BULLETIN DE L'INSTITUT ROYAL DES SCIENCES NATURELLES DE BELGIQUE SCIENCES DE LA TERRE , 77: 117-129, 2007
BULLETIN VAN HET KONINKLIJK BELGISCH INSTITUUT VOOR NATUURWETENSCHAPPEN AARDWETENSCHAPPEN, 77: 117-129, 2007

Homaletarhynchia SIMON & OWEN, 2001 - a genus transferred to the Basiliolidae (Pugnacoidea, Rhynchonellida, Brachiopoda)

by Neda MOTCHUROVA-DEKOVA & Eric SIMON

MOTCHUROVA-DEKOVA, N. & SIMON, E., 2007 — *Homaletarhynchia* SIMON & OWEN, 2001 – a genus transferred to the Basiliolidae (Pugnacoidea, Rhynchonellida, Brachiopoda). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, 77: 117-129, 2 pls, 2 figs, Brussels, October 15, 2007 – ISSN 0374-6291.

Abstract

The brachiopod rhynchonellide subgenus *Cretirhynchia (Homaletarhynchia)* SIMON & OWEN, 2001 is removed from the late Cretaceous genus *Cretirhynchia* PETTITT, 1950 and elevated to a genus level. On the basis of comprehensive revision of the internal morphology of the type species *Terebratulites limbatus* VON SCHLOTHEIM, 1813 by using serial sections, excavations of the umbonal part and investigations of the shell ultrastructure, *Homaletarhynchia* is now placed in the family Basiliolidae, superfamily Pugnacoidea. For the first time in rhynchonellide taxonomy the peculiarities of the shell ultrastructure were used to distinguish the representatives of a new genus, removed from another one, in which they were originally placed by the founder of the genus, when the serial sections were not informative enough and before revealing the internal morphology in detail by excavation.

Keywords: Upper Cretaceous, Brachiopoda, Rhynchonellida, *Homaletarhynchia*, subfalciform crura, shell ultrastructure.

Résumé

Parmi les brachiopodes rhynchonellides, le sous-genre *Cretirhynchia (Homaletarhynchia)* SIMON & OWEN, 2001 est retiré du genre *Cretirhynchia* PETTITT, 1950 et est élevé au rang de genre. Une révision basée sur la morphologie interne de l'espèce type *Terebratulites limbatus* VON SCHLOTHEIM, 1813 utilisant des sections transversales sériées, l'excavation de la partie umbonale et l'étude ultrastructurale de la coquille permet de transférer *Homaletarhynchia* dans la famille des Basiliolidae au sein de la superfamille des Pugnacoidea. Pour la première fois dans la taxonomie des rhynchonellides, les particularités de l'ultrastructure de la coquille ont été utilisées pour distinguer les représentants d'un nouveau genre, lui-même extrait d'un genre plus ancien dans lequel ils étaient placés au préalable par le fondateur du genre, lorsque seules les sections sériées n'offraient pas une information suffisante. L'excavation de la coquille a contribué également à cette démarche en révélant leur morphologie interne en détail.

Mots-clefs: Crétacé Supérieur, Brachiopoda, Rhynchonellida, *Homaletarhynchia*, crura subfalciformes, ultrastructure de la coquille.

Introduction

A first step in the revision of the taxonomically problematic late Cretaceous rhynchonellide brachiopod genus *Cretirhynchia* PETTITT, 1950 was made by SIMON & OWEN in 2001. In their work they made a comprehensive critical review of all the literature dealing with *Cretirhynchia*. They discussed exhaustively the various aspects of the "*Cretirhynchia* problem": the validity of species and the lack of knowledge about the internal morphology of many species included in the content of *Cretirhynchia*. These authors published new serial sections of a total for 17 species belonging originally to *Cretirhynchia* and compared them to the serial sections of the type species *Rhynchonella plicatilis* (J. SOWERBY, 1816). As a consequence, SIMON & OWEN (2001) subdivided *Cretirhynchia* into four subgenera; some of the species were placed in the new genus *Woodwardirhynchia*, and some were removed from *Cretirhynchia* without specifying their new position. All descriptions of the internal morphologies of the discussed taxa were based on serial sections. The described new genus and four subgenera of *Cretirhynchia* were said to be all characterized by raduliform crura, typical of the superfamily Hemithiridoidea RZHONSNITSKAIA, 1956.

Later MOTCHUROVA-DEKOVA *et al.* (2007) discussed the necessity of using multiple techniques in order to reveal an objective image of the internal characters of some post-Paleozoic rhynchonellides,

including representatives of *Cretirhynchia*. They recommended that a range of methods including optical examination, low vacuum SEM and serial sections should be used whenever possible to fully describe the morphological characters of post-Paleozoic rhynchonellides. They also pointed out that there was a contrast between the working practices of Mesozoic and Cenozoic rhynchonellide workers. The former prefer serial sections, while the latter, working with more poorly consolidated matrix, prefer excavation. These different methods can yield contrasting results and a combination of both methods is preferred in order to describe and illustrate these taxa more properly. MOTCHUROVA-DEKOVA *et al.* (2007) first mentioned that subfalciform crura were exposed when investigating some representatives of the subgenus *Cretirhynchia (Homaletarhynchia)*. They illustrated the interior of the type specimen *C. (Homaletarhynchia) limbata* (MOTCHUROVA-DEKOVA *et al.*, 2007; fig. 5C), and the difference between the type species of the nominative subgenus C. *(Cretirhynchia,)* i.e. *C. (Cretirhynchia) plicatilis* (with raduliform crura), and the group of species belonging to *C. (Homaletarhynchia)* was confirmed by shell ultrastructure data.

The aim of this paper is to revise the subgenus *Cretirhynchia (Homaletarhynchia)* SIMON & OWEN, 2001 with an exhaustive study of its type species *Terebratulites limbatus* VON SCHLOTHEIM, 1813 using all possible methods: serial sectioning, SEM observations of dissected umbonal internal structures and investigations of the shell ultrastructure.

Abbreviations used: IRScNB – Institut royal des Sciences naturelles de Belgique, Brussels; NMNHS – National Museum of Natural History, Sofia; BMNH – Natural History Museum, London; L – length of the specimen.

Material and methods

Specimens to be macro-photographed were coated with ammonium chloride. Serial sections were produced by the method summarised by AGER (1965, pp. 212-218) at a distance of 0.1 mm, subsequently acetate peels were prepared following STERNBERG & BELDING's method (1942). Specimens chosen for excavation were manually opened and prepared using steel needle and fine brush. Cross sections at the mid shell length for investigation of shell ultrastructure were polished and etched in 5 % HCl for 20-30 seconds. Both dissected specimens and the samples for ultrastructure were mounted on stubs then coated in gold palladium and imaged using a JEOL JSM-6335 F field emission SEM. The shell thickness and fibres of the secondary layer were measured close to the symmetry plane.

Taxonomy

Phylum Brachiopoda DUMÉRIL, 1806
Subphylum Rhynchonelliformea WILLIAMS, CARLSON, BRUNTON, HOLMER & POPOV, 1996
Class Rhynchonellata WILLIAMS, CARLSON, BRUNTON, HOLMER & POPOV, 1996
Order Rhynchonellida KUHN, 1949
Superfamily Pugnacoidea RZHONSNISKAIA, 1956
Family Basiliolidae COOPER, 1959
Subfamily Aphelesiinae, COOPER, 1959

Genus *Homaletarhynchia* SIMON & OWEN, 2001
[Name transferred herein, *ex Cretirhynchia (Homaletarhynchia)* SIMON & OWEN, 2001]

Diagnosis
Subpentagonal to subcircular, dorsibiconvex, symmetrical, medium sized to small rhynchonellides; uniplicate, smooth (or very finely striate) with faint or incipient rounded costae developed only in the anterior half. Squama and glotta not developed. Hypothyrid, umbo short, erect to suberect, foramen small, deltidial plates conjunct, beak ridges distinct, interarea narrow. Umbonal part thickened. Convergent to medially convex short dental plates, disappearing before the full development of the crura. Strong subquadrate teeth. Euseptoidum well expressed in the dorsal valve. Inner socket ridges expanding anteriorly. In juvenile and young individuals crura attached directly to the inner socket ridges. Adults develop swollen inner hinge plates. Crura subfalciform, not curved longitudinally, distally serrate, short, widening anteriorly as a shovel. Peculiar crater-like negative attachment area developed in the tip of the dorsal umbo.

