

New data about the evolution and phylogenetic relations of brachiopod families Basiliolidae and Cyclothyrididae on the basis of Late Cretaceous rhynchonellids from Bulgaria

Neda Motchurova-Dekova

National Museum of Natural History, 1000 Sofia

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Н. Мочурова-Декова — Новые данные об эволюции и филогенетических связях брахиоподных семейств Basiliolidae и Cyclothyrididae на основе позднемиоценовых ринхонеллид из Болгарии. На основе исследований болгарских позднемиоценовых ринхонеллид сделан опыт выяснить некоторые закономерности их развития и филогенетических связей. Сем. Basiliolidae представлено рр. *Orbirhynchia* и *Parthirhynchia*. Предполагается, что *Parthirhynchia* произошел непосредственно или через неизвестную междинную связь из *Orbirhynchia*. Сем. Cyclothyrididae представлено рр. *Cyclothyris*, *Cretirhynchia* и *Septatoechia*. Учитывая установленную широкую изменчивость внутренней и внешней морфологии *Cyclothyris*, автор разделяет мнение Лобачевой и Смирновой, что р. *Lamellaerhynchia* является синонимом р. *Cyclothyris*. Намечены и некоторые направления эволюции *Cyclothyris*. Что касается р. *Cretirhynchia*, на взгляд автора, вид ребер не может иметь высокую таксономическую стоимость и не может быть использован для его подразделения, так как установлены переходы между сериями „*Cr. limbata*” и „*Cr. plicatilis*”. С другой стороны, присутствие или отсутствие ребер может быть использовано для подразделения рода. Автор полагает, что р. *Septatoechia* произошел из р. *Cretirhynchia*, точнее из тех его представителей, которые характеризуются простыми ребрами.

Abstract. On the basis of investigations of Bulgarian Late Cretaceous Rhynchonellida an attempt is made to outline some trends in the development and phylogenetic relations among them. The fam. Basiliolidae is represented by the genera *Orbirhynchia* and *Parthirhynchia*. It is suggested that *Parthirhynchia* derived from *Orbirhynchia* directly or by unknown till now link. Fam. Cyclothyrididae is represented by the genera *Cyclothyris*, *Cretirhynchia* and *Septatoechia*. The author maintains the view of Lobacheva and Smirnova that *Lamellaerhynchia* should be considered as synonym of *Cyclothyris* taking into consideration the established vast variability within the inner and outer shell morphology of *Cyclothyris*. Some evolutionary trends in the development of *Cyclothyris* are outlined. For *Cretirhynchia* it is suggested that the type of the ribs cannot have a high taxonomic value and cannot be used for subdividing the genus because transitions between „*Cr. plicatilis*” and „*Cr. exculpta*” series are found. But the presence or absence of ribs can be used as characteristic for subdividing. It is considered that *Septatoechia* derived from some of simple ribbed *Cretirhynchia*.

Introduction

The evolution of the Mesozoic Rhynchonellida is discussed in detail by Ager et al. (1972). This work reflects the stage of knowledge of the rhynchonellid taxonomy at that time and the data about the Late Cretaceous Rhynchonellida are rather scanty. The

