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LITERATURE ON THE SHELL STRUCTURE OF PELECYPODS,

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Introduction.

The rich field of shell structure has scarcely been scratched by those interested in the classification of the Pelecypoda. Microscopists, physiologists and mineralogists have been the chief investigators and they have not had taxonomic problems uppermost in mind during their studies. Literally hundreds of publications contain notes on the mineralogical and chemical composition of the shells of mollusks, yet no one has attempted in recent years to bring these data clearly to the attention of conchologists. The literature here cited is that which has come into my hands from time to time and although limited in number I believe that the papers are sufficiently diverse to present a fair sample of the literature on the subject. The following survey may serve, therefore, to give the reader an indication of the trend of thought along this line; it should aid him in understanding the terminology and vagaries thereof; and it indicates where additional research is needed.

Epoch 1799-1849.

Shells were divided into porcellanous and nacreous types as early as 1799, the date of Hatchett's (1799) often-cited paper (2).

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(2) Dates in parentheses refer to the bibliography, pages .

The author « never obtained any trace of phosphate of lime », but chiefly carbonate of lime upon testing nacreous shells. His remarks show that he recognized the lamellar (« stratified ») nature of the nacreous material.

Wood (1815, pp. VIII-XVI) gave a few general remarks on the formation of the shell in mollusks, remarking (p. XV) that in bivalves the « shells increase by a perfect juxtaposition of calcareous beds ».

Gray (1833) adopted Hatchett's classification. He believed that the pearly lustre of nacreous shells « depends in great measure on the thinness and number of the laminae of which the shell is formed » (p. 794). Shells may be segregated, according to his views, on the basis of the way in which the calcium carbonate is deposited; i. e. *crystalline* and *granular.*

That « the structural arrangement in bivalve shells appears to be subject to a greater degree of variation in different genera than we observe to be the case among the univalves » was the opinion of Bowerbank (1844). He thought he saw Hauversian canals in both bivalves and univalves, and figured some (× 300) « in the membranous tissue of the shell of *Ostrea edulis* » on his plate 16, fig. 5. The author was convinced by his investigations that a study of the shells will be of « powerful assistance towards a natural arrangement of genera, and a most efficient aid in determining doubtful species » (p. 152). Speaking of *Cypraea* (p. 128) he said that when the shell « was fractured at right angles to the lines of growth », it was found to consist of « three distinct strata », the outer one being of (p. 153) « plates of prismatic cellular structure, exhibiting the basaltiform columnar appearance arising from the section being at right angles to the planes of the plates ». The prisms of *Pinna* seen under « a power of 500 linear » assume an appearance « which strongly resembles that of the fasciculi of muscular fibres ». The forms mentioned are under the following names: *Arca, Ampullaria, Bulinus, Conus, Cypraea, Haliotis, Helix, Lymnea, Modiola, Mytilus, Oliva, Ostrea, Pinna, Pyrula, Solen, Strombus, Trigonia, Unio, Venus* and *Voluta.* The author does not differentiate between calcite and aragonite.

Carpenter's famous work on shell structure (1845, 1848) is a fundamental one because of the breadth of the author's observations. The main divisions of shell structures are, according to him : (a) *prismatic cellular* (as illustrated by *Pinna)* and (b) *membranous.* The latter is now generally spoken of as *lamel-*

lar.) The « structures » described are prismatic cellular, nacreous, tubular, and cancellated. He asserted (1845, p. 15) that « the conformity in structure between all the shells of one natural family is usually so close, that any strongly-marked differences in a particular genus would make me hesitate in admitting it into the group ». In the case of the families of pelecypods where the « lobes of the mantle are disunited », « it is very interesting to find how completely the Prismatic Cellular substance is restricted to the group thus constituted » (1845, p. 22). The second part of the work is devoted chiefly to a description of the shells of different families of Mollusca, with some attention to Brachiopoda, Echinodermata, and Crustacea.

Epoch 1850-1899.

G. Rose (1858) reviewed the work of Bournon, Hatchett, de la Beche, von Brewster, Necker, Gray, Carpenter, Bowerbank, and von Leydolt. The author stated (p. 98) that the shells of mollusks are of three kinds: they consist of either (a) calcite and aragonite (*Pinna, Inoceramus, Mytilus,* etc.) ; or (b) only of calcite *(Ostrea, Pecten, Spondylus)*; or (c) only of aragonite *(Arca,* etc.). Specific gravity was an important means of differentiating the minerals. Shells like « *Unio* », *Inoceramus, Anodonta,* and *Pinna* have an outer « fibrous layer » (*Faserlage*) and on inner pearly layer, the former being calcite and the latter aragonite (p. 84).