Shell ultrastructure
Shell built of two calcite layers primary microgranular and secondary fibrous. The fibrous layer is differentiated (not homogeneous), composed of alternating sublayers of two types of fibres: coarser and finer. Rhomboidal to subquadrate in cross-section coarser fibers prevail. Anisometric anvil-like (=halberd-like) finer fibers are in subordinated quantity, often developed only close to the primary layer.

Type species
Terebratulites limbatus VON SCHLOTHEIM, 1813

Other species likely included
The list of species which should be included in *Homaletarhynchia* will be later discussed elsewhere. This list will be based on close similarity in external morphology and peculiarities of their serial sections which also suggest subfalciform crura, previously misidentified as raduliform. Thus all former representatives of the ex subgenus *Cretirhyncha (Homaletarhynchia)* should be considered. Morphology of the excavated crura and shell ultrastructure will be studied. Here only the type species of *Homaletarhyncha* is discussed.

Stratigraphical range
Coniacian? – Maastrichtian.

Geographical distribution
Northern and Central Europe, The Ukraine, Southernmost Russia, Caspian depression, the plateaux between Caspian and Aral seas and SW Turkmenistan.

Remarks
The type of the crura is one of the most important characters defining the superfamilies in the revised classification of the order Rhynchonellida KUHN, 1949, adopted in the Treatise on Invertebrate Paleontology, part H (Revised), volume 4 by SAVAGE *et al.* (2002) and in some precursor works (MANCEÑIDO & OWEN, 1996; MANCEÑIDO, 2000; MANCEÑIDO & OWEN, 2001).

Thanks mainly to our detailed observations of dissected cardinalia of *H. limbata* using SEM, which allows higher magnifications and deeper focus, compared to the normal light microscope, some details not clear when analyzing the serial sections were easily revealed. The 3-dimentional images of the hinge and the crura revealed that previous authors had misidentified the type of the crura relying only on serial sections. The crura in *Homaletarhynchia* turned out to be clearly subfalciform.

Homaletarhynchia SIMON & OWEN, 2001 was a subgenus proposed subordinated to the genus *Cretirhynchia* with *C. (H.) limbata* designated as its type species and several other referred species which all present typical external and internal morphocharacters in common. During our study we discovered that in the type species and in some other species included in this subgenus the crura morphology was in fact subfalciform and not raduliform *sensu lato* as previously presumed. For this reason the diagnosis of the subgenus is here corrected, accordingly.

As the kind of the crura determines the placement of this material at a rank above the family level, the whole subgenus must be transferred to another family and superfamily. Therefore, *Homaletarhynchia* should be also elevated in rank and becomes a genus. As a consequence, this correction requires relocation of the whole genus in the Basiliolidae (superfamily Pugnacoidea). These modifications should not affect the priority rights of the name in consideration, which are guaranteed by the Principle of Coordination (see Art. 43 of ICZN, 1999). Thus the name, the spelling of the name, the composition of the list of species originally involved in the former subgenus and the authors are not changed.

Homaletarhynchia limbata is now accommodated in the family Basiliolidae, subfamily Aphelesiinae because of the presence of well developed euseptoidum in the dorsal valve and because of the relative reduction of the hinge plates compared to representatives of the other possible subfamily Basiliolinae COOPER, 1959, which usually develop broad outer hinge plates.

By the presence of the crater-like attachment area in the dorsal umbo (unfortunately not visible in serial sections) *Homaletarhynchia* differs from all known smooth rhynchonellide genera with falciform and subfalciform crura. Externally *Homaletarhynchia* is similar to *Aphelesia* COOPER, 1959 and *Phapsirhynchia* PAJAUD, 1976. The last two genera are tentatively regarded distinct in the new Treatise (MANCEÑIDO & OWEN, 2002). However LLOMPART & CALZADA (1982) and later GAETANI & SACCÀ (1985) consider *Phapsirhynchia* a junior subjective synonym of *Aphelesia.* Like *Homaletarhynchia, Aphelesia* has also a thickened umbonal part, but its crura are wider and slightly bending ventrally, it does not develop inner hinge plates, has less convergent and thinner dental plates. *Phapsirhynchia* is larger in size, has ventrally deflected larger subfalciform crura and no inner hinge plates. The recently described basiliolid genus *Basiliocostella* DULAI, BITNER & MÜLLER, 2007 (DULAI *et al.*, 2007) has subfalciform crura and similarly convergent and medially convex dental plates, but the dental plates are longer and thinner and externally the shell is fully costate.

Homaletarhynchia limbata
(VON SCHLOTHEIM, 1813)
Text-Figs 1, 2; Pls 1, 2

1803?[for 1799] — *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 — *Terebratula 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. – PUGGARD, p. 16.
1856 — *Rhynchonella limbata* V. SCH. sp. – BOLL, p. 47.
1860 — *Rhynchonella limbata* V. SCH. sp. – BOSQUET, p. 392, Nr. 585.
1866 — *Rhynchonella subplicata* D'ORB. – CORNET & BRIART, pp. 150, 189 (= *H. limbata*).
1868 — *Rhynchonella limbata*, SCHL. sp. – BOSQUET, p. 19.
1870 — *Rhynchonella subplicata* D'ORB. – CORNET & BRIART, pp. 8, 9 (=*H. limbata*).
pp 1871 — *Terebratula octoplicata subplicata* – QUENSTEDT, p. 169, pl. 41, figs 59, 63 (*non* fig. 58, 60-62 = *C. retracta*, non fig. 64).
.*v* 1879 — *Rhynchonella limbata* V. SCHLOTH. sp. – VON HANSTEIN, p. 37.
1888 — *Rhynchonella limbata* SCHL. – GEINITZ, F.E., p. 742.
.*v* 1894 — *Rhynchonella limbata* SCHLOTHEIM – POSSELT, p. 27, pl. 2, fig. 16.
pp 1895 — *Rhynchonella octoplicata* SOW. – DEECKE, pp. 73-74 (cit. in STEINICH, 1965, p. 24)
pp v 1909 — *Rhynchonella limbata* SCHLATHEIM (Sic) – NIELSEN, p. 157, Nr. 17, pl. 1, fig. 26, (*non* figs 24-25).
.*v* 1938 — *Rhynchonella limbata* SCHLOT. – POŻARYSKI, p. 20.
.*v* 1950-54 — *Cretirhynchia limbata* (SCHLOTHEIM, 1813) – PETTITT, p. 27, pl. 1, fig. 1a-c, pl. 2, fig. 12, text-figs 7a-c, 8, 9.
1961 — *Cretirhynchia limbata* (SCHLOT) – KOVALEVA, pp. 66, 70.
.1965 — *Cretirhynchia limbata* (SCHLOTHEIM, 1813) – STEINICH, p. 24, pl. 2, fig. 4a-d, text-fig. 13.
?1965 — *Cretirhynchia limbata limbata* (SCHLOTH.) – MAKRIDIN & KATZ, pp. 4-6.
.1966 — *Cretirhynchia limbata limbata* (SCHLOTH.) – MAKRIDIN & KATZ, p. 101, pl. 1, fig. 6.
?1972 — *Cretirhynchia limbata* (SCHLOTHEIM) – SURLYK, p. 24, text-fig. 5.
?1974 — *Cretirhynchia limbata* – PAJAUD, p. 25.
non 1974 — *Cretirhynchia limbata limbata* (SCHLOTHEIM) – KATZ, p. 251, pl. 83, fig. 11.
non 1982 — *Cretirhynchia limbata* (SCHLOTHEIM, 1813) – NEKHRIKOVA, p. 39, pl. 3, figs 12-25.
non v 1984 — *Cretirhynchia limbata* (SCHLOTHEIM, 1813) – POPIEL-BARCZYK, p. 384, pl. 151, figs 5, 6.
non v 1988 — *Cretirhynchia limbata* (SCHLOTHEIM, 1813) – POPIEL-BARCZYK, pp. 6-8, text-figs 3-4, pl. 1, figs 1-6.
.*v* 1988 — *Cretirhynchia subplicata* (MANTELL) – POPIEL-BARCZYK, text-fig. 9.
?1990 — *Cretirhynchia limbata* (SCHLOTHEIM, 1813) – JOHANSEN & SURLYK, p. 838, pl. 2, figs 3-5.
pp 1992 — *Cretirhynchia limbata* (SCHLOTHEIM, 1813) – POPIEL-BARCZYK, pp. 14-15
.*v* 1993 — *Cretirhynchia limbata* (SCHLOTHEIM, 1813) – SIMON, p. 83, text-fig. 8; pl. 3, figs 4a-e, 5a-b; pl. 4, fig. 1a-e.
non 1997 — *Cretirhynchia limbata* (SCHLOTHEIM, 1813) – TITOVA, p. 162, pl. 66, fig. 10.
.*v* 1998 — *Cretirhynchia limbata* (SCHLOTHEIM, 1813) – SIMON, pp. 183-185, 195, text figs 2, 3.
.*v* 2001 — *Cretirhynchia (Homaletarhynchia) limbata* (VON SCHLOTHEIM, 1813) – SIMON & OWEN, p. 91-95, 99, 101; text-fig. 19, pl. 7 figs 1a-e, 2a-e.
non 2002 — *Cretirhynchia (Homaletarhynchia) limbata* (SCHLOTHEIM, 1813) – GASPARD, p. 578, fig. 1:5.
? 2002 — *Cretirhynchia (Homaletarhynchia) limbata* (SCHLOTHEIM, 1813) – GASPARD, p. 578, fig. 1:6
.*v* 2005 — *Cretirhynchia (Homaletarhynchia) limbata* (VON SCHLOTHEIM, 1813) – SIMON, p. 136.
.*v* 2007 — *Cretirhynchia (Homaletarhynchia) limbata* (VON SCHLOTHEIM, 1813) – MOTCHUROVA-DEKOVA *et al.*, figs 4C, 5C.

