appear nearly subcircular in section. In both sectioned specimens (NHMM 2002 139, NHMM 2003 208, see Text-Fig. 2, 3) as in the prepared individual (NHMM 2002 140), the troughs formed by combined outer hinge plates, crural bases and inner socket ridges are always nearly subcircular and never keeled. This character is of specific value because it is observed in all the specimens studied, and moreover, appears independently of the growth stage. Inner hinge plates are weakly but clearly developed as for example in specimen NHMM 2002 140 (Pl. 2, Fig. 3a). The development of inner hinge plates does not depend on the size of the shell. In specimen NHMM 2002 139, which is quite large, inner hinge plates are only developed as thick ridges, present on the inner part of the ventral edges of crural bases. These inner hinge plates are triangular in transverse serial sections (Text-Fig. 2). In NHMM 2003 208, a young individual (Text-Fig. 3), inner hinge plates are not developed.

Crural processes are very high and their tips are gently curved inwards. Tips of crural processes are placed anteriorly to mid-loop and this character seems specifically distinctive. Crural processes are developed anteriorly to the place where outer hinge plates are tapering the crural structure.

Quite long, but relatively low and thin descending branches are developed from the anterior part of the crural processes. They support a broad transverse band which is highly arched. The lateral sides of the transverse band are weakly concave in section, sometimes nearly straight. The median part is nearly flat, gently concave dorsally. Terminal points are very short.

Transverse serial sections made through a very young specimen (NHMM 2003 208, Text-Fig. 3) show a very similar loop structure to the brachidium in a fully-grown individual (NHMM 2002 140, Text-Fig. 2) except for the development of inner hinge plates.

Loop statistics are presented in Table 2. The ratio WI/LI is fairly low (mean value: 0.56) for this species because the brachidium is relatively narrow but long. The ratio c/LI has also a low mean value of 0.33 due to the relative important length of the brachidium compared to the length of the outer hinge plates. On the contrary, the ratio d/LI shows a high mean value (0.23) due to the development of crural processes anterior to mid-loop. The high mean value observed for the ratio g/WI (1.02) confirms that the brachidium is narrow and is as wide as the hinge.

Comparison with other species of *Cyranoia*

Terebratula depressa VALENCIENNES *in* LAMARCK, 1819 var. *visae* HADDING, 1919 originally described from Blaksudden (Ifö, Sweden) from the *Belemnellocamax mammillatus* Zone (upper Lower Campanian), is the type species of the genus *Cyranoia* COOPER, 1983. Specimens illustrated by HADDING (1919, pl. 9, figs. 1-3) are less elongated in outline than representatives of *C. bosqueti* n. sp. Their dorsal valve is more subcircular (ratio LDV/W: 1.0 for the specimen illustrated in HADDING, pl. 9, fig. 1). The beak is also more erect in *Terebratula depressa* var. *visae* than in *Cyranoia bosqueti* n. sp. Beak ridges appear stronger in the former than in the new species (see HADDING 1919, pl. 9, figs 1b, 2b). In dorsal view, the apical angle formed by beak ridges is much wider in *Terebratula depressa* var. *visae* than in *Cyranoia bosqueti* n. sp. The anterior commissure of *Terebratula depressa* var. *visae* is rectimarginate to slightly sulcate while in *Cyranoia bosqueti* n. sp. it is sulciplicate.

The slightly sulcate specimen (USNM 73465a) of *C. visae* (HADDING, 1919) in COOPER, 1983 (pl. 21, figs. 22-24) is also less elongated (ratio LDV/W: 1.1) than representatives of *C. bosqueti* n. sp. (ratio LDV/W: 1.35). A similar observation is made for a second specimen (USNM 112312) illustrated by COOPER, 1983 (pl. 54, figs. 25-26).

The brachidia of *Cyranoia visae* illustrated by COOPER, 1983 (pl. 21, figs. 21, 25-26 and pl. 54, figs. 25-26) show several similarities to the loop observed in the prepared specimen of *C. bosqueti* n. sp. (see Plate 2, Figures 2a-2b). The architecture of the sockets and socket ridges is very similar. There is a plate-like, half elliptical, cardinal process in both species. The crural bases are thin, with acute edges and they are relatively high in both species. Inner hinge plates are present both in *C. visae* and in *C. bosqueti* n. sp.