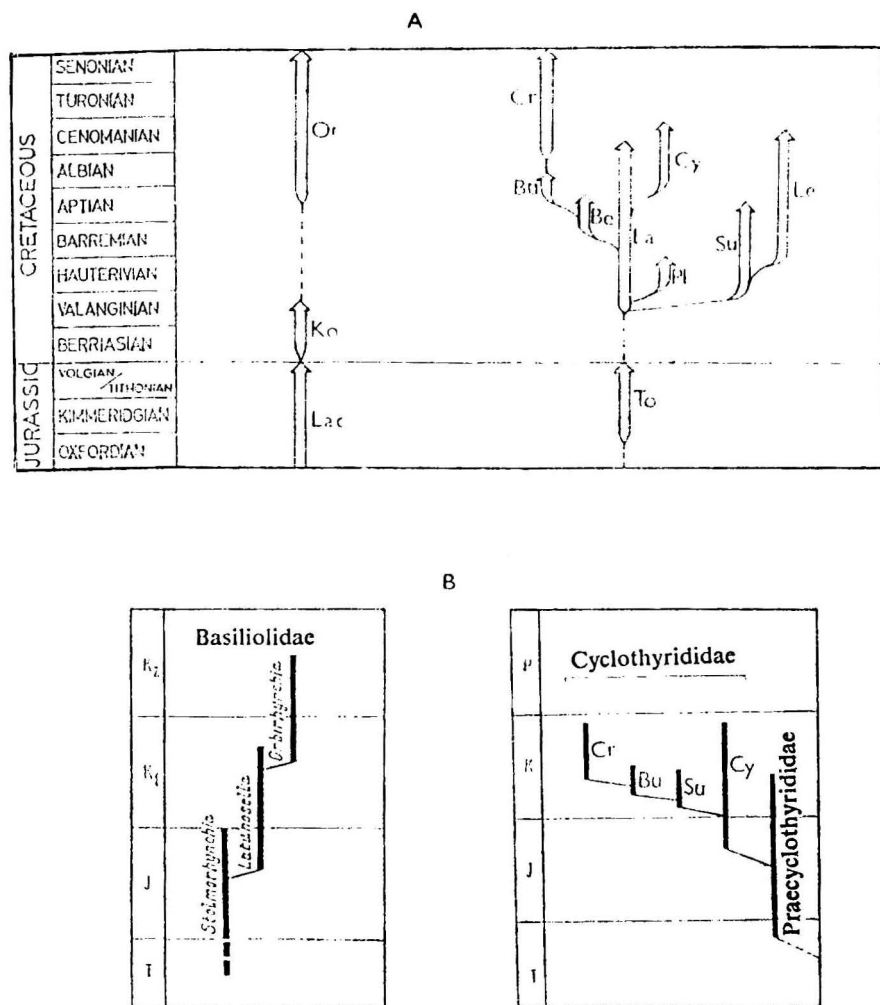


Fig. 1. Evolution of Cretaceous Rhynchonellida:

A — after Ager et al. (1972)

B — after Смирнова (1984)

Key to genera — Basiliolidae: *Kolhidaella*, *Lacunocella*, *Orbirhynchia*, *Parthirhynchia*, *Stomorhynchia*; Cyclothyrididae: *Belbekella*, *Burrihynchia*, *Cretirhynchia*, *Cyclothyris*, *Lamellaerhynchia*, *Lepidorhynchia*, *Plicarostrium*, *Septalocchia*, *Sulcirhynchia*, *Torquirhynchia*

evolution of the Late Cretaceous Rhynchonellida that will be discussed in the present paper according to Ager et al. (1972) is shown on Fig. 1, A. The taxonomic and phylogenetic problems of the Early Cretaceous Rhynchonellida are worked up at a modern level by Smirnova (Смирнова, 1984). In their exposition the author treats also the genera *Orbirhynchia*, *Cyclothyris* and *Cretirhynchia* that are widely distributed during the Late Cretaceous, too. Smirnova's phylogenetic schemes are shown on Fig. 1, B.

In the published taxonomic papers on Late Cretaceous Rhynchonellida the evolution and phylogenetic problems were not discussed. On the basis of Bulgarian material, as well as through a critical study of the works on Cretaceous Rhynchonellida an attempt