Stratigraphical range
Uppermost Campanian? to base of the Upper Maastrichtian.

Geographical distribution
Northern and Central Europe, southern part of the Ukraine up to the Caspian depression.

Type specimen
Since the original specimen of FAUJAS DE SAINT-FOND (1803?, pl. 26, fig. 4), collected from the Maastrichtian of "Montagne Saint Pierre" was not traced, PETTITT (1950, pl. 1, figs 1a-c) has chosen and illustrated a specimen from another quite remote locality - the Grey Beds of the Upper Chalk (*Lunata* zone) of Trimingham, Norfolk, England. This specimen is housed in BMNH under the reference B 52745. PETTITT (1954, p. 27) erroneously listed the specimen, chosen by him, under the subheading *holotype* (see Article 73.1.3 of ICZN 1999). In fact his figured specimen could be named a *neotype*. However, it does not even fulfil all qualifying conditions of Article 75.3 to be a neotype, especially because it comes from Norfolk, England which is in contradiction with Art. 75.3.6. Thus the situation with the stability of the type specimen of *Homaletarhynchia limbata* is problematic. A further study could possibly help in designating a correct neotype for this species.

Material
All material discussed by SIMON & OWEN (2001,

p. 93); new specimens from Lower Maastrichtian, Ciply-Malogne Phosphatic Chalk Formation (CIP), Phosphatic Chalk of Ciply, *B. obtusa* Zone, Ciply: material housed in IRScNB (registration numbers IRScNB MI-11043, MI-11044, MI-11050 and specimens housed in NMNHS (NMNHS 31299-313003, which were excavated and NMNHS 313004,5, which were sectioned for shell ultrastructure).

External morphology

Medium-sized rhynchonellide brachiopod about 12 mm long, 15 mm wide and 7 mm thick, transversely oval in outline, flatly dome-shaped in anterior contour and depressed cuneiform in lateral profile. Dorsibiconvex, maximum convexity of the dorsal valve in the anterior half. Dorsal valve with sharp, elevated median fold. Ventral valve much less convex with its main convexity in its posterior part. The ventral valve has a deep, narrow rounded sinus and the antero-lateral parts of this valve surface are very flat. The beak is delicate, sharply pointed and slightly curved, when observed in lateral profile. Small hypothyrid foramen, deltidial plates conjunct, often auriculate. Shell surface nearly smooth but presenting under magnification numerous, regular, faint and extremely narrow, radial grooves. A few short subrounded costae are developed near the anterior commissure.

Internal morphology

The serial sections available in the literature were analyzed. A new set of serial sections was made (Text-Figure 1). Five additional specimens from Ciply were opened and the umbonal part excavated (Plate 2). The thick convergent, often medially deflected, dental plates are short and disappear before the full development of the crura. Very shallow umbonal chambers. Teeth strong, subquadrate. No pedicle collar observed. The better preserved adult specimen revealed perfectly shaped subfalciform crura (Plate 2, Fig. 1a-d). They slightly diverge and widen anteriorly as a shovel, but do not bend towards the ventral valve. Their edges are serrated and encrusted with secondary calcite. Serration is perceptible on some previously published serial section too (see POPIEL-BARCZYK, 1988, text-fig. 9). The crural bases are not clearly perceptible on the well preserved dissected specimen, illustrated here (Plate 2, Fig. 1a-d). They could be better observed on another specimen with broken crura (Plate 2, Fig. 3). They are clearly crescent like, but obsolete by additional material. In serial section the crural bases are often indistinct from the thickening material. Here we illustrate a detail of a serial section just before the full appearance of the crus (Text-Figure 2). The subfalciform condition in serial sections is best observed in STEINICH (1965, p. 25, text-fig. 13). Robust inner socket ridges expand anteriorly. The hinge plates are very much reduced. In younger individuals (Plate 2, Fig. 2a, b) inner hinge plates are not developed. In adult specimens slight but swollen inner hinge plates are developed (Plate 2, Figs 1a,b, 3). Euseptoidum well expressed. Only in adult specimens a peculiar negative crater like muscle attachment area is developed in the tip of the dorsal umbo when the hinge plates meet (Plate 2, Figs 1e, 3).

Shell ultrastructure

The peculiarities of the ultrastructure will be discussed briefly here; they will be the subject of another paper dealing with all the former *Cretirhynchia* species. Two cross sections at the mid shell length were studied. The impunctate shell is about 300 - 400 μm thick. Posteriorly the shell becomes much thicker. Two calcite layers were observed - primary and secondary fibrous (WILLIAMS, 1997). The primary layer is about 20 μm thick, recrystallised (Pl. 1, Fig. 3a). Here we use the terminology of KAMYSHAN (1977, 1986), who distinguished two types of fibrous ultrastructures of the secondary layer in rhynchonellides: *fine fibrous rhynchonellidine type* and *coarse fibrous basiliolidine type*. The secondary fibrous layer is differentiated (not homogeneous), composed of alternating sublayers of two types of fibres. Anisometric anvil-like (=halberd-like) *rhynchonellidine type* fibres are developed close to the primary layer; they are 5 to 12 μm thick and 30 to 40 μm wide. More isometric rhomboidal *basiliolidine type* fibres prevail (Pl. 1, Fig. 3a, b) towards the interior of the shell. They are 10-23 μm thick and 30 to 45 μm wide. At some spots laterally a second thin sublayer of anisometric anvil like fibres appear.

Remarks

The external variability of this species, its distinct morphocharacters, and the comparison with other species, its functional morphology and possible way of life were exhaustively commented in previous papers (STEINICH, 1965; SIMON, 1993, 1998, SIMON & OWEN, 2001).