Sorby's (1879) investigations proved that certain genera have tests composed entirely of calcite, others are of aragonite, but in others the inner layer is aragonite and the outer is calcite. Thus he is in general accord with Rose, whose work Sorby was « able to confirm, extend, and modify ». That aragonite is less stable than calcite is deduced from several observations, and he remarked (p. 68-69) that :

« This difference in the state of preservation of fossils, according as they were originally composed of calcite or aragonite, appears to be so well established in all those cases in which we are able to ascertain the true mineral nature of closely allied living organisms, that I feel myself justified in concluding that certain doubtful fossil forms were originally calcite, because they are preserved like those in the same thin section known to have been so, whilst those known to have been aragonite have become quite crystalline and lost their original structure. »

The monograph by Tullberg (1882) contains a review of some literature on the method of formation and structure of the shell (pp. 12-14) and also descriptions of the shells of *Mytilus edulis* (pp. 14-31), *Modiola modiolus* (pp. 31-33), *Margaritana margaritifera* (pp. 34-37), *Ostrea edulis* (pp. 37-39) and *Buccinum undatum* (pp. 39-49). The shells are believed to be a secretion product of the cells of the mantle. In the shell of *Mytilus* were recognized (a) the periostracum; (b) the « outer substance » of lamellar structure oblique to the inner surface; (c) the outer layer of the « inner substance »; (d) the transparent substance; and (e) the inner layer of the inner substance, which is laid down parallel to the inner surface of the shell. The illustrations are drawings.

Long quotations are in Fischer's (1887) « Manuel de Conchyliologie ». Well known at that time was the fact that there is a correlation between the resting stages and the shell characters. As for structures the following is a quotation (p. 17):

« La texture des coquilles est variée et caractéristique. Quelques-unes, lorsqu'elles sont cassées, présentent un faible éclat, comme celui du marbre ou de la porcelaine et sont nommées *porcellanées;* d'autres sont nacrées; quelques-unes ont une structure *fibreuse;* certaines sont cornées, et d'autres *vitreuses* et *translucides.* »

Oysters (p. 18) have a « structure *lamelleuse* », but in many bivalves one finds a fine « structure *tubuleuse* » (p. 19), such as in *Pinna* and oysters, but one must be careful to distinguish such tubes from borings of other organisms. The nacreous shells are destroyed more readily than those with a fibrous structure (e. g. *Inoceramus*).

Also known at Fischer's time was the fact that the shell is formed by the mantle, for Carpenter and others clearly established that fact.

Cornish and Kendall (1888) devoted a part of a paper recording the experimental evidence that explains « the inferior stability of aragonite fossils as compared with those formed of calcite, with observations on the geological conditions favourable to the removal of aragonite fossils (p. 66). The experiments led them to conclude (p. 67) that « the more rapid solution of aragonite fossil shells is not due directly to difference of mineralogical constitution, but to difference of structure ». « With regard to the question of structure, aragonite fossil shells have a hard surface, but the interior, though close-grained, is porous.

The calcite shells on the other hand are compact throughout » (p. 68) (3).

The shell structure of *Cardium* was described, in a general way, by Johnstone (1889), who found the shell to be made up of « inner and outer shell layers since the terms prismatic and nacreous layers are not applicable here ». (For more precise observations consult Böggild (1930, pp. 284-285).

Steinmann (1889) remarked that the influence of the surrounding medium is shown by the relatively thick shells of the marine Mollusca and the thin shells of land mollusks (p. 290). The genera mentioned are *Unio, Limax, Helix, Argonauta, Nautilus,* and *Teredo.* The geological significance of his observations is briefly pointed out.

Epoch 1900-1914.

Stempell (1900) was chiefly concerned with the secretion of the shell of mollusks. This monograph includes a bibliography of papers to and including the year 1899.

Biedermann (1902) discussed at greath length the mode of origin of the molluscan shells, recognizing that each lamella is a secretion product of the epithelial cells of the mantle; and that there is a relationship between the sculpture of the molluscan shell and the mantle margin of the animal. A number of pages were devoted to the « finer » structure of *Anodonta, Pinna,* and « *Meleagrina* » to show that each one of the many superimposed lamellae was laid down evenly and unwrinkled and as a continuous layer. He dealt with the physical, and especially with the optical, properties of the prismatic and nacreous layers. To a lengthy review of previous work on the mineralogical constitution of shells are appended the personal observations of the author, who was impressed by the facts that the prismatic layer is built up of prisms having the qualities of true calcite crystals and that the pearly layer is double refracting.

Dakin (1909) presented some notes on the shell of *Pecten* and on the theories of the formation of bivalve shells. The secretion theory is the one « now generally accepted ». « The inner nacreous layer, or that part of the lamellar layer of the Pecten shell corresponding to it, is unlimited in growth, and is formed

(3) Dr. E. Wayne Galliher, when I questioned him on this subject, pointed out to me (written communication dated September 28, 1932) that aragonite is less stable than calcite *under wet conditions.*

by the outer surface cells of the mantle » (p. 17). He believed that the shell of *Pecten* is composed mainly of aragonite, but for more accurate observation, the reader is referred to the paper by Böggild (1930).

