

A first step in the revision of the genus *Cretirhynchia* PETTITT, 1950

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Abstract

The rhynchonellid brachiopod genus *Cretirhynchia* PETTITT, 1950 was in need of revision. Representatives of this genus together with the original material studied by PETTITT in 1950 and 1954 were reviewed. Transverse serial sections were made and the internal structures observed in this study allow us to remove some species from the genus *Cretirhynchia* and to split the genus into four subgenera. A new species and a new subspecies of *Cretirhynchia* are described here. In addition a new genus, related to the genus *Cyclothyris* M'COY, 1844 has been erected.

Key-words: Brachiopods, *Cretirhynchia*, Revision, Cretaceous, Europe.

Résumé

Une révision du genre *Cretirhynchia* PETTITT, 1950 était souhaitée, depuis fort longtemps, par de nombreux auteurs. La plupart des espèces incluses dans ce genre et surtout le matériel original étudié par PETTITT en 1950 et 1954, ont fait l'objet de nouveaux examens. Des sections transversales sériées ont été réalisées et les structures internes observées ont permis d'extraire certaines espèces du genre *Cretirhynchia* et d'ériger au sein de ce genre quatre nouveaux sous-genres. Une nouvelle espèce et une nouvelle sous-espèce de *Cretirhynchia* sont décrites. De plus, un nouveau genre, montrant des affinités avec le genre *Cyclothyris* M'COY, 1844 est érigé.

Mots-clés: Brachiopodes, *Cretirhynchia*, Révision, Cretacé, Europe.

Introduction

A persistent problem for establishing distinct species among Upper Chalk rhynchonellid brachiopods has been observed, since the publication, in 1816, of the second volume of "The Mineral Conchology of Great Britain" by J. SOWERBY. Abundant comments and erroneous applications, concerning *Terebratula plicatilis* J. SOWERBY, 1816 and *Terebratula octoplicata* J. SOWERBY, 1816 have been published for more than a century.

DAVIDSON tried to distinguish valid species among the numerous specimens collected from Great Britain. In his monograph of the British Fossil Brachiopoda (1855, Part II, The Cretaceous Brachiopoda) several species from the Upper Chalk were discussed and illustrated. The material

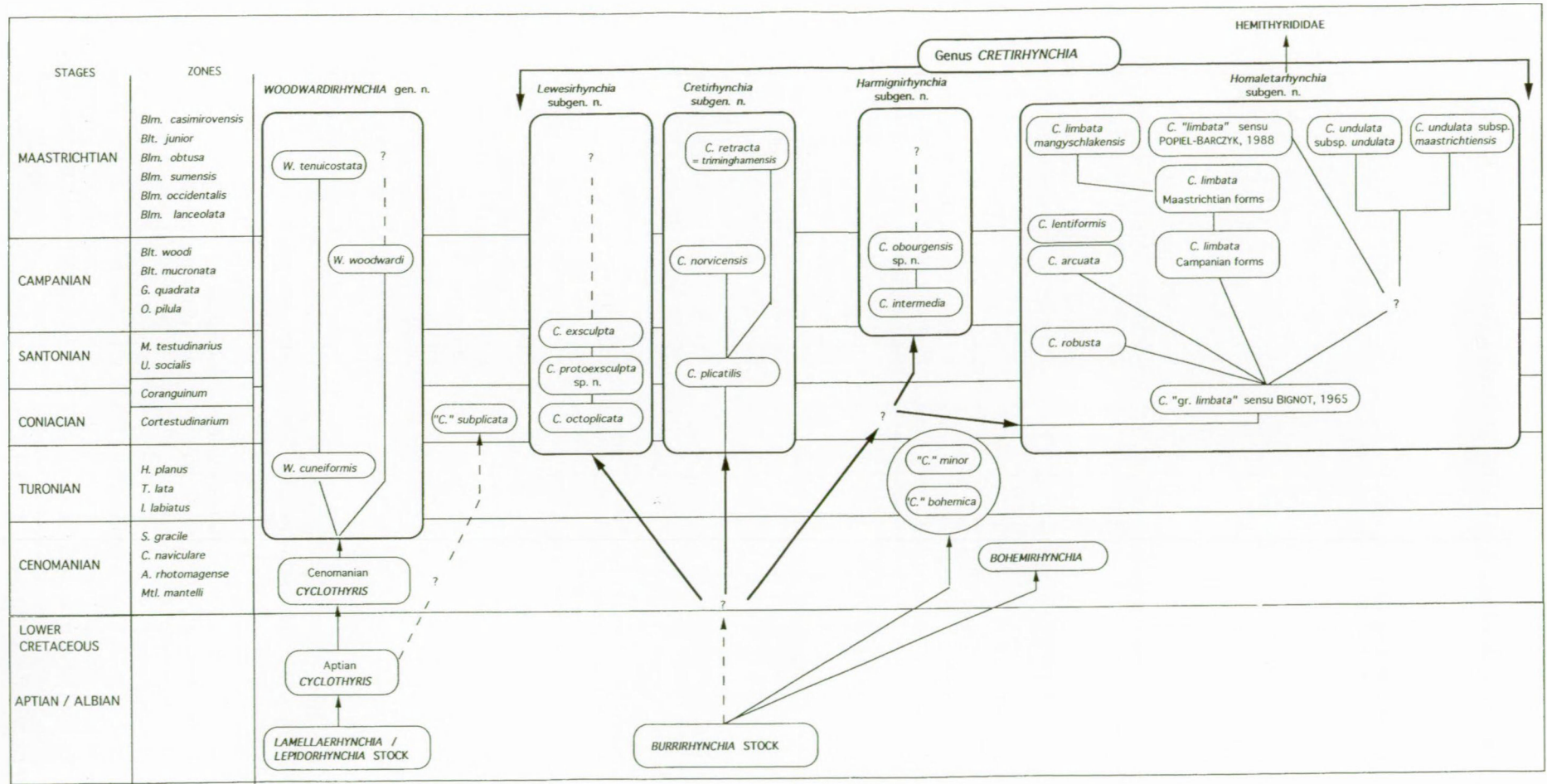
collected from Britain has been compared with other European rhynchonellid brachiopods. Observations made by other palaeontologists as, for instance, the remarks of WOODWARD (1833), were reported in this work which remains a masterpiece on the subject.

However, as these studies were based only on the external characters of the shell, problems subsided for erecting valid species. DAVIDSON (1855, p. 75) clearly described this problem in one sentence: "...it is often almost impossible to draw up a diagnosis embodying the character of every variety." Great confusion in this subject was thus maintained for several decades.

In 1950, PETTITT, using transverse serial sections, erected the genus *Cretirhynchia* and established the distinction between this genus and the genus *Cyclothyris* M'COY, 1844. He also erected, in 1954, the genus *Orbirhynchia* represented by numerous species collected from the European Upper Cretaceous chalk.

Species included by PETTITT in the genus *Cretirhynchia* were presented in three series. The first (*Cretirhynchia plicatilis* series) deals with ribbed species, showing a reduced number of costae near the commissure. The second (*Cretirhynchia exsculpta* series) includes ribbed species, exhibiting incipient splitting of the costae near the commissure. The third series (*Cretirhynchia limbata* series) is not accurately defined but includes all species with a "smooth shell".

The series of PETTITT are mainly based on external characters and no taxonomic relationships have been drawn by this author. These series do not represent taxonomic units. However, PETTITT carefully described a lot of different species, collected from Great Britain and the stratigraphy of these species was indicated (PETTITT, 1950, tables 1-3, pp. 3-5). The work of PETTITT was a major step in improving the knowledge of Upper Cretaceous rhynchonellid brachiopods. However, this work was not immediately acknowledged by palaeontologists in Western Europe. The new species erected by PETTITT were sharply criticized. For instance, STEINICH (1965, p. 23) thought that the variability inside a species was often larger than the variation of the characters chosen by PETTITT for separating his species. The need of revision and of subdivision of the genus *Cretirhynchia* was already expressed by AGER (1965) and AGER *et al.* (1972). POPIEL-BARCZYK (1988, p. 5) and JOHANSEN & SURLYK (1990, p. 838) also suggested the necessity of a revision of the genus *Cretirhynchia* and its possible subdivision. The doubt, concerning the species of PETTITT,



partly results from the lack of knowledge of the whole morphological variation inside the representatives of the genus *Cretirhynchia* and of their precise and complete geographical and stratigraphical distributions. Moreover, it is rather difficult to recognize the different species, without a direct and concrete comparison with the original type specimens. This introduced erroneous identifications of species into the literature (see the taxonomic part of this paper).

Relationships between the genus *Cretirhynchia* and other rhynchonellid genera have been studied by OWEN (1962). He stressed that the genus *Cretirhynchia* probably arose from the Aptian genus *Burrirhynchia* (OWEN, 1962, p. 58) and not from the genus *Cyclothyris* M'COY, 1844. *Burrirhynchia* and *Cretirhynchia* representatives have much in common. Both do not have a pedicle collar and they possess narrow, thickened hinge-plates. The median septum present in the dorsal valve persists for well over one half the length of the shell. The raduliform crura are given off dorsally from subquadrate crural bases (OWEN, 1962, p. 61).

The present paper is a first step in the revision of the genus *Cretirhynchia*. The species erected by PETTITT (1950) are reviewed and serial sections of the original material have been completed. The validity of PETTITT's species diagnoses and series is discussed. Tentatively, a new light is thrown on the affinities existing between Upper Chalk rhynchonellid brachiopods. Several species have been removed from the genus *Cretirhynchia* and lastly, the genus *Cretirhynchia* has been split into four subgenera. Their diagnoses are sustained by both external and internal morphological characters.

Material and methods

The material used by PETTITT in 1950 constitutes the largest part of the rhynchonellid brachiopods studied in this paper. Only two species could not be investigated due to the lack of material: *Cretirhynchia lenticularis* PETTITT, 1950 and *C. magna* PETTITT, 1950. The collections, preserved in the Natural History Museum in London (NHM), and some type specimens of PETTITT, preserved in the British Geological Survey, are taken into account. Large numbers of *Cretirhynchia* specimens, pre-

served in the Institut royal des Sciences naturelles de Belgique in Brussels (IRScNB) are included in this study. Specimens from Poland are also considered here, and their specific attribution is discussed. They have been studied previously by POPIEL-BARCZYK in 1988. This Polish material is preserved in the Museum of the Earth in Warsaw (Muzeum Ziemi PAN). Rhynchonellid brachiopods, collected by VON HANSTEIN (1879) from Cipluy (Hainaut, Belgium) and preserved in the Geological and Palaeontological Institute of the University of Bonn are reviewed. Upper Cretaceous specimens more recently collected in Belgium (Mons basin and Maastricht area), France (Seine-maritime), Germany (Ahlden near Hanover), and Denmark (Møns Klint and Stevns Klint) are added to our study.

Transverse serial sections were made by the method described by AGER (1965, pp. 212-218) and peels were taken on cellulose acetate following the method of STERNBERG & BELDING (1942). In some cases, the matrix of the specimens sectioned consisted of very soft white chalk. With such a material, the use of acetic acid is not possible and peels of the serial sections cannot be made. In this case, macrophotographs of the sections were taken and enlargements used to draw the serial sections for these specimens. Peels or photographs of the serial sections made from British specimens are preserved in the NHM, whereas those made on specimens from the other European countries are kept in the IRScNB.

A sharper concept of the genus *Cretirhynchia* PETTITT, 1950

Terebratulina plicatilis J. SOWERBY, 1816 is the type species of the genus *Cretirhynchia*. PETTITT (1950, text-fig. 4, p. 11) published transverse serial sections of a specimen of *Cretirhynchia plicatilis* collected from the *Coranguinum* Zone of Northfleet (Kent, England). All the important elements of the generic diagnosis are visible on this figure which can be consulted.

No pedicle collar is observed. The dental plates are ventrally convergent. The hinge plates are short and subtriangular. The septum in the dorsal valve is well developed and persistent. Crural bases are subquadrate and raduliform crura remain close together. All these characters, considered as a whole, are the most essential for assigning a rhynchonellid brachiopod to the genus *Cretirhynchia*. They also allowed OWEN (1962, p. 59) to propose the Aptian genus *Burrirhynchia* OWEN, 1962 as potential ancestor to the genus *Cretirhynchia*. Although dental plates are less convergent, and the dorsal septum is less developed in *Burrirhynchia* than in *Cretirhynchia*, there is a structural similarity between these two types of rhynchonellid brachiopods. Hinge plates are very similar and crural bases, given off dorsally, are subquadrate in both genera. Another important feature clearly visible in *Burrirhynchia*, is the fact that raduliform crura remain close together. The slight concavity of the crura is similar in *Burrirhynchia* and *Cretirhynchia*: they are inwardly concave. They are never dorsally concave as in the representatives of the genus *Cyclothyris* M'COY, 1844. This proposition, considering



Fig. 1 — Relationships between Upper Chalk rhynchonellid brachiopods. One group of genera, arising from the genus *Cyclothyris* M'COY, 1844, has the *Lamellaerhynchia/Lepidorhynchia* stock as potential ancestor, while the second group of genera, which includes *Cretirhynchia* PETTITT, 1950, has the genus *Burrirhynchia*, OWEN, 1962 as potential ancestor. The species of rhynchonellid brachiopods have been placed in a genus or subgenus following the results of this paper. They are placed on the figure in function of their known stratigraphical position.

Mtl.: Mantelliceras, A.: *Acanthoceras*, C.: *Calycoceras*, S.: *Sciponoceras*, I.: *Inoceramus*, T.: *Terebratulina*, H.: *Holaster*, U.: *Uintacrinus*, M.: *Marsupites*, O.: *Offaster*, G.: *Goniot euthis*, Blt.: *Belemnitella*, Blm.: *Belemnella*.

Burrirhynchia as potential ancestor of *Cretirhynchia* is thus reconfirmed here.

In 1994, MOTCHUROVA-DEKOVA emended the diagnosis of the genus *Cretirhynchia*. She pointed out that the shell microstructure of *Cretirhynchia* is characterized by three calcitic layers: primary, secondary and prismatic. The secondary layer is fine-fibrous. The fibres are diamond-shaped to square in cross section (MOTCHUROVA-DEKOVA, 1994, p. 88).

Among the species included by PETTITT (1950) in the genus *Cretirhynchia*, only three species simultaneously exhibit the external and internal features described in the diagnosis. This group, includes *Cretirhynchia plicatilis* (J. SOWERBY, 1816), *C. norvicensis* PETTITT, 1950 and *C. triminghamensis* PETTITT, 1950 which is a junior synonym of *C. retracta* (ROEMER, 1841). These species illustrate a restricted concept of the genus *Cretirhynchia*.

Other species, previously included by PETTITT in the genus *Cretirhynchia*, show the essential features of this genus. They have no pedicle collar, their dental plates are clearly convergent, the hinge plates are small and subtriangular, the raduliform crura are given off dorsally from more or less subquadrate crural bases and a dorsal septum is present. They can be considered as representatives of the genus *Cretirhynchia*. But, in these species, some secondary characters, which are absent in *C. plicatilis*, *C. retracta* and in *C. norvicensis*, become evident in transverse serial sections. These secondary characters allow the erection of distinct subgenera within the genus *Cretirhynchia*. These characters mainly affect the aspect of the hinge plates and the development of the crura, but some external features are also taken into account. This splitting of the genus *Cretirhynchia* into four subgenera, is developed further. The diagnoses of these subgenera can be found in the taxonomic part of this paper. Proposed relationships between Upper Chalk rhynchonellid brachiopod species are illustrated in Figure 1.

The internal features observed in "*Cretirhynchia*" *cuneiformis* PETTITT, 1950 and in "*C.*" *woodwardi* (DAVIDSON, 1855) indicate a close relationship with the genus *Cyclothyris* M'COY, 1844. These rhynchonellid species are now removed from the genus *Cretirhynchia* and a new genus is erected for them (see taxonomic part of this paper).

Cretirhynchia bohémica (SCHLOENBACH, 1868) and *C. aff. cuneiformis* PETTITT, 1950 are Turonian rhynchonellid brachiopods. They have several features in common with representatives of the genus *Cretirhynchia*: no well developed pedicle collar, convergent dental plates (rarely subparallel), presence of a coarse persistent dorsal septum, subquadrate crural bases and raduliform crura remaining close together. But the hinge plates are much wider, often slightly forked (NEKVASILOVA, 1974, text-figs. 5-6, 9). Moreover the hinge plates are nearly parallel to the hinge axis or are even dorsally deflected. We consider that these species constitute a homogenous group distinct from the typical *Cretirhynchia*. As similar internal features are observed in *Cretirhynchia minor* PETTITT, 1950 this Upper Turonian species is removed from the genus *Cretirhynchia* and is placed in this group, near "*C.*" *bohémica* and "*C.*" *aff. cuneiformis*. Further studies are necessary to decide if these species should be

placed together in one new genus or in two new genera. For this reason, it is better to allow them to remain for the present with uncertain generic affinity.

The Cenomanian rhynchonellid brachiopod *Bohemirhynchia soukupi* NEKVASILOVA, 1973 (pp. 78-84, text-figs. 1-3, pl. 1, figs. 1-4, pl. 5, fig. 4, pl. 7, figs. 1-2) has several characters in common with *Burrirhynchia* and *Cretirhynchia*. In this species, a pedicle collar is not developed, dental plates are ventrally convergent and a persistent septum is developed on the dorsal valve floor. The hinge plates are much narrower than those observed in "*C.*" *bohémica* and are subtriangular in outline. The raduliform crura, which remain close together, are given off from more or less subquadrate crural bases. But, the crura in *Bohemirhynchia soukupi* are dorsally concave and this specific character is never observed in representatives of *Cretirhynchia* or *Burrirhynchia*. The genus *Bohemirhynchia* NEKVASILOVA, 1973 is herein considered to be related to *Burrirhynchia* but remains distinct from the genus *Cretirhynchia*.

About the series proposed by PETTITT (1950)

Species included in the genus *Cretirhynchia* were arranged by PETTITT (1950, p. 2) in three distinct series. In the light of present knowledge, these series are no longer tenable. Some examples are presented here to justify this position.

The serial sections of *C. octoplicata* (J. SOWERBY, 1816) are identical to the sections of *C. exsculpta* PETTITT, 1950 (Figs. 11-12). In PETTITT, *C. octoplicata* was placed in the first series ("*plicatilis* series") and *C. exsculpta* was placed in the second series ("*exsculpta* series"). Obviously, the first series of PETTITT is not homogenous and in the present paper, *C. octoplicata* and *C. exsculpta* have been placed in a new subgenus within the genus *Cretirhynchia*.

The second series, the "*exsculpta* series" as described by PETTITT (1950, p. 2), which was based on the tendency towards incipient splitting of the costae in the latest stages of growth, is not acceptable. The species included in the "*exsculpta*" series are *C. minor* PETTITT, 1950, *C. exsculpta* PETTITT, 1950, *C. woodwardi* (DAVIDSON, 1855) and *C. magna* PETTITT, 1950. When the internal features of these species are analyzed, it appears that they have little in common and it can now be demonstrated that the second series of PETTITT (1950) included several species which do not belong to the same genus.

The third series of PETTITT (1950, p. 2) which seems more homogenous, includes all the "smooth" species. *Cretirhynchia limbata* (VON SCHLOTHEIM, 1813) has been chosen as "typical representative" of this series. PETTITT (1950, p. 2) considered that this group had special features which might be held to justify the generic segregation of the series.

Transverse serial sections made of species of this series confirm that a segregation can easily be considered. But, an astonishing internal structure was discovered for "*Cretirhynchia*" *subplicata* (MANTELL, 1822). This species was considered by DAVIDSON (1855, pp. 79-80) as a junior synonym of *C. limbata* (VON SCHLOTHEIM, 1813) because of the superficial similarity affecting the external outline of both brachiopod species. PETTITT (1950, pp. 23-24) pointed out constant differences

between these two species and gave a very accurate description for "*C.*" *subplicata*. Our serial sections (Fig. 7) of "*C.*" *subplicata* confirm the opinions of MANTELL (1822) and PETTITT (1950). This rhynchonellid brachiopod must be considered as a valid species, absolutely distinct from *C. limbata*. The internal aspect of "*C.*" *subplicata* is different from the typical structure of the genus *Cretirhynchia*. The dental plates are not convergent ventrally but parallel to subparallel. The hinge plates are relatively wide and forked. Although the crural bases are subquadrate, the crura are strongly concave and they do not remain very close together. These serial sections of "*C.*" *subplicata* are closer to the *Cyclothyris* structures than to the *Burrirhynchia* structures. "*C.*" *subplicata* is thus removed from the genus *Cretirhynchia* and tentatively placed near the genus *Cyclothyris* (Fig. 1). But, as no other "smooth" species, exhibiting cyclothyridid internal structures are known, "*C.*" *subplicata* remains of uncertain generic affinity.

About the "Passage forms" described by PETTITT (1950)

In his monograph, PETTITT often described "passage forms" between two species of *Cretirhynchia*. He recognized such "passage forms" between "*Cretirhynchia*" *cuneiformis* and *C. octoplicata* (J. SOWERBY, 1816), and between *C. plicatilis* (J. SOWERBY, 1816) and *C. lenticularis* PETTITT, 1950 (p. 7, 9, 12). Other "passage forms" between *C. intermedia* PETTITT, 1950 and *C. norvicensis* PETTITT, 1950 are pointed out (PETTITT, 1950, p. 15, 17). Concerning the species included in his second series, "passage forms" between *Cretirhynchia Woodwardi* (DAVIDSON, 1855) and *C. exsculpta* PETTITT, 1950 are described. For species included in the third series, no "passage forms" were observed.

In the light of present knowledge, these passage forms of PETTITT are not acceptable. The internal structures observed by serial sections demonstrate that passage forms between "*Cretirhynchia*" *cuneiformis* (PETTITT, 1950), a species related to the genus *Cyclothyris* M'COY, 1844, and *Cretirhynchia plicatilis* (J. SOWERBY, 1816) cannot be taken into account. For the same reasons, passage forms between "*C.*" *cuneiformis* and *Cretirhynchia octoplicata* are not possible. A similar remark can be stressed for passage forms between "*Cretirhynchia*" *woodwardi* (DAVIDSON, 1855) and *Cretirhynchia exsculpta* PETTITT, 1950 which are now rhynchonellid species placed in two different genera (see taxonomic part of this paper).

These "passage forms" were only described on the basis of their external characters and they represent only intraspecific or taphonomical variations. These morphological variations or taphonomical distinctive aspects can sometimes be important. Some individuals are so different from the type specimen, that they could easily be considered as candidates to a new specific designation. In this case, the serial sections which are much less variable than the external characters, make it possible to assign this "intermediate form" to an already described species. An example is given, with the specimens of "*Cretirhynchia*" *cuneiformis* collected from Bardouville (Rouen, France) which have been sectioned for the present paper.

On the other hand, it has never been demonstrated that the evolutionary process in the Upper Chalk rhynchonellid brachiopods is a progressive and continuous process. Further studies are needed to more accurately establish this evolutionary process.

Taxonomic descriptions

Phylum Brachiopoda DUMÉRIL, 1806

Subphylum Rhynchonelliformea WILLIAMS *et al.*, 1996

Class Rhynchonellata WILLIAMS *et al.*, 1996

Order Rhynchonellida KUHN, 1949

Superfamily Rhynchonelloidea D'ORBIGNY, 1847

Family Rhynchonellidae D'ORBIGNY, 1847

Nomenclative note: the family-group names based on *Rhynchonella* should be attributed to D'ORBIGNY, 1847 and not to GRAY, 1848 (MANCENIDO, OWEN & MORRIS, 1993 p. 193).

Subfamily Cyclothyridinae MAKRIDIN, 1955 emended
OWEN, 1962

Genus *Woodwardirhynchia* gen. n.

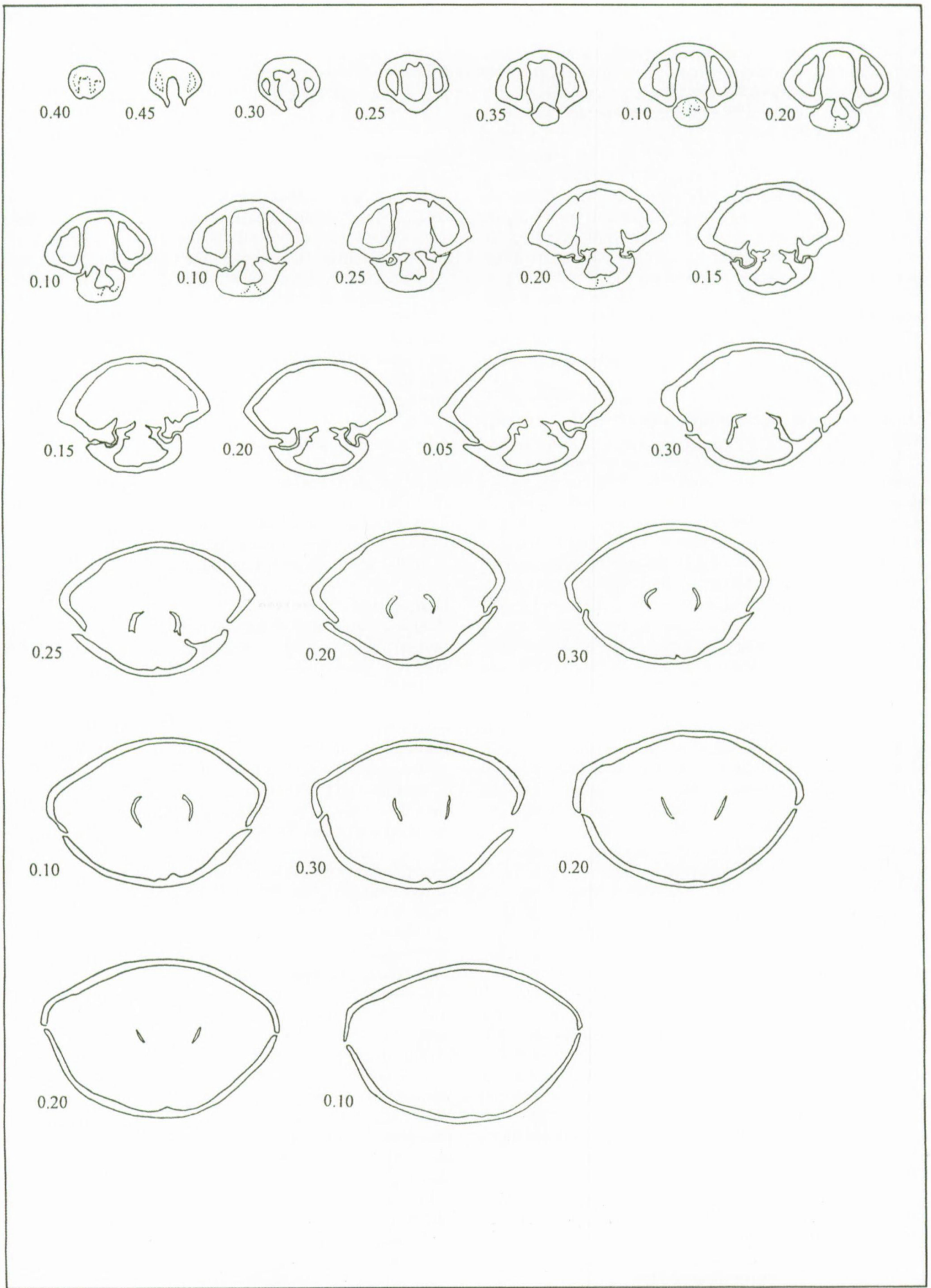
Type species: *Cretirhynchia cuneiformis* PETTITT, 1950
Derivatio nominis: in honour of S.P. WOODWARD and from the greek *Rugcos* meaning beak.

Diagnosis of the genus

Costate rhynchonellid brachiopod with a cyclothyridid outline. Shell slightly wider than long. Beak short and curved. Beak ridges distinct. Extensive interarea. Hypothyridid, auriculate foramen. Well developed pedicle collar. Dental plates divergent ventrally in their early stages and subparallel to slightly convergent anteriorly. Forked hinge plates, generally short, triangular in outline with a ventral concave surface. Raduliform crura, inwardly concave and becoming straight in transverse section near distal end. Crura diverging laterally. Septum persistent on dorsal valve floor.

Comparison with other genera

Woodwardirhynchia gen. n. has several features in common with the genus *Cyclothyris* M'COY, 1844 as the development of a pedicle collar, subparallel thin dental plates and forked hinge plates. But, in *Cyclothyris*, the hinge plates are more parallel to the hinge axis whereas in *Woodwardirhynchia* gen. n. they are ventrally oriented and ventrally concave. The crura in *Cyclothyris* are dorsally concave whereas they are inwardly concave in *Woodwardirhynchia* gen. n. In *Parthirhynchia* TITOVA, 1980 (Basiliolidae COOPER, 1959) a pedicle collar is present, ventrally concave and forked hinge plates are developed, and the subfaliform crura are inwardly concave. The dental plates are ventrally divergent, the hinge plates are deflected dorsally and the dorsal septum is weakly developed. In *Woodwardirhynchia* gen. n. the dental plates are never ventrally divergent in their medium or anterior part. The hinge plates are not deflected dorsally and the crura are raduliform. The dorsal septum is more persistent.



***Woodwardirhynchia cuneiformis* (PETTITT, 1950)**

Text-Figures 2-3, Plate 8, Figures 1a-d, 2a-e.

- * 1950 *Cretirhynchia cuneiformis*, sp. nov. - PETTITT, pp. 2, 6-7, table 1, text-fig. 3, pl. 2, figs. 4a-c.
 . 1965 *Cretirhynchia cuneiformis* Pettitt - BIGNOT, p. 5.
 . 1974 *Cretirhynchia cuneiformis* Pettitt, 1950 - NEKVASILOVA, p. 48.
 non 1974 *Cretirhynchia* aff. *cuneiformis* Pettitt, 1950 - NEKVASILOVA, pp. 45-49, text-figs. 8-9, pl. 3, figs. 1-4, pl. 4, fig. 3, pl. 7, figs. 3-4.
 . 1988 *Cretirhynchia cuneiformis* Pettitt, 1950 - POPIEL-BARCZYK, p. 16.
 . 1997 *Cretirhynchia cuneiformis* (Pettitt) - MORTIMORE, pp. 37, 93.

Stratigraphical range: Upper Turonian, *Holaster planus* Zone.

Type specimen: holotype from the Upper Turonian (*H. planus* Zone) of Aston Hill, Aston Rowant, near Stockenchurch (Oxfordshire, England). Illustrated in PETTITT (1950, pl. 2, figs. 4a-c). Preserved in the NHM under the reference BB. 9990.

Material

Material preserved in the NHM.

The holotype cited above.

Two specimens from Santon Downham (Suffolk), *H. planus* Zone (B. 40863-64).

One specimen from Gillingham (Kent), *H. planus* Zone (B. 97336).

Two specimens from Bridgwick Pit, South Malling, Lewes (Sussex), *H. planus* Zone (B. 55846-47).

Material preserved in the IRScNB in Brussels.

42 complete, bivalved specimens collected from the Hayez quarry in "Hameau de Beaulieu", Bardouville, (near Rouen, Seine-Maritime, France). Hardground, Upper Turonian, *H. planus* Zone.

Original diagnosis in PETTITT (1950, pp. 2, 6).

"*Cretirhynchia*, about 20 mm long, 24 mm wide and 16 mm thick, subtriangular to subpentagonal in outline, domical (*sic*) to oval in anterior contour and cuneiform in lateral profile.

Brachial valve of considerable convexity, but medianly flattened, with broad, somewhat faint median fold on the anterior commissure. Pedicle valve less convex, with broad median sinus and large linguiform extension. Linguiform extension broad, fairly long, arcuate, turning until almost at right angles to the line of junction of the valves.

Umbo short, erect; umbonal slopes straight, long. Foramen

moderately large, circular; deltidial plates slightly produced around foramen. Beak-ridges distinct, only slightly curved.

Ornament of about 50 fine depressed costae, becoming sub-angular and reduced in number to about 35 near the commissure; the intervening sulci are narrow. Concentric ornament of very fine growth-lines and a few laminae, especially near the commissure. Apical angle 109°."

Comments

Externally, the outline and the ornamentation of the shell of this rhynchonellid brachiopod have much in common with the representatives of the genus *Cyclothyris* M'COY, 1844. This is the first rhynchonellid brachiopod species described in the work of PETTITT (1950) as representative of the genus *Cretirhynchia*. In his diagnosis, PETTITT did not mention any internal characters, but he illustrated transverse serial sections for this species (1950, fig. 3 p. 7). A very short description of the internal characters (1950, p. 7) stressed "the presence of a median septum and raduliform crura in the brachial valve". Although the diagnosis of the genus *Cretirhynchia* given by PETTITT (1950, p. 1) is accurate, this author did not strictly apply the criteria of this diagnosis to each species described in his monograph. In fact, PETTITT was often satisfied with the presence of a dorsal septum and of raduliform crura for including a species in the genus *Cretirhynchia*.

The serial sections made by PETTITT (1950, fig. 3 p. 7) show several characters which are quite different from the specific characters seen in the type species *Cretirhynchia plicatilis* (see PETTITT, 1950, text-fig. 4, p. 11 and this paper Figs. 2-3). The dental plates are slightly divergent during young stages of growth, they become subparallel and lastly, are slightly convergent. The dental plates are especially thin, a character which is not observed in the type species of *Cretirhynchia*. A well developed pedicle collar is visible. The hinge plates are forked, thin and nearly parallel to the hinge line. Crural bases are concave. The crura are slightly divergent.

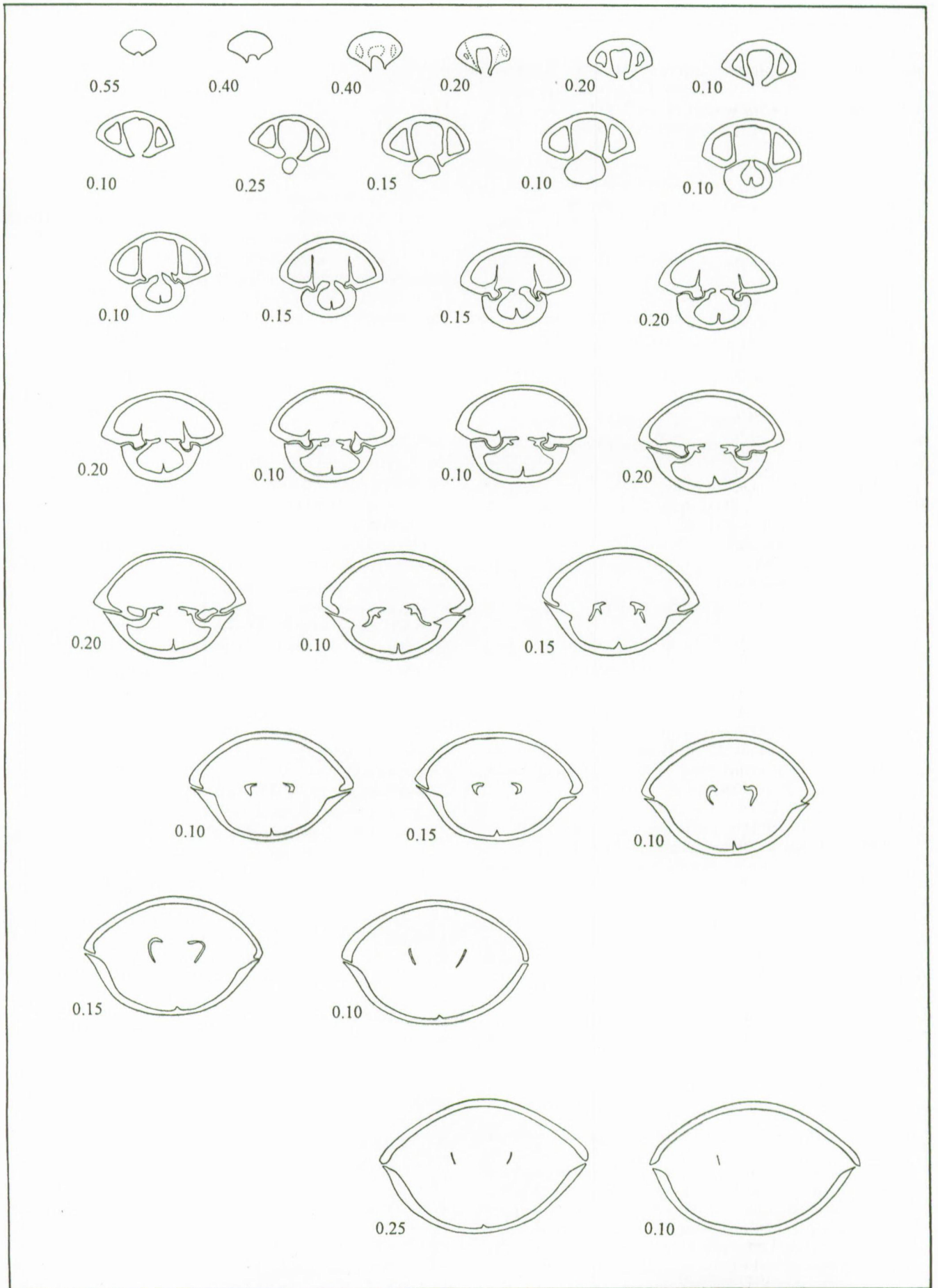
Specimens collected by the first author in Bardouville (Seine-maritime, Rouen, France) from the *H. planus* Zone were sectioned (Figs. 2-3). These sections are virtually identical to those of PETTITT for a specimen from Aston Hill.

In *Cretirhynchia plicatilis*, there are strong and thick convergent dental plates, short triangular hinge plates and subquadrate crural bases. The anterior parts of the crura remain close together. "*C.*" *cuneiformis* cannot, therefore, be maintained in the genus *Cretirhynchia*. The internal structures observed, mainly the forked hinge plates which are subparallel to the hinge line and the subparallel dental plates, indicate that "*C.*" *cuneiformis* probably arose from the genus *Cyclothyris* and not from the genus *Burrirhynchia* (OWEN, 1962, pp. 58-60) justifying the erection of the genus *Woodwardirhynchia* gen. n.

Cretirhynchia aff. *cuneiformis* PETTITT, 1950 described by NEKVASILOVA (1974, pp. 45-49, text-figs. 8-9) is a rhynchonellid brachiopod collected from the Upper Turonian of North-West Bohemia. Compared with *Woodwardirhynchia cuneiformis* from England or France, this material exhibits narrower hinge plates which are slightly forked but the dental plates are thick and clearly convergent. The crural bases are more or less subquadrate. *Cretirhynchia* aff. *cuneiformis sensu* NEK-



Fig. 2 — Serial transverse sections through the umbonal part of *Woodwardirhynchia cuneiformis* (PETTITT, 1950) collected from the Upper Turonian (*Holaster planus* Zone), Bardouville, Hameau de Beaulieu (near Rouen, Seine-Maritime, France). This specimen was collected in the hardground. Length of the specimen: 19.2 mm. IRScNB. - IST. N° 10831. The distances between the sections are indicated in mm (method of STERNBERG & BELDING, 1942).