However, the cardinal process in *C. visae* is much more developed and the loop angle is much wider than in *C. bosqueti* n. sp. Inner hinge plates are much more developed in *C. visae* and may sometimes coalesce (COOPER, 1983, pl. 21, figs. 21). Crural processes in *C. visae* are placed "almost opposite the fulcral plate" as pointed out by COOPER, 1983 (p. 186). In *C. bosqueti* n. sp., crural processes are placed in a more anterior position.

Anomites longirostris WAHLENBERG, 1821, subsequently referred to as *Terebratula longirostris* by NILSSON (1827, p. 33, pl. 4, Figs. 1a-c), HISINGER (1837, p. 82, pl. 23, figs. 9a-c) and LUNDGREN (1885, p. 49, pl. 2, figs. 22a-c) was placed in the genus *Cyranoia* by COOPER (1983, p. 185, pl. 55, fig. 13).

Cyranoia longirostris (WAHLENBERG, 1821) is a large terebratulid from the Kristianstad area (Sweden) occurring in the *Belemnellocamax mammillatus* Zone. Externally, *C. longirostris* could be confused with *C. bosqueti* n. sp. but a closer look at specimens illustrated in the literature shows that, in outline, the largest width of the shell is always situated in its anterior part. In *C. bosqueti* n. sp. the largest width is placed in the middle of the shell. This character is also valid for young specimens of the two species.

Concerning the internal structures, *C. longirostris* exhibits a strong development of the inner hinge plates. The specimen illustrated by COOPER (1983, pl. 55, fig. 13) shows completely coalescent, fused inner hinge plates. Such a development of inner hinge plates has never been observed in representatives of *C. bosqueti* n. sp.

Comparison with other terebratulid brachiopods

"Terebratula" scaphula VON SCHLOTHEIM 1813

This rectithyridine was named by VON SCHLOTHEIM (1813, p. 113), who referred to a species illustrated and described as "Térébratulite de forme allongée" by FAUJAS DE SAINT-FOND in 1803 (p. 160, pl. 26, fig. 8). FAUJAS's collection is supposed to be housed at the Museum national d'Histoire naturelle in Paris but appears mostly to have been lost. However, FAUJAS's drawings seem correct, since other well known brachiopod species illustrated from the Maastricht area are easily identifiable. *"Terebratula" scaphula* VON SCHLOTHEIM 1813 is represented by a unique ventral valve with a wide, convex symphytium, similar to that of the Rectithyridinae. FAUJAS's valve is represented at natural size in dorsal and lateral views. The symphytium of *"T." scaphula* is nearly rectangular whereas that of *C. bosqueti* n. sp. is trapezoidal. The beak of *"T." scaphula*, in dorsal view, is shorter and more massive than that of *C. bosqueti* n. sp. which is more subtriangular, regular and provided with more visible beak ridges. The relative size of the foramen is larger in *"T." scaphula* than in *C. bosqueti* n. sp.

Rectithyris depressa (VALENCIENNES *in* LAMARCK, 1819)

At first glance, medium-sized individuals of *Cyranoia bosqueti* n. sp. might be confused with specimens of *Rectithyris depressa* (VALENCIENNES *in* LAMARCK, 1819), a Cenomanian terebratulid brachiopod commonly found in the Tourtia of Tournai (Hainaut, Belgium) and subsequently designated by D'ARCHIAC (1847, p. 313, pl. 17, figs. 2a-d, 3-10) as *Terebratula nerviensis*. The specimen represented in D'ARCHIAC pl. 17, fig. 6 in particular appears closely similar to representatives of *Cyranoia bosqueti* n. sp. Both species have an elongated outline, a slightly curved beak, a mesothyrid foramen and a wide, wholly visible, striated, convex symphytium. *Rectithyris depressa* was described by D'ARCHIAC (1847, p. 313) as a smooth shell only ornamented by "*des stries transverses, convexes, serrées et peu régulières*". Several authors also described *R. depressa* as a smooth species (e.g. SAHNI 1929, p. 9 and COOPER 1983, p. 213). However, all the numerous, intact specimens, preserved in the collection of the Royal Belgian Institute of natural Sciences in Brussels, are obviously capillate. These capillae are very faint but easily visible on the shell surface of several individuals. On other shells, this character is more attrite and can only be seen under special lighting conditions. This character has thus been often overlooked. However, the character "capillate shell surface" is not a valid feature for distinguishing between *Rectithyris depressa* and *Cyranoia bosqueti* n. sp.