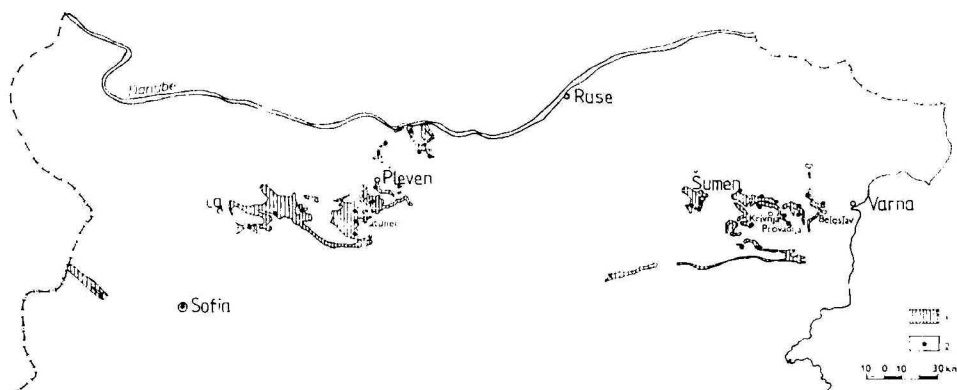


Fig. 2. Sketch map of the rhynchonellid localities in the Bulgarian Upper Cretaceous
1 — Upper Cretaceous outcrops; 2 — major rhynchonellid localities

is made below to outline some trends in the development and phylogenetic relations among the Late Cretaceous representatives.

Material

The investigations carried out on a plentiful collection of Late Cretaceous Rhynchonellida from Bulgaria served as factual background of the present paper. The collection consists of 2270 specimens of 48 species and subspecies from 42 localities in the Bulgarian Upper Cretaceous (Fig. 2). The taxonomical descriptions will be subjects of other separate papers. The phylogenetic relations among the Late Cretaceous rhynchonellids are discussed below at genus level, in some cases, when there was a sufficiency of material, also at species level, as Bulgarian representatives include 5 genera all together of two families: Basiliolidae and Cyclothyrididae.

Late Cretaceous development of fam. Basiliolidae Cooper, 1959

In the Bulgarian Upper Cretaceous the Basiliolidae are represented mainly by genus *Orbirhynchia* Pettitt (19 taxa). Only one well preserved specimen of genus *Parthirhynchia* Titova is found in the Middle-Upper Turonian rocks and its inner shell structure is not investigated. That is why, at this stage of knowledge, I share Smirnova's view (Смирнова, 1984) that *Orbirhynchia* derived from *Lacunosella*. *Orbirhynchia* appeared in the Albian and till now it was recorded for certain last in Upper Maastrichtian rocks. (These are *Orbirhynchia granum* Pettitt and *Orbirhynchia* sp. found in the Bulgarian Upper Cretaceous.) The genus *Parthirhynchia* is known only from one publication so far (Титова, 1980). The unique Bulgarian specimen found, judging by its outer morphology, belongs to that genus for certain. Proceeding from the published set of serial sections (Титова, 1980), where thin dental plates, wide divided hinge plates, euseptum, and also the typical for *Lacunosella* and *Orbirhynchia* additional crural plates (although the crura are prefalcifer) can be seen, I presume quite relatively that *Parthirhynchia* derived directly or through unknown intermediate link from *Orbirhynchia* in Turonian time. The last *Parthirhynchia* are known from Upper Maastrichtian rocks in Turkmenistan (Титова, 1980).

The phylogenetic scheme proposed here for *Orbirhynchia* and *Parthirhynchia* is shown on Fig. 3, A.

Explanations to the plates

PLATE I

- 1a, b, c — *Cyclothyris?* sp., spec. No 3067, Katunec, Kalen Formation, Upper Santonian; $\times 1$, 22.
2a, b, c — *Cyclothyris?* sp., spec. No 3670, Krivnja, Šumen Formation, Upper Santonian; $\times 1$, 9.
3a, b, c — *Cyclothyris globata* (Arnau d), 1877, spec. No 3680, Krivnja, Šumen Formation, Upper Santonian; $\times 1$, 9.
4a, b, c — *Cyclothyris globata* (Arnau d), 1877, spec. No 1696, Šumen, Šumen Formation, Upper Santonian; $\times 1$, 9.