The fact that the type of the crura in *Cretirhynchia limbata* was not previously recognised in serial section is a bit puzzling. One explanation could be that usually the specimens were not burned before sectioning, as recommended in BUCKMAN (1918), a method that often helps, but sometimes results in

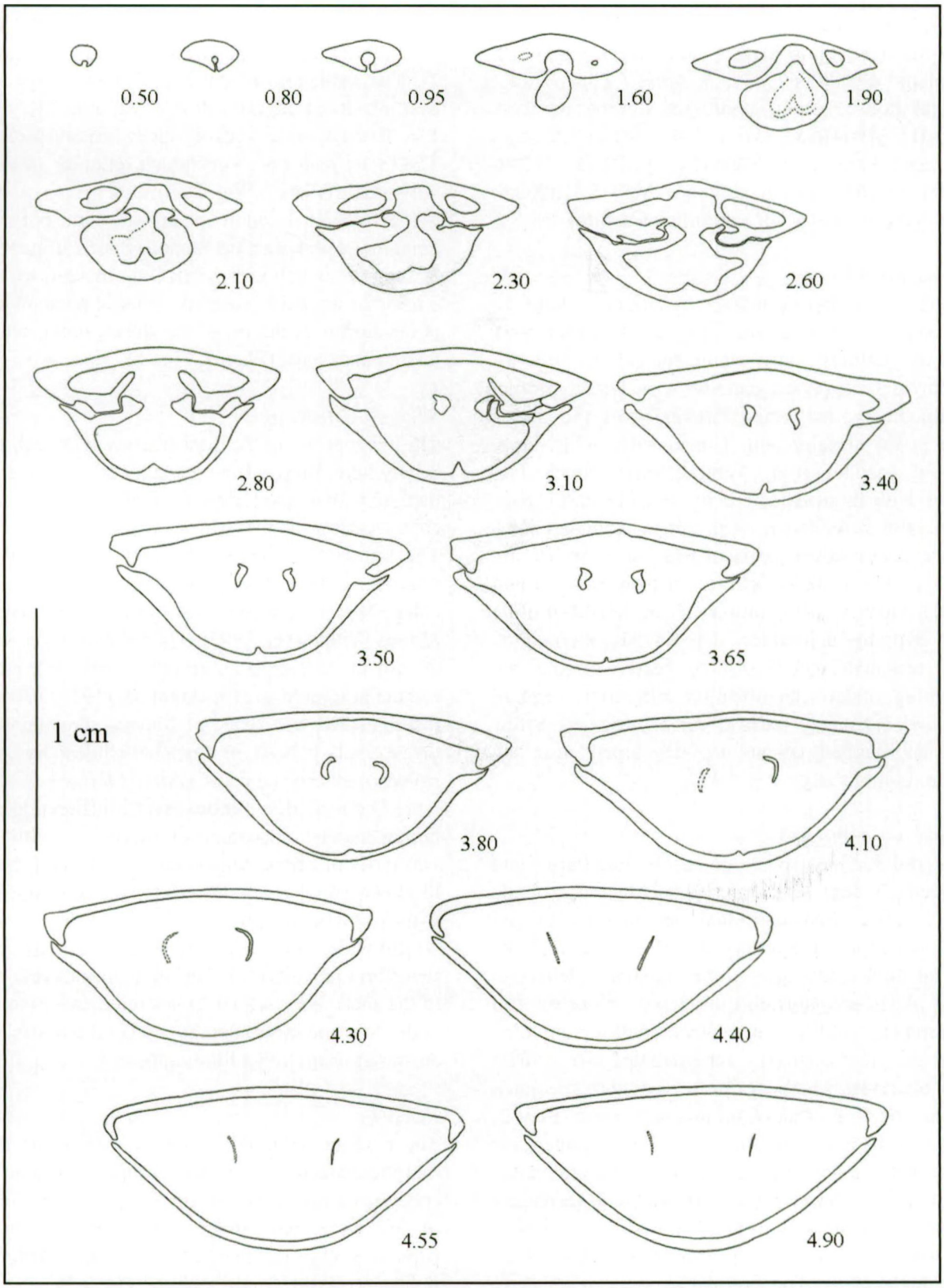


Fig. 1 — Nineteen selected transverse serial sections through the umbonal portion of an adult specimen (IRScNB MI-11050) of *Homaletarhynchia limbata* (VON SCHLOTHEIM, 1813), from the phosphatic chalk of Ciply, Lower Maastrichtian, Ciply-Malogne-Phosphatic Chalk Formation, *Belemnella obtusa* Zone. Van Damme quarry in Ciply, Mons basin, Province of Hainaut, Belgium (x 4.1). Scale bar = 1 cm. Distance from the tip of ventral umbo of each section given in mm. Drawings from peels.

Note: The authors prefer to use the traditional way of presenting the serial sections with the ventral valve up in order to compare more effectively and in detail with most of the originally published serial sections of the genera *Cretirhynchia*, *Homaletarhynchia* and other post-Palaeozoic rhynchonellides.

crushing of the specimen. So the calcite of the crura sometimes diagenetically amalgamates with the carbonate infilling of the shell and if recrystallised it is difficult to differentiate between the structural elements and the matrix.

Conclusions

This research could be regarded as a second revision work on the taxonomically problematic genus *Cretirhynchia* PETTITT, after the work of SIMON & OWEN (2001). However, it is the first case-study following the recommendations of MOTCHUROVA-DEKOVA *et al.* (2007) to combine all possible methods to investigate the internal morphology of post-Palaeozoic rhynchonellides. Our study is the first based on peculiarities of shell ultrastructure for distinguishing representatives of *Homaletarhynchia*, from typical specimens of the genus *Cretirhynchia sensu stricto*. The shell ultrastructure of the remnant of the sectioned and figured by PETTITT (1950, text-fig. 4, p. 11) topotype specimen of *Cretirhynchia plicatilis* (J. SOWERBY, 1816) was first examined (see MOTCHUROVA-DEKOVA *et. al.*, 2007, fig. 4A). It revealed a secondary layer of monotonously arranged anvil-like anisometric fibres. Its ultrastructure was determined as typically *fine-fibrous rhynchonellidine type*. Later we studied sections of *C. limbata* and some other representatives of the subgenus *C. (Homaletarhynchia)*. We discovered that in cross section about the mid shell length they have quite different ultrastructure displaying prevailing quantity of more isometric and larger rhomboidal fibres of *basiliolidine type*. Only later as a second step in our study we tried excavating and examining directly the 3-dimensional morphology of the cardinalia of *C. (Homaletarhynchia) limbata*. After successful excavation of some specimens from Ciply our hypothesis that *C. (Homaletarhynchia) limbata* belongs to another genus, quite distinct from the true *Cretirhynchia* was confirmed. Compared to the true *Cretirhynchia,* characterised by raduliform crura (see MOTCHUROVA-DEKOVA *et al.*, 2007, figs 2B-D, 3A, C), *Cretirhynchia (Homaletarhynchia) limbata* revealed totally different type of crura – subfalciform, which should place it in another superfamily. Thus for the first time in rhynchonellide taxonomy, the shell ultrastructure was used as a first chronologic method to distinguish representatives of a new genus removed from another one, in which they were previously placed by the founder of the genus.

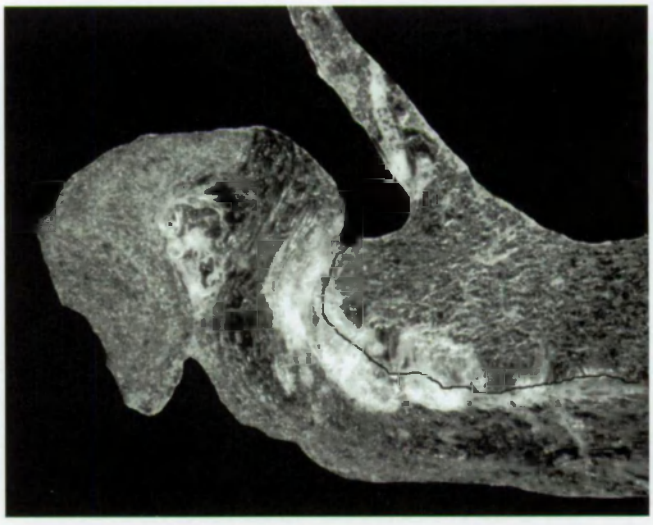


Fig. 2 — The same specimen presented on Figure 1. Photograph of a peel. Magnified detail of the tenth transverse serial section at 3.1 mm from the umbo. Note the crescent-like crural base, shallow and wide socket ridge and robust tooth.

Determining properly the type of the crura at the present state of knowledge has permitted us to place *Homaletarhynchia* in Pugnacoidea, family Basiliolidae.

The precision of the taxonomic work is the key stone of all subsequent interpretations in biostratigraphy, paleobiogeography and evolutional theory. Our work on a single species *Homaletarhynchia limbata*, widely cited and often confused in the literature since two centuries, has shown that much care is needed in order to properly describe a taxon, for subsequently being able to compare it with occurrences of similar material in other areas and finally drawing conclusions about its value in biostratigraphy and paleobiogeography. When examining different sized specimens it appeared that some elements as inner hinge plates and the crater like negative attachment scar appear in adult specimens, while in young individuals they are not developed. Thus much care is needed when describing scarce material, especially juveniles or only adult forms. Not taking into account the ontogenetic changes may lead to wrong taxonomical decisions.

It could be suggested that the Late Cretaceous *Homaletarhychia* was a possible forerunner of the Eocene to Pliocene *Aphelesia* and *Phapsirhynchia.*

In the Maastrichtian different representatives of the genus *Homaletarhynchia* inhabited the epicontinental seas along the northern margin of the

Tethys Ocean. To our knowledge, the distribution of type species - the true *Homaletarhynchia limbata sensu stricto* - is restricted to the Lower and base of Upper Maastrichtian in western European area. While in the Late Maastrichtian some larger forms, determined as subspecies by MAKRIDIN & KATZ (1965, 1966) have inhabited more eastern parts of the northern margin of the Tethys Ocean. The available data show that representatives of *Homaletarhynchia* did not survive the Cretaceous/Paleogene boundary. The Paleocene time gap of lack of Aphelesiines is still not filled and possible intermediate forms should be searched there. The reasons and mechanism of migration of the representatives of Aphelesiinae from the Central-North European epicontinental seas to the Mediterranean region should also be established in future studies.

Acknowledgments

This work was inspired and preliminary laboratory work was done during a visit of N. Motchurova-Dekova in BMNH, London in 2001, supported by a Sys-Resource grant. E.F. Owen and S. Long (BMNH) have encouraged this revision. S. Long participated in discussing the first results in revealing the interior of other representatives of "*Cretirhynchia*" by excavation. All SEM pictures of prepared cardinalia and shell ultrastructure were made in the Natural History Museum of Denmark, University of Copenhagen during a Synthesys visit of N. Motchurova-Dekova in 2005, grant DKTAF-939. This research was also partly supported by the Bulgarian National Science Fund - grant MU F 08/96. V. Dekov (Sofia) is thanked for excavating the interior and preparing the crura of the studied material. This is a contribution to the project "Revision of the genus *Cretirhynchia*" (IRScNB, Brussels). The authors are no end grateful for the scrupulous reviews of M. Manceñido (La Plata, Natural Sciences Museum) and E.F. Owen (London, BMNH) which helped to improve the first version of this paper.

References

AGER D.V., 1965. Serial grinding techniques. *In*: B. KUMMEL & D.M. RAUP (eds). Handbook of Paleontological techniques. Freeman and Co., San Francisco, London, pp. 212-224.

BOLL, E., 1846. Geognosie der deutschen Ostseeländer zwischen Eider und Oder. Neubrandenburg, 284 pp.

BOLL, E., 1856. Die Brachiopoden der Kreideformation in Mecklenburg. *Archiv des Vereins der Freunde der naturgeschichte Mecklenburg*, **10**: 29-48.

BOSQUET, J., 1860. Versteeningen uit het Limburgsche Krijt. *In:* W.C.H. STARING (ed.). De Bodem van Nederland. De zamenstelling en het ontstaan der gronden in Nederland ten behoeve van het algemeen beschreven. Tweede deel, A.C. Kruseman, Haarlem. pp. 361-418.

BOSQUET, J., 1868. Liste des fossiles du massif crétacé du Limbourg. *In*: G. DEWALQUE. Prodrome d'une description géologique de la Belgique. J.-G. Carmanne (Ed.), Liège, 1-35.

BRONN, H.G., 1848. *Lethaea geognostica*, oder Übersicht der bis jetzt bekannten Fossilen Organismen. Erste Abtheilung, E. Schweizerbart'sche Verlags, Stuttgart, 1381 pp.

BUCKMAN, S.S. 1918. The Brachiopoda of the Namyau Beds, Northern Shan States, Burma. *Memoirs of the Geological Survey of India, Palaeontologia Indica*, New Series **3** (2): 1-299.

COOPER, G.A. 1959. Genera of Tertiary and Recent rhynchonelloid brachiopods. *Smithsonian Miscellaneous Collection*, **139**: 1-90.

CORNET, F.L. & BRIART, A., 1866. Description minéralogique, paléontologique et géologique du Terrain Crétacé de la Province du Hainaut. Dequesne-Masquillier, Mons, 199 pp.

CORNET, F.L. & BRIART, A., 1870. Sur la Division de l'étage de la Craie Blanche du Hainaut en quatre Assises. *Mémoires Couronnés et Mémoires des Savants Etrangers de l'Académie royale de Belgique*, **35**: 1-26.

DEECKE, W., 1895. Die mesozoischen Formationen der Provinz Pommern. *Mitteilungen des naturwissenschaftlichen Vereins für Neu-Forpommern und Rügen in Greifswald*, **26**: 1-115.

DULAI, A., BITNER, M.A. & MÜLLER, P., 2007 (in press). A monospecific assemblage of a new rhynchonellide brachiopod from the Paleocene of Austria. *Fossils and Strata. Proceedings of the 5th International Brachiopod Conference*, Copenhagen 2005, **54**.

DUMÉRIL, A.M.C., 1806. Zoologie analytique ou méthode naturelle de classification des animaux. Allais, Paris, xxiv + 344 pp.

FAUJAS DE SAINT-FOND, B., 1803(?) [for 1799]. Histoire naturelle de la Montagne de Saint-Pierre de Maëstricht. H.J. Jansen, Paris, 263 pp., 54 pls.

GAETANI, M. & SACCÀ, D., 1985. Il genere *Aphelesia* (Rhynchonellida, Brachiopoda) nel Mio-Pliocene Italiano. *Rivista Italiana di Paleontologia e Stratigrafia*, **91** (3): 357-378.

GASPARD, D., 2002. Les Brachiopodes de la craie blanche de Meudon (Campanien supérieur) de la collection d'Orbigny (NMNH, Paris). *C. R. Palevol*, **1**: 573-585.

GEINITZ, F.E., 1888. Die Kreidegeschiebe des mecklenburgischen Diluviums. Zeitschrift der deutschen Geologischen Geselschaft, **40**: 720-749.

HAGENOW, F. VON, 1842. Monographie der Rügen'schen Kreide-Versteinerungen, III. Abtheilung: Mollusken. *Neues Jahrbuch für Mineralogie, Geognosie, Geologie und Petrefactenkunde*, **5**: 528-575.

HANSTEIN, R. VON, 1879. Die Brachiopoden der oberen Kreide von Ciply. Inaugural-Dissertation zur Erlangung der Doctorwürde bei der philosophischen Fakultät der Rheinischen Friedrich-Wilhems-Universität zu Bonn, 56 pp.

ICZN, 1999. International Code of Zoological Nomenclature. Fourth edition. The International Trust for Zoological Nomenclature, London, 306 pp.

JOHANSEN, M.B. & SURLYK, F., 1990. Brachiopods and stratigraphy of the Upper Campanian and Lower Maastrichtian chalk of Norfolk, England. *Palaeontology*, **33** (4): 823-872.

KAMYSHAN, V.P., 1977. Organizational levels of the shell substance, structure and texture of the shell of Mesozoic and Cenozoic rhynchonellides. *III-ia vsesoiuznaia konferentsia po mezozoiskim i kainozoiskim brahiopodam, Tezisy dokladov*: 21-24. [in Russian]

KAMYSHAN, V.P., 1986. On the microstructure features of the shell growth in Jurassic rhynchonellides (Brachiopoda). *Vestnik Khar'kovskogo Universiteta, seria Geologicheskaia*, **16:** 75-77. [in Russian]

KATZ YU.I., 1974. Tip Brachiopoda. *In:* G. IA. KRYMGOL'TS (ed.). Atlas verhnemelovoi fauny Donbassa, Nedra edition, Moskva, pp. 240-275. [in Russian]

KOVALEVA, N.P., 1961. New data on the specific composition of the brachiopods from the Upper Cretaceous and Lower Paleogene deposits in Mangyshlak. *Vestnik Leningradskogo Universiteta. Geologia*, **6**: 65-72. [in Russian]

KUHN, O. 1949. Lehrbuch der Paläozoologie. E. Schweizerbart'sche Verlagsbuchhandlung. Stutgart. 326 p.

LLOMPART, C. & CALZADA, S., 1982. Braquiópodos messinienses de la Isla de Menorca. *Boletin de la Real Sociedad Española de Historia Natural. (Seccion Geologica)*, **80**: 185-206.

MAKRIDIN, W.P. & KATZ, YU.I., 1965. The significance of the generalizing paleontological investigations for stratigraphy and palaeogeography. *Paleontologicheskii Zhurnal*, **3**: 3-15. [in Russian]

MAKRIDIN, W.P. & KATZ, YU.I., 1966. Some questions on the methodology of palaeogeographical research. *In:* R.F. GEKKER, (ed.). Organism i sreda v geologicheskom proshlom. Nauka edition, Moskva, pp. 98-115. [in Russian]

MANCEÑIDO, M.O., 2000. Crural types among post-Palaeozoic Rhynchonellida (Brachiopoda). *The Millennium Brachiopod Congress, London, Abstracts*: 57.

MANCEÑIDO, M.O. & OWEN, E.F. 1996. Post-Palaeozoic Rhynchonellides: an overview. *In:* P. COOPER, & J. JIN (eds). *Brachiopods.* Proceedings of the Third International Brachiopod Congress, 1995, Balkema, Rotterdam, p. 368.

MANCEÑIDO, M.O. & OWEN, E.F. 2001. Post-Palaeozoic Rhynchonellida (Brachiopoda): classification and evolutionary background. *In*: C. H. Brunton, L. R. M. Cocks & S. L. Long (eds). *Brachiopods past and present.* Systematics Association Special Volume Series **63,** pp. 189-200. Taylor and Francis, London, New York.

MANCEÑIDO, M.O. & OWEN, E.F., 2002. Family Basiliolidae COOPER, 1959. *In:* R.L. KAESLER (ed.) Treatise on Invertebrate Paleontology, Part H, Brachiopoda (revised). Volume 4, Rhynchonelliformea (part), Geological Society of America & University of Kansas Press, Boulder, Colorado & Lawrence, Kansas, pp. 1199-1214.

MOTCHUROVA-DEKOVA, N., LONG, S., SAITO, M., 2007 (in press). Unravelling taxonomy of some Post Palaeozoic rhynchonellides by using multiple techniques to investigate their internal morphology. *Fossils and Strata. Proceedings of the 5th International Brachiopod Conference*, Copenhagen 2005, **54**.

NEKHRIKOVA, N. I., 1982. Brachiopods. *In:* B. A. SOBETSKI (ed.). Atlas bespozvonochnyh pozdnemelovyh morei Prikspiiskoi vpadiny. Akademia Nauk SSSR, Trudy paleontologicheskogo instituta, Moskva, pp. 26-49. [in Russian]

NIELSEN, K.B., 1909. Brachiopoderne i Danmarks Kridtaflejringer. *Det Kongelige Danske Videnskabernes Selskab Skrifter* **7**, 6 (4): 129-178.

PAJAUD, D., 1974. Etude Paléontologique de la Thiérache et du Marlois (Nord-Est du Bassin de Paris). *Bulletin Inf. Géologie du Bassin de Paris*, **39**: 15-26.

PAJAUD, D., 1976. Les Brachiopodes du Pliocène I de la Sierra de Santa Paula (sud d'Alicante, Espagne): *Terebratula terebratula* (Linné, 1758) et *Phapsirhynchia sanctapaulensis* nov. gen., nov. sp. *Annales de la Société Géologique du Nord*, **96** (2): 99-106.

PETTITT, N.E. 1950. A Monograph on the Rhynchonellidae of the British chalk. Part 1. *Palaeontographical Society*, **103**: 1-26.

PETTITT, N.E., 1954. A Monograph on some Rhynchonellidae of the British Chalk. Part 2. *Palaeontographical Society*, **107**: 27-52.

POPIEL-BARCZYK, E. 1984. Typ Brachiopoda. *In*: L. MALINOVSKA (ed.). Budowa geologiczna Polski. III. Atlas skamienialosci, czesc 2c, Mezozoik, Kreda, pp. 342-358.

POPIEL-BARCZYK, E.. 1988. Upper Cretaceous Rhynchonellids (Brachiopoda) from the middle Vistula river valley in Poland. *Prace Museum Ziemi*, **40**: 3-21.

POPIEL-BARCZYK, E. 1992. Mesozoic and Cenozoic

Brachiopods. Catalogue of the collection. Polish Academy of Sciences, Museum of the Earth, Warszawa, 55 pp.

POSSELT, J.H., 1894. Brachiopoderne i den danske Kridtformation. *Danmarks geologiske Undersøgelse*, **6**: 1-59.

POŻARYSKI, W., 1938. Stratygrafia Senonu w przelomie wisly miedzy Rachowem i Pulawami. *Panstwowy Instytut Geologiczny*, **6**: 1-147.

PUGGARD, C., 1852. Geologie der Insel Möen. Leipzig, 116 pp.

QUENSTEDT, F.A., 1868-1871. Petrefactenkunde Deutschlands. 1. Abt., Zweiter Band, Brachiopoden, Fues's Verlag (R. Reisland), Leipzig, 748 pp + atlas (1871).

ROEMER, F.A., 1841. Die Versteinerungen des norddeutschen Kreidegebirge. Hahn'schen Hofbuchhandlung (ed.), Hannover, 145 pp.

RZHONSNISKAIA, M. A., 1956. Systematization of Rhynchonellida. *In:* E. GUZMÁN *et. al.* (eds). Resumenes de Los Trabajos Presentados. International geological congress, Mexico, Report, **20**: pp. 125-126.

SAVAGE, N.M., MANCEÑIDO, M.O., OWEN, E.F., CARLSON, S.J., GRANT, R.E., DAGYS, A.S. & DONG-LI, S. 2002: Rhynchonellida. *In:* R.L. KAESLER (ed.). Treatise on Invertebrate Paleontology, Part H, Brachiopoda (revised). Volume 4, Rhynchonelliformea (part), Geological Society of America & University of Kansas Press, Boulder, Colorado & Lawrence, Kansas, pp. 1027-1376.

SCHLOTHEIM, E.F. VON, 1813. Beiträge zur Naturgeschichte der Versteinerungen in geognostischer Hinsicht. *Leonhard's Taschenbuch für die gesammte Mineralogie*, **7** (1): 3-134.

SCHLOTHEIM, E.F. VON, 1820. Die Petrefactenkunden auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreiches der Vorwelt erläutert. Gotha, 437 pp.

SIMON, E., 1993. Possible presence of *Cretirhynchia undulata* (PUSCH, 1837) in de Vijlen Chalk (Upper Maastrichtian) from Hallembaye (Belgium). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **63**: 73-98.

SIMON, E., 1998. Maastrichtian brachiopods from Ciply: palaeoecological and stratigraphical significance. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **68**: 181-232.