Nevertheless, other clear distinctions can be established. The shell of *Cyranoia bosqueti* n. sp. is equally biconvex at the adult stage whereas that of *Rectithyris depressa* is more depressed and remains typically ventribiconvex. The anterior commisssure of *Cyranoia bosqueti* n. sp. is sulciplicate in adult specimens whereas it is rectimarginate or narrowly uniplicate in *R. depressa*. The beak ridges are present but weakly developed in *Cyranoia bosqueti* n. sp. while they are stronger in *Rectithyris depressa*.

The brachidium of *Rectithyris depressa* is relatively shorter and wider than that of *Cyranoia bosqueti* n. sp. In *Rectithyris depressa*, the crural processes are placed much nearer to where the anterior ends of outer hinge plates taper. In *Cyranoia bosqueti* n. sp. crural processes are placed more anteriorly, resulting in a larger mean value for the ratio d/LI (Table 2). The combination of inner socket ridges, outer hinge plates and crural bases forms a keeled pattern in *Rectithyris depressa* whereas a wide U-shaped pattern is observed in *Cyranoia bosqueti* n. sp. But the most striking difference between loops of these two terebratulids is that inner hinge plates are lacking in *Rectithyris depressa* but clearly visible in *Cyranoia bosqueti* n. sp. Another striking difference between architectures of these two brachidia is seen in the distance between crural process to bridge (=e). This distance is much greater in *C. bosqueti* than in *Rectithyris depressa*, resulting in a higher value for the ratio e/LI in the former. (Table 2).

Comparison with ?*Rectithyris viquesneli* (D'ARCHIAC, 1847)

This Cenomanian species (Tourtia de Tournai in Tournai, Hainaut, Belgium) described by D'ARCHIAC (1847, p. 316, pl. 18, figs. 1a-c), is much smaller than *C. bosqueti* n. sp. and has a more subcircular outline. The beak of the former is truncate and relatively larger than that of *C. bosqueti* n. sp., and also shows a much wider foramen. The internal structures of the Belgian Cenomanian specimens remain unknown. The ?*Rectithyris viquesneli* specimen from Albian sandstones near Annopol (Poland), illustrated by POPIEL-BARCZYK (1972, pl. 3, figs. 6-9), has a very different outline than the original specimen of D'ARCHIAC, especially in lateral profile. This Polish shell is more biconvex and its beak is less truncate than the topotypical material from Belgium, which suggests that Polish and Belgian material is not conspecific. The brachidium of?*R. viquesneli* illustrated by POPIEL-BARCZYK (1972, pl. 3, fig. 8) has strongly developed inner hinge plates, a character not established in the genus *Rectithyris* SAHNI, 1929). The cardinal process of ?*Rectithyris viquesneli* and its socket structures are very distinct from those observed in *C. bosqueti* n. sp.

Generic attribution of the species

Cyranoia bosqueti n. sp. is thus considered to belong to the genus *Cyranoia* COOPER, 1983. The differences in the position of crural processes, loop length, loop width, size of the cardinal process, structure of typical troughs made by inner sockets ridges, outer hinge plates and crural bases, are considered to represent interspecific variation.

Distribution

Collected from the Meerssen Member (Upper Maastrichtian) in The Netherlands, *Cyranoia bosqueti* n. sp. is known from the Maastricht area and also from Valkenburg (southern Limburg). In Belgium, *C. bosqueti* n. sp. has been collected from Vroenhoven (Meerssen Member, Upper Maastrichtian) but also from the base of the Tuffeau de Saint Symphorien at Ciply (Mons basin, Hainaut Province). This paper was already in press, when two new specimens of *C. bosqueti* n. sp. from Ciply become available for study. They have been collected from the top of the Phosphatic Chalk of Ciply (Lower Maastrichtian, *Belemnella obtusa* Zone). The stratigraphical range for *C. bosqueti* n. sp. is thus now from the Lower Maastrichtian to the upper part of the Upper Maastrichtian.