VASILOVA (1974) is distinct from *Woodwardirhynchia cuneiformis* (PETTITT, 1950) but has much in common with other Turonian brachiopods such as "*Cretirhynchia*" *bohémica* (SCHLOENBACH, 1868).

Woodwardirhynchia woodwardi (DAVIDSON, 1855)

Text-Figures 4-5, Plate 8, Figures 3a-e, 4a-d.

- 1833 *Terebratula gallina* - WOODWARD, p. 49, pl. 6, fig. 12. (non BRONGNIART, 1822)
- *v 1855 *Rhynchonella plicatilis* var. *woodwardi* - DAVIDSON, pp. 77-78, pl. 10, figs. 43, 44 (non figs. 45, 46).
- . 1866 *Rhynchonella octoplicata*, d'Orb. - CORNET & BRIART, p. 126, 187 (non p. 189).
- 1874 *Rhynchonella plicatilis*, Sow. - CORNET & BRIART, p. 549.
- ? 1871 *Terebratula plicatilis* Sw. - QUENSTEDT, p. 167, pl. 41, fig. 57.
- . 1879 *Rhynchonella plicatilis* Sow. sp. - UBAGHS, pp. 128, 217.
- . 1887 *Rhynchonella plicatilis*, Sow. - RUTOT & VAN DEN BROECK, pp. 155, 156.
- 1938 *Rhynchonella plicatilis* var. *woodwardi* Dav. - POŻARYSKI, p. 20.
- . v 1950 *Cretirhynchia woodwardi* (Davidson) - PETTITT, pp. 1, 4, 16, 21-22, table 2, pl. 1, figs. 4a-c, pl. 2, figs. 5a-c.
- . 1954 *Cretirhynchia woodwardi* (Davidson) - PETTITT, pp. 48, 49.
- . 1961 *Cretirhynchia woodwardi* (Davidson) - PEAKE & HANCOCK, p. 320.
- . 1968 *Cretirhynchia woodwardi* - LEEDER, pp. 6-7, tables 1-2, text-fig. 2, p. 10.
- . 1983 *Cretirhynchia woodwardi* - BAILEY *et al.*, text-fig. 3.
- . 1988 *Cretirhynchia woodwardi* Pettitt - WOOD, pp. 25, 29, 34-35, 54-55, 61, 63-65, 81.
- v non 1988 *Cretirhynchia woodwardi* (Davidson, 1852) - POPIEL-BARCZYK, p. 15, pl. 3, figs. 5-6.
- . 1990 *Cretirhynchia woodwardi* (Davidson) - JOHANSEN & SURLYK, p. 838.
- non 1992 *Cretirhynchia woodwardi* (Davidson, 1852) - POPIEL-BARCZYK, p. 15.
- non 1995 *Cretirhynchia woodwardi* (Davidson, 1852) - SIMON in JAGT *et al.*, p. 11.
- . 2000 *Cretirhynchia woodwardi* (Davidson, 1855) - SIMON, p. 139, text-fig. 3, pl. 5, figs 4a-e.

Stratigraphical range: Upper Campanian, from *Blt. mucronata* Zone to *Blt. woodi* Zone.

Type specimen: lectotype from the Upper Chalk of Norwich, Norfolk, Norwich Castle Museum (Fitch

Collection), N° 2069. Specimen figured by DAVIDSON (1855, pl. 10, figs. 43-44) and also illustrated by PETTITT (1950, pl. 1, figs. 4a-c).

Material

Material preserved in the NHM.

Five specimens from the *Blt. mucronata* Zone in Norwich (Norfolk, England).

BB. 10069: this specimen is a topotype illustrated by PETTITT (1950, pl. 2, figs. 5a-c).

B. 11928-1: one specimen (a second specimen, B. 11928-2 is from Brighton and it is considered here as specimen of *Cretirhynchia exsculpta* PETTITT, 1950).

B. 467-1, B. 467-2, B. 467-3: three specimens.

One specimen from the *Blt. mucronata* Zone in Alderbury near Salisbury (Wiltshire, England). B. 91960.

Material preserved in the IRScNB in Brussels.

Specimens collected from the Mons basin (Hainaut, Belgium):

From the "Craie de Trivières", *Blt. mucronata* Zone

43 bivalved specimens and several fragments from the "Craie de Trivières", collected by the first author in Cuesmes, Craibel quarry.

From the "Craie d'Oubourg", *Blt. mucronata/Blt. woodi* Zones

58 bivalved specimens collected from Cuesmes, 472 bivalved specimens collected from Harmignies, 23 bivalved specimens from Ciplly and seven bivalved specimens from Nimy.

From the "Craie de Nouvelles", *Blt. woodi* Zone

Eight bivalved specimens from Nouvelles and 47 bivalved specimens from Harmignies.

Material preserved in the Museum of the Earth in Warsaw (PAN Muzeum Ziemi).

Two Maastrichtian specimens from Nasiłow (MZ VIII Bra-1466 and MZ VIII Bra-1466a) which should be studied for their internal characters. Their description as *Cretirhynchia woodwardi* is doubtful. This material has been illustrated by POPIEL-BARCZYK (1988, pl. 3, figs. 5-6).

Original diagnosis in DAVIDSON (1855, p. 77).

"Shell transversely oval: valves moderately convex, with a shallow sinus in the ventral, and slightly produced mesial fold in the opposite one. Externally each valve is ornamented by from 24 to 44 simple plaits, often split close to the margin".

Emended description in PETTITT (1950, p. 21).

PETTITT placed *Cretirhynchia woodwardi* in his second series because he recognized that the costae show incipient splitting near the commissure.

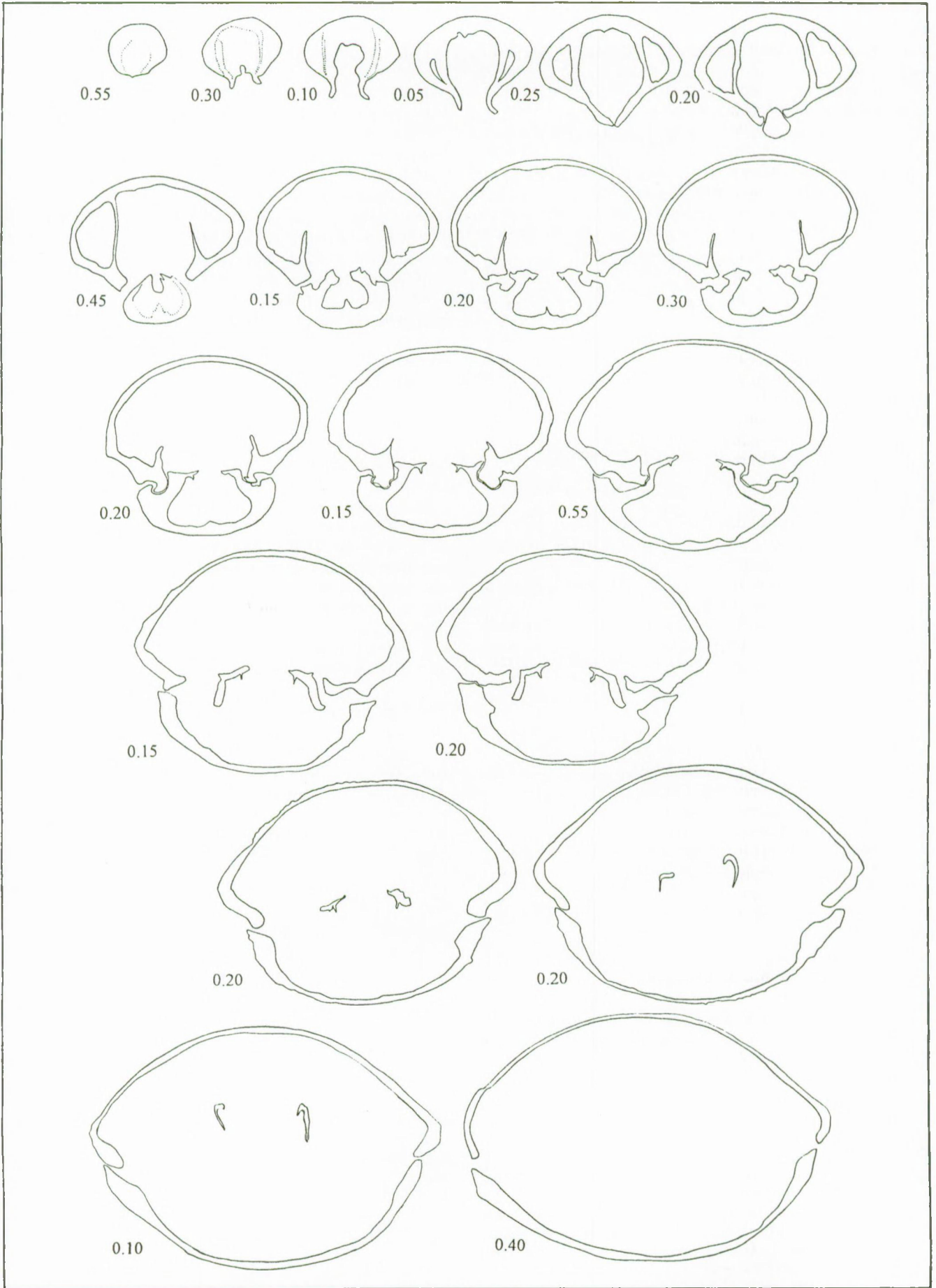
"*Cretirhynchia*, about 17 mm long, 21 mm wide, and 12 mm thick, transversely oval in outline, lenticular to oval in anterior contour. Brachial valve convex with broad, anterior median fold. Pedicle valve slightly less convex, with broad, shallow sinus. Linguiform extension broad, arcuate. Umbo erect. Ornamentation with 30 low costae, with narrow intervening sulci. Apical angle 106°."

Comments

In a further description concerning the internal characters



Fig. 3 — Serial transverse sections through the umbonal part of *Woodwardirhynchia cuneiformis* (PETTITT, 1950) collected from the Upper Turonian (*Holaster planus* Zone), Bardouville (near Rouen, Seine-Maritime, France). This specimen was collected in a soft chalk. Length of the specimen: 23.0 mm. IRScNB. - IST. N° 10832.



of this species, PETTITT (1950, p. 21) wrote: "The dental lamellae can be seen through the test in the lectotype; they are distant and divergent. The median septum can also be seen through the test."

Transverse serial sections were made on specimens collected from the "Craie d'Obourg" (Upper Campanian, *Blt. mucronata/Blt. woodi* Zones) in Harmignies (Mons basin, Hainaut, Belgium). It is seen (Fig. 4-5) that thin dental plates, ventrally divergent in the posterior part of the shell, become anteriorly subparallel or slightly convergent. A pedicle collar is observed. In the dorsal valve, a septum is present on the valve floor, but it is rather short. The hinge plates, relatively narrow and thin in section, are typically forked. The crural bases are not subquadrate but concave. The raduliform crura which are laterally diverging, are inwardly concave but they become straight in transverse section near their distal end. All those cyclothyridid characters are consistent with the diagnosis of the genus *Woodwardirhynchia* gen. n.

Externally, *Woodwardirhynchia woodwardi* is an Upper Chalk rhynchonellid brachiopod resembling the representatives of the genus *Orbirhynchia* PETTITT, 1954. But the well developed beak ridges and the internal characters observed in the serial sections avoid any confusion with this genus.

The Polish Maastrichtian specimens of "*Cretirhynchia woodwardi* (DAVIDSON, 1852)" from Nasiłow studied and illustrated by POPIEL-BARCZYK (1988, p. 15, pl. 3, figs. 5-6) are in need of revision. The very small size and general outline of the shell, the sharp angular "roof shaped" costae present in these specimens are quite different from the characters observed in the typical *Woodwardirhynchia woodwardi*. In *W. woodwardi*, the costae are relatively flat near the commissure. Serial sections should be made for these specimens.

On the other hand, Campanian specimens determined and illustrated by POPIEL-BARCZYK (1988, pp. 16-17, text-fig. 18, pl. 3, figs. 7-8) as *Cyclothyris* sp., exhibit a similarity with *W. woodwardi*. The specimen sectioned on her text-fig. 18 shows subparallel dental plates, a pedicle collar and narrow, forked hinge plates.

W. woodwardi is fairly common in the West European Upper Campanian white chalks. It seems to be limited to the *Belemnitella mucronata* - *Blt. woodi* Zones and could provide a good stratigraphical marker for these zones.

Woodwardirhynchia tenuicostata (VON HANSTEIN, 1879)

Text-Figure 6, Plate 8, Figures 5a-e.

* 1879 *Rhynchonella tenuicostata* sp. n. - VON HANSTEIN, p. 42.

←
Fig. 4 — Serial transverse sections through the umbonal part of *Woodwardirhynchia woodwardi* (DAVIDSON, 1855) collected from the Upper Campanian (*Belemnitella woodi* Zone), "Craie d'Obourg", Harmignies (Mons basin, Hainaut, Belgium). Length of the specimen: 17.5 mm. IRScNB. - IST. N°10833.

1996 *Cretirhynchia tenuicostata* (von Hanstein, 1879) - SIMON, pp. 102-104, tables 3-4, text-fig. 2, pl. 2, figs. 1-6.

Stratigraphical range: Lower Maastrichtian, *Belemnitella obtusa* Zone.

Type specimen: lectotype from the phosphatic chalk of Cibly (Hainaut, Belgium) chosen among the four specimens of the type series of VON HANSTEIN, preserved in the Geological and Palaeontological Institute of the University of Bonn and registered under the number G.P.I.B.O.-HANSTEIN-5. The lectotype is illustrated in SIMON (1996, pl. 2, figs. 2a-e).

Material

Material from Cibly (Mons basin, Hainaut, Belgium) preserved in the IRScNB in Brussels: 30 specimens.

Original diagnosis in VON HANSTEIN (1879, pp. 42-43)

"Kleine, dreiseitige Rhynchonellen mit wenig hervortretendem Wulst und Sinus, meist scharf rechtwinklig gebogenem Stirnrand und sehr zahlreichen, feinen, sich nicht vermehrenden Rippen, die häufig antidichotomiren.

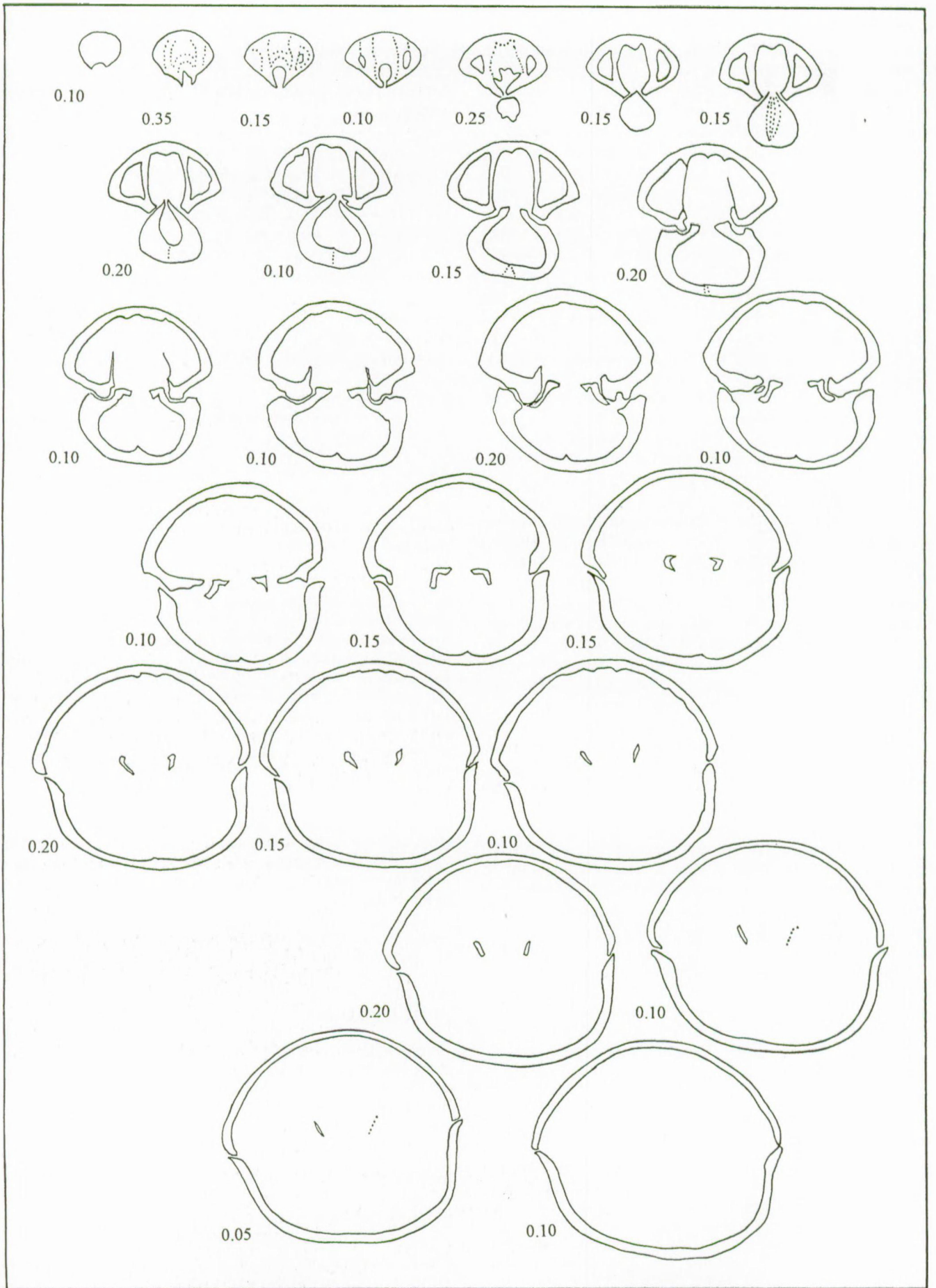
Auch diese Species scheint mir den bisher bekannten gegenüber wohl charakterisirt zu sein. Ihre Gestalt ist ungefähr die eines an den Ecken abgerundeten gleichseitigen Dreiecks. Sie zeigt eine gewisse Aehnlichkeit mit denjenigen Formen von *Rh. plicatilis*, welche dem Typus Dav. l. c. f. 16 entsprechen. Doch, abgesehen von andern Verschiedenheiten, trennt sie von der Sowerby'schen Species die bedeutend grössere Anzahl (60-70) der sehr feinen Rippen bei stets viel geringere Grösse. Die Rippen vermehren sich nicht, dagegen scheinen Exemplare mit antidichotomirenden Rippen nicht selten zu sein. Wenigstens liegt mir eine ganze Reihe von Individuen vor, bei denen am Stirnrande die Rippen zu 2 bis 3 sich vereinigen. Dass das Antidichotomiren der Rippen keine für bestimmte Species charakteristische Eigenschaft, sondern eine in sehr verschiedenen Arten afiretend individuelle Erscheinung sei, hat bereits Davidson (*Cret. Brach.* p. 78) und Herm. Credner (*a. a. O.* p. 555 ff.) gezeigt. Der Wulst auf der kleinen und der Sinus der grossen Klappe sind bei allen normal ausgebildeten Exemplaren sehr schwach entwickelt. Dagegen ist der Stirnrand bei der überwiegenden Mehrzahl scharf rechtwinklig umgebogen. - Rückichtlich der Beschaffenheit des Schnabels hält unsere Species ungefähr die Mitte zwischen den beiden vorhergehenden. Derselbe ist deutlich umgebogen, aber nicht so stark, wie bei *Rh. plicatilis*. Die Oeffnung liegt der Längsaxe parallel. Unter derselben ist das Deltidium stets zu sehen. Die Area ist von scharfen Kanten begrenzt. Im innern zeigt die kleine Klappe ausser den beiden kurzen, das Armgerüst repräsentirenden Lamellen, ein kurzes, niedriges Septum, welche jedoch die Mitte der Klappe nicht erreicht."

Emended description in SIMON (1996, p. 103).

It can be consulted mainly for the description of the internal characters. Transverse serial sections are also illustrated in SIMON (1996, text-fig. 2).

Comments

This species was included by SIMON (1996, p. 102) in the genus *Cretirhynchia* PETTITT, 1950 mainly because a persistent septum on the dorsal valve floor, simple hinge plates, raduliform crura, anteriorly convergent dental plates were observed in transverse serial sections. However, the dental plates which are relatively thin, are



slightly divergent posteriorly and they are mainly subparallel in their median parts. They are only convergent at their distal end (SIMON, 1996, text-fig. 2). The hinge plates are wider than the hinge plates usually found in the representatives of the genus *Cretirhynchia*. The crural bases are not subquadrate and the crura appear clearly concave. For these reasons, new serial sections were made on four specimens collected from the phosphatic chalk of Ciply. These specimens were chosen for their relatively large size (fully adult specimens). An illustration of these results is given in Fig. 6.

A new observation was the presence of a short pedicle collar which was overlooked in the sections made by SIMON (1996, text-fig. 2). Dental plates are ventrally divergent in the first stage of growth, becoming parallel and slightly convergent anteriorly. Dental plates are relatively thin and their development resembles those observed in *Woodwardirhynchia cuneiformis* and *W. woodwardi*. In the dorsal valve, a persistent, low septum is observed. The hinge plates appear variable in serial sections but in some specimens (Fig. 6) they are typically forked. Crural bases are inwardly concave and the raduliform crura which are posteriorly concave, become straight in section in their anterior part. Although this character is variable, the crura are divergent. These new observations lead us to include this species in the genus *Woodwardirhynchia* gen. n.

An external homeomorphy has been observed between *Woodwardirhynchia tenuicostata* (VON HANSTEIN, 1879) and some medium-sized Campanian forms of *Cretirhynchia norvicensis* PETTITT, 1950 (Pl. 2 Fig. 1a-e). Transverse serial sections of such specimens should exclude any confusion between these two rhynchonellid brachiopods.

Species removed from the genus *Cretirhynchia* PETTITT, 1950 and placed in open nomenclature near the “*Cyclothyris* group”

“*Cretirhynchia*” *subplicata* (MANTELL, 1822)
Text-Figure 7, Plate 8, Figures 6a-e, 7a-e.

- * 1822 *Terebratula subplicata*. - MANTELL, p. 211, pl. 26, figs. 5, 6, 11.
- non 1841 *Terebratula subplicata* Mantell - ROEMER, F.A., p. 38, n° 10 (= *C. limbata*).
- non 1842 *Terebratula subplicata* Mant. - VON HAGENOW, p. 534, n° 4 (= *C. limbata*).
- non 1846 *Terebratula subplicata* Mant. - BOLL, p. 209 (= *C. limbata*).
- non 1847 *Rhynchonella subplicata* d’Orb., 1847 - D’ORBIGNY, p. 48, pl. 499, figs. 13-17.



Fig. 5 — Serial transverse sections through the umbonal part of *Woodwardirhynchia woodwardi* (DAVIDSON, 1855) collected from the Upper Campanian (*Belemnitella woodi* Zone), “Craie d’Obourg”, Cuesmes (Mons basin, Hainaut, Belgium). Length of the specimen: 15.5 mm. IRScNB. - IST. N° 10835.

- non 1852 *Terebratula subplicata* Mant. - PUGGAARD, p. 16 (= *C. limbata*).
- pp 1855 *Rhynchonella limbata* (Schlotheim) - DAVIDSON, p. 79-80, non pl. 12, figs. 1-5.
- non 1866 *Rhynchonella subplicata* d’Orb. - CORNET & BRIART, pp. 150, 189 (= *C. limbata*).
- non 1870 *Rhynchonella subplicata* d’Orb. - CORNET & BRIART, pp. 8, 9 (= *C. limbata*).
- non 1871 *Terebratula octoplicata subplicata* - QUENSTEDT, p. 169, pl. 41, fig. 59 (= *C. limbata*), figs. 58, 60, 62 (= *C. retracta*).
- 1950 *Cretirhynchia subplicata* (Mantell) - PETTITT, pp. 23-24, pl. 2, figs. 2a-c.
- 1965 *Cretirhynchia subplicata* (Mantell) - STEINICH, pp. 23, 24, 26.
- 1965 *Cretirhynchia subplicata* (Mantell, 1822) - BIGNOT, p. 6, non pl. 1, figs. 10a-c.
- 1983 *Cretirhynchia subplicata* - BAILEY *et al.*, text-fig. 2.
- non 1988 *Cretirhynchia subplicata* (Mantell, 1822) - POPIEL-BARCZYK, pp. 10-11, text-fig. 8, pl. 2, figs. 1-3 (?= *C. arcuata*).
- non 1988 *Cretirhynchia subplicata* (Mantell, 1822) - POPIEL-BARCZYK, text-fig. 9, p. 11 (= *C. limbata*).
- non 1992 *Cretirhynchia subplicata* (Mantell, 1822) - POPIEL-BARCZYK, p. 15.
- 1997 *Cretirhynchia subplicata* (Mantell) - MORTIMORE, p. 54.

Stratigraphical range: Coniacian, *Cortestudinarium* Zone.

Type specimen

The specimen figured by MANTELL (1822, pl. 26, figs. 5, 6, 11) has not been found (PETTITT, 1950, p. 23). A neotype has been chosen by PETTITT (1950, p. 23) from the *Cortestudinarium* Zone of Offham Hill, near Lewes, Sussex, England. This type specimen is preserved in the NHM under the reference B. 47876 (See PETTITT 1950, pl. 2, figs. 2a-c).

Material

Material preserved in the NHM.

Numerous specimens collected from the *Cortestudinarium* Zone from Dover, Kent, England. References: B. 29723, B. 96854, B. 96856, B. 79964-74, B. 79994.

One specimen collected from the *Cortestudinarium* Zone in Holmes Lane, Rustington near Littlehampton, Sussex, England, reference B. 81425.

Two specimens from the *Cortestudinarium* Zone in Whiteleaf, Surrey, England, reference B. 19352-53.

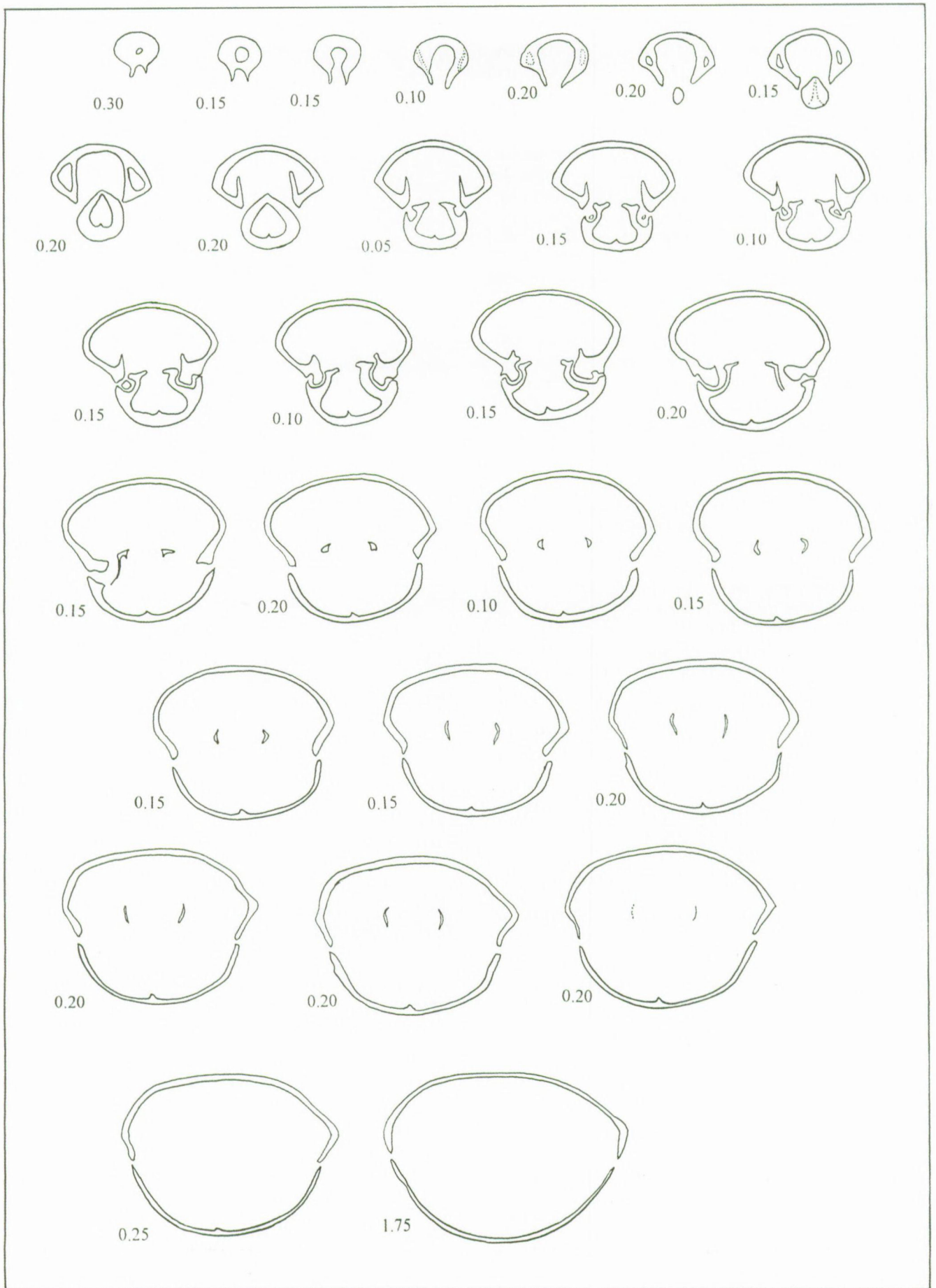
Eleven specimens from the *Cortestudinarium* Zone in Chalk Pitton, Offham Hill, Lewes, reference B. 47876-86.

Thirteen specimens from the *Cortestudinarium* Zone in foreshore S. of Kingston Farm near Angmering-on-Sea, Sussex, England, reference B. 81426-38.

Six specimens from the *Cortestudinarium* Zone in Beachy Head, Sussex, England, reference B. 97171-76.

Original diagnosis in MANTELL (1822, p. 211)

“Transversely ovate, gibbous, nearly smooth; lower valve depressed, upper valve convex; margin serrated; front sinuate, with three or four sharp plicae; beak slightly produced. This is



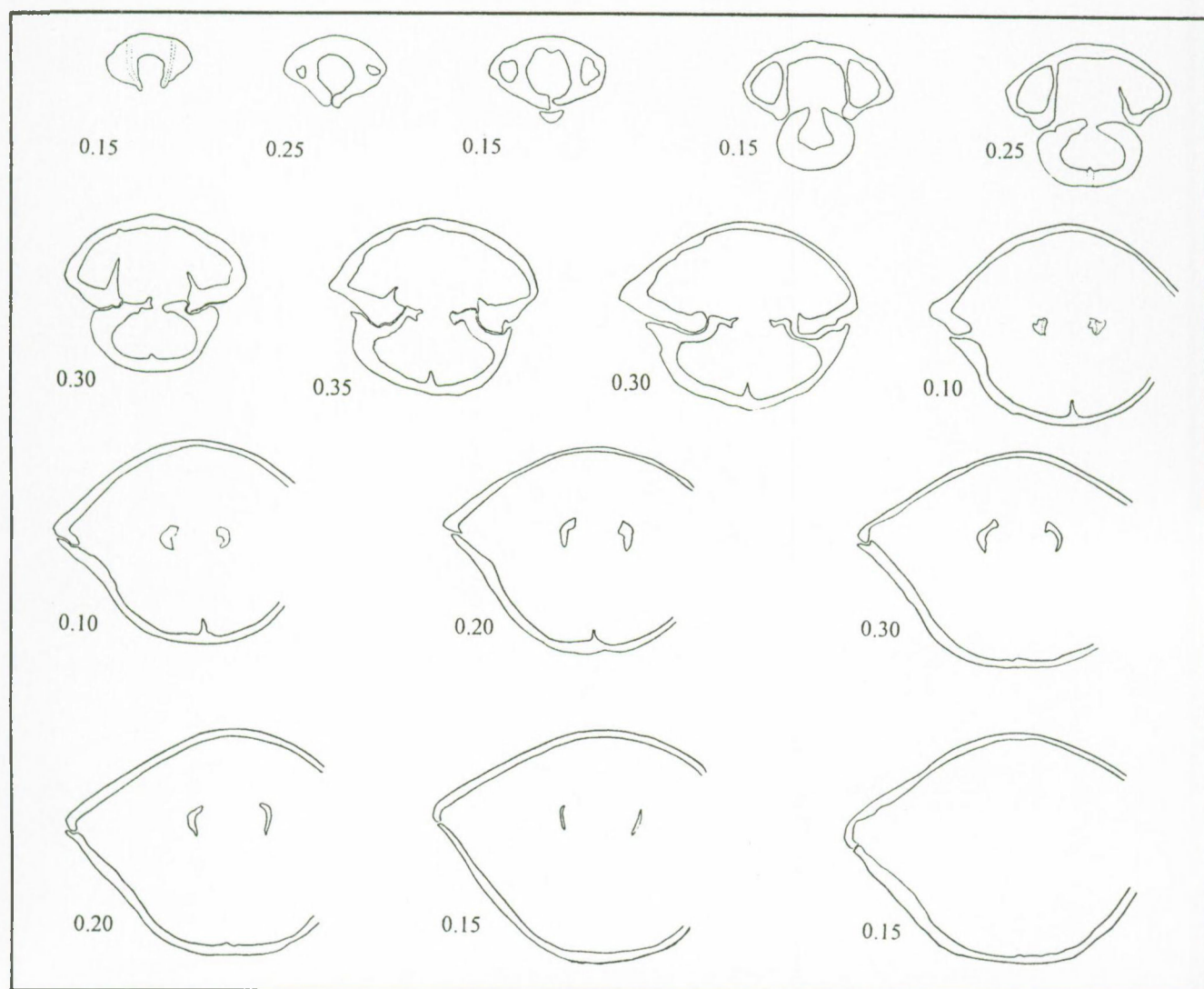


Fig. 7 — Serial transverse sections through the umbonal part of ex *Cretirhynchia subplicata* (MANTELL, 1822) collected from the Coniacian (*Cortestudinarium* Zone), Dover (Kent, England). Length of the specimen: 10.0 mm. NHM. B. 79974.

a small species, well characterized by its smooth surface, and elevated plicated front."

Emended diagnosis in PETTITT (1950, p. 23)

"*Cretirhynchia*, about 11 mm long, 11 mm wide and 8.0 mm thick, subpentagonal to oval in outline; anterior contour domical, lateral profile cuneiform.

Brachial valve depressed at first, convex later, especially on lateral slopes; with faint median fold.

Pedicle valve less convex, with shallow sinus; linguiform extension fairly broad, subarcuate to U-shaped, turns at 90°.

Umbo broad. Foramen small, circular.

Ornament of about 15 low costae, near commissure only. Concentric growth-lines fine, distinct. Apical angle 117°."

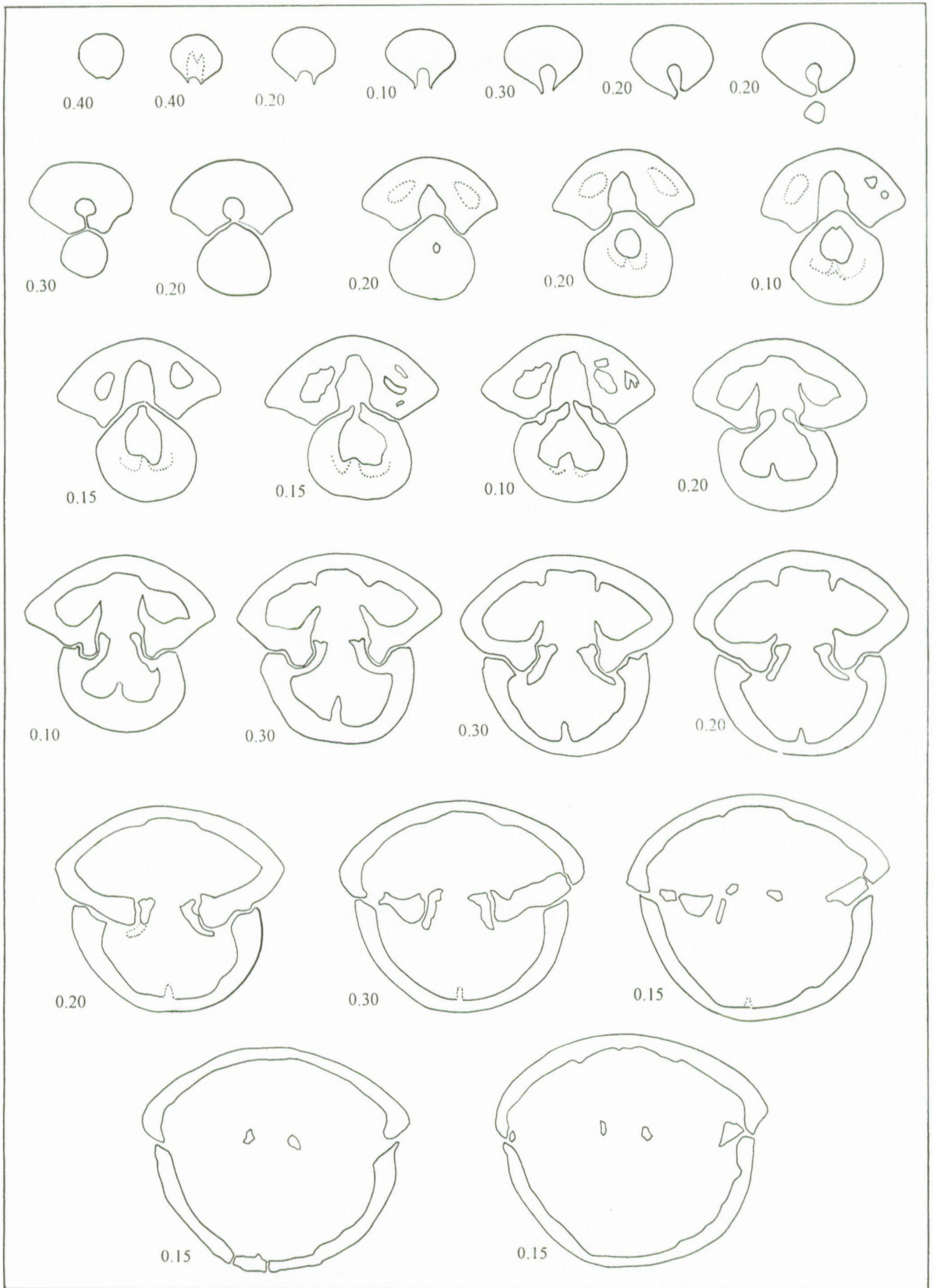
Comments

Concerning the internal characters, PETTITT (1950, p. 24) pointed out that "a median septum and raduliform crura are present in the brachial valve. The inner socket-ridges are well developed". He did not published any serial sections for this species, but exhaustively described the external characters (PETTITT, 1950, pp. 23-24) and this description should be consulted. Its comparison between "*C.* *subplicata* (MANTELL, 1822) and *C. limbata* (VON SCHLOTHEIM, 1813) is noteworthy (PETTITT, 1950, p. 24).

"... There are, however, several differences between the two forms. The lateral profile in *C. limbata* is depressed, but becomes cuneiform in the adult stage



Fig. 6 — Serial transverse sections through the umbonal part of *Woodwardirhynchia tenuicostata* (VON HANSTEIN, 1879) collected from the Lower Maastrichtian (*Belemnella obtusa* Zone), Phosphatic chalk, Ciplu (Mons basin, Hainaut, Belgium). Length of the specimen: 20.0 mm. IRScNB. - IST. N° 10836.



owing to elevation of the median fold; the lateral parts of the brachial valve remain low and the lateral slopes are not steep. In *C. subplicata* the lateral profile is cuneiform, but the median fold is barely perceptible, and the lateral slopes are steep. The posterior part of the brachial valve is nearly flat, not convex as in *C. limbata*. The linguiform extension quickly reaches an angle of 90°; in *C. limbata* it turns at a smaller angle and is V-shaped. The umbo is short in *C. subplicata*, and not incurved as in *C. limbata*."

We agree with these distinctions which have been observed in all the specimens investigated in our study. In addition, it can be stated that in *C. limbata* the antero-lateral parts of the ventral valve are nearly flat, whereas in "*C.*" *subplicata* they are obviously convex.

Transverse serial sections (Fig. 7) were made from a specimen from the *Cortestudinarium* Zone of Dover, Kent, England (B. 79974). The sections made from a second specimen (B. 47876) from the *Cortestudinarium* Zone of Offham Hill, Lewes (Sussex, England) offered similar structures. The dental plates are slightly divergent to subparallel posteriorly and they are parallel anteriorly. The anterior parts of the dental plates are relatively thin in section. The hinge structures of "*C.*" *subplicata* are totally different from the typical hinge structures described for the representatives of the subgenus in which *C. limbata* has now been placed. In the dorsal valve, the hinge plates are nearly flat and forked. The crural bases are strongly concave and the crura remain inwardly concave. They are only straight in section near their distal ends. Crura are also slightly divergent. All these observations show that a possible synonymy between "*C.*" *subplicata* and *C. limbata* must be excluded. Moreover the cyclothyridid aspect of the internal characters, *i. e.* subparallel dental plates and forked hinge plates, lead us to remove this species from the genus *Cretirhynchia* PETTITT, 1950 and to place it much nearer the representatives of the "*Cyclothyris* group". As "*C.*" *subplicata* (MANTELL, 1822) is the only smooth rhynchonellid brachiopod in this taxonomic position, it remains of uncertain generic affinity.

Genus *Cretirhynchia* PETTITT, 1950

Type species: *Terebratula plicatilis* J. SOWERBY, 1816

Original diagnosis in PETTITT (1950, p. 1)

"Shell biconvex, symmetrical; brachial valve convex, with median fold on anterior part of the valve; pedicle valve less convex, with anterior median sinus; linguiform extension arcuate - V-shaped.

Hypothyrid; umbo short, erect to slightly incurved; foramen small; deltidial plates small, conjunct, produced; beak ridges distinct; interarea well defined.



Fig. 8 — Serial transverse sections through the umbonal part of *Cretirhynchia* (*Cretirhynchia*) *plicatilis* (J. SOWERBY, 1816) collected from the Santonian (*Marsupites testudinarium* Zone), Northfleet (Kent, England). Length of the specimen: 23.3 mm. NHM. B. 79815.

Shell multicostate (or smooth, owing to costae becoming obsolete); costae low, rounded, faint near umbo, becoming elevated and subangular along antero-lateral commissure, and either reduced in number or showing incipient splitting in final adult stages.

Teeth large; dental lamellae short to moderately long, slightly divergent, partly joined to lateral wall.

Median septum of brachial valve moderately strong, commencing at short distance from umbo; septalium absent; cardinal process absent. Hinge plate broad, divided; dental sockets large, striated; crura raduliform, short, fairly broad; crural bases given off dorsally.

Muscle-scars broad-spreading".

Subgenus *Cretirhynchia* PETTITT, 1950

Diagnosis of the subgenus

Multicostate rhynchonellid brachiopods with a biconvex, symmetrical shell. Costae low, rounded, faint near umbo, becoming elevated and more subangular and either sharply reduced in number near the commissure. Thick-shelled, umbo thickened with secondary callose material. Pedicle collar absent. Thick dental plates, convergent ventrally. Hinge plates ventrally deflected, simple, subtriangular, never forked. Crural bases subquadrate. Raduliform crura straight or moderately concave in section and remaining close together. Crura ventrally deflected but not steeply.

Cretirhynchia (*Cretirhynchia*) *plicatilis*

(J. SOWERBY, 1816)

Text-Figures 8, Plate 1, Figures 1a-e, 2a-e, 3a-e, 4a-e.

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|-----|---------|--|
| * v | 1816 | <i>Terebratula plicatilis</i> - SOWERBY, J., ii, p. 37, pl. 118, fig. 1. |
| non | 1822 | <i>Terebratula plicatilis</i> - BRONGNIART, pl. 4, figs. 5a-c. |
| pp. | 1822 | <i>Terebratula plicatilis</i> . - MANTELL, p. 210, n°81, var. a. |
| | 1828 | <i>Terebratula plicatilis</i> , Sow. - DEFRANCE, fig. 3, p. 159 (considered as a variety of <i>T. octoplicata</i> , Sow.). |
| non | 1833 | <i>Terebratula plicatilis</i> - WOODWARD, p. 49. |
| . | 1836 | <i>Terebratula plicatilis</i> - DESHAYES, 7, p. 357, n°77. |
| . | 1838 | <i>Terebratula plicatilis</i> Sow. - VON BUCH, pl. 15, fig. 24. |
| pp. | 1838 | <i>Terebratula plicatilis</i> Sow. - VON BUCH, pp. 153-154. |
| ? | 1841 | <i>Terebratula plicatilis</i> - ROEMER, F.A., p. 39, n°14. |
| non | 1842 | <i>Terebratula plicatilis</i> Sow. - HAGENOW, p. 534, n°2 (= <i>C. retracta</i>) |
| non | 1846 | <i>Terebratula plicatilis</i> - GEINITZ, H.B., pl. 21, figs. 9 a-b. |
| non | 1846 | <i>Terebratula plicatilis</i> Sow. - BOLL, p. 209 (cit. HAGENOW, 1842). |
| ? | 1846 | <i>Terebratula plicatilis</i> - REUSS, p. 47, n°6, pl. 25, figs. 10-13. |
| non | 1848 | <i>Terebratula plicatilis</i> (So.) Br. - BRONN, p. 1246 (except the type of SOWERBY cited in the synonymy). |
| non | 1851-52 | <i>Rhynchonella plicatilis</i> Br. - BRONN & ROEMER, F., pl. 30, fig. 9. |
| non | 1852 | <i>Terebratula plicatilis</i> (Sow.) Bronn - PUGGAARD, p. 14, fig. 19, p. 17. (= <i>C. retracta</i>) |
| pp. | 1854 | <i>Terebratula plicatilis</i> , Sow. - MORRIS, p. 150. |

- pp. 1855 *Rhynchonella plicatilis* J. Sowerby - DAVIDSON, pp. 75-77, pl. 10, fig 40 (non figs. 37-39, 41-42).
- non 1866 *Rhynchonella plicatilis*, Sow. - CORNET & BRIART, p. 189.
- non 1868 *Rhynchonella plicatilis*, Sow. sp. 1816 - SCHLOENBACH, pp. 159-160 (= *C. aff. cuneiformis* sensu NEKVASILOVA, 1974).
- non 1873 *Rhynchonella plicatilis* Sow. - GEINITZ, H.B., pl. 7, figs. 5, 7, 8.
- non 1874 *Rhynchonella plicatilis*, Sow. - CORNET, F.L. & BRIART, A., p. 549.
- non 1871 *Terebratulula plicatilis* Sw. - QUENSTEDT, p. 167, pl. 41, figs. 55-57.
- non 1877 *Rhynchonella plicatilis* Sow. sp. - FRIČ, ii, p. 144, fig. 147.
- non v 1879 *Rhynchonella plicatilis* Sow. sp. - VON HANSTEIN, pp. 38-40.
- non 1879 *Rhynchonella plicatilis* Sow. sp. - UBAGHS, pp. 128, 217.
- non 1885 *Rhynchonella plicatilis*, Sow. sp. - LUNDGREN, p. 16, pp. 37-38, n°4, pl. 1, figs. 29-31.
- non 1887 *Rhynchonella plicatilis*, Sow. - RUTOT & VAN DEN BROECK, pp. 155, 156 (= *C. woodwardi*).
- non 1888 *Rhynchonella plicatilis* Sow. - GEINITZ, F.E., p. 742 (= *C. retracta*).
- non 1894 *Rhynchonella plicatilis*, Sowerby - POSSELT, p. 26, n°13 (= *C. retracta* + *C. limbata* + *C. octoplicata*).
- non 1895 *Rhynchonella plicatilis* Sow. - GEINITZ, H.B., pp. 6-7 (= *C. retracta*).
- non 1895 *Rhynchonella plicatilis* Sow. - DEECKE, pp. 105, 108-109, 112 (= *C. retracta*).
- non 1921 *Rhynchonella plicatilis* - CORNET, J., p. 21.
- v 1950 *Cretirhynchia plicatilis* (J. Sowerby) - PETTITT, pp. 9-12, text-fig. 4, p. 11, text-fig. 5, p. 12, pl. 1, figs. 9 a-c, 10, 11, pl. 2, figs. 8 a-b.
- 1962 *Cretirhynchia plicatilis* (J. Sowerby) - OWEN, p. 60.
- 1965 *Cretirhynchia plicatilis* (J. Sowerby) - AGER, p. 166.
- 1965 *Cretirhynchia plicatilis* (Sow.) - STEINICH, p. 17.
- 1965 *Cretirhynchia plicatilis* (Sow.) - BIGNOT, p. 5.
- 1968 *Cretirhynchia plicatilis* Pettitt - LEEDER, p. 6.
- 1974 *Cretirhynchia plicatilis* - NEKVASILOVA, p. 48.
- non 1974 *Cretirhynchia plicatilis* (Sowerby) - KAEVER *et al.*, p. 107, pl. 1, figs. 7 a-c.
- 1974 *Cretirhynchia plicatilis* (Sow.) - PAJAUD, pp. 24-25.
- non 1981 *Cretirhynchia plicatilis* (J. Sowerby), 1816 - GIOVANNONI, p. 210, table 1, p. 202, pl. 4, figs. 1-3.
- 1983 *Cretirhynchia plicatilis* (J. Sowerby) - BAILEY *et al.*, text-fig. 2, p. 33, pp. 36-37.
- 1987 *Cretirhynchia plicatilis* (J. Sowerby) - OWEN, p. 57, pl. 11, figs. 8 a-c.
- non 1988 *Cretirhynchia plicatilis* (Sowerby, 1816) - ALIEV & TITOVA, p. 228, text-fig. 66, pl. 5, figs. 1-5.
- 1988 *Cretirhynchia plicatilis* (J. Sowerby) - POPIEL-BARCZYK, p. 16.
- 1997 *Cretirhynchia plicatilis* - MORTIMORE, p. 130.
- Gravesend, Kent, England. NHM, SOWERBY Collection, B. 61513. Figured by J. SOWERBY, 1816, pl. 118, fig. 1. Illustrated by PETTITT (1950), pl. 1, figs 9 a-c.

Material

Material preserved in the NHM.

From Upper Chalk, Northfleet, Kent

The holotype cited above.

Topotype. B. 79813, *Coranguinum* Zone. Figured by PETTITT (1950, pl. 1, fig. 11, interior of brachial valve).Topotype. B. 79814, *Coranguinum* Zone. Figured by PETTITT (1950, pl. 1, fig. 10, lateral view). One complete adult specimen.Topotype. B. 79815, *Coranguinum* Zone. Figured in this study, Pl. 1, Figs. 1a-e, sectioned (Fig. 8).Topotype. B. 79809, *Coranguinum* Zone. sectioned and illustrated by PETTITT (1950, text-fig. 4, p. 11).

Topotype. B.44664, Dibley Coll. (oct. 1922): 1 adult complete specimen. Figured in this study Pl. 1, Figs. 2a-e.

B.79811, an altered adult specimen.

B.79808, an adult complete specimen with a more trapezoidal linguiform extension which is slightly wider than in the type specimen.

B.79810, one ventral valve with an internal mould.

From the Snowdown Colliery, Kent, England.

B. 93648, *Coranguinum* Zone. Younger complete specimen figured in this study, Pl. 1, Figs. 4a-e.

From the Upper Chalk, Grays, Essex

B.44662, *Coranguinum* Zone. One complete, adult specimen which is opened. Its internal structure fits perfectly with the type specimen.B. 44663, *Coranguinum* Zone. One complete adult specimen similar to the type.

From Amesbury near Salisbury, Wiltshire

B. 94062, a complete adult shell which exhibits finer costae than the type.

From Devizes Road, W. of Salisbury, Wiltshire.

B. 91832, *Uintacrinus* Zone. One complete adult specimen with slightly coarser costae. Figured in this study, Pl. 1, Figs. 3a-e.

From Thanet Coast

B. 79820, *Uintacrinus* Zone. One complete adult specimen.B. 79821, *Uintacrinus* Zone. One complete adult specimen.B. 79822, *Uintacrinus* Zone. One ventral valve.

From unknown origin

B. 9036-37. Two specimens transferred from the Zoological Department in February 1896 determined erroneously as *Cretirhynchia tringhamensis* PETTITT, 1950. B.79816. Young specimen of *Cretirhynchia plicatilis*.Specimens originally determined as *Cretirhynchia plicatilis* (J. SOWERBY, 1816) and not accepted as representatives of this species in this study.Stratigraphical range: Santonian, *Coranguinum* and *Testudinarius* Zones.

Type specimen

Holotype from the Upper Chalk, Northfleet, near

In most cases, they can be attributed to other species of *Cretirhynchia*, mainly *Cretirhynchia exsculpta*, *C. intermedia* or *C. norvicensis*. Their references in the NHM collection are: B. 4809, B. 8380, B. 10677, B. 11724, B. 19868, B. 19869, B. 19870, B. 19871, B. 22886, B. 25068, B. 79818, B. 79852, B. 79883., BB. 922 and BB. 76525.

Material preserved in the Geological and Palaeontological Institute of the University of Bonn.

Three specimens of *Rhynchonella plicatilis* Sow. sp. sensu VON HANSTEIN (1879, pp. 38-40) from the chalk of Ciply, Hainaut, Belgium (G.P.I.B.O.- Hanstein: 6). These specimens cannot be accepted as *Cretirhynchia plicatilis* (J. SOWERBY, 1816). Such material has not been found by SIMON (1998) in the phosphatic chalk of Ciply, despite extensive research. A specimen, extremely similar in character was collected in the Chalk of Vijlen, in Altembroeck (Maastrichtian, *Belemnella sumensis* Zone). This isolated specimen was determined as *Cretirhynchia* gr. *exsculpta* PETTITT, 1950 by SIMON (1995, p. 11).

Original diagnosis in J. SOWERBY, 1816, p. 37.

"Gibbose, transversely obovate, finely and obtusely plaited; middle elevated by twelve plaits; fifteen or more plaits on each side; beak slightly projecting."

Emended diagnosis in PETTITT, 1950, pp. 9-10.

"*Cretirhynchia*, about 22 mm. long, 28 mm. wide and 19 mm. thick, transversely oval to subpentagonal in outline, oval in anterior contour, subcircular in lateral profile.

Brachial valve of considerable convexity, with slight, broad, flattened fold on anterior part. Pedicle valve less convex, with broad, flat, shallow sinus on anterior part. Linguiform extension broad, trapezoidal, nearly rectangular, turning sharply in the dorsal direction until at right angles to the plane of junction of the valves.

Umbo small, erect; umbonal slopes concave. Deltidial plates small, just conjunct. Foramen small, circular to longitudinally oval. Beak-ridges distinct, curved.

Ornament of about 70 or more depressed, rounded costae, about 11 on fold and 10 in sinus, and about three on each flank of the fold, with shallow subangular intervening sulci. Many closely set and very fine concentric growth-lines with several laminae near the commissure. Apical angle 105-120°."

Comments

Special attention must be paid to the wide place occupied by *Cretirhynchia plicatilis* in the literature. Since the description of *Terebratula plicatilis* appeared in the Mineral Conchology of Great-Britain (J. SOWERBY, 1816, p. 37), this name has been widely used by numerous authors for describing many rhynchonellid brachiopods from the European chalk facies. The concise description given by SOWERBY was very freely interpreted by several palaeontologists. The binomen *Terebratula* (or *Rhynchonella*) *plicatilis* was applied to several distinct species collected from the Cenomanian to the uppermost Maastrichtian. *Terebratula* (or *Rhynchonella*) *plicatilis* became an abstract concept applied to nearly all ribbed rhynchonellid brachiopods from the Chalk. Most of the distinctive characters which allow us to recognize different species in the genus *Cretirhynchia* PETTITT (1950) have been considered as "variations". These variations were never measured or demonstrated and an extraordi-

nary confusion was installed. Some examples illustrate this problem.

STEINICH (1965) stressed the fact that the Maastrichtian *Cretirhynchia retracta* (ROEMER, 1841) had been confused with *C. plicatilis* (J. SOWERBY) by HAGENOW (1842), BOLL (1846), BRONN (1848), PUGGAARD (1852), QUENSTEDT (1871), GEINITZ, F.E. (1888), POSSELT (1894), GEINITZ, H.B. (1895) and by DEECKE (1895).

Cretirhynchia plicatilis (J. SOWERBY, 1816) had often been confused with *C. octoplicata* (J. SOWERBY, 1816). The latter species was often considered as a variety of the former. These confusions are discussed further when dealing with *Cretirhynchia octoplicata*.

The Campanian *Rhynchonella plicatilis* var. *woodwardi* DAVIDSON, 1855 has been confused with *Cretirhynchia plicatilis* (J. SOWERBY) by CORNET & BRIART (1866 and 1874), QUENSTEDT (1871), UBAGHS (1879), and by RUTOT & VAN DEN BROECK (1887).

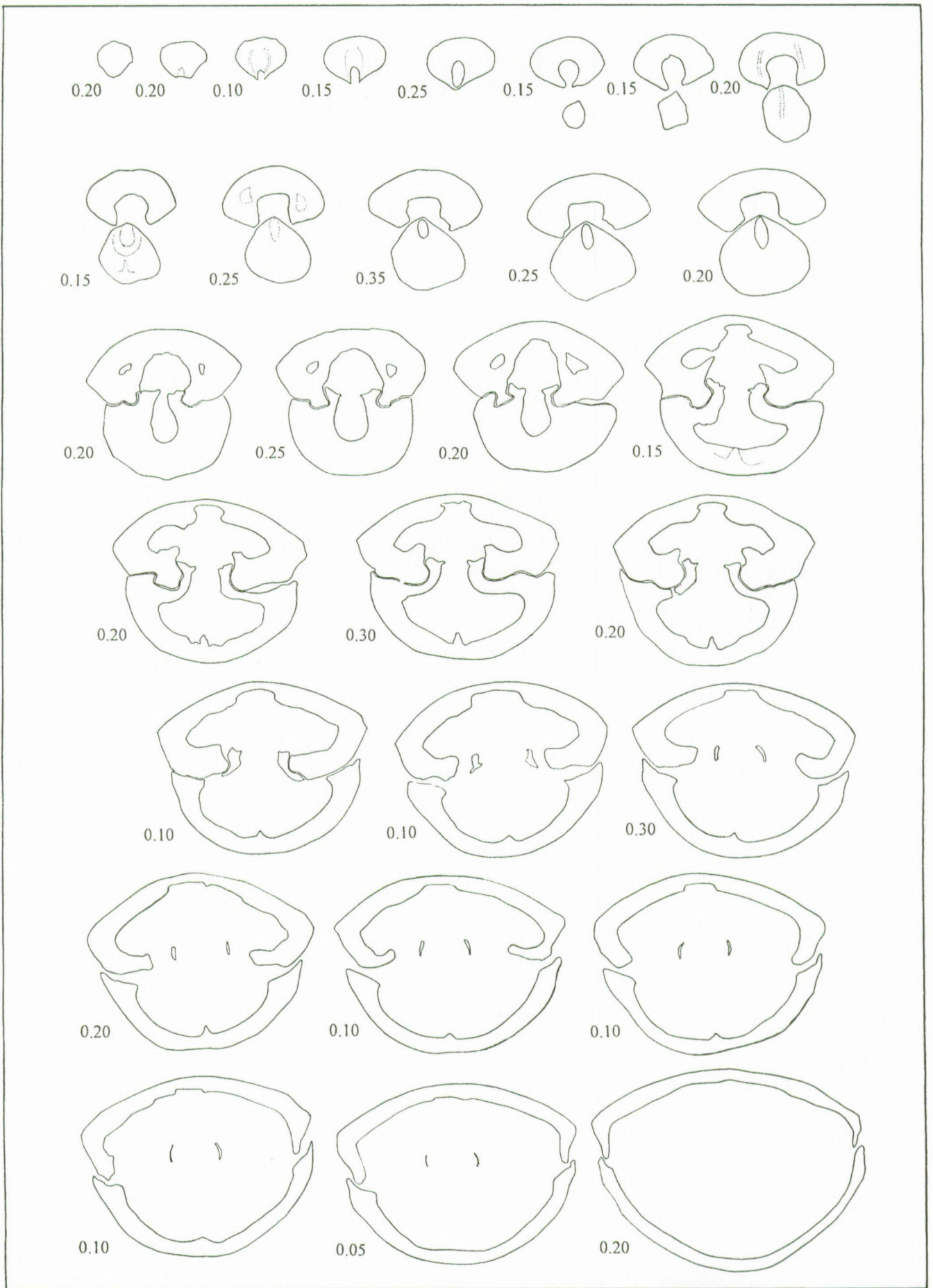
Even "smooth" species such as *Cretirhynchia limbata* (VON SCHLOTTHEIM, 1813) and *C. subplicata* (MANTELL, 1822) were included as varieties of the true *C. plicatilis* by several authors as BRONN (1851), QUENSTEDT (1871) and also by D'ORBIGNY (1847, pp. 46, 47, 48) who included *Terebratula subplicata* MANTELL, 1822 in his *Rhynchonella octoplicata* D'ORBIGNY (*non Terebratula octoplicata* J. SOWERBY, 1816), together with the true *T. plicatilis* (J. SOWERBY).

DAVIDSON (1855, pp. 75-79) repeated D'ORBIGNY's opinion (1847) namely that "SOWERBY's descriptions of *Terebratula plicatilis* and *Terebratula octoplicata* are so entirely similar, that no one is able to perceive in them distinguishing features". DAVIDSON, admitting D'ORBIGNY's point of view, interpreted *Terebratula plicatilis* in a very wide sense. But, he reported the opinion of WOODWARD (1833) who considered *Terebratula plicatilis* and *T. octoplicata* as distinct species. Moreover, DAVIDSON (1855, p. 77) created a variety (var. *woodwardi*) for separating the Campanian rhynchonellid brachiopod designated here as *Woodwardirhynchia woodwardi* (DAVIDSON, 1855) from *Terebratula plicatilis* (SOWERBY, 1816). PETTITT (1950, p. 9), pointed out that only the fig. 40, pl. 10 in DAVIDSON's monograph is a true *Cretirhynchia plicatilis*.

Some authors however restricted the use of the specific name *plicatilis* to the true *Terebratula plicatilis* J. SOWERBY, 1816: see DEFRANCE (1828, p. 159) in his "Dictionnaire des Sciences naturelles" and DESHAYES (1836, p. 357) who insisted on a possible confusion in literature between *Terebratula plicatilis* and some Cenomanian rhynchonellid species placed today in the genus *Cyclothyris* M'COY, 1844. PETTITT (1950, pp. 9-12) has accurately reviewed the whole material available and his detailed description restricts this species to a very distinct *Cretirhynchia* found in precise stratigraphical levels of the British Chalk; the *Coranguinum* and *Testudinarius* Zones. For PETTITT, *Cretirhynchia plicatilis* is distinct from *C. octoplicata* and also from all other ribbed rhynchonellid brachiopods from the Chalk.

Recent works (OWEN, 1962 and 1987; AGER, 1965; STEINICH, 1965 and BAILEY *et al.*, 1983) generally admit and confirm the point of view of PETTITT.

However, KAEVER *et al.* (1974, p. 107, pl. 1, figs. 7a-c) continue to apply the binomen *Cretirhynchia plicatilis* to



German material which appears different from the English species.

ALIEV & TITOVA (1988, text-fig. 67, pl. 5, figs. 1-5.) illustrated and published serial sections of a Coniacian-Santonian rhynchonellid brachiopod which they described as *Cretirhynchia plicatilis*. However, the general outline of their sections is different from the outline seen in sections of *C. plicatilis*. The dental plates are thinner and the dorsal septum is weakly developed. Externally this material exhibits a different type of ribbing and an anterior contour which is oval-lenticular. In *C. plicatilis* the anterior contour is more oval, never lenticular and the costae are much finer. Differences in the linguiform extension are also observed. Moreover the specimen illustrated on pl. 5, figs. 1a-d appears fairly distinct from the specimen figured pl. 5, figs. 5a-d.

Observations made on the reviewed material

The specimen chosen by J. SOWERBY in 1816 is a perfectly preserved specimen from Northfleet, Kent. It is a gerontic representative of the species. The whole material examined by PETTITT (1950) consists in fully adult, often gerontic, specimens. Younger specimens are nearly absent from the collections investigated. The whole variability and the ontogeny of the species is not well known. PETTITT (1950, p. 10) indicated that the convexity of the shell increases in the dorsal valve during growth. This increase of convexity is "accompanied by increased growth along the posterior and lateral margins, tending to the formation of a depression on either side of the dorsal umbo". This has been deduced from the observation of the shape of concentric laminae present on the surface of a specimen. A younger shell is illustrated here (Pl. 1, Figs. 4a-e) which shows a reduced convexity. Its other external characters, such as the shape of its linguiform extension, the structure of its costae, the shape of its beak and the size and shape of its foramen, fit within the limit of the description given by PETTITT. As the original material mainly consists of gerontic specimens, new material is needed for describing the ontogenic process.

PETTITT (1950, p. 10) studied "numerous specimens from the Upper Chalk". In the collections reviewed in the Natural History Museum, 19 specimens are considered here as true representatives of the species. Many other specimens, labelled *Cretirhynchia plicatilis* (see above for references) must be discarded.

The fact that most European, non-British, specimens attributed to *Cretirhynchia plicatilis* (J. SOWERBY, 1816) are misidentified, restricts *C. plicatilis* to its original geographic area. It is not excluded, a priori, that *C. plicatilis* could be present elsewhere in Europe, but material, candidate to this determination, should be imperatively confronted with the original English material for avoiding new taxonomical errors.

The specimen sectioned and illustrated in PETTITT (1950, text-fig. 4, p. 11) shows the important internal characters of the genus and subgenus *Cretirhynchia* PETTITT, 1950.

New serial sections were made on another specimen from Northfleet, Kent, England (Fig. 8). These sections confirm the internal structures observed by PETTITT (1950, text-fig. 4, p. 11). The dental plates are thick and ventrally convergent. The hinge plates are very small and triangular whereas the crural bases are subquadrate. The raduliform crura which remain close together are slightly and inwardly concave in their posterior part. The sections illustrated here (Fig. 8) and the sections illustrated by PETTITT (1950, text-fig. 4, p. 11) distinguish *Cretirhynchia* (*Cretirhynchia*) *plicatilis* from *C. octoplicata* (J. SOWERBY, 1816).

Cretirhynchia (*Cretirhynchia*) *retracta*

(ROEMER, 1841)

Text-Figure 9, Plate 3, Figures 2a-e, 3a-e, 4a-e, 5a-e.

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| * | 1841 | <i>Terebratula retracta</i> N. - ROEMER, F.A., p. 38, n° 9, pl. 7, figs. 2. |
| | 1842 | <i>Terebratula plicatilis</i> Sow. - VON HAGENOW, p. 534, n° 2. |
| | 1842 | <i>Terebratula octoplicata</i> Sow. - VON HAGENOW, p. 534, n° 3. |
| | 1846 | <i>Terebratula octoplicata</i> Sow. - BOLL, pp. 148, 209. |
| | 1846 | <i>Terebratula plicatilis</i> Sow. - BOLL, p. 209. |
| | 1846 | <i>Terebratula pisum</i> Sow. - BOLL, p. 209. |
| | 1851 | <i>Terebratula octoplicata</i> Sow. - BOLL, p. 446. |
| | 1852 | <i>Terebratula octoplicata</i> Sow. - BOLL, p. 62. |
| | 1852 | <i>Terebratula plicatilis</i> (Sow.) Bronn - PUGGAARD, p. 14, fig. 19, p. 17. |
| | 1856 | <i>Rhynchonella octoplicata</i> Sow. - BOLL, p. 46. |
| | 1871 | <i>Terebratula octoplicata subplicata</i> - QUENSTEDT, p. 168, pl. 41, figs. 58, 60-62. |
| | 1885 | <i>Terebratula retracta</i> - QUENSTEDT, p. 697. |
| ? | 1885 | <i>Rhynchonella retracta</i> Roem. - LUNDGREN, pp. 16, 36-37, n° 3, pl. 1, fig. 23. |
| | 1888 | <i>Rhynchonella plicatilis</i> Sow. - GEINITZ, F.E., p. 742. |
| | 1894 | <i>Rhynchonella octoplicata</i> (Sow.) Davidson. - POSSELT, p. 28, n° 4, pl. 3, figs. 17, 18d-f. |
| pp | 1894 | <i>Rhynchonella retracta</i> , Roemer. - POSSELT, p. 28, n° 2. |
| | 1895 | <i>Rhynchonella plicatilis</i> Sow. - GEINITZ, H.B., pp. 6-7. |
| | 1895 | <i>Rhynchonella octoplicata</i> Sow. - GEINITZ, H.B., pp. 6-7. |
| | 1909 | <i>Rhynchonella retracta</i> Roemer - BRÜNNICH NIELSEN, p. 156, n° 16. |
| | 1950 | <i>Cretirhynchia triminghamensis</i> , sp. nov. - PETTITT, pp. 17-18, pl. 2, figs. 7a-c. |
| | 1961 | <i>Cretirhynchia retracta</i> (Roem.) - KOVALEVA, pp. 66, 70. |
| | 1965 | <i>Cretirhynchia retracta</i> (Roemer, 1841) - STEINICH, pp. 7-9, 16-24, 196, 203-207 text-figs. 4-12, pl. 2, figs. 1a-d, 2a-d, 3a-d, pl. 3, figs. 1a-b, pl. 21, figs. 5-6. |
| | 1965 | <i>Cretirhynchia triminghamensis</i> Pettitt - STEINICH, pp. 17, 23-24. |
| ? | 1967 | <i>Cretirhynchia triminghamensis</i> Pettitt, 1950 - NECHRIKOVA, pp. 30-31, pl. 1, figs. 1, 1a, 1b. |
| | 1972 | <i>Cretirhynchia retracta</i> (Roemer) - SURLYK, p. 24, text-figs. 5, 12 |



Fig. 9 — Serial transverse sections through the umbonal part of *Cretirhynchia* (*Cretirhynchia*) *retracta* (ROEMER, 1841) collected from the Lower Maastichtian, Trimingham (Norfolk, England). Length of the specimen: 22.2 mm. NHM. BB. 43335.

- non 1974 *Cretirhynchia retracta* (Roemer, 1842) - KATZ, p. 251, pl. 83, figs. 10a-c.
- 1982 *Cretirhynchia triminghamensis* Pettitt - NECHRIKOVA, table 2, pp. 39-40, pl. 3, figs. 8-11.
- ? 1984 *Cretirhynchia retracta* (Roemer, 1841) - POPIEL-BARCZYK, p. 350, pl. 151, fig. 2.
- ? 1988 *Cretirhynchia retracta* (Roemer, 1841) - POPIEL-BARCZYK, p. 13, text-figs. 13-14, pl. 2, figs. 4-6.
- 1988 *Cretirhynchia triminghamensis* Pettitt, 1950 - POPIEL-BARCZYK, p. 16.
- 1988 *Cretirhynchia ex gr. limbata retracta* - JOHANSEN, text-fig. 2.
- 1989a *Cretirhynchia ex gr. limbata* (Schlotheim 1813) *retracta* (Roemer 1841) - JOHANSEN, text-fig. 2.
- 1989b *Cretirhynchia ex gr. limbata retracta* - JOHANSEN, text-fig. 2.
- non 1992 *Cretirhynchia retracta* (Roemer, 1841) - POPIEL-BARCZYK, p. 15.

Stratigraphical range: Lower Maastrichtian

Type specimen

Specimen from the Lower Maastrichtian of Rügen (Germany), illustrated by ROEMER, F.A. (1841, pl. 7, fig. 2) not traced, but it could be useful to check the collection of Roemer preserved in the Pelizaeus Museum in Hildesheim.

STEINICH (1965) illustrated three specimens from Rügen (1965, pl. 2, figs. 1a-d, 2a-d, 3a-d) but he did not designate a lectotype for this species.

Material

Material preserved in the NHM.

Material collected from Trimingham (Norfolk, England).

One specimen which is the holotype of *Cretirhynchia triminghamensis* PETTITT, 1950, illustrated by PETTITT (1950, pl. 2, figs. 7a-c). Reference B. 52635.

Eleven specimens labelled as *Cretirhynchia triminghamensis* PETTITT, 1950 with the following references: B. 96744-45, B. 96961 and BB. 43329-36. The specimen BB. 43335 has been sectioned (Fig. 9).

Material preserved in the Geologisk Museum in Copenhagen.

One complete specimen labelled as *Cretirhynchia retracta* (ROEMER, 1841) from Stevns under reference n° 1918.95. Lower Maastrichtian.

Material preserved in the IRScNB in Brussels.

Three specimens of *Cretirhynchia retracta* (ROEMER, 1841) collected from Møns Klint, Denmark. Lower Maastrichtian.

One specimen of *Cretirhynchia retracta* (ROEMER, 1841) collected from Kronsmoor, Schleswig-Holstein, Germany. Lower Maastrichtian. Illustrated on Pl. 3, Figs. 5a-e.

Two specimens of *Cretirhynchia retracta* (ROEMER, 1841) collected from Lägerdorf, Germany. Lower Maastrichtian.

Original diagnosis in ROEMER (1841, p. 38)

“*Ist etwas breiter als lang, breit queer oval, wenig dreiseitig und hat 27 einfache, flache, erst seit der Mitte sichtbare Falten,*

von denen drei in dem tiefen, glattseitigen, nach dem Buckel der Bauchschale zurückgebogenen Sinus liegen; Bauschale vor der Stirn am höchsten; sie steigt am Buckel anfangs senkrecht, dann sehr allmählig in die Höhe.”

Emended diagnosis in STEINICH (1965, pp. 16-17)

“*Umriss breit-subpentagonal bis breit-subtriangulär; Dorsalklappe kräftig gewölbt, mit hohem, abgeflachtem Wulst; Ventralklappe an den Seiten flach, der tiefe Sinus greift mehr oder weniger rechtwinklig zur Lateralkommissur trapezoidal bis rektangulär in den Dorsalwulst ein; grösste Dicke vor der Schalenmitte; über 60 sehr niedrige Rippen, deren Zahl an Schalenrand i. d. R. auf um 20 kräftige reduziert wird, im Sinus 3 bis 14, meist aber 5 bis 7; Schnabel kurz, spitz, leicht eingebogen; Schnabelkanten scharf; Deltidium kragenförmig; Foramen sehr klein, rund.*”

Original diagnosis of *Cretirhynchia triminghamensis* in PETTITT (1950, p. 17).

“*Cretirhynchia*, about 20 mm long, 23 mm wide and 15 mm thick, subpentagonal to oval in outline, oval to domical in anterior contour, lateral profile oval to subcircular. Brachial valve convex, with moderately elevated median fold, rather flattened. Pedicle valve less convex, with rather deep, rounded median sinus; linguiform extension trapezoidal to U-shaped, turning at 45° to 60° to lateral commissure. Umbo short, erect to slightly incurved; foramen minute, circular. Ornament of numerous fine, very low costae, becoming more elevated and reduced in number near the commissure; about seven on fold. Apical angle 120°.”

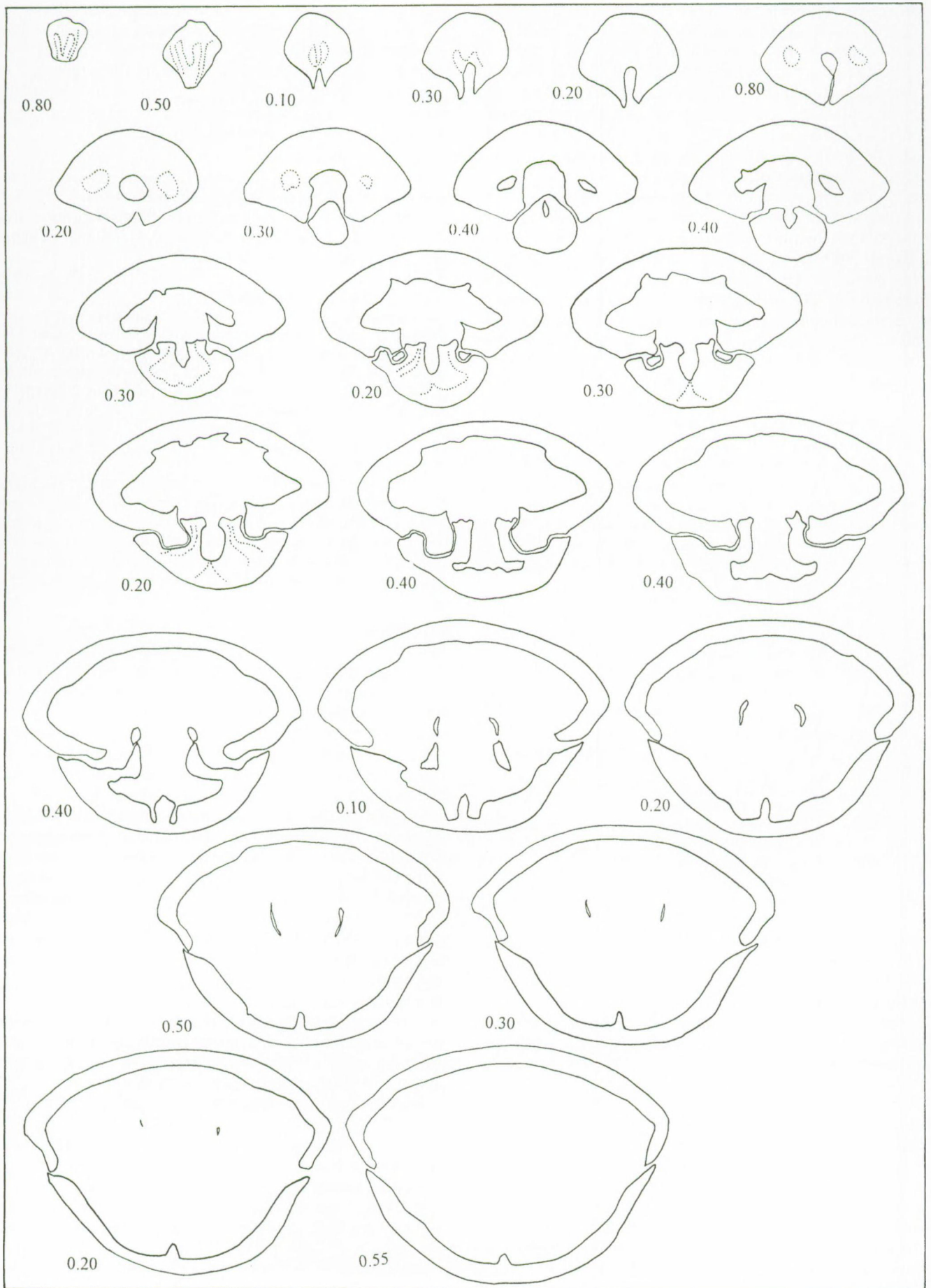
Comments

An exhaustive description of *Cretirhynchia retracta* (ROEMER, 1841) was published by STEINICH (1965, pp. 16-23). The ontogenetic development of this species (STEINICH, 1965, fig. 7, p. 20) and the detailed structure of the brachidium (STEINICH, 1965, fig. 5, p. 18) are fully illustrated. Transverse serial sections of *C. retracta* from Rügen are also figured (STEINICH, 1965, fig. 6, p. 19). All the internal characters of the subgenus *Cretirhynchia* PETTITT, 1950 are visible on these serial sections.

The extended description of *Cretirhynchia triminghamensis* given by PETTITT (1950, pp. 17-18) is very similar to the description of *C. retracta* reproduced above. PETTITT (1950, p. 17) did not investigate the internal characters of *C. triminghamensis* owing to lack of material.

STEINICH (1965, pp. 23-24) pointed out that *C. triminghamensis* could be a junior synonym of *C. retracta*. The material from Trimingham, from Lägerdorf and Kronsmoor (Germany) and the Danish specimens from Stevns and Møns Klint were compared. As already suggested by STEINICH, it is rather difficult to separate the English “*triminghamensis*” specimens from the German and Danish individuals of *C. retracta*. The beak structure and the interarea, especially, are strictly identical for the

→
Fig. 10 — Serial transverse sections through the umbonal part of *Cretirhynchia* (*Cretirhynchia*) *norvicensis* PETTITT, 1950 collected from the Upper Campanian (*Belemnitella mucronata* Zone), Norwich (Norfolk, England). Length of the specimen: 26.1 mm. NHM. B. 24902.



specimens investigated. These characters are fairly important as it has been demonstrated that *C. retracta* is a secondary free living brachiopod.

Transverse serial sections of a specimen of *C. triminghamensis* were made and the results are illustrated in Fig. 9. These sections can be compared with the results published by STEINICH (1965, text-fig. 6, p. 19) and it is difficult to point out any significant differences between them. The posterior part of the shell is thickened and ventrally convergent, thick dental plates are observed. They are rather short. The hinge plates are very small and subtriangular in section. Crural bases are more or less subquadrate and the raduliform crura are slightly concave. The crura, in the sectioned specimen, remain close together till their anterior end. The similarity between external and internal characters of *C. triminghamensis* and *C. retracta* confirms the opinion of STEINICH and we also consider *C. triminghamensis* PETTITT, 1950 and *C. retracta* (ROEMER, 1841) as synonyms.

Cretirhynchia (Cretirhynchia) norvicensis

PETTITT, 1950

Text-Figure 10, Plate 2, Figures 1a-e, 2a-e, 3a-e, 4a-e, 5a-e, Plate 3, Figures 1a-e.

- 1855 *Rhynchonella plicatilis* var. *octoplicata* Sow. - DAVIDSON, pl. 10, figs. 1-11, 16, 17.
- * 1950 *Cretirhynchia norvicensis*, sp. nov. - PETTITT, pp. 15-17, pl. 2, figs. 6a-c.
- 1961 *Cretirhynchia norvicensis* Pettitt - PEAKE & HANCOCK, p. 320.
- 1962 *Cretirhynchia norvicensis* Pettitt - OWEN, Text-fig. 9, p. 58, p. 61.
- 1965 *Cretirhynchia norvicensis* Pettitt - STEINICH, p. 24.
- 1968 *Cretirhynchia norvicensis* Pettitt - LEEDER, pp. 6-7, tables 1-2.
- 1982 *Cretirhynchia norvicensis* Pettitt - NECHRIKOVA, pp. 38, 40.
- 1988 *Cretirhynchia norvicensis* Pettitt - POPIEL-BARCZYK, pp. 13, 14.
- 1988 *Cretirhynchia norvicensis* Pettitt - WOOD, pp. 21, 29, 36, 54, 61, 64, 71-72, 89, 92-93.
- 1990 *Cretirhynchia norvicensis* Pettitt - JOHANSEN & SURLYK, p. 838.

Stratigraphical range: Upper Campanian, *Belemnitella mucronata* Zone

Type specimen

Holotype (in PETTITT, 1950, p. 16) from the *Blt. mucronata* Zone, Mousehold pit, Norwich, Norfolk, England, preserved in the NHM; reference B. 93138 and figured by PETTITT (1950, pl. 2, figs. 6a-c).

Material

Material preserved in the NHM.

From Norwich, Norfolk, England.

The holotype cited above.

B. 477 (young individual), B. 9638-40 (from Mousehold pit), B. 10681 (3 specimens), B. 22033, B. 24902 (29 specimens), B. 25078, B. 31340 (3 specimens), B. 44192-94 (from Mousehold pit), B. 45244-45 (from Harford Bridge), B. 47580-86 and B. 47588-93, B.

70201, B. 93354-56 (from Mousehold pit), B. 97815-26 (several specimens from this collection figured in this paper on Plate 2, 3).

B. 83341, B. 83344 and B. 83348 are three representatives of *C. norvicensis* although they were originally determined as *C. cuneiformis* PETTITT, 1950.

From Trimmingham, Norfolk, England.

One specimen: B. 29731.

Material preserved in the IRScNB in Brussels.

One specimen from Wansin (Brabant, Belgium) and one specimen from Waremme (Liège, Belgium) incidentally collected during waterworks.

Original diagnosis in PETTITT (1950, p. 15)

"*Cretirhynchia*, about 25 mm long, 27 mm wide and 18 mm thick, triangular to subpentagonal in outline, oval in anterior contour, depressed oval in lateral profile. Brachial valve moderately convex, with broad, flattened fold on the anterior third of the valve. Pedicle valve less convex, with broad, moderately deep but somewhat flattened median sinus. Linguiform extension trapezoidal. Umbo short, erect to slightly incurved, beak-ridges distinct. Foramen small, auriculate; deltidial plates slightly produced.

Ornament of about 50 fine depressed costae, reduced in number to about 20 near the commissure, with about 7 on fold and 6 in sinus; the intervening sulci are narrow but are wider and deeper near the commissure. There are fine concentric growth-lines and occasional laminae; they are particularly well developed near the commissure. Apical angle 99°."

Comments

The external characters of this species have been exhaustively described by PETTITT (1950, pp. 16-17) and his accurate description can be consulted. The external distinctions between *C. norvicensis* PETTITT, 1950, *C. plicatilis* (J. SOWERBY, 1816), *C. octoplicata* (J. SOWERBY, 1816), *C. intermedia* PETTITT, 1950, *Woodwardirhynchia cuneiformis* (PETTITT, 1950) and *Woodwardirhynchia woodwardi* (DAVIDSON, 1855) are exposed in this text.

For the internal characters of *C. norvicensis*, PETTITT (1950, p. 16) indicated that "the teeth are large, but the dental lamellae are considerably reduced. In the brachial valve the hinge plate is wide and thickened and the dental sockets are large; a median septum and raduliform crura are present". No transverse serial sections were illustrated by PETTITT. OWEN (1962, text-fig. 9, p. 58) figured serial sections for this species. From these sections it can be seen that the umbo is strongly thickened and dental plates are not as reduced as indicated by PETTITT. They are very thick and ventrally convergent. The hinge plates are small, subtriangular in section and the crural bases are subquadrate. The crura are a little more laterally divergent than in the type species *C. plicatilis*.

Another specimen from the *Blt. mucronata* Zone of Norwich (B. 24902) was used for serial sections (Fig. 10). The shell is thickened in its posterior part. The thick and ventrally convergent dental plates, are shorter in this specimen. Hinge plates are small and subtriangular and crural bases are subquadrate. The crura remain close together but they are slightly more divergent than in *C. plicatilis*.

Usually, *C. norvicensis* has a clear triangular outline. Among the specimens investigated, some exhibit a trans-

versely oval outline. These specimens can be confused with *Woodwardirhynchia tenuicostata* (VON HANSTEIN, 1879). Serial sections will help to dispell confusion between these two rhynchonellid brachiopods. It is probable that these transversely oval specimens were considered by PETTITT as passage forms between *C. norvicensis* and *C. intermedia* PETTITT, 1950 (another species with a transversely oval outline). However, such passage forms are doubtful. The internal features observed in serial sections for both species indicate that *C. intermedia* has little in common with *C. norvicensis*.

C. norvicensis preserves a primitive crural structure which is not very distinct from the crural structure observed in the genus *Burrirhynchia* OWEN, 1962. *C. intermedia* PETTITT, 1950 which is now placed in the subgenus *Harmignirhynchia* subgen. n., strongly exhibits concave crural structures which are steeper than the crura observed in *C. norvicensis*. It is difficult to imagine a passage from the elaborate crural structure of *C. intermedia* to a more ancestral aspect observed in *C. norvicensis*.

The similarity proposed by STEINICH (1965, p. 24) between *C. retracta* and *C. norvicensis* PETTITT, 1950 is not confirmed here and *C. norvicensis* remains a distinct and valid species.

C. norvicensis which occurs commonly in the Campanian chalk of Norwich (Norfolk, England) is a large rhynchonellid species which is rarely found outside England. In Belgium, only two specimens are present in the collections of the IRScNB in Brussels and they were incidentally collected during waterworks in the area of Liège. In Norfolk, *C. norvicensis* is found together with *C. arcuata* PETTITT, 1950 in the Beeston Chalk (WOOD, 1988, p. 36). This stratigraphical level is rarely exposed in Belgium resulting in the absence of these two species in the Belgian material.

Subgenus *Lewesirhynchia* subgen. n.

Derivatio nominis: from the name of the town of Lewes (Sussex, England) and from the greek "Πυγχοσ" meaning beak.

Diagnosis of the subgenus

Multicostate rhynchonellid brachiopods with a biconvex, symmetrical shell. Numerous costae, generally faint near umbo, becoming elevated near the commissure. Costae may be reduced in number near the commissure. Incipient splitting of the costae near the commissure is observed in some species. Thick-shelled, umbo filled with callus. No pedicle collar. Thick dental plates, convergent ventrally. Inner socket ridges extending anteriorly. Hinge plates very small, triangular becoming anteriorly indistinct. Crural base inwardly concave, developing with the hinge plate and the anterior part of the inner socket ridge, an original hook structure, visible in transverse section. Crura raduliform, slightly diverging.

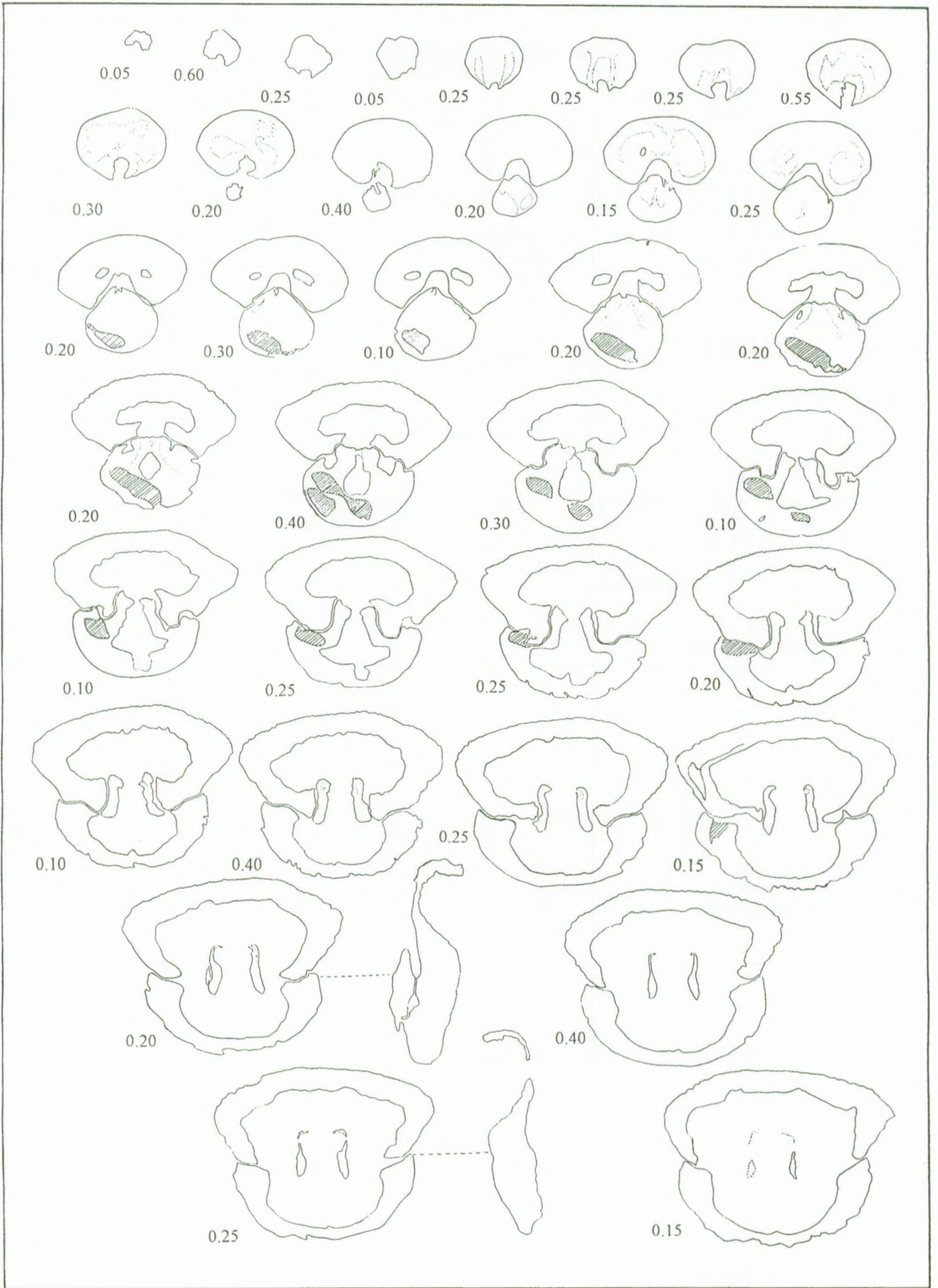
Type species: *Terebratula octoplicata* J. SOWERBY, 1816.

Cretirhynchia (Lewesirhynchia) octoplicata (J. SOWERBY, 1816)

Text-Figure 11, Plate 4, Figures 1a-e.

* 1816 *Terebratula octoplicata* - J. SOWERBY, ii, pp. 37-38, pl. 118, fig. 2 (left-hand figure only).

- non 1822 *Terebratula octoplicata* - BRONGNIART, pl. 4, figs. 8 a-c.
- pp. 1822 *Terebratula plicatilis* var. *b. octoplicata* - MANTZELL, p. 210.
- ? 1827 *Terebratula octoplicata* - NILSSON, p. 36.
- non 1833 *Terebratula octoplicata* - WOODWARD, p. 49.
- non 1837 *Terebratula octoplicata* - HISINGER, pl. 22, fig. 12.
- 1838 *Terebratula octoplicata* Sow. - VON BUCH, pl. 15, fig. 18 (opened specimen).
- pp. 1838 *Terebratula octoplicata* Sow. - VON BUCH, pp. 147-148 (cit. the type specimen of SOWERBY).
- non 1842 *Terebratula octoplicata* Sow. - HAGENOW, p. 534, n°3. (= *C. retracta*).
- non 1845 *Terebratula octoplicata* Sow. - D'ORBIGNY, ii, pt. 3, pl. 43, figs. 15-17.
- non 1846 *Terebratula octoplicata* Sow. - BOLL, pp. 148, 209 (= *C. retracta*).
- pp. 1847 *Rhynchonella octoplicata*, d'Orb. - D'ORBIGNY, pp. 46-48, n° 1111. non 1851 *Rhynchonella octoplicata*, d'Orb. - D'ORBIGNY, pl. 499, figs. 9-12.
- ? 1846 *Terebratula plicatilis* var. *octoplicata* Sow. - GEINITZ, H.B., pl. 16, fig. 16.
- non 1851 *Terebratula octoplicata* Sow. - BOLL, p. 446 (= *C. retracta*).
- non 1852 *Terebratula octoplicata* Sow. - BOLL, p. 62 (= *C. retracta*).
- non 1852 *Terebratula octoplicata* (Sow.) Bronn - PUGGAARD, p. 14, fig. 19, p. 17 (= *C. retracta*).
- non 1855 *Rhynchonella plicatilis* var. *octoplicata* Sow. - DAVIDSON, i, p. 77, pl. 10, figs. 1-17 (= *C. norvicensis*).
- non 1856 *Terebratula octoplicata* Sow. - BOLL, p. 46 (= *C. retracta*).
- non 1860 *Rhynchonella plicatilis* Sow. sp. var. *octoplicata* Sow (Davids). - BOSQUET, N° 586.
- non 1866 *Rhynchonella octoplicata*, d'Orb. - CORNET & BRIART, pp. 128, 187.
- non 1866 *Rhynchonella octoplicata*, d'Orb. - CORNET & BRIART, p. 189.
- non 1870 *Rhynchonella octoplicata*, d'Orb. - CORNET & BRIART, pp. 7, 8, 9
- non 1871 *Terebratula octoplicata subplicata* - QUENSTEDT, pp. 168-169, pl. 41, figs. 58, 60-62 (= *C. retracta*), pl. 41, figs. 59, 63-64 (= *C. limbata*).
- non 1871 *Terebratula octoplicata* - QUENSTEDT, pl. 41, figs. 65-73.
- non 1889 *Rhynchonella plicatilis* var. *octoplicata* - FRIČ, fig. 91.
- pp. 1894 *Rhynchonella octoplicata* (Sow.) Davidson - POSSELT, pp. 28-29, n°4 (*pro partim*), non pl. 2, figs. 17-18. (= *C. retracta*).
- non 1895 *Rhynchonella octoplicata* Sow. - GEINITZ, H.B., pp. 6, 7. (= *C. retracta*).
- non 1895 *Rhynchonella octoplicata* Sow. - DEECKE, pp. 55, 73, 74, 87. (= pp. *C. retracta*, pp. *limbata*).
- non 1907 *Rhynchonella octoplicata* Lam. - DEECKE, pp. 105, 108, 109, 112. (= *C. retracta*).
- 1950 *Cretirhynchia octoplicata* (J. Sowerby). - PETTITT, pp. 8-9, pl. 1, figs 12 a-c.
- 1965 *Cretirhynchia octoplicata* (Sow.) - BIGNOT, p. 5.
- 1965 *Cretirhynchia octoplicata* (Sow.) - STEINICH, p. 17.
- non 1974 *Cretirhynchia octoplicata* (Sowerby) - KAEVER *et al.*, p. 107, pl. 1, figs. 8 a-c.
- 1982 *Cretirhynchia octoplicata* (Sowerby) - NECHKOVA, p. 38.



- 1988 *Cretirhynchia octoplicata* (Sowerby) - POPIEL-BARCZYK, p. 16.
 1997 *Cretirhynchia octoplicata* (J. Sowerby). - MORTIMORE, pp. 37, 93.

Stratigraphical range: Coniacian, *Cortestudinarium* Zone

Type specimen

Lectotype from the Chalk (*Cortestudinarium* Zone ?) of Lewes, Sussex. Figured by J. SOWERBY (1816, pl. 118, fig. 2, left-hand figure). Illustrated by PETTITT (1950, pl. 1, figs 12 a-c). This lectotype is preserved in the NHM (SOWERBY collection), reference B. 61478.

Material

Material preserved in the NHM.

Lectotype (B. 61478) from the Chalk (*Cortestudinarium* Zone?) of Lewes, Sussex. Figured by J. SOWERBY, 1816, pl. 118, fig. 2, left-hand figure). Illustrated by PETTITT (1950), pl. 1, figs 12 a-c.

One specimen from the Chalk of Lewes. B. 8379-1. This specimen has been prepared for serial sections (Fig. 11) and it is illustrated here on Pl. 4, Figs. 1a-e.

Original description in J. SOWERBY (1816, pp. 37-38)

"Gibbose, transversely obovate, obtusely plaited; middle elevated by eight plaits; twelve or fourteen plaits on each side; beak projecting."

Emended diagnosis in PETTITT (1950, pp. 9-10)

"*Cretirhynchia*, about 21 mm. long, 23mm. wide, and 17 mm. thick, transversely oval to sub-circular in outline, cuneiform in lateral profile, and domical in anterior contour. Brachial valve convex, with slight, rounded anterior fold. Pedicle valve less convex, with slight, rounded sinus. Linguiform extension broad, U-shaped. Umbo erect.

Ornament of about 40 depressed costae, about eight on fold. Concentric laminae, chiefly developed along commissure. Apical angle 110°."

Comments

The remarks formulated above for *Cretirhynchia plicatilis* can be repeated for *C. octoplicata*. STEINICH (1965) stressed the fact that the Maastrichtian *C. retracta* (ROEMER, 1841) has been confused with *C. octoplicata* (J. SOWERBY) by HAGENOW (1842), BOLL (1846, 1852, 1851 & 1856), QUENSTEDT (1871), POSSELT (1894), GEINITZ, H.B. (1895) and by DEECKE (1895 & 1907).

The very succinct description of J. SOWERBY (1816, p. 37) distinguishing *C. octoplicata* from *C. plicatilis* only by the number of costae observed on their respective fold, introduced a confusion among these species in many

works published by several authors. This was the case with GEINITZ (1846), DAVIDSON (1855), FRIČ (1889) and POSSELT (1894).

DAVIDSON (1855, pl. 10, figs. 1-11) included in *Rhynchonella octoplicata* (SOWERBY, 1816) Campanian specimens from the *Blt. mucronata* Zone of Norwich which were later described by PETTITT (1950, p. 15) as *Cretirhynchia norvicensis*.

The specimens described and illustrated by KAEVER *et al.* (1974) are not consistent with the diagnosis given by PETTITT (1950). Moreover, the distribution "from Turonian to Campanian" given in that paper fit not with the specially restricted stratigraphical distribution of the type material.

PETTITT (1950, p. 9) insisted in keeping *Cretirhynchia octoplicata* as a valid species distinct from *C. plicatilis* (SOWERBY, 1816), from *C. cuneiformis* PETTITT, 1950 and from *C. norvicensis* PETTITT, 1950.

Despite his efforts to separate *C. plicatilis* and *C. octoplicata* by an accurate description of their respective external characters, an easy distinction between these species remains quite difficult. Both *C. octoplicata* and *C. plicatilis* are species with numerous costae, reduced in number near the commissure. No incipient splitting of the costae is observed. Furthermore, PETTITT (1950, p. 8) restricted *C. octoplicata* to SOWERBY specimen represented in 1816, pl. 118, fig. 2 (left -hand figure). The second specimen [B. 61479] of SOWERBY (1816, pl. 118, fig. 2 right-hand) has been diagnosed by PETTITT (1950, p. 13) as a new species: *Cretirhynchia lenticularis*.

The emended diagnosis of PETTITT (1950, p. 8) is based on three specimens only and his illustrations of this species are limited to the lectotype from J. SOWERBY's collection.

Although *Rhynchonella octoplicata* was one of the most cited (erroneously) Cretaceous rhynchonellid brachiopod during the 19th century, after PETTITT's work, it became an extremely rare species.

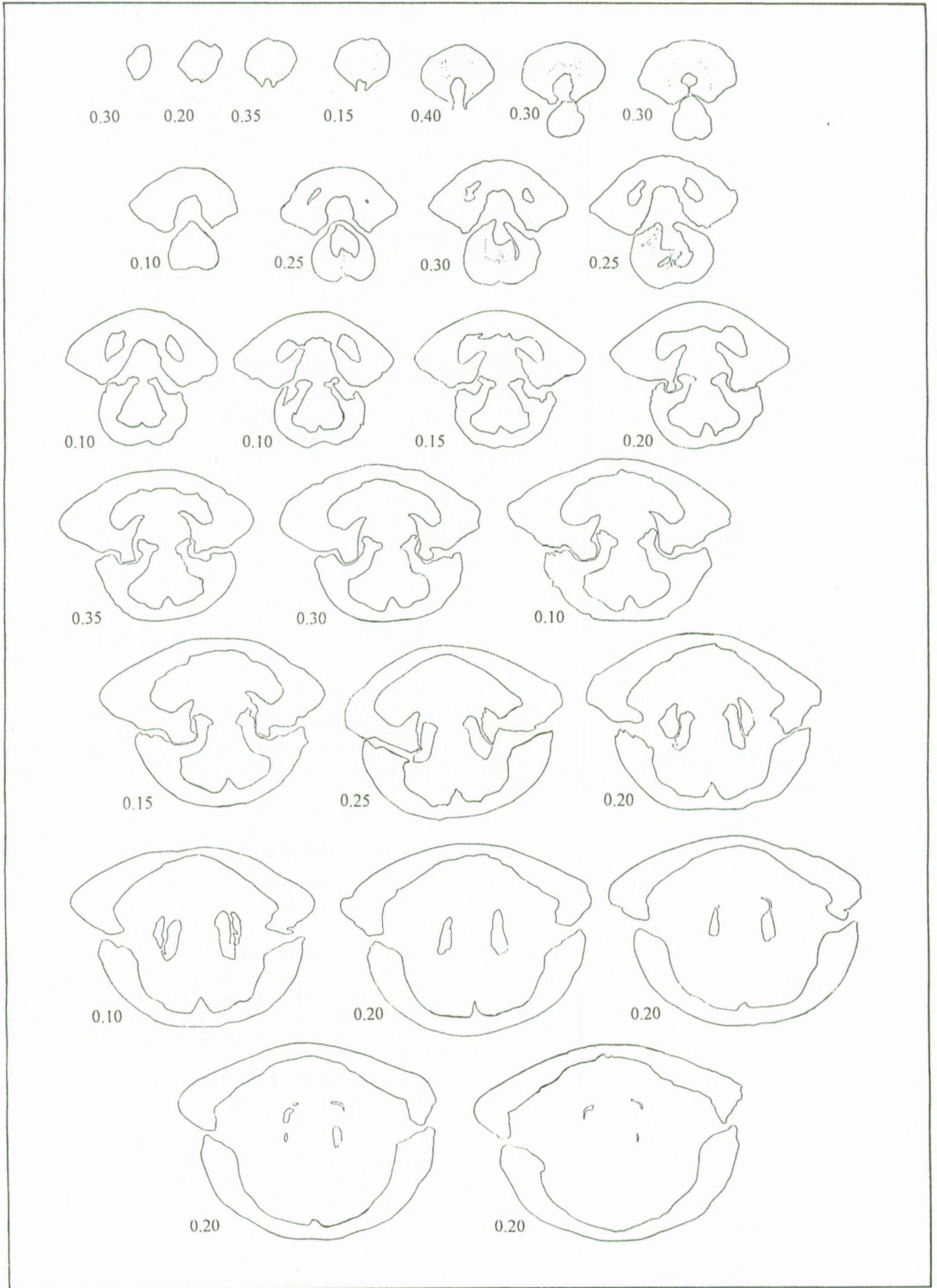
C. octoplicata, *sensu stricto*, has never been collected with certainty, outside England. For PETTITT (1950, p. 9) *C. octoplicata* is not a common species in the *Coranguinum* Zone and he considered it as a variant of *Cretirhynchia cuneiformis* (PETTITT, 1950). But no sections were made, owing to lack of material.

Among the material preserved in the NHM, one specimen, collected from Lewes, Sussex (B 8379-1) has been chosen for serial sections. It has an external outline, very similar to the lectotype of *Cretirhynchia octoplicata*. This specimen has been collected from the same locality as the SOWERBY lectotype.

The sections obtained for this specimen (Fig. 11) confirm the hypothesis of PETTITT (1950, p. 9). Strong convergent dental plates are observed in the ventral valve. On the dorsal valve floor, a persistent septum is developed. Very short, subtriangular hinge plates are visible. These characters are typical for the genus *Cretirhynchia*. The specimen investigated is a gerontic specimen and the anterior parts of its crura are broken. But, crural bases are visible on the sections and they are quite different from the crural bases observed in *C. plicatilis*. They are strongly concave. As the anterior parts of the hinge plates are nearly indistinct, crural bases appear ventrally attached



Fig. 11— Serial transverse sections through the umbonal part of *Cretirhynchia* (*Lewesirhynchia*) *octoplicata* (J. SOWERBY, 1816) collected from the Coniacian (*Cortestudinarium* Zone), Lewes (Sussex, England). Length of the specimen: 19.2 mm. NHM. B. 8379-1.



to the expanded anterior parts of the inner socket ridges. They build a pair of symmetrical "hook structures". This structure which is easily seen in serial sections, is observed in all the species of the subgenus *Lewesirhynchia* subgen. n., and is a distinctive character. A tendency to produce such a "hook" structure is observed in serial sections of *C. norvicensis* (Fig. 10) but it is not fully realized.

Undoubtedly, *C. octoplicata* is a distinct species from *C. plicatilis*. New material from Lewes and other places in England should be collected in order to improve the knowledge of this species and for establishing its potential of variation.

The "passage forms" between *C. octoplicata* and *C. cuneiformis* proposed by PETTITT (1950, p. 9) cannot be taken into account as the internal structures of the second species, placed here in the genus *Woodwardirhynchia* gen. n. (Figs. 2-3, show that it arose from the *Cyclothyrus* stock.

Cretirhynchia (Lewesirhynchia) exsculpta

PETTITT, 1950.

Text-Figure 12, Plate 4, Figures 3a-e, 4a-e.

- * 1950 *Cretirhynchia exsculpta*, sp. nov. - PETTITT, pp. 19-21, text-fig. 6, pl. 1, figs. 6a-c.
- ? 1965 *Cretirhynchia exsculpta* Pettitt, 1950 - BIGNOT, p. 6, pl. 1, figs. 7a-c, 8a-c.
- . 1968 *Cretirhynchia exsculpta* Pettitt - LEEDER, p. 6.
- . 1974 *Cretirhynchia exsculpta* - PAJAUD, p. 25.
- non 1982 *Cretirhynchia exsculpta* Pettitt, 1950 - NECHRIKOVA, p. 38, pl. 2, figs. 35-41.
- . 1983 *Cretirhynchia exsculpta* - BAILEY *et al.*, text-fig. 3, p. 36.

Stratigraphical range: Santonian, *Uintacrinus* and *Marsupites* Zones to Lower Campanian, *O. pilula* Zone.

Type specimen in PETTITT (1950, p. 19).

Holotype from the *Marsupites* Zone collected in Brighton or Friar's Bay, Sussex, England. Illustrated in PETTITT (1950, pl. 1, figs. 6a-c). Preserved in the NHM, reference B. 79824.

Material

Material preserved in the NHM.

Material from Sussex, England.

24 topotypes from the *Marsupites* Zone in Brighton and Friar's Bay (B. 79833-47 and B. 79823-32). 13 specimens from the *Marsupites* Zone in Brighton (B. 19869, B. 22886-1 to 5, BB. 68-70, BB. 4631-32, BB. 561-62, BB. 565). 14 specimens collected from cliffs, east of Brighton (B. 47956-62, BB. 577, BB. 776-80, BB. 922 from the *Marsupites* Zone and BB. 24 from the *O. pilula*

Zone). Three specimens (*Marsupites* Zone) from a railway cutting at Preston Park (BB. 563, BB. 574, BB. 775). Two specimens from the Mantell collection without precise locality (B. 4809-10). 22 specimens from Sussex coast without precise locality collected from the lower part of the *Goniot euthis quadrata* Zone (B. 79756-75, B. 97137-40). One specimen (*O. pilula* Zone) from a roadside, south of Tich Hill farm, west of Dankton Cottages in Sompting (BB. 589). Three specimens (*O. pilula* Zone) collected east of Saltdean Cottages (BB. 937, BB.940, BB. 983). Four specimens (*O. pilula* Zone) collected from the Gap to Saltdean Gap (BB. 28-31). 11 specimens (*O. pilula* Zone) without precise locality (B. 47908-18). Two specimens from the chalk of Lewes from the Mantell collection (B. 10677-78). Six specimens from the *Marsupites* Zone in the Meeching quarry at Newhaven (BB. 914-20).

Material from Dorset, England.

One specimen from the *Uintacrinus* Zone in White Nothe (B. 79819). Two specimens (*Marsupites* Zone) from the Dorset coast (B. 79834-35).

Material from Paulsgrove Pit, Portsdown Hills, Hampshire, England.

10 specimens from the lower part of the *Goniot euthis quadrata* Zone (B. 79776-85).

Original diagnosis in PETTITT (1950, p. 19)

"*Cretirhynchia*, about 19 mm long, 20 mm wide, and 16 mm thick, subpentagonal in outline, domical (*sic*) in anterior contour, and subdomical in lateral profile. Brachial valve convex, with slight, fairly broad and flat median fold on the anterior part. Pedicle valve less convex, with shallow to moderately deep median sinus. Linguiform extension trapezoidal, almost rectangular. Umbo erect. Ornament of about 40 rounded, clearly defined costae, with incipient splitting near the commissure and with moderately deep intervening sulci. Concentric growth-lines, with occasional laminae, especially near the anterior and lateral commissures. Apical angle 109°."

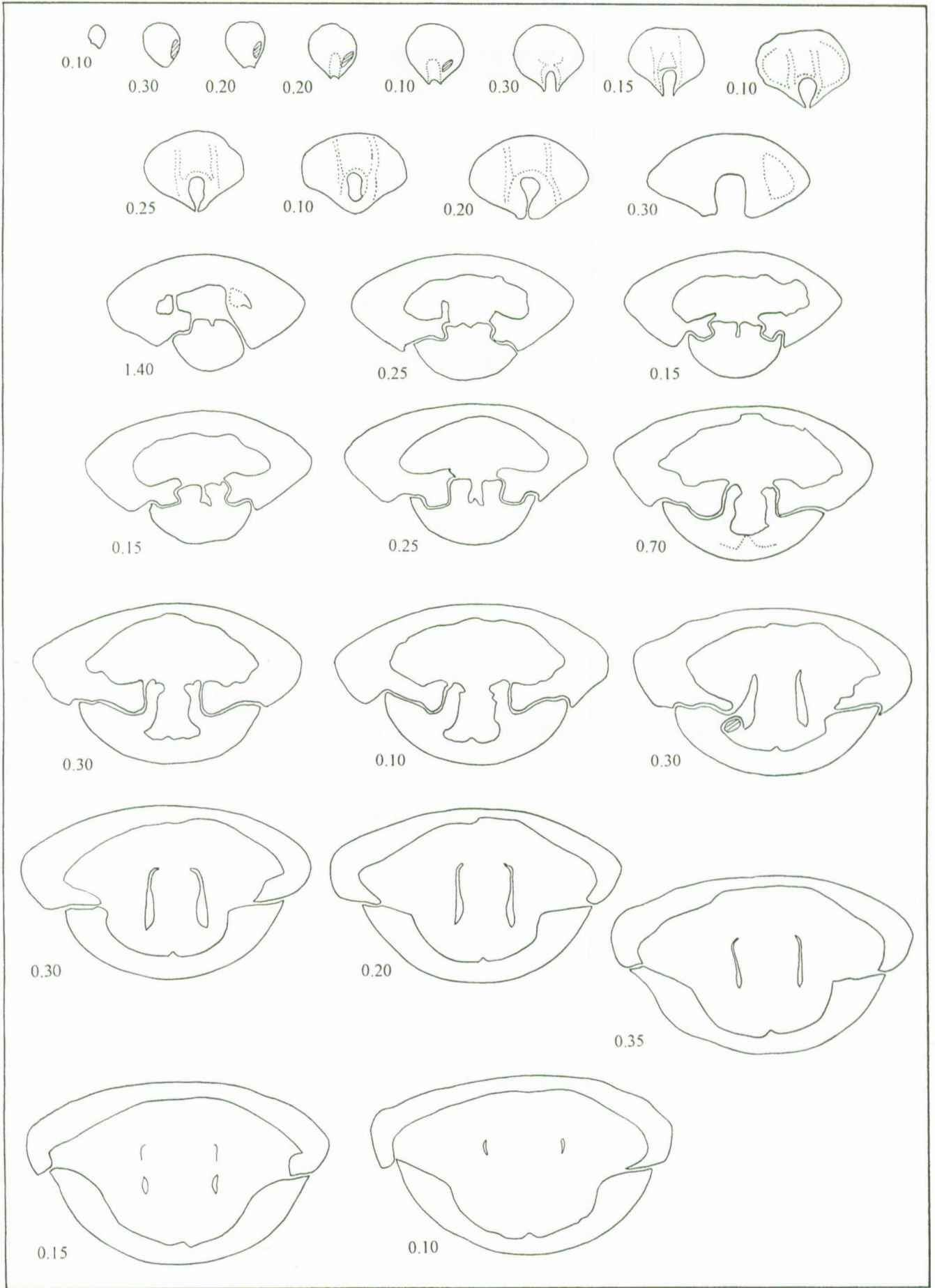
Comments

Cretirhynchia (Lewesirhynchia) exsculpta PETTITT, 1950 is a fairly abundant species in the Santonian and the Lower Campanian of England. It has never been collected, with certainty, outside England. The external morphological characters were exhaustively described by PETTITT (1950, pp. 19-20). For the internal characters, PETTITT (1950, p. 20) pointed to the existence of a dorsal septum and of raduliform crura only. Despite the large amount of material available, no transverse serial sections were illustrated.

Sections made for the present paper (Fig. 12) show that the posterior part of the shell is greatly thickened. In the ventral valve, the dental plates are thick and strongly convergent. They are fused with the lateral walls of the shell, a character already observed by PETTITT (1950, text-fig. 6, p. 20). Robust teeth are present. In the dorsal valve, a persistent septum is present on the valve floor. The outer socket-ridges are very low in transverse section whereas the very high, robust inner socket-ridges are much more developed. The hinge plates are small and subtriangular. The structure built by the anterior parts of the inner socket ridges and the hinge plates, is strikingly similar, in transverse sections, to the structures observed in *C.*



Fig. 12 — Serial transverse sections through the umbonal part of *Cretirhynchia (Lewesirhynchia) exsculpta* PETTITT, 1950 collected from the Santonian (*Marsupites testudinarius* Zone), Brighton (Sussex, England). Length of the specimen: 21.1 mm. NHM. B. 9464.



(*Lewesirhynchia*) *octoplicata* (Fig. 11). Crural bases are inwardly concave forming, with the hinge plates and the anterior parts of the inner socket ridges, symmetrical hook-like figures. In *C. exsculpta*, this hook-like structure is a little thicker than those observed in *C. octoplicata* and in *C. protoexsculpta*.

***Cretirhynchia* (*Lewesirhynchia*) *protoexsculpta* sp. n.**
Text-Figure 13, Plate 4, Figures 2a-e, Plate 6,
Figures 1a-e.

Diagnosis

Medium-sized, multicostate, rhynchonellid brachiopod, subpentagonal to transversely oval in outline, lenticular, dome-shaped in anterior contour and lenticular in lateral profile. Dorsal valve regularly convex with slight, fairly broad and flat median fold on the anterior part. Ventral valve less convex with a very broad, shallow sinus. Linguiform extension trapezoidal. Beak strong, curved, pointed and erect. About 40 costae, clearly defined, not reduced in number near the commissure and showing faint incipient splitting. Inner socket ridges, hinge plates and crural bases associated in very slender hook structures.

Derivatio nominis: from "πρωτο", greek prefix indicating that this species is a potential ancestor of *C. exsculpta*.

Locus typicus: Lewes, Sussex, England.

Stratum typicum: Coniacian, *Cortestudinarium* Zone.

Holotype

Cretirhynchia (*Lewesirhynchia*) *protoexsculpta* sp. n. Text-Figure 13, Plate 4, Figures 2a-e. The holotype is a prepared specimen for transverse serial sections (Fig. 13). The cast, peels and photographs of the serial sections are preserved in the NHM. B. 8379-2.

Dimensions of holotype: 19.8 mm long, 22.3 mm wide and 13.6 mm thick.

Paratype

One specimen collected from Lewes, illustrated Pl. 6, Figs. 1a-e., and preserved in the Natural History Museum in London under reference B. 8379-3.

Description

The shell is relatively depressed, transversely oval in outline (dorsal view) and subpentagonal in ventral view. The convexity of the dorsal valve is moderate and regular, the lateral part of the shell remaining gently convex. The short, median fold occurs on the anterior part of the valve and it is limited by relatively sharp ridges. The ventral

valve is slightly convex mainly in its posterior part and the sulcus is more clearly developed than the corresponding fold on the dorsal valve. The sinus is much wider than the corresponding fold. The linguiform extension is wide and sharply trapezoidal. It turns at an angle of about 60°-70° to the plane of junction of the valves. The beak is slightly curved and erect. The beak-ridges are sharply defined. The hypothryidid foramen is very small and perfectly circular. The deltidial plates are conjunct and produced.

The costae (± 40), relatively flat and rounded, are well defined, very faint near umbo and widening towards the commissure. The costae on the lateral parts of the shell are finer near the commissure than the costae ornamenting the ventral sulcus (± 9) or the dorsal fold (± 8). The deep, intervening sulci, are extremely narrow. Incipient splitting is observed for several costae near the commissure. On the specimens investigated, no growth-lines or growth laminae are detected.

Internal characters (Fig. 13)

The posterior parts of the shell are fairly thickened. In the ventral valve, no pedicle collar has been observed in serial sections. The dental plates are subparallel posteriorly and they become anteriorly convergent. The outer socket-ridges are rather low whereas the inner socket-ridges are very thick in section and quite elevated. Teeth are strong. The hinge plates are small, subtriangular posteriorly, but they become indistinct anteriorly and develop, with the distal parts of the inner socket-ridges and the crural bases, symmetrical hook-like structures. These structures are especially thin and slender in transverse sections. The raduliform crura are slightly concave in their anterior part and are slightly divergent laterally. A persistent septum is present on the dorsal valve floor.

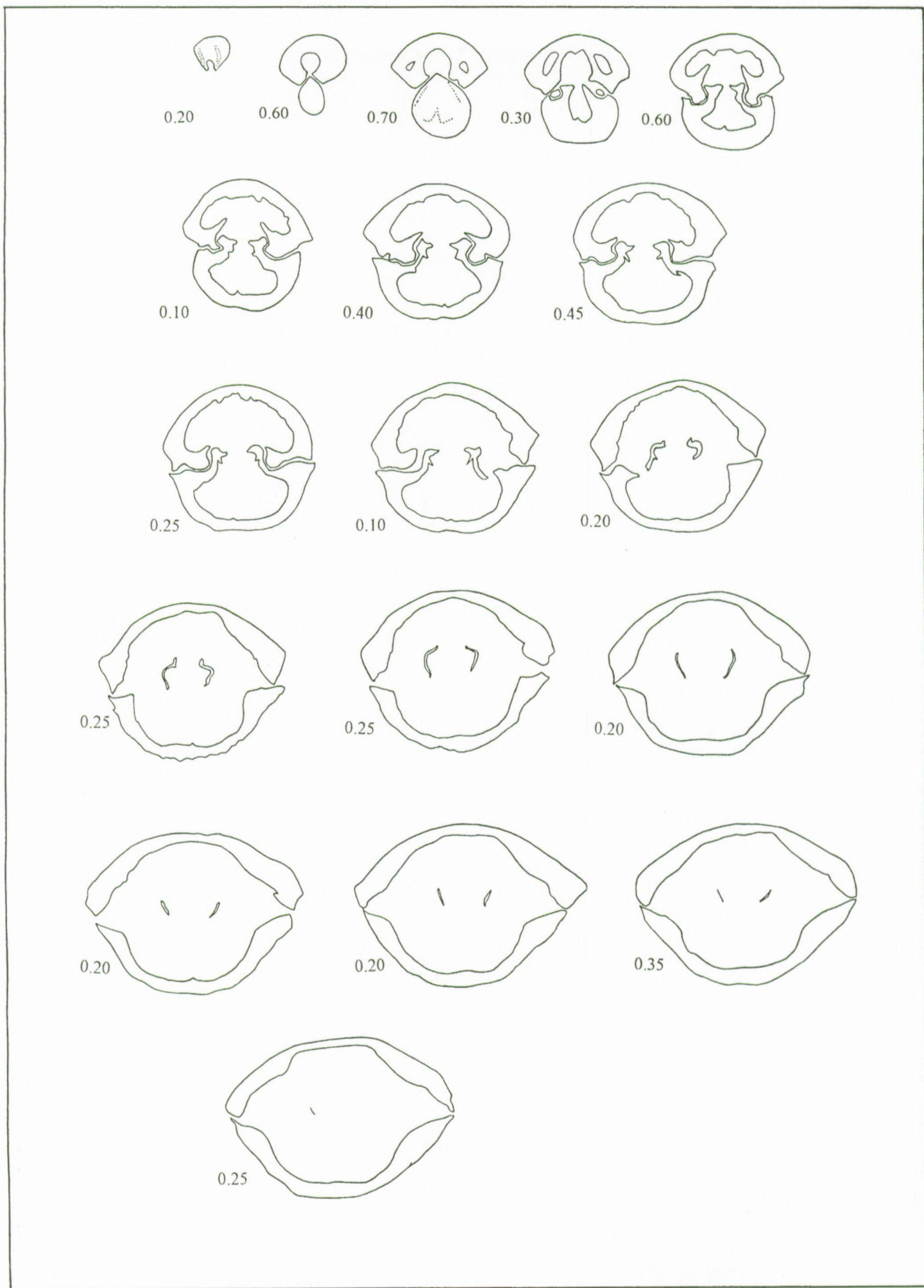
Comparison with other species

Cretirhynchia (*Lewesirhynchia*) *protoexsculpta* sp. n. must be compared with *C. (Lewesirhynchia) exsculpta* PETTIT, 1950. Generally, the dorsal valve of *C. exsculpta* is much more convex and the lateral flanges are much steeper in *C. exsculpta*. The beak is a little more curved in *C. exsculpta* but the beak of *C. protoexsculpta* sp. n. appears wider in dorsal view. The interarea is much more reduced in *C. exsculpta*. In *C. protoexsculpta* sp. n. the interarea is fairly wide. The linguiform extension of *C. exsculpta*, which turns at an angle of 90° to the plane of the commissure, is often rectangular, although a trapezoidal linguiform is more rarely observed. In *C. protoexsculpta*, the linguiform extension turns rarely above an angle of 70° and in the specimens investigated, it is widely trapezoidal. These two species exhibit a similar number of costae showing incipient splitting near the commissure. But, in *C. exsculpta*, the costae ornamenting the anterolateral zone of the dorsal valve, are slightly wider than the costae situated on the fold and in the sulcus. On the contrary, in *C. protoexsculpta* sp. n., the costae present on the fold and in the sulcus are slightly wider than the costae present on the anterolateral parts of the dorsal valve.

Concerning the internal characters, it is observed that the dental plates are more convergent ventrally in *C. exsculpta* than in *C. protoexsculpta* sp. n. The hook-like



Fig. 13 — Serial transverse sections through the umbonal part of the holotype of *Cretirhynchia* (*Lewesirhynchia*) *protoexsculpta* sp. n. collected from the Coniacian ? (*Cortestudinarium* Zone ?), Lewes (Sussex, England). Length of the specimen: 21.5 mm. NHM. B. 8379-2.



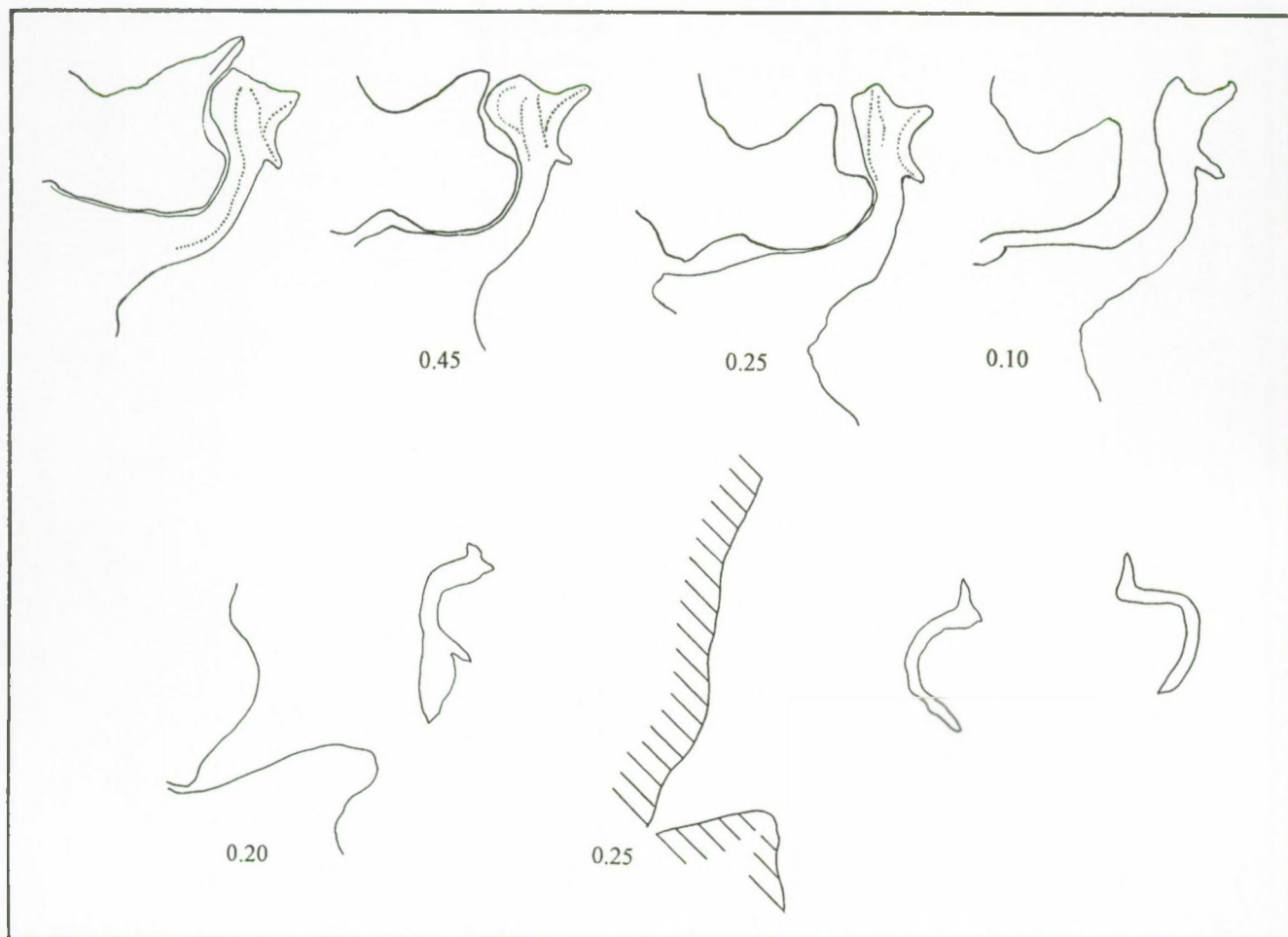


Fig. 15 — Detail of some serial transverse sections through the umbonal part of *Cretirhynchia* (*Harmignirhynchia*) *intermedia* PETTITT, 1950 collected from the Lower Campanian (*Offaster pilula* Zone), East Harnham (Wiltshire, England). Same specimen as in Fig. 14. NHM. B. 92742-4.

structure seen in transverse sections is much more slender in *C. protoexsculpta* sp. n. than in *C. exsculpta*.

Confusion can also be made between *C. protoexsculpta* sp. n. and some flat or depressed specimens of *Woodwardirhynchia cuneiformis* (PETTITT, 1950). In *W. cuneiformis*, incipient splitting of the costae near the commissure never occurs. The number of costae is generally reduced near the commissure in *W. cuneiformis* but some specimens do not exhibit this reduction of the number of costae. The structure of dental plates, hinge plates and crural bases is totally different in *W. cuneiformis* and transverse serial sections avoid any confusion.

As the incipient splitting of the costae is not always clearly present in the specimens of *C. protoexsculpta* sp. n., it is possible that the passage forms between *W. cuneiformis* and *C. octoplicata* (J. SOWERBY, 1816) described

by PETTITT (1950, p. 9) were in fact specimen of *Cretirhynchia* (*Lewisirhynchia*) *protoexsculpta* sp. n.

Subgenus *Harmignirhynchia* subgen. n.

Derivatio nominis: from the name of the village of Harmignies (Mons basin, Hainaut, Belgium) and from the greek “Πυγχοσ” meaning beak.

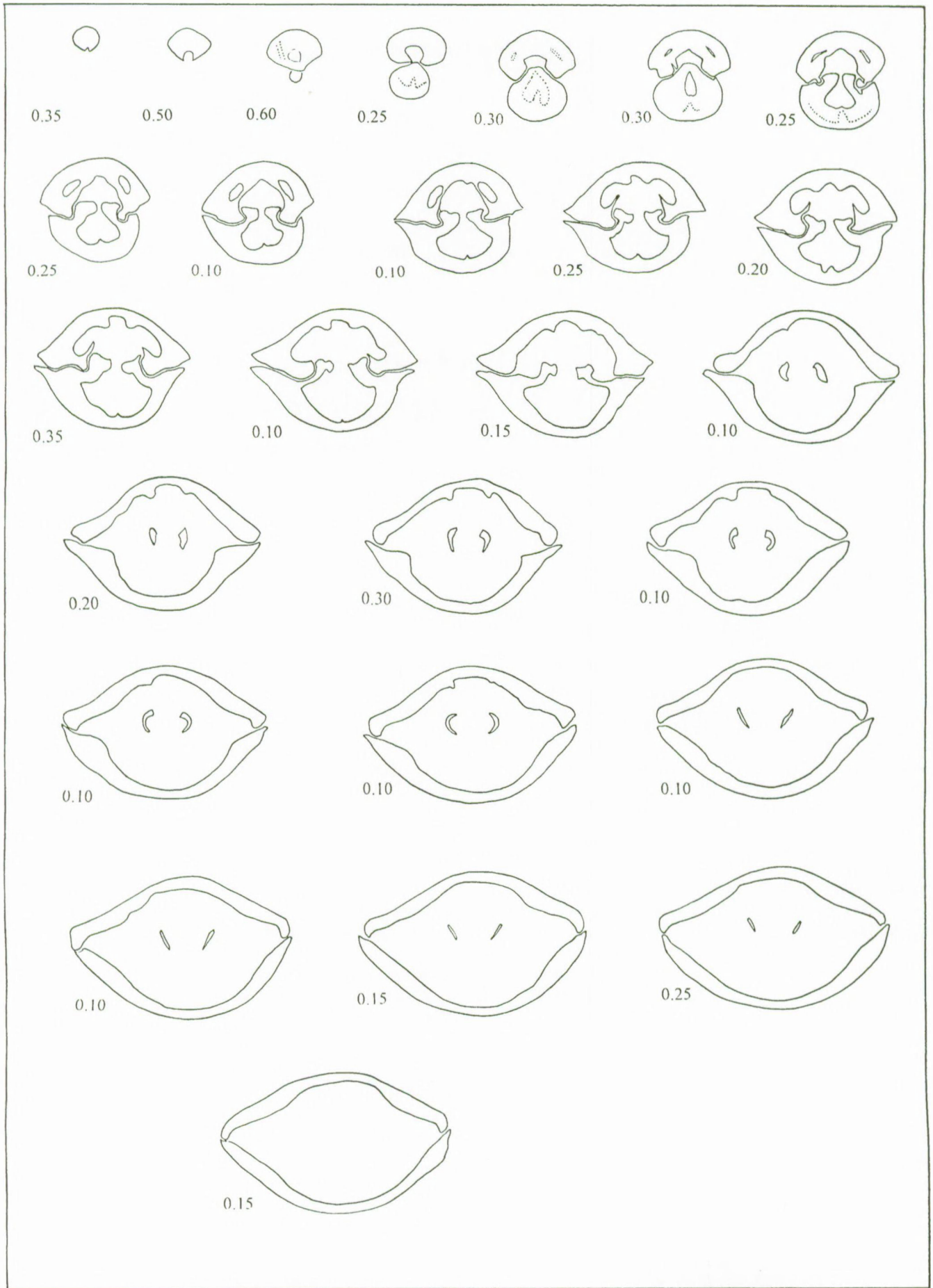
Diagnosis of the subgenus

Multicostate rhynchonellid brachiopods with a slightly biconvex, symmetrical shell. Shell transversely oval in outline, always wider than long. Anterior contour and lateral profile lenticular. Numerous faint costae reduced or not reduced in number near the commissure. No incipient splitting of the costae near the commissure. Dental plates convergent ventrally. Hinge plates relatively wide and crural bases subquadrate but often inwardly concave. Posterior part of the crura strongly concave. Crura steep, deflected ventrally, remaining close together or slightly diverging laterally. Angle formed by the posterior parts of the crura widely obtuse in transverse section.

Type species: *Cretirhynchia intermedia* PETTITT, 1950



Fig. 14 — Serial transverse sections through the umbonal part of *Cretirhynchia* (*Harmignirhynchia*) *intermedia* PETTITT, 1950 collected from the Lower Campanian (*Offaster pilula* Zone), East Harnham (Wiltshire, England). Length of the specimen: 11.9 mm. NHM. B. 92742-4.



Cretirhynchia (Harmignirhynchia) intermedia

PETTITT, 1950

Text-Figures 14-16, Plate 5, Figures 1a-e, 2a-e, 3a-e.

- * 1950 *Cretirhynchia intermedia* sp. nov. - PETTITT, pp. 14-15, pl. 1, figs. 5a-c, 8a.

Stratigraphical range: Lower Campanian, *Offaster pilula* and *Goniot euthis quadrata* Zones.

Type specimen

Holotype from the *O. pilula* Zone of East Harnham, Wiltshire, England, illustrated by PETTITT (1950, pl. 1, figs. 5a-c) and preserved in the NHM under the reference B. 92723.

Material

Material preserved in the NHM.

Specimens from the *O. pilula* Zone of East Harnham, Wiltshire, England

The holotype cited above. 74 topotypes [B. 92705-19, B. 92742 (24 specimens), B. 92743-44, B. 92746-63, B. 92764-73, BB. 43306-11).

Specimens from the *O. pilula* and/or *G. quadrata* Zones of Whaddon near Salisbury, Wiltshire, England.

24 specimens (B. 92043-46, B. 92055-57, B. 92059-61, B. 92069-71, B. 92075-80, B. 92094, B. 92984-87).

Specimens from the *O. pilula* Zone of Harnham Hill, Salisbury, Wiltshire, England.

Three specimens (B. 25068-70).

Original Diagnosis in Pettitt (1950, p. 14)

"*Cretirhynchia*, about 19 mm long, 22 mm wide and 14 mm thick, subpentagonal to oval in outline, oval in lateral profile, lenticular, thick in anterior contour. Brachial valve convex, with low median fold on anterior part; pedicle valve slightly less convex, with moderately deep median sinus; linguiform extension U-shaped, turns at 45° to 60°. Umbo short, thick; foramen small, circular. Costae numerous, low and fine; sulci shallow".

Comments

Cretirhynchia intermedia has never been collected outside England. However, the material preserved in London is quite abundant and relatively homogenous. Numerous specimens available, mostly collected in East Harnham, fit the description given by PETTITT.

Cretirhynchia intermedia is a species with numerous (up to 50 in large specimens) very low and faint costae. However, in some specimens, the costae can be more acutely developed. The shell is transversely oval in outline with very rounded lateral parts. A flat median fold, which is fairly broad and moderately elevated, corresponds to a relatively wide sinus which is moderately

deep. PETTITT stressed the evolution of the linguiform extension in this species: arcuate in early stages of growth and U-shaped in later stages. In some larger specimens, the linguiform extension can be subrectangular. Another typical feature is the very narrow interarea which is curved. The apical, hypothyriddid, foramen is oval and the deltidial plates are produced, forming a well developed tube. The beak ridges are acutely distinct in this species. Transverse serial sections were made on two specimens collected from the type area (Figs. 14, 16). The dental plates, convergent ventrally, are thick in the umbo but relatively thin anteriorly. No pedicle collar has been observed in transverse section. A dorsal septum is present in the dorsal valve but it is rather short and very low. The hinge plates are small and subtriangular. The crural bases are fairly coarse and inwardly concave. They are not strictly subquadrate. They remain associated with the internal side of the anterior portion of the inner socket ridges, below their ventral edge. This gives, in transverse section, a very peculiar image resembling a "cockfighting" situation (Fig. 15). In their posterior part, the crura are thick and deeply concave. They become wider, up to the middle of their length. In the anterior part, they become narrower again, appearing straight in transverse sections. An obtuse, wide angle is formed by the distal parts of the crura. The crura are steep and ventrally oriented.

Cretirhynchia intermedia represents a special lineage among the species of the genus *Cretirhynchia*. Its shape and external ornamentation suggest that *C. intermedia* was a deep water species. Among the internal characters, the convergent dental plates, the small subtriangular hinge plates and the anterior parts of the crura which are close together, are all typical characters for representatives of the genus *Cretirhynchia*. The dorsal septum which is relatively short and poorly developed, the sharply concave crural bases and posterior parts of the crura, and the wide obtuse angle formed by the distal parts of the crura, are original features of the subgenus *Harmignirhynchia* subgen. n.

PETTITT (1950) named this species "intermedia" because its shape was a kind of "go-between" form among several species of *Cretirhynchia*. He described passage forms between *C. intermedia* and *C. norvicensis*. These forms are not considered here as passage forms. They are only more subtriangular than the usual transversely oval specimens. The serial sections easily distinguish *C. norvicensis* from *C. intermedia*.

***Cretirhynchia (Harmignirhynchia) obourgensis* sp. n.**

Text-Figures 17-18, Plate 5, Figures 4a-e, 5a-e, Plate 6, Figures 2a-e.

- 2000 *Cretirhynchia* sp. - SIMON, pp. 139-140, text-fig. 3, pl. 5, figs. 5a-e, 6a-c.

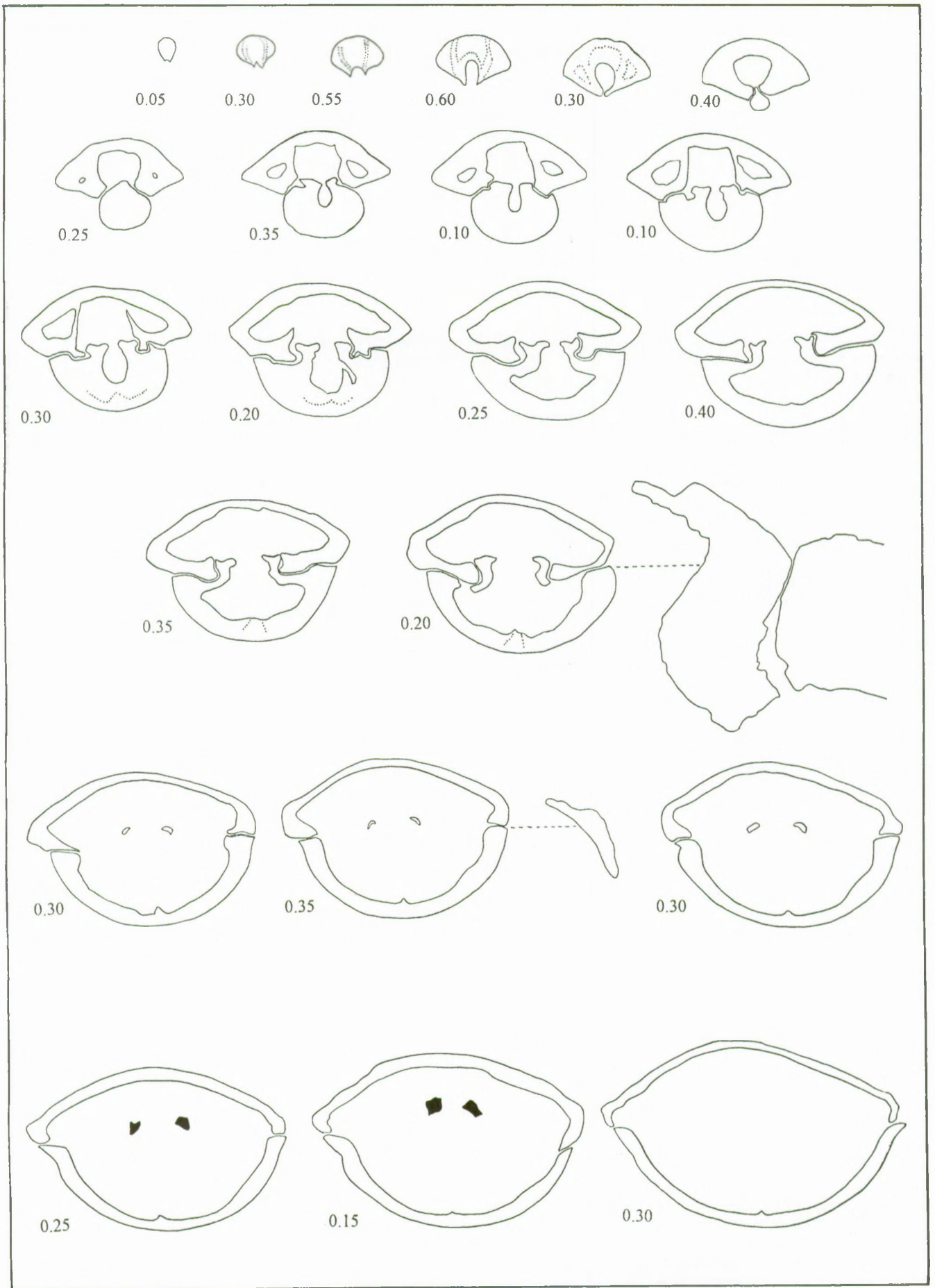
Stratigraphical range: Upper Campanian, from uppermost part of the *Blt. mucronata* Zone to the *Blt. woodi* Zone.

Diagnosis

Medium-sized, multicostate rhynchonellid brachiopod, transversely oval in outline, always wider than long,



Fig. 16 — Serial transverse sections through the umbonal part of *Cretirhynchia (Harmignirhynchia) intermedia* PETTITT, 1950 collected from the Lower Campanian (*Offaster pilula* Zone), East Harnham (Wiltshire, England). Length of the specimen: 11.9 mm. NHM. B. 92742-5.



lenticular in anterior contour and lenticular in lateral profile. Dorsal valve slightly more convex than the ventral valve. Slight, relatively broad and flat median fold limited to the anterior part of the dorsal valve. Ventral valve with a very broad, shallow sulcus with very sharp lateral limits. Linguiform extension trapezoidal. Beak small, curved and pointed, erect. About 50 costae, clearly defined, slightly reduced in number near the commissure. No incipient splitting of the costae. Dental plates subparallel in the posterior part of the ventral valve, becoming ventrally convergent in their anterior part. No pedicle collar. Persistent, low dorsal septum. Hinge plates simple, subtriangular. Crural bases inwardly concave. Crura very steep, laterally diverging. Wide, obtuse angle formed by the anterior parts of the crura.

Derivatio nominis: The species name is derived from the name of the village of Obourg near Mons (Mons Basin, Hainaut, Belgium) and refers also to the "Craie d'Obourg" from which the species has been collected.

Locus typicus: Harmignies near Mons, C.C.C. (Crayères, Cimenteries et Chaux) quarry.

Stratum typicum: "Craie d'Obourg-Nouvelles", Upper Campanian, *Blt. woodi* Zone.

Holotype

Cretirhynchia (*Harmignirhynchia*) *obourgensis* sp. n. Text-Figure 17, Plate 6, Figures 2a-e. The holotype is a prepared specimen for transverse serial sections. The cast, peels off and photographs of the serial sections are preserved in the IRScNB in Brussels under the reference IRScNB - IST n°10847.

Dimensions of holotype: 15.7 mm long, 17.9 mm wide and 10.2 mm thick.

Paratypes

C. (Harmignirhynchia) obourgensis sp. n. Plate 5, Figures 4a-e. IRScNB - IST n° 10844. Complete bivalved specimen collected from the "Craie de Nouvelles", Upper Campanian (*Blt. woodi* Zone) in Harmignies near Mons (Hainaut, Belgium).

C. (Harmignirhynchia) obourgensis sp. n. Plate 5, Figures 5a-e. IRScNB - IST n° 10846. Complete bivalved specimen collected from the "Craie de Nouvelles" (*Blt. woodi* Zone) in Harmignies near Mons (Hainaut, Belgium).

C. (Harmignirhynchia) obourgensis sp. n. Slightly damaged, bivalved specimen collected from the top of the "Craie de Trivières", Upper Campanian (*Blt. mucronata*

Zone) in Cuesmes near Mons (Hainaut, Belgium). Specimen described and illustrated in SIMON (2000, pp. 139-140, pl. 5, figs. 5a-e). IRScNB - IST n° 10830.

C. (Harmignirhynchia) obourgensis sp. n. Slightly damaged, bivalved specimen collected from the top of the "Craie de Trivières", Upper Campanian (*Blt. mucronata* Zone) in Cuesmes near Mons (Hainaut, Belgium). Specimen described and illustrated in SIMON (2000, pp. 139-140, pl. 5, figs. 6a-e). IRScNB - IST n° 10824.

Material

Material from the Mons basin (Hainaut, Belgium) preserved in the IRScNB in Brussels.

Specimens collected from the "Craie de Trivières", Upper Campanian, *Blt. mucronata* Zone.

12 complete, bivalved specimens collected from the Craibel quarry in Cuesmes.

Specimens collected from the "Craie d'Obourg", Upper Campanian, uppermost part of the *Blt. mucronata* and *Blt. woodi* Zones.

Two specimens from Cuesmes, one from the base of the "Craie d'Obourg" in the Craibel quarry (see SIMON, 2000, pl. 5, figs. 5a-e, 6a-c) and one specimen without precise locality (Collection Cornet).

48 specimens from Harmignies. Three specimens from Cibly. Seven specimens without precise locality.

Specimens collected from the "Craie de Nouvelles", Upper Campanian, *Blt. woodi* Zone (Mons basin, Hainaut, Belgium).

One specimen from Harmignies and one specimen from Nouvelles.

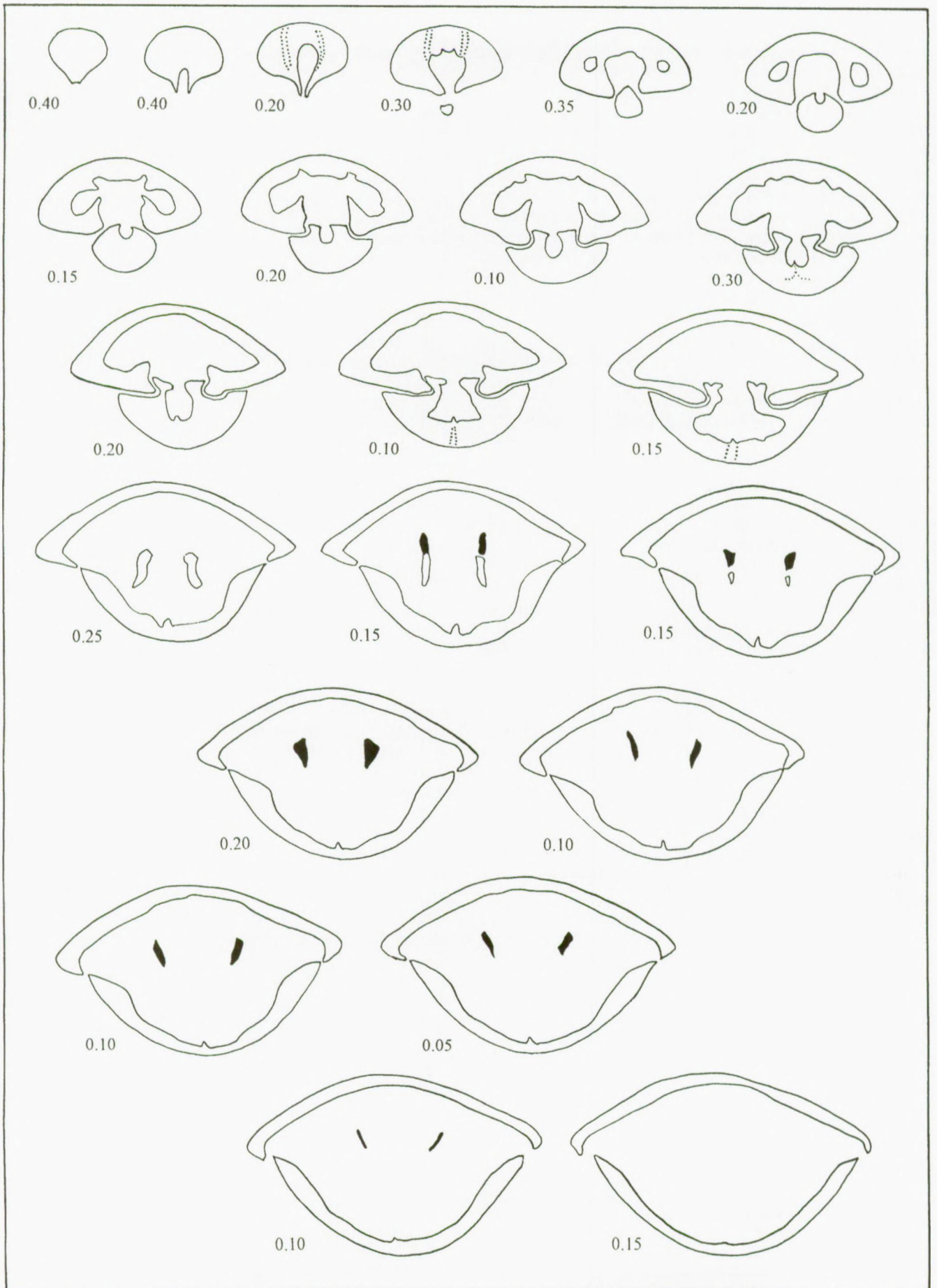
Description

External characters

Medium sized rhynchonellid brachiopod, about 14.0 / 19.5 mm long, 14.5 / 21.2 wide and 7.3 / 11.5 mm thick, transversely oval in outline, oval-lenticular in lateral profile and lenticular in anterior view. Young specimens are more subtriangular in outline. The dorsal valve is slightly more convex than the ventral valve. The maximum convexity is situated in the middle of the dorsal valve. A very low dorsal median fold is only developed on its anterior part and is bounded by sharp edges. The ventral valve shows a maximal posterior convexity near the umbo and its sulcus is low, flattened but slightly wider than the corresponding dorsal fold. The sulcus is restricted to the anterior part of the ventral valve and it is limited by sharp edges. The broad linguiform extension is sharply trapezoidal. The relative width of the linguiform extension is variable. The beak is very short, curved and erect with a pointed tip. The beak ridges are very distinct. The hypothryrid foramen is circular with conjunct, protruding deltidial plates. The interareas are slightly curved but the posterior commissure is nearly straight. Numerous costae are visible (38 to 53). They are low, very faint in the posterior part of the shell but wider anteriorly. The costae are slightly reduced in number near the anterior part of the shell, but in some specimens, reduction of the number of costae does not occur. Incipient splitting is never observed. Eight to ten costae are visible in the bottom of the sulcus at the anterior commissure whereas seven to nine costae are present on the dorsal fold. Fine



Fig. 17 — Serial transverse sections through the umbonal part of *Cretirhynchia* (*Harmignirhynchia*) *obourgensis* sp. n. collected from the Upper Campanian (*Belemnitella woodi* Zone), Harmignies (Mons basin, Hainaut, Belgium). Holotype. Length of the specimen: 22.2 mm. IRScNB. - IST. N° 10847.



concentric growth lines are perceptible on the shell surface and sometimes, a few laminae are developed near the commissure. A major growth line is often perceptible in the anterior part of the shell.

Internal characters

In transverse serial sections (Figs. 17-18), dental plates are subparallel in the posterior part of the umbo and they become anteriorly convergent. No pedicle collar is observed. Outer socket ridges are extremely low and the sockets, in this species, are fairly wide in transverse section. Inner socket ridges are much more elevated. The hinge plates are simple and subtriangular. Crural bases subquadrate but slightly concave inwardly. Very steep, ventrally directed, raduliform crura are observed. In transverse section, they are nearly vertical in their anterior part. A persistent, low dorsal septum is developed on the dorsal valve floor.

Comparison with other species

The general outline of large shells of *C. (Harmignirhynchia) obourgensis* sp. n. is quite similar to the shell outline of *C. (Harmignirhynchia) intermedia* PETTITT, 1950. But, the latter species is relatively thicker in anterior contour and the maximum convexity of its dorsal valve is situated near the umbo. Reduction of the number of costae near the anterior commissure is stronger in *C. intermedia*. Moreover, the linguiform extension of *C. intermedia* is generally U-shaped or arcuate, it is sharply trapezoidal in *C. obourgensis* sp. n.. However, in the collections of the NHM, specimens of *C. intermedia*, from East Harnham near Salisbury, have a more trapezoidal linguiform extension.

The smaller specimens of *C. obourgensis* sp. n. have a subtriangular outline similar to those of *C. norvicensis* PETTITT, 1950. In the latter species the linguiform extension is trapezoidal but a strong reduction of the number of costae is always observed on the anterior part of the shell. The foramen is relatively smaller in *C. norvicensis* than in *C. obourgensis* sp. n. *C. norvicensis* is generally much larger than *C. obourgensis* sp. n.

For its internal characters, *C. obourgensis* sp. n. is nearer *C. intermedia*, the internal structures of *C. norvicensis* being much heavier and similar to the structures observed in *C. plicatilis*.

Subgenus *Homaletarhynchia* subgen. n.

Derivatio nominis: from the greek "Homales" (ὁμαλῆς) meaning "flat", "without relief" and "Πυγχοσ" meaning beak.

Diagnosis of the subgenus

Medium-sized, symmetrical, biconvex rhynchonellid brachiopods. Shell ornamentation generally smooth or with very faint radial grooves. Development of costae limited to the antero-lateral commissure. Beak small, pointed and generally curved. Beak ridges well developed. Hypothyridid foramen with conjunct, protruding deltidial plates.

Ventrally convergent dental plates. Pedicle collar rarely developed. Very strong hinge structure, with ventrally expanded inner socket ridges. Crural bases subquadrate. raduliform crura slightly concave in their posterior part, remaining close together.

Type species: *Terebratulites limbatus* VON SCHLOTHEIM, 1813.

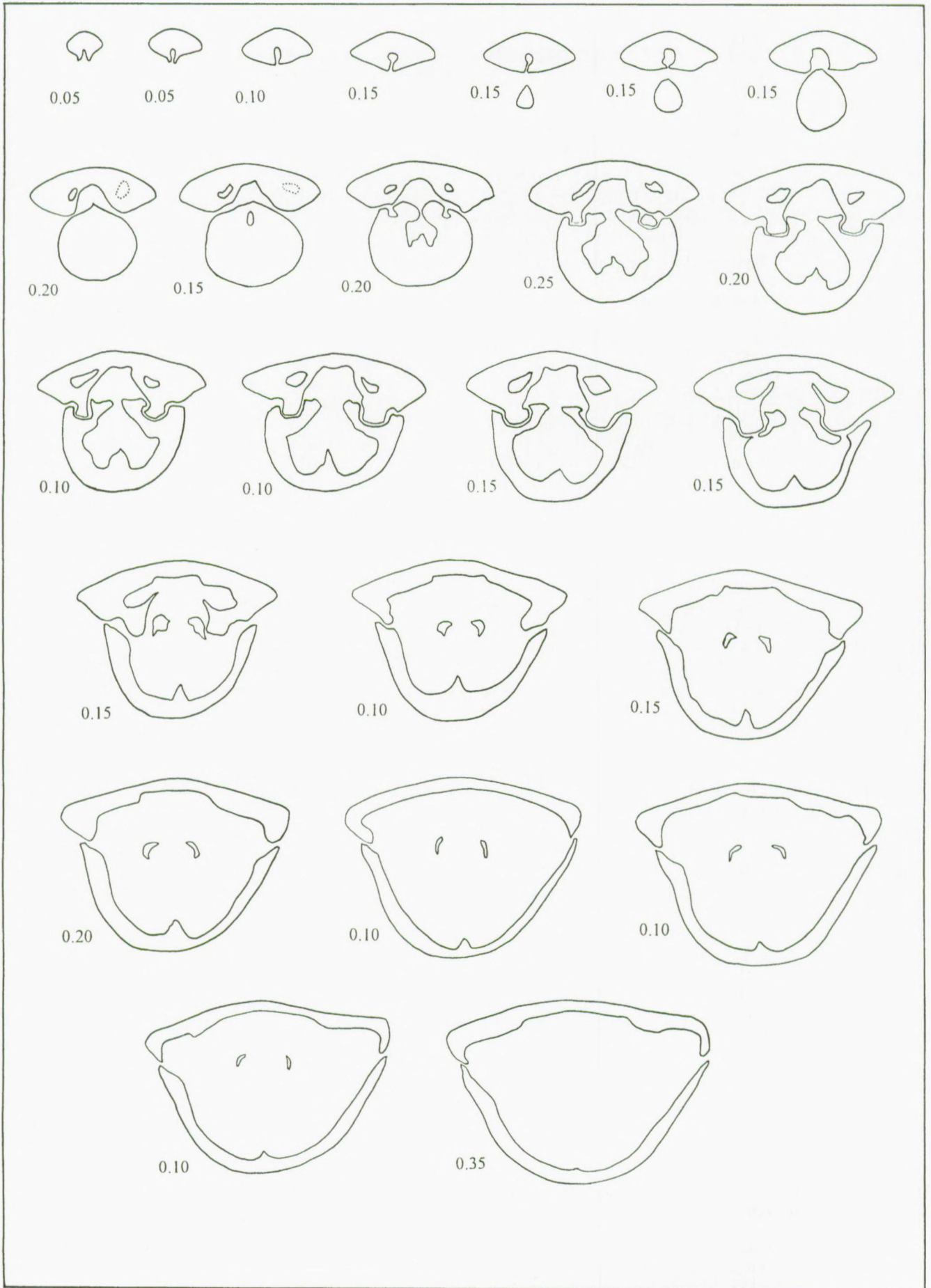
Cretirhynchia (Homaletarhynchia) limbata (VON SCHLOTHEIM, 1813)

Text-Figure 19, Plate 7, Figures 1a-e, 2a-e.

- (1803?) *Térébratules fossiles* - FAUJAS DE SAINT-FOND, pl. 26, fig. 4.
- * 1813 *Terebratulites limbatus* - VON SCHLOTHEIM, p. 113 (cit. FAUJAS, 1803?)
- 1820 *Terebratulit. Limbatus* - VON SCHLOTHEIM, p. 286.
- 1841 *Terebratula subplicata* Mantell - ROEMER, F.A., p. 38, Nr. 10.
- 1842 *Terebraiula subplicata* Mant. - VON HAGENOW, p. 534, Nr. 4.
- 1846 *Terebratula subplicata* Mant. - BOLL, p. 209
- 1848 *Terebratula limbata* - BRONN, p. 1240.
- 1852 *Terebratula subplicata* Mant. - PUGGAARD, p. 16.
- 1856 *Rhynchonella limbata* v. Sch. sp. - BOLL, p. 47.
- 1860 *Rhynchonella limbata* v. Schl. sp. - BOSQUET, N° 585.
- 1866 *Rhynchonella subplicata* d'Orb. - CORNET & BRIART, pp. 150, 189 (= *C. limbata*).
- 1870 *Rhynchonella subplicata* d'Orb. - CORNET & BRIART, pp. 8, 9 (= *C. limbata*)
- 1871 *Terebratula octoplicata subplicata* - QUENSTEDT, p. 169, pl. 41, fig. 59 (d, f, non fig. 58, 60-62 = *C. retracta*).
- 1879 *Rhynchonella limbata* v. Schloth. sp. - VON HANSTEIN, p. 37.
- 1888 *Rhynchonella limbata* Schl. - GEINITZ, F.E., p. 742.
- 1894 *Rhynchonella limbata*, Schlotheim - POSSELT, p. 27, fig. 16.
- pp 1895 *Rhynchonella octoplicata* Sow. - DEECKE, pp. 73-74 (cit. in STEINICH, 1965, p. 24)
- pp 1909 *Rhynchonella limbata* Schlatheim (*Sic*) - BRÜNNICH NIELSEN, p. 157, N° 17, pl. 1, fig. 26 (non figs. 24-25).
- . v 1938 *Rhynchonella limbata* Schlot. - POŻARYSKI, p. 20.
- . 1954 *Cretirhynchia limbata* (Schlotheim); - PETTITT, p. 27, pl. 1, fig. 1a-c, pl. 2, fig. 12 a-c, text-fig. 7a-c, 8, 9.
- 1961 *Cretirhynchia limbata* (Schlot.). - KOVALEVA, p. 66, 70.
- . 1965 *Cretirhynchia limbata* (Schlottheim, 1813) - STEINICH, p. 24, pl. 2, fig. 4a-d, text-fig. 13.
- . 1966 *Cretirhynchia limbata limbata* (Schloth.) - MAKRIDIN & KATZ, p. 191, pl. 1, fig. 6.



Fig. 18 — Serial transverse sections through the umbonal part of *Cretirhynchia (Harmignirhynchia) obourgensis* sp. n. collected from the Upper Campanian (*Belemnitella mucronata* Zone), Cuesmes (Mons basin, Hainaut, Belgium). Holotype. Length of the specimen: 19.1 mm. IRScNB. - IST. N° 10849.



- 1968 *Cretirhynchia limbata* Pettitt - LEEDER, p. 6.
 1972 *Cretirhynchia limbata* (Schlottheim) - SURLYK, p. 24, text-fig. 5.
 1974 *Cretirhynchia limbata limbata* (Schlottheim, 1813) - KATZ, p. 251, pl. 83, fig. 11.
 1974 *Cretirhynchia limbata* - PAJAUD, p. 25.
 non v 1984 *Cretirhynchia limbata limbata* (Schlottheim, 1813) - POPIEL-BARCZYK, p. 384, pl. 151, fig. 5, 6.
 non v 1988 *Cretirhynchia limbata limbata* (Schlottheim, 1813) - POPIEL-BARCZYK, p. 6-8, text-figs. 3-4, pl. 1, figs. 1-6).
 v 1988 *Cretirhynchia subplicata* (Mantell) - POPIEL-BARCZYK, text-figs. 9.
 1990 *Cretirhynchia limbata* (Schlottheim, 1813) - JOHANSEN & SURLYK, p. 838, pl. 2, fig. 3-5.
 pp 1992 *Cretirhynchia limbata* (Schlottheim, 1813) - POPIEL-BARCZYK, pp. 14-15.
 v 1993 *Cretirhynchia limbata* (von Schlottheim, 1813) - SIMON, p. 83, text-fig. 8, pl. 3, fig. 4a-e, fig. 5a-b, pl. 4, fig. 1a-e, text-fig. 8.
 v 1998 *Cretirhynchia limbata* (von Schlottheim, 1813) - SIMON, pp. 183-185, 195, text-fig. 2-3.

Stratigraphical range: uppermost Campanian to Upper Maastrichtian.

Type specimen

The original of FAUJAS (1803?, pl. 26, fig. 4) from the Maastrichtian of the "Montagne Saint-Pierre" near Maastricht has not been traced. VON HANSTEIN (1879, p. 37) indicated that the specimen of FAUJAS was in fact collected in Cibly. PETTITT (1954, p. 27, pl. 1 figs. 1a-c) designated and illustrated a specimen from the Grey Beds of the Upper Chalk (*Lunata* Zone) of Trimmingham, Norfolk, England for *Cretirhynchia limbata* (VON SCHLOTHEIM, 1813). This specimen is preserved in the NHM under the reference B. 52745.

Material

Material preserved in the NHM.

Lower Maastrichtian specimens collected from Trimmingham, Norfolk, England

The type specimen cited above (B. 52745). Three specimens (B. 92004-5, B. 92006).

Material preserved in the IRScNB in Brussels.

407 Lower Maastrichtian (*Blm. obtusa* Zone) complete, bivalved young, adult and gerontic specimens, 113 ventral valves 37 dorsal valves collected from the phosphatic chalk of Cibly (Hainaut, Belgium).

Two specimens collected in the CPL quarry in Hallembaye (Vijlen chalk), near Liège (Upper Maastrichtian, *B. junior* Zone) and illustrated by SIMON (1993, pl. 3, figs. 4-5).

Material preserved in the Museum of the Earth in Warsaw (Muzeum Ziemi PAN).

One Lower Maastrichtian specimen collected from Kamien, "horizon u", middle Vistula river, Poland (MZ VIII Bra 1516a).

143 specimens determined as *Cretirhynchia limbata* (Schlottheim, 1813) in POPIEL-BARCZYK (1988, pp. 6-8) which must be removed from this species.

Diagnosis in Faujas (1803?): none (parait être inédite).

Original diagnosis in VON SCHLOTHEIM (1813, p. 113): none.

Diagnosis in VON HANSTEIN (1879, p. 37)

"Da der Hauptunterschied zwischen dieser Species [*Rh. limbata*] und *Rh. plicatilis* Sow. darin besteht, dass bei unserer Art die Klappen ganz glatt sind und die Rippen erst kurz vor der Stirnrand auftreten, so ist es möglich, dass sie, wie dies bereits Davidson *Cret.* p. 80 und Quenstedt *Petr.* p. 168 ff. vermuteten, nur eine glatte Varietät der Sowerby'schen Species darstellt. Doch scheint es mir, dass auch die geringere - kaum bemerkliche - Wölbung der durchbohrten Klappe und die steile Area sie von derselben unterscheiden, ich habe sie daher von ihr getrennt gelassen. Während die Klappen bis zu dem dem Stirnrande nächsten Anwachsstreifen keinerlei Spur von radialer Sculptur erkennen lassen, treten die Rippen nun plötzlich sehr stark hervor, etwa 12 an der Zahl, davon 3-4 im Sinus der grossen Klappe liegen".

Emended diagnosis in PETTITT (1954, p. 27)

"*Cretirhynchia*, about 12 mm long, 15 mm wide and 7 mm thick, oval in outline, low domical in anterior contour, depressed cuneiform in lateral profile. Brachial valve moderately convex, with sharp, elevated median fold. Pedicle valve less convex, with deep, narrow, rounded sinus. Umbo slightly incurved. Surface of shell nearly smooth, with a few costae developed near the commissure".

Emended diagnosis in STEINICH (1965, p. 24)

"Relativ klein; stets deutlich breiter als lang, oval bis subtriangular. Stirnrand oft leicht eingebuchtet; Dorsalklappe kräftig konvex, am Wirbel steil ansteigend; Ventralklappe sehr niedrig, am Wirbel schwach gewölbt, sonst plan; etwa ab Schalenmitte erscheint ein kräftiger Ventralsinus, der v-förmig bis trapezoidal in den deutlichen Dorsalwulst eingreift; grösste Höhe am Schalenvorderrand; Schalenoberfläche glatt, erst unmittelbar am Rand, oft nach einer kräftigen Anwachslinie erscheinen ca. 14 Rippen, von denen 3 oder 4 im Sinus liegen; Schnabel kurz, spitz, mehr oder weniger erect; Schnabelkanten deutlich; Deltidium kragenförmig; Foramen sehr klein, rund".

Comments

Cretirhynchia (Homaletarhynchia) limbata (VON SCHLOTHEIM, 1813) is a species which was often confused with other rhynchonellid brachiopods in the past but which is now accurately described. The descriptions in PETTITT (1953, pp. 27-29) and in STEINICH (1965, pp. 24-26) avoid any possible confusion with other *Cretirhynchia* species. SIMON (1993, p. 83) pointed out the essential differences between *C. limbata* and *C. undulata* (PUSCH, 1837). The same author (1998, pp. 183-184, text-fig. 3) discussed the palaeoecology of *C. limbata*, a species thought to have been fixed directly in the sediment by means of its pedicle. It was probably living with its dorsal fold down, partly inserted in the sediment (SIMON, 1998, text-fig. 3).

Transverse serial sections of an original specimen, col-



Fig. 19 — Serial transverse sections through the umbonal part of *Cretirhynchia (Homaletarhynchia) limbata* (VON SCHLOTHEIM, 1813) collected from the Upper Maastrichtian, Jandrain (Brabant, Belgium). Length of the specimen: 20.9 mm. IRScNB. - IST. N° 10838.

lected from the phosphatic chalk of Ciplly (Lower Maastrichtian, *Blm. obtusa* Zone) were illustrated by POPIEL-BARCZYK (1988, text-fig.9) under the name *Cretirhynchia subplicata* (MANTELL). A specimen from Rügen, Germany (Lower Maastrichtian) was prepared for serial sections and the results were illustrated in STEINICH (1965, text-fig. 13). Serial sections of a specimen collected from the Vijlen chalk in the CPL quarry in Hallembaye, near Liège, Belgium (Upper Maastrichtian, *B. junior* Zone) were illustrated by SIMON (1993, text-fig. 8). In this paper, serial sections of a specimen from Jandrain, Brabant, Belgium (Upper Maastrichtian) are presented in Fig. 19. Serial sections show the typical features of the genus *Cretirhynchia*; convergent dental plates, persistent dorsal septum, simple and subtriangular hinge plates, subquadrate crural bases and raduliform crura remaining close together. The strong hinge associated with expanded inner socket ridges is an important character of the subgenus *Homaletarhynchia* subgen. n.

Cretirhynchia (*Homaletarhynchia*) *limbata* is a variable species for its size. Campanian representatives are

rather small and thin-shelled. Lower Maastrichtian specimens (Pl. 7, Figs. 2a-e) are larger and their shell is much thicker. Specimens from Jandrain (Pl. 7, Figs. 1a-e) are still larger and they are slightly different in outline from the type material. They seem adapted to a higher rate of sedimentation inducing a larger development of their dorsal fold.

On the contrary, other characters are very stable in this species. The clearly cuneiform aspect of the shell in lateral view, the very thin and pointed beak which is only suberect, the v-shaped linguiform extension and the antero-lateral parts of the ventral valve which are always flat, are specific characters for *C. limbata*.

The Upper Maastrichtian material from the middle Vistula River studied and illustrated by POPIEL-BARCZYK (1988, pp. 6-8, pl. 1, figs. 1-6) is removed from *Cretirhynchia limbata*. These specimens are very large-sized *Cretirhynchia* which are clearly biconvex. Even if some specimens are cuneiform in lateral profile, most of them are oval lenticular (POPIEL-BARCZYK, 1988, pl. 1, fig. 2a). The beak is much thicker and more

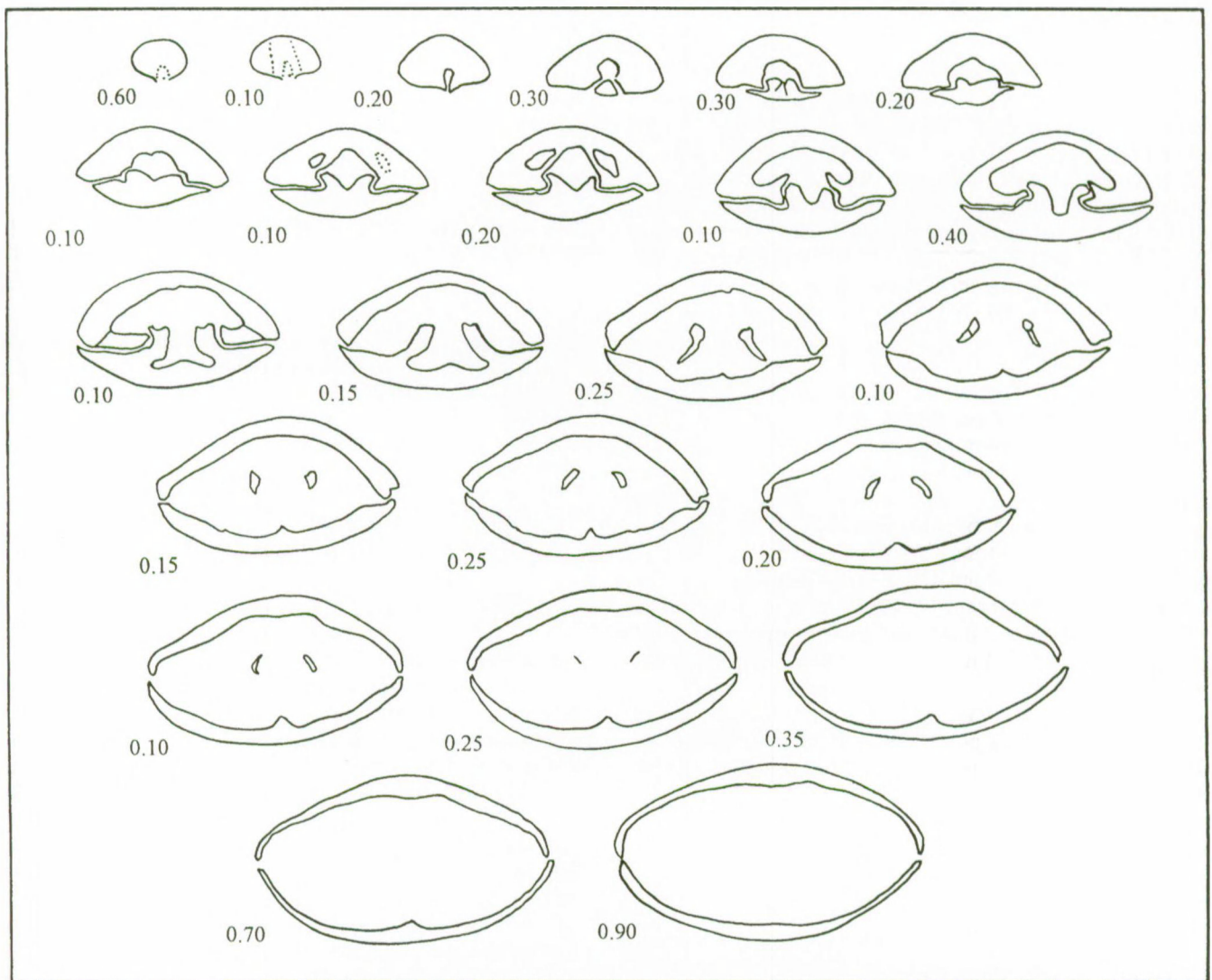


Fig. 20 — Serial transverse sections through the umbonal part of *Cretirhynchia* (*Homaletarhynchia*) *lentiformis* (WOODWARD, 1833) collected from the Upper Campanian (*Belemnitella mucronata* Zone), Cuesmes (Mons basin, Hainaut, Belgium). Length of the specimen: 9.2 mm. IRScNB. - IST. N° 10821.

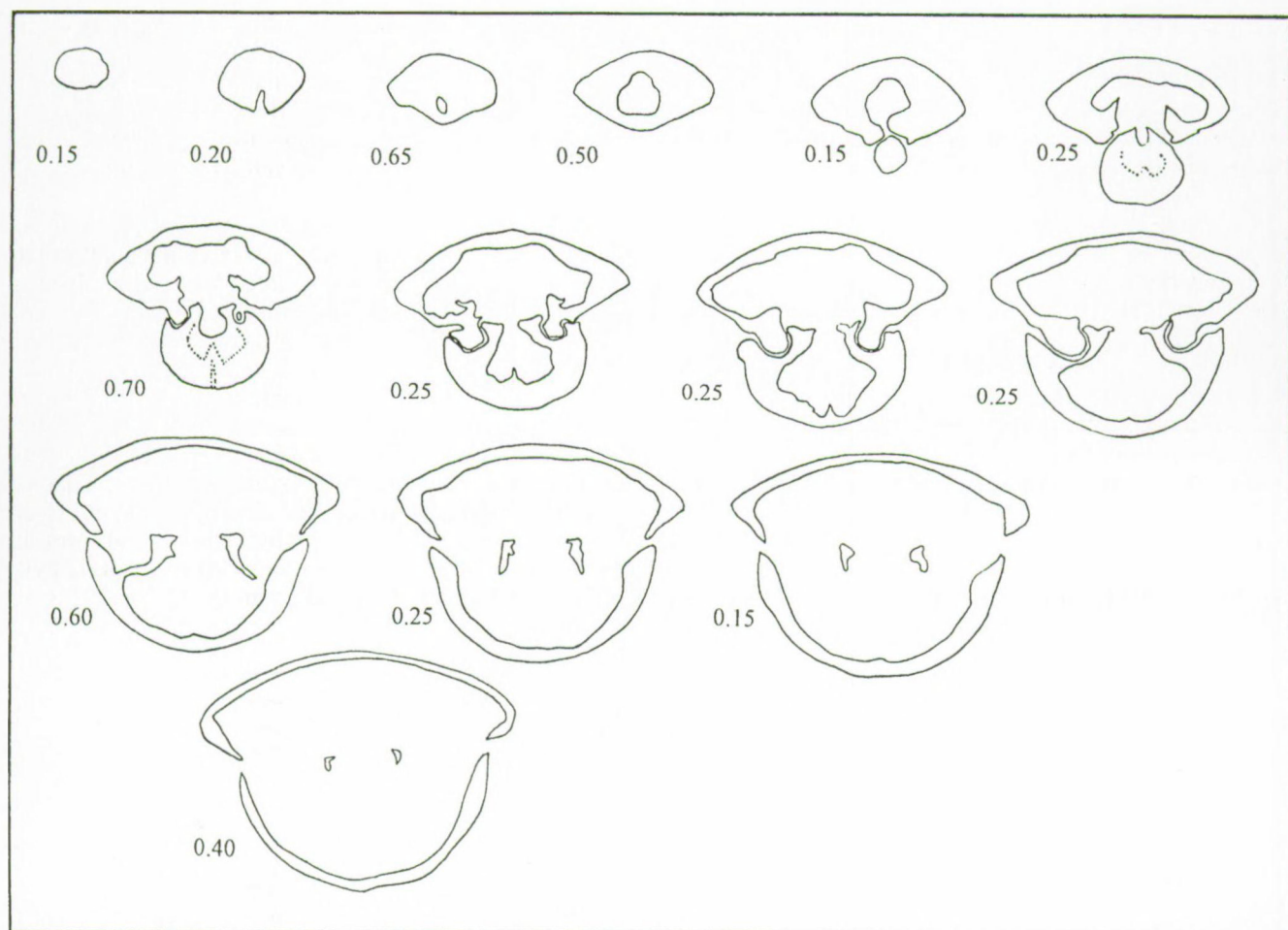


Fig. 21 — Serial transverse sections through the umbonal part of *Cretirhynchia (Homaletarhynchia) robusta* (TATE, 1865) collected from the Santonian, Woodburn, Northern Ireland. Length of the specimen 13.5 mm. NHM. B. 25152.

curved and erect. The antero-lateral parts of the ventral valve are always convex, never flat. These specimens are related to the *limbata* - group but the erection of a new species in the *Homaletarhynchia* subgen. n. is suggested.

In 1965, BIGNOT (p. 6, pl. 1, figs. 7-8) described some rhynchonellid brachiopods as *Cretirhynchia* gr. *limbata* (v. SCHLOTHEIM) from the Lower Senonian of Ballastière d'Etran and Arques-la Bataille (Area of Dieppe, Normandy, France). Although no transverse serial sections are available for this material, the illustrations given by BIGNOT suggest a close relationship between this material and *C. (Homaletarhynchia) limbata*. This material is considered as a potential ancestor (Fig. 1) for the "limbata-undulata group" included in *Homaletarhynchia* subgen. n. but it should be reviewed for further information.

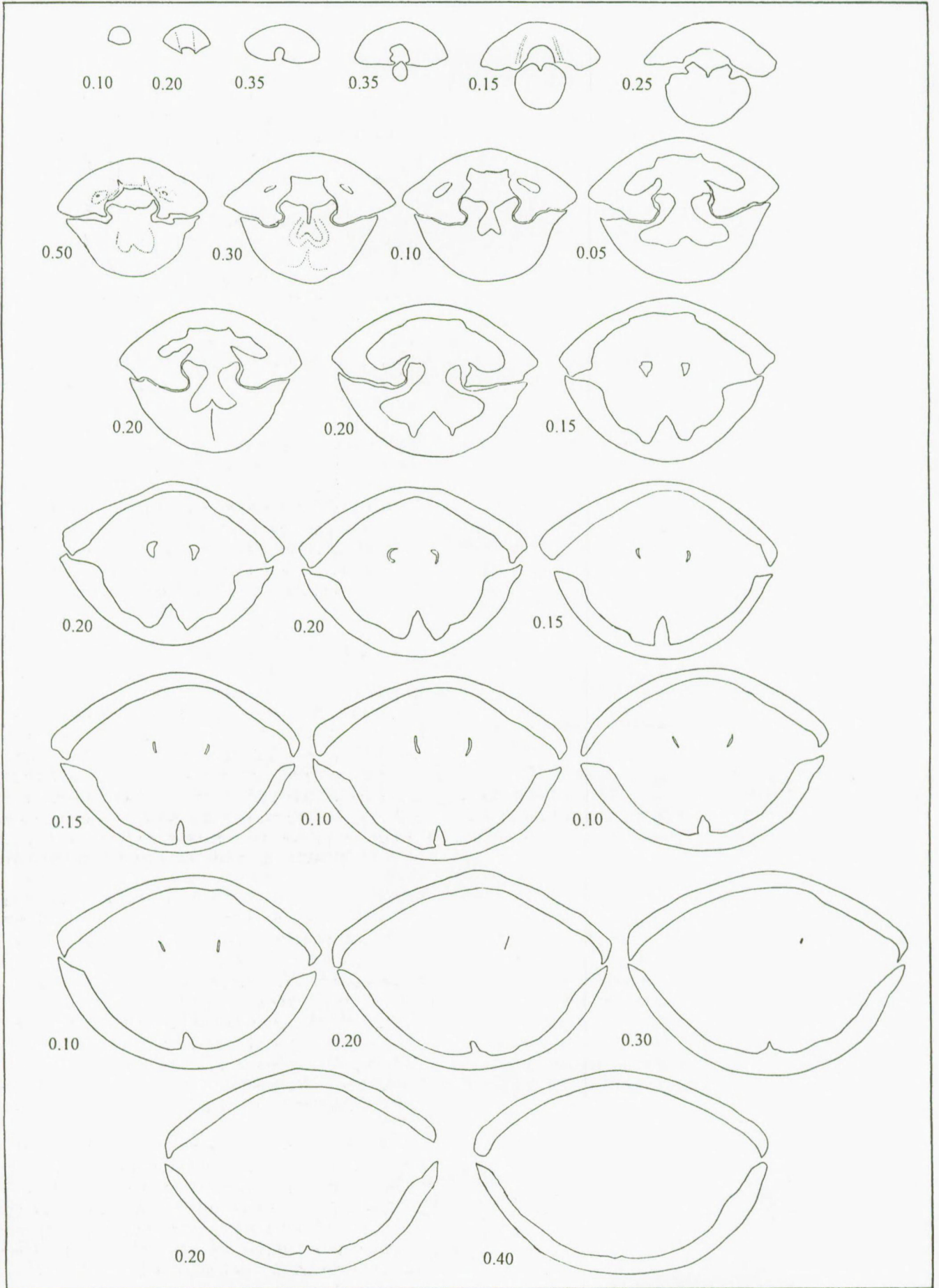
Cretirhynchia (Homaletarhynchia) lentiformis

(WOODWARD, 1833)

Text-Figure 20, Plate 7, Figures 5a-e.

- * 1833 *Terebratula lentiformis* - WOODWARD, S., p. 49, pl. 6, fig. 11.
 pp. 1855 *Rhynchonella limbata* Schlotheim - DAVIDSON, pp. 79-80, pl. 12, figs. 4-5.

- .v 1950 *Cretirhynchia lentiformis* (S. Woodward) - PETTITT, pp. 1, 26-27, 29, table 3, pl. 2, figs. 1a-c.
 . 1961 *Cretirhynchia lentiformis* (S. Woodward) - PEAKE & HANCOCK, p. 320.
 . 1968 *Cretirhynchia lentiformis* Woodward - LEEDER, pp. 6-7, 9, tables 1-2, text-fig. 1, p. 8.
 . 1988 *Rhynchonella lentiformis* - ROWE in WOOD, pp. 10, 21, 58, 59, 86.
 . 1988 *Cretirhynchia lentiformis* - WOOD, pp. 21, 25, 29, 34-35, 42, 49-50, 53-56, 58-59, 61, 79, 81-82, 87-88.
 pp v 1988 *Cretirhynchia lentiformis* (Woodward, 1833) - POPIEL-BARCZYK, pp. 11-12, text-fig. 11, non text-fig. 10, pl. 2, figs. 7-9 (= *C. arcuata* PETTITT, 1950).
 .v 1988 *Cretirhynchia arcuata* Pettitt, 1950 - POPIEL-BARCZYK, pl. 2, fig. 10.
 . 1989 *Cretirhynchia lentiformis* (Woodward, 1833) - POPIEL-BARCZYK, p. 245, pl. 152, figs. 1a-c.
 . 1990 *Cretirhynchia lentiformis* (Woodward) - JOHANSEN & SURLYK, p. 838.
 pp 1992 *Cretirhynchia lentiformis* (Woodward, 1833) - POPIEL-BARCZYK, p. 14.
 . 2000 *Cretirhynchia lentiformis* (Woodward, 1833) - SIMON, pp. 138-139, table 1, text-fig. 3, pl. 5, figs. 2a-e, 3a-e.



Stratigraphical range: lower to middle Upper Campanian.

Type specimen

Holotype, the original of WOODWARD (1833, pl. 6, fig. 11) from the Upper of Norwich, Norfolk, England, not traced. PETTITT (1950, p. 26) designated and figured a topotype as neotype from the Upper Chalk (*Blt. mucronata* Zone) of Harford Bridge, Norwich, Norfolk.

Material

Material preserved in the NHM.

The neotype cited above. 49 specimens from the *Blt. mucronata* Zone in Norwich, under the reference B. 93067-110. 41 specimens (topotypes) from the *Blt. mucronata* Zone in Hartford Bridge, Norwich, Norfolk (B. 25067-107). Four specimens, from Norwich without precise locality (B. 24900-3). Five specimens from the *Blt. mucronata* Zone of Ballard Head and Studland Bay, Dorset, England (B. 79946-50).

Material preserved in the IRScNB in Brussels.

Specimens collected from the Mons Basin (Hainaut, Belgium).

From the "Craie de Trivières", *Blt. mucronata* Zone: 230 complete bivalved specimens collected from the Craibel quarry in Cuesmes.

From the "Craie d'Obourg", *Blt. mucronata*-*Blt. woodi* Zones: 30 complete bivalved specimens collected from Harmignies.

Original diagnosis in WOODWARD (1833, p. 49)

None.

Diagnosis in PETTITT (1950, p. 26)

"*Cretirhynchia*, about 10 mm in length, 9 mm in width, 5 mm in thickness, subcircular in outline, lenticular to oval in anterior contour and lateral profile. Brachial valve moderately convex, with slight median fold on anterior margin; pedicle valve equally convex, with shallow and narrow median sinus; or fold and sinus may be absent. Linguiform extension very small, arcuate, or anterior commissure may be rectimarginate. Surface nearly smooth."

Comments

Cretirhynchia lentiformis held a juvenile structure throughout its whole life and specimens with a more adult internal aspect are rarely collected. However, the hinge and crural structures are very similar to the structures observed in *C. arcuata* and in *C. limbata* and they are typical for the subgenus *Homaletarhynchia* subgen. n.

The numerous specimens investigated are relatively

small, about 10 mm long, 9-10 mm wide and 5-7 mm thick. Valves are equally convex with a slight median fold on the dorsal valve corresponding to a narrow and shallow sulcus on the ventral valve. The linguiform extension is small, but clearly trapezoidal in most studied specimens. More rarely, some flat specimens exhibit a slightly arcuate linguiform extension. The umbo is fairly broad. The beak is thin and the hypothrydid foramen is extremely small. At first glance, the shell surface seems nearly smooth, except for faint growth-lines. But, careful study of a large sample, observed under good light condition, show numerous faint costae which are constantly present on the anterior part of the shell. The posterior part and in some cases, the middle part of the shell remain smooth. Only very young specimens are totally smooth. This character distinguishes *Cretirhynchia lentiformis* from *C. arcuata* PETTITT, 1950. In *C. arcuata*, the shell is smooth on its whole surface and "costae" are only developed on large specimens near the antero-lateral commissure.

PETTITT (1950, p. 26, pl. 2, figs. 1a-c) based his description on a poorly developed specimen. He stated in his diagnosis: "linguiform extension very small, arcuate, or anterior commissure may be rectimarginate". This diagnosis was the subject of confusion between *C. lentiformis* and *C. arcuata*. In most specimens of *C. lentiformis* investigated, we observed a small but clearly trapezoidal linguiform extension. Confusion arose over the material collected from the middle Vistula river valley in Poland (POPIEL-BARCZYK, 1988, pp. 11-13, pl. 2, Figs. 7-9, 10). In that paper, POPIEL-BARCZYK describes some specimens of *C. lentiformis* (pl. 2, fig. 10) under the name *C. arcuata*. Specimens presented as *C. lentiformis*. (pl. 2, figs. 7-9) must be interpreted as the real *C. arcuata*. The serial sections presented in POPIEL-BARCZYK (1988, text-fig. 10) under the name *C. lentiformis*, are typical of *C. arcuata*. The dorsal septum is very thick and high, a character not observed in *C. lentiformis*. The sections presented in POPIEL-BARCZYK (1988, text-fig. 11) are consistent with our sections obtained on specimens of *C. lentiformis* (Fig. 20) but those presented in her text-fig. 12 must be considered as *C. lentiformis* and not as *C. arcuata*.

The material collected from Norfolk is identical to the material collected from Cuesmes. However, two forms α and β , have been described by LEEDER (1968, p. 9, text-fig. 1ac, 1d-f) and they have a stratigraphical value. The form α has a broad trapezoidal linguiform extension and up to nine small costae near the anterior commissure. It ranges from the top of the Basal *Mucronata* Chalk to the middle of the Weybourne Chalk. The form β has only four broad costae and its linguiform extension is much narrower and tends to a V-shaped. It occurs from the middle of the Weybourne Chalk to the Paramoudra Chalk.

Transverse serial sections of specimens of *C. lentiformis* collected from Cuesmes (Fig. 20) show that no pedicle collar is observed and that dental plates are ventrally convergent. The strong hinge structure, with its ventrally expanded inner socket ridges, is typical of the subgenus *Homaletarhynchia* subgen. n. Crural bases are inwardly concave as are the crura in their posterior part. The dorsal septum is present but it is relatively low.



Fig. 22 — Serial transverse sections through the umbonal part of *Cretirhynchia* (*Homaletarhynchia*) *arcuata* PETTITT, 1950 collected from the Upper Campanian (*Belemnitella mucronata* Zone), Mousehold Pit, Norwich (Norfolk, England). Length of the specimen: 14.0 mm. NHM. B. 93163.

Cretirhynchia (Homaletarhynchia) undulata

(PUSCH, 1837)

Plate 7, Figures 6a-e.

- * 1837 *Terebratula undulata* m. - PUSCH, p. 20, pl. 4, figs. 4a-c.
- 1938 *Rhynchonella limbata* v. *undulata* Pus. - POŻARYSKI, p. 20.
- 1942 *Rhynchonella limbata* Schl. var. *undulata* Pusch - PUTZER, p. 373.
- .v 1958 *Cretirhynchia limbata* (Schlotheim, 1813) - FEDOROWSKI, p. 9, pl. 1, figs. b, d.
- 1966 *Cretirhynchia limbata undulata* (Pusch) - MAKRIDIN & KATZ, p. 101, pl. 1, figs. 7-8.
- .v 1984 *Cretirhynchia limbata undulata* (Pusch) - POPIEL-BARCZYK, p. 349 pl. 151, figs. 7-8.
- .v 1988 *Cretirhynchia undulata* (Pusch, 1837) - POPIEL-BARCZYK, p. 8, text-figs. 5-7, pl. 1, figs. 7-12.
- . 1989 *Cretirhynchia limbata undulata* (PUSCH, 1837) - POPIEL-BARCZYK, p. 245, pl. 152, figs. 7-8.
- . 1992 *Cretirhynchia undulata* (PUSCH, 1837) - POPIEL-BARCZYK, p. 15.
- . 1993 *Cretirhynchia undulata* (PUSCH, 1837) - SIMON, pp. 78-86, text-figs. 4-7, pl. 1, figs. 1-5, pl. 2, figs. 1-5, pl. 3, figs. 1-3, pl. 4, figs. 2-4, pl. 5, figs. 1-4.