PLATE II

- 1a, b, c — *Cretirhynchia?* sp., spec. No 2054, Provadija, Šumen Formation, Upper Santonian; $\times 1$, 9.
2a, b, c — *Cretirhynchia?* sp., spec. No 1695, Šumen, Šumen Formation, Upper Santonian; $\times 1$, 8.
3a, b, c — *Cretirhynchia?* sp., spec. No 3151, Šumen, Šumen Formation, Upper Santonian; $\times 1$, 7.
4a, b, c — *Cretirhynchia* sp., spec. No E-240, unique symmetrical specimen found, Šumen, Šumen Formation, Upper Santonian; $\times 1$, 22.

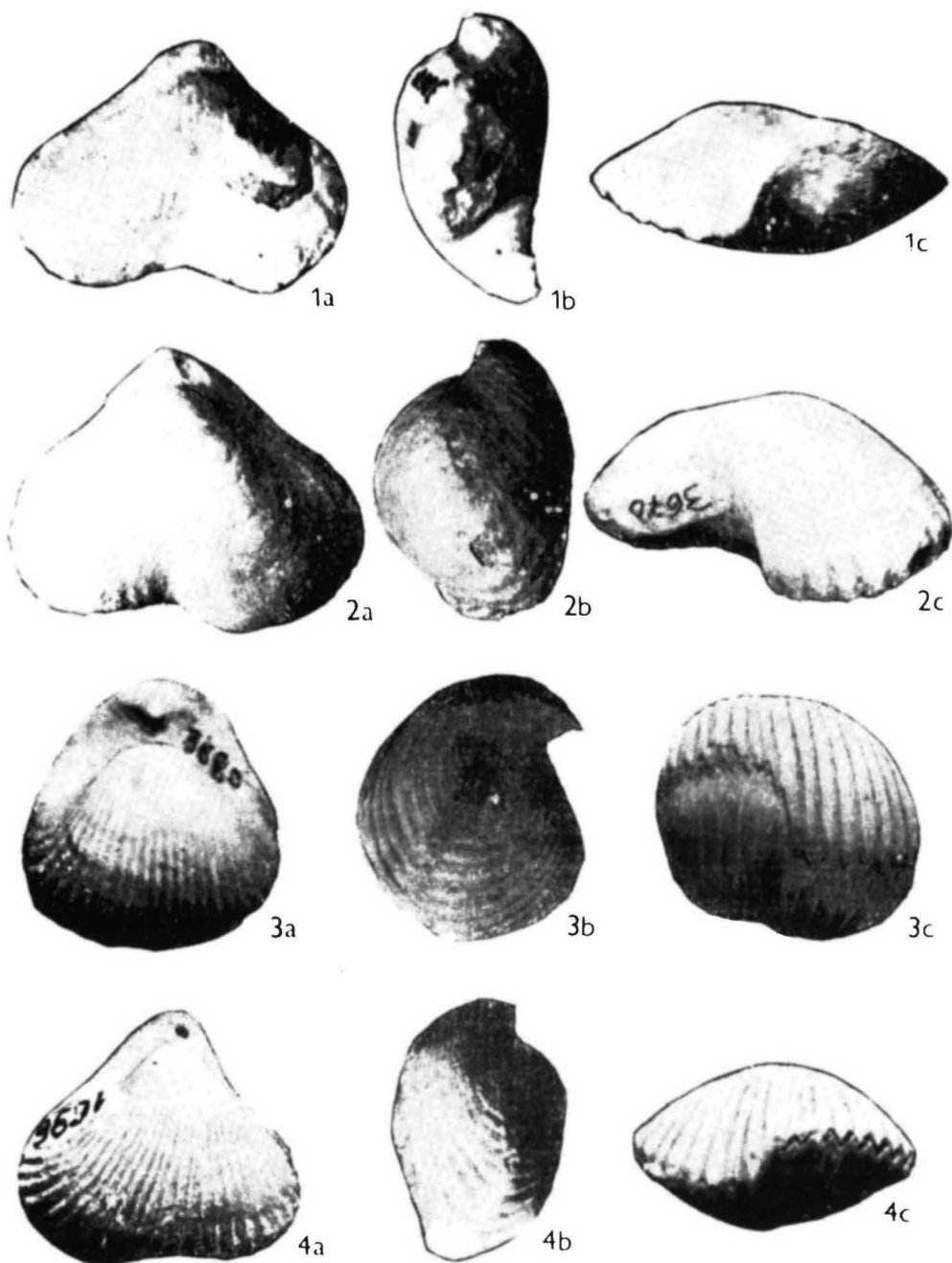
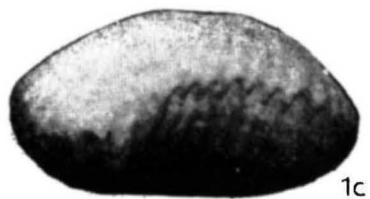
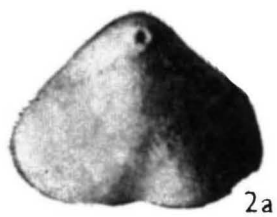