Palaeoecology

Cyranoia bosqueti n. sp., a brachiopod found in living position

The Meerssen Member as exposed in the Maastricht area comprises "poorly indurated white yellowish coarse – to very coarse grained chalks" (JAGT 1999, p. 30). ALBERS & FELDER (1979) noted that this unit represented a fully marine, euphotic, subtropical environment, formed with a relative high level of hydrodynamic energy which produced a high biological diversity allowing the evolution of rich and complex biocoenoses. The rich fauna includes numerous bivalves, corals, echinoderms and brachiopods. All specimens of *C. bosqueti* n. sp. are preserved articulated. Dissociated dorsal or ventral have not been observed. In contrast, "*Terebratula*" *scaphula* VON SCHLOTHEIM, 1813 is only known from a ventral valve. In such a high energy environment, one might expect to find a large number of loose valves or crushed shells. The fact that shells are found intact probably indicates that the live animals were rapidly buried during storms. The gerontic NHMM n° JJ8323 (Pl. 2, Figs. 1a-e) was found in living position (pers. comm. J.W.M. JAGT), upright with its beak down in fairly coarse sediment. The large foramen indicates that the pedicle was fairly thick, allowing the animal to withstand very strong wave effects. The attrition of the foramen is due to the development of a very short, strong pedicle and this is also suggestive of a high level of hydrodynamic energy.

Bite-marks

Out of sixteen specimens studied, three show bite-marks near the lateral commissure or in the middle of the valves. Such marks are seen on the specimen NHMM n° 2003 208 (Pl. 1, Fig. 5c) – the shell was pinched on both dorsal and ventral valves near the lateral commissure, on left and right sides. These traces are so similar that they can be considered to represent a single bite. The predator (a fish or a reptile) must have had pointed teeth, placed in opposition, and well separated from each other (the two traces near the lateral commissures are separated by a distance of 28.1 mm, nearly the width of the shell). The specimen repaired the damaged part of the shell. In the middle of the same shell (Pl. 1, Fig. 5a, 5b) again on both ventral and dorsal valves, the shell reveals a second fracture which was not repaired, probably leading to the death of the animal.

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Explanation of Plates

PLATE 1

Cyranoia bosqueti n. sp. from the Meerssen Member (Maastricht Formation, Late Maastrichtian), in dorsal (a), ventral (b), lateral (c), anterior (d) and posterior (e) views, respectively.

Fig. 1 — NHMM 001388 (holotype); fully-grown, articulated specimen from Valkenburg aan de Geul (December 1925, leg. Caselli). Length of shell 75 mm, x 0.75.

Fig. 2 — NHMM 2002 139 (ex Senden Colln, paratype); medium-sized, adult specimen from Vroenhoven, used for transverse serial sections (Text-fig. 2) – peels are housed in the NHMM collections. Length of shell 62.3 mm, x 0.98.

Fig. 3 — NHMM 2002 140 (paratype, leg. R. Langeveld, Eindhoven); smaller-sized, adult specimen from Vroenhoven; prepared to reveal the brachidium. Length of shell 42.5 mm, x 0.97.

Fig. 4 — NHMM 2003 208 (paratype, leg. E. Simon, Brussels); young individual from Ankerpoort-Marnebel quarry (Eben-Emael), from dumped material originally excavated at Vroenhoven, used for transverse serial sections (Text-fig. 3). Peels are housed in the NHMM collections. Length of shell 26.6 mm, x 0.98.

Fig. 5 — NHMM 2003 209 (paratype, leg. E. Simon, Brussels); medium-sized, adult specimen from Ankerpoort-Marnebel quarry (Eben-Emael), from dumped material originally excavated at Vroenhoven. Specimen shows bitemarks and repaired traces at mid-length near the lateral commissure (Fig. 5c). Shell was bitten and broken a second time – this damage remained unrepaired (Fig. 5a, b). Length of shell 47 mm, x 1.

PLATE 2

Cyranoia bosqueti n. sp.

Fig. 1 — NHMM JJ 8323 (paratype) ; gerontic specimen from the Meerssen Member, ENCI-Maastricht bv quarry, probably representing the largest terebratulid brachiopod ever recorded from Upper Cretaceous strata, found in living position, with beak down and anterior commissure up, in dorsal (a), ventral (b), lateral (c), anterior (d) and posterior (e) views. Length of shell 98.6 mm, x 0.6.

Fig. 2 — NHMM 2002 140; brachidium prepared (see Pl. 1, Fig. 3a-e), in ventral (a) and oblique lateral (b) views. The left crural process was broken during preparation and the right one was repaired. Note the U-shaped troughs formed by the combination of inner socket ridges, outer hinge plates and crural bases, and the relative length of the loop. Such a narrow loop (28°) is not a consistent character for this species. Length of loop 14.04 mm, x 3.5.