Douvillé (1912) viewed shell structure from a different angle — that of its significance in the classification of bivalves. Especially important is this in his discussion of the evolutionary characters; a passage, freely translated (from pages 435-436), is as follows :

« Among these (evolutionary characters) may be cited the character of the shell. I have shown that the ancient forms were nacreous, and that the porcellanous ones originated from them by evolution. One could not then place nacreous forms in the same branch as porcellanous. I do not know of a single case of regression: the living nacreous forms are related to the primitive forms by a continuous series of equally nacreous forms. The forms that are derived from porcellanous types are always porcellanous. »

Rubbel (1913) paid attention to the shell of « *Margaritana* », giving cross sections showing the interrelations of the periostracum, prismatic layer, and nacreous layer. The layers differ with age: in young animals the nacreous layer is thin, whereas the periostracum and prismatic layer make up the greatest part of the shell, as seen in cross sections. The nacreous layer is divided into an inner and an outer layer, the former being less homogeneous.

Like Rubbel, Rassbach (1912) showed that in the case of certain mollusks the animal can regenerate the three layers (periostracum, prismatic, and pearly) and van Deinse's (1912) observations led the same results as those by Rubbel and Rassbach.

Karney (1913) described the shell of *Pinna, Malleus, Meleagrina,* and *Unio.* Some of his conclusions (pp. 258-259) are that (a) the calcareous shell of the Aviculidae and Unionidae consists of a prismatic and a nacreous layer; (b) the prismatic layer of *Pinna* is calcite; it is called the *orthoprismatic* layer because the prisms are at right angles to the shell's upper surface, in contrast to (c) the *klinoprismatic* layer in Aviculidae, in which the constituent elements of the prisms have no direct directional relation to the shell's upper surface and to the form of the prisms; (d) in the Unionidae the prisms are of aragonite and the structure calls for the proposal of the designation

« *Späroprismatic* » layer; (e) the nacreous layer is of aragonite, just as Rose (1858) and many others have stated.

Epoch 1915-1929.

Cayeux's (1916) treatment of the shell structure of pelecypods is, in outline form, as follows :

I. Prismatic layer (external).

- A. *Prismatic structure,* as in Pinnidae, Unionidae, etc. Prisms (in the geometrical sense of the word) are independent of each other; they are of crystalline calcite, illustrated by figures 1-4 on plate 48 of his monograph.
- B. *Cellulo-prismatic* structure, as in the rudistids; illustrated by fig. 5, pl. 48, and fig. 2, pl. 49.
- C. *Fasciculated* structure, characterized by fascicles of lamellae, as in *Mytilus edulis, Cardium edule,* and *Chama.* The constituent elements are not geometrical. Each element is resolved into a bundle of fine, parallel lamellae, and all are united in such a way that they are inseparable. Illustrated by fig. 3, 5, pl. 49; fig. 2, 3, pl. 50. (Böggild (1930), reviewing Cayeux's description of this structure in *Mytilus,* says : « I must confess that I have not been able to find any similar structure.»)

II. Lamellar layer (internal; nacreous or porcellanous).

- A. *Laminated parallel to the surface.* Illustrated by *Pinna, Corbis,* and *Cardita;* fig. 1, pl. 48, fig. 4, pl. 50.
- B. *Crossed structure;* two systems of lamellae that cross at variable angles, as in *Corbis,* « *Pectunculus* » *obovatus, Mytilus,* etc. Illustrated by figs. 2 and 4, pl. 51. (This is perhaps the « crossed lamellar layer » of Böggild's terminology.)
- C. *Undulated and folded structure,* as in *Meleagrina margaritifera* and *Ostrea edulis.* Illustrated by fig. 3, pl. 51.

The monograph by Clarke and Wheeler (1917 and 1922) gives the chemical composition of the shells of numerous bivalves; namely, *Astarte, Callista, Macoma, Pecten, Calyptogena, Nucula, Placuna,* « *Venericardia* », *Cardium,* and *Acila.* The authors affirm (1922, p. 40) that « from the evidence now at hand from many older data it is clear that molluscan shells consist almost entirely of calcium carbonate with quite insignificant impurities ».

Pelseneer (1920) perpetuated Kelly's « conchite » error, but gives some interesting notes on the extraction of lime from the *milieu,* which, he believes, effects the quantity of lime in the shell.

Loppens (1920) endeavoured to learn if the chemical composition of shells varies under environmental influences. The analyses are in terms of « conchyoline » and calcium carbonate, and are of *Anodonta anatina, Scrobicularia piperata, Pinna pectinata, Pