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ERIDOSTRACA — A NEW SUBORDER OF OSTRACODS AND ITS PHYLOGENETIC SIGNIFICANCE

Abstract. — This paper reports the results of investigations on the structure and texture of multilamellar ostracod carapaces and of comparative studies on the microstructure of the shell in Leperditiidae Jones and Healdiidae Harlton. The writer's inferences are that the multilamellar ostracod carapace has been derived from Conchostraca (Phyllopoda) with concentric growth lines. The consequent result is the separation of the group Eridoconchinae Henningsmoen into a distinct suborder — the Eridostraca. A new genus, *Aberroconcha*, has been established in this suborder and two species from the Middle Devonian of Poland are described as new: *Aberroconcha plicata* and *A. devonica.* Moreover, one new species of *Eridoconcha* Ulrich & Bassler, equally of Devonian age, is described: *Eridoconcha granulifera.* A concept of the diphyletic origin of ostracods is postulated, based on the morphology and microstucture of their carapace.

INTRODUCTION

The here reported results of studies on the origin and structure of the ostracod carapace do not clear up all the problems concerning this matter. The question, given here the most attention, is that of the occurrence of multilamellar shells of certain ostracods which have, since long, been recorded in palaeontological literature and known as Eridoconchinae Henningsmoen, 1953. Detailed studies on the morphology of the carapace of Ordovician and Devonian representatives of these ostracods reasonably suggest their separation into a new suborder, for which the name Eridostraca is introduced.

The shells of these ostracods are multilamellar, being composed of up to 11 lamellae underlying one another and expressing the successive growth stages. In morphology and structure they resemble the carapace of Conchostraca (Phyllopoda). In these, however, the carapace is made up mostly of chitin, or of chitin permeated with calcium carbonate, less often of calcium carbonate only. To the new suborder Eridostraca the writer has referred, besides the genus *Eridoconcha,* in 1923 established by Ulrich and Bassler, also his new genus *Aberroconcha* described in the present paper, as well as genera with the carapace up to 6 lamellae, sometimes even only unilamellar, but displaying close morphological and genetic relationships with the just mentioned genera. Such are the genera *Cryptophyllus* Levinson, 1951, *Milleratia* Swartz, 1936, *Schmidtella* Ulrich, 1892, and probably *Paraschmidtella* Swartz, 1936. The above enumerated genera correspond to a morphological series permitting to understand the origin of the unilamellar carapace of typical ostracods.

The supposition here made as to the derivation of the ostracod carapace from a conchostracoid type is based on a purely theoretical conception, advanced in 1892 by the zoologist Grobben. It is confirmed by fossil material with regard to the Eridoconchidae and to the genera *Cryptophyllus* Levinson, *Milleratia* Swartz and *Schmidtella* Ulrich, probably also to the family Conchoprimitiidae Henningsmoen (emend. Pokorný, 1958). On the other hand, the Leperditiidae Jones, 1856, owing to fundamental structural differences of the carapace, have most probably different ancestors, not closely allied with Eridostraca n. subordo.

The ancestors of the multilamellar ostracods may possibly be certain Conchostraca with concentric growth lines, such as the Lower Cambrian genera *Fordilla* Walcott and *Lepiditta* Matthew, known already from the Lower Cambrian and united by Kobayashi (1952) into the family Lepidittidae. On the base of ornamentation their carapace may be presumed to have consisted, similarly as in representatives of recent Conchostraca, of numerous lamellae underlying one another. It is not impossible that these forms may have been the ancestors not only of the Palaeozoic, but also of the living representatives of this group of animals. Eridostraca may possibly also have evolved from this assemblage of forms. The evolution of this group was expressed by the gradual increase of the ability to moult, which finally led to the development of a strong, unilamellar carapace of the ostracoid type. The above considerations have suggested a revision of Levinson's (1951) hypothesis, known as the „retention of moults" which, it is shown, does not adequately interpret the occurrence of multilamellar shells.

The hypothesis here advanced, as regards the carapace of ostracods consisting of successive moultings, is based, in the first place, on an analysis of the structure of multilamellar valves of living Conchostraca whose carapace, formed of successive instars, increases throughout the animal's life-time. Analogous conditions must have occurred in the group of Eridostraca. Their carapace consists of calcareo-chitinous lamellae displaying a cryptocrystalline microscopic structure. In this it does not differ from representatives of the group of Palaeocopa, the Leperditiidae Jones excepted. The latter ostracod group is known to have the carapace built of distinct calcite prisms. A similar structure of the shell is likewise noted in one of the most primitive Podocopa (sensu G. W. Müller, 1894), namely the Healdiidae Harlton, 1933. Studies on the microstructure of the carapace of Eridostraca and many representatives of the Beyrichiacea

Jones, 1854, have revealed many features in common, while fundamental structural differences have been ascertained in this respect in Leperditiidae and Healdiidae. Detailed comparative studies of the shells in these groups suggest the origin of the ostracoid carapace to have been associated with many groups of Cambrian crustaceans referred to Archaeostraca Claus. This problem, however, is far from being definitely cleared up in the present paper. Some light only is being thrown on phylogenetic relations, suggested by shell structure, but these call for additional more extensive comparative studies in other groups.

The basic and comparative materials used in preparing this paper include: Cambrian representatives of the Archaeostraca (collected by late Prof. J. Samsonowicz), fossil and living Conchostraca and many groups of ostracods from various periods and regions. The basic material has been collected from Middle Devonian strata in the Holy Cross Mountains — Góry Świętokrzyskie (the Łysogóra region) which represents a classical section of that age in Poland. Abundant ostracods of this section indicate close connections with the Devonian ostracod fauna in the Eifel Mountains. The occurrence is here noted of ostracod species and genera, lately recorded from Western Germany (Krömmelbein, 1950, 1952, 1953, 1954, 1955), namely: *Polyzygia symmetrica* Gürich (Adamczak, 1956), *Poloniella tertia* Krömmelbein (Adamczak, 1959), *Bairdia seideradensis* Krömmelbein (Přibyl, 1953), representatives of *Kozłowskiella* (Přibyl) and many species belonging to the genera *Bairdiocypris* (Kegel), *Pachydomella* Ulrich, *Condracypris* Roth, and others. It is not excluded that a number of them may be used in stratigraphic correlation of these far distant areas.

Faunal similarities are likewise noted with analogous deposits in the Soviet Union, in the first place with the „Main Devonian Area" where the presence has been ascertained of the same species as those occurring in the Holy Cross Mountains, partly also in Western Germany, namely: *Polyzygia symmetrica* Gürich (Adamczak, 1956), *Poloniella* (= *Dizygopleura*) *curta* (Polenova) and *Bairdia seideradensis* Krömmelbein. There is a number of genera common to all these areas, such as *Bairdiocypris* (Kegel), *Euglyphella* Warthin (Polenova, 1960c), *Bufina* Coryell & Malkin and others occasionally represented by extremely numerous species. Some faunistic elements of the Łysogóra region are likewise present in North-American faunas, such are: *Poloniella cingulata* Warthin, *Ponderodictya punctulifera* (Hall), *Eridoconcha rugosa* Ulrich & Bassler, *E. arsiniata* (Stover), *Ctenoloculina cicatricosa* (Warthin) and the genera *Aberroconcha* n. gen., *Hollinella* Coryell, *Abditoloculina* Kesling, and others.

The excellent state of preservation of ostracods from the Devonian of the Holy Cross Mountains, their diversity and abundance, make this region one of marked palaeogeographical interest. It is a cross-road of faunal elements from the east and the west, as is among others also indicated by the presence of representatives of Eridoconchidae. Genera of this group (*Aberroconcha* n. gen. and *Eridoconcha* Ulrich & Bassler) have a very wide geographic and stratigraphic range. Beginning with the Ordovician they occur throughout the United States of America, as well as in the Siberian Platform (USSR) and in later times (Devonian) in Europe, too.

Use has been made in the preparation of this paper of fossil material collected from four Middle Devonian profiles, involving Couvinian beds at Wydryszów and Grzegorzowice, and Givetian — at Skały and Świętomarz-Śniadka. Devonian outcrops at the just mentioned localities have yielded, in addition to ostracods, representatives of Tabulata (Stasińska, 1958), Tetracoralla (Różkowska, 1954, 1956), Brachiopoda (Biernat, 1954, 1959) and Trilobita (Kielan, 1954; Osmólska, 1957). The ostracod fauna is diversified and many species are very abundant, however such groups as the Eridoconchidae are extremely rare. On the whole, only some scores of specimens belonging to species of the genera *Aberroconcha* n. gen. and *Eridoconcha* Ulrich & Bassler have been discovered in the material containing many tens thousands of various ostracod carapaces. These have been obtained by washing marly and marly-argillaceous rocks more than half a ton in weight. With a few exceptions, the specimens are in a very satisfactory state of preservation. The shells are often filled with calcite, thanks to which very delicate internal chitinous structures have not been damaged.

Besides forms described at some length in the present paper, the writer had the advantage of having at his disposal comparative material collected outside of Poland, most useful in his studies on the structure and texture of the carapace. Very valuable specimens of *Aberroconcha* from the Ordovician of the Siberian Platform have been most kindly supplied by Dr V. A. Ivanova of the Palaeontological Institute in the Academy of Sciences of U.S.S.R. in Moscow. These have been likewise described and included in the chapter on systematics. Moreover, several specimens of representatives of the genera „*Eridoconcha*" and *Cryptophyllus* Levinson have been graciously sent by Dr S. A. Levinson of the Humble Oil and Refining, Co. of Houston, Texas. Specimens of *Conchoprimitia* Öpik were received through the courtesy of Dr A. I. Netzkaja from the VNIGRI Institute of Leningrad, while many Devonian species from the Soviet Union have been kindly contributed by Dr E. N. Polenova of the same Institute.

For the sake of comparison the writer has made use of living Adriatic ostracods turned over to him by Dr J. Małecki of the Palaeozoological Laboratory at the Academy of Mining and Metallurgy of Cracow, also of Conchostraca (*Estheria* sp.) kindly supplied by the Zoological

Institute of the Warsaw University. Moreover the writer has found some interesting material of Conchostraca among Prof. R. Kozłowski's material of Upper Silurian rocks from Podolia. Many valuable specimens have also been collected by the writer from Ordovician and Silurian erratic blocks in Poland.

The present paper has been written at the Palaeozoological Laboratory of the Warsaw University, under the guidance of Prof. R. Kozłowski, to whom the writer here expresses the warmest thanks for the unrestricted assistance tendered to him. Acknowledgements are also due to all the persons mentioned hereabove, for their friendly attitude in making available to him so many, often very valuable, specimens.

The drawings and figures in this paper have been done by Mrs K. Budzyńska and Mrs D. Platajs, the microscopic sections have been photographed by Miss L. Łuszczewska, the English translation of this paper has been made by Mrs J. Humnicka, and the writer thanks them cordially, too.

METHODS

Problems here discussed concerning the origin and phylogeny of ostracods have been studied in the first place on an analysis of the skeletal parts of fossil forms. Particular attention was focussed on the structure and microscopic texture of shells. Palaeontological literature contains but very meagre data connected with such problems. Comparative systematic studies of this type have not, thus far, been made of shells pertaining to different groups of ostracods, even though they have proved of importance in what phylogeny is concerned. This is all the more so considering that criteria for recent forms cannot always be used in the case of many fossil groups. These studies necessitate very special and time-consuming methods, such as thin precisely oriented sections, serial sections, fluoridization (Sohn, 1956; Upshaw, Todd & Allen, 1957), treatment of shells in acids, etc.

The complicated structure of the carapace of Eridoconchidae Henningsmoen has, in the first place, been investigated by means of serial sections and fluoridization. The latter method is a very helpful one since it permits the observation of internal morphology without destroying the shell. The sections through carapaces of Eridoconchidae, as well as of Leperditiidae Jones and Healdiidae Harlton, have led to a thorough knowledge of their structural elements having taxonomic significance. By those methods it has been possible to clarify the complicated internal structure of the carapace of *Aberroconcha* n. gen. The dorso-central parts of carapace lamellae invaginated into the interior of the valve (fig. 1), occupy a space hardly 0.1 mm in width. In order to ascertain the exact sequence of the growth stages and their mutual relation, the section must cut these elements centrally, for outside of the area of maximum convexity of lamellae they are intimately confluent and resemble the structure of valves in the genus *Eridoconcha* Ulrich & Bassler. Observations of valves in transversal plane were supplemented by serial sections (text-pl. I), cut parallel to the longitudinal axis of the carapace. These serial sections have made it possible at least partly to reconstruct the spatial structure of the shell and the mode of development of the dorsal part (fig. 2 and 6).

On thin slides the presence has been ascertained in valves of *Bairdiocypris* (Kegel), *Pachydomella* Ulrich and *Condracypris* (?) sp. of an internal, extremely thin and strongly chitinized lamella (fig. 14 *A-C*).

As has already been mentioned above, fluoridization of shells is markedly helpful in the morphological studies of the carapace. Moreover, this method has been used when investigating the structure of the carapace. Recent ostracod valves are known to consist of three layers, the outer and the inner ones being chitinous, the middle one — calcareous. Among fossil forms a three-layered carapace has been ascertained in Leperditiidae only (Levinson, 1951). In other groups of fossil ostracods the carapace is not so well differentiated. Though a kind of inner layer has been noted in *Bairdiocypris üxheimensis* (Kegel), particularly so within the free marginal area (Krömmelbein, 1952, pl. 4, fig. 1 a-c), Krömmelbein's interpretation (*l.c.*, p. 322) of that occurrence arouses some doubts (comp. p. 65—66 of the present work). No such structures have been observed on thin slides of the carapace of Palaeocopa, whose shell is colourless and with a cryptocrystalline structure.

Fluoridization and thin slides cut through shells of various groups of Palaeozoic ostracods have revealed the presence in Leperditiidae and *Bairdiocypris* sp., as well as in other Podocopa (*Condracypris* (?) sp.), of a distinctly three-layered structure (fig. 13 *A*, *B*), while in representatives of Palaeocopa the carapace is most commonly two-layered (fig. 12 *C*; pl. II, fig. 1). In the course of fluoridization of shell, e.g. in Leperditiidae, the prismatic structure is not obscured, but quite contrary it becomes more stressed (pl. II, fig. 7). On the other hand, in Podocopa which have the shell with extremely fine calcite prisms, the primary microstructure is sometimes completely effaced (pl. II, fig. 5).

In the group of Palaeocopa (the Leperditiidae excepted) presence of muscle scars is still an open question. In spite of the use of diverse methods such as fluoridization, polishing of the outer shell layer and cutting of thin slides, etching of shells by weak acid solutions, immersion in liquids with strong light refraction, particularly so in monobromnaphtaline (Triebel, 1941), no adequate results have been obtained. These methods have only revealed the position of the muscle attachment which, as a rule, is indicated as a rounded area with stronger light refraction. In what the muscle scars are concerned, excellent results have been obtained in *Bairdiocypris* sp. by treatment in a weak solution of hydrochloric acid, and for *Bairdia* sp. by fluoridization of shells.

In treating rocks yielding ostracod shells, marly and argillaceous deposits have been washed in water after being reduced to fragments by means of Glauber salt or lixiviation. In the case of limestone rocks roasting at high temperature (up to 900°C) and rapid cooling in water have been used. For this purpose the sediment was broken up into fragments of ca. 3 cm, which crumbled up after being subjected to repeated heating and cooling. A disadvantage of this method is the large percentage of damaged shells (particularly so in the case of larger ostracods and of strongly ornamented forms). Sudden temperature change did not cause such strong disintegration of the shell in small and smoother forms resulting in a smaller number of damaged specimens. Neither does their microscopic structure alter, but they become whiter than the uncalcinated specimens, and covered with a minute network of cracks. By using the above described method it has been possible to isolate from the rock numerous shells of various groups of ostracods which have served as comparative material in the preparation of the present paper.

TERMINOLOGY

The terminology here used to define the morphological elements of the carapace of Eridoconchidae Henningsmoen is taken partly from earlier palaeontological and zoological works concerning Conchostraca (Grube, 1865; Raymond, 1946; Novoshilov, 1954, 1960). Terms accepted for and used in papers on ostracods (Schmidt, 1941; Hessland, 1949; Kesling, 1951 *c*; Jaanusson, 1957; Triebel, 1958 *b*) and other groups of animals have been introduced by the writer. Here below are given the morphological definitions for the main structural elements of the carapace in Eridoconchidae. Definitions of terms concerning the structure of the carapace in other ostracods cited in this paper are not given since they are commonly known and used. Brief explanations only accompany their illustrations.

Nauplioconch = shell of the first (post-embryonal) growth stage, forming the umbo on a multilamellar carapace (fig. 1).

Multilamellar carapace = a carapace consisting of moults not shed off during growth. The most common occurrence of this type of carapace is encountered in the Conchostraca.

Lamella = an instar or a moult stage corresponding to a given growth phase of the multilamellar carapace with which it is closely morphologically connected. In a single lamella, not yet quite calcified, the following parts may be distinguished: a proximal calcified portion, by the present writer commonly referred to as the *dorsal* or *hinge* *lamella,* the central one consisting of chitin — hence the *chitin lamella,* and finally the *distal lamella,* calcified as the dorsal one, and including the growth band (Raymond, 1946; Novoshilov, 1954) whose peripheral ends form the free edge of the shell during successive growth stages. At the base of the invagination of the lamella occurs a semicircular list.

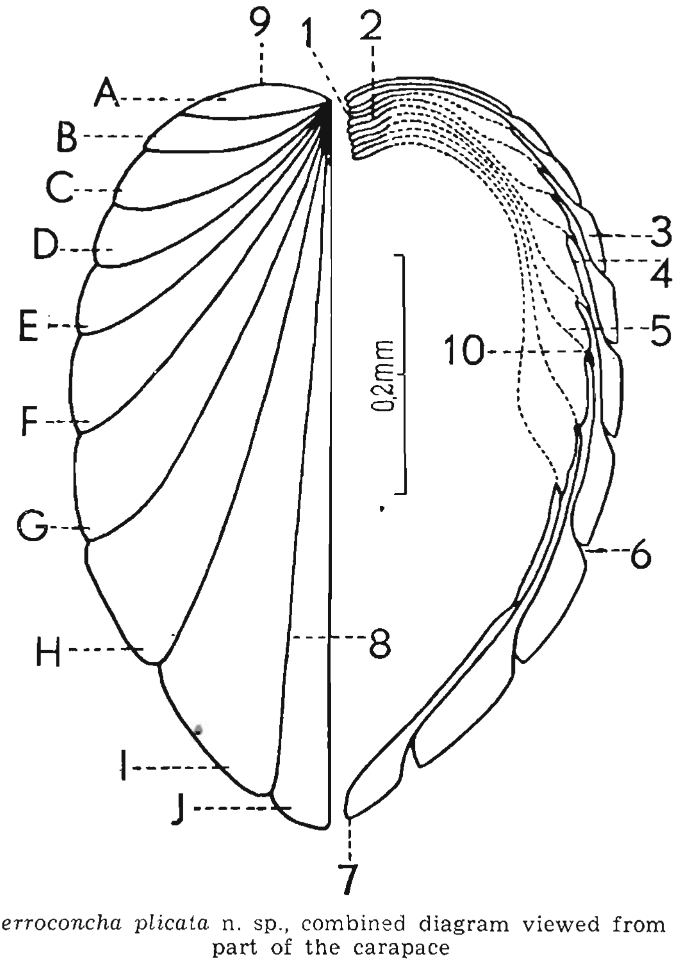


Fig. 1. — *Aberroconcha plicata* n. sp., combined diagram viewed from the anterior part of the carapace

A nauplioconch, *B-J* successive growth stages, *1* hinge, *2* dorsal lamellae, *3* growth bands (distal part of lamella), *4* interlamellar chamber, *5* chitinous lamella, *6* concentric groove, *7* free edge, *8* growth lines (concentric groove), *9* dorsal margin, *10* semicircular list.

Growth band = the outer distal part of the carapacial lamella, corresponding to adventral structures (Jaanusson, 1957) in ostracod carapaces from the Palaeocopa group. On a multilamellar carapace these elements are called concentric rings (Ulrich & Bassler, 1923*a*), ridges (Levinson, 1951), which indicate the number of lamellae composing the carapace. The particular growth bands are separated by grooves, the so-called growth lines (Raymond, 1946; Novoshilov, 1954).

Interlamellar chambers = free spaces produced by chitin lamellae, invaginated into the interior of the valve. Neither their origin nor function is fully understood (comp. p. 56—57).

Bisecting line (Jaanusson, 1957) = a dark line (Adamczak, 1958) cutting — parallel to the surface of shell — the adventral structures. It constitutes the first stage (sinus) in the formation of a small free space within the growth band, in the present paper referred to as the lacuna.

GENERAL PART

ON THE ORIGIN OF OSTRACODS

The origin and phylogeny of ostracods have not as yet been definitely clarified. Many of the problems connected therewith are still highly hypothetical. Zoological and palaeontological concepts advanced with regard to the phylogeny of these animals often disagree. A distinct lack is felt in this field of a constructive theory supported by both — palaeontological and recent materials. Neither will a solution of these problems be found in the views of Pokorný (1953, 1954, 1958), based on investigations of earlier authors (Müller, 1894; Raymond, 1946), or in the classification and new systematic groups introduced by him. Many of the ostracod groups differentiated by Pokorný are not mutually related (Leperditiida Pokorný, Beyrichiida Pokorný, Podocopida Pokorný).

In spite of the great abundance of the available fossil material it has not been possible more closely to correlate many of the extinct ostracod groups with the living forms. Essential differences occur even among fairly well known groups of primitive ostracods, to which in the first place belong Leperditellidae Ulrich & Bassler, 1906, and Leperditiidae Jones, 1856. Even though some authors (Bassler & Kellett, 1934; Henningsmoen, 1953*a*) unite these groups into one superfamily, the Leperditacea, yet this standpoint has not been commonly accepted[1].

In what regards the Leperditellidae and the division of this family by Henningsmoen (1953*a*) into smaller taxonomic units: Leperditellinae Ulrich & Bassler, 1906, Eridoconchinae Henningsmoen, 1953, Conchoprimitiinae Henningsmoen, 1953, this conception was then quite correct and expressed the opinions held and the state of knowledge at that

[1] Quite recently the genus *Aparchites* Jones, 1889, has by Polenova (1960*b*) been included into the Leperditellidae. Eo ipso, this family has automatically become a synonym of Aparchitidae Jones, 1901 (Pokorný, 1958). Moreover, Polenova has erected the superfamily of Aparchitacea to contain the families: Aparchitidae, Graviidae Polenova, Aechminidae Bouček. This group, together with the Leperditacea, has been included into the Leperditiida Pokorný.

time concerning the morphological structure of shells of this group. Recent investigations, and particularly so data relating to the internal structure of Eridoconchidae have revealed some fundamental structural and morphological differences (fig. 2). Since they involve not only the remaining subfamilies of Leperditellidae, but the Palaeocopa as a whole, too, they have — on the base of their multilamellar carapace — been

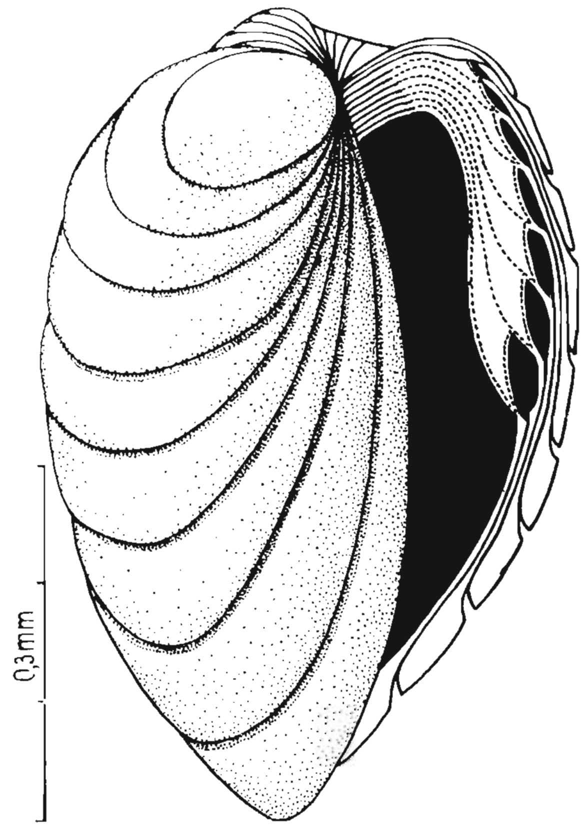


Fig. 2. — *Aberroconcha plicata* n. sp., schematic drawing of the carapace, oriented slightly obliquely towards the anterior part. Left valve shows in cross section a reconstructed spatial picture of chitinous lamellae.

separated by the present writer into a distinct family, the Eridoconchidae, and placed in a new suborder — the Eridostraca. This new group has some features in common not only with the Conchostraca (multilamellar carapace), but with the Ostracoda, too (ability to produce a unilamellar calcite carapace). Among the ostracods the Eridostraca occupies an exceptional phylogenetic position.