Stratigraphical range: Upper Maastrichtian

Type specimen

Holotype not designated by PUSCH (1837). PUSCH's collection has been destroyed (KIEPURA, 1984), a neotype from the Upper Maastrichtian of Kazimierz (Poland) has been designated by POPIEL-BARCZYK (1988, p. 8, pl. 1, fig. 11). The neotype is preserved in the Museum of the Earth (Muzeum Ziemi PAN) in Warsaw under the reference MZ VIII Bra-943, 33.

Comments

Cretirhynchia undulata (PUSCH, 1837) has been studied by POPIEL-BARCZYK (1988) and more recently by SIMON (1993). Numerous illustrations have been published in these two papers concerning the Polish and the Belgian material of *C. undulata*. The external characters and the internal characters, presented in the transverse serial sections published by POPIEL-BARCZYK (1988, text-figs. 5-7) and by SIMON (1993, text-figs. 4-5), are consistent with the diagnosis of *Homaletarhynchia* subgen. n.

A pedicle collar has been observed in one Belgian specimen from Hallembaye by Motchurova-Dekova & Bitner (Personal communication, 1998). This species has a fairly strong hinge structure with very low outer socket ridges and extremely elevated, expanded, inner socket-ridges. Subquadrate crural bases and concave raduliform crura which remain close together are observed. *C. undulata* developed small umbonal chambers in the dorsal valves.

It is proposed here to erect two subspecies, one for the original Polish material and one for the Belgian material collected in the area of Maastricht.

Cretirhynchia (Homaletarhynchia) undulata(PUSCH, 1837) subsp. *undulata*

This is the original Polish material described by PUSCH

(1837) and by POPIEL-BARCZYK (1988). At adult growth stage, *C. undulata undulata* is a large shell, triangular in outline and with distinct sharp cardinal margin. In the Polish subspecies, adult and gerontic specimens exhibit a large trapezoidal linguiform extension. Weak folds (4-10) are visible on the anterior margin.

Cretirhynchia (Homaletarhynchia) undulata(PUSCH, 1837) subsp. *maastrichtiensis* subsp. n.

This subspecies is erected for the material collected from the Vijlen chalk (Upper Maastrichtian, *B. junior* Zone) in the CPL quarry in Hallembaye and the CBR quarry in Lixhe (Liège, Belgium), studied and illustrated by SIMON in 1993 (pp. 78-83, pl. 1, figs. 1-5, pl. 2, figs. 1-5, pl. 3, figs. 1-3).

Type specimen of the subspecies

Cretirhynchia (Homaletarhynchia) undulata (PUSCH, 1837) subsp. *maastrichtiensis* subsp. n. collected at the base of the Lixhe chalk (Upper Maastrichtian, *Blt. junior* Zone) from the CBR quarry in Lixhe (Liège, Belgium) and illustrated in SIMON (1993, pl. 2, figs. 5a-d). The type specimen is preserved in the IRScNB in Brussels under the reference IRScNB - IST n° 10842.

Morphological measurements of the type specimen: length of the shell 17.7 mm, width of the shell 20.4 mm and thickness of the shell 11.4 mm.

Diagnosis of the subspecies

Shell small to medium-sized, subtriangular in outline, lenticular to oval-lenticular in anterior contour, oval-lenticular to slightly cuneiform in lateral profile. The maximum width of the shell is observed just below the middle of the valves. Ventral valve less convex than the dorsal valve but a strong convexity takes place at the base of the beak.

Beak short, erect, thick in lateral profile and curved. Beak ridges distinct. Hypothyridid small foramen, circular. Flat ventral median sulcus and relatively narrow, flat dorsal fold. Linguiform extension arcuate in young specimens becoming trapezoidal in gerontic specimens. Absence of large weak folds on the top of the linguiform extension, anterior commissure simply plicate. Ornamentation of the shell consisting of numerous regular, faint and extremely narrow grooves. Dental plates convergent. Pedicle collar sometimes developed. Umbonal chambers in the umbo of the dorsal valve. Strong hinge with ventrally expanded, elevated inner socket ridges, simple hinge plates, crural bases inwardly concave, crura concave posteriorly and remaining close together.

Comments

Juvenile or young specimens of both subspecies of *C. undulata* are not distinguishable. The adult specimens of the subspecies *maastrichtiensis* subsp. n. are much smaller and the dorsal valve is less convex than in the representatives of the subspecies *undulata*. The sulci-plicate anterior commissure of gerontic Polish specimens referred to the subspecies *undulata* is the most obvious external difference from the Belgian specimens. Anterior commissure of the specimens referred to the sub-

species *maastrichtiensis* subsp. n. is always simply plicate.

Cretirhynchia (Homaletarhynchia) robusta

(TATE, 1865)

Text-Figure 21, Plate 6, Figures 6a-e.

- * 1865 *Rhynchonella limbata* Schlotheim var. *robusta* - TATE, p. 42, pl. 5, figs. 2a-c.
- 1950 *Cretirhynchia robusta* (Tate) - PETTITT, pp. 24-25, pl. 2, figs. 3a-c.
- 1988 *Cretirhynchia robusta* (Tate) - POPIEL-BARCZYK, p. 10.

Stratigraphical range: Santonian.

Type specimen

Specimen illustrated in TATE (1865, pl. 5, figs. 2a-c) not traced. Lectotype in PETTITT (1950, p. 24, pl. 2, figs. 3a-c) from the Santonian but originally considered from "the Zone of *Inoceramus crispus*" (*sic*) of Carrickfergus, North-East Ireland. The lectotype is preserved in the Museum of the British Geological Survey, under the reference GSM. 83078.

Material

The lectotype chosen by PETTITT, cited above.

Ten specimens from Woodburn, Northern Ireland, preserved in the NHM (unregistered specimens). On the original label, the mention "chloritic sand, *Inoceramus crispus* Zone ? (*sic*) is indicated. One specimen (B. 25152) has been chosen for transverse serial sections (Text-Fig. 21, Pl 6, Figs 6a-e).

Original diagnosis in TATE (1865, p. 42)

"This well marked variety of *R. limbata* is very distinct on account of the exceeding gibbosity of the shell; it is moreover of larger dimensions than specimens of *R. limbata* usually are. It is exceedingly common in the Zone of *Inoceramus crispus*, [*sic*] at Woodburn, Whitehead, and Island Magee. It is not found in any other zone".

Emended diagnosis in PETTITT (1950, p. 24)

"*Cretirhynchia*, about 16 mm long, 17 mm wide and 12 mm thick, subtriangular to subpentagonal in outline, domical in anterior contour, cuneiform in lateral profile. Brachial valve convex; pedicle valve less convex, with rounded median sinus. Linguiform extension arcuate to V-shaped. Umbo short, broad, erect. A few low and broad costae near the anterior commissure. Concentric ornament of fine growth-lines; a few laminae near the anterior and lateral commissure. Apical angle 120°".

Comments

Among the species of *Cretirhynchia* included here in the subgenus *Homaletarhynchia* subgen. n., *C. robusta* (TATE, 1865) is a species which has most characters in common with *C. limbata*, and it is important to point out the differences between these two species. Externally, the shell of *C. robusta* is dome-shaped in anterior contour and its dorsal valve is more convex than the dorsal valve of *C. limbata*. The lateral parts of the shell are steeper in *C. robusta*. The ratio thickness (in mm)/width (in mm) has a mean value of 0.7 in *C. robusta* and of 0.6 in *C. limbata*. The antero-lateral parts of the ventral valve are

slightly convex in *C. robusta* and always flat in *C. limbata*. But some specimens of *C. robusta* exhibit a so weak convexity of the anterior part of the ventral valve that this difference can be difficult to appreciate. The linguiform extension is U-shaped or sometimes narrowly trapezoidal in *C. robusta* whereas it is V-shaped in *C. limbata*. Very young specimens of *C. limbata* have an arcuate linguiform extension but it is never U-shaped. The beak is much shorter in *C. robusta* and less curved than in *C. limbata*.

PETTITT (1950, p. 25) made transverse serial sections (not illustrated) from a specimen of *C. robusta*, and he observed that "...the shell showed the presence of a median septum and raduliform crura in the brachial valve. No cardinal process or septalium were seen. Of particular interest are the inner socket-ridges, which are considerably elevated, the remainder of the hinge plate being much reduced".

The sections presented in the present paper (Fig. 21) and made on a specimen from Woodburn (Northern Ireland) confirm the remarks of PETTITT, especially that inner socket ridges are considerably elevated. All the external characters and this internal character, associated with the small subtriangular hinge plates, the subquadrate crural bases and the raduliform crura which remain close together, places *C. robusta* in *Homaletarhynchia* subgen. n.

Compared with *C. limbata* for its internal features, *C. robusta* has a shorter dorsal septum. *C. robusta* possesses more expanded inner socket ridges and narrower crura which are less concave in their posterior part.

At first glance, *Cretirhynchia (Homaletarhynchia) arcuata* PETTITT, 1950 can be rather difficult to distinguish from *C. robusta*. Specimens of both species exhibit the same ratio T/W, a similar narrow interarea and extremely short costae near the antero-lateral commissure. Generally, *C. arcuata* is more biconvex than *C. robusta*. A clear difference between these species concerns the anterior part of the dorsal fold. In *C. robusta*, the anterior part of the dorsal fold is elevated and nearly parallel to the plane of the ventral valve. In *C. arcuata*, the fold is less elevated and slopes towards the anterior commissure. When seen in lateral profile, the beak is more curved in *C. arcuata*. The apical angle is narrower in *C. arcuata*. The linguiform extension is generally arcuate in *C. arcuata* and U-shaped in *C. robusta*, but some gerontic specimens of *C. arcuata* can exhibit a more trapezoidal linguiform extension and confusion with *C. robusta* is possible. Serial sections will avoid all possible confusion because *C. arcuata* is distinguished by its thick, elevated and long dorsal septum. In *C. robusta*, the septum is much weaker, lower and shorter.

"*Rhynchonella*" *subplicata* MANTELL, 1822 is much smaller than *C. robusta* and its cyclothyridid internal structures cannot be confused with the internal characters of *C. robusta*.

Cretirhynchia (Homaletarhynchia) arcuata

PETTITT, 1950

Text-Figure 22, Plate 7, Figures 3a-e, 4a-e.

- * 1950 *Cretirhynchia arcuata*, sp. nov. - PETTITT, pp. 25-26, pl. 1, figs. c 3a-c pl. 2, fig. 13.

- 1954 *Cretirhynchia arcuata* - PETTITT, p. 28.
 1965 *Cretirhynchia arcuata* - STEINICH, p. 25.
 1968 *Cretirhynchia arcuata* Pettitt - LEEDER, pp. 6, 9, tables 1-2.
 1987 *Cretirhynchia arcuata* Pettitt - OWEN, p. 57, pl. 11, figs. 6a-c.
 pp 1988 *Cretirhynchia arcuata* Pettitt, 1950 - POPIEL-BARCZYK, pp. 12-13, text-figs. 10, 12, pl. 2, figs 7-9. non pl. 2, fig. 10, 10a, 10b (= *C. lentiformis*).
 1990 *Cretirhynchia arcuata* Pettitt - JOHANSEN & SURLYK, p. 838.
 pp 1992 *Cretirhynchia arcuata* Pettitt, 1950 - POPIEL-BARCZYK, p. 14.
 2000 *Cretirhynchia arcuata* Pettitt, 1950 - SIMON, pp. 138-139.

ta'' Zone) of Mousehold Pit, Norwich, Norfolk, England. This holotype was preserved in the NHM under the reference BB. 9991, but it has been recently lost.

A paratype from Mousehold has been illustrated by PETTITT, pl. 2, fig. 13 (BB. 9989).

Material

Material preserved in the NHM.

Material from Norwich, Norfolk (*Blt. mucronata* Zone)

The paratype cited above.

Six large specimens originally labelled as *Cretirhynchia limbata* (B. 25066-71). 24 topotypes from Mousehold Pit n°160 (B. 93163-76).

Material preserved in the IRScNB in Brussels.

Six specimens collected from the uppermost part of the Upper Campanian at Ahlten near Hanover, Germany (ex collection Leiptnitz, Uelzen, Germany).

Stratigraphical range: Upper Campanian, *Blt. mucronata* Zone.

Type specimen

Holotype designated and illustrated by PETTITT (1950, p. 25, pl. 1, figs. 3a-c) from the Upper Chalk (B. "mucrona-

Original diagnosis in PETTITT (1950, p. 25)

"*Cretirhynchia*, about 13 mm long, 14 mm wide and 9 mm

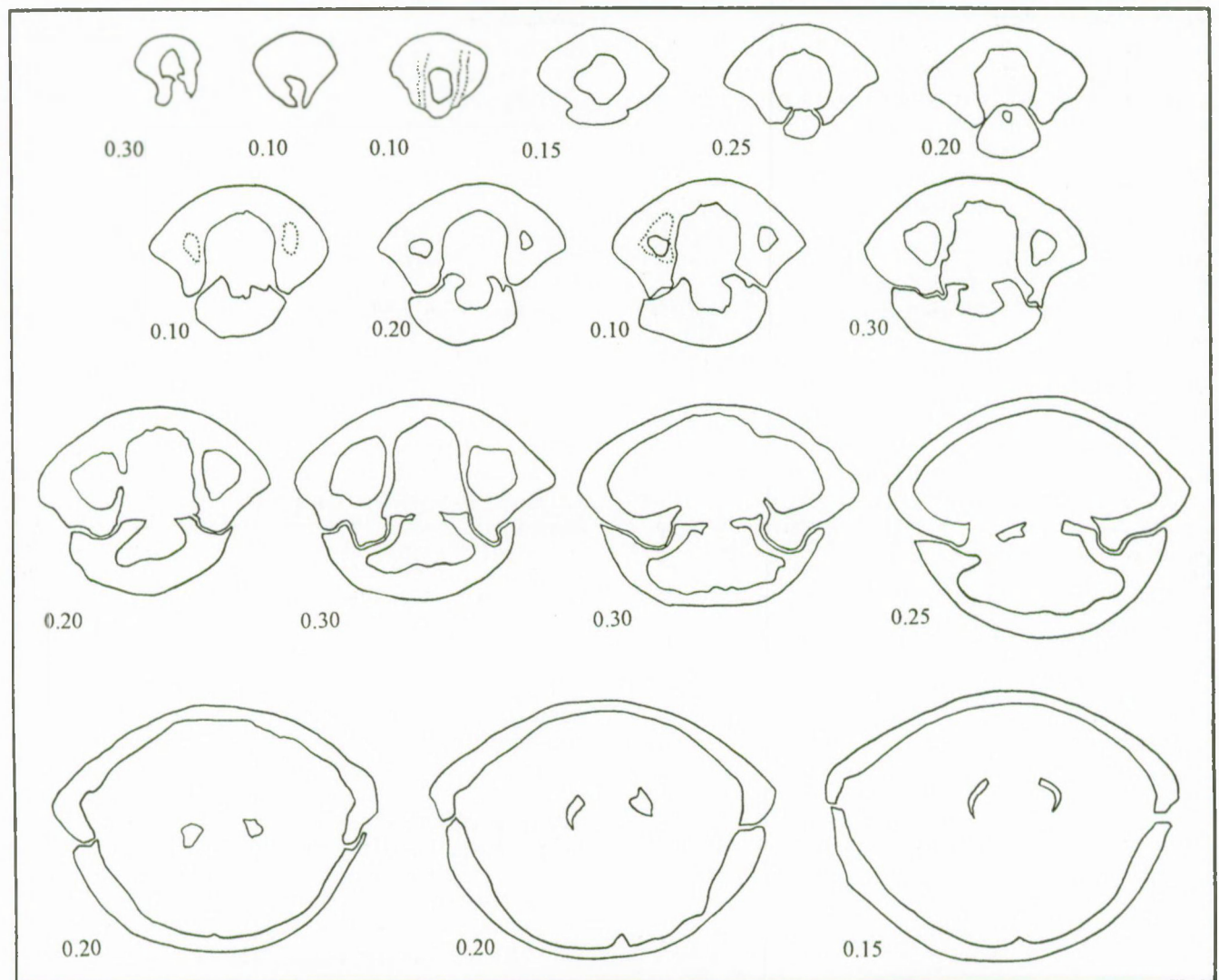


Fig. 23 — Serial transverse sections through the umbonal part of ex *Cretirhynchia minor* PETTITT, 1950 collected from the Upper Turonian (*Holaster planus* Zone), West Firle (Sussex, England). Length of the specimen: 9.0 mm. NHM. BB-73.

thick, subcircular to subtriangular in outline, anterior contour oval to lenticular. Brachial valve convex, with low median fold on anterior part; pedicle valve less convex, with shallow to moderately deep sinus on anterior part; linguiform extension short, arcuate to trapezoidal. Umbo thin, long, slightly incurved. Costae only developed along antero-lateral commissure (in late stages of growth); about 14, with 3 to 4 on fold; low, broad, subrounded to subangular."

Comments

PETTITT (1950, p. 26) observed a fairly strong median septum in the dorsal valve and raduliform crura. He indicated that "the adductor muscle-scars are posterior to the diductors, and only partly surrounded by them".

The transverse serial sections made from a topotype collected from Mousehold Pit (Fig. 22) show coarse dental plates, strongly convergent. No pedicle collar is observed. The hinge structure is very strong and typical of *Homaletarhynchia* subgen. n. The outer socket ridges are very low whereas thick inner socket ridges are ventrally expanded. The dorsal septum seen on the valve floor, is extremely thick, elevated and rather long. The hinge plates are very small. Crural bases are subquadrate and raduliform crura are inwardly concave. The crura remain close together.

C. arcuata has an absolutely smooth shell. Ribs only occur along the commissure. This is a difference with *C. lentiformis* which possesses very faint costae on the anterior part of the shell.

C. arcuata, a species of possible stratigraphical value, is an abundant brachiopod in the *Blt. mucronata* Zone of Norwich and it is often associated with *C. norvicensis*. In Belgium, *C. arcuata* has never been collected and *C. norvicensis* is a very exceptional species. On the contrary, *C. arcuata* seems well present in Northern Germany.

A phylogenetical relation, between *Homaletarhynchia* subgen. n. and *Harmignirhynchia* subgen. n., is suggested by a closer examination of the serial sections (Fig. 1). In the sections of the posterior part of *C. arcuata* and *C. limbata*, the juvenile crura are embedded in the material constituting the adult hinge plates. These juvenile crura are very concave and obviously similar to the adult crura observed in the representatives of *Harmignirhynchia* subgen. n. A common ancestor to these two subgenera is plausible (Manceñido, personal communication, July, 2000).

Species removed from the genus *Cretirhynchia*

PETTITT, 1950

"*Cretirhynchia*" *minor* PETTITT, 1950

Text-Figures 23-24, Plate 6, Figures 3a-d, 4a-e, 5a-d.

- | | | |
|---|------|--|
| ? | 1873 | <i>Rhynchonella plicatilis</i> Sow. - GEINITZ, H.B., pl. 7, figs. 9, 10, 12, 13. |
| * | 1950 | <i>Cretirhynchia minor</i> , sp. nov. - PETTITT, pp. 18-19, pl. 1, figs. 2a-c. |
| . | 1961 | <i>Cretirhynchia minor</i> Pettitt - PEAKE & HANCOCK, p. 309. |
| . | 1965 | <i>Cretirhynchia minor</i> Pettitt, 1950 - BIGNOT, p. 6. |
| . | 1974 | <i>Cretirhynchia minor</i> Pettitt, 1950 - NEKVASILOVA, pp. 48-53, 61-62, table 1, text-figs. 7, 10-14, pl. 4, figs. 1-6, pl. 7, figs. 1-2, pl. 8, fig. 3. |

1992 *Cretirhynchia minor* Pettitt, 1950 - POPIEL-BARCZYK, p. 15.

1997 *Cretirhynchia minor* - MORTIMORE, pp. 36, 93.

Stratigraphical range: Upper Turonian, *H. planus* Zone.

Type specimen

Holotype designated and illustrated by PETTITT (1950, p. 18, pl. 1, figs. 2a-c) from the base of the *H. planus* Zone, New Pit, Lewes, Sussex, England. The holotype is preserved in the Museum of the British Geological Survey, under the reference GSM. 88778.

Material

Material preserved in the NHM.

Six specimens from the *H. planus* Zone, Firle Chalk, West Firle, Sussex (BB. 73-9). One specimen has been chosen for transverse serial sections (Fig. 23).

Material preserved in the Museum of the Earth in Warsaw (Muzeum Ziemi PAN).

30 specimens from the Upper Turonian of Cizkovice in North-West Bohemia, under the reference MZ VIII bra-1498. This is a part of the material studied by NEKVASILOVA, 1974.

Material preserved in IRScNB in Brussels.

Three specimens collected by the first author in Bardouville near Rouen (Seine-Maritime, France) from the Upper Turonian, *H. planus* Zone. One specimen has been sectioned for the present study (Fig. 24).

Original diagnosis in PETTITT (1950, p. 18)

"*Cretirhynchia*, about 12 mm long, 12 mm wide and 9 mm thick, subcircular to subpentagonal in outline, oval to subcircular in lateral profile; anterior contour domical.

Brachial valve of considerable convexity, with flattened, barely perceptible fold on the anterior commissure. Pedicle valve less convex, with broad, shallow, median sinus. Linguiform extension trapezoidal, long (in adult forms) and fairly broad.

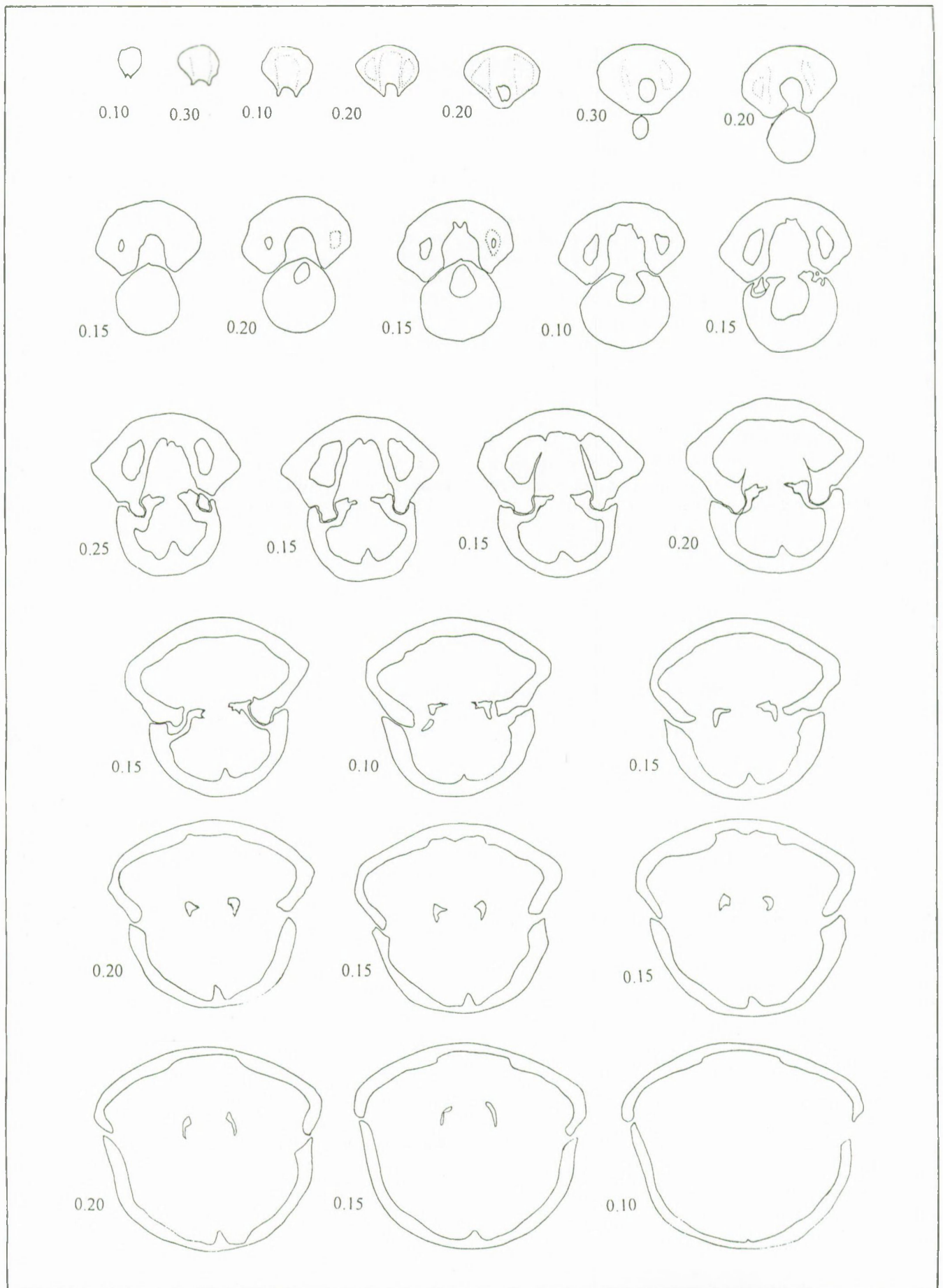
Hypothyridid; umbo short, erect, extremity pointed. Foramen moderate in size, tubular. Deltoidal plates conjunct, produced (alar). Beak-ridges distinct; interarea well defined.

Ornament of about 36 rounded to subangular costae, with angular intervening sulci; 8 costae on fold and 7 in sinus. Concentric ornament faint; fine growth-lines and a few growth laminae. Apical angle 105°."

Comments

PETTITT (1950, p. 19) did not illustrate his serial sections made on *Cretirhynchia minor*. He merely pointed out the presence of a dorsal septum and raduliform crura and considered (1950, p. 21) *C. minor* as a small *Cretirhynchia* species very similar to *C. exsculpta* PETTITT, 1950. The external similarities between both species, including incipient splitting of the costae, lead PETTITT to assign to *C. minor* a taxonomic position close to *C. exsculpta* in his "second series".

NEKVASILOVA (1974, pp. 49-57) published an exhaustive study of *C. minor* collected for North-West Bohemia. This material from North-West Bohemia was also compared to the original material of PETTITT preserved in the Natural History Museum and in the Geological Survey in



London, and in the Sedgwick Museum in Cambridge (NEKVASILOVA, 1974, p. 53). It is noteworthy that no incipient splitting of the costae has been observed on this Bohemian material. The serial sections of NEKVASILOVA (1974, text-figs. 11-12) show dental plates which are divergent ventrally at first and becoming clearly convergent in their anterior part. The presence of a poorly developed pedicle collar has been shown only in the specimen sectioned. Hinge plates are almost parallel to the hinge-axis or slightly deflected dorsally. Dorsally, crural bases are slightly concave. Crura are generally strongly concave in their posterior part. These serial sections are extremely similar to the sections obtained for *Cretirhynchia* aff. *cuneiformis* PETTITT, 1950, another larger Bohemian rhynchonellid species (NEKVASILOVA, 1974, text-figs. 8-9).

In the Upper Turonian (*H. planus* Zone) from Bardouville near Rouen (Seine maritime, France), three specimens of *C. minor* were collected by SIMON. A poorly developed incipient splitting of the costae near the commissure was only visible on two specimens. The sections made on one specimen from Bardouville (Fig. 24) are similar to the sections made by NEKVASILOVA (1974) on the North-West Bohemian material. Moreover, transverse serial sections were also made on a specimen from West Firl, Sussex, England (Fig. 23). It exhibits convergent dental plates, hinge plates subparallel to the hinge-axis, concave crural bases and raduliform crura which are clearly concave in their posterior parts.

All those characters are quite different from those observed in the sections of *Cretirhynchia* (*Lewesirhynchia*) *exsculpta* PETTITT, 1950 (Fig. 12). In *C. exsculpta*, the dental plates are much thicker and more convergent and the hinge plates are smaller and subtriangular. The typical "hook structure" of *Lewesirhynchia* subgen. n. built by the distal end of the inner socket ridges, the hinge plates and the crural bases, visible in *C. exsculpta*, has never been observed in the sections of *C. minor*. Despite an external broad similarity between these two rhynchonellid brachiopods, these species are taxonomically distinct from each other, when their internal characters are taken into account.

We think that *C. minor* forms, with other Turonian brachiopods such as *Cretirhynchia* aff. *cuneiformis* sensu NEKVASILOVA (1974) and *C. bohémica* (SCHLOENBACH, 1868), an homogenous group of rhynchonellid brachiopods. When transverse serial sections of *Bohemirhynchia soukupi* NEKVASILOVA, 1973 (NEKVASILOVA, 1973, text-figs. 1-2) are confronted with those obtained for *C. minor*, *C. bohémica* and *C. aff. cuneiformis*, a relationship between these species and the genus *Bohemirhynchia* seems probable. It must be noted that *Bohemirhynchia soukupi* exhibits intermediate internal struc-

tures between *Burrirhynchia* and *Cretirhynchia* representatives. *Bohemirhynchia soukupi* has many characters in common with *Cretirhynchia* but it has dorsally concave crura subparallel to the hinge-axis, a character which has never been observed in *Cretirhynchia* representatives. In the group of *C. minor*, *C. bohémica* and *C. aff. cuneiformis* sensu NEKVASILOVA (1974) the crura are not really facing each other, as in most representatives of the genus *Cretirhynchia*, but they have a concavity which is more dorsally oriented. A revision of this material is suggested before a new genus could be erected for it. This is the reason why, it seems preferable to leave "*C.*" *minor* and other members of this group without precise generic attribution.

Stratigraphical interest of Upper Chalk rhynchonellid brachiopods

Rhynchonellid brachiopods have been successfully used for establishing stratigraphical correlations between English Chalk deposits (PEAKE & HANCOCK, 1961, BAILEY *et al.*, 1987, LEEDER, 1968, WOOD, 1988). Using rhynchonellid brachiopods, stratigraphical correlations were established between the British, French and Belgian Cenomanian deposits (OWEN, 1988).

These stratigraphical results are consistent with the correlations obtained with the ammonites (KENNEDY, 1971, WRIGHT & KENNEDY, 1981). The Upper Turonian material collected from Bardouville near Rouen (Seine-Maritime, France) and presented in this paper show that an excellent stratigraphical correlation can be demonstrated between this French area and the Turonian Chalk Rock of England. These areas are from the *H. planus* Zone and ammonites such as *Lewesiceras mantelli* (WRIGHT & WRIGHT, 1951) and *Subprionocyclus neptuni* (GEINITZ) have been collected from both areas. The rhynchonellid brachiopod *Woodwardirhynchia cuneiformis* (PETTITT, 1950) is relatively abundant in these French and English chalk deposits.

A study of the Upper Campanian brachiopods (*Belemnitella mucronata* Zone and *Belemnitella woodi* Zone) from the Mons basin (SIMON, 2000) indicates that stratigraphical correlations can be established between the "Craie de Trivières" (Mons basin, Belgium) and the Weybourne¹ faunal belt described by WOOD (1988). *Cretirhynchia* (*Homaletarhynchia*) *lentiformis* (WOODWARD, 1833) is fairly abundant at this level in Belgium and in England. The "Craie d'Obourg" (Mons Basin, Hainaut, Belgium) can be correlated with the Weybourne² faunal belt and *Woodwardirhynchia woodwardi* (DAVIDSON, 1855) associated with *C. (Harmignirhynchia) obourgensis* sp. n., a species described in this paper, appear as good markers of this stratigraphical level.

A correlation between the Lower Maastrichtian chalk from Trimingham (Norfolk) and the Lower Maastrichtian chalk from Rügen (Germany) has been established (STEINICH, 1965) and *Cretirhynchia retracta* (ROEMER, 1841) is the most striking rhynchonellid brachiopod species present in both places.

On the other hand, misidentifications of rhynchonellid brachiopod species produce wrong stratigraphical results or simply mask possible correlations. *Cretirhynchia plicatilis* (J. SOWERBY, 1816) and *C. octoplicata* (J. SOWERBY, 1816) are extreme examples of this type of



Fig. 24 — Serial transverse sections through the umbonal part of *exCretirhynchia minor* PETTITT, 1950 collected from the Upper Turonian (*Holaster planus* Zone), Bardouville (near Rouen, Seine-Maritime, France). Length of the specimen: 13.0 mm. IRScNB.-IST. N° 10843.

misidentification but confusion between *C. (Homaletarhynchia) lentiformis* (WOODWARD, 1833) and *C. (Homaletarhynchia) arcuata* PETTITT, 1950 are also seen in the literature. The latter species is of special interest because it is often associated with *C. (Cretirhynchia) norvicensis* PETTITT, 1950 in a restricted Upper Campanian stratigraphical level. This level is well exposed in Norfolk and near Ahlten (Hanover, Germany) but it is not visible in Belgium.

Cretirhynchia (Cretirhynchia) plicatilis and *C. (Lewesirhynchia) octoplicata* must be considered as English endemic species since they were never collected with certainty outside England. They are respectively good markers for the *Cortestudinarium* and *Coranguinum-Marsupites* Zones of Sussex and Kent (PEAKE & HANCOCK, 1961, BAILEY *et al.*, 1987, MORTIMORE, 1997). This suggests that English Coniacian and Santonian deposits could represent special facies which are not similar to the Coniacian-Santonian facies exposed on the continent.

The Lower Campanian *Cretirhynchia (Harmignirhynchia) intermedia* PETTITT, 1950 from the *Offaster pilula* Zone is actually known from Wiltshire and Hampshire, England. In Belgium, Lower Campanian white chalk is not exposed, resulting in the absence of *C. intermedia*. This species, which has a restricted stratigraphical range, should be searched for elsewhere in Europe as it is now better described and could be more easily recognized.

Conclusions

The proposed revision of the genus *Cretirhynchia* PETTITT, 1950 throws a new light on this interesting problem. The original material used by PETTITT in 1950-1954 for his monograph was accurately reviewed and the large amount of European material used in this study have afforded a sharper concept of the genus *Cretirhynchia*.

After this revision, "*Cretirhynchia*" *cuneiformis* PETTITT, 1950, "*C.*" *woodwardi* (DAVIDSON, 1855) and "*C.*" *tenuicostata* (VON HANSTEIN, 1879) are removed from the genus *Cretirhynchia*. The new genus *Woodwardirhynchia* gen. n. is erected for these species exhibiting numerous distinct characters which indicate that it probably arose from the *Cyclothyris* rhynchonellid stock.

For specific reasons, "*Cretirhynchia*" *minor* PETTITT, 1950 and "*C. subplicata* (MANTELL, 1822) are also removed from the genus *Cretirhynchia* and left with uncertain generic affinity. "*C.*" *subplicata* exhibits internal features more resembling the structure of the genus *Cyclothyris* M'COY, 1844. "*C.*" *minor* is a species related to "*C.*" *bohémica* (SCHLOENBACH, 1868). Further studies are necessary to assign a more precise taxonomic position to these rhynchonellid species.

The genus *Cretirhynchia* has been split into four subgenera. Three new subgenera based on typical external and mainly internal features have been erected: *Lewesirhynchia* subgen. n., *Harmignirhynchia* subgen. n. and *Homaletarhynchia* subgen. n.

The species erected by PETTITT in 1950 and revised in this work are valid and distinct species, except *Cretirhynchia triminghamensis* which is a junior synonym of *C.*

retracta (ROEMER, 1841). Further studies are necessary to assign a correct taxonomic position to *C. lenticularis* PETTITT, 1950 and *C. magna* PETTITT, 1950 which were not considered here due to lack of material.

The series of PETTITT (1950) are no more tenable, and this system must be discarded.

The passage forms described by PETTITT were discussed and cannot be taken into account.

The taxonomic relationships between the Upper Chalk rhynchonellid brachiopods proposed in this paper are a first step in the revision of the genus *Cretirhynchia*. The numerous species from Eastern Europe and from Western and Central Asia should be now revised in the light of present knowledge.

Most species of *Cretirhynchia* have, without doubt, restricted stratigraphical ranges. But the stratigraphical use of such brachiopods is sometimes restricted to a regional scale, such as several English species, mainly those collected from the Coniacian to the lowermost Campanian, appear endemic or extremely rare outside England. On the contrary, good stratigraphical correlations can be made between other English and some Western European chalk. This is especially true for the Cenomanian, Turonian, Upper Campanian and Lower Maastrichtian white chalks.

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Captions of plates

PLATE 1

Cretirhynchia (Cretirhynchia) plicatilis (J. SOWERBY, 1816)

a: ventral view, b: dorsal view, c: lateral view, d: anterior view, e: posterior view
All the specimens are preserved in the Natural History Museum in London (NHM)
Magnification: x 1.76

- Fig. 1 — Specimen from the *Coranguinum* Zone in Northfleet, Kent (England) used for serial transverse sections (Figure 8). B. 79815.
Fig. 2 — Specimen from the *Coranguinum* Zone in Northfleet, Kent (England). B. 44664.
Fig. 3 — Specimen from the *Uintacrinus* band, Devices Road, West of Salisbury, Wiltshire (England). B. 91832.
Fig. 4 — Younger specimen from the *Coranguinum* Zone, Snowdown Colliery, Kent (England). B. 93648.

PLATE 2

Cretirhynchia (Cretirhynchia) norvicensis PETTITT, 1950

a: ventral view, b: dorsal view, c: lateral view, d: anterior view, e: posterior view
All the specimens are preserved in the Natural History Museum in London (NHM)

Specimens collected from the Upper Campanian (*Belemnitella mucronata* Zone) of Norwich, Norfolk, England. Variations of shape and size, observed among individuals from a same locality.

- Fig. 1 — Small-sized specimen illustrating the possible homeomorphy between *C. (Cretirhynchia) norvicensis* PETTITT, 1950 and *Woodwardirhynchia tenuicostata* (VON HANSTEIN, 1879) a Lower Maastrichtian rhynchonellid brachiopod from the phosphatic chalk of Cipluy (Hainaut, Belgium). B. 97815-1. (Magnification: x 1.85).
Fig. 2 — Small-sized specimen with a typical triangular outline. B. 97815-2. (Magnification: x 1.85).
Fig. 3 — The smallest specimen observed in this study. B. 97815-3. (Magnification: x 1.78).
Fig. 4 — Medium-sized specimen with a typical triangular outline. B. 97815-4. (Magnification: x 1.78).
Fig. 5 — Medium-sized specimen exhibiting a more transversely-oval outline. Such specimens can be confused with *Woodwardirhynchia tenuicostata* (VON HANSTEIN, 1879) or with *Cretirhynchia (Harmignirhynchia) intermedia* PETTITT, 1950. B. 97815-5. (Magnification: x 1.78).

