

New representatives of the genus *Septatoechia* LOBATSCHIEVA & TITOVA, 1977 (Brachiopoda, Rhynchonellida, Tetrarhynchiidae) from the Maastrichtian of Western Europe

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Abstract

PETTITT (1950) erected the species *Cretirhynchia magna* for a rhynchonellide brachiopod collected from the Upper Chalk of Trimmingham, Norfolk, England. On the basis of specimens of this species made available to the authors, serial transverse sections and SEM examination of the shell microstructure were performed. Macro-morphological characters observed assign this material to the genus *Septatoechia* LOBATSCHIEVA & TITOVA, 1977. The early Maastrichtian *Cyclothyris elegans* (VON HANSTEIN, 1879) collected from Ciplly (Hainaut, Belgium) is reappraised and its generic allocation is also changed due to the macromorphological characteristics fitting the genus *Septatoechia*. The shell microstructure pattern of the secondary shell layer of both species is 'fine fibrous' (leptinoid). The discrepancy in the shell microstructure patterns between western representatives (*S. magna* and *S. elegans*) and the eastern representatives (*S. inflata* and *S. amudariensis*) stimulated revision of previous published information. Careful re-examination of unpublished results revealed problems with the original description of the shell microstructure of *S. inflata* and *S. amudariensis* due to the use of oblique lateral sections of the fibres. Emended description of the shell microstructure of *S. inflata* and *S. amudariensis* is herein provided. Thus all four species belonging to the genus *Septatoechia* have 'fine fibrous' (leptinoid) shell microstructure, typical of superfamily Hemithiridoidea.

Keywords: Cretaceous, Brachiopoda, Rhynchonellida, *Septatoechia*, serial transverse sections, shell microstructure.

Résumé

PETTITT (1950) érigea l'espèce *Cretirhynchia magna* pour un brachiopode rhynchonellide Maastrichtien collecté à Trimmingham, Norfolk, Angleterre. Quelques spécimens ont pu être étudiés

par les auteurs. Des sections transversales sériées ainsi que des observations au MEB de l'ultrastructure de la coquille ont été menées. Les caractères macromorphologiques observés placent cette espèce dans le genre *Septatoechia* LOBATSCHIEVA & TITOVA, 1977. La révision de *Cyclothyris elegans* (VON HANSTEIN, 1879) provenant du Maastrichtien Inférieur de Ciplly permet de transférer également cette espèce vers le genre *Septatoechia*. Pour ces deux espèces, la microstructure de la couche secondaire du test est 'finement fibreuse' (leptinoïde). Les différences de microstructure observées entre les espèces ouest-européennes (*S. magna* et *S. elegans*) et les espèces orientales (*S. inflata* et *S. amudariensis*) ont induit une révision des informations précédemment publiées. Un examen attentif de sections sériées non-publiées a révélé quelques problèmes dans les interprétations de microstructures de *S. inflata* et de *S. amudariensis* dus à l'utilisation de coupes latérales obliques des fibres. Une description modifiée est donc proposée pour *S. inflata* et *S. amudariensis*. Il est établi que toutes les espèces décrites au sein du genre *Septatoechia* ont une microstructure 'finement fibreuse' (leptinoïde) caractéristique pour tous les représentants de la superfamille des Hemithiridoidea.

Mots-clefs: Crétacé, Brachiopodes, Rhynchonellida, *Septatoechia*, sections transverses sériées, microstructure.

Introduction

Between 1950 and 1965, PETTITT published an important monograph dealing with the rhynchonellide brachiopods from the British chalk in which he erected two new genera: *Cretirhynchia* and *Orbirhynchia*. The genus *Cretirhynchia* as proposed by PETTITT included as many as 16 distinct species, all of them supposedly having raduliform crura. Problems appeared with PETTITT's interpretation and, in 2001, SIMON & OWEN made a first step in the revision of this taxonomically problematic genus. They provided serial transverse sections for 17 species belonging initially to the genus *Cretirhynchia*. As a result of their taxonomic reappraisal they subdivided this genus into 4 subgenera; some of the species being placed in a new genus: *Woodwardirhynchia*. However, some species were

removed from the genus *Cretirhynchia* and left without any new generic position. The type of crura present in all the studied species in the latter work was considered raduliform, a character that in this state (or a variation thereof) is typical for the whole rhynchonellide superfamily Hemithiridoidea (MANCENIDO *et al.*, 2002).

Later, MOTCHUROVA-DEKOVA *et al.* (2008a) proposed the use of multiple techniques for investigating this kind of problematic palaeontological material. To the method of serial transverse sections, they added the use of SEM observations for analysing excavated umbonal parts of the specimens and for establishing the microstructure of the shell (mainly the structure of the secondary layer). They succeeded in investigating more thoroughly the morphology of the crura and they pointed out the presence of subfalciform crura in *Cretirhynchia limbata* (VON SCHLOTHEIM, 1813), the type species for the subgenus *Homaletarhynchia* SIMON & OWEN, 2001. A clear distinction between *Cretirhynchia* (*Cretirhynchia*) *plicatilis*, with true raduliform crura, and *Cretirhynchia* (*Homaletarhynchia*) *limbata*, with subfalciform was established. The new results allowed MOTCHUROVA-DEKOVA & SIMON (2007) to remove the subgenus *Homaletarhynchia* from the genus *Cretirhynchia* and to elevate it to genus level within another family Basiliolidae, and superfamily, the Pugnacoidea.

All these deep changes inside a large group of rhynchonellide brachiopods indicate that the taxonomical problem with the historic concept of *Cretirhynchia* is quite complex and other changes and discoveries are awaited for improving our knowledge of the taxonomical structure of this group.

In 1950 PETTITT erected the species *magna* within the genus *Cretirhynchia*. This species has been collected from the Upper Chalk (*Lunata* Zone, *Porosphaera* Beds) from Trimmingham, Norfolk. The *Porosphaera* Beds correspond to the Lower Maastrichtian, *Belemnella pseudobtusa* and *B. obtusa* Zones (CHRISTENSEN *et al.*, 2000). In 2001, SIMON & OWEN did not have access to material from this species. Later, the late Paul Whittlesea from Eaton, Norwich, Norfolk, UK sent some specimens of *C. magna* to E.S. for investigation. The aim of this paper is to reveal the internal structure of this species by using all possible methods and to establish its taxonomical position accurately. After this study, it became apparent that this material should be removed from the genus *Cretirhynchia* and a possible taxonomical solution, based on morphological macro-characters, was to transfer it to the genus *Septatoechia* LOBATSHEVA & TITOVA, 1977. However, this

analysis indicated that such generic assignment could be doubtful if the known shell ultrastructure of the genus *Septatoechia* was taken into account. As similar external and internal morphological characters found in *C. magna* were also previously observed in *Cyclothyris elegans* (VON HANSTEIN, 1879) a rhynchonellide brachiopod collected at Ciplly (Hainaut, Belgium) from the Ciplly-Malogne Phosphatic Chalk Formation (*Belemnella obtusa* Zone, Lower Maastrichtian), a revision of this latter species appeared necessary and it has been included in this study.

Methods and Material

Macro-photographed specimens were coated with ammonium chloride. Serial transverse sections were made following the method proposed by AGER (1965, pp. 212-218) at a distance of 0.1 mm. Subsequently, acetate peels were prepared after the STERNBERG & BELDING's method (1942). Drawings were made with a Wild camera lucida. Macrophotographs of the serial sections were also taken to provide a permanent record of the coloured view of the sections during their preparation. Each morphological structure appears with a distinct colour and aspect (such as hinge plates and crural bases for instance) and this facilitates the interpretations of the peels.