PLATE II



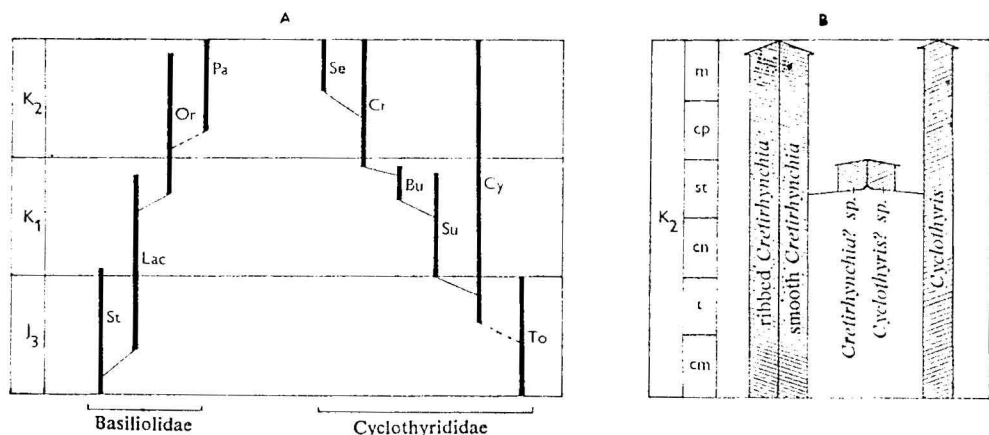


Fig. 3. A — schemes of the evolutionary relations among Late Cretaceous Rhynchonellida according to the present work; B — scheme of the taxonomical problem about the Late Santonian *Cyclothyris?* sp. and *Cretirhynchia?* sp. found in Bulgaria Key to genera — Basiliolidae: *Lacunosella*, *Orbithynchia*, *Patrhirhynchia*, *Stolomorphynchia*; Cyclothyrididae: *Burrirhynchia*, *Cretirhynchia*, *Cyclothyris*, *Septatoechia*, *Sulcirhynchia*, *Torquirhynchia*

Late Cretaceous development of fam. Cyclothyrididae M a k r i d i n, 1964

This family is one of the main stocks of Mesozoic Rhynchonellida. Brachiopods of different size are referred to it, most often with coarse ribs, average developed or reduced median septum, absent septalium, without cardinal process, crura are radulifer or turn into canalifer. Another common characteristic is the development of the beak, which is erect or suberect, with a big hypothryid foramen, surrounded by outer pedicle collar (Ager et al., 1972). Unlike Basiliolidae, Cyclothyrididae are characterized by development of fibres of a smaller size in the secondary shell layer (К а м ы ш а н, 1977; М о т ч у р о в а - Д е к о в а, 1994).