Fig. 3 — NHMM 2003 207 (paratype); medium-sized, adult specimen with asymmetric outline, from St. Pietersberg, south of Maastricht; Meerssen Member (Maastricht Formation), in dorsal (a), ventral (b), lateral (c), anterior (d) and posterior (e) views. Length of shell 56.7 mm, x 0.75.

Fig. 4 — Scanning electron microscope illustration showing development of capillae on shell surface in *C. bosqueti* n. sp.; a – capillae developed on lateral part of beak (ventral valve) near the commissure; b – other zone on lateral part of the same beak with a more densely capillate surface, x 17.5.

Fig. 5 — IRScNB MI 10937 (paratype); large, gerontic individual from the Tuffeau de Saint-Symphorien at Ciply (Hainaut, Belgium), Late Maastrichtian. Length of shell 87.7 mm, x 0.60.

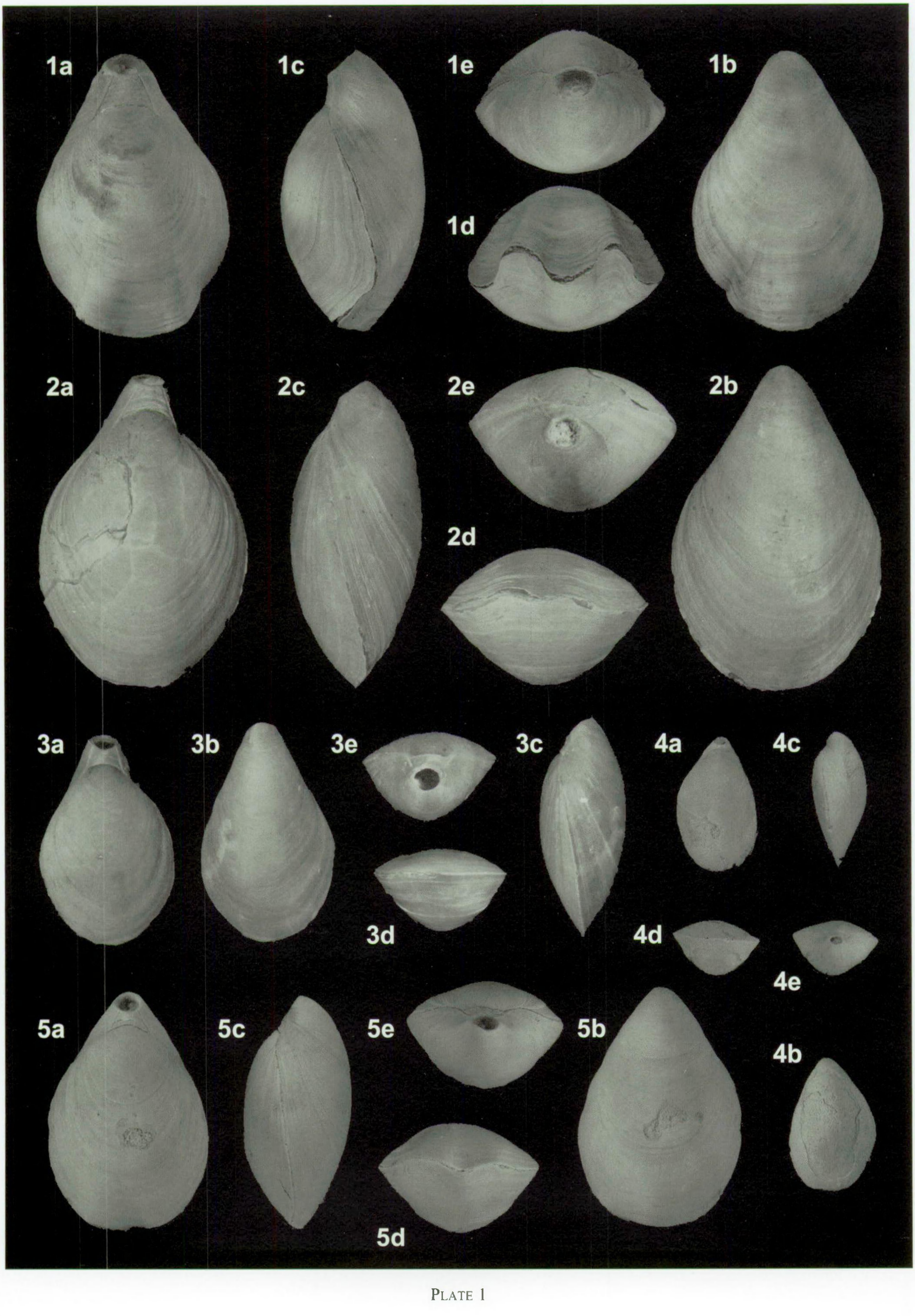
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PLATE 1