Three specimens of "*Cretirhynchia*" *magna* collected by Paul Whittlesea from the *Porosphaera* Beds at Sidestrand near Cromer, Norfolk, England were available for investigation. One of them, a large, fully adult, undistorted specimen was chosen for serial sections and for SEM examination of its shell microstructure. A second one, also with regular outline, but with a stronger anterior fold, has been chosen for illustrating a possible variation for this species. The third specimen was not suitable for this type of study as it was strongly compressed.

"*Cyclothyris*" *elegans* was studied by SIMON in 1996. The original material collected by VON HANSTEIN in Ciplly (3 specimens), preserved at the University of Bonn (Germany), was re-examined in that study. Moreover, 29 specimens, from Ciplly (Hainaut Province, Belgium), kept in the "Institut royal des Sciences naturelles de Belgique" in Brussels (IRScNB), were measured and some of them were illustrated (SIMON, 1996, pl. 1, fig. 1, 3, 4). Two specimens were sectioned and the serial transverse sections were published (SIMON 1996, text-fig. 1 A & B). The remnants of these two-sectioned specimens (IRScNB MI – 10663 and IRScNB MI – 10664) are used in this study again for

SEM examination and shell microstructure. For an easy and direct comparison with *S. magna*, photographs of one of the sectioned specimens (IRScNB MI – 10663) and illustrations of another specimen (IRScNB MI – 11046) are given again on Pl. 2, Fig. 2a-e, 3a-d).

Investigation of the shell microstructure of "*Cretirhynchia*" *magna* and "*Cyclothyris*" *elegans* was made on cross sections at mid shell length, polished and finally etched in 5% HCl for about 10 seconds. The samples were subsequently coated with gold and observed using a low vacuum SEM - an ESEM FEI Quanta 200. The shell thickness and fibres of the secondary layer were measured close to the symmetry plane.

For ease of comparison between the serial sections made in this paper and sections already published earlier by LOBATSHEVA & TITOVA (1977, p. 104, fig. 1) and by SIMON (1996, p. 100, fig. 1) the orientation of the sections are presented here with the ventral valve up. This follows also the recommendation of MOTCHUROVA-DEKOVA *et al.* (2008b).

Taxonomic description

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 Hemithiridoidea RZHONSNITSKAIA, 1956
 Family Tetrarhynchiidae AGER, 1965(a)
 Subfamily Viarhynchiinae
 MANCEÑIDO & OWEN, 2002
 Genus *Septatoechia* LOBATSHEVA & TITOVA, 1977

Type species: Septatoechia inflata LOBATSHEVA & TITOVA, 1977.

Diagnosis

S. inflata is an Upper Maastrichtian (*Inoceramus dobrovi* Zone) large rhynchonellide brachiopod collected from Tuarkyr, Turkmenistan. The original diagnosis pointed out the following morphological characters: a symmetric rounded to subtriangular shell, a strongly erect, short or medium sized beak, a small submesothyrid foramen, parallel or convergent dental plates and thicker and short, slightly ventrally deflected hinge plates. Possible rudimentary septal plates were also noted. The presence of a very high, long and thin median septum and of raduliform crura is the most

important diagnostic character. Based on extensive observations of new representatives from Bulgaria (unpublished material), MOTCHUROVA-DEKOVA (1994) published an emended diagnosis adding some new morphological characters such as: a possible subpentagonal outline; a variable convexity; a beak which is straight; deltidial plates which are conjunct; simple costae which are subangular or slightly rounded and a septum which is never complicated by callus; and a secondary shell layer, which is of fine-fibrous rhynchonellide type (*sensu* KAMYSHAN, 1977) with diamond-shaped to square in cross sections fibres (9-30 µm). In 2001, MOTCHUROVA-DEKOVA additionally published SEM micrographs of the shell microstructure of the type species *S. inflata* collected from Upper Maastrichtian deposits at Tuarkyr, Turkmenistan and from Novachene, Bulgaria (MOTCHUROVA-DEKOVA, 2001, p. 325; fig. 4, B, C). She also illustrated (MOTCHUROVA-DEKOVA, 2001, fig. 4, D) detail of the shell microstructure of *S. amudariensis* (KATZ, 1964) from Nardyvaly (Badhyz Region, Turkmenistan). This species is distinct morphologically from *S. inflata* but has a similar secondary layer structure. During the present study the published and unpublished results from previous SEM observations of the shell microstructure of these two eastern representatives of *Septatoechia* were critically revised and we report new data below.

Septatoechia magna (PETTITT, 1950)

Pl. 1, Figs 1a-i, 2a-e; Pl. 2, Figs 1a-d; Fig. 1; Table 1

- *1950 — *Cretirhynchia magna*, sp. nov. – PETTITT, p. 22, pl. 2, fig. 9a-c.
 1990 — *Cretirhynchia magna* – JOHANSEN & SURLYK, p. 838.
 2001 — *Cretirhynchia magna* – MORTIMORE *et al.*, p. 16.
 2001 — *Cretirhynchia magna* – SIMON & OWEN, p. 56.

Type specimen

The holotype is preserved in the Sedgwick Museum, Cambridge, England with the number B.52623.

Locus typicus

Trimingham, Norfolk, England.

Stratum typicum

Upper Chalk, *Lunata* Zone, *Porosphaera* Beds. Following CHRISTENSEN *et al.*, 2000 this is equivalent to the *Belemnella pseudobtusa* and *B. obtusa* Zones (Lower Maastrichtian).

*Description**External characters.*

Medium to large rhynchonellide brachiopod with a subpentagonal to transversely oval outline. The shell is lenticular in lateral view and appears, at first glance, equibiconvex. However, when the precise position of the lateral commissure is taken into account, the shell is clearly dorsibiconvex. In anterior view, the shell is dome-shaped. In posterior view, the squamaglottal junction appears arched dorsally. The convexity of the dorsal valve is strong in adults but weaker in juveniles. The erect beak is strong, short and pointed and the beak ridges are clearly developed determining a submesothryid foramen. The medium-sized foramen is complete and elliptical. The conjunct deltidial plates are often produced, forming auriculate extensions. The interarea is wide and gently curved. A wide sulcus is present on the ventral valve. It develops along the two thirds of the length of the valve and it is rather deep in the anterior part of the valve. A corresponding fold is present on the dorsal valve. The linguiform extension is generally arcuate (Pl. 1, Fig. 2d) but it can be subtrapezoidal (Pl. 1, Fig. 1d). The shell surface is ornamented with 50-55 costae in large adults. The costae are subrounded, not angular, in section. They are very narrow in the posterior part of the shell but their width increases regularly till the anterior commissure. There is sometimes a very faint median groove on the costae producing an incipient splitting near the anterior commissure (Pl. 1, Fig. 2c). There are 8 costae present on the fold and 9 costae in the sulcus. These costae are much wider and stronger than the costae present on the lateral flanks of the shell. Interspaces are relatively narrow. Three major growth lines are present. However, they are not equally strong on all specimens.

Internal characters.

The internal characters of this species are observed for the first time using serial transverse sections (Fig. 1).

Ventral valve. - A long pedicle collar is visible in the posterior sections of the ventral valve. Relatively thin dental plates, which limit the umbonal cavities, are subparallel in their posterior part and they become ventrally convergent in their anterior part. Teeth are strong, deeply inserted in the sockets. Peculiar ventral low and short ridge is developed in the posterior part of the shell.

Dorsal valve. - Cardinal process is absent. The socket ridges are well-developed, inner ones being stronger. A blade-like, very long, high and thin median septum is developed. No callus has been observed associated with the dorsal septum. The hinge plates are slender,

dorsally concave and ventrally convergent. The crural bases are ventrally deflected. Crura are raduliform, relatively long and given off ventrally. Their inner side is concave in their posterior part. Anteriorly, they become parallel, wider and very thin.

Microstructure of the shell (Pl. 2, Figs 1-4; Table 1)

The whole shell thickness ranges between 400 μm (in the sulcus) and 480 μm (in the ribs). The primary layer is relatively thin (17-21 μm). It is made of obviously recrystallized calcite granules. The fibres of the secondary layer are anisometric in cross section (25 to 35 μm wide and 5 to 9 μm thick). The ratio between the width and the thickness of the fibre in cross section ranges between 3 and 7 (see also Table 1). The inner part of the shell is made of somewhat larger, regular subrhombic fibres. The edges of these fibres have sharp angles. The external part of the shell is built of thinner fibres, which are more anvil-like (formed by two arcs – larger and smaller – connected laterally by two sides). The secondary layer is fine fibrous or leptinoid type (*sensu* RADULOVIĆ *et al.*, 2007 or MANČEŇIDO *et al.*, 2007 respectively). A myotest up to 100 μm thick is observed in the internal part of the shell. The microtexture is homogeneous and this pattern of shell microstructure is characteristic of the representatives of the Hemithiridoidea (RADULOVIĆ *et al.*, 2007, MANČEŇIDO & MOTCHUROVA-DEKOVA, 2010).

Septatoechia elegans (VON HANSTEIN, 1879)

Pl. 2, Figs 2a-e; Pl. 3, Figs 1a-d, 2a-d; Table 1

*1879 — *Rhynchonella elegans* – VON HANSTEIN, p. 40.

1996 — *Cyclothyris elegans* – SIMON, pp. 97-101; text-fig. 1; pl. 1, fig. 1-4.

1998 — *Cyclothyris elegans* – SIMON, p. 194.

Type specimen

A lectotype has been designated by SIMON (1996, p. 98) among the type series collected by VON HANSTEIN and preserved at the University of Bonn under the reference G.P.I.BO. – Hanstein: 4.

Fig. 1 – Thirty-eight transverse serial sections through the umbonal portion of an adult specimen (IRScNB MI-11061) of *Septatoechia magna* (PETTITT, 1950), from the *Porosphaera* Beds at Sidestrand near Cromer, Norfolk, England. Lower Maastrichtian, *Belemnella pseudobtusa* and *B. obtusa* Zones. Scale bar = 10 mm. The same specimen is figured on Plate 1, Fig. 2. Distance from the tip of ventral umbo of each section given in mm. Drawings from peels.

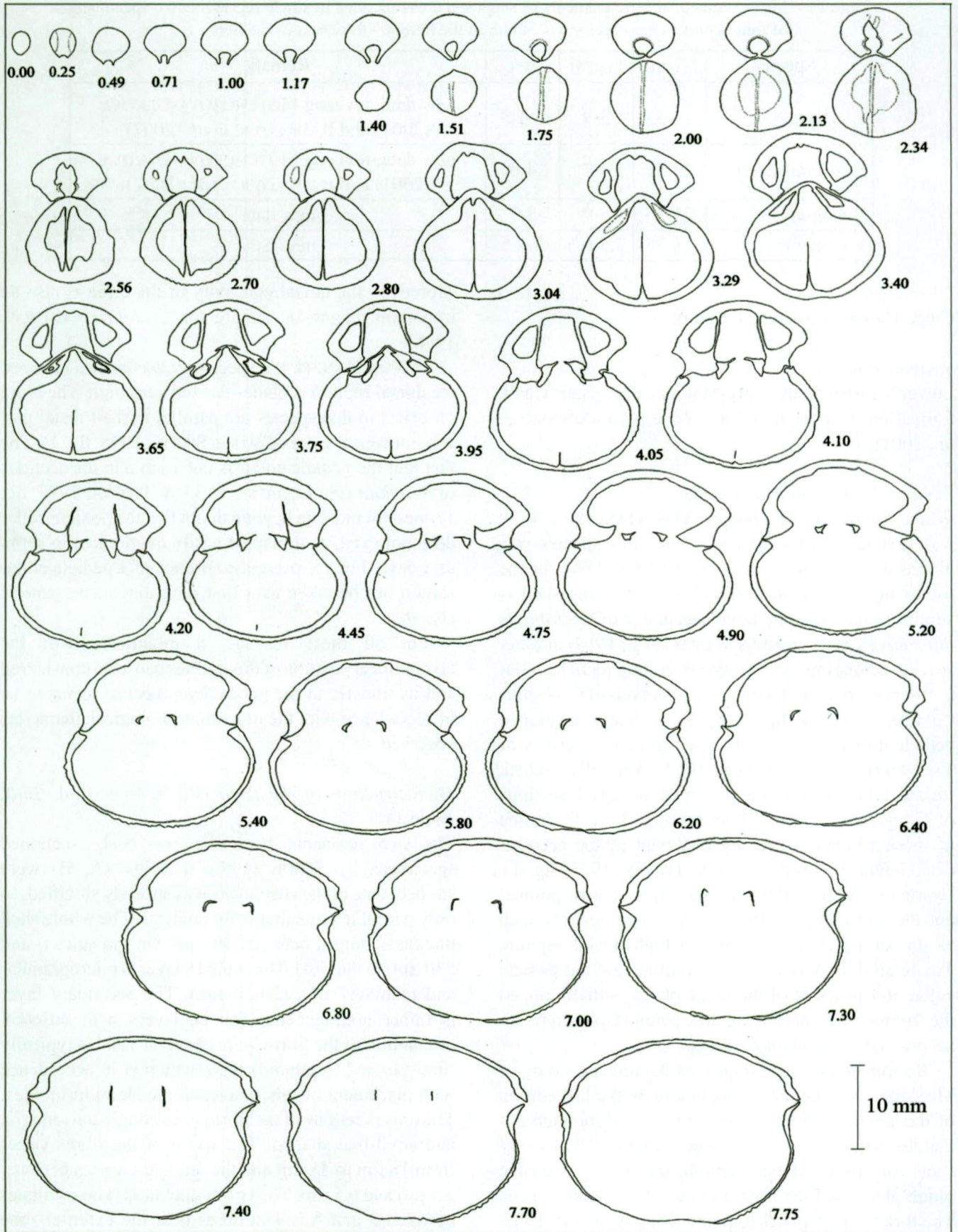


Table 1 – Measurements of fibre elements of supposed cross sections in single representative specimens of four *Septatoechia* species; w – width of the fibre; t – thickness of the fibre.

Species	w (µm)	t (µm)	w/t	Remark
<i>S. inflata</i>	19-33	3-9	3-7.5	new data, revising MOTCHUROVA-DEKOVA (2001) and RADULOVIĆ <i>et al.</i> (2007)
<i>S. amudariensis</i>	20-31	4-7	4-6	new data, revising MOTCHUROVA-DEKOVA (2001) and RADULOVIĆ <i>et al.</i> (2007)
<i>S. magna</i>	25-35	5-9	3-7	new data
<i>S. elegans</i>	18-35	3.5-6.5	3-8.5	new data

Locus typicus

Ciply, Hainaut Province, Belgium.

Stratum typicum

Lower Maastrichtian, Ciply-Malogne Phosphatic Chalk Formation, *Belemnella obtusa* Zone (ROBASZYNSKI *et al.*, 2001).

Revised description and remarks

When *Rhynchonella elegans* VON HANSTEIN, 1879 was first revised by SIMON (1996), this species was placed in the genus *Cyclothyris* M'COY, 1844 for the following reasons: the general outline of the shell is similar to that of some large specimens of *Cyclothyris difformis* (VALENCIENNES in LAMARCK, 1819) or other species belonging to *Cyclothyris*. A long pedicle collar is observed in the serial transverse sections of *C. elegans* (SIMON, 1996, text-fig. 1, A, B). A clearly developed pedicle collar has been observed in many sections of *Cyclothyris* species (OWEN, 1962). Ventrally arched, forked hinge plates are observed in serial sections of *C. elegans* (SIMON, 1996, text-fig. 1, A, B). Some of these characters are not observed in the sections of *S. inflata* (LOBATSCHEVA & TITOVA, 1977, fig. 1). However, (SIMON 1996, p. 101) has clearly pointed out the similarities with the genus *Septatoechia* such as the strong development of a high dorsal septum. The relative importance of the outline and the pedicle collar and structure of the hinge plates, initially tipped the balance for preferring the genus *Cyclothyris* to accommodate *Rhynchonella elegans*.