SIMON, E., 2005. New Lower Maastrichtian brachiopods (Gulpen Formation, Vijlen Member) from southern Limburg (The Netherlands). *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **75**: 127-165.

SIMON, E. & OWEN, E.F. 2001. A first step in the revision of the genus *Cretirhynchia* Pettitt, 1950. *Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre*, **71**: 53-118.

SOWERBY, J. & SOWERBY, J. DE C. 1812-1846. The Mineral Conchology of Great Britain. Vol. I - VII. 803 pp, pls. 1--383 by J. Sowerby (1812-1822); 558 pp., pls. 384-648 by J. de C. Sowerby (1823-1846), London.

STEINICH, G., 1965. Die artikulaten Brachiopoden der Rügener Schreibkreide (Unter-Maastricht). *Paläontologische Abhandlungen, Abteilung A. Paläozoologie*, **2** (1): 1-220.

STERNBERG R.M. & BELDING H.F., 1942. Dry-peel technique. *Journal of Paleontology*, **16**: 135-136.

SURLYK, F., 1972. Morphological adaptations and population structures of the Danish Chalk brachiopods (Maastrichtian, Upper Cretaceous). *Det Kongelige Danske Videnskabernes Selskab, Biologiske Skrifter*, **19** (2): 1-57.

TITOVA, M. V., 1997. Brachiopods. *In:* V.B. ARKADIEV & T.N. BOGDANOVA (eds). Atlas verhnemelovoi fauny zapadnogo Kryma, Pangea, Sankt-Peterburg, pp. 156-176. [in Russian]

WILLIAMS A., 1997. Shell structure. *In*: R. L. KAESLER (ed.). Treatise on Invertebrate Paleontology. Part H. Brachiopoda, Volume 1, Geological Society of America and University of Kansas, Boulder, Colorado & Lawrence, Kansas, pp. 267-320.

WILLIAMS, A., CARLSON, S.J., BRUNTON, C.H.C., HOLMER L.E. & POPOV, L., 1996. A supra-ordinal classification of the Brachiopoda. *Philosophical Transactions of the Royal Society of London*, **B351**(4): 1171-1193.

Neda MOTCHUROVA-DEKOVA
National Museum of Natural History
1, Tsar Osvoboditel Blvd,
Sofia 1000
Bulgaria
E-mail: neda@nmnh.bas.bg;
neda_dekova@yahoo.com

Eric SIMON
Département de Paléontologie
Section des Invertébrés fossiles
Institut royal des Sciences
naturelles de Belgique
Rue Vautier, 29
B-1000 Bruxelles
Belgique
E-mail: ericsimon98brach@yahoo.fr

Typescript received: 9 October 2006
Revised typescript received: 7 May 2007

Explanation of the plates

PLATE 1

Homaletarhynchia limbata (VON SCHLOTHEIM, 1813)
Material collected from the Van Damme quarry at Ciply (Province of Hainaut, Belgium). Phosphatic chalk, Lower Maastrichtian, Ciply-Malogne-Phosphatic Chalk Formation, *Belemnella obtusa* Zone:

Figs 1-2 — Specimens housed in the Institut royal des Sciences naturelles de Belgique (IRScNB) in Brussels, Belgium. **1**. Fully adult, complete articulated specimen (IRScNB MI- 11044), L = 13.2 mm. **a**: dorsal view; **b**: ventral view, note the muricid gastropod boring; **c**: lateral view; **d**: anterior view; **e**: posterior view, **2**. Gerontic, complete articulated specimen (IRScNB MI- 11043), L = 13.8 mm. **a**: dorsal view; **b**: ventral view; **c**: lateral view; **d**: anterior view; **e**: posterior view. Note the almost flat ventral valve on Figs 1 c, e and 2 c, e.

Fig. 3 — SEM micrographs of a section of adult specimen NMNHS 31305 (sample K-18), housed in National Museum of Natural History, Sofia. **a**: dorsal valve, whole shell thickness, recrystallised primary layer above, secondary layer differentiated, composed of thinner anisometric fibres closer to the primary layer and close to the internal surface and central sublayer of more isometric rhombic fibres; silicified organic sheets in the lower part; **b**: dorsal valve, another spot, detail of the sublayer of rhombic to subquadrate fibres (below) and part of the sublayer of anisometric anvil-like fibres (above).

PLATE 2

Homaletarhynchia limbata (VON SCHLOTHEIM, 1813).
Cardinalia of opened specimens, collected from the Van Damme quarry at Ciply (Province of Hainaut, Belgium). Phosphatic chalk, Lower Maastrichtian, Ciply-Malogne-Phosphatic Chalk Formation, *Belemnella obtusa* Zone. Material housed in National Museum of Natural History, Sofia.

Fig. 1 — Complete articulated adult specimen (NMNHS 31299), L=13.5mm. Different views of prepared internal umbonal part of both valves with subfalciform crura. **a:** oblique ventro-anterior view of the crura, note the inner hinge plates; **b:** oblique ventro-lateral view of the crura; note the medially deflected dental plates; **c:** frontal view of the crura and crater-like attachment scar in the top of the dorsal umbo; **d:** frontal dorsal view of the crura; **e:** detail of **c** to show the crater-like attachment scar in the dorsal umbo.

Fig. 2 — Articulated young specimen (NMNHS 31300), L=10.1 mm. Two views of prepared internal umbonal part of both valves with subfalciform crus, the second crus broken. **a:** oblique ventro-anterior view of the young crus, note the lack of inner hinge plates; **b:** oblique ventro-lateral view of the crus.

Fig. 3 — Articulated gerontic specimen (NMNHS 31302), L=14,0 mm. Almost frontal anterior view of prepared internal umbonal part of both valves with crura broken, but with clearly seen crescent shaped crural bases, thickened inner socket ridges, swollen inner hinge plates, crater-like attachment scar in the dorsal umbo and foramen in the ventral umbo.