Moult stages are of particular significance in the study of ostracod phylogeny. They are an important factor in the study of the past history of these animals. Moreover, they permit to ascertain the modes of changes through which their evolution was realized (Adamczak, 1959). Palingenetic characters are frequently preserved on young shells; these provide very sound suggestions for the determination of mutual relationships between the lower taxonomic groups. The youngest stages would indeed be here of greatest significance, but unfortunately, owing to unfavourable conditions, they are but seldom preserved in the fossil state.

During the latest years, with the purpose of clearing up taxonomic and phylogenetic problems, much attention has been focussed on the study of the microscopic structure of the carapace by means of thin slides (Hessland, 1949; Triebel, 1950; Spjeldnaes, 1951; Levinson, 1951; Krömmelbein, 1952; Jaanusson, 1957; Kesling, 1957*a*; Adamczak, 1958). Application of this method permits to take into account characters which, thus far, have scarcely received due attention. It seems that, besides ontogeny, investigations carried on from this standpoint permit to trace changes of phyletic importance independently of those in the ornamentation of shell. In the course of research work on the Eridoconchidae, it was found that structural studies of fossil ostracods may help to solve many problems other than taxonomic. It has been ascertained that the cryptocrystalline structure of the carapace of Eridoconchidae is common to many groups of Palaeocopa, the Leperditiidae excepted. These, on the other hand, display an astonishing resemblance with the Podocopa (in the sense of Müller, 1894). Observations made during the study of this problem likewise shed some light on the origin of the ostracod carapace and on ostracods in general. They permit to understand better the evolutionary trends of these animals from a different aspect than has been done heretofore. It seems that considering the origin of the carapace, the ostracods correspond to a group rather diphyletic than monophyletic.

In what regards the opinions held by palaeontologists concerning the phylogeny of ostracods, probably the most popular hypothesis is that first advanced by Ulrich and Bassler (1931) postulating that the bivalved Cambrian Archaeostraca from the group of Bradoriidae Matthew and Beyrichionidae Ulrich & Bassler may correspond to the ancestors of ostracods. These authors write: „For the reasons mentioned we are confident that the Bradoriidae and allied Cambrian Crustacea are not true Ostracoda. However, as they precede the Ostracoda in time, it is quite probable that the latter were derived from the earlier Bradoriidae and Beyrichionidae" (*l.c.*, p. 3). This standpoint was subsequently accepted by Raymond (1946) and many other palaeontologists.

The Cambrian Archaeostraca have no definite taxonomic position; they are considered as Arthropoda incertae ordinis (Shrock & Twenhofel, 1953). This does not diminish the interest they arouse since it is among them that we should most likely search for ancestors not of ostracods only, but of other groups of Entomostraca, too.

Without now developing in detail these ideas, the writer wishes to recall here the opinions of zoologists concerning the problem of ostracod phylogeny (Grobben, 1892; Giesbrecht, 1921) which, as a rule, are neglected by the palaeontologists. Müller's (1894) conception will not be here considered, as not bearing much significance on questions studied in this paper. That author does not, indeed, concern himself with the concrete group of the ancestors of these animals, but presents only the hypothetical „prae-ostracod" form (Protoostracoda Skogsberg). Far more interesting are the opinions advanced by Grobben whose chief assertments have been confirmed by palaeontological evidence.

In a short report „Zur Kenntnis des Stammbaumes und des Systems der Crustaceen" Grobben (1892) discusses three morphological types of the living Phyllopoda (*Branchipus, Apus* and *Estheria*) which simultaneously reflect the evolutionary trends in this group of animals. According to that author, the type *Estheria* has certain features in common with ostracods, as well as with Cladocera, and this does not certainly arouse the slightest doubts. As regards the ostracods, Grobben thinks (*l.c.*, p. 247) that „... lassen sich auch hier genügende Anhaltspunkte gewinnen, welche die Herleitung der Ostracoden von einer *Estheria*-Typus angehörigen Urphyllopoden zu stützen vermögen". These „Anhaltspunkte" are foremost the laterally compressed body and the „bivalved" carapace protecting the body. The latter is, according to Grobben, an element of a great significance in the interpretation of ostracod phylogeny. Grobben's considerations were based on Myodocopa, representing today the most primitive body type, and providing suitable material for comparative studies. Disregarding, however, this side of the problem, the present writer focusses his attention chiefly on palaeontological materials (Eridoconchidae), which support Grobben's hypothesis that forms of the conchostracoid type with concentric growth lines may have been the ancestors of ostracods (though of not all of them).

Giesbrecht (1921) disputes the main concepts of Grobben and rejects his leading idea. He discusses but the aspect of the problem of phyletic significance, namely the comparative anatomy of the body, disregarding elements studied palaeontologically. In Giesbrecht's opinion (*l.c.*, p. 227) the shells are convergent structures, consequently of small significance in phylogenetic speculations. Hence that author does not, contrary to Grobben, trace the ostracods back to the Conchostraca, but to Protostraca, i.e. to a hypothetical ancestral group from which may, indeed, descend all the Crustacea after they had passed the stage differentiating them from the Copepoda. Giesbrecht's views are not confirmed by fossil evidence and it seems that his inferences are one-sided, since they are based on evaluation of recent materials only.

STRUCTURE OF CARAPACE OF ERIDOCONCHIDAE

Outer morphology of shell

The carapaces of *Aberroconcha* n. gen. and *Eridoconcha* Ulrich & Bassler are distinguished by an extremely characteristic type of ornamentation due to their peculiar mode of growth. The outer surface of

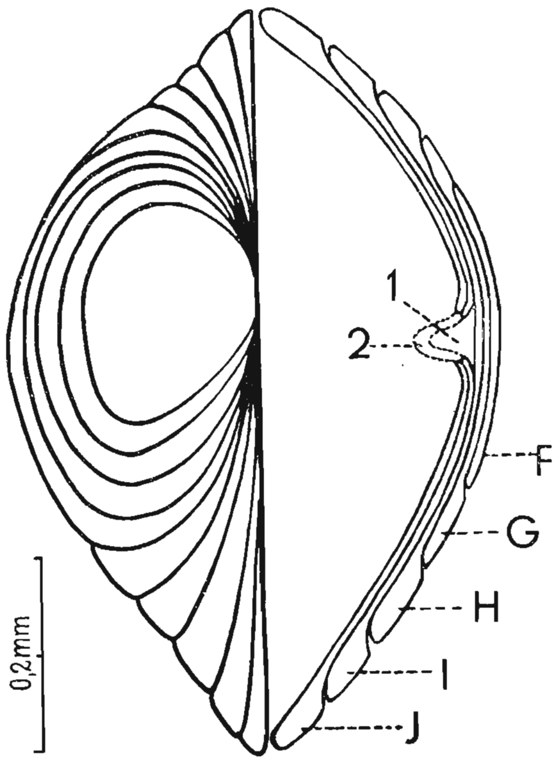


Fig. 3. — *Aberroconcha plicata* n. sp., combined diagram as seen from the dorsal part of the carapace; right valve polished up to midheight
F-J lamellae of last growth stages, *1* interlamellar chamber, *2* chitinous lamella.

the carapace, consisting of calcite, is marked by numerous (up to 10) concentric bands and grooves (fig. 1, 2), in literature frequently referred to as ridges (Ulrich & Bassler, 1923*a*; Levinson, 1951) or concentric rings (Harris, 1931), sometimes as concentric bands (Matern, 1929). This type of ornamentation displays certain analogies with pelecypod ornamentation, as is mentioned by Coryell and Williamson (1936). As regards comparison with the last named group, it must be stressed that the growth pattern is here entirely different. In pelecypods the growth of shell is essentially continuous, while in Eridoconchidae distinctly periodical. In the latter group each band may be interpreted as a definite growth or moult stage.

In Eridoconchidae the carapace outline is ovate, posteriorly cordate (Harris, 1931; Keenan, 1951). The particular grooves and bands parallel

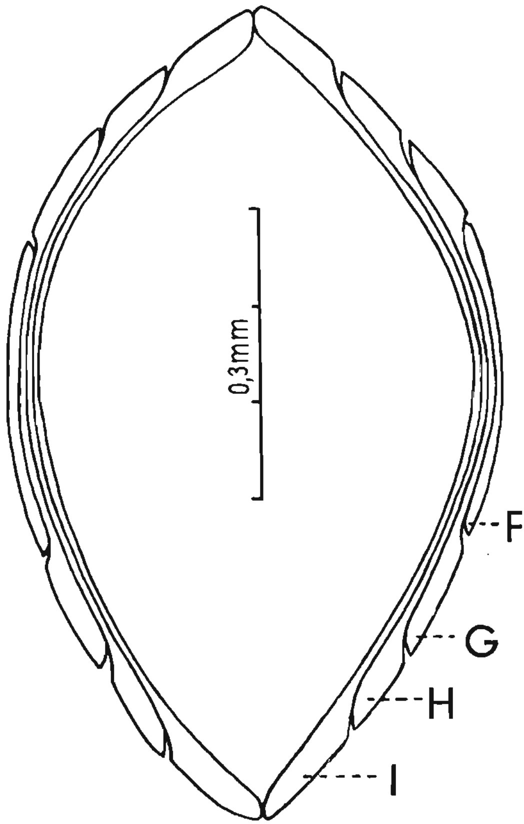


Fig. 4. — *Aberroconcha plicata* n. sp., longitudinal section of carapace, cut below the invagination of the last growth stage
F-I layers of last growth stages

the free edge and converge below the umbo (fig. 3), which is formed by the first growth stage, here referred to as nauplioconch. This is directed slightly to the front and hence is helpful in determining the orientation of carapace. The umbo is variously shown. In *Aberroconcha* it is conspicuous, in *Eridoconcha* (though this is no rule) the apex of the carapace is slightly flattened.

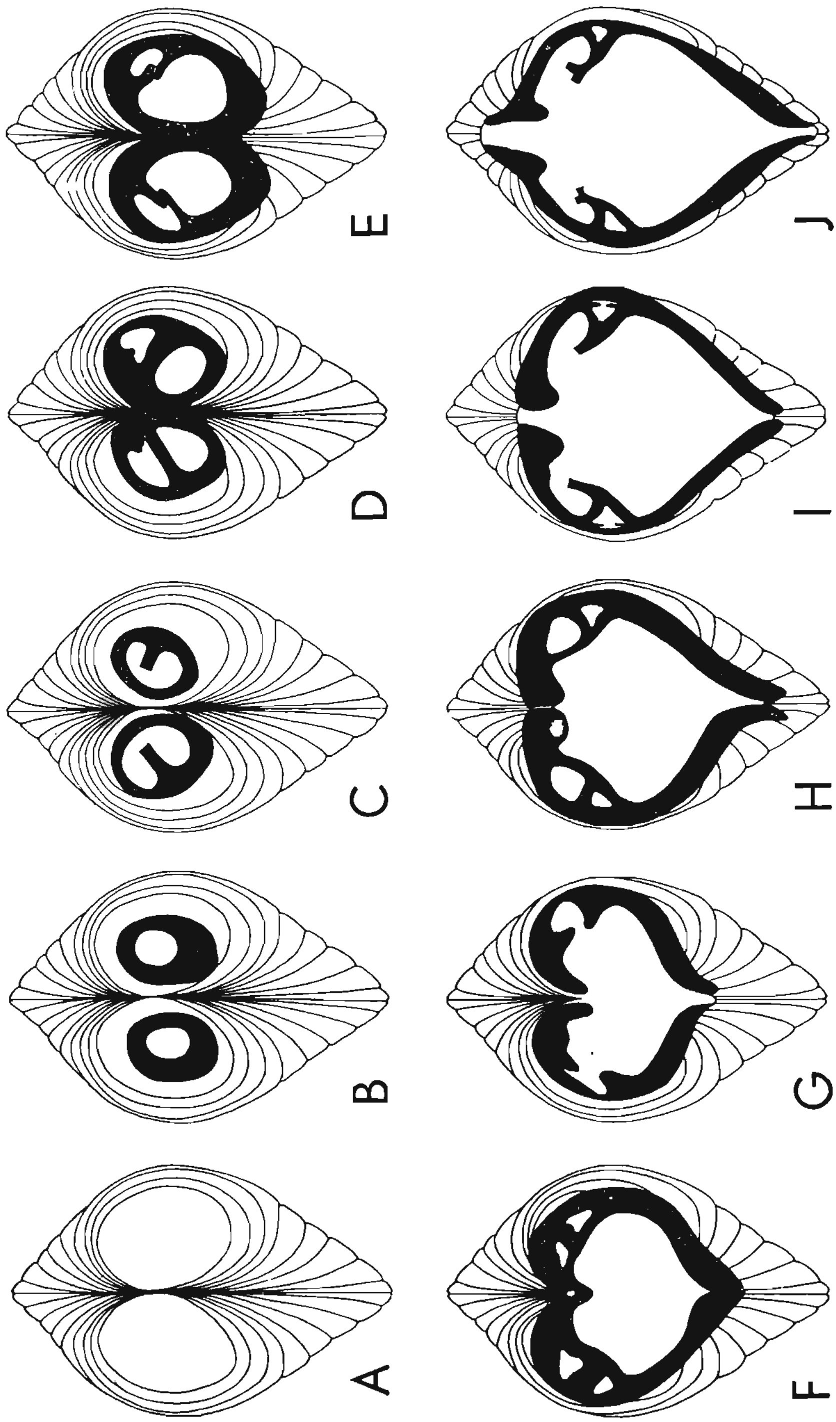
Shape of the carapace of Eridoconchidae varies. Most likely it was strongly affected by environmental conditions and depends also on the development of the animal's body. It may be considered to be a resultant of the action of these two factors. Dorsally and ventrally they are distinctly stream line in shape, with a smooth surface, occasionally only marked by minute punctae on the growth bands.

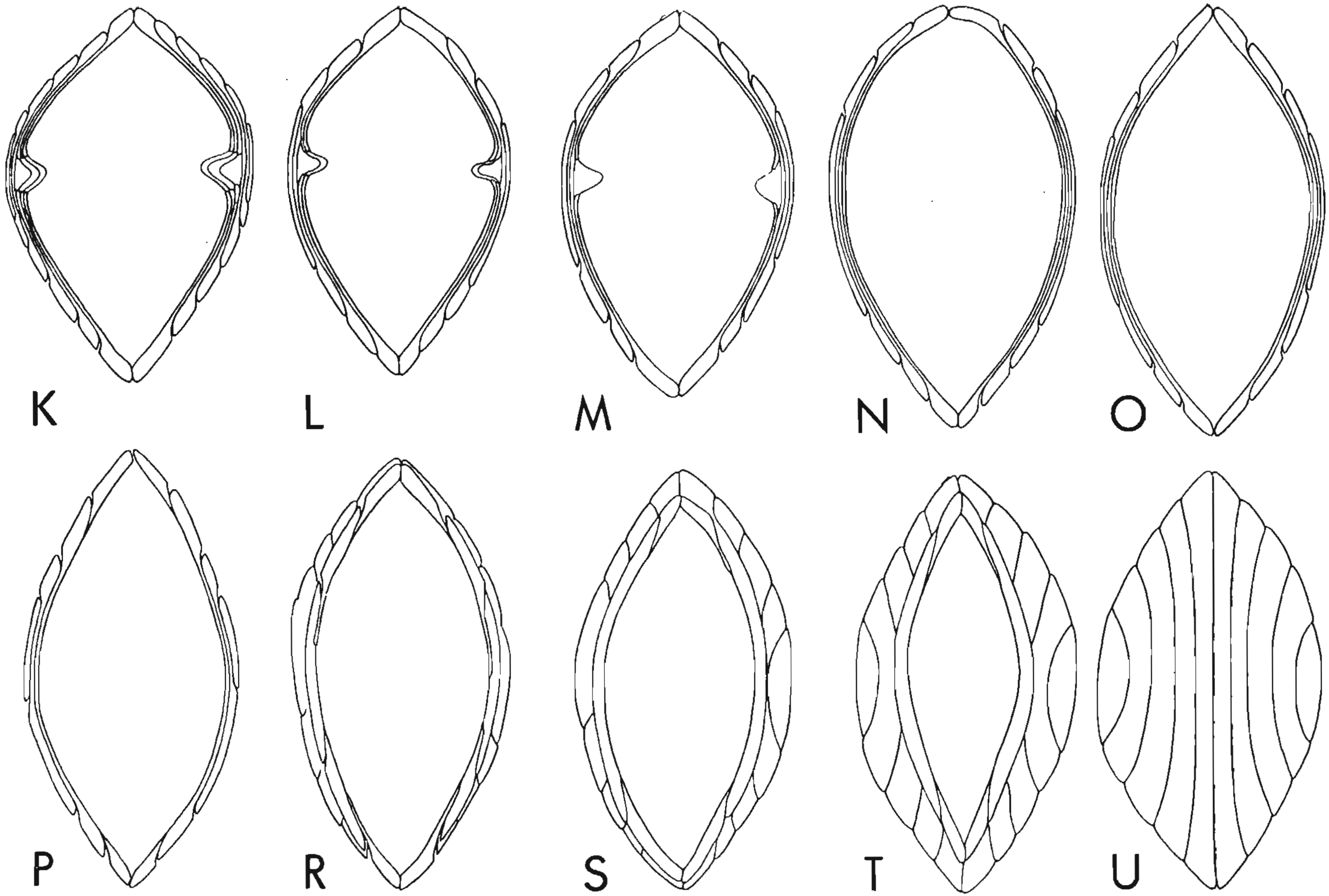
The valves of the carapace are symmetric. No overlapping or shifting of valves has been noted (fig. 1, 4). The hinge-line is straight and short, placed in a depression, with both its ends meeting the free edge at an obtuse angle. The hinge is simple, freely confluent with one another on either valve, without forming differentiated structures. The free edge of the valve is formed by the last band. The number of the bands in Eridoconchidae varies from 6 to 10 (without the nauplioconch). This number reflects the primitive character of the carapacial structure and is of marked taxonomic and phylogenetic significance. The maximum number of growth (moult) stages, ascertained in Beyrichiidae Matthew, is eleven (Spjeldnaes, 1951). These agree with the number of growth stages in Eridoconchidae. We may infer that this character (11 growth stages) is the upper limit attainable by ostracods of the Beyrichiidae group and that it corresponds to the number of growth stages in primitive Eridostraca.

The individual variability of shell is likewise connected with its individual development. Ontogeny of the carapace may be traced on one specimen in which all the growth stages have been preserved. In the fossil state, however, young shells are known with a small number of lamellae (growth bands). They are markedly smaller than the adult individuals. Moreover, they differ from adult forms in the valve outline which varies strongly during the growth process (fig. 18, 21). Usually the posterior area of the carapace is more strongly developed than the anterior, so that the mutual ratio of these parts is 1:1.83. With growth these proportions gradually alter and in adult forms they are 1:1.24. The more intense growth of valve in the caudal direction during the initial growth stages may probably be accounted for by the addition to the body of new segments. In connection with problems concerning the young forms we should take into the account that frequently such individuals may be described as adult forms with a lesser number of lamellae on the carapace. It is not excluded that *Eridoconcha minutissima* Ivanova, described from the Ordovician of the Siberian Platform, represents indeed such a young form. This is indicated by the small size of shell and the few growth bands (comp. p. 83).

The size of shell in Eridoconchidae varies. The largest shells in the Devonian of the Holy Cross Mountains are noted in *Aberroconcha plicata* n. sp.: approx. 1.08 mm, while the smallest ones are those in *E. granulifera* n. sp. — 0.62 mm, and *E. arsiniata* (Stover) — 0.50 mm. The length/height ratio within the studied species of the genus *Aberroconcha* and *Eridoconcha* varies, too. In *A. plicata* n. sp. the mean length/height ratio is 1:1.26, in *A. devonica* n. sp. 1:1.16. Shells of the

TEXT-PL. I





Aberroconcha plicata n. sp., serial polished surfaces of the carapace, parallel to the longitudinal axis; *A-J* dorsal view, *U-K* ventral view (sections placed in reverse order as compared with fig. *A-J*).

last named species are more circular, while in the former one they are slightly elongate. Analogous changes have been observed in *E. rugosa* Ulrich & Bassler (mean L/H being 1:1.39) and in the related *E. granulifera* n. sp., where it is 1:1.33. On the whole, it may be observed that during the process of phylogeny these extremely conservative representatives of Eridoconchidae tend to produce a rounded carapace.

A peculiar problem is presented by the microornamentation of the carapace noted on detached valves of *E. granulifera* n. sp. in transmitted light and under strong magnification (× 450), (see fig. 22). It consists of a network with polygonal meshes. Moreover, in one of the species (*E. rugosa*), on partly decalcified valves, minute pits (canalicules) strongly resembling the pores (fig. 8) in living Conchostraca (Grube, 1865) have been noted to occur in the free margin area, as well as on the last growth band.

Detailed morphology and architecture of the carapace

A shell of the Eridoconchidae is a structure consisting of numerous lamellae, underlying one another, each successive lamella being larger that the preceding one by a fixed value, approximately corresponding to the numerical values of Brooks' law (*vide* Kesling, 1951*b*, 1952*c*, 1953*d*). Observations described in the present chapter are based on thin and serial sections (text-pl. I) and fluoridized shells belonging to *Aberroconcha* and *Eridoconcha*. As a rule within these forms two architectural patterns of the carapace may be differentiated: 1) aberroconchoidal and 2) eridoconchoidal.

The *aberroconchoidal* type is distinguished by a highly complex structure, readily observable only in sections normal to the longitudinal axis of the shell, or in longitudinal sections (fig. 1, 3).

The cross section of the shell reveals a number of lamellae, each one being a structure independent from the preceding one. This structural pattern has been ascertained in *Aberroconcha magna* (Harris), *A. plicata* n. sp. and *A. devonica* n. sp. In the first named species (fig. 9 *A*, 17) lamellae of the early growth stages (I — III) consist of calcite and are closely adherent. The first lamella is referred to as the nauplioconch. Beginning with stage IV the growth stage displays a different structure. In the proximal part sloping into the dorsum and in the free edge they are calcareous, while centrally they are chitinous. This structural pattern is consistently followed to the last stage of growth. Chitinous lamellae, forming each moult stage of which the carapace is composed, call for special attention. They are domed into the interior of the shell and do not lie close together, but produce a sort of chambers. So far this pattern of structure has not been noted

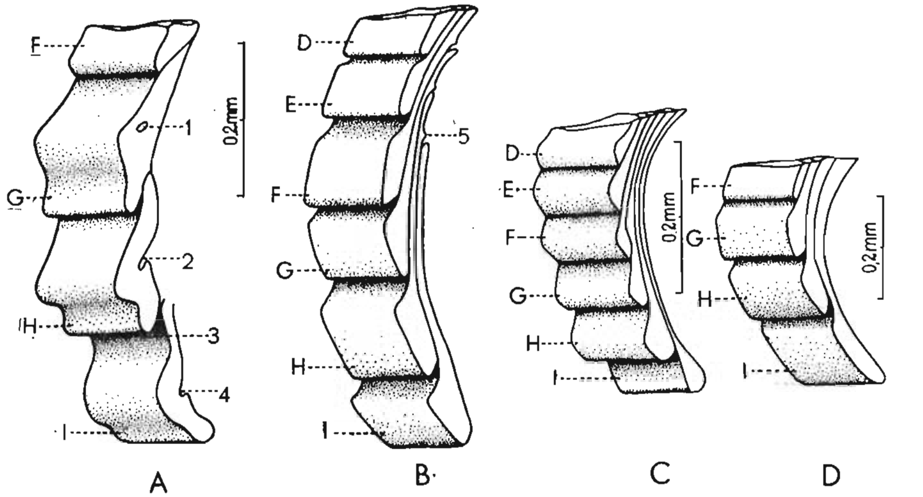


Fig. 5 *A*. — Diagrammatic sections of the distal part of carapace in outer view: A *Aberroconcha magna* (Harris), B *A. plicata* n. sp., C *Eridoconcha rugosa* Ulrich & Bassler, D *Cryptophyllus oboloides* (Ulrich & Bassler)

D-I successive phases of the last growth stages, *1* lacuna, *2* bisecting line (shallow bay — sinus), *3* concentric (U-shaped) groove, *4* broad bay or fold, *5* semicircular list.