Recent studies have improved the understanding of Mesozoic rhynchonellide taxonomy. In the last edition of the *Treatise* (2002), MANCENIDO *et al.* pointed out that the genus *Cyclothyris* can be recognized by its very short (or absent) dorsal septum, the distally concave hinge plates and the long and dorsally concave crura. The forked hinge plates as pointed out by OWEN (1962, p. 44) are no more considered of special taxonomical importance. The development of the dorsal septum seems to be more important in generic diagnoses.

Moreover, the dorsal concavity of the crura is also an important diagnostic feature for *Cyclothyris* (SIMON, 1996).

In VON HANSTEIN's species *Rhynchonella elegans*, the dorsal septum is blade-like and very high. The crura observed in this species are parallel in their distal part and not concave dorsally (see SIMON, 1996, fig. 1). The fact that the pedicle collar is not visible in the sections of *S. inflata* (see LOBATSCHEVA & TITOVA, 1977, fig. 1) does not indicate beyond doubt that the pedicle collar does not exist, as it may be easily overlooked in serial sections. Thus the presence/absence of a pedicle collar should not be taken as a first rank diagnostic generic character.

For all these reasons, a modification of the taxonomical position of this species had to be considered and its transfer to the genus *Septatoechia* seems to be in accordance with the macromorphological characters observed.

Microstructure of the shell (Pl. 3, Figs 1a-d, 2a-d; Table 1)

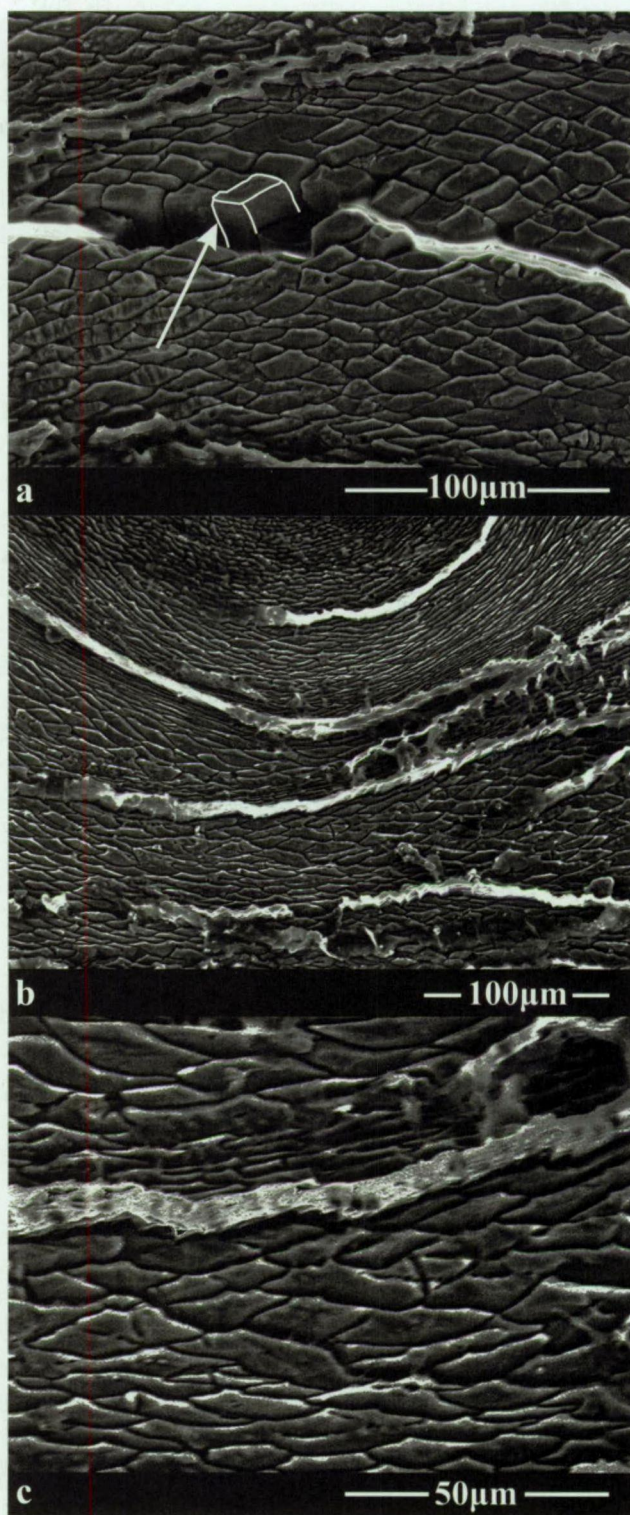
The two remnants from the previously sectioned specimens by SIMON (1996, text-figs 1A, B) were studied. One of the specimens was strongly silicified, so only part of it was suitable for analysis. The whole shell thickness ranges between 300 µm (in the sulcus) and 530 µm (in the ribs). The primary layer is microgranular and relatively thin (20-30 µm). The secondary layer is rather homogeneous (no sublayers with different orientation of the fibres were observed) and is typically 'fine-fibrous' (leptinoid) type, which is in accordance with placement of this species to the Hemithiridoidea. The cross sections of the fibres are strongly anisometric and anvil-like shaped. The width of the fibres varies from 18 µm to 35 µm and the thickness varies between 3.5 µm and 6.5 µm. The width/thickness ratio oscillates between 3 and 8.5. The fibres near the external zone of the shell are much thinner. This type of structure is inconsistent with those observed in the representatives of the genus *Septatoechia* as previously reported (see

Fig. 2 – Shell microstructure and microtexture of *Septatoechia inflata*, Tuarkyr, Turkmenistan, Upper Maastrichtian, ventral valve of the specimen studied by MOTCHUROVA-DEKOVA (2001), deposited in the National Museum of Natural History, Sofia, NMNHS F-31364 [sample 26b], (revision of data published by MOTCHUROVA-DEKOVA, 2001). a: detail of the old fig. 4B (MOTCHUROVA-DEKOVA, 2001) showing the orientations of the fibres in a lateral part of the shell. Note that the studied section was not properly chosen because the long axes of the fibres (arrow) are not perpendicular to the study plane. As a result the rhombic sections of the fibres are not true cross sections, but rather oblique cuts of the fibres; b: section through a sulcus that is closer to the plane of symmetry of the shell. Note the prevailing anisometric sections of the fibres; c: detail of b.

MOTCHUROVA-DEKOVA, 2001). Surprisingly, this type of microstructure is more similar to that observed in representatives of the genus *Cyclothyris*. However, in *Cyclothyris*, the secondary layer is not homogeneous but is usually made of several “packages of fibres” as noted by MOTCHUROVA-DEKOVA (2001, p. 323). In *S. elegans* the microtexture of the secondary shell layer is particularly homogeneous.