According to Ager et al. (1972) the traces of the forerunners of this group fade into the beginning of the Triassic. In the Early Jurassic the flourishing of this stock began. One of its offshoots is the Late Jurassic genus *Torquirhynchia* C h i l d s (Fig. 1, A). These are asymmetrical rhynchonellids, some of them are found in perireefal limestones. It is considered that *Torquirhynchia* is the link between Jurassic and Cretaceous cyclothyrids, grouped around *Cyclothyris* M c C o y. Most of them are introduced by Burri (1953, 1956). Ager et al. (1972) accept for valid the names of all genera, described by Burri — *Lamellaerhynchia*, *Sulcirhynchia*, *Lepidorhynchia*, *Plicarostrum*. The same authors consider that *Belbekella* (М о й с е е в, 1939) existed separately from *Cyclothyris*, although they doubt that most probably in Western and Soviet literature are introduced parallel names for one and the same genera. Smirnova and Lobacheva (С м и р н о в а, 1963, 1984; Л о б а ч е в а, 1974) consider *Lamellaerhynchia* and *Belbekella* as junior synonyms of *Cyclothyris*. Ager et al. (1963), Ager (1964) and Ager et al. (1972) take the view that *Lamellaerhynchia* is a separate genus from *Cyclothyris*, although they do not fail to mention their great similarity. According to them the differences are in minor internal details in dental lamellae, hinge-plates and median septum and the outer differences are more important — *Lamellaerhynchia* has bifurcating costae, shorter beak and a stronger tendency towards asymmetry. I think the last pointed out difference has to be rejected because this feature is quite often observed in *Cyclothyris*. Although typical representatives of *Lamellaerhynchia* are absent in Bulgaria, I maintain the view of Smirnova and Lobacheva. A reason for

this are the investigations of the intraspecies variability of the inner and outer shell morphology in a set of sections from the Cenomanian species *Cyclothyris difformis* (Valenciennes in Lanmarch) found in one locality in the same layer of Madara Formation near Beloslav. In some specimens bifurcating costae can be observed and some serial sections show the typical for *Lamelaerhynchia* inner shell structure. The same problem is treated and the same point of view is supported by Nekvasilova (1973). The earlier proposed emended diagnosis of g. *Cyclothyris* (Motchurova - Dekova, 1994) includes in its content *Lamelaerhynchia*, too. If one takes such point of view, *Cyclothyris* turns out to be a wide distributed and a long existing genus. The lowest stratigraphic level where it occurs is Upper Valanginian and I extend the highest one to Maastrichtian. A number of evolutionary trends were outlined during the investigations of Bulgarian material. They will be mentioned in brief: 1. Shells of smaller size in the beginning and at the end of the period of existence and bigger shells in the middle of it (Albian — Cenomanian); 2. From a development only of symmetrical representatives in the beginning, through species that develop symmetrical as well as asymmetrical specimens ("difformis" type), towards species of only asymmetrical specimens (although some species continue developing "difformis" type); 3. Decreasing of the foramen size and distinctness of the beak ridges, most probably related with change of the functional role of the pedicle; 4. Possible tendency towards passing from ribbed to smooth shell is also outlined having in mind the not described yet probably new species *Cyclothyris?* sp. (Plate I, figs. 1, 2) which is found in the highest levels of Upper Santonian in North-East and Central-North Bulgaria. I think that *Cyclothyris globata* (Arnau d), (Plate I, figs. 3, 4) should be considered as a forerunner of *Cyclothyris?* sp. in the evolutionary chain. These two species are almost identical, except for the smooth shell of *Cyclothyris?* sp. The bulk of ribbed *Cyclothyris globata* are found just below the level with *Cyclothyris?* sp.

Another typical Late Cretaceous genus found in Bulgaria is *Cretirhynchia* Pettitt. Inwardly it has radulifer crura and not very high median septum. Outwardly it is characterized by poorly developed sulcus and fold and various ribbing: simple ribs, dichotomizing of some of them, reduction of ribs near the commissures or nearly smooth shell. Ager et al. (1972) and Smirnova (Смирнова, 1984) presume that *Cretirhynchia* derived from *Burrirhynchia* Owen (Fig. 1, A, B). In some authors' opinion *Cretirhynchia* has to be divided but this has not been done so far. Because of the limited number Bulgarian representatives the subdivision of the genus has not been undertaken. In my opinion, however, the ribbed "*Cr. plicatilis*" and "*Cr. exculpta*" series should be separated from the smooth "*Cr. limbata*" series. The united first two series should include not only specimens with dichotomous or reducing ribs, but also such with simple ribs (the later have not been differentiated in a separated series till now). Such approach is supported mostly by the fact that in Bulgaria mainly species with simple ribs were found and they cannot be always distinguished from the representatives of "*Cr. plicatilis*" and "*Cr. exculpta*" series. In the case when specimens from the last two series have not developed a mature stage it also cannot be determined exactly to which group they belong to. It can be concluded that the character of the ribs have not a high taxonomic value and cannot be used for subdividing the genus *Cretirhynchia*. But the presence or absence of ribs can be used as characteristic for subdividing the genus because transitions between ribbed and smooth *Cretirhynchia* are not registered till now. From the smooth or the so-called "*Cr. limbata*" forms probably derived the tertiary fine-ribbed or smooth Hemithyrididae (Popiel - Barczyk, 1988).

I refer with a certain doubt to *Cretirhynchia* the probably new and not described yet *Cetirhynchia?* sp. (Plate II, figs. 1-3). These rhynchonellids are asymmetrical that is untypical for *Cretirhynchia*, but that is often observed in other Cyclothyrididae. By inner shell morphology *Cetirhynchia?* sp. corresponds to the generic diagnosis of *Cretirhynchia*. Presumably this uncommon species derived from some smooth *Cretirhynchia*.

chia when by unknown till now reason in the genetic fund of some representatives of the genus the asymmetry came into existence and stabilized. As a certain proof of this statement may serve a unique find of a symmetrical smooth specimen *Cretirhynchia* sp. (Plate II, fig. 4). I found it together with many specimens of *Cretirhynchia*? sp. and it is outwardly almost identical to them except for the symmetrical shell. It can be suggested that it is a specimen in which the feature asymmetry has not stabilized in the genetic fund. While studying the ontogenies of *Cretirhynchia*? sp. in a set of specimens of different size I established that the younger the specimen was, the better the typical features of *Cretirhynchia* were distinguished. But with age the inner shell structure "drifted away" from the characteristics of *Cretirhynchia*. That supports the assumption that *Cretirhynchia*? sp. derived from some typical smooth *Cretirhynchia* (Fig. 3, B).

It is interesting to note also that the inner shell structure of the unusual species *Cyclothyris*? sp. and *Cretirhynchia*? sp. corresponds to the genus, they are referred to under question, whereas the outer one corresponds to the other genus. Still more curious is the fact that these two strange groups can be found together in one and the same localities in the Upper Santonian in North-East Bulgaria. Their representatives could not be distinguished by outer morphology and it was necessary to make serial sections and only then do one determine that some correspond to *Cyclothyris* diagnosis and other — to *Cretirhynchia* diagnosis. The taxonomical problem could not be definitely settled at this stage of study (Fig. 3, B). I consider, however, that it doesn't concern simple homeomorphy. I exclude absolutely the possibility the smoothing of the shell to be a result of bad preservation of the material. In many Upper Santonian localities the smooth *Cyclothyris*? sp. and *Cretirhynchia*? sp. are found together with the ribbed *Cyclothyris globata*. The latter has well distinguished ribs and neither the process of fossilization, nor the subaerial weathering influenced its ribbing. Of course the possibility the costal *Cyclothyris globata* to be synchronously transported or resedimented should not be excluded. But the fact that the smooth and the ribbed rhynchonellids are buried together is an evidence a priori that they "endured together" all processes after that and their stage of preservation is one and the same. Thus, there is no reason to assume that a particular process could have a selective influence over a part of the buried fauna, i. e. the possible "smoothing" is a process or fact that existed before the burial. It is likely that it is a genetic characteristic. But before this assumption would be accepted the rest of the macrofauna should be investigated in order to search for possible similar aberrations and to discuss the probability some external factors to have caused them. It is important also to study the chemical composition of the shell and embedding sediments in order to search for positive anomalies of some elements, which at this stage could only be assumed.