PLATE 3

a: ventral view, b: dorsal view, c: lateral view, d: anterior view, e: posterior view

- Fig. 1 — Fully adult specimen of *Cretirhynchia (Cretirhynchia) norvicensis* PETTITT, 1950 with an oval outline collected from Norwich, Norfolk, England. Upper Campanian (*Belemnitella mucronata* Zone). Specimen preserved in the NHM. B. 97815-6. (Magnification: x 1.80).
Fig. 2 — Small, adult specimen of *Cretirhynchia (Cretirhynchia) triminghamensis* PETTITT, 1950 from S. Bluff, Trimingham, Norfolk, England. Lower Maastrichtian. *C. (Cretirhynchia) triminghamensis* is a junior synonym of *Cretirhynchia (Cretirhynchia) retracta* (ROEMER, 1841). Specimen preserved in the NHM. B. 96961. (Magnification: x 2.84).
Fig. 3 — Gerontic specimen of *Cretirhynchia (Cretirhynchia) triminghamensis* PETTITT, 1950 from Trimingham, Norfolk, England. Lower Maastrichtian. *C. (Cretirhynchia) triminghamensis* is a junior synonym of *Cretirhynchia (Cretirhynchia) retracta* (ROEMER, 1841). Specimen prepared for serial sections (Figure 9) and preserved in the NHM. BB. 43335. (Magnification: x 1.81).
Fig. 4 — Adult specimen of *Cretirhynchia (Cretirhynchia) triminghamensis* PETTITT, 1950 from Trimingham, Norfolk, England. Lower Maastrichtian. *C. (Cretirhynchia) triminghamensis* is a synonym of *Cretirhynchia (Cretirhynchia) retracta* (ROEMER, 1841). Specimen preserved in the NHM. BB. 43333. (Magnification: x 1.81).
Fig. 5 — *Cretirhynchia (Cretirhynchia) retracta* (ROEMER, 1841) collected from Krons Moor, Schleswig-Holstein, Germany. Lower Maastrichtian. Specimen preserved in the IRScNB, IST. n° 10840. (Magnification: x 1.78).

PLATE 4

Cretirhynchia PETTITT, 1950 - Subgenus *Lewesirhynchia* subgen. n.

a: ventral view, b: dorsal view, c: lateral view, d: anterior view, e: posterior view.

All this material is preserved in the Natural History Museum, London (NHM).

- Fig. 1 — Gerontic specimen of *Cretirhynchia* (*Lewesirhynchia*) *octoplicata* (J. SOWERBY, 1816) from the chalk of Lewes (*Cortestudinarium* Zone), Lewes, Sussex, England. B. 8379-1. This specimen has been sectionned (Figure 11). (Magnification: x 1.77).
- Fig. 2 — Holotype of *Cretirhynchia* (*Lewesirhynchia*) *protoexsculpta* sp. n. from the chalk of Lewes (*Cortestudinarium* Zone), Lewes, Sussex, England. B. 8379-2. This specimen has been sectionned (Figure 13). (Magnification: x 1.60).
- Fig. 3 — Fully adult specimen of *Cretirhynchia* (*Lewesirhynchia*) *exsculpta* PETTITT, 1950 collected from the Santonian (*Marsupites testudinarius* Zone) in Brighton, Sussex, England. B. 9464. (Magnification: x 2.12).
- Fig. 4 — Smaller specimen of *Cretirhynchia* (*Lewesirhynchia*) *exsculpta* PETTITT, 1950 collected from the "Senonian" chalk of Elmer, Middleton, Sussex. BB. 76525. (Magnification: x 1.9).

PLATE 5

Cretirhynchia PETTITT, 1950 - Subgenus *Harmignirhynchia* subgen. n.

a: ventral view, b: dorsal view, c: lateral view, d: anterior view, e: posterior view.

- Fig. 1 — Gerontic specimen of *Cretirhynchia* (*Harmignirhynchia*) *intermedia* PETTITT, 1950 from East Harnham, Wiltshire, England. Lower Campanian (*Offaster pilula* Zone). The numerous faint costae, reduced in number near the commissure are well preserved. Specimen preserved in the NHM. B. 92742-2. This specimen has been sectionned (Figure 16). (Magnification: x 2.4).
- Fig. 2 — Adult specimen of *Cretirhynchia* (*Harmignirhynchia*) *intermedia* PETTITT, 1950 from East Harnham, Wiltshire, England. Lower Campanian (*Offaster pilula* Zone). Specimen preserved in the NHM. B.92742-3. (Magnification: x 1.94).
- Fig. 3 — Adult specimen of *Cretirhynchia* (*Harmignirhynchia*) *intermedia* PETTITT, 1950 from East Harnham, Wiltshire, England. Lower Campanian (*Offaster pilula* Zone). Specimen preserved in the NHM. B. 92742-4. (Magnification: x 2.5).
- Fig. 4 — Paratype of *Cretirhynchia* (*Harmignirhynchia*) *obourgensis* sp. n. from Harmignies, Mons basin, Hainaut, Belgium. Upper Campanian, "Craie de Nouvelles" (*Belemnitella woodi* Zone). Specimen preserved in the IRScNB - IST n° 10844. (Magnification: x 2.27).
- Fig. 5 — Paratype of *Cretirhynchia* (*Harmignirhynchia*) *obourgensis* sp. n. from Harmignies, Mons basin, Hainaut, Belgium. Upper Campanian, "Craie de Nouvelles" (*Belemnitella woodi* Zone). Specimen preserved in the IRScNB - IST n° 10846. (Magnification: x 1.60).

PLATE 6

a: ventral view, b: dorsal view, c: lateral view, d: anterior view, e: posterior view.

- Fig. 1 — Paratype of *Cretirhynchia* (*Lewesirhynchia*) *protoexsculpta* sp. n. from the chalk of Lewes (*Cortestudinarium* Zone), Lewes, Sussex, England. Specimen preserved in the NHM. B. 8379-3. (Magnification: x 1.5).
- Fig. 2 — Holotype of *Cretirhynchia* (*Harmignirhynchia*) *obourgensis* sp. n. collected from Harmignies, Mons basin, Hainaut, Belgium. Upper Campanian, "Craie de Nouvelles". (*Belemnitella woodi* Zone). Specimen preserved in the IRScNB. - IST n° 10847. This specimen has been sectionned (Figure 17). (Magnification: x 2.1).
- Fig. 3 — Adult specimen of ex "*Cretirhynchia*" *minor* PETTITT, 1950 collected from Bardouville, hameau de Beaulieu, Seine Maritime, France. Upper Turonian (*Holaster planus* Zone). This specimen has been sectionned (Figure 24). Specimen preserved in the IRScNB. IST- n° 10843. (Magnification: x 3.1).
- Fig. 4 — Adult specimen of ex "*Cretirhynchia*" *minor* PETTITT, 1950 collected from West Firle, Firle Chalk, Sussex. Upper Turonian (*Holaster planus* Zone). This specimen has been sectionned (Figure 23). Specimen preserved in the NHM. B. 73. (Magnification: x 4.3).
- Fig. 5 — Adult specimen of ex "*Cretirhynchia*" *minor* PETTITT, 1950 collected from Cizkovic, North-West Bohemia. Upper Turonian. Specimen preserved in the IRScNB. IST n° 10844. (Magnification: x 3.7).
- Fig. 6 - Adult specimen of *Cretirhynchia* (*Homaletarhynchia*) *robusta* (TATE, 1865) collected from Woodburn, Northern Ireland. Santonian. This specimen has been sectionned (Figure 21). Specimen preserved in the NHM. B. 25152. (Magnification: x 2.3).

PLATE 7

Cretirhynchia PETTITT, 1950 - Subgenus *Homaletarhynchia* subgen. n.

a: ventral view, b: dorsal view, c: lateral view, d: anterior view, e: posterior view.

- Fig. 1 — Adult specimen of *Cretirhynchia* (*Homaletarhynchia*) *limbata* (VON SCHLOTHEIM, 1813) from Jandrain, Brabant, Belgium. Upper Maastrichtian. Specimen preserved in the IRScNB. IST n° 10838. This specimen has been sectionned (Figure 19). (Magnification: x 1.87).
- Fig. 2 — Adult specimen of *Cretirhynchia* (*Homaletarhynchia*) *limbata* (VON SCHLOTHEIM, 1813) from Ciplly, Mons basin, Hainaut, Belgium. Lower Maastrichtian (*B. obtusa* Zone). Specimen preserved in the IRScNB. IST n° 10839. (Magnification: x 1.84).
- Fig. 3 — Gerontic specimen of *Cretirhynchia* (*Homaletarhynchia*) *arcuata* PETTITT, 1950 from Ahlten, Germany. Upper Campanian. Ex collection Leipzig, Uelzen, Germany. Specimen preserved in the IRScNB. IST n° 10841. (Magnification: x 2.0).
- Fig. 4 — Adult specimen (paratype) of *Cretirhynchia* (*Homaletarhynchia*) *arcuata* PETTITT, 1950 from Mousehold Pit, Norwich, Norfolk, England. Upper Campanian. Specimen preserved in the NHM. B. 93163. This specimen has been sectionned (Figure 22). (Magnification: x 2.0).
- Fig. 5 — Adult specimen of *Cretirhynchia* (*Homaletarhynchia*) *lentiformis* (WOODWARD, 1833) from Cuesmes, Mons basin, Hainaut, Belgium. Upper Campanian. "Craie de Trivières" (*Belemnitella mucronata* Zone). Specimen preserved in the IRScNB. IST n° 10821. This specimen has been sectionned (Figure 20). (Magnification: x 2.74).
- Fig. 6 — Type specimen of *Cretirhynchia* (*Homaletarhynchia*) *undulata* (PUSCH, 1837) subsp. *maastrichtiensis* n. subsp. collected from C.P.L. quarry in Hallembaye, Liège, Belgium. Upper Maastrichtian, Vijlen Chalk (*B. junior* Zone). Specimen preserved in the IRScNB. IST n° 10842. (Magnification: x 2.0).

PLATE 8

a: ventral view, b: dorsal view, c: lateral view, d: anterior view, e: posterior view.

Woodwardirhynchia gen. n.

- Fig. 1 — Fully adult specimen of *Woodwardirhynchia cuneiformis* (PETTITT, 1950) collected from Bardouville near Rouen, Seine Maritime, France. Upper Turonian (*Holaster planus* Zone). IRScNB. IST n° 10831. This specimen has been sectionned (Figure 2). (Magnification: x 1.7).
- Fig. 2 — Fully adult specimen of *Woodwardirhynchia cuneiformis* (PETTITT, 1950) collected from Bardouville near Rouen, Seine Maritime, France. Upper Turonian (*Holaster planus* Zone). The numerous costae are better preserved in this specimen. Specimen preserved in the IRScNB. IST n° 10832. This specimen has been sectionned (Figure 3). (Magnification: x 1.7).
- Fig. 3 — Large adult specimen of *Woodwardirhynchia woodwardi* (DAVIDSON, 1855) collected from Harmignies, Mons basin, Hainaut, Belgium. Upper Campanian, top of the "Craie de Trivières" (*Belemnitella mucronata* Zone). Specimen preserved in the IRScNB. IST n° 10834. (Magnification: x 1.1).
- Fig. 4 — Smaller adult specimen of *Woodwardirhynchia woodwardi* (DAVIDSON, 1855) collected from Harmignies, Mons basin, Hainaut, Belgium. Upper Campanian, top of the "Craie de Trivières" (*Belemnitella mucronata* Zone). Specimen preserved in the IRScNB. IST n° 10837. (Magnification: x 1.6).u
- Fig. 5 — Adult specimen of *Woodwardirhynchia tenuicostata* (VON HANSTEIN, 1879) collected from the phosphatic chalk of Ciplly, Mons basin, Hainaut, Belgium. Lower Maastrichtian (*Belemnella obtusa* Zone). Specimen preserved in the IRScNB. IST n° 10665. (Magnification: x 2.1).

Species removed from the genus *Cretirhynchia* PETTITT, 1950 and left without precise generic affinity.

ex "*Cretirhynchia*" *subplicata* (MANTELL, 1822)

- Fig. 6 - Adult specimen collected from Dover, Kent, England. Coniacian (*Cortestudinarium* Zone). Specimen preserved in the NHM. B. 79974. This specimen has been sectionned (Figure 7). (Magnification: x 2.6).
- Fig. 7 - Smaller specimen collected from Offham Hill near Lewes, Sussex, England. Coniacian (*Cortestudinarium* Zone). Specimen preserved in the NHM. B. 47876. This specimen has been sectionned. (Magnification: x 3.4).

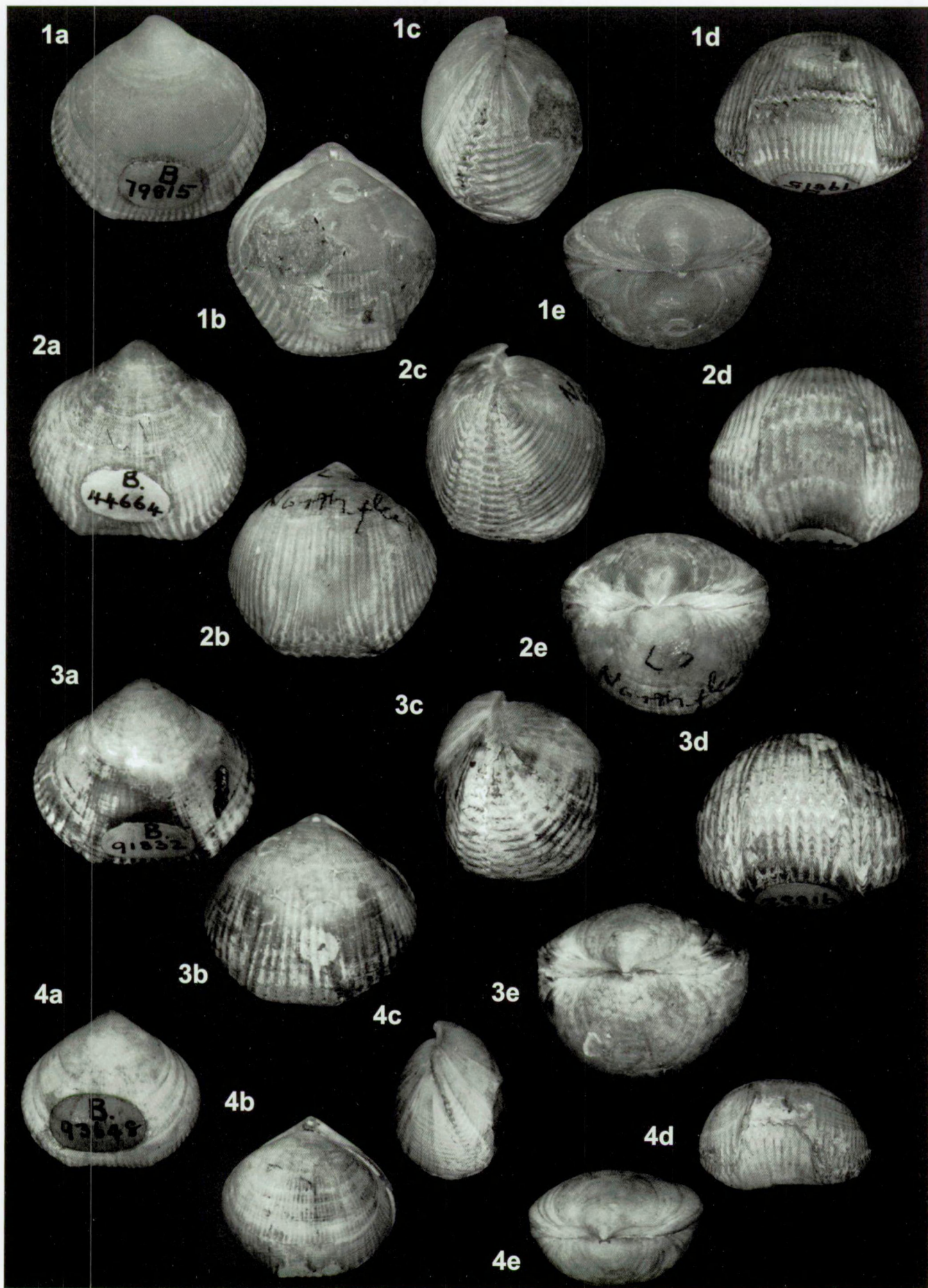


PLATE I

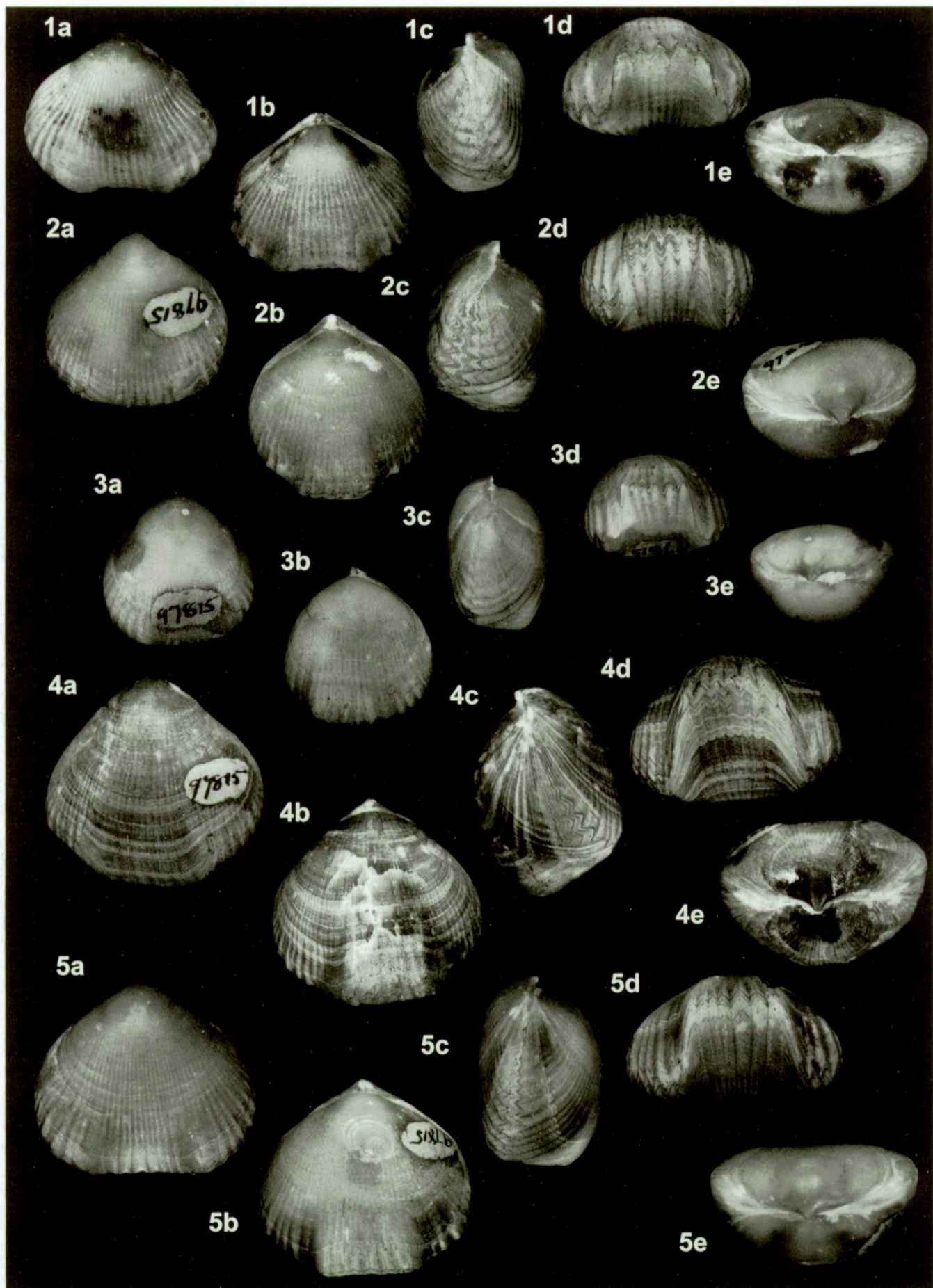


PLATE 2

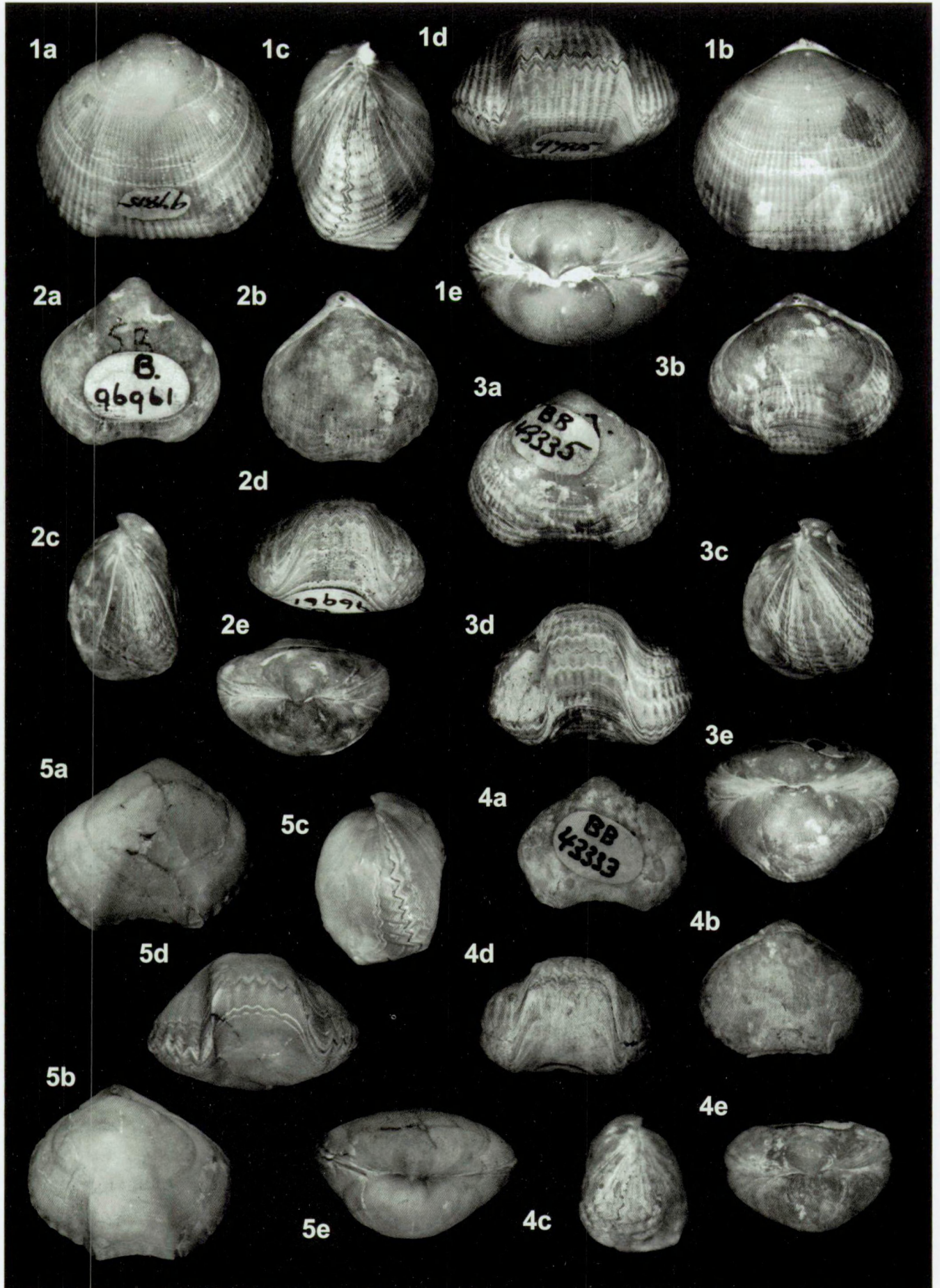


PLATE 3

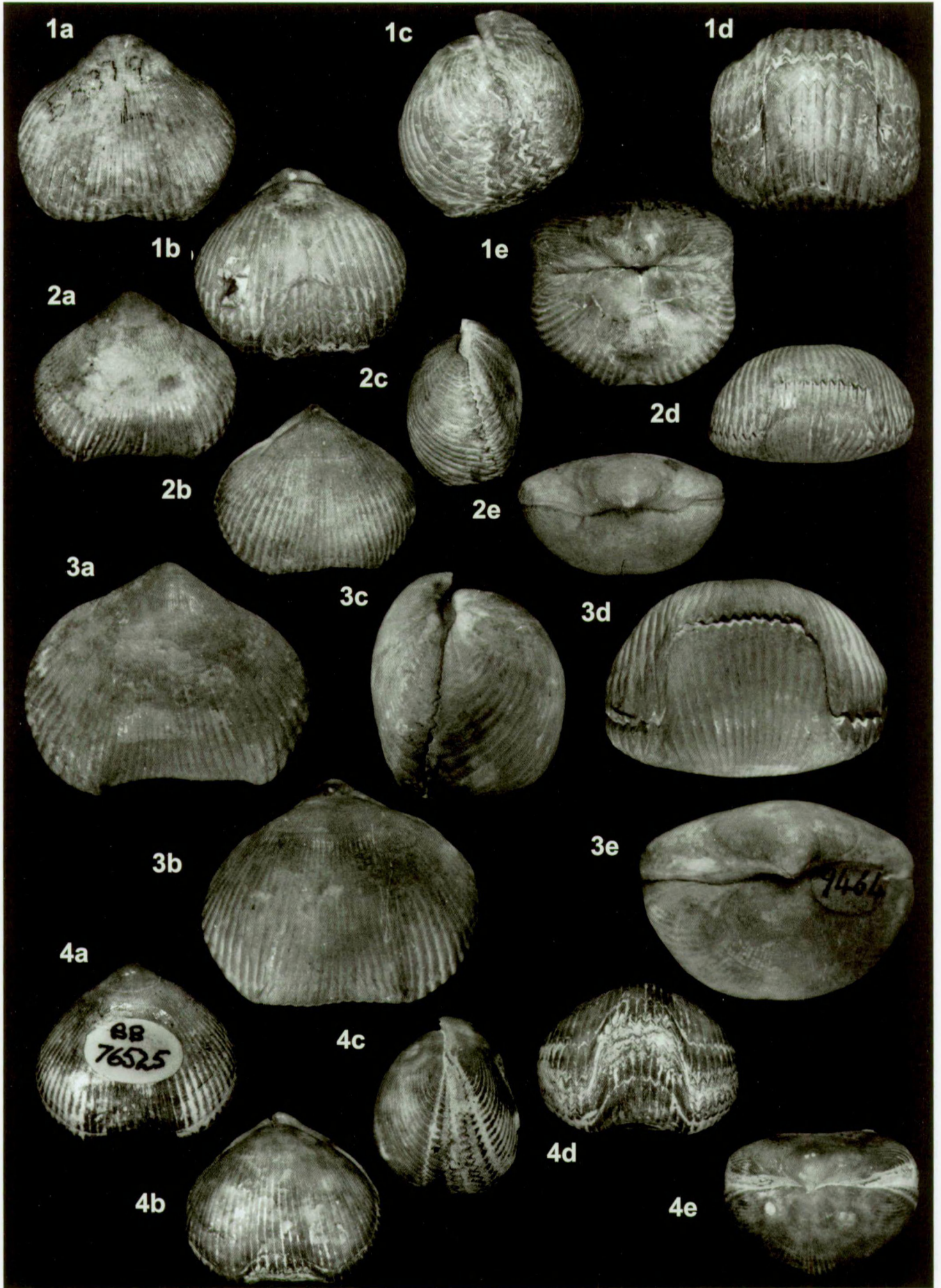


PLATE 4

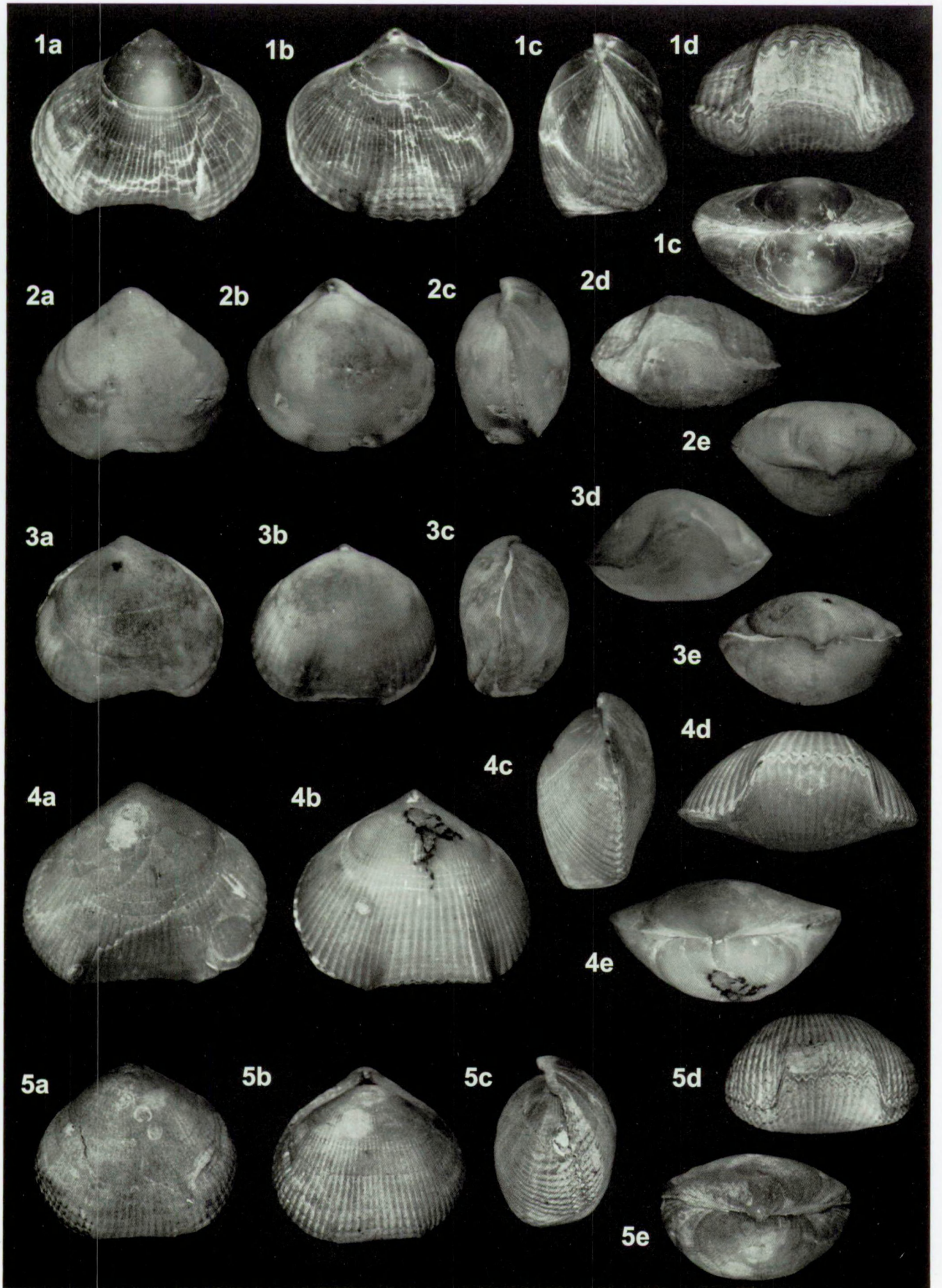


PLATE 5

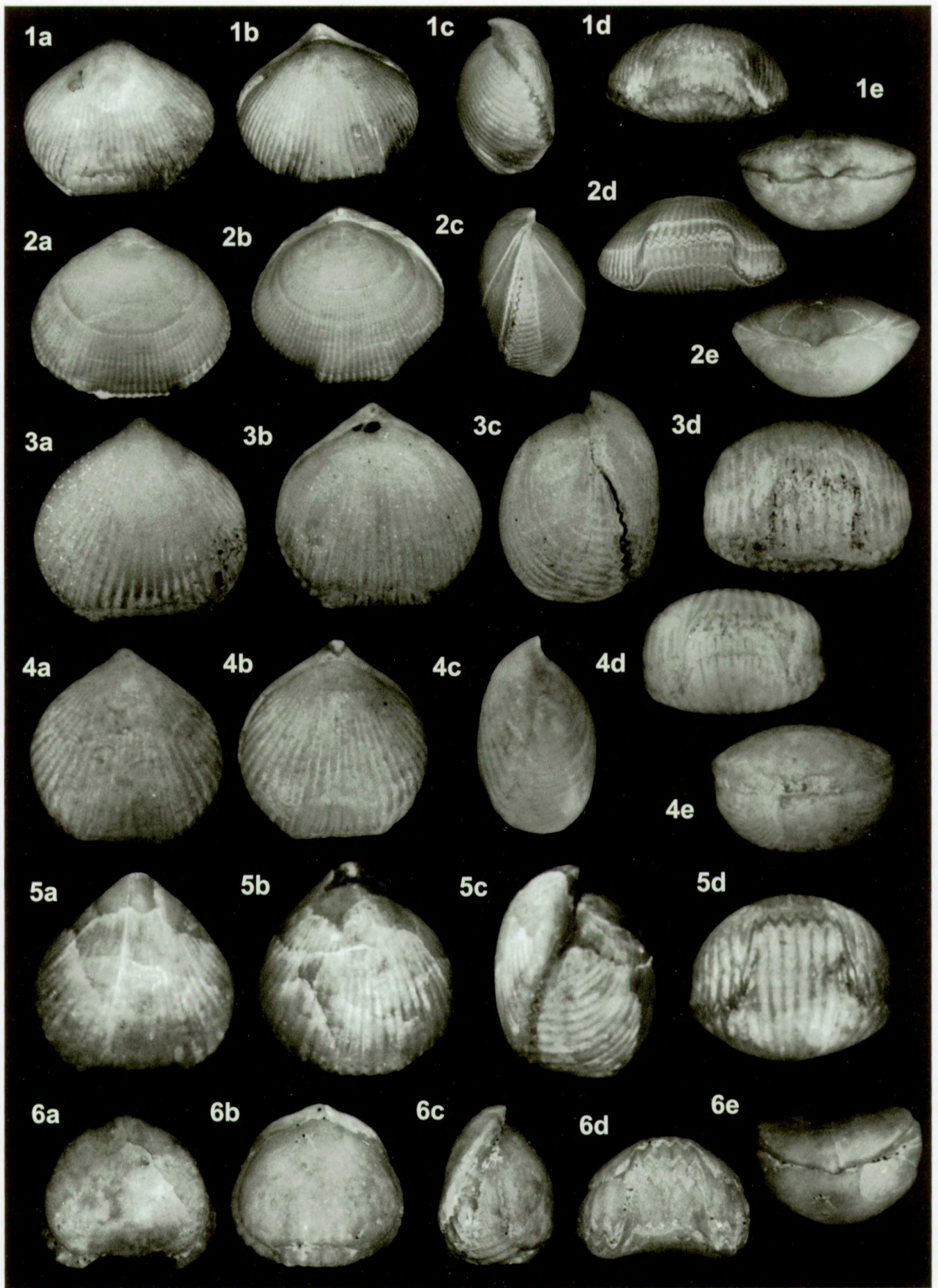


PLATE 6

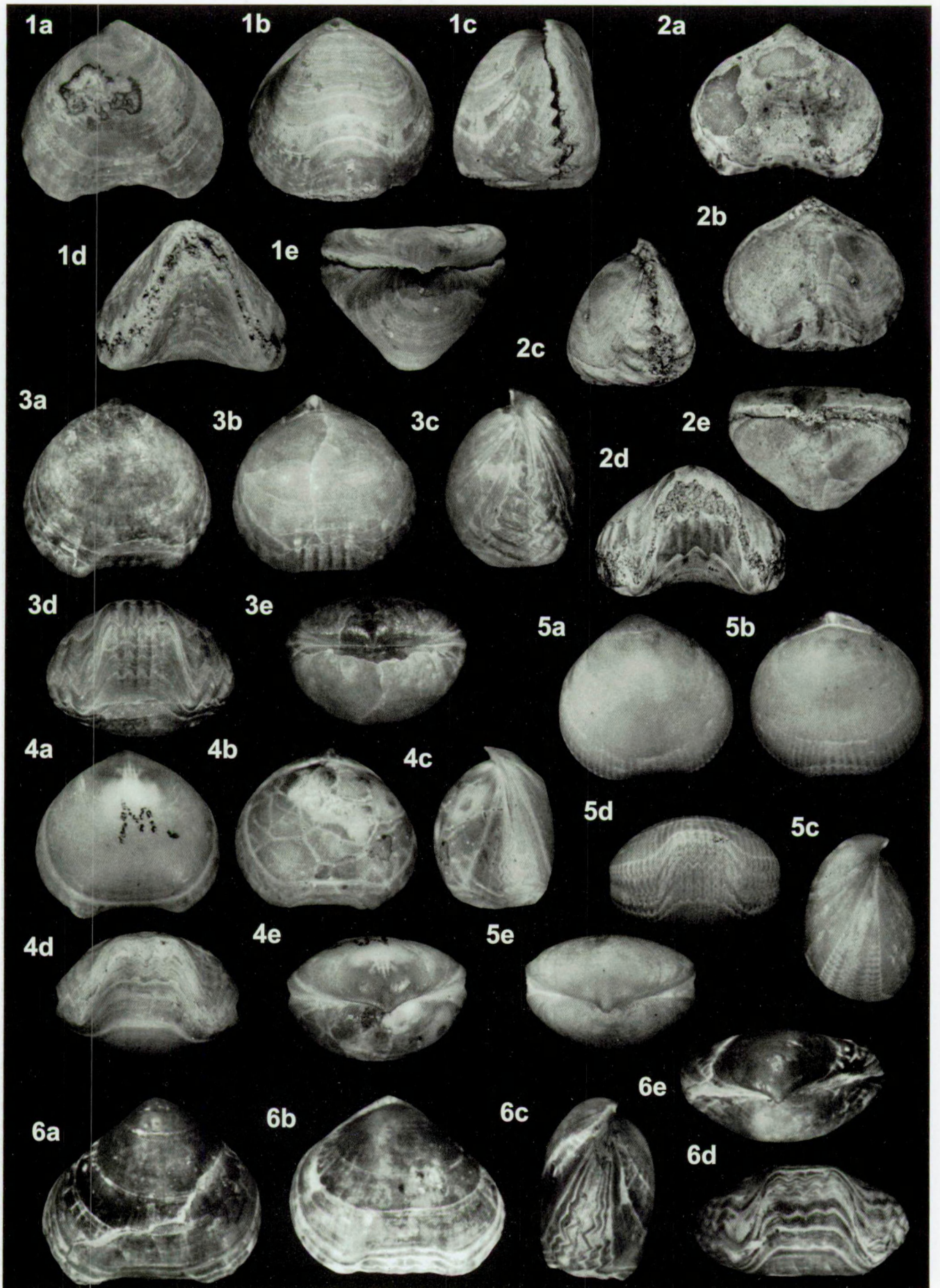


PLATE 7



PLATE 8