Revision of previously published shell microstructure data for *Septatoechia inflata* and *Septatoechia amudariensis*

The peculiarities of the shell microstructure of *S. magna* and *S. elegans* revealed in this study which seemed inconsistent with published data on *Septatoechia* stimulated us to reappraise the initial scarce information about the shell microstructure of the type species *S. inflata* and another previously available species *S. amudariensis* from the Maastrichtian of Turkmenistan. A closer re-examination of the old laboratory notes (1999–2000) of N.M.-D. showed that unfortunately during the preparation of the manuscript (MOTCHUROVA-DEKOVA, 2001) the micrographs and the measurements taken from them were not the most informative ones. Looking in closer detail at the published illustrations of *S. inflata* and *S. amudariensis* (see MOTCHUROVA-DEKOVA, 2001, figs 2B, D) demonstrates that the studied sections are not perpendicular to the long axes of the fibres. Therefore the exposed sections are not transverse, but rather oblique sections of the fibres, so that measurements taken from such sections are misleading. The ‘relatively isometric rhombic’ cross sections of



the fibres are thus an artefact, because the sections are slanted, hence extended in some lateral direction. Detail from MOTCHUROVA-DEKOVA (2001, fig 2B) is here illustrated again under a larger magnification (see Fig. 2a) to show that the real orientation of the long axes of the fibres is not perpendicular to the studied section. Unfortunately, other similar SEM micrographs, which were not perpendicular to the long axes of the fibres

were chosen for the description and measurements of this species in MOTCHUROVA-DEKOVA (2001). In summary, we realise that most of the SEM micrographs of *S. inflata* and *S. amudariensis* taken in 1999-2000 present oblique and rather laterally extended sections of the fibres. These misleading results were duplicated in the compilation for the shell microstructure of all post-Palaeozoic rhynchonellides made by RADULOVIC *et al.* (2007, table 2).

Septatoechia inflata LOBATSHEVA & TITOVA, 1977

When re-examining the data set of multiple SEM micrographs made for this taxon in 1999-2000 only two of them are found to be located close to the standard reference section (= close to the sagittal plane), where the long axis of the fibres are supposed to be perpendicular to the section. One of these 2 micrographs is illustrated here (Fig. 2 b, 2 c). Not surprisingly the fibres observed in this section are rather anisometric, with prevailing anvil like sections and only some of them have rhomb-like and other anisometric sections. The width of the measured fibres varies from 19 μm to 33 μm and the thickness varies between 3 μm and 9 μm . The ratio width/thickness ranges from 3 and 7.5 (see Table 1). The fibres near the external part of the shell are much thinner and smaller in width. The secondary layer is thus of fine fibrous (leptinoid) type. As reported before (MOTCHUROVA-DEKOVA, 2001), the microtexture of the section seems not quite homogeneous, it is composed of some packages of slightly differently oriented long axes of the fibres. However, a definite conclusion about the microtexture pattern cannot be drawn from a single micrograph only. The myotest is rather thick, as reported before.

Septatoechia amudariensis (KATZ, 1964)

Among the previously analyzed SEM micrographs of this species taken at the mid shell length of one specimen, only one was in fact taken close to the median plan, where the long axes of the fibres are almost perpendicular to the plane of the section. The micrograph illustrated by MOTCHUROVA-DEKOVA (2001, fig. 2D) was taken from a lateral portion of the shell, where the sections of the fibres are oblique, thus their outline and size is misleading and not suitable for comparative purposes. The outlines of the cross sections of the fibres in the representative section illustrated here (Fig. 3) are anvil-like and unambiguously anisometric. The measured width of the fibres is from 20 to 31 μm , the thickness is from 4 to 7 μm and the ratio width/thickness varies from 4 to 6 (see Table 1). The secondary layer pattern is of 'fine-fibrous' (leptinoid)

type. The studied cross section through a rib has rather homogeneous microtexture.

Comparisons between the *Septatoechia* species

Comparison between S. magna and S. inflata

S. magna is more transversely oval and the sulcus and fold are wider. The costae of *S. magna* widen out much more anteriorly. The hypothryd foramen is larger in *S. magna* and it is auriculate, indicating that it was really used to fix the brachiopod by its pedicle. The raduliform

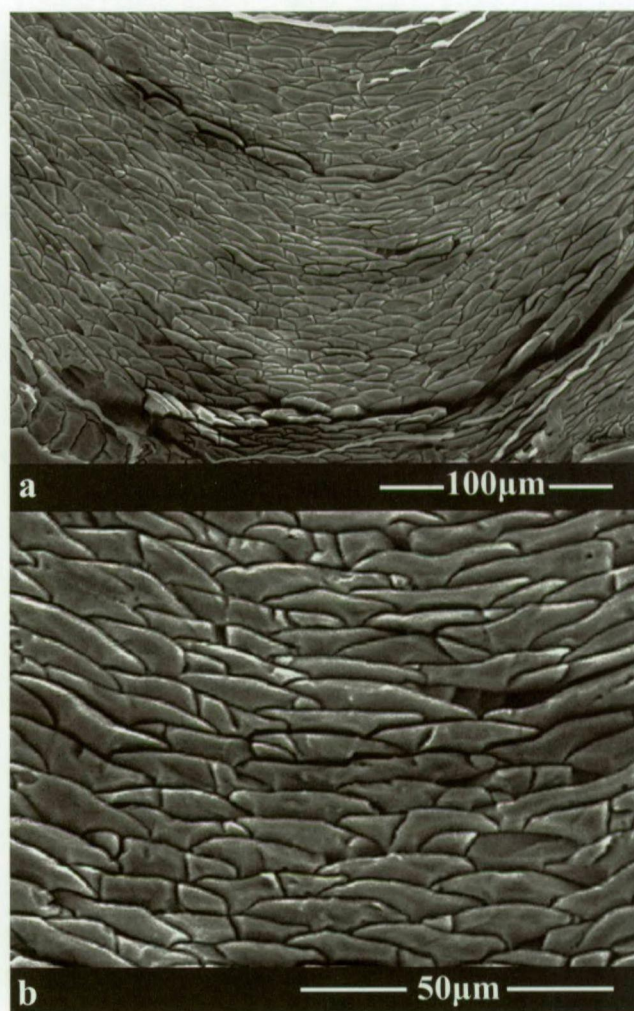


Fig. 3 – Shell microstructure and microtexture of *Septatoechia amudariensis*, Nardyvaly, Badkhyz region, eastern Turkmenistan, Upper Maastrichtian, the specimen studied by MOTCHUROVA-DEKOVA (2001), deposited in the National Museum of Natural History, Sofia, NMNHS F- 31364-a [sample 27a]. a: dorsal valve, section through a rib close to the median plane of the shell external part of the shell below. Note the anisometric anvil-like cross section of the fibres; b: detail of a.

crura observed in *S. magna* are parallel anteriorly.

In *S. inflata*, the width of the costae is more regular and the costae on the fold and sulcus resemble the costae observed on the lateral parts of the shell. The submesothyrid foramen in *S. inflata* is comparatively smaller. The dental plates in *S. inflata* are slightly less convergent in their anterior part. The crura in *S. inflata* as seen on the original serial transverse sections of LOBATSHEVA & TITOVA (1977, p. 104, fig. 1) are more canaliform in their anterior part and not simply subparallel. The pattern of the shell microstructure of both species is fine fibrous, with the dimensions of the fibres (Table 1) very homogeneous in the same range of values. The only difference seems to be the heterogeneous microtexture of *S. inflata* (however, see the remark above).

Comparison between *S. elegans* and *S. inflata*

S. elegans is a rhynchonellide brachiopod which externally most resembles the representatives of the genus *Cyclothyris*. Its outline is thus more transversely oval. The costae are stronger, roof-shaped in transverse sections and the top of the costae is sharp. As the costae are also wider they are not numerous in *S. elegans*. In the sulcus, for instance, 9 costae are observed in *S. elegans* and 16 costae in *S. inflata*. The foramen in *S. elegans* is large and circular whereas it is relatively small in *S. inflata*. Both have a very biconvex shell but *S. elegans* is more dorsibiconvex. Internally these two species have much in common including a blade-like, long and very high dorsal septum and raduliform crura with subparallel anterior parts. The hinge plates are given off ventrally in both species but they are terminally forked (=the crural bases attached to their tips are more crescent like, or boomerang like) in *S. elegans*.