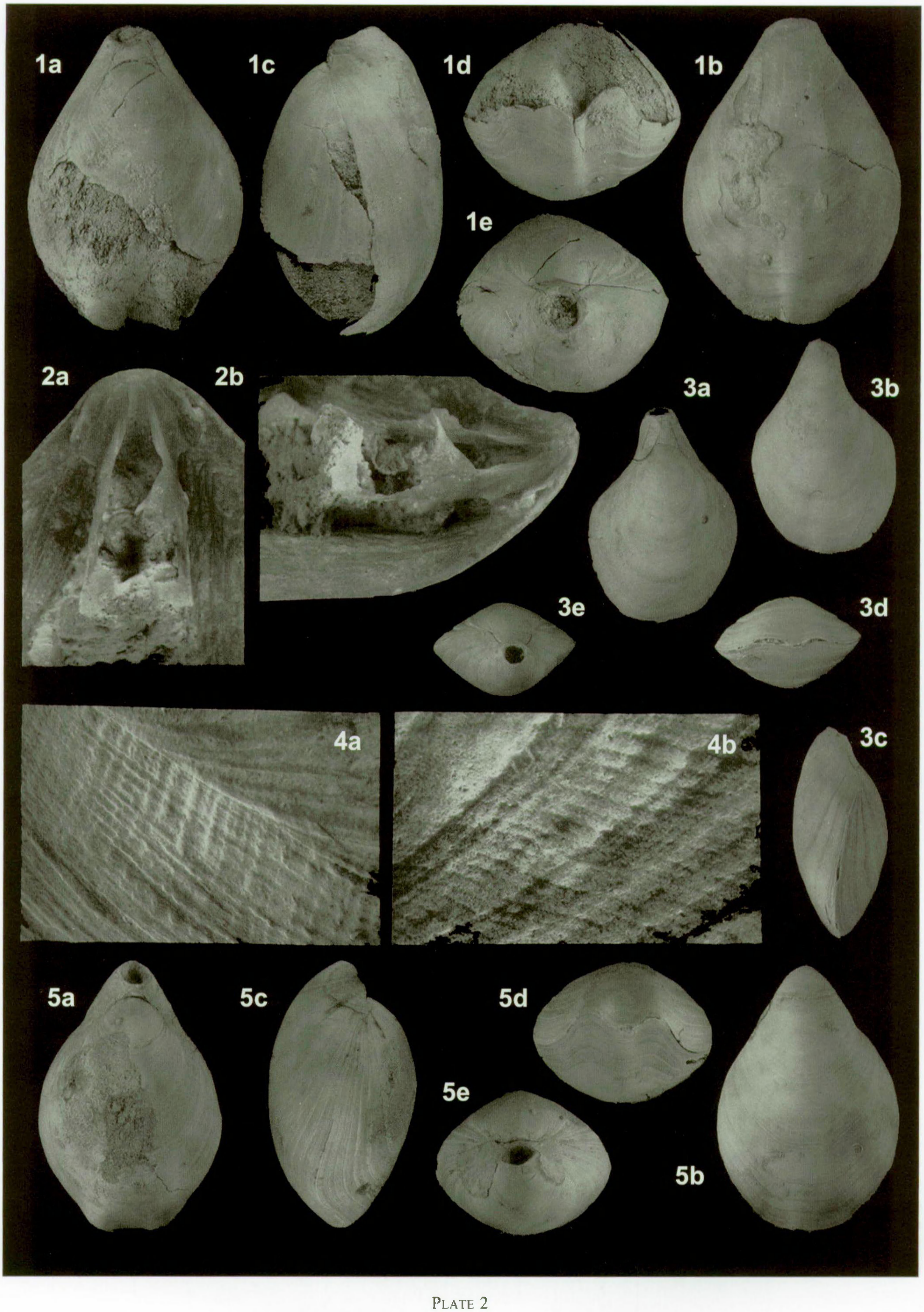

PLATE 2