When Lobacheva and Titova (Лобачева, Титова, 1977) introduced the genus *Septatoechia* they referred it to Cyclothyrididae without commenting upon its phylogenetic relations with other representatives of the family. Although this genus has high and thin median septum (not typical for *Cyclothyrididae*) the rest of its characteristics refers it certainly to this family: well developed ribs, outer pedicle collar; hinge plates, crural bases and radulifer crura similar to those of the nominate genus *Cyclothyris*. When the authors described *Septatoechia* they referred to it 3 species: the Maastrichtian *S. inflata* Titova and *S. amudariensis* (Katz) and the Late Albian *S. globulosa* Lobacheva. A set of serial sections was published for each of them. It is interesting that the septum of the first two Maastrichtian species is well-notable in the inner relief of the brachial valve and is not "coated" with callus, although other inner structure elements are blurred by such thickening. So the septum has needle-shaped profile (Лобачева, Титова, 1977; p. 104, 107). However the septum of the Late Albian *S. globulosa* is "submerged" in callus and shows itself on the relief of the brachial valve not until 2.7 mm after the valve appearance on the serial sections. Till its disappearance the septum remains thick and round spike-like (Лобачева, Титова, 1977, p. 110). The median septum of all Bulgarian representatives of

Septatoechia shows morphology similar to the first type, i. e. it is thin and not complicated by callus. Going back to the description of *S. globulosa* (Лобачева, Титова, 1977, p. 108) the reader can note that its deltidial plates are divided. This fact absolutely excludes *S. globulosa* from the framework of genus *Septatoechia* and makes it very close to the Late Aptian — Early Albian genus *Burrirhynchia* Owen, 1962. The median septum of the later is high too, the hinge plates, crura and teeth have similar morphology to those of *S. globulosa*. If one excludes *S. globulosa* from the species belonging to *Septatoechia*, the question about the rather long interval of absence of its finds is settled also (till now *Septatoechia* was absent from Cenomanian to Lower Campanian). Thus representatives of *Septatoechia* are found with certainty from Upper Campanian to Upper Maastrichtian without a break. I consider that *Septatoechia* is connected with *Cretirhynchia* (Fig. 3, A) and to be more precise with the simple ribbed *Cretirhynchia*. The following can support this statement: similarity in the morphology of the dental plates (parallel or more often convergent), dorsally directed arcs of the radulifer crura, a symmetrical shell, a shorter beak, a smaller foramen and more rounded beak ridges, and also diamond-shaped to square fibres of the secondary shell layer in the representatives of both genera (unlike the same characteristics in *Cyclothyris*). But in contrast to *Cretirhynchia* the morphology "formation" in *Septatoechia* passed in the direction of confirming a high and thin septum, without "affinity" of callus heaping, shells of larger size and always simple, slightly sharp costae.

At the end of Maastrichtian all the three examined genera of Cyclothyrididae disappeared which are its last representatives.

Conclusion

The investigations of Bulgarian Late Cretaceous rhynchonellids afforded an opportunity to add to the picture of the evolution of the Late Cretaceous representatives of Basiliolidae and Cyclothyrididae a number of new elements and to outline some trends in the development and phylogenetic relations among them. I adopt the phylogenetic schemes of Smirnova (1984) and supplement them.

As regards the fam. Basiliolidae I suggest that *Parthirhynchia* derived from *Orbirhynchia* directly or by unknown till now link. As for genus *Cyclothyris* I maintain the view of Lobacheva and Smirnova (Лобачева, 1974; Смирнова, 1984) that *Lamellaerhynchia* should be considered as synonym of *Cyclothyris* taking into consideration the vast variability within the inner and outer shell morphology established in the course of the taxonomic work on Bulgarian representatives of the later. I consider that the type of the ribs cannot have a high taxonomic value for genus *Cretirhynchia* and cannot be used for subdividing it. I suggest that *Septatoechia* derived in Late Campanian from some of simple ribbed *Cretirhynchia* which is supported by a number of morphological similarities.

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