Comparison between *S. magna* and *S. elegans*

Both species have a transversely oval outline and externally they have a 'cyclothyrid' aspect. The costae in *S. magna* are slightly narrower, more numerous and they are not roof-shaped in section but subrounded to relatively flat. Internal characters such as the septum, the subparallel dental plates, the raduliform crura which are subparallel in their anterior part and the hinge plates given off ventrally are present in both species. The dental plates in *S. elegans* are, in their posterior part, ventrally divergent, parallel in their median part and slightly convergent in their anterior part. In *S. magna* they are subparallel in their posterior part and a little more convergent ventrally in their anterior part. In both species the shell microtexture pattern is homogeneous.

The fibres in the secondary layer are anisometric with comparable values (see Table 1); this pattern is of the 'fine-fibrous' (leptinoid) type. The fibres observed in *S. magna* are elongate rhombic in the central part whereas those observed in *S. elegans* are only anvillike. This may be regarded as intrageneric variation. However, more material has to be studied to check if this difference is applicable to more specimens from both taxa.

Discussion and conclusions

The present work investigates for the first time the internal morphological characters and shell microstructure of the rhynchonellide brachiopod '*Cretirhynchia*' *magna* erected by PETTIT in 1950. Morphological characters observed in serial sections such as subparallel dental plates, short hinge plates given off ventrally, ventrally deflected crural bases, parallel and straight distal parts of the crura and a blade-like, long and high dorsal septum in the dorsal valve, are not typical features for the genus *Cretirhynchia*. In the latter genus, the dental plates are more ventrally convergent, the distal parts of the crura are clearly concave and the dorsal median septum, though present, is never developed to such extent. Considering the macro-morphological characters, a transfer of this species to the genus *Septatoechia* LOBATSHEVA & TITOVA, 1977 seems reasonable and is proposed in this paper.

The recent, more restrictive description (MANCENIDO *et al.*, 2002) of the genus *Cyclothyris* M'COY, 1844 led us to reconsider the generic attribution for *Cyclothyris elegans* (VON HANSTEIN, 1879) favoured by SIMON (1996). Some characters such as the presence of a blade-like high and long dorsal septum, raduliform crura which are not canaliform, anterior parts of the crura which are subparallel and not dorsally concave suggest the removal of this species from the genus *Cyclothyris*. Its transfer to the genus *Septatoechia* is here proposed.

SEM investigations of the shell microstructures of *Septatoechia magna* and *S. elegans* revealed that their secondary layer is of fine fibrous or leptinoid type (*sensu* RADULOVIĆ *et al.*, 2007 or MANCENIDO *et al.*, 2007, respectively). Both have a very homogeneous microtexture characteristic for the secondary shell layer observed in the Hemithiridoidea (RADULOVIĆ *et al.*, 2007, MANCENIDO & MOTCHUROVA-DEKOVA, 2010).

The discrepancy between the new results obtained for the shell microstructure pattern of the two western representatives of *Septatoechia* (*S. magna* and *S.*

elegans) and the previously published results on the type species *S. inflata* and another eastern representative, *S. amudariensis*, (MOTCHUROVA-DEKOVA, 2001) initially led us to think about a possible evolutionary convergence process in *Septatoechia*, involving two different stocks – eastern and western which reveal different patterns of the shell microstructure, whereas the internal macromorphology of their shells is similar and suggests allocation in the same genus. However, such a discrepancy between stable similar internal morphology (in the four available species of *Septatoechia*) and quite different shell microstructure pattern (between the eastern and western representatives of *Septatoechia*) might also be a result of subjectivity while choosing the representative sections of the shell to study the shell microstructure peculiarities. Therefore on occasion of the present study we revised the published data about the pattern of the shell microstructure of the type species in *S. inflata* and in *S. amudariensis*. The more lateral sections used for descriptions and measurements of the fibre elements by (MOTCHUROVA-DEKOVA, 2001) are not informative and should not be used for comparative purposes. We have chosen for this study only the few available micrographs of *S. inflata* and of *S. amudariensis* (eastern representatives of the genus), which were taken closer to the plane of symmetry of the shell and which were initially neglected. We now consider such sections suitable for comparative purposes. The revised results obtained for the eastern representatives are in accordance with the new data obtained here for the western representatives of *Septatoechia* (*S. magna* and *S. elegans*). Thus, the shell microstructure pattern of all four taxa is fine fibrous with prevailing anisometric anvil-like transverse sections of the fibres. The values of the width and thickness of the fibres seem quite homogeneous for the genus as a whole (see Table 1).

Further studies on representatives collected from a wider stratigraphical and paleogeographical range are needed to obtain a more comprehensive knowledge of the variation of the shell microstructure in the genus *Septatoechia* and other rhynchonellide genera. Our results indicate that the shell microstructure pattern is a useful taxonomic character and detailed investigations of multiple specimens from one taxon are regarded to confirm the stability of the character.

The present research stresses the importance of precise technical work in order to reveal the internal morphology and the pattern of the shell microstructure. The present list of species of *Septatoechia* includes taxa that were previously assigned either to *Cretirhyncha* (*S. magna*) or to *Cylothyrus* (*S. amudariensis*, *S. elegans*). The external morphological characters of the shell in

these three Mesozoic rhynchonellide genera are similar and serial sectioning, dissection of the umbonal part (when possible) and study of the shell microstructure should be involved before proposing a taxonomic placement of a given species.

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Explanation of the plates

PLATE 1

Septatoechia magna (PETTITT, 1950). Fully adult specimens housed in the Institut royal des Sciences naturelles de Belgique (IRScNB) in Brussels, Belgium. Material collected from the Porosphaera Beds at Sidestrand near Cromer, Norfolk, England. Lower Maastrichtian, *Belemnella pseudobtusa* and *B. obtusa* Zones.

a: dorsal view; b: ventral view; c: lateral view; d: anterior view; e: posterior view.
Size of the specimens given by scale bars.

Fig. 1 – Complete articulated specimen (IRScNB MI-11062) with a strong dorsal fold limited by relatively abrupt lateral sides. The linguiform extension is subtrapezoidal.

f: detailed dorsal view of the suberect beak and of the complete auriculate submesothyrid foramen;

g: detailed view of the costae on the middle part of the dorsal valve;

h: enlarged detailed view of the costae on the dorsal view with subrounded section and nearly flat top; i: detailed view of a part of the anterior commissure.

Predation attempt scars are visible on both dorsal and ventral views, affecting the edge of the dorsal median fold just before the 2nd major growth line.

Fig. 2 – Complete articulated specimen (IRScNB MI-11061) with an outline similar to those observed in the type specimen (PETTITT 1950, pl. 2, fig. 9a-c). The linguiform extension is broadly arcuate. The auriculate submesothyrid foramen is fully preserved. This specimen has been used for serial transverse sections (Fig. 1).

f: detailed ventral view of the costae developed on the right side of the shell.

PLATE 2

Fig. 1 – *Septatoechia magna* (PETTITT, 1950) collected from the *Porosphaera* Beds at Sidestrand near Cromer, Norfolk, England. Lower Maastrichtian, *Belemnella pseudobtusa* and *B. obtusa* Zones. Shell microstructure observed on a polished cross section made at mid shell length of the ventral valve in the specimen used for serial transverse sections. Material housed in the Institut royal des Sciences naturelles de Belgique (IRScNB) in Brussels, Belgium (IRScNB MI-11061).

- a: section through the whole shell thickness at the plane of symmetry. General view of two ribs, external surface above;
 b: section through the whole shell thickness, section through a sulcus, a more lateral section than in a. Note the primary layer above and the myotest below;
 c: detail of a showing one of the ribs only. Note the gradual transition between thicker fibres often with rhombic sections (close to the central and internal part of the shell towards thinner fibres externally. Strong myotest developed at the internal side of the shell;
 d: detail of c showing the fibres.

Fig. 2 – Fully adult specimen of *Septatoechia elegans* (VON HANSTEIN, 1879) collected in Cibly (Hainaut Province, Belgium) from the Cibly-Malogne-Phosphatic Chalk Formation, *Belemnella obtusa* Zone, Lower Maastrichtian and housed in the Institut royal des Sciences naturelles de Belgique (IRScNB) in Brussels, Belgium. a: dorsal view. b: ventral view. c: lateral view. d: anterior view. e: posterior view. Size of the specimens given by scale bars.

Photographs of the specimen IRScNB MI- 10663 used for serial transverse sections already published in SIMON (1996, fig. 1-A, p. 104) and its shell microstructure is illustrated in Plate 3, Figs 1a-d.

Fig. 3 – Specimen IRScNB MI – 11046: a fully adult specimen of *Septatoechia elegans* (VON HANSTEIN, 1879), exhibiting a stronger dorsal fold and a deeper ventral sulcus, collected from the same level as the above mentioned specimen (Pl. 2, Fig. 2).

PLATE 3

Septatoechia elegans (VON HANSTEIN, 1879) collected in Cibly (Hainaut Province, Belgium) from the Cibly-Malogne-Phosphatic Chalk Formation, *Belemnella obtusa* Zone, Lower Maastrichtian and housed in the Institut royal des Sciences naturelles de Belgique (IRScNB) in Brussels, Belgium. Shell microstructure observed on a polished cross section made at mid shell length in two different specimens.

Fig. 1 – Specimen IRScNB MI-10663 illustrated on Pl. 2, Fig. 2a-e. This specimen has been used for serial transverse sections which are illustrated in SIMON 1996, fig. 1A, p. 104. Sections at the plane of symmetry of the dorsal valve (a, b) and ventral valve (c, d).

- a: section through the whole shell thickness, primary layer below, secondary layer strongly silicified (the higher relief on the micrograph), however 'islands' of unaltered fibres are seen;
 b: detail from a to show the unaltered anvil like fibres close to the internal surface of the shell. Diagenetic calcite prisms overgrow the internal surface of the shell (top);
 c: section through a rib to show the homogeneous development of the fibres in the secondary layer;
 d: detail from c to show the shape of the innermost fibres.

Fig. 2 – Specimen IRScNB MI- 10664 illustrated in SIMON 1996, pl. 1, fig. 4a-c. This specimen has been used for serial transverse sections, which are illustrated in SIMON 1996, fig. 1B, p. 104.

- a: section through a rib, whole shell thickness in the ventral valve at the median plane. A silicified band developed in a crack subparallel to the shell interior (white colour);
 b: a small lateral portion of the dorsal valve, section through a rib showing the homogeneous development of the fibres in the secondary layer;
 c: section through a rib, whole shell thickness in the dorsal valve at the median plane. Primary layer below;
 d: detail from c to show anvil-like cross sections of the fibres.