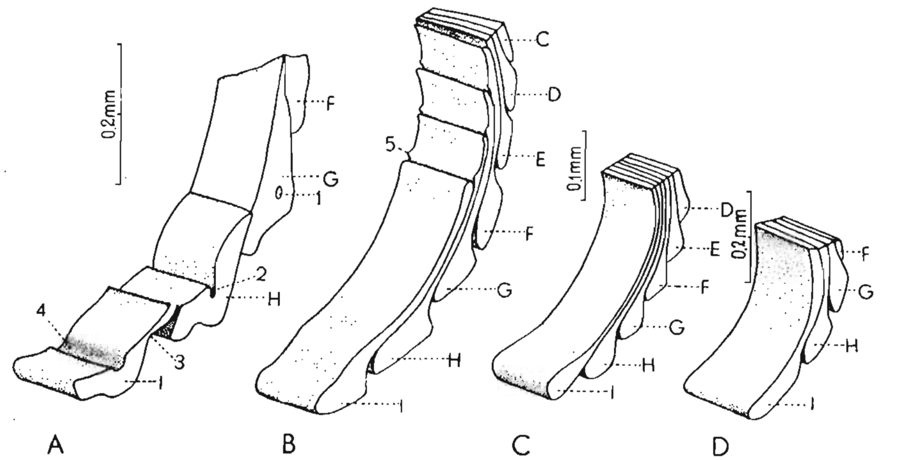


Fig. 5 *B*. — Diagrams of inner surfaces of valves; for explanations — see fig. 5 *A*.

in any one ostracod group and it seems that among Eridostraca they are typical solely in representatives of *Aberroconcha* n. gen. The species *A. magna* represents the most primitive type of carapacial structure within the group of Eridoconchidae. Its lamellae are but slightly calcified, while their chitinous parts occupy a fairly large area of the shell. In thin sections of these forms the chitinous lamellae are distinct as dark lines (pl. I, fig. 3). During the process of fossilization, secondary impregnation of calcium carbonate has been noted on these dark lines, displaying a different microstructure than the remaining elements of the carapace which have a cryptocrystalline structure.

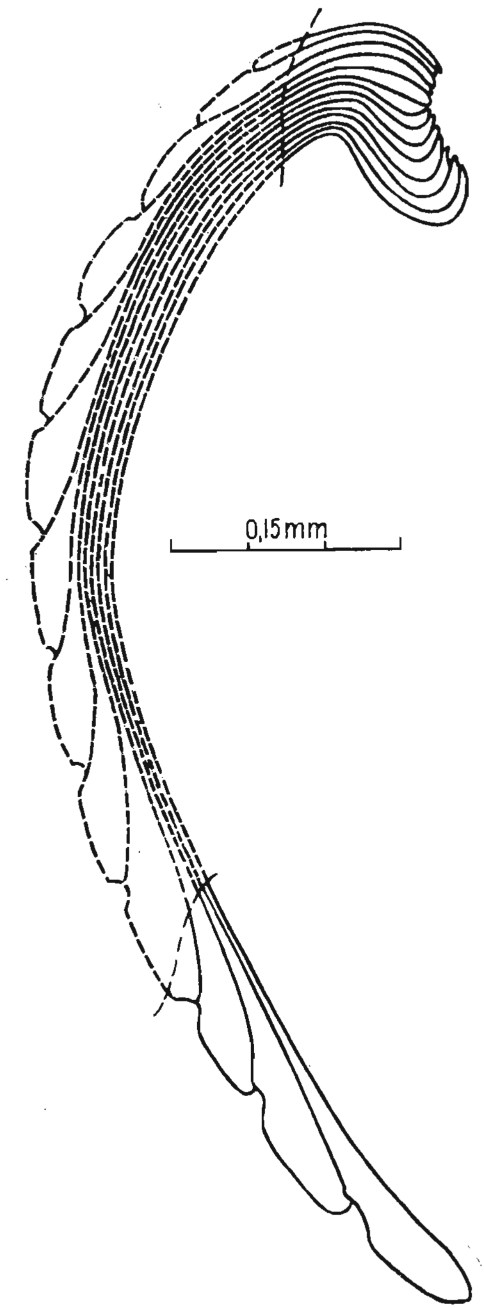
Stronger morphological differentiation is displayed by the aberroconchoidal type of carapace in *Aberroconcha plicata* n. sp. (fig. 1, 2; pl. I, fig. 1, 2 *a, b*). It seems very probable that this species is a successive morphological link of the same evolutionary trend. Both these species although congeneric are not closely related to one another, belonging to different phylogenetic trends. Independently of that fact they probably represent the gradual transformations of forms belonging to the group of *A. magna* (Harris) in the early evolutionary stage during the Ordovician, or maybe at the boundary of the Cambrian and Ordovician. In the species *A. plicata* n. sp. the calcification of lamellae is further advanced. Their chitinous surface has decreased in favour of the calcareous ones. These differences are particularly striking when comparing the final growth stages in forms *A. magna* and *A. plicata* n. sp. (fig. 9 *A, B*). In the latter species the distal calcareous parts of lamellae have grown proximally. The surface of calcareous lamellae converging to the dorsal area has likewise increased. These changes have resulted in increased capacity of the domicilium, while the chitinous lamellae form smaller air chambers. The particular growth bands in *A. plicata* are characterized by great uniformity. Morphologically they are but little differentiated, while in *A. magna* they form a kind of „podium" — in the last bands particularly so (fig. 5 *A, B*). The concentric grooves separating them are U-shaped in section. According to Levinson (1951), the shape of the groove is taxonomically important. However, it may be actually asserted that on the same individual of *Aberroconcha magna* the section of the sulcus varies with the growth of the shell. An analogous phenomenon has been noted also in representatives of the genus *Eridoconcha* (*E. granulifera* n. sp.), (comp. p. 84). During the early growth stages the groove is V-shaped, being U-shaped in the last growth stages. In *A. plicata* n. sp. or *A. devonica* n. sp. the groove is invariably V-shaped in section. The realization of either of these two types of sulcus is controlled in the first place by the structure of the growth band. The more this resembles the „velate ridge", the greater probability to produce a U-shaped sulcus.

As has already been mentioned, the chitinous elements invaginated into the interior of the valve do not touch one another. In longitudinal section (fig. 3) it is seen that lamellae of the older growth stages overlap the younger stages. The maximum number of chambers formed by chitinous lamellae (text-pl. I, *K*), noted on one section, is three. On the outer surface of fluoridized carapaces the chambers resemble a string of vesicles decreasing dorsally. On the inner surface of shell they form surfaces (fig. 6) diverging at the base of the dorsal area. The process of calcification involves a larger area dorsally and this gradually shifts to the ventral side. In *A. devonica* n. sp. this process is fairly well advanced. Dorsally nearly all the lamellae have been calcified and this process is accompanied by the disappearance of chambers in this zone, while in the central portion of shell changes are but small (fig. 9 *C*). This species ends up the morphological series of the aberroconchoidal type. The last two species of *Aberroconcha* (*A. plicata* n. sp. and *A. devonica* n. sp.) are closely allied with one another and at the same time they correspond to the same phylogenetic line.

The *eridoconchoidal* type of carapace morphology is, in the first place, encountered in representatives of the genus *Eridoconcha* Ulrich & Bassler, and in some Conchostraca species found by the writer in Upper Silurian beds of Podolia. Species *E. rugosa* Ulrich & Bassler, *E. granulifera* n. sp. and *E. arsiniata* (Stover) are representatives of the eridoconchoidal type of the carapace. In these forms the lamellae of the carapace have been completely calcified and mutually adhere throughout the surface. Hence, the shell is massive and heavy. The number of lamellae continues to be considerable, ranging from seven to eleven. This morphological type of the carapace is linked by transitions with the preceding one and there is no sharp boundary between them. The fundamental difference lies in that the latter forms lack air chambers, though some carapaces bear traces of them preserved as slightly corrugated calcite lamellae.

In representatives of *Eridoconcha* the carapace morphology is simple. On the whole they are poorly differentiated forms with monotonous ornamentation. Size and contour of shell are, in the first place, subject to some variations. The growth bands, i.e. the distal parts of lamellae are still more conservative characters, subject to only unimportant changes. Practically speaking, the shells of *Eridoconcha* are hardly distinguishable from those of *Aberroconcha* n. gen. on outer morphology only. This question is far simpler in the case of representatives of the genus *Cryptophyllus* Levinson (Levinson, 1951) related with them. The latter have distinctly fewer lamellae on the carapace and their valves are subject to far more important variations. The decreased number of lamellae is correlated with a process of marked biological significance, i.e. the ability to shed moults which, in their ancestors (*Aberroconcha* n. gen. and *Eridoconcha*), formed a carapace morphologically greatly complicated. The species referred to the genus *Cryptophyllus* and the allied representatives of the genera *Milleratia* Swartz and *Schmidtella* Ulrich are, taxonomically speaking, a separate group, but nevertheless related to the Eridoconchidae.

In what concerns the structure of carapace in *Eridoconcha*, it displays strong resemblance to shells of certain more closely not



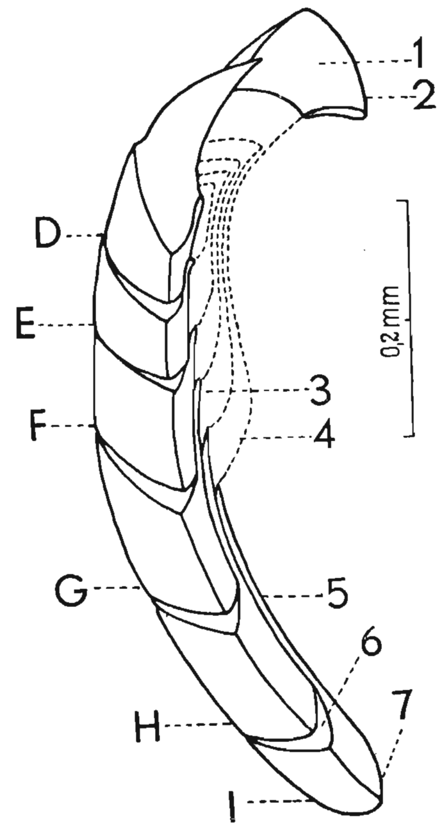


Fig. 6. — *Aberroconcha plicata* n. sp.; schematic drawing, showing a fragment of the right valve from which the earliest growth stages (*A-C*) have been removed

D-I growth stages, *1* dorsal lamella, *2* hinge, *3* interlamellar chamber, *4* chitinous lamella, *5* distal part of lamella, *6* concentric groove, *7* free edge.

Fig. 7. — Conchostraca gen. & sp. indet., transverse section of left valve, partly reconstructed (broken lines); Upper Silurian of Podolia.

determinate Conchostraca from the Upper Silurian of Podolia, collected by Kozłowski from the Czortków formation, which has yielded the well known brachiopod fauna with *Mutationella podolica* Kozł. (Kozłowski, 1929). These shells, unfortunately strongly damaged, were built exclusively of calcium carbonate. In cross section (fig. 7) we may observe their lamellae and thickened growth bands. The dorsal margin area forms a strongly extended surface, resembling analogous structures in living Conchostraca. The number of lamellae was up to 13. The most noteworthy fact is that so far Conchostraca with calcareous shells and concentric growth bands have not been recorded from Silurian rocks. Devonian forms which, in the opinion of many authors (Raymond, 1946; Novoshilov, 1953, 1960), represent the earliest type of these crustaceans, have a chitinous carapace. Representatives of this group of animals found in Silurian beds reasonably suggest that its history lasts over a far greater span of time than has heretofore been supposed. It is not excluded that they constitute a link between the Cambrian representatives of Lepidittidae Kobayashi and the Devonian forms. Neither are they referable to the Eridoconchidae, for they display a number of fundamental differences from that group, such as: large number of lamellae (13), development of the hinge margin and dimensions greater than those in typical Eridoconchidae.

Observations made during the study on Eridoconchidae reveal that: 1) their carapace was a multilamellar (up to 11) structure reflecting the growth stages of the valve, and 2) that the calcification of lamellae was gradually realized during the evolutionary process of this group of animals, while in their ancestors the lamellae were most likely built of chitin.

Differences and affinities of shell in Eridoconchidae and living Conchostraca

Schmidt (1941) was the first to call attention to the fact that the carapace of the genus *Eridoconcha* greatly resembles that of Conchostraca. Hence, he referred them to one of the families (Cyclestheriidae Sars) of that group of animals. Novoshilov (1953), an outstanding authority on fossil Phyllopoda, thinks the genus *Eridoconcha* to be a representative of the ostracods, postulating that the concentric ornamentation is not a diagnostic taxonomic criterion of fossil Conchostraca (1953, p. 6). Moreover, in all the works available to the writer, the genus *Eridoconcha* is invariably assigned to the ostracods. Actually, however, in what the structure of carapace is concerned, this group shows marked similarities with Conchostraca. With a view of clearing up these relations, the writer has investigated the carapace of certain living Conchostraca. In the light thrown by these studies the multilamellar structure of Eridoconchidae and the problem of the „retention of moults" (Levinson, 1951) seems to be soundly clarified.

The carapace of the Conchostraca is chitinous and is but to a small extent subject to calcification. Nevertheless, as it has been afore mentioned, in certain fossil forms from the marine Silurian deposits of Podolia, the carapace was completely calcified (fig. 7). Probably, in connection with their gradual migration from salt to brackish and fresh water basins, these forms lost the ability to accumulate carbonate salts, whose concentration percentage among organisms living in this environment is markedly low. Their shells are made up of many chitinous lamellae underlaying one another. On the outer surface of the carapace they form growth bands separated by concentric grooves. Grube (1865) has studied the carapacial morphology of these animals in great detail and the comparative studies here described have been based, among others, on that author's data.

The shell of the living genus *Estheria* Rüppel is easily etched after being for some hours immersed in KOH (Grube, 1865), where it becomes swollen. Subsequently, therefore, the successive lamellae of the carapace may be easily separated one from another. Under the microscope these lamellae reveal a characteristic mesh-like ornamentation, by Grube referred to as „Netzwerk". It also occurs on the bands of growth, but there it is obscured by additional ornamentation of this part. In fossil forms, in which the ornamentation pattern on concentric bands is subject to strong variations, this reticulation has, among others, been encountered in Glyptoasmussidae Novoshilov (Novoshilov, 1960). Traces of it have by the writer been observed also in *Eridoconcha granulifera* n. sp. (comp. p. 46). Moreover, this reticulated pattern likewise occurs in living ostracods of the species *Cythereis prava* Baird (Müller, 1894, p. 97-98). In the last named species the network consists of chitinous rods, often invading the calcareous lamella, while in other forms they adhere to them on the inner side (*Bairdia* McCoy). It seems that some vestiges of analogous structures may be observed in other fossil forms of the group Palaeocopa, e.g. in *Kozłowskiella* (Přibyl) (Adamczak, 1958), *Hibbardia* Kesling (Kesling, 1957*a*) and in *Trachyleberis tubulosa* Triebel (Cytheridae Baird), (Triebel & Klinger, 1959).

The reticulated ornamentation on the surface of chitinous carapace has likewise been noted in Cambrian Archaeostraca (*Hipponicharion* Matthew). It resembles the ornamentation of Glyptoasmussidae. In Cambrian forms the structure of this type of ornamentation suggests that it re-inforced the carapace, contributing to its elasticity and resistance to deformation. How far these structures are homologous, still remains an open question. Is the „Netzwerk" a vestige of the primary chitinous carapace, or is it a convergent structure produced independently by the various crustacean groups? The solution of this problem may be of great phylogenetic significance, since certain Cambrian crustaceans (Bradoriidae Matthew and Beyrichionidae Ulrich & Bassler) have been supposed to be the ancestors of ostracods (Ulrich & Bassler, 1931).

Comparative studies on the Eridoconchidae and Conchostraca, and still more so morphological observations of the representatives of

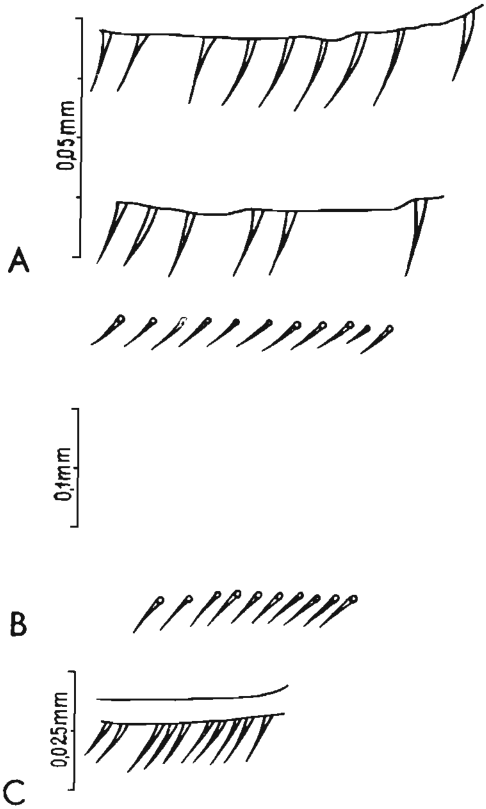


Fig. 8. — A *Eridoconcha rugosa* Ulrich & Bassler; schematic drawing, showing pores on partly decalcified shells at the boundary of the growth bands; B *Estheria* sp., schematic drawing, showing presence of pores at the boundary of growth bands in a recent form; C *Estheria* sp., fragment of chitinous mantle with setae.

Aberroconcha and *Eridoconcha*, lead to the conclusion that these two groups are related. This is indicated by the following characters: 1) multilamellar carapace, 2) minute pits of the growth bands (*E. rugosa*) (fig. 8), and 3) reticulation-„Netzwerk", which may be traced in *Eridoconcha* (*E. granulata* n. sp.).

The multilamellar carapace, common to both these groups, is the essential feature suggesting the relationship between Eridoconchidae and Conchostraca. Though in the opinion of most authors the Conchostraca did not occur before the Devonian (comp. Raymond, 1946; Novoshilov, 1954), forms with concentric growth lines of the conchostracoid type occur already in the Cambrian (*Fordilla* Walcott and *Lepidita* Matthew). According to Raymond (1946, p. 304), „... both show growth-lines, and, technically I do not see any way of excluding them from the Lioestheriidae. Possibly they are ancestors of the Conchostraca, but until Upper Cambrian, Ordovician, Silurian and Lower Devonian connecting links are found, it is probably wise to leave them in their present uncertain position." The present writer does not believe their position so uncertain as is thought by Raymond, since the hiatus between the Upper Cambrian and the Lower Devonian is partly filled up by a specimen of Conchostraca, found by the writer in the Silurian (comp. p. 51), and, to a certain extent, by the Ordovician Eridoconchidae.

Retention or initiation of moults?

Multilamellar carapaces must be considered as quite exceptional among ostracods, for as a rule the shell of these animals consists of one lamella only. Levinson (1951) was the first thoroughly to investigate the multilamellar carapace. Independently of that author, this problem has also been studied by Egorov (1954).

Levinson, who was the first to take up the problem of multilamellar carapaces, asserts that: „Both of the genera *Eridoconcha* and the new genus *Cryptophyllus* exhibit a many-layered shell which appears to be formed by the retention of molts. It is proposed that the cohesion of these molts is not dependent on the carapace but it is a specialised adaptation of generic importance" (Levinson, 1951, p. 553). As is stated by Levinson himself, the hypothesis of the retention of moults had been advanced in earlier papers by Swain and Bollin, and by Drake, in 1940 (Levinson, 1951). Henningsmoen (1953*a*) also concerned himself with that problem and succeeded to discover analogous occurrences in representatives of the genus *Conchoprimitia* Öpik and *Ectodemites plummeri* Cooper. Of some interest is also a report by Egorov (1954) on the multilamellar shells in forms of the *„Astarte" socialis* Eichwald group. These used to be assigned among the pelecypods, but Egorov proved that they actually belong to *Eridoconcha*. He states that: „In sections, thin sections and samples it may be observed that the shells of *Astarte socialis* Eichw. consist of several layers whose numbers correspond to the numbers of growth lines" (*l.c.*, p. 25).

In the light of Levinson's studies (1951) the „retention" is a distinctly adaptative feature, restricted to a small group of forms. When viewed from this standpoint, this process acquires peculiar characters, since the purpose of the adaptation itself is not clear. We do not know what factors influenced the animals to carry the burden of the moultings and subsequently, with the lapse of time, to lose this ability, for, as is mentioned by Levinson on p. 557: „The evolution of this group is toward a decrease in the number of specimens consisting of only one or two molts".

According to Levinson, the problem of the retention of moults suggests, too, that these multilamellar forms descended from ancestors with a unilamellar carapace. Such a conception explains well that author's statement that the carapace of the genera *Eridoconcha* and *Cryptophyllus* „... is a specialized adaptation of generic importance". Our knowledge of these ancestors is very inadequate. The collected materials and observations, however, permit the problem of „the retention of moults" to be put in a different light. In *Eridoconcha* and *Aberroconcha* the shells consisted of many lamellae (7-11) and it is reasonable to suppose that this was the original condition of the structure of the carapace, inherited from ancestors of the Conchostraca group. The remaining forms with fewer lamellae (6-1), to which *Cryptophyllus* belongs foremost, referred by the present writer to Eridostraca, too (comp. p. 71—72), realize a new structural type of the carapace. It seems highly probable that shells in representatives of this genus do not, as has been suggested by Levinson (1951), illustrate „retention", but the initiation of moults (fig. 9). In this connection we may infer that the reduced number of lamellae in shells of these animals (the maximum number of lamellae in *Cryptophyllus* being 6) is to be regarded as a proterogenetic character (Schindewolf, 1927, 1950). Species of *Cryptophyllus* may be considered as a link in the morphological chain uniting forms of the conchostracoidal type (Eridoconchidae) with the typical representatives of ostracods such as *Milleratia* and *Schmidtella*. Observations thus far made suggest that representatives of *Conchoprimitia* Öpik, which had made their appearance as early as in the Ordovician, evolved according to a similar pattern as *Cryptophyllus*. This is indicated by traces of earlier moult stages, the simple structure of the carapace, the medial sulcus and a kind of velar structure within the free edge of valve (fig. 11 *B*). A number of species of this genus (*Conchoprimitia gammae* Öpik, *C. deminuata* Öpik, *C. tallinnensis* Öpik, et alii) have coherent valves of moult stages (Henningsmoen, 1953*a;* Jaanusson, 1957; Sarv, 1959). In this case, too, we may speak about moult stages fixed on the carapace of mature forms as of a proterogenetic phenomenon. These animals had acquired the ability for nearly complete moulting which in our considerations here is regarded as a taxonomic and phylogenetic factor of great importance. They probably descend from forms of the Eridoconchidae-type. This group though provided with many primitive features, e.g. partly calcified lamellae (*A. magna, A. plicata* n. sp.), displays many progressive features during its evolutionary process. The most noteworthy of them are the ability to assimilate carbonate salts and their excretion as calcified lamellae. The bulky multilamellar carapace safely protected the animal's

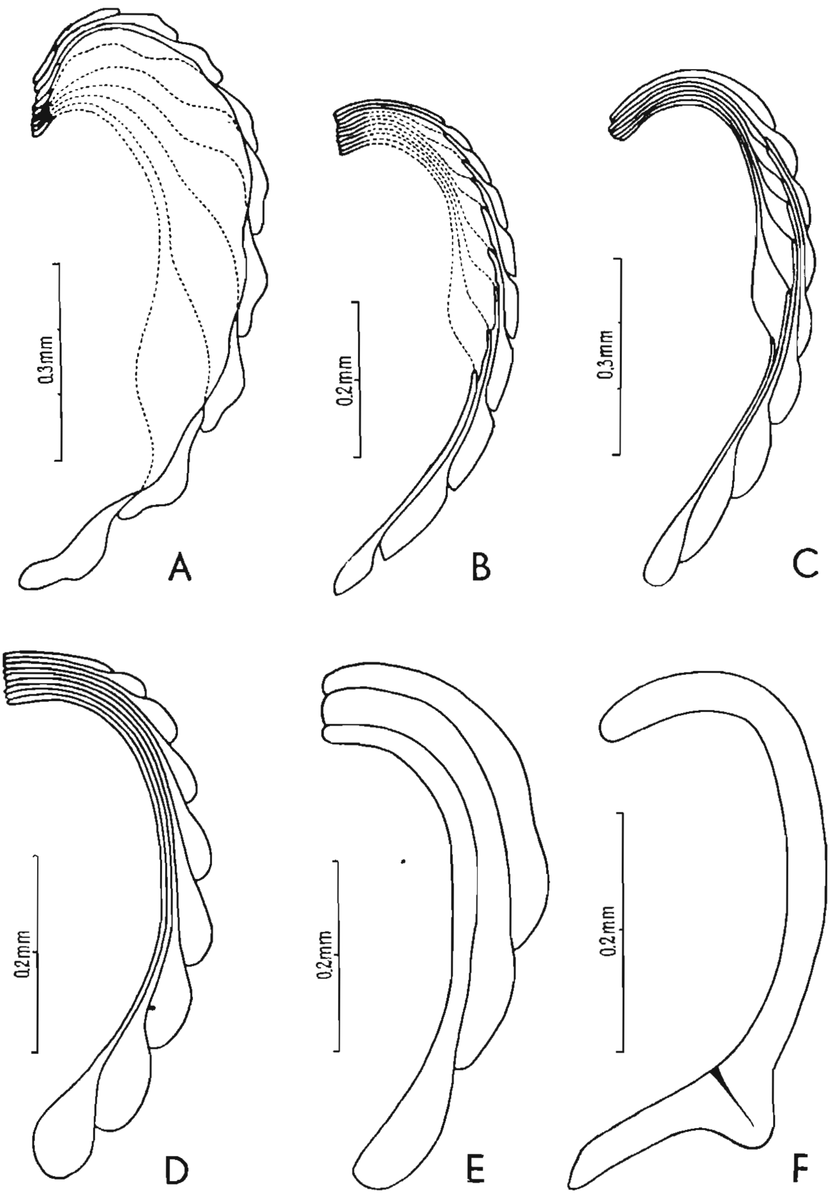


Fig. 9. — Schematic transverse sections of shells: A *Aberroconcha magna* (Harris), B *A.* plicata n. sp., C *A. devonica* n. sp., D *Eridoconcha rugosa* Ulrich & Bassler, *E Cryptophyllus oboloides* (Ulrich & Bassler), *F Milleratia shideleri* Levinson (after Levinson, 1951).

Carapaces of these species correspond to a morphological series passing from the multilamellar carapace of Eridostraca to the unilamellar carapace of typical ostracods.

body against danger, but at the same time hampered its free movements on the sea floor. It seems that interlamellar chambers (comp. fig. 1, 2; pl. I, fig. 1, 2*b*) to a certain extent counteracted this ballast. They were produced by chitinous lamellae invaginated into the interior of shell and corresponding to the successive growth stages (*Aberroconcha*). This type of „hydrostatic" organ, however, did not occur consistently as is suggested by their complete calcification and compactness in carapaces of *Eridoconcha* Ulrich & Bassler (fig. 9 *D*, 23). The occurrence of an essential change, corresponding to Severtzoff's (1949) aromorphosis, was most likely responsible for the establishment of the process of moulting. During the first evolutionary stage, it involved the youngest growth stages only, while the older moults were not shed. This pattern of evolutionary change resembles — as has already been mentioned — Schindewolf's proterogeny (1950, p. 251), in which „die Ascendenten sind also hier nicht mit Hilfe der jugendlichen und mittleren Entwicklungsstadien zu ermitteln, sondern auf Grund der Altersformen".

A few remarks must here be made on the so-called „combined retention" discussed by Levinson (1951, p. 555). This process consists in the disturbed sequence of the moult stages. Namely e.g. instars III, V and VI are present on the carapace, while instar IV is missing. Actually, however, it is the last growth stages that come here into the question (the examples are taken from representatives of *Cryptophyllus*), namely instars VI, VII, VIII and IX, instar VII corresponding to Levinson's instar IV. The shells of the earlier instars have already been shed (I-V). The lack of one of the intervening instars (VII) is difficult to explain. Possibly we might in this case be dealing with a disturbance of the growth process (longer break between the moult stages), but a natural falling out of that instar without disturbing instar VI is inadmissible.

In what concerns the process of „retention" in *Ectodemites plummeri* Cooper (Henningsmoen, 1953*a*), the writer believes to be dealing here and in several other cases mentioned later with retained moulting. In this species the preceding growth stage had, indeed, been stopped, but owing to a probable purely mechanical reason. These are highly specialized forms and the earlier growth stage still present on the carapace is but very loosely connected with the adult stage. Valves thus joined do not adhere tightly (*vide* Cooper, 1945, pl. 57, fig. 32) as in *Cryptophyllus* or *Conchoprimitia*. Analogous occurrences have been noted in *Kozłowskiella* (Přibyl), (Adamczak, 1958, p. 79) and in very doubtful forms of „*Conchoprimitia*" *polinae* Nazarova (*vide* Egorov, 1954). Structures observed in these forms have nothing in common with the multilamellar carapace of Eridoconchidae, nor may these cases be correlated with the initiation of moulting in *Cryptophyllus* and *Conchoprimitia*. In these forms the young moult stages are tightly adhering, while the marginal area forms a sort of growth bands. The initiation of moulting is fairly well illustrated by examples taken from Levinson (1951, pl. 77, fig. 6 a-9 a), concerning *Eridoconcha* and *Cryptophyllus*. In Keenan's paper an analogous phenomenon is exemplified in representatives of „*Eridoconcha*" *marginata* (Ulrich), (*vide* Keenan, 1951, pl. 79, fig. 13-15). Forms figured by Levinson and Keenan, and referred to *Eridoconcha* Ulrich & Bassler, are, in the writer's opinion, rather to be regarded as representatives of the genus *Cryptophyllus* (comp. p. 72).

The origin of the unilamellar carapace in some representatives of the ostracods

The origin of the unilamellar ostracoid carapace is a complex question. Its realization may be traced through the genera *Aberroconcha*, *Eridoconcha*, *Cryptophyllus*, *Milleratia* and *Schmidtella*. Morphologically these genera not only display many comparable elements in the structure of shell, but moreover they indicate close mutual relationships (Levinson, 1951; Keenan, 1951).

The genus *Aberroconcha*, occurring since the early Palaeozoic, belongs to very primitive crustaceans which, on the one hand, exhibit features common in Conchostraca (multilamellar carapace), on the other hand—those of ostracods (calcareous carapace tending to produce a unilamellar shell). It is not excluded that its ancestor is to be found among some Cambrian representatives of Lepidittidae Kobayashi, provided with a calcareo-phosphatic carapace, from which the representatives of living Conchostraca may have descended, too.

The genera *Aberroconcha* and *Eridoconcha* have a wide geographical distribution (North America, Europe, Asia) and stratigraphic range (Ordovician — Devonian). Along with very primitive forms, such as Ordovician *Aberroconcha magna* (Harris), existed more specialized, progressive forms, too. Among these are representatives of the genus *Cryptophyllus* Levinson, provided with a few lamellae on the carapace. The evolutionary trend of these forms distinctly tends toward unilamellar carapace.

It has been asserted in the preceding chapters that the multilamellar carapace in *Cryptophyllus* and *Conchoprimitia* does not express a retention of moults, but an initiation of moults, and on this conception are based the considerations discussed in the present chapter. Many features indicate close relationship of the genera *Aberroconcha*, *Eridoconcha, Cryptophyllus, Milleratia, Schmidtella;* they are: a convex dorsal border and a straight hinge-line, mode of development of the free edge of valve (kind of velar structures) and the cryptocrystalline structure of the carapace.

In the case of Eridostraca the process of differentiation must have been markedly ununiform, occurring at varying rate. In result, along with closely allied genera, forming a nearly unbroken evolutionary line, we encounter others, whose separation from that group

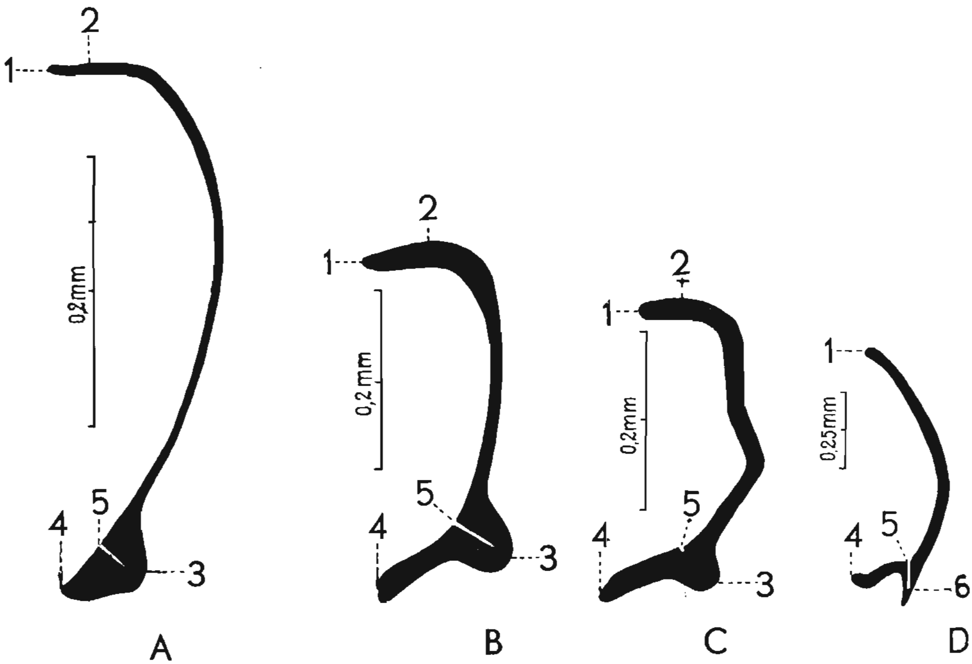


Fig. 10. — *A-C* transverse sections of single lamellae, illustrating structure of the free edge: A *Eridoconcha granulifera* n. sp., B „*Eridoconcha*" *multiannulata* Levinson (schematic drawing after a photo given by Levinson, 1951), C „*Eridoconcha*" *multiannulata* Levinson (remark as to fig.B), *D* transverse section of shell of *Euprimites suecicus* (Thorslund) after Jaanusson, *1957*

1 hinge line, *2* dorsal border, *3* growth band forming a kind of adventral structures, *4* free edge, *5* bisecting line, *6* velar dolon.

(*Conchoprimitia*) had occurred at an early time. These had been subjected to many morphologically significant modifications, but had inherited, too, some characters from their multilamellar ancestors, such as the development of the marginal area in the shell and the unshed moults during the growth process. Besides *Conchoprimitia* (in the Ordovician of Europe) representatives of *Cryptophyllus* make their appearance during the Ordovician (North America, Siberian Platform). The latter are connected with forms of the type of *A. magna* and some eridoconchs. The genera *Milleratia* and *Schmidtella* constitute the next link of that evolutionary chain. Representatives of the just mentioned genera are characterized by the lateral outline of valve, distinctly convex in the dorsal border with the hinge-line like the chord of an arch (Triebel, 1941). Its development was dependent upon the architecture of carapace. *Milleratia* and *Schmidtella* have the umbonal outline similar to that in Eridoconchidae. The most striking resemblance is noted when comparing lamellae isolated from the carapace of *Eridoconcha* and *Cryptophyllus* (fig. 9 *F*, 10 *A-C*).

The kind of velar structures occurring in the free edge of many Palaeozoic ostracods are an important not only morphological, but also phylogenetic character. They are of marked taxonomic significance. Schmidt (1941) was the first to turn his attention to these structures, making use of them in systematics. Subsequent investigations by Hessland (1949), Henningsmoen (1953*a*, 1954*b*, 1955) and Jaanusson (1957) confirmed Schmidt's suggestions. Jaanusson (*l.c.*, p. 188, 191-197) mentions various types of adventral structures which he regards, together with Levinson (1951) as products of the outer epidermal layer of the outer lamella. Triebel (1941, p. 357-358) supposes that both, the outer and the inner lamellae, participated in the formation of that kind of structure. Triebel's opinion, however, does not seem correct in view of evidence provided by studies on the adventral structures in *Aberroconcha magna* (Harris). In this form it is possible to trace the mode of development of the so-called bisecting line (Jaanusson, 1957) traversing these structures. In the Eridoconchidae they may be taken to be the first stage in the differentiation of the free edge of the carapace. This kind of structures does not occur among typical representatives of Conchostraca since in most of them the carapace has been but slightly calcified (excepted *Rhabdostichus*). In all of the known Eridoconchidae the carapace is calcified with the particular lamellae showing strong accumulation of calcium carbonate, mostly so in the free marginal area. Moreover, the extent of modifications to which they are subjected, varies, not only during ontogeny, but phylogeny, too. During the first growth stages of the carapace (stages I-III) in *Aberroconcha magna* (Harris), the free marginal area of lamellae is not much differentiated in relation to the remaining surface. The growth bands do not produce an adventral thickening. Some changes occur in this respect during the next stages of growth. The free marginal areas of laminae are thickened and form a sort of „podium" thickest about the centre. It is possible to trace the development of these structures by means of cross sections. The last growth band is usually gently folded. In the earlier bands the fold is decreasing — the excretion of calcium carbonate having continued in spite of the next growth stage — and a bisecting line is produced (fig. 5 *a*, *b*; pl. I, fig. 4). Stage VII, third but last, now exhibits the presence of a small lumen only. Analogous structures occur in *Cryptophyllus multiannulatus* (Levinson), (*Erido-*

concha multiannulata Levinson, 1951, pl. 77, fig. 6 e). The most striking resemblance of adventral structures is noted between *Aberroconcha* n. gen. and *Eridoconcha* on the one side, and *Cryptophyllus, Milleratia* and *Conchoprimitia* — on the other (fig. 11). Similarities are likewise observable in sections through „*Eridoconcha*" *multiannulata* (Levinson, 1951, pl. 77, fig. 6 c, 7 c), *Euprimites suecicus* (Jaanusson, 1957, fig. 31), *Eridoconcha granulifera* n. sp. Histal structures (Jaanusson, 1951) seem to have the same origin and to be a modification of the adventral structures in representatives of Eridoconchidae (fig. 10). Convergence does not seem a very likely supposition for these structures. The eridoconchoid type of adventral structures may be considered as the first step of differentiation of velar structures, occurring in Palaeozoic ostracods of the Palaeocopa. During individual development the velar structures make a very early appearance and are almost fully developed from the very first moults. This has been ascertained, among others, during investigation of *Kozłowskiella* (Přibyl), (Adamczak, 1958). In species of this genus a dark line (Adamczak, *l.c.*) is produced on velar structures as early as in the first stage. It corresponds to the bisecting line of Jaanusson (1957).

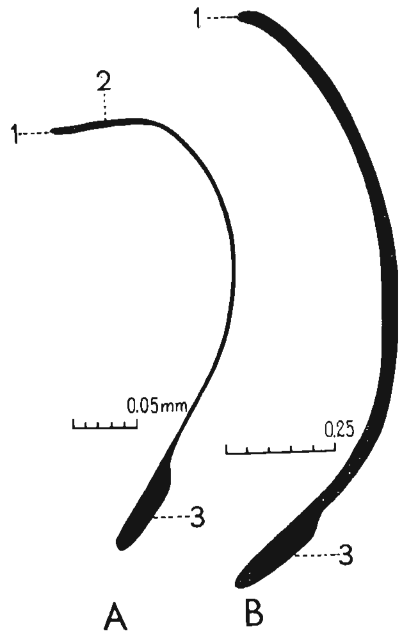


Fig. 11. — *A* transverse section of a single lamella of *Eridoconcha arsiniata* (Stover) *B* transverse section of shell of *Conchoprimitia gammae* (?) Öpik

1 hinge line, *2* dorsal margin, *3* adventral structures.

The microstucture of the carapace is another problem. Müller (1894) was the first to study it on recent materials, and to postulate the amorphic or finely crystalline structure of the shell. Distinct prismatic structures (fibrous structure of the calcified lamella) were first ascertained in Leperditiidae Jones (*Leperditia gigantea* Roemer) by Roemer (1858). Similarly prismatic structures with minute calcite fibres were observed in *Cythreis prava* Baird (Müller, 1894), within the dorsal area. In Palaeocopa, on the other hand, microstructure is cryptocrystalline. It is exhibited by *Conchoprimitia* Öpik, *Beyrichia* McCoy, *Hibbardia* Kesling, *Kozłowskiella* Přibyl, *Hollinella* Coryell, Eurychilinidae Ulrich & Bassler, and many other ostracods. Representatives of Eridostraca have an analogous structure, too.

The morphology of the carapace of some species of *Cryptophyllus* Levinson is characteristic by the shape of the median sulcus (S2). It resembles that on valves of species of *Milleratia*, also of certain *Conchoprimitia*. In representatives of *Aberroconcha* n. gen. and *Eridoconcha* this sulcus is missing. It is interesting to note that steinkern of *Aberroconcha plicata* n. sp. bear a very characteristic impression of the invaginated shell lamellae, having a close resemblance with median sulcus (S2). In some species of *Eridoconcha* (*E. granulifera* n. sp., *E. arsiniata* (Stover)) an elongate ridge is occasionally observable on the inner side. Its impression, resembling the sulcus in *Milleratia shideleri* Levinson, is likewise left on internal molds. In representatives of Eridoconchidae convexities on the internal side occur mostly during the last moult stages. In descendants of these animals they have disappeared completely and it is very probable that the median sulcus is their equivalent in representatives of the genus *Cryptophyllus* and in some Conchoprimitiidae Henningsmoen. In *Aberroconcha* the position of the muscle scar was probably near the point of maximum invagination of the last lamella. The appearance of sulcus (S2) was probably to some extent affected by that adductor muscle, but it has not been possible to identify it and its presence may be but indirectly inferred. In *Pyxion* Thorslund, *Parapyxion* Jaanusson and *Craspedopyxion* Jaanusson, as well as in many other genera, by Jaanusson (1957) referred to the Leperditellidae, the median sulcus closely resembles an analogous groove in *Milleratia*. These genera are mutually interrelated and derived from conchoprimitial forms (Jaanusson, *l.c.*, p. 415).

Comparative studies on primitive ostracods from the Palaeocopa suggest close connections of a number of morphological elements of the carapace, in the first place of the free marginal area, with analogous structures in *Aberroconcha* and *Eridoconcha*. The last named genus is closely allied with Conchostraca, as is evidenced by its multilamellar carapace. In the evolution of these animals the lamellae (moult stages) are subject to gradual calcification. During this process, or directly after its completion these animals acquired the ability to moult. The youngest moult stages were shed during the first phase of evolution, while the older ones were still attached on the shell (*Cryptophyllus*). However, this phase did not, indeed, persist even within one species. Some forms moult definitely, others have a tendency to „withstand" it (Levinson, 1951, pl. 77, fig. 6, 7; Keenan, 1951, pl. 79, fig. 13-15). The last evolutionary stage tending to produce a unilamellar ostracoid carapace is represented in *Milleratia* and *Schmidtella* related to the just mentioned genera. Representatives of the genus *Conchoprimitia* may, likewise, be correlated with this final stage. In the here mentioned ostracods the unilamellar carapace has evolved from a multilamellar one probably during the span of time from the Upper Cambrian to the early Ordovician. They have evolved in two distinct geographical regions. Forms of the cryptophylloid type developed in North America and Asia, those of the conchoprimitial type — in Europe.

STRUCTURE OF THE CARAPACE IN LEPERDITIIDAE JONES AND SOME HEALDIIDAE HARLTON

The prismatic structure of the leperditiid carapace is a well known fact (Roemer, 1858; Hessland, 1949; Levinson, 1951). A similar microscopic structure is also displayed by Podocopa (in the sense of Müller, 1894), such as *Bairdiocypris* (Kegel), *Pachydomella* Ulrich, *Condracypris* Roth, *Bairdia* McCoy, *Bythocypris* Brady. In these genera the calcite prisms are smaller than in leperditiids. Levinson (1951, p. 554), who has investigated the carapacial structure of various Leperditiidae genera, writes that „... shell is characteristically composed of two layers, a third layer being present on only one specimen (pl. 77, fig. 5 a, b)". Krömmelbein (1952, p. 322-323) when giving a very full analysis of the representatives of *Bairdiocypris*, writes about their carapace that: „Die Schale is dick und besteht wahrscheinlich aus zwei Lagen, von denen die innere meist dunkel gefärbt ist (besonders deutlich bei Fig. la, Chitin?), während die äussere durchscheinend hell ist. Besonders stark pigmentiert sind jeweils die Schalenränder, sowohl ventral wie auch in der Schlossgegend". A similar occurrence has been observed by Levinson (1951) in Leperditiidae in which the inner shell layer „... on most specimens is restricted to the dorsal and ventral margins" (*l.c.*, p. 554). The prismatic structure and so complex a structure of the carapace as in the Leperditiidae and Podocopa (not in all but in many early Palaeozoic forms) are not encountered in the Palaeocopa and Eridostraca. The phenomena discussed by Levinson and Krömmelbein call for a more extensive study. It seems that carapacial similarities in these two groups are not accidental. Detailed examinations of the shells of these animals undertaken by the present writer reveal more features in common than may be supposed at first sight.

A comparative study has been made of fluoridized and subsequently polished shells. Three layers are discernible in the thin sections of these shells: 1) outer — dark; 2) median — colourless and transparent; 3) inner — dark. In leperditiids these three layers are sharply delimited and have a distinctly prismatic structure (fig. 12 *A;* pl. II, fig. 6). The outer layer is markedly thin, the median one is thickest, while the inner is slightly thinner than the median. The outer layer is usually dark-coloured owing to strong permeation by organic substances. This has also been observed on shells of *Bairdiocypris, Pachydomella* and *Bairdia*. Though there are some differences between these forms and the leperditiids, they are not so important as those between the leperditiids and the other Palaeocopa. In these genera the outer layer is thicker and, similarly as in leperditiids, sharply delimited from the median layer (fig. 12 *B*). The last named layer passes gradually to the inner (darker)

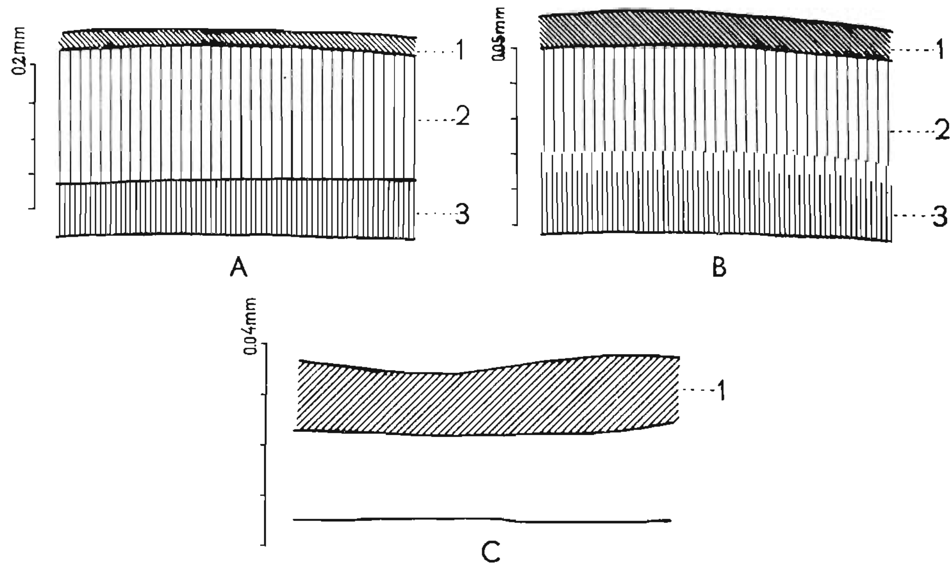


Fig. 12. — Schematic transverse sections of a fluoridized shell: A *Leperditia* sp., B *Bairdiocypris* sp., C *Hollinella* sp.
1 outer layer, 2 median layer, 3 inner layer.

layer (comp. pl. II, fig. 5). In Podocopa the prismatic structure partly disappears owing to fluoridization.

Analogous investigations of the shells of Eridoconchidae and Palaeocopa (*Hollinella* Coryell, *Kozłowskiella* (Přibyl), *Poloniella* Gürich, and others), have shown the carapace in all these cases to be composed of two layers (comp. fig. 12 *C*; pl. II, fig. 1) — a darker outer one and a transparent inner one.

These structural similarities do not provide direct evidence, but may, indeed, be indicative of different evolution of the carapace than that of the Palaeocopa. It is the muscle scars that provide sound evidence of their relationship. In the Leperditiidae the muscle area consists of many minute ligaments of adductor muscle. A similar type of muscle pattern is found in Healdiidae. Such adductors are not encountered in any other ostracod group outside of these families. Many authors believe these numerous minute muscles to be proof of the primitive character of these forms (Triebel, 1941, 1950; Pokorný, 1950, 1952, 1953, 1958). They are of great taxonomic and phylogenetic importance, possibly of greater value than such character as the duplicature of the carapace.

In what the free edge of shell is concerned, the Leperditiidae (fig. 13 *A;* pl. II, fig. 6) display the most primitive structure among all the here discussed groups. A similar structure is also displayed by *Bairdiocypris* (Kegel) and *Pachydomella* Ulrich (fig. 13 *B*, 14 *A*, *C;* pl. II, fig. 4). In the two just mentioned genera, however, appears an inner layer consisting of a thin chitinous membrane permeated by calcium carbonate.

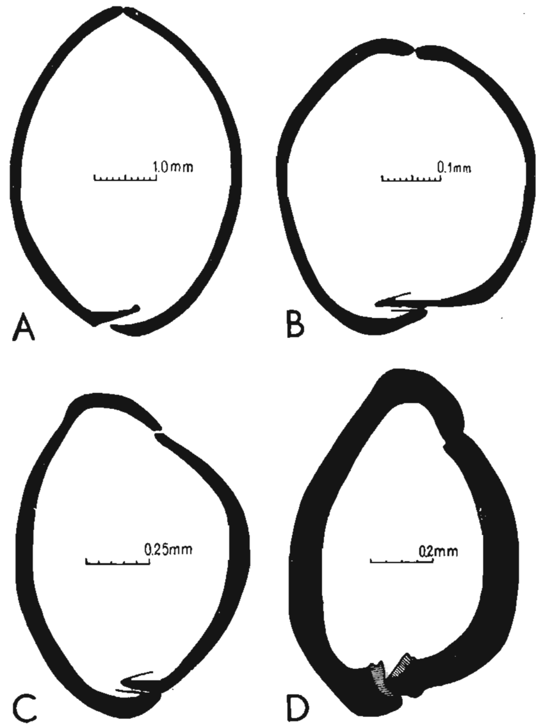


Fig. 13. — Schematic transverse sections of carapaces: A *Leperditia* sp., B *Pachydomella* sp., C *Bairdiocypris* sp., D *Bairdia* sp.

Krömmelbein (1952, p. 322) supposed that in these forms (*Bairdiocypris*) the inner layer partly contained the marginal area of shell (outer lamella), resembling in this the genus *Ogmoconcha* Triebel (Triebel, 1950). No such modifications have been ascertained by the present writer. It seems to him that the inner lamella occurring on *Bairdiocypris* (Kegel) marks among ostracods the first stage or the beginning of formation of the carapacial duplicature.

A typical development pattern of this layer is to be found in representatives of *Bairdia* McCoy (fig. 14 *D;* pl. II, fig. 2, 3). In thin sections of these forms the inner lamella is strongly calcified and probably permeated by chitin (dark colouration). Outside of the zone of concrescence in this genus a dark line occurs. This, according to Jaanusson's terminology (1957), corresponds to the bisecting line, while according to Triebel's (1950) terminology it would be the „Verschmelzungszone" which „... offensichtlich auf die chitinige Zwischenlage zurückzuführen ist" (*l.c.*, p. 115). In what concerns the dark line in *Bairdia*, running parallel or slightly obliquely to the zone of concrescence, its origin seems to be different than that supposed by Triebel

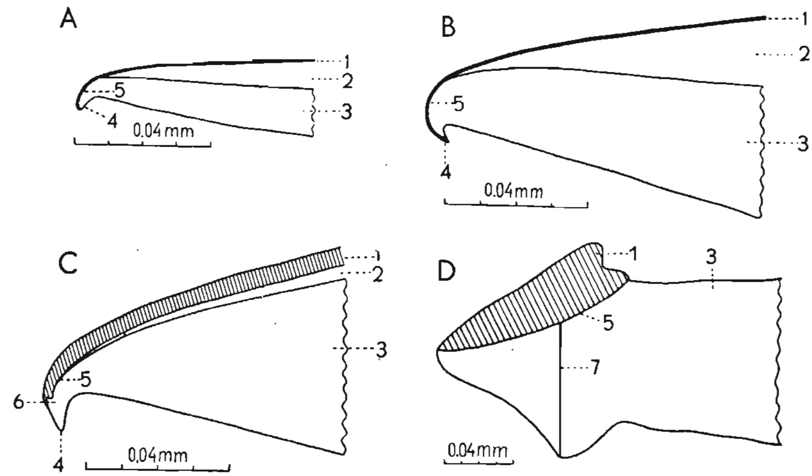


Fig. 14. — Schematic transverse sections of the free edge of right valve: A *Pachydomella* sp., B *Bairdiocypris* sp., C *Condracypris* sp., D *Bairdia* sp.
1 inner lamella, 2 vestibulum, 3 outer lamella, 4 extramarginal list, 5 zone of concrescence, 6 inframarginal list, 7 bisecting line.

for this type of structures. Under strong magnification (fig. 15) a most characteristic fan-like arrangement of the calcite prisms is seen in the part of shell bearing the dark line, resulting in a „Verschmelzungszone" like picture. In this part of the carapace the outer layer is strongly curved, hence it seems quite probable that the epidermal layer here was conspicuously folded, too, producing this structural pattern of the calcite prisms. With regard to *Ogmoconcha* Triebel and *Cytherella* Jones, it is not impossible that the transversal dark line in these forms had formed, as has been supposed by Triebel (1950). In this connection, Henningsmoen's statement (1953 *a*, p. 262), that „... the Platycopa type (of the margin — *F. A.*) is a reduced Podocopa type", seems partly correct. This supposition is categorically rejected by Pokorný (1956*b*), but apparently without adequate grounds.

Studies on *Bairdiocypris* (Kegel) and *Pachydomella* Ulrich evidently call for a revision of the views of palaeontologists ascribing considerable systematic importance to the duplicature of the carapace, that according to Triebel (1950, p. 116) constitutes „... ein taxonomisches Merkmal ersten Ranges angesehen werden...". Undoubtedly structures ascertained in these genera correspond to the inner lamella, hence they form the double margin of shell.

In connection with these problems comes to light the question of the systematic and phylogenetic significance of muscle scars. Their systematic value has, indeed, been fully appreciated in ostracod studies (Triebel, 1941, 1950; Scott, 1944; Pokorný, 1950, 1952, 1953, 1958; Krömmelbein, 1952), but so far underestimated in what phylogeny is concerned. In Pokorný's opinion (1950, 1952) the number of scars is a primitive character. Actually muscle scars do, most likely, play a decisive role and are the fundamental element providing evidence of relationship even between distant ostracod groups.

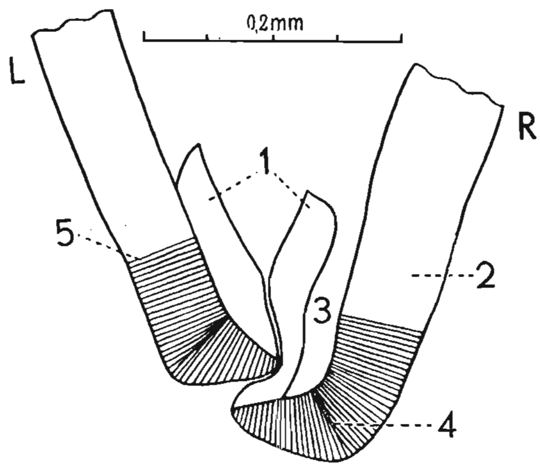


Fig. 15. — *Bairdia* sp., schematic longitudinal section of anterior border of the free edge of carapace

L left valve, *R* right valve, *1* inner lamella, *2* outer lamella, *3* vestibulum, *4* bisecting line, *5* calcite prisms.

Observations on the leperditiids indicate that the Healdiidae may have differentiated from that group. The following are characters pointing out their mutual relationship: 1) rounded muscle scars composed of many elements of adductor muscles; 2) prismatic structure of the carapace; 3) three-layered shell.

These three characters, common to both the mentioned groups, reasonably suggest that the Leperditiidae may have been the ancestors of Healdiidae. We do not encounter in other ostracods (in the first place not among Palaeocopa) carapacial structures characteristic of these two groups. The type of muscle scars must here be recognized as the most important character determining their relationship.

PROBLEM OF DIPHYLETISM IN OSTRACODS

Observations discussed in the two preceding chapters indicate distinct divergence of the ostracods from their very beginning. It is so suggested by studies on their carapace structure. In the Eridostraca and Palaeocopa the carapace structure has many features in common, while the leperditiids and the healdiids point out to a different origin, probably to the connections with another group of Cambrian crustaceans having a unilamellar shell. Indeed, as early as during the Cambrian — together with forms showing concentric growth lines, such as *Fordilla* Walcott — occur unilamellar chitinous Bradoriidae Matthew, whose morphology approaches that of the leperditiids, suggesting them as their possible ancestors (Ulrich & Bassler, 1931; Raymond, 1946). On the other hand, we do not find, within the Bradoriidae, equivalents displaying any similarities whatever to the carapace of Eridoconchidae. Solely some few Cambrian forms (*Fordilla, Lepiditta*) approach them. This standpoint and still more the results of studies on the carapace of Eridoconchidae, as well as of Leperditiidae and Podocopa, reasonably suggest the diphyletic origin of the Ostracoda. Thus far, the family-trees of ostracods have always been represented as monophyletic (Müller, 1894; Jaanusson, 1957; Zanina & Polenova, 1960), with the Leperditiidae and the Leperditellidae families placed by the palaeontologists at its base. A similar standpoint is accepted by Henningsmoen (1953*a*, p. 250) though he asserts that „the position of the Leperditellidae is uncertain", and later on states that „it is possible that the Leperditellidae are intermediate between the Leperditiidae and the Beyrichiacea". However, it is hardly possible to detect characters common to both the just named groups. All the morphological elements mentioned in discussing these groups express differences only. Jaanusson (1957, p. 221) criticizes Henningsmoen's views stating: „The degree of relationship between the Leperditiidae and other Palaeocopa is in fact as yet little known". Pokorný's inferences (1953, 1954, 1958) concerning leperditiids are the most radical: he separates them into a distinct order — the Leperditiida. That author's standpoint seems reasonably justifiable in view of the lack of relationship between this group and the remaining Palaeocopa from which it differs in many fundamental characters. Muscle scars and the probable presence of the heart in Leperditiidae are among the most important ones. According to Pokorný (1953, 1954) the last named feature suggests a very primitive character and fully justifies their high taxonomic value. Jaanusson (1957, p. 228) disputes Pokorný's opinion concerning differences between the Leperditiidae and Palaeocopa, stating that they have been overemphasized by that author. In what the heart is concerned (marks of blood canals), these are not restricted to Leperditiidae and Myodocopa, but have likewise been encountered in Leperditellidae, Beyrichiacea and probably Kloedenellacea (Henningsmoen, 1954*a*, p. 56). It seems that the presence of heart blood canals is not a feature of decisive systematic value, since this organ was, most

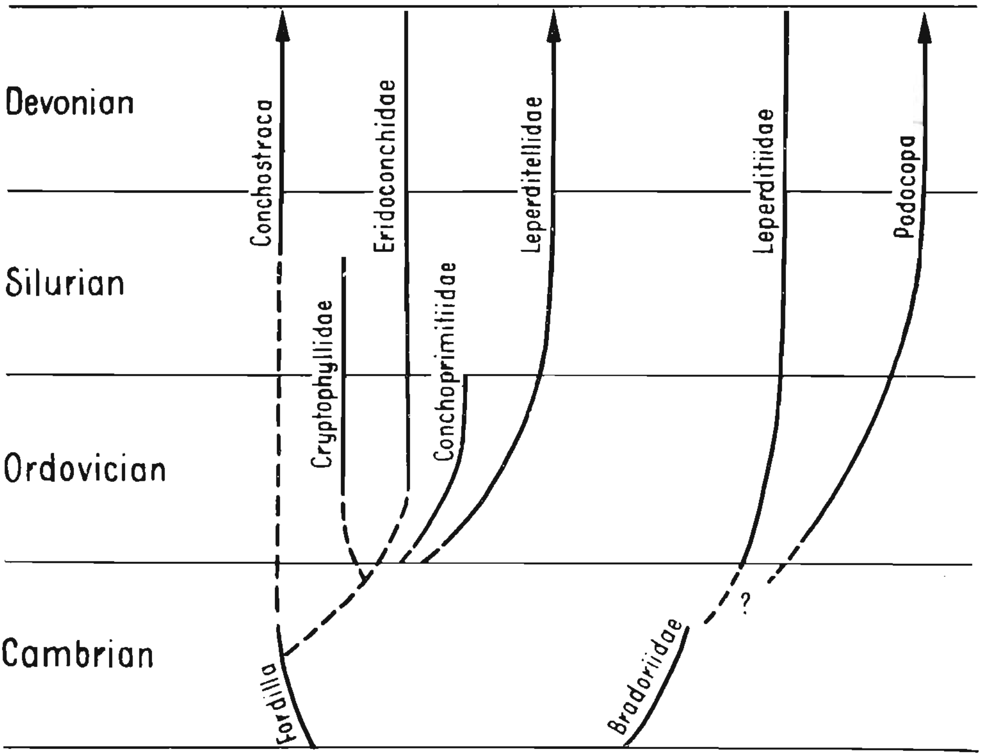


Fig. 16. — Diagram showing the supposed relationships and stratigraphic distribution of certain ostracod groups.

likely, present in all the early-Palaeozoic ostracods, being subject to a varying degree of reduction in its various groups.

Jaanusson (1957) considers the Leperditiidae in a similar manner as the Leperditellidae, i.e. as distinct superfamilies, and states (*l.c.*, p. 223) that „Leperditellacea represent the simplest type of the palaeocope ostracodes, and are apparently also the most primitive. It is well possible that the other Ordovician palaeocope superfamilies (Eurychilinacea + Hollinacea and Leperditiacea) have been derived from this group". The two first mentioned groups actually do exhibit close relationship with the Leperditellacea, while the Leperditiacea cannot be allied with them.

Zanina and Polenova (1960) have advanced a very peculiar concept as to the phylogeny of Palaeocopa. They establish this suborder as an order to contain the two suborders of Beyrichiida Pokorný and Leperditiida Pokorný. The phylogenetic scheme given by these writers (*l.c.*, p. 281), however, suggests three fairly independent evolutionary trends, all derived from *Cambria sibirica* Netzkaja & Ivanova, which is considered as the most primitive and earliest ostracod.

In the writer's opinion, *C. sibirica* is not an ostracod, but a representative of Archaeostraca, as is suggested by ornamentation and the structural type of the carapace. This has no bearing, however, on the phylogenetic scheme given by the just mentioned authors, but it does seem that Zanina and Polenova have not studied all the aspects of Aparchitacea and have underestimated their significance. As a matter of fact, this group (containing representatives of Leperditellidae, too) is of a far greater phylogenetic importance (comp. Jaanusson, 1957, p. 224).

It is the present writer's opinion that Eridostraca and Palaeocopa must be decidedly separated from the Leperditiacea since the latter correspond to a phylogenetic branch independent of the two former groups.

SYSTEMATIC PART

Suborder **Eridostraca** n. subordo

Diagnosis. — Ostracods with multilamellar carapace, rarely unilamellar, with short straight hinge-line, and convex dorsal margin. Greatest number of shell lamellae — eleven. Microstructure of carapace cryptocrystalline.

Occurrence. — Ordovician-Devonian (Jurassic?).

Remarks. — The separation of forms, so far assigned to the family Leperditellidae Ulrich & Bassler, 1906, into a distinct suborder is reasonably justified on the basis of the characteristic multilamellar structure of the carapace and many other morphological characters. A number of structural elements in the carapace of these animals points out that they are related with Conchostraca Sarv (Phyllopoda). This ostracod group is known in the fossil state only and occupies an intermediate systematic position among the lower Entomostraca, linking Conchostraca with Palaeocopa. In the course of its evolution the structure of the carapace underwent modifications, changing from a multilamellar one into a unilamellar. This process has a great phylogenetic importance. In distinction from the earlier term „retention of moults" proposed by Levinson (1951), it should rather be referred to as the initiation of moults.

Two families are to be distinguished in this new suborder: the Eridoconchidae Henningsmoen, 1953, and the proposed new family of Cryptophyllidae.

Henningsmoen (1953*a*) who separated the Eridoconchidae into a subfamily within the family of Leperditellidae, included into it the following genera: *Eridoconcha* Ulrich & Bassler, *Cryptophyllus* Levinson, *Milleratia* Swartz, *Schmidtella* Ulrich and ?*Paraschmidtella* Swartz.

Moreover, Leperditellinae Ulrich & Bassler, 1906, and Conchoprimitiinae Henningsmoen, 1953, have likewise been referred to the Leperditellidae. This standpoint, however, was not commonly accepted. Jaanusson (1957, p. 414) among others thinks that „*Leperditiella* and *Conchoprimitia* are evidently closely related, and the differences between them are not of subfamiliar value". Actually, however, these differences do exist, so that the recognition of the genus *Conchoides* Hessland (Hessland, 1949) as a synonym of *Conchoprimitia* Öpik (Henningsmoen, 1953*a;* Jaanusson, 1957; Sarv, 1959) is not justifiable. Some species of *Conchoides* have been ascertained (Hessland, 1949) to have a prismatic shell structure (*C. micropunctatus* Hessland) and they are probably representatives of Leperditiidae.

The proposed new family Cryptophyllidae would include middle-sized Eridostraca with carapace composed of several (6) or of one lamella, having a straight hinge margin and a well formed median sulcus. Genera referable to this new family are distinguished by their ability to moult (*Cryptophyllus, Milleratia, Schmidtella* and *?Paraschmidtella*).

In general morphology of the carapace they approach the Eridoconchidae. The fundamental difference between them concerns the number of carapacial lamellae which have persisted after their multilamellar ancestors (Eridoconchidae). They differ from the Conchoprimitiidae Hennigsmoen, 1953 (emend. Pokorný, 1958), too, in shape of the carapace, as well as in stratigraphic and geographic range. The Conchoprimitiidae made their appearance during the Lower Ordovician; similarly as in Cryptophyllidae n.fam. unshed moults may be encountered on shells of mature individuals. The ostracoid type of structure of the carapace has been realized by them at a much earlier moment and they have undergone greater modifications as compared with the Cryptophyllidae which are to be considered as direct descendants of the Eridoconchidae. Hence, the writer considers that they ought to be retained within Leperditellacea Ulrich & Bassler (emend. Jaanusson, 1957).

Genera referred to that new family, particularly so *Cryptophyllus* Levinson, ought probably to be separated into two independent taxonomic units, for this genus contains two morphologically different types of forms:

a) *Group 1,* includes typical cryptophylloidal species such as *Cryptophyllus oboloides* (Ulrich & Bassler) (= *Eridoconcha oboloides* Ulrich & Bassler), and *Cryptophyllus latimarginatus* (Keenan) (= *Schmidtella latimarginata* Keenan), (part.: Keenan, 1951, pl. 79, fig. 16). They display a distinctly umbonal shape of the carapace, cordate posterior outline and V-shaped section of the groove between the growth bands.

Species of this group are very closely related with the Eridoconchidae and most likely constitute a link joining the latter with *Milleratia* and *Schmidtella;*

b) *Group 2,* contains the species: „*Eridoconcha*" *multiannulata* Levinson, „*Placentula*" *marginata* Ulrich (emend. Keenan, 1951), „*Eridoconcha*" *elegantula* Keenan. All these species are characterized by a subrectangular outline of the shell, the presence of a well marked median sulcus and U-shaped section of the concentric groove.

Family **Eridoconchidae** Henningsmoen, 1953 (emend.)

Diagnosis. — Rather small multilamellar Eridostraca with distinct umbo. Hinge-line short, straight. Number of lamellae composing the carapace between 7 and 11.

Occurrence. — Ordovician through the Devonian.

Geographical distribution. — North America, Europe, Asia (Siberian Platform).

Genera: *Aberroconcha* n. gen. and *Eridoconcha* Ulrich & Bassler, 1923.

Remarks. — The most important character of the ostracods assigned to this family is the multilamellar structure of shell. The lamellae reflect the successive growth stages of the carapace. It is possible that in some representatives of this family the moulting process (shedding of moult stages) may have involved the earliest growth stages.

The writer has not ascertained on these shells the occurrence of sexual dimorphism. It rather seems that secondary sexual features have not affected the morphology of the carapace. Measurements made on *Aberroconcha plicata* n. sp., most copiously represented in the available material, do not provide sound suggestions for clearing up this problem.

Genus *Aberroconcha* n. gen.

Genotypus: Aberroconcha plicata n. sp.
Derivatio nominis: aberro — deviate, *concha* — shell.

Diagnosis. — Oval Eridoconchidae with numerous (between 9 and 11) lamellae on the carapace, and straight hinge-line. The uncalcified lamellar elements, invaginated into the interior of shell, form chambers. Dimorphism unknown.

Occurrence. — Ordovician through the Devonian.

Geographical distribution. — North America, Europe, Asia (Siberian Platform).

Species:

Aberroconcha plicata n. sp.	*Eridoconcha magna* Harris
A. devonica n. sp.	?*E. simpsoni* Harris

Remarks. — This genus is distinctly characteristic in the first place by the inner structure of the carapace which consists of many overlapping lamellae. They are mostly invaginated into the interior of the shell where they form a kind of chambers. The invaginated parts of lamellae are chitinous (?), or slightly saturated with calcium carbonate (*Aberroconcha devonica* n. sp.). Some of the here described species of this genus occur in Middle Devonian strata and these belong to a conservative lineage. Others, as e.g. *A. magna* (Harris), make their appearance as early as in the Ordovician of North America and Asia. They represent progressive forms probably showing rapid modifications, as is suggested by the occurrence together with them of *Cryptophyllus* Levinson which may possibly be regarded as their descendants. In the Ordovician representatives of *Aberroconcha* n. gen. are rare fossils. They include one of the most primitive groups of ostracods, while many carapacial features in these animals indicate that they are closely allied with Conchostraca (comp. p. 51—54).

Species ?*A. simpsoni* (Harris), referred to that genus, displays strong morphological resemblance with the remaining species, but its taxonomic position is not certain owing to our lack of knowledge of its internal structure. Considerable difficulties are encountered in investigating the internal structure of shell in species of the genus *Aberroconcha*. It may be analysed in thin slides only, or on fluoridized shells, revealing on the outer side of the carapace a characteristic chain of vesicles (interlamellar chambers) going from the centre of shell to the dorsal margin. The internal structure is doubtlessly taxonomically important. Hence, it should be taken into account in specific identification, for representatives of the genus *Eridoconcha* have the same ornamentation pattern with the closely allied genus *Aberroconcha*.

Aberroconcha magna (Harris, 1931)

(fig. 17; pl. I, fig. 4)

Holotypus: right shell figured by Harris (1931) in pl. V, fig. 3.
Stratum typicum: Middle Ordovician, Carter County, South Oklahoma, USA.
Locus typicus: Springer.

Diagnosis. — Multilamellar, umbonal carapace, with numerous (up to 10) concentric growth bands. The particular lamellae calcified along the free and the dorsal margins, but uncalcified in central parts invaginated into the interior of shell, and probably chitinous.

Material. — Several badly damaged shells, not isolated from the rock material. Specimens of this species have been kindly offered to the writer by Dr V. A. Ivanova, who had collected them from Middle Ordovician strata within the area of the Siberian Platform (Asia).

Dimensions (in mm):

Length	1.72
Height	1.44

Description. — These are the largest Eridostraca thus far recorded. Outline of carapace oval, dorsally forming a distinct umbo. Numerous

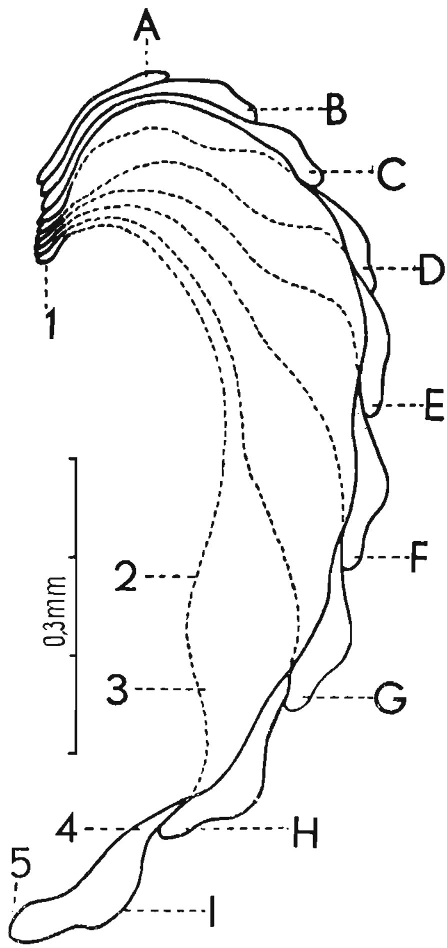


Fig. 17. — *Aberroconcha magna* (Harris), cross section of right valve
A nauplioconch, *B-I* successive growth stages, *1* dorsal lamella, *2* chitinous lamella, *3* interlamellar chamber, *4* distal part of lamella, *5* free edge.

(between 8 and 10) concentric growth bands, with intervening grooves marked on the surface. Shells well symmetric. Carapace thick, composed of many lamellae whose dorsal and free edge areas are subject to calcification. Hinge-line straight, dorsal border convex.

Structure of the carapace (fig. 17). In cross sections, oriented parallel to the umbo formed by the nauplioconch and directed towards the ventral edge of shell, may be seen the particular overlapping lamellae of the carapace. The first two or three lamellae are entirely calcified. On the dorsal side of shell they are adjacent to one another, forming multilamellar calcareous structures. Lamellae of the next growth stages are calcified in that part only which forms the growth band, also in the dorsal area, taking part in the hinge margin. The uncalcified chitinous surfaces of lamellae are invaginated into the interior of shell. Each lamella was successively a uniform cover of the animal's body, lining the carapace on its inner side. The chitinous parts of lamellae do not adhere to one another and occupy considerable space within the shell.

Hinge structures. These are multilamellar elements, closely touching one another over a small surface of the dorsal area. The particular lamellae composing these structures show no differentiation whatever; they have straight ends in both the left and the right valves. Growth bands form characteristic concentric ridges on the surface of the carapace, separated by grooves whose shape varies strongly even within one individual. The growth bands push on within a small area, according to an imbricating pattern. One part of the growth band, directly underlying the earlier growth stage, is thin and tapers out over a relatively small distance, to pass into the chitinous band. The calcium carbonate, laid down on the chitinous lamellae, has a different microstructure than that of the remainder of shell. This calcite has not been secreted by the animal, but is most likely associated with the process of fossilization. Distally the growth band thickens and forms a kind of „velar structure". This part has been probably formed through the folding of the epidermal layer, as is suggested by a small sinus (pl. I, fig. 4) closing up in the earlier growth stages. The free edge does not produce any definite structures; it is rounded and slightly thickened on the last bands.

Variability. — The extent of variability of this genus cannot be determined owing to scarcity of the available material. Modifications of the carapace are detectable in thin slides only, on account of the unsatisfactory state of preservation and owing to the specimens being in the rock matrix. Hence, observations on variability are limited to changes affecting the shell during the process of its postembryonal development. The building up of the carapace continued all through the lifetime of an animal, and the story of individual development is discernible on mature specimens. The first stage consists of the nauplioconch. This is of simple structure lacking any ornamentation. During the next stages the growth bands are thickened to produce a kind of „velar structure". The groove separating the growth bands is V-shaped. In stages III and IV the median part of the band thickens up; it is provided with a small central lumen. In the successive growth stage an embayment is visible within the thickened part of the band, while the groove separating the growth elements becomes U-shaped in section. This is the picture presented by the carapace, whose thin section is oriented somewhat obliquely and away from the side of the main invagination axis (pl. I, fig. 4); this displacement, however, is expressed by the hundredth fractions of a millimetre.

Occurrence. — Specimens of this species have been found by Dr V. A. Ivanova in Middle Ordovician deposits of the Siberian Platform (in districts drained by the rivers Podkamennaja Tunguska and Lena). So far representatives of this species have been reported from analogous formations of North America only. Thus the geographical range of the species is very wide, indeed. Its occurrence, however, being very rare, it could not play the role of an index fossil.

Remarks. — In view of the strong resemblance of ornamentation in the Siberian specimens with the American ones, the writer did not hesitate to refer them to *Aberroconcha magna* (Harris). Even though the American forms are known from very incomplete descriptions, it may reasonably be supposed that they represent the same morphological type of the carapace as the examined specimen from the Siberian Platform. *A. magna* approaches the Devonian representatives of this genus (*A. plicata* n. sp.), though in the latter form the calcification process of the carapace has advanced much further. *A. magna* is not, in most probability, directly ancestral of the Devonian forms. Most likely it represents another evolutionary trend and belongs to the progressive representatives of that group. Along with forms of the *A. magna*-type, shells approaching the genus *Cryptophyllus* have also been discovered by the writer in samples of Ordovician rocks from the Siberian Platform. This might suggest that representatives of the last named genus occurred over a wide geographical range (America-Asia) in Ordovician time. From that territory Ivanova (1955) also described representatives of *Eridoconcha* (*E. minutissima* Ivanova), *Schmidtella* (*S. dorsicostata* Ivanova) and others.

Aberroconcha plicata n. sp.

(pl. III, fig. 1 *a–c*)

Holotypus: carapace figured in pl. III, fig. 1 *a–c*.

Stratum typicum: Middle Devonian (Couvinian), Holy Cross Mountains.

Locus typicus: Wydryszów.

Derivatio nominis: Lat. *plica* — fold, with reference to folds formed by chitinous lamellae invaginated into the interior of shell.

Diagnosis. — Carapace of moderate size, umbonal, multilamellar, with numerous (up to 10) growth bands. Chitinous lamellae, invaginated into the interior of shell, form rather small chambers.

Material. — About 80 well preserved shells, isolated from the rock matrix. Young individuals with few layers have also been encountered among this material.

Dimensions (in mm):

	Holotype	Paratype
Length	0.966	1.080
Height	0.775	0.829
Thickness	0.538	0.535

Description. — Carapace oval, posterior part higher than the anterior. Shells perfectly symmetric. Particular growth bands separated from one another by grooves, which are V-shaped in section. Last growth band narrow. Umbo formed by the nauplioconch.

Structure of carapace. Transverse sections allow better knowledge concerning the complicated structure of this species. A thin section, cutting the carapace slightly obliquely from the umbo to the ventral edge of shell, reveals the presence of thin lamellae whose dorso-central parts are chitinous. The surface of lamellae, which invaginate into the interior, occupies one-tenth of the carapace length. The calcified parts of the particular lamellae are larger than those in *Aberroconcha magna*. The first two lamellae are completely calcified; they are adjacent to one another. The nauplioconch has a simple morphology and does not produce any adventral structures within the free edge area. In the next growth stages this part of the shell is already provided with structures resembling the velate ridge. Beginning with stage III, the carapace lamellae are over a small area invaginated into the interior of the carapace, where they are not calcified. Secondary calcium carbonate is often deposited on them. The hingements are multilamellar and show simple construction.

Growth bands and the morphology of lamellae. The concentric bands on the surface of shell correspond to these parts of the lamellae that are protruding during successive stages beyond the preceding ones. Along the free edge the band is gently rounded and thickens gradually in the proximal direction, attaining its maximum thickness at the „growth line". The band is a part of the lamella whose remaining (internal) part is thin and slightly sigmoidal. The lamella of the last stage of growth (its distal part without the growth band) is thin; dorsally it occupies the width of three preceding growth bands. At the level of the third band, counting from its bottom, the layer curves gently passing into the thin membrane, invaginated into the interior of shell. It coats the inner side of shell. Overlying it is the one but last layer which is somewhat different. It is provided with a subcircular list just at the termination of the calcareous part of the lamella of the last stage (fig. 1; pl. I, fig. 2 *b*). The remaining lamellae of the earlier growth stages display similar development pattern.

Ontogeny. — The carapace of Conchostraca is known to develop all through the animal's lifetime. The new growth stages are not shed, but superimposed on the earlier ones thus producing a multilamellar shell.

The mature carapace of these forms gives at the same time a full picture of shell ontogeny.

In Eridoconchidae the growth process was analogous to that in Conchostraca. Along with shells of mature individuals of *Aberroconcha plicata*, carapaces have also been found exhibiting a smaller number

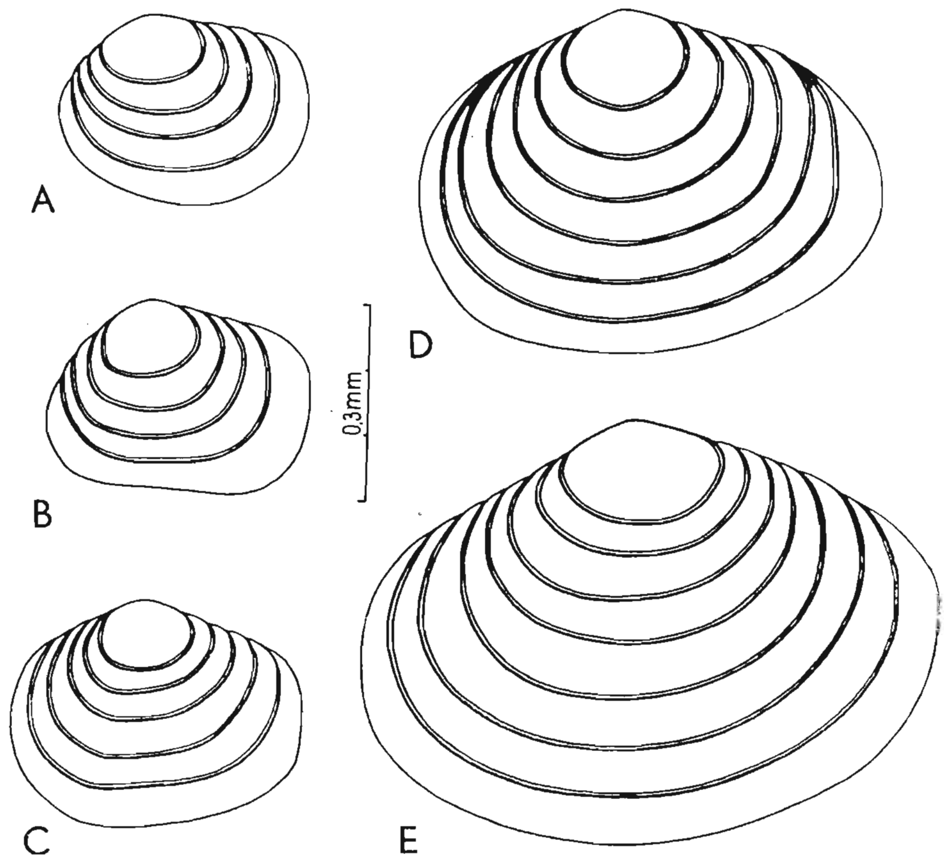


Fig. 18. — *Aberroconcha plicata* n. sp., *A-E* young carapaces of various growth stages.

of growth bands and, most probably, corresponding to young individuals. The most characteristic feature of the shells here is their shape, subject to strong modifications during the growth process. The youngest individuals found by the writer are with 4 bands (fig. 18 *A*). The shape of the carapace in these forms differs from that in mature specimens. The posterior part of shell is more strongly developed. The bands are wide. Gradually, with the addition of new growth stages, the shell outline changes from one nearly rectangular (fig. 18 *A-C*) into an oval one (*D-E*) which characterizes mature forms.

Variability. — As has already been mentioned, the carapace of *A. plicata* n. sp. is subject to certain variations during the growth process. Mature forms are more uniform and their shell outline is not affected by major modifications. Respective data concerning the variability range are given in tabular form in fig. 19.

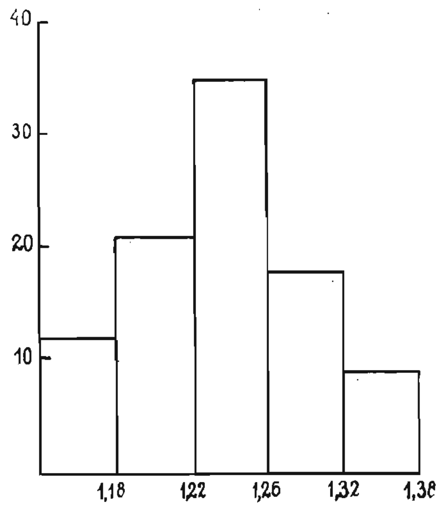


Fig. 19. — *Aberroconcha plicata* n. sp., variability diagram: number of specimens on ordinate; length/height of shell ratio quotients — on abscissa.

Occurrence. — *A. plicata* n. sp. is encountered in Middle Devonian strata of the Holy Cross Mountains. It occurs already within the lowermost Couvinian horizons at Wydryszów and Grzegorzowice. In the first locality some tens of these shells have been collected from Couvinian beds. In relation to the other ostracod groups this amount is 1:250. In the Grzegorzowice profile only a very few shells have been discovered.

Remarks. — *Aberroconcha plicata* n. sp. represents morphologically a transition from *A. magna* (Harris) to *Eridoconcha (E. rugosa)*. These forms, however, are not directly related, for they occur at different periods. *A. plicata* probably belongs to a conservative lineage of forms whose evolution progressed at a very slow rate. Forms approaching *A. magna* were most probably their ancestors. After acquiring a fair ability for carapace calcification, they lingered on for a greater period of time at that evolutionary stage. Nor is it improbable that they appeared at a later time and played no role in the evolution of ostracods.

Aberroconcha devonica n. sp.

(pl. III, fig. 2 *a–c*)

Holotypus: carapace figured in pl. III, fig. 2 *a–c*.
Stratum typicum: Middle Devonian (Couvinian), Holy Cross Mountains.

Locus typicus: Grzegorzowice.
Derivatio nominis: *devonica* — occurring in the Devonian.

Diagnosis. — Carapace subovate, of moderate size, with numerous (9) lamellae on the carapace. The particular lamellae calcified and partly invaginated into the interior of shell. Anterior part of carapace sharply truncated.

Material. — A dozen or so of well preserved shells.

Dimensions (in mm):

	Holotype	Paratype
Length	0.924	0.922
Height	0.777	0.775
Thickness	0.505	0.515

Description. — Carapace subovate, anteriorly sharply truncated. Umbo directed to the front. Particular growth bands of nearly uniform breadth, the last ones somewhat narrower.

Structure of carapace. Thin sections show invaginations of lamellae so characteristic of the genus *Aberroconcha* n. gen. The lamellae are almost entirely calcified. The first four growth stages adhere to one another, while the subsequent are gently invaginated into the interior of shell. In the dorsal area the invaginations gradually disappear. Lamellae of the last growth stages form analogous chambers as in *A. plicata* n. sp. The multilamellar hinge is of simple structure, dorsal border convex.

Remarks. — *A. devonica* n. sp. is closely allied with *A. plicata* n. sp. This is suggested foremost by its internal structure, the appearance of the hinge margin and its occurrence. The process of calcification of carapace lamellae though much further advanced than in *A. plicata* n. sp. is not yet definitely completed in *A. devonica* n. sp. The chitinous layers, especially in the last growth stages, have a very low calcium carbonate content.

A. devonica n. sp. differs from its ancestor (*A. plicata*) in the shell outline being more rounded and the length/height ratio 1.16, while in *A. plicata* it is 1.26. They are extremely rare fossils in the Couvinian deposits of the Grzegorzowice profile.

Genus *Eridoconcha* Ulrich & Bassler, 1923

Genotypus: Eridoconcha rugosa Ulrich & Bassler.

Diagnosis. — Multilamellar ovate Eridoconchidae, with short hinge line and distinct umbo. Number of lamellae on the carapace ranges from 7 to 11. Dimorphism unknown.

Occurrence. — Ordovician through the Devonian. A genus with cosmopolitan distribution.

Species:

Astarte socialis Eichwald, 1860
Eridoconcha rugosa Ulrich & Bassler, 1923
E. materni Bassler & Kellett, 1934
E. concentrica Coryell & Williamson, 1936
E. raychmani Egorov, 1954
E. tokmovoensis Egorov, 1954
E. minutissima Ivanova, 1955
Cryptophyllus arsinius Stover, 1956
Eridoconcha baschcirica Ljaschenko, 1960
E. granulifera n. sp.

Remarks. — Ulrich and Bassler (1923*a*) established the genus *Eridoconcha* to accommodate Ordovician and Silurian forms with concentric ridges and grooves. Their diagnosis read: „Small, apparently unequivalved carapaces with concentric, simple or rugose bands or rows of punctae, resembling an equilateral pelecypod or brachiopod in shape and markings" (*l.c.*, p. 297). The broad generic diagnosis admitted of the inclusion into it of forms with a unilamellar carapace, too, e.g. *Eridoconcha placentula* Ulrich & Bassler. Not all of the species described by those authors have been here considered.

In the course of the following years Matern (1929) identified as *E. rugosa* Ulrich & Bassler a form which Bassler and Kellett (1934) recognized as a new species (*E. materni* Bassler & Kellett). *E. magna* and *E. simpsoni* — species established by Harris (1931) — have been referred by the present writer to the new genus — *Aberroconcha*.

Revision of the genus *Eridoconcha* was made simultaneously, but independently by Levinson (1951) and Keenan (1951). They have contributed to a better knowledge of this genus, and have had a decisive bearing on its taxonomic and phylogenetic evaluation given in the present paper. On the U-shaped section of grooves the genus *Cryptophyllus* has been separated by Levinson (1951) from the genus *Eridoconcha*. This separation is justifiable, but the character on which the new genus was established has no systematic significance, for both V-shaped and U-shaped grooves may occur on the carapace of the same individual. To the genus *Cryptophyllus* are here being assigned all the forms of *Eridoconcha* with less than 7 lamellae on the carapace. The fundamental feature in taxonomic evaluation is, indeed, the ability for shedding the juvenile growth stages. This character has likewise markedly influenced the writer's interpretation of their phylogenetic position in relation to the Eridoconchidae and has provided a base for the creation of a new family — the Cryptophyllidae. All forms assigned to this family are distinguished by the limited ability to moult, hence on shells of these animals we may observe a much smaller number of lamellae than in the case of Eridoconchidae.

Keenan (1951) believes that it is not *E. rugosa*, but *Placentula marginata* Ulrich, 1890, by Bassler and Kellett (1934) assigned to the genus *Jonesites* Coryell, which is the genotype of *Eridoconcha*. Figures published by Keenan (1951, pl. 79, fig. 13-15) suggest that these forms are referable to the genus *Cryptophyllus* Levinson on the ground of the small number of growth bands on the carapace.

The species of *Eridoconcha*, described from the Siberian Platform (Ivanova, 1955) and from the European part of the Soviet Union (Egorov, 1954; Ljaschenko, 1960), do not arouse doubt as to their generic assignment.

Schmidtella latimarginata Keenan (Keenan, 1951) is interesting in that the forms it contains differ in the morphology of the carapace. Some of them (Keenan, 1951, pl. 79, fig. 16) ought to be referred to the genus *Cryptophyllus* Levinson, as is suggested by their multilamellar carapace.

Eridoconcha rugosa Ulrich & Bassler, 1923
(pl. IV, fig. 3 *a-c*)

Holotypus: shell of *Eridoconcha rugosa*, figured by Ulrich & Bassler in text-pl. 14, fig. 9.
Stratum typicum: Upper Ordovician (Maysville), Ohio, USA.
Locus typicus: Cincinnati.

Diagnosis. — Shell suboval in shape, with numerous (up to 10) growth bands. Hinge line straight, the dorsal border convex. Carapace lamellae adjacent to one another on the whole surface.

Material. — Some dozens (35) of well preserved carapaces.

Dimensions (in mm):

	1	2
Length	0.777	0.714
Height	0.546	0.588
Thickness	0.400	0.398

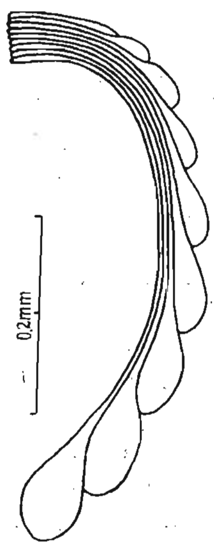


Fig. 20. — *Eridoconcha rugosa* Ulrich & Bassler, transverse section of right valve.

Description. — The valves are with conspicuous growth bands separated by concentric grooves. The bands are smooth, with the surface occasionally finely granulated (especially so during the last growth stages). The free edge of shell is gently convex, rounded both anteriorly and posteriorly. A line drawn from the umbo to the ventral edge divides the shell into two nearly symmetric halves. In posterior view the carapace is heart-shaped.

Structure of shell. Lamellae composing the carapace are visible in thin sections. The nauplioconch is of simple structure, smooth in the free edge area. The succeeding growth stages have developed adventral structures. The hinge parts formed by the dorsal lamellae terminate straight and are equally developed on both valves (fig. 20).

On partly decalcified shells (fig. 8 *A*), on the boundary of the growth bands, minute, virgulate pores are visible, most likely vestiges after the setae of the chitinous layer in the marginal area.

Ontogeny. — The young carapaces have been found, too, among the collected material. They are characterized by rather small dimensions (between 0.336 to 0.540 mm) and fewer lamellae on the carapace (the smallest ones having 5 lamellae only). In shape of shell these forms strongly resemble the juvenile carapaces of *Aberroconcha plicata* n. sp. During the earliest growth stages the shell is nearly rectangular and caudally more developed. In the following stages these proportions are modified, the shape of shell becoming analogous to that in mature individuals (fig. 21).

Variability. — The height of the carapace of mature individuals shows fairly strong variations. The length/ /height ratio ranges from 1.31 to 1.52. Ornamentation does not, on the whole, vary to any considerable extent. Occasionally only, extremely fine granulation may be encountered on the last growth stages.

Occurrence. — As has been stated by Ulrich and Bassler, *Eridonconcha rugosa* occurs in the Upper Ordovician (Maysville division of the Ordovician) and Silurian. In Europe it has been recorded from the Devonian of the Holy Cross Mountains.

Remarks. — The description of this species, as given by Ulrich and Bassler (1923*a*) is very concise. The structure of its carapace has not been investigated. The figure of this species

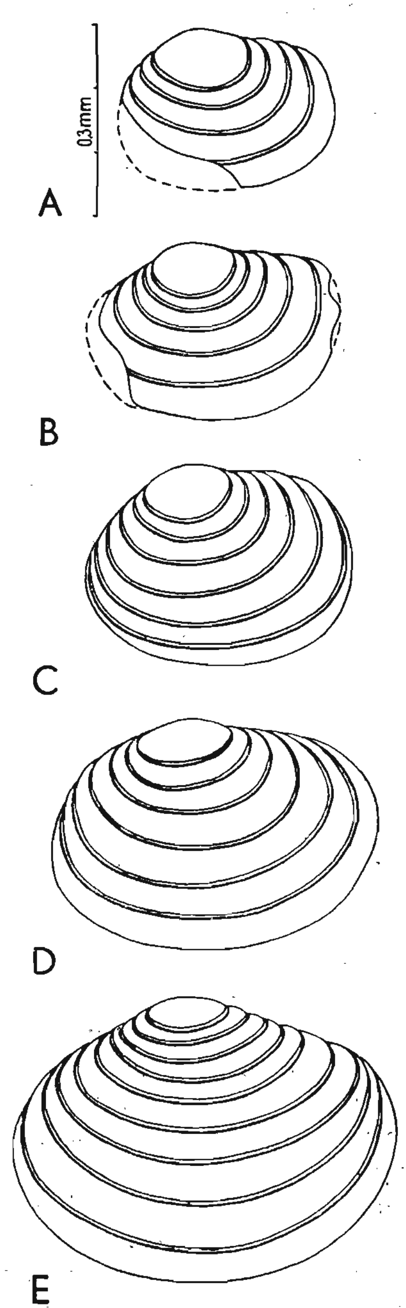


Fig. 21. — *Eridoconcha rugosa* Ulrich & Bassler, *A-E* young carapaces of various growth stages.

given by the authors is a very schematic drawing, hardly to be relied upon for specific identification. Specimens from the Holy Cross Mountains closely resemble the American form in that they have the same shell outline and dimensions. On this evidence specimens from Middle Devonian strata of Poland are regarded as conspecific.

Eridoconcha granulifera n. sp.

(pl. IV, fig. 2 *a-c*)

Holotypus: carapace figured in pl. IV, fig. 2 *a-c*.
Stratum typicum: Middle Devonian (Givetian) of the Holy Cross Mountains.
Locus typicus: Skały.
Derivatio nominis: Lat. *granum* — grain, *ferro* — to bear, with reference to the granulation on the growth bands.

Diagnosis. — Outline of valve ovate. Numerous minute granulations on the last growth bands. Lamellae completely calcareous, adhering to one another on the whole surface. Lamellae 9 in number.

Material. — A dozen or so of detached valves and fairly well preserved carapaces.

Dimensions (in mm):

	Holotype	Paratype
Length	0.567	0.580
Height	0.420	0.440
Thickness	0.357	0.340

Description. — Shell subovate with very distinct growth bands. The carapace umbonal, with the straight hinge line in a depression. Minute grains occurring on the last four growth bands. On the last growth band they are the largest and slightly obliquely directed towards the outside of the shell. The carapaces of this form are swollen, which may not, however, be associated with dimorphism, thus far not observed either in this species or in others here discussed. The depressed hinge line is of simple structure. On the dorsal side the concentric grooves are conspicuous and converge below the umbo. On the ventral side the grooves run parallel to the free edge of shell.

The carapace is composed of 9 calcareous lamellae, whole distal ends form a sort of velar structures. Grooves separating the bands are V-shaped during the early growth stages, later to become more or less U-shaped. The lamellae of the early stages are distally somewhat thickened. In the subsequent stages a kind of velar structures are first formed. In cross section a distinct dark line is marked on these structures, probably formed owing to the folding of the epidermal layer; it may be correlated with Jaanusson's (1957) „bisecting line".

The hinge areas are multilamellar with analogous development of lamellae in both valves.

In transmitted light vestiges of minute reticulation refracting light (Netzwerk) have been observed (fig. 22). This reticulation resembles analogous structures present in Conchostraca (comp. p. 52—53). They are most likely vestiges of the chitinous skaffolding which was included in the layer on the calcareous shell, or lined it on the inner side. In living ostracods these structures have been studied in full detail by Müller (1894).

Variability. — The marginal parts of growth bands are in the first place subject to modifications during the growth process. It has been noted, too, that with growth of the carapace, the shape of the concentric grooves changes very fundamentally. During the early growth stages they passe through V-shaped phase subsequently to become U-shaped. That part of the growth band forming adventral structures deserves special attention. The adventral structures are formed gradually during the growth process of the carapace. Initially they are folded, as is suggested by the dark line bisecting it at right angle to the surface.

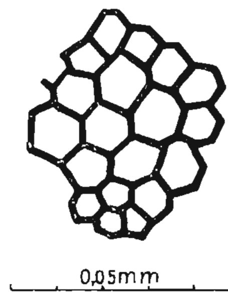


Fig. 22. — *Eridoconcha granulata* n. sp., fragment of shell reticulation.

The outline of carapace is subject to some variations, too. On the available material it has been ascertained that the length/height ratio of the carapace ranges from 1.22 to 1.40. As compared with *E. rugosa* Ulrich & Bassler, the variation curve is here shifted towards greater sphaericity of shell.

Occurrence. — *E. granulifera* n. sp. occurs in Poland within Givetian deposits at Skały, but is very rare.

Remarks. — Forms referred to this species display certain similarities with *E. rugosa*, expressed mostly in ornamentation pattern and shell outline. Apparently, these species are interrelated and represent links of one evolutionary trend. They have not acquired the ability to moult, since all the moult stages are preserved on their carapace.

Eridoconcha arsiniata (Stover, 1956)

(pl. IV, fig. 1 *a-c*)

Holotypus: carapace figured by Stover (1956) in pl. 119, fig. 37.
Stratum typicum: Windom shale (Moscow formation), western New York.
Locus typicus: Genesee County, N. Y.

Diagnosis. — Shell small, ovate, with numerous (9) lamellae. Umbo slightly anteriorly directed. Hinge line short, straight.

Material. — Several well preserved valves and carapaces.

Dimensions (in mm):

	1	2
Length	0.545	0.505
Height	0.462	0.460
Thickness	0.360	—

Description. — This is one of the smallest species of *Eridoconcha.* The average size of the shell does not exceed 0.52 mm. The carapace is multilamellar, with thin lamellae. The growth bands are of nearly uniform breadth, the last ones being as a rule the narrowest. The gently rounded anterior part of shell is lower than the posterior part. In the centro-dorsal part of shell a distinct umbo is present, consisting of the nauplioconch. In cross section the carapace is cordate.

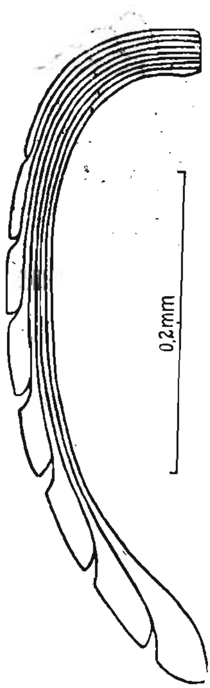


Fig. 23. — *Eridoconcha arsiniata* (Stover), transverse section of left valve.

Structure of carapace. The carapace lamellae tightly adhere to one another on the whole surface, and only occasionally detached valves are in these elements gently folded in the dorsal carapace area. The last stage lamella is gently rounded along the free edge (fig. 23).

The hinge structures do not show any differentiation, the particular layers within the hinge area on both shells being straightly terminated and adjacent. The hinge line is short; in the anterior part of shell it passes into the free edge at an obtuse angle. In the distal part of the carapace the analogous angle is wider.

Occurrence. — *E. arsiniata* occurs in Upper Givetian beds of the United States of America (New York) and in analogous formations of Poland (Świętomarz-Śniadka and Skały).

Remarks. — *E. arsiniata* (Stover) differs from all the so far studied species of *Eridoconcha* in its very small dimensions. The studied specimens are not young forms since they bear 9 lamellae. These are thin, with the growth bands forming a sort of adventral structures, not much differentiated in the successive stages. In these characters *E. arsiniata* differs from *E. rugosa* and *E. granulifera* n. sp. which have the growth bands rounded and forming a sort of ridges. In shape of lamellae and of the growth bands *E. arsiniata* (Stover) approaches nearest to representatives of *Aberroconcha plicata* n. sp., *A devonica* n. sp. and *Eridoconcha concentrica* Coryell & Williamson (Stover, 1956).

In view of the very strong resemblance of the Polish specimens in exterior appearance and dimensions, they have been referred to the species established by Stover on specimens from the Givetian strata (Moscow form.) of North America. The American specimens differ in dimensions only, while in what concerns other external features they are similar with the Holy Cross Mountains specimens.

*

ADDENDUM

After the present paper had been sent to the press, Ivanova (1960) published a paper in which she revised the position of Archaeostraca, erected a new subclass Ostracoidea to include the orders of Bradoriida Raymond, Leperditiida Pokorný and Ostracoda Latreille, and opposed (in a diagram) the Leperditiida group to the ostracods which she postulated to be the descendants of Beyrichionidae Ulrich & Bassler, while the Leperditiida are considered as derived from Bradoriidae Matthew.

In what concerns Ivanova's revision of the Archaeostraca the present writer does not think reasonably justifiable the separation of Bradoriida from that group of crustaceans merely on a supposition that the shell of these animals covered their entire body. Among Bradoriida many genera are encountered (e. g. Alutidae Huo Shih-Cheng, 1956), whose valves are invariably connected in the hinge area, and continuously spread at the base. No evidence is available suggesting that a shell of this type covers the animal's whole body which has been laterally compressed. It rather seems that the order Bradoriida is artificial, including different groups of crustaceans.

In what regards the Leperditiida the writer's view is that they are primitive ostracods, but he nearly agrees with Ivanova's suggestion to oppose them to the group of Palaeocopa (but to that one group only). On the other hand, it is not the Beyrichionidae but the Conchostraca that seem the most probable ancestors of that suborder.

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Warszawa, September 1960

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FRANCISZEK ADAMCZAK

ERIDOSTRACA — NOWY PODRZĄD OSTRACODA I JEGO FILOGENETYCZNE ZNACZENIE

Streszczenie

Rozprawa ta zawiera rezultaty badań nad morfologią Eridoconchidae Henningsmoen i obserwacje nad mikrostrukturą pancerzy przedstawicieli kilku prymitywnych grup paleozoicznych Ostracoda. Rozpatrywany w niej problem obejmuje również zagadnienia związane z genezą pancerza ostrakodowego. Wysunięte w tej pracy tezy oparte zostały na obserwacjach zarówno Ostracoda, jak i kambryjskich Archaeostraca oraz współczesnych Conchostraca.

Materiały, na których dokonane zostały te badania, zebrano z dewonu środkowego w Górach Świętokrzyskich (Wydryszów, Grzegorzowice, Skały, Świętomarz-Śniadka). Prócz tego zbadano okazy *Aberroconcha magna* (Harris) z ordowiku Platformy Syberyjskiej, przekazane autorowi przez Dr W. A. Iwanową z Instytutu Paleontologicznego Akademii Nauk ZSRR w Moskwie.

Do celów porównawczych wykorzystano również Ostracoda ze Związku Radzieckiego (Estonia, Platforma Rosyjska, Platforma Syberyjska) i ze Stanów Zjednoczonych, jak również materiały z głazów narzutowych pochodzenia skandynawskiego oraz współczesne z Adriatyku i wiele innych.

W badaniach tych uwzględniono w szerokim zakresie studia porównawcze nad mikrostrukturą pancerzy, oparte na szlifach cienkich i seryjnych naszlifowaniach. Stosowano też fluorydyzację skorupek w celu zbadania struktury pancerza, jego laminacji i budowy wewnętrznej Eridoconchidae.

Szczegółowa analiza morfologiczna skorupek Eridoconchidae wykazała, że pancerze tych zwierząt zbudowane były z licznych blaszek ułożonych jedna pod drugą, odzwierciedlających kolejne fazy wzrostu zwierzęcia. Poszczególne blaszki stanowią elementy wylinkowe, nie zrzucane w procesie wzrostu. Pod tym względem pancerze Eridoconchidae przypominają stosunki panujące u Conchostraca (Phyllopoda), różnią się jednak od tych ostatnich ilością blaszek na pancerzu, która w obrębie rodzajów *Aberroconcha* n. gen. i *Eridoconcha* Ulrich & Bassler dochodzi do 11 i liczby tej nie przekracza. Poza tym, skorupki tych zwierząt są z reguły wapienne, a tylko partie centralne blaszek są chitynowe i wpuklone do środka skorupki, tworząc komory, jak to jest u przedstawicieli rodzaju *Aberroconcha*. Reprezentują one jeden z najprymitywniejszych typów Ostracoda; nie osiągnęły jeszcze zdolności linienia, która jest cechą charakterystyczną dla małżoraczków.

Obok form typu *Aberroconcha*, zarówno z Polski, jak i z Platformy Syberyjskiej, zbadano i opisano gatunki rodzaju *Eridoconcha*, z których dwa (*E. rugosa* Ulrich & Bassler, *E. arsiniata* (Stover)) znane są ze Stanów Zjednoczonych. Ich pancerze mają wszystkie blaszki całkowicie wapienne. Stanowi on dalsze ogniwo morfologiczne rozwoju pancerza ostrakodowego. Liczba faz wzrostu u tego rodzaju pozostaje nadal wysoka (do 11), a poszczególne blaszki ściśle do siebie przylegają.

Swoisty typ budowy pancerza Eridoconchidae uzasadnia wyodrębnienie tej grupy ostrakodów w samodzielny podrząd — Eridostraca n.subordo. Stanowisko filogenetyczne tego podrzędu, do którego włączono również proponowaną nową rodzinę — Cryptophyllidae, cechującą się skorupkami zbudowanymi z niewielkiej liczby blaszek (od 6 do 1), — jest pośrednie między Conchostraca a Ostracoda, z grupy Palaeocopa.

Wysunięta przez Levinsona (1951) dla skorupek wieloblaszkowych Ostracoda hipoteza „retencji linienia", jako cechy przystosowawczej dla niewielkiego kręgu form, wydaje się niesłuszną, ponieważ mała liczba blaszek na pancerzu takich form, jak np. *Cryptophyllus* Levinson, nie ilustruje retencji, lecz przypuszczalnie inicjację linienia, zaś skorupki wieloblaszkowe Eridoconchidae (*Aberroconcha* i *Eridoconcha*) wskazują na pierwotny stan budowy, odziedziczony po swoich wieloblaszkowych przodkach z grupy Conchostraca. Pod względem morfologicznym istnieją stopniowe przejścia od pancerza wieloblaszkowego (*Aberroconcha*, *Eridoconcha*), poprzez pancerz o niewielkiej liczbie blaszek (*Cryptophyllus*), do pancerza trzy-, dwu- i jednoblaszkowego (*Conchoprimitia* Öpik, *Milleratia* Swartz, *Schmidtella* Ulrich). Wskazują one równocześnie na sposób powstania dużej grupy paleozoicznych Ostracoda, a przede wszystkim prymitywnej i ważnej pod względem filogenetycznym grupy Leperditellidae Ulrich & Bassler.

Badania prowadzone nad Eridoconchidae rzucają jednocześnie światło na pochodzenie Ostracoda. Okazało się, że znana od dawna koncepcja paleontologiczna pochodzenia Ostracoda z grupy Bradoriidae Matthew (Ulrich & Bassler, 1931; Raymond, 1946), nie wyczerpuje całkowicie zagadnienia. Autor uważa, że z grupy kambryjskich Bradoriidae (Archaeostraca) mogły wyodrębnić się tylko bardzo prymitywne ostrakody, a mianowicie Leperditiidae Jones. Odznaczają się one dużymi rozmiarami pancerza, obecnością odcisków mięśniowych na skorupce, których w grupie Palaeocopa na ogół brak. Pancerz tych małżoraczków (Leperditiidae) ma strukturę pryzmatyczną, a w jego jednoblaszkowej skorupce wyróżnić można trzy warstwy: 1) zewnętrzną, ciemno zabarwioną; 2) środkową, przezroczystą; 3) wewnętrzną, grubszą od zewnętrznej i również ciemno zabarwioną.

Podobny typ struktury pancerza i wyraźne odciski mięśniowe, złożone z licznych śladów przyczepów adduktorów, mają przedstawiciele Healdiidae Harlton (Podocopa). W związku z tym autor jest skłonny wyprowadzić te ostatnie z Leperditiidae.

Jeśli chodzi o mikrostrukturę pancerza Eridostraca, to jest ona kryptokrystaliczna. Po sfluorydyzowaniu można na ich skorupkach wyróżnić dwie warstwy: 1) zewnętrzną, ciemno zabarwioną, 2) wewnętrzną, przezroczystą. Poza tym na skorupkach przedstawicieli tego podrzędu mięśnie zwierające nie pozostawiają śladów przyczepu ścięgien. Analogiczne stosunki panują wśród prymitywnych Leperditellidae (Conchoprimitia), których przodkami, według wszelkiego prawdopodobieństwa, były wieloblaszkowe Eridostraca.

Ta ostatnia grupa, jak już wspomniano, wykazuje duże podobieństwo do jednego z najprymitywniejszych szczepów skorupiaków, a mianowicie Conchostraca, których pancerz jest z reguły chitynowy (bardzo rzadko wapienny). Powstanie pancerza ostrakodowego dokonało się na drodze głębokich przeobrażeń, polegających m.in. na uzyskanej stopniowo zdolności przyswajania soli węglanowych i wydalania ich w postaci blaszek wapiennych oraz na zdolności zrzucania skorupek wylinkowych.

Na podstawie dokonanych obserwacji i badań można z dużym prawdopodobieństwem przyjąć, że występujące w paleozoiku grupy małżoraczków wskazują na difiletyczne pochodzenie tego rzędu. Szczep Leperditiidae wywodziłby się z Archaeostraca (Bradoriidae), szczep zaś obejmujący Eridostraca związany byłby z Conchostraca (Lepidittidae Kobayashi).

DIAGNOZY

Podrząd **Eridostraca** n. subordo

Ostracoda o pancerzu wieloblaszkowym, rzadziej jednoblaszkowym, wapiennym, z krótkim, prostym brzegiem zawiasowym i wypukłym dorsalnym. Maksymalna liczba blaszek na skorupce — 11. Mikrostruktura pancerza kryptokrystaliczna.

Występowanie: ordowik — dewon (jura?).

Rozprzestrzenienie geograficzne: Ameryka, Azja, Europa.

Aberroconcha n. gen.

Owalne Eridoconchidae z licznymi (9-11) blaszkami na pancerzu, o prostym brzegu zawiasowym. Niezwapniałe elementy blaszek, wpuklone do środka skorupki, tworzą komory. Dymorfizm nie znany.

Występowanie: ordowik — dewon.

Rozprzestrzenienie geograficzne: Ameryka Północna, Europa (Góry Świętokrzyskie), Azja (Platforma Syberyjska).

Aberroconcha plicata n. sp.
(pl. III, fig. 1 *a-c*)

Pancerz średniej wielkości, umbonalny, wieloblaszkowy, z licznymi (do 10) pasmami przyrostowymi. Blaszki chitynowe, wpuklone do środka skorupki, tworzą niewielkie komory.

Aberroconcha devonica n. sp.
(pl. IV, fig. 2 *a-c*)

Pancerz prawie owalny, średniej wielkości, z licznymi (9) blaszkami na pancerzu. Poszczególne blaszki zwapniałe i częściowo wpuklone do wnętrza skorupki. Przednia część pancerza ostro ścięta.

Eridoconcha granulifera n. sp.
(pl. III, fig. 2 *a-c*)

Zarys skorupki owalny. Liczne drobne granulacje na ostatnich pasmach przyrostowych. Blaszki, całkowicie wapienne, przylegają do siebie na całej powierzchni, Liczba blaszek — 9.

OBJAŚNIENIA DO ILUSTRACJI

Fig. 1 (p. 36)

Aberroconcha plicata n. sp., rysunek schematyczny, kombinowany, widziany od strony przedniej pancerza; *A* naupliokoncha, *B-J* kolejne stadia wzrostu, *1* brzeg zawiasowy, *2* blaszki dorsalne, *3* pasmo przyrostowe (dystalna część blaszki), *4* komora międzyblaszkowa, *5* blaszka chitynowa, *6* bruzda koncentryczna, *7* wolny brzeg, *8* linia narastania (bruzda koncentryczna), *9* brzeg dorsalny, *10* listewka półkolista.

Fig. 2 (p. 38)

Aberroconcha plicata n. sp., rysunek schematyczny. Pancerz lekko skośnie nachylony ku przodowi. Lewa skorupka w przekroju poprzecznym odsłania zrekonstruowany, przestrzenny obraz blaszek chitynowych.

Fig. 3 (p. 41)

Aberroconcha plicata n. sp., rysunek schematyczny, kombinowany, od strony dorsalnej. Prawa skorupka zeszlifowana do połowy wysokości; *F-J* blaszki ostatnich faz wzrostu, *1* komora międzyblaszkowa, *2* blaszka chitynowa.

Fig. 4 (p. 42)

Aberroconcha plicata n. sp., przekrój podłużny pancerza, poniżej wpuklenia ostatniej fazy wzrostu; *F-I* blaszki ostatnich faz wzrostu.

Fig. 5 (p. 47)

A Diagramatyczne przekroje dystalnej części skorupek, widziane od strony zewnętrznej: A *Aberroconcha magna* (Harris), B *A. plicata* n. sp., C *Eridoconcha rugosa* Ulrich & Bassler, D *Cryptophyllus oboloides* (Ulrich & Bassler); *D-I* kolejne stadia ostatnich faz wzrostu, *1* lacuna, *2* linia przecięcia (wąska zatoka-sinus), *3* bruzda koncentryczna (U-kształtna), *4* szeroka zatoka lub fałd, *5* listewka półkolista.

B Diagramy wewnętrznych powierzchni skorupek. Objaśnienia — jak do fig. *A*.

Fig. 6 (p. 50)

Aberroconcha plicata n. sp., rysunek schematyczny przedstawiający fragment prawej skorupki, z której usunięto najwcześniejsze stadia wzrostowe (*A-C*); *D-I* stadia wzrostu, *1* blaszka dorsalna, *2* brzeg zawiasowy, *3* komora międzyblaszkowa, *4* blaszka chitynowa, *5* blaszka dystalna, *6* bruzda koncentryczna, *7* brzeg wolny skorupki.

Fig. 7 (p. 50)

Conchostraca gen. et sp. indet., przekrój poprzeczny skorupki lewej częściowo zrekonstruowany (linie przerywane); górny sylur, Podole.

Fig. 8 (p. 53)

A *Eridoconcha rugosa* Ulrich & Bassler, rysunek schematyczny przedstawiający pory na częściowo odwapnionych skorupkach, na granicy pasm przyrostowych; B *Estheria* sp., rysunek schematyczny przedstawiający pory na skorupce na granicy pasm przyrostowych formy współczesnej; C *Estheria* sp., fragment płaszcza chitynowego z rzęskami.

Fig. 9 (p. 56)

Diagramatyczne przekroje poprzeczne skorupek: A *Aberroconcha magna* (Harris), B *A. plicata* n. sp., C *A. devonica* n. sp., D *Eridoconcha rugosa* Ulrich & Bassler, E *Cryptophyllus oboloides* Ulrich & Bassler, F *Milleratia shideleri* Levinson (wg Levinsona, 1951). Pancerze tych gatunków obrazują szereg morfologiczny, prowadzący od pancerza wieloblaszkowego Eridostraca do jednoblaszkowego typowych Ostracoda.

Fig. 10 (p. 59)

A-C Przekroje poprzeczne pojedynczych blaszek, ilustrujące budowę brzegu wentralnego: *A Eridoconcha granulifera* n. sp., *B, C „Eridoconcha" multiannulata* Levinson (rys. schem. wg fotografii z Levinsona, 1951), *D* przekrój poprzeczny skorupki *Euprimites suecicus* (Thorslund), (wg Jaanussona, 1957); *1* brzeg zawiasowy, *2* brzeg dorsalny, *3* pasmo przyrostowe tworzące rodzaj struktur adwentralnych, *4* brzeg wolny skorupki, *5* linia przecięcia, *6* dolon welarny.

Fig. 11 (p. 61)

A Przekrój poprzeczny pojedynczej blaszki *Eridoconcha arsiniata* (Stover), *B* skorupki *Conchoprimitia gammae* (?) Õpik; *1* brzeg zawiasowy, *2* brzeg dorsalny, *3* struktury adwentralne.

Fig. 12 (p. 64)

Schematyczne przekroje poprzeczne skorupek sfluorydyzowanych: A *Leperditia* sp., B *Bairdiocypris* sp., C *Hollinella* sp.; *1* warstwa zewnętrzna, *2* warstwa środkowa, *3* warstwa wewnętrzna.

Fig. 13 (p. 65)

Schematyczne przekroje poprzeczne pancerzy: A *Leperditia* sp., B *Pachydomella* sp., C *Bairdiocypris* sp., D *Bairdia* sp.

Fig. 14 (p. 66)

Schematyczne przekroje poprzeczne wentralnego brzegu skorupki prawej: A *Pachydomella* sp., B *Bairdiocypris* sp., C *Condracypris* sp., D *Bairdia* sp.; *1* blaszka wewnętrzna, *2* vestibulum, *3* blaszka zewnętrzna, *4* listewka ekstramarginalna, *5* strefa zrośnięcia blaszek, *6* listewka inframarginalna, *7* linia przecięcia.

Fig. 15 (p. 67)

Bairdia sp., schematyczny przekrój podłużny przedniej części wolnego brzegu pancerza; *L* lewa, *R* prawa skorupka, *1* blaszka wewnętrzna, *2* blaszka zewnętrzna, *3* vestibulum, *4* linia przecięcia, *5* pryzmaty kalcytu.

Fig. 16 (p. 69)

Diagram ilustrujący prawdopodobne stosunki pokrewieństwa i rozprzestrzenienie stratygraficzne pewnych grup Ostracoda.