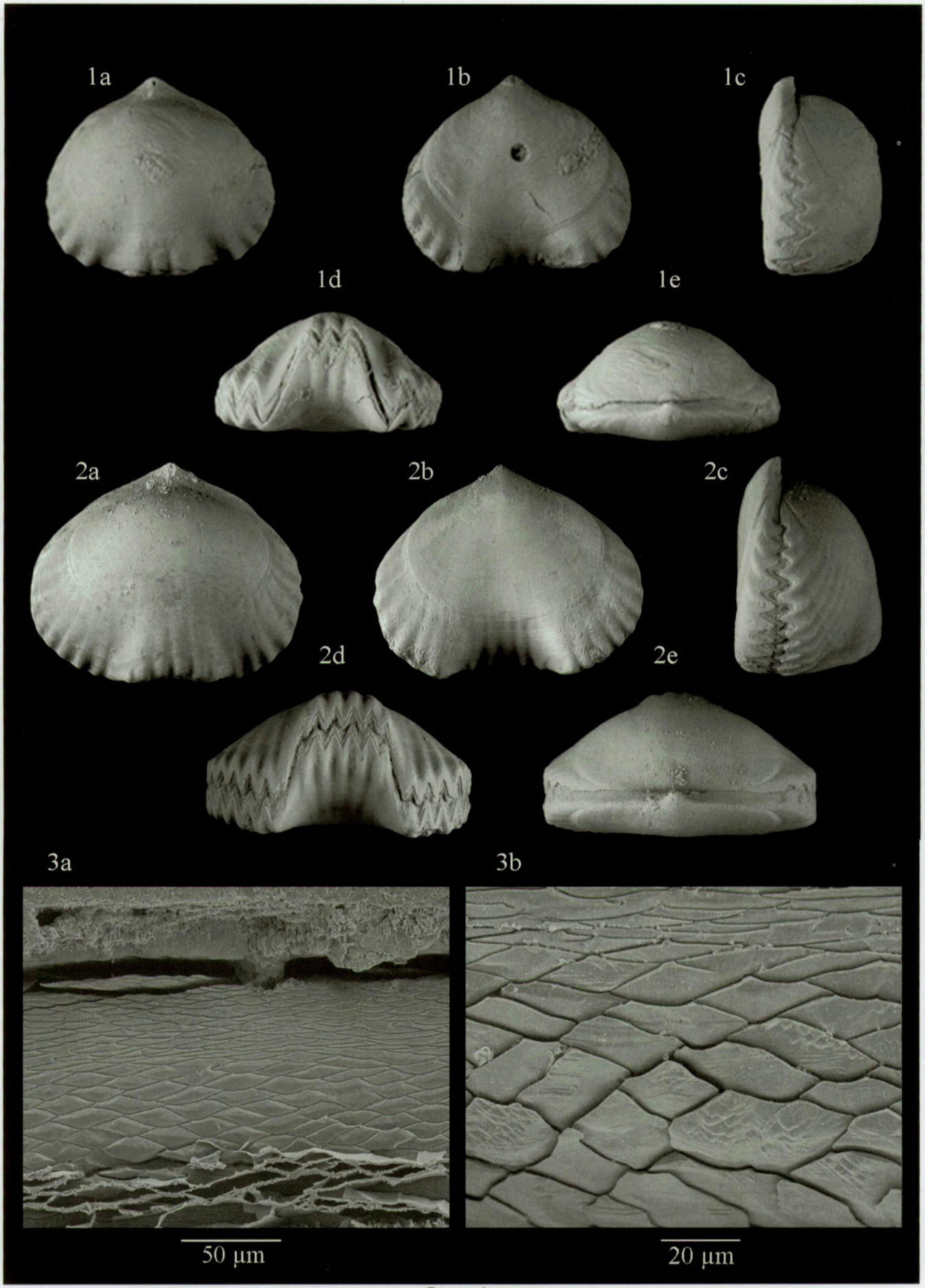
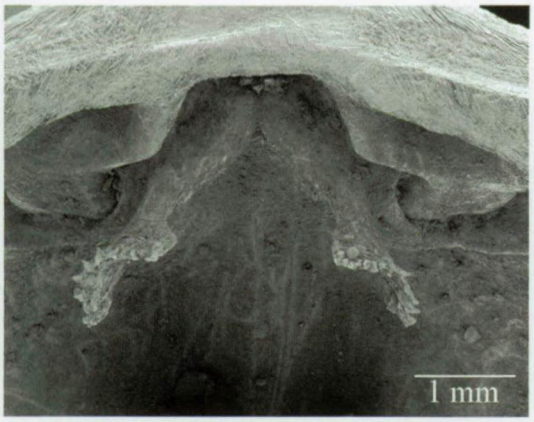
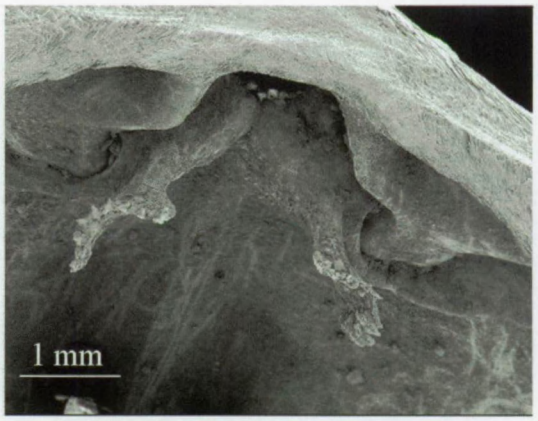


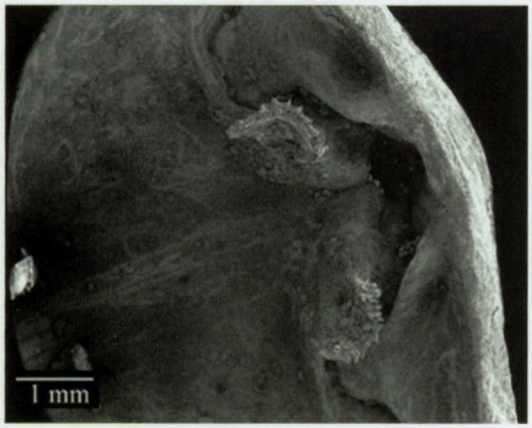
PLATE 1



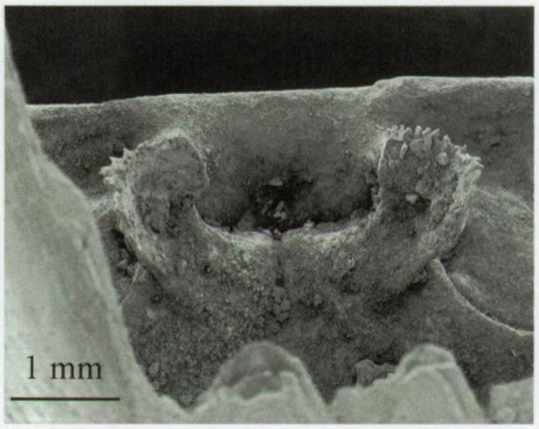
1a



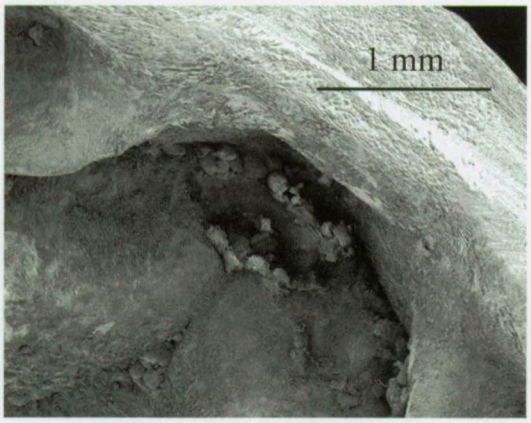
1b



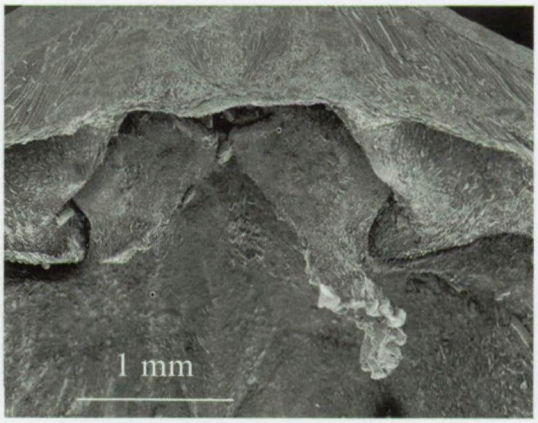
1c



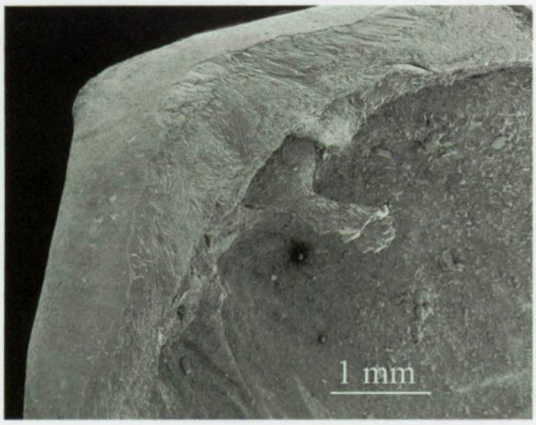
1d



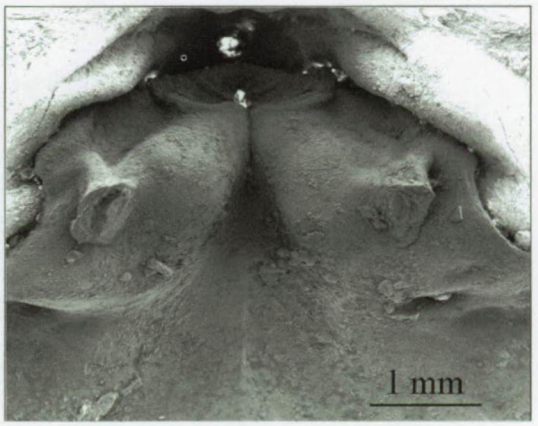
1e



2a



2b



3

PLATE 2