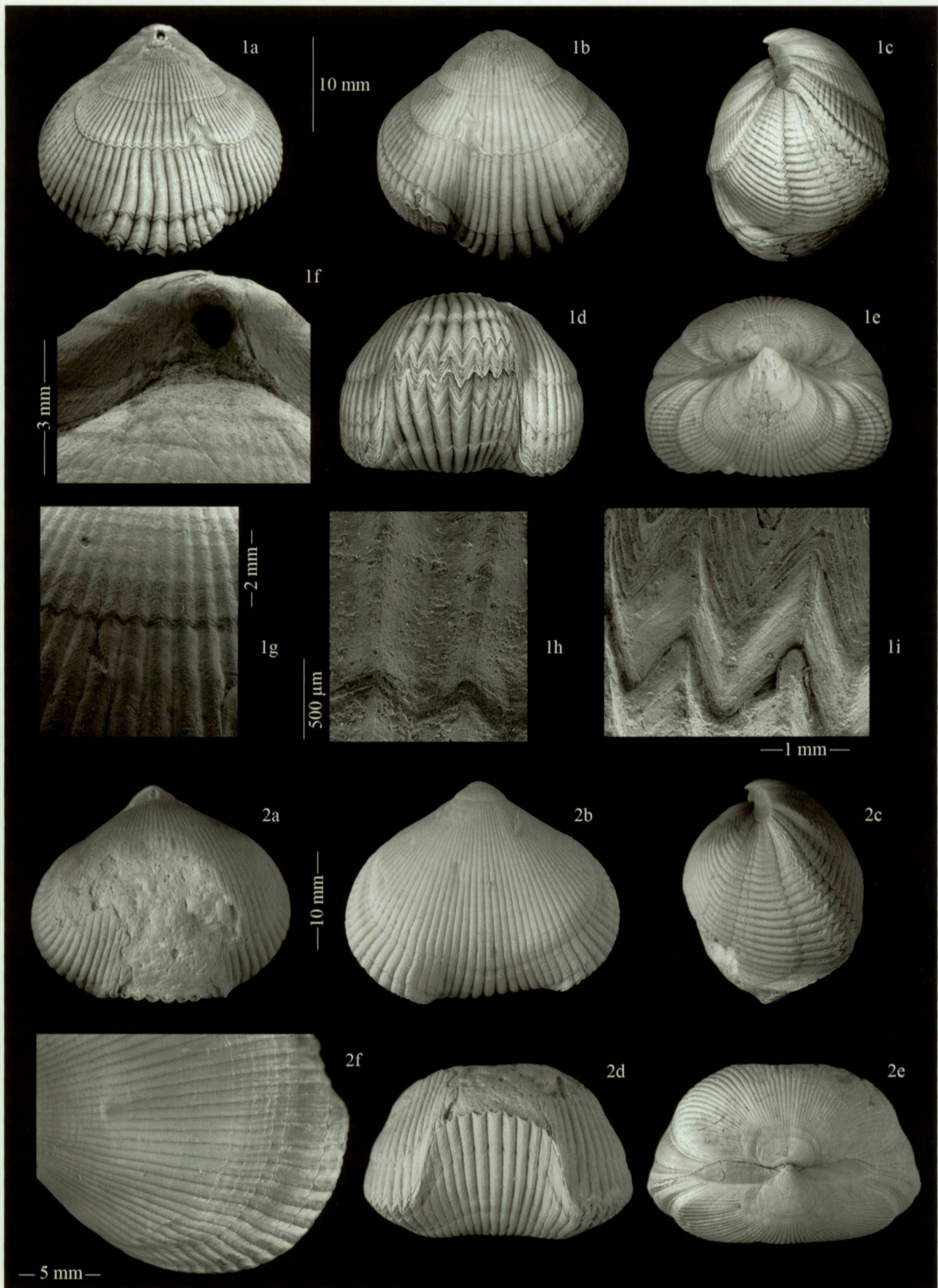


PLATE 1

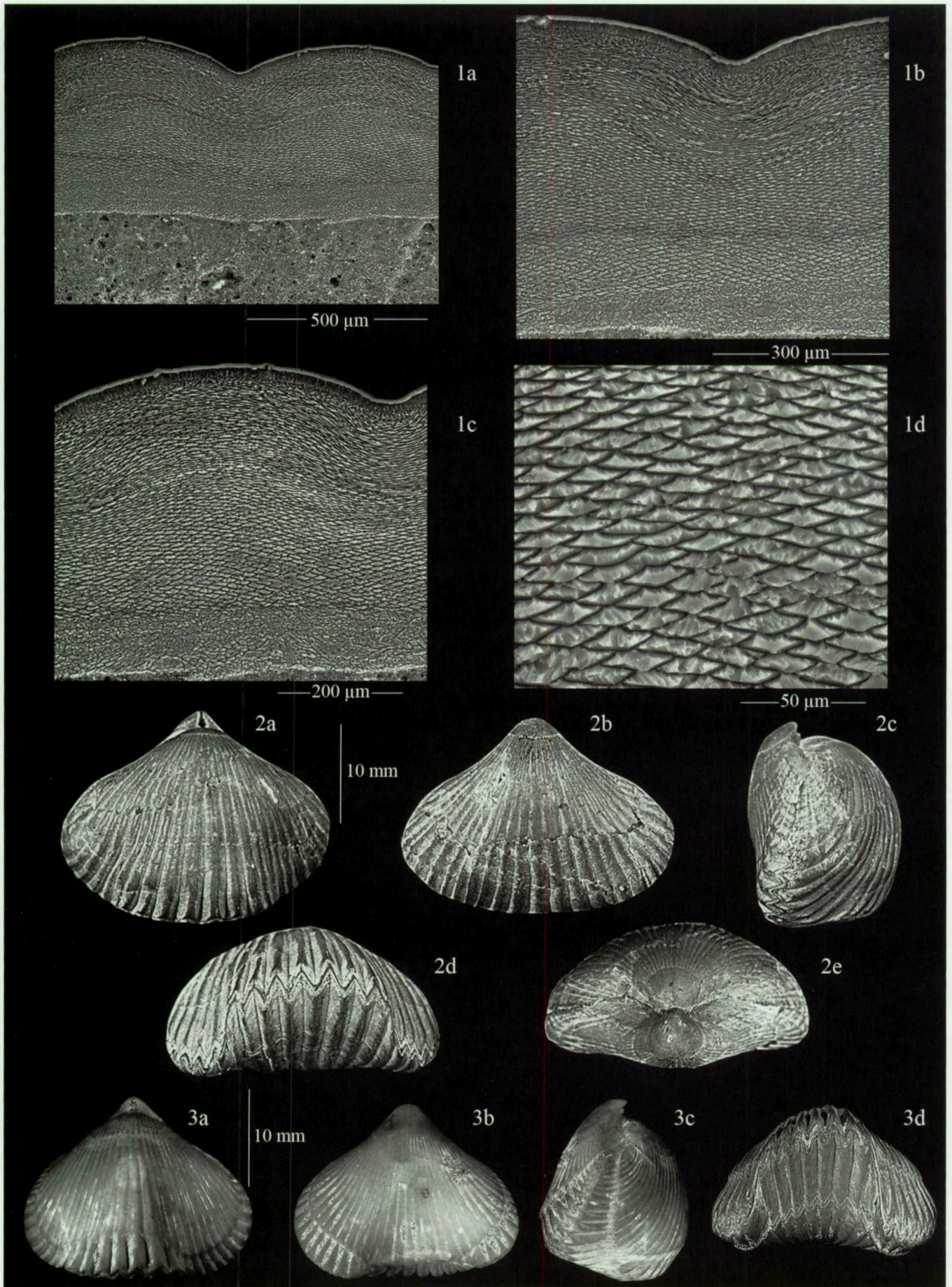
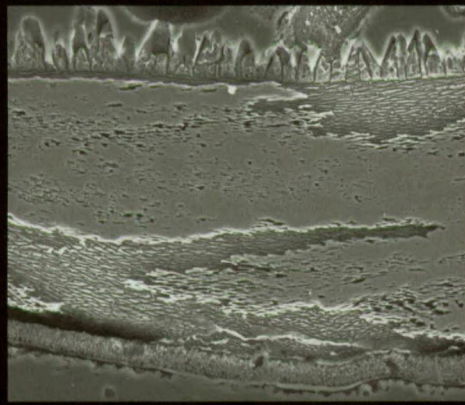
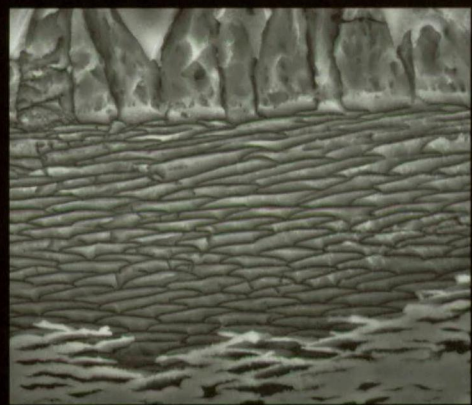


PLATE 2



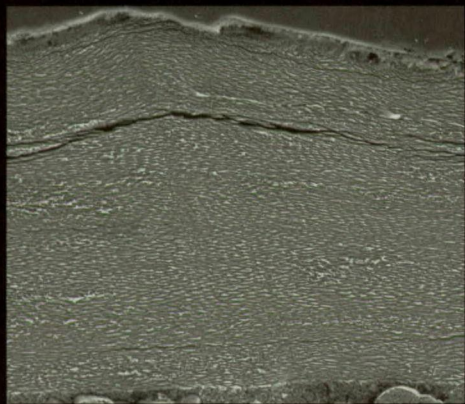
1a

—200 μm —



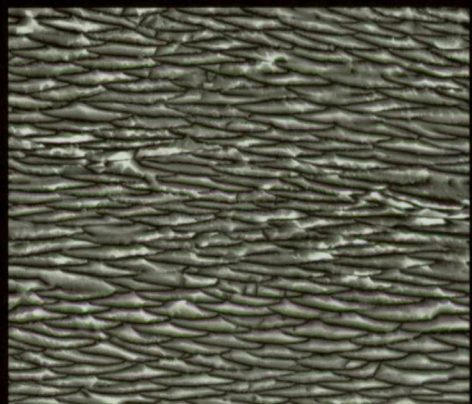
1b

—50 μm —



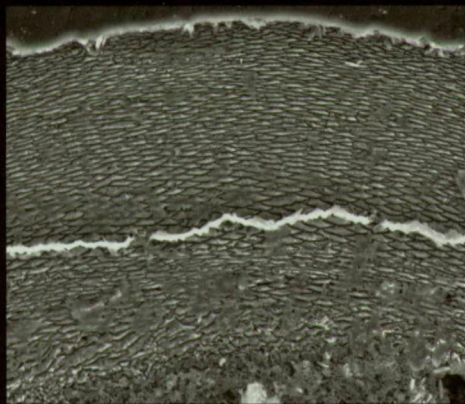
1c

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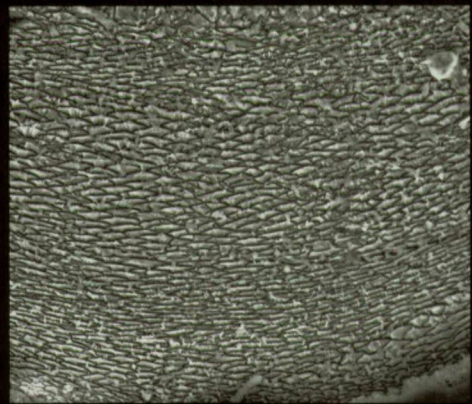
1d

—50 μm —



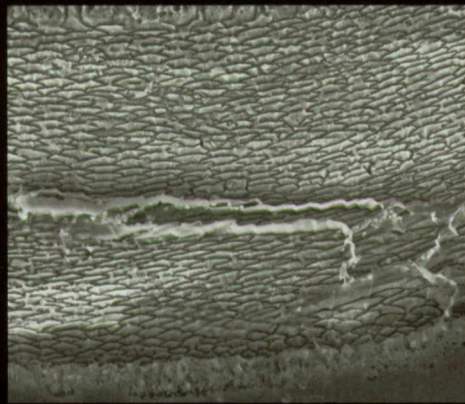
2a

—200 μm —



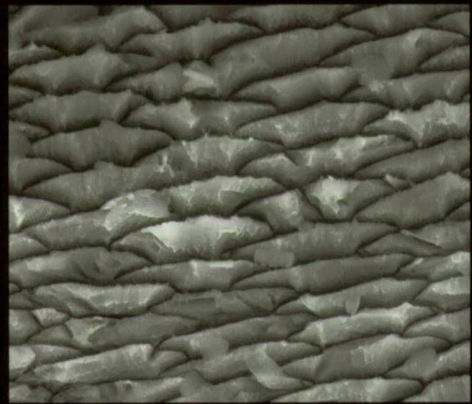
2b

—100 μm —



2c

—100 μm —



2d

—30 μm —