Fig. 17 (p. 74)

Aberroconcha magna (Harris), przekrój poprzeczny prawej skorupki: *A* naupliokoncha, *B-I* kolejne stadia wzrostu, *1* blaszka dorsalna, *2* blaszka chitynowa, *3* komora międzyblaszkowa, *4* blaszka dystalna, *5* brzeg wolny skorupki.

Fig. 18 (p. 78)

Aberroconcha plicata n. sp., *A-E* skorupki młodociane w różnych stadiach wzrostu.

Fig. 19 (p. 79)

Aberroconcha plicata n. sp., diagram zmienności; na osi rzędnych — ilość osobników, na osi odciętych — ilorazy stosunku długości do wysokości skorupki.

Fig. 20 (p. 82)

Eridoconcha rugosa Ulrich & Bassler, przekrój poprzeczny prawej skorupki.

Fig. 21 (p. 83)

Eridoconcha rugosa Ulrich & Bassler, *A-E* skorupki młodociane w różnych stadiach wzrostu.

Fig. 22 (p. 85)

Eridoconcha granulifera n. sp., fragment retikulacji skorupki.

Fig. 23 (p. 86)

Eridoconcha arsiniata (Stover), przekrój poprzeczny lewej skorupki.

Text-pl. I (p. 44-45)

Aberroconcha plicata n. sp., szlify seryjne pancerza, równolegle do osi podłużnej: *A-J* od strony dorsalnej, *U-K* od strony wentralnej.

Pl. I

Fig. 1, 2. *Aberroconcha plicata* n. sp., przekroje poprzeczne: *1* pancerza, × 95: *2a* strefy zawiasowej, × 375; *2b* skorupki lewej, obejmujący komory międzyblaszkowe ostatnich faz wzrostu, × 375.

Fig. 3, 4. *Aberroconcha magna* (Harris), przekroje poprzeczne: *1* skorupki lewej, × 88; *4* skorupki prawej, obejmujący ostatnie fazy wzrostu, × 200.

a blaszki zawiasowe, *b* blaszki chitynowe, *c* blaszka dystalna, *d* komora międzyblaszkowa, *e* listewka półkolista, *f* zatoka (sinus), *g* lacuna.

Pl. II

Fig. 1. *Hollinella* sp., przekrój poprzeczny brzegu wolnego skorupki sfluorydyzowanej, × 190.

Fig. 2, 3. *Bairdia* sp.: *2* przekrój poprzeczny wentralnej części brzegu wolnego skorupki, × 88; *3* przekrój przedniej części brzegu wolnego skorupki, × 144.

Fig. 4, 5. *Bairdiocypris* sp., przekroje poprzeczne: *4* brzegu wolnego skorupki, × 180; *5* skorupki sfluorydyzowanej, × 225.

Fig. 6, 7. *Leperditia* sp., przekroje poprzeczne: *6* brzegu wolnego skorupki, × 77; *7* skorupki sfluorydyzowanej, × 73.

a warstwa zewnętrzna (pigmentowana), *b* warstwa środkowa, *c* warstwa wewnętrzna, *d* blaszka wewnętrzna, *e* linia przecięcia, *f* strefa zrośnięcia, *v* vestibulum.

Pl. III

Fig. 1. *Aberroconcha plicata* n. sp., holotyp: *a* skorupka lewa, *b* od strony dorsalnej, *c* od strony wentralnej; × 66.

Fig. 2. *Aberroconcha devonica* n. sp., holotyp: *a* skorupka lewa, *b* od strony dorsalnej, *c* od strony wentralnej; × 66.

Pl. IV

Fig. 1. *Eridoconcha arsiniata* (Stover): *a* skorupka lewa, *b* od strony dorsalnej, *c* od strony wentralnej; × 102.

Fig. 2. *Eridoconcha granulifera* n. sp., holotyp: *a* skorupka lewa, *b* od strony dorsalnej, *c* od strony wentralnej; × 100.

Fig. 3. *Eridoconcha rugosa* Ulrich & Bassler: *a* skorupka lewa, *b* od strony dorsalnej, *c* od strony wentralnej; × 92.

ФРАНЦИШЕК АДАМЧАК

ERIDOSTRACA — НОВЫЙ ПОДОТРЯД OSTRACODA И ЕГО ФИЛОГЕНЕТИЧЕСКОЕ ЗНАЧЕНИЕ

Резюме

В настоящей работе представлены результаты исследований над морфологией Eridoconchidae Henningsmoen и наблюдения над микроструктурой раковин нескольких примитивных групп палеозойских остракод. Рассматриваемая тут проблема обнимает тоже вопросы генезиса остракоидной раковины. Выдви-

нутые тезисы основаны на наблюдениях касающихся не только остракод, но и кембрийских Archaeostraca и ископаемых и современных Conchostraca.

Для сравнения использовано материалы из Советского Союза (Эстонская ССР, Русская платформа, Сибирская платформа), Соединенных Штатов, материалы из скандинавских ледниковых валунов и многие другие.

В исследованиях учтено в широком объеме микроструктуру раковин, применяя разнообразные технические методы.

Подробный морфологический анализ створок Eridoconchidae показал, что раковина этих животных была построена из многочисленных пластинок наложенных одна под другой, отражающих последовательные возрастные фазы животного. Отдельные пластинки составляют элементы линьки не сброшенные в процессе возрастания. В этом отношении раковины Eridoconchidae напоминают соотношения господствующие среди Conchostraca (Phyllopoda), но отличаются от этих последних количеством пластинок раковины, которое в пределах родов *Aberroconcha* n. gen. и *Eridoconcha* Ulrich & Bassler доходит до 11, но не превышает этого числа. Кроме того створки этих животных как правило известковые, а только центральные части пластинок состоят из хитина и вогнуты внутрь створки, образуя иногда камеры, как это имеет место у рода *Aberroconcha*. Представители этого рода являются одними из самых примитивных типов остракод. Они не достигнули еще способности линьки, характерной для остракод.

Рядом с формами типа *Aberroconcha*, исследованы и описаны виды рода *Eridoconcha*, которых раковина тоже состоящая из многих пластинок, но целиком известковая, составляет следующее морфологическое звено в развитии остракоидной раковины. Количество пластинок у представителей этого рода всё еще высокое (до 11). Отдельные пластинки тесно прилегают друг к другу.

Особенный тип строения раковины Eridoconchidae обосновывает выделение этой группы в самостоятельный подотряд — Eridostraca n. subordo. Филогенетическое положение этого подотряда, в который включено тоже предлагаемое новое семейство — Cryptophyllidae, отмечающееся створками состоящими из небольшого количества пластинок (максимально из 6), занимает промежуточное положение между Conchostraca и Ostracoda, из группы Palaeocopa.

Выдвинутый Левинсоном (Levinson, 1951) для многопластинчатых створок остракод гипотез „задержки линьки" (retention of moults), как приспособительного свойства для небольшого круга форм, кажется неверным, так как небольшое количество пластинок в раковинах представителей рода *Cryptophyllus* Levinson является иллюстрацией не задержки, но начала линьки (initiation of moults), а многопластинчатые Eridoconchidae (*Aberroconcha* и *Eridoconcha*) указывают на примитивное состояние строения, унаследованное от своих многопластинчатых предков из группы Conchostraca. По отношению морфологии имеются постепенные переходы от многопластинчатой до однопластинчатой остракоидной раковины. Указывают они одновременно на путь возникновения большой группы палеозойских остракод, а прежде всего примитивной и филогенетически важной группы Leperditellidae Ulrich & Bassler.

Исследования описанные в этой работе проливают свет на происхождение остракод. Оказалось, что давно известная палеонтологическая концепция происхождения остракод из группы Bradoriidae Matthew (Ulrich & Bassler, 1931; Raymond, 1946), не исчерпывает проблемы. Автор настоящей работы думает, что из группы кембрийских Bradoriidae могли выделиться только очень примитивные остракоды, а именно Leperditiidae Jones. Отличаются они присутствием мускульных отпечатков на створке, которых нет в большой группе Palaeocopa. Их раковина обладает призматической структурой. В однопластинчатой створке можно выделить три слоя. Выше упомянутые признаки встречаются в группе Healdiidae Harlton (Podocopa) и поэтому автор склоняется к тому, чтобы этих последних выводить из Leperditiidae. Таким образом, выступающие в нижнем палеозое группы остракод указывают на дифилетическое происхождение этого отряда: Leperditiidae происходили бы из Archaeostraca, а Eridostraca были бы связаны с Conchostraca.

ДИАГНОЗЫ

Eridostraca n. subordo

Остракоды с раковиной многопластинчатой, реже однопластинчатой, известковой, с коротким, простым замковым краем и выпуклым дорсальным. Максимальное количество пластинок в створке — 11. Микроструктура раковины криптокристаллическая.

Выступание: ордовик — девон (юра?).

Географическое распространение: Америка, Азия, Европа.

Aberroconcha n. gen.

Овальные Eridoconchidae, с многочисленными (9 — 11) пластинками в раковине, с простым замковым краем. Необизвествленные элементы пластинок вогнуты внутрь створки, образуя камеры. Диморфизм не известный.

Выступание: ордовик — девон.

Географическое распространение: Северная Америка, Европа (Свентокржиские Горы), Азия (Сибирская платформа).

Aberroconcha plicata n. sp.

Раковина средней величины, умбональная, многопластинчатая, с многочисленными (до 10) полосами нарастания. Хитиновые пластинки вогнуты внутрь створки, образуя небольшие камеры.

Aberroconcha devonica n. sp.

Раковина почти овальная, средней величины, с многочисленными (9) пластинками в раковине. Отдельные пластинки обизвествленные и частично вогнуты внутрь створки. Передняя часть раковины остро срезана.

Eridoconcha granulifera n. sp.

Очертание створки овальное. Многочисленные мелкие грануляции на последних полосах нарастания. Пластинки, целиком обизвествленные прикасаются друг с другом на всей поверхности. Число пластинок — 9.

PLATES

EXPLANATIONS OF PLATES

Pl. I

Fig. 1, 2. *Aberroconcha plicata* n. sp., transverse sections: *1* of carapace, × 95; *2a* of hinge area, × 375; *2b* of left valve, showing interlamellar chambers of the last growth stages, × 375.

Fig. 3, 4. *Aberroconcha magna* (Harris), transverse sections: *3* of left valve, × 88; *4* of right valve, showing last growth stages, × 200; *a* dorsal lamellae, *b* chitinous lamellae, *c* distal lamellae, *d* interlamellar chamber, *e* semicircular list, *f* sinus, *g* lacuna.

Pl. II

Fig. 1. *Hollinella* sp., transverse section of free edge of a fluoridized shell, × 190.

Fig. 2, 3. *Bairdia* sp.: *2* transverse section of the ventral part of free edge of shell, × 88; *3* the same of the anterior part × 144.

Fig. 4, 5. *Bairdiocypris* sp., transverse sections: *4* of free edge of shell, × 180; *5* of a fluoridized shell, × 225.

Fig. 6, 7. *Leperditia* sp., transverse sections: *6* of free edge of shell, × 77; *7* of a fluoridized shell, × 73; *a* outer (pigmented) layer, *b* median layer, *c*, *d* inner layers, *e* bisecting line, *f* zone of concrescence, *v* vestibulum..

Pl. III

Fig. 1. *Aberroconcha plicata* n. sp., holotype: *a* left valve, *b* dorsal view, *c* ventral view; × 66.

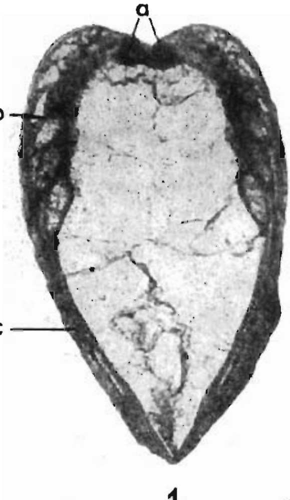
Fig. 2. *Aberroconcha devonica* n. sp., holotype: *a* left valve, *b* dorsal view, *c* ventral view; × 66.

Pl. IV

Fig. 1. *Eridoconcha arsiniata* (Stover): *a* left valve, *b* dorsal view, *c* ventral view; × 102.

Fig. 2. *Eridoconcha granulifera* n. sp., holotype: *a* left valve, *b* dorsal view, *c* ventral view; × 100.

Fig. 3. *Eridoconcha rugosa* Ulrich & Bassler: *a* left valve, *b* dorsal view, *c* ventral view; × 92.



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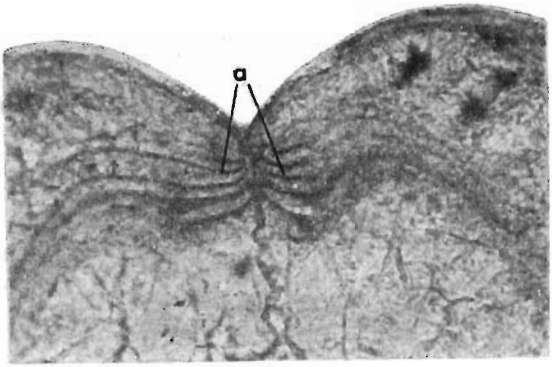

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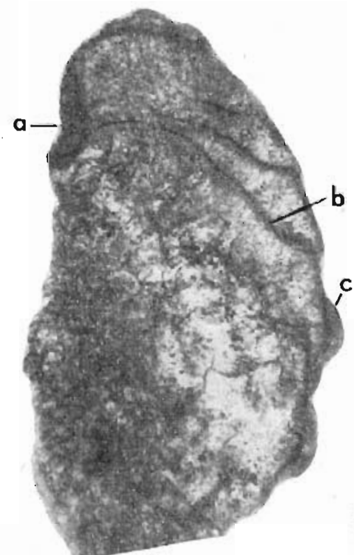

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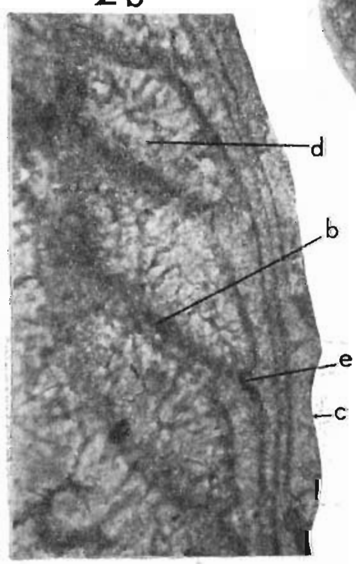

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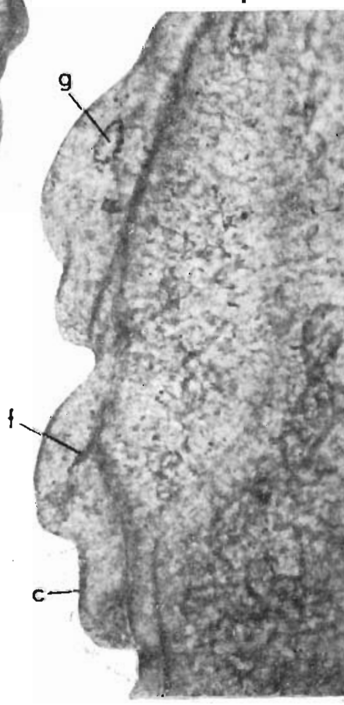

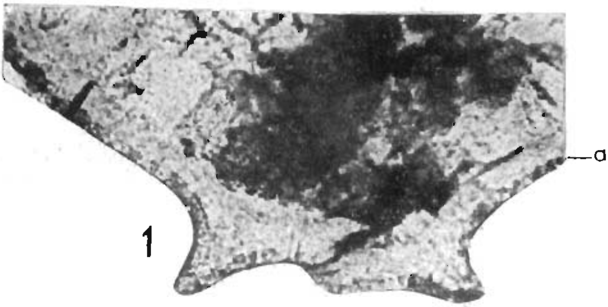

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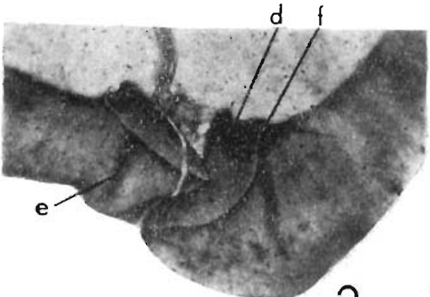

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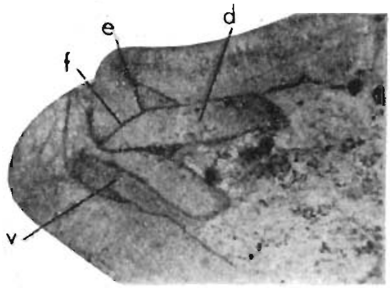

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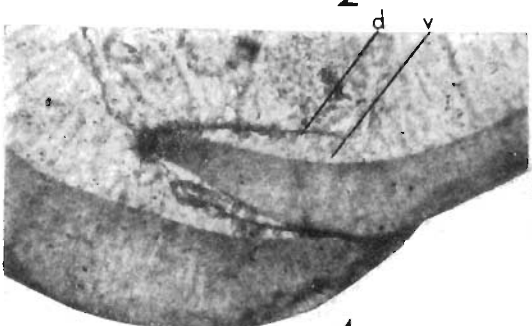

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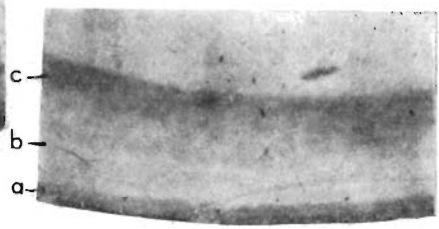

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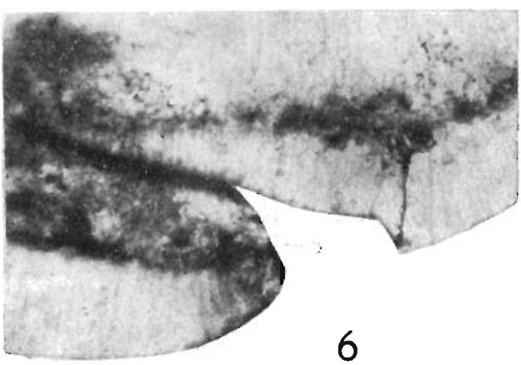

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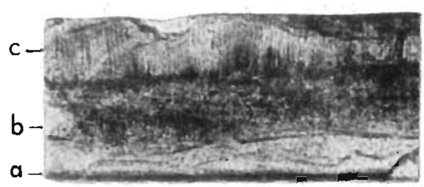

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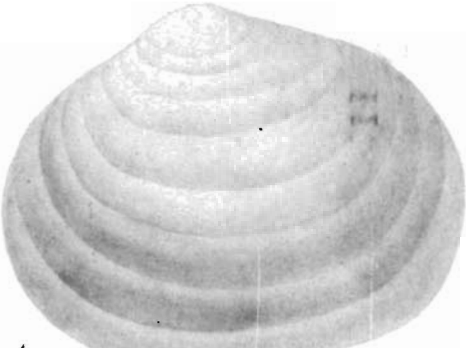

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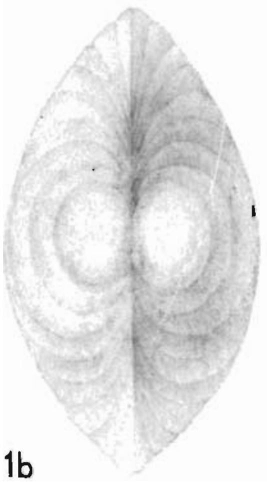

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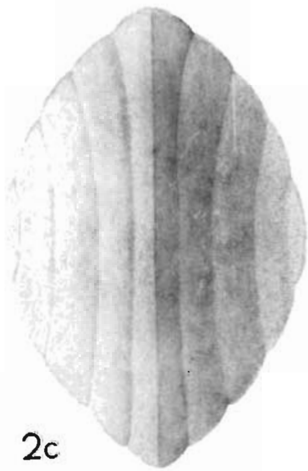

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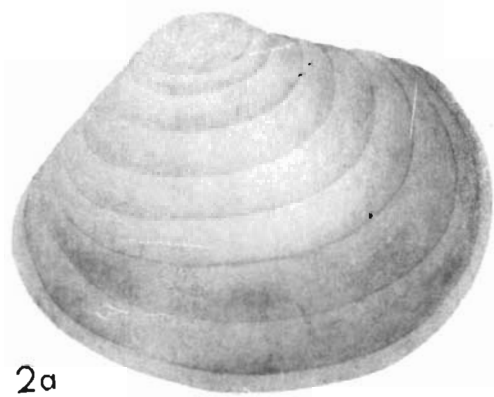

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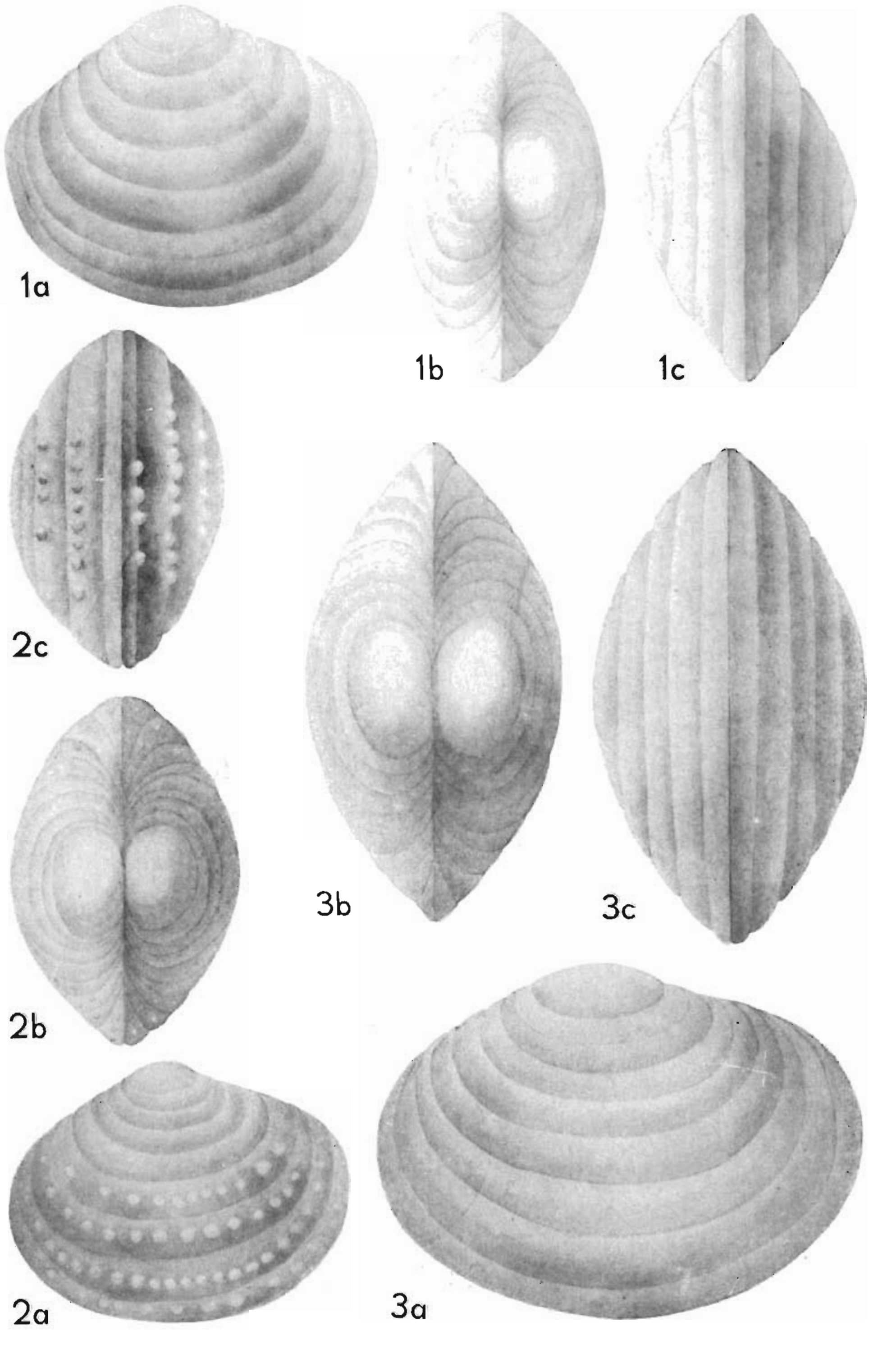
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1b
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2b
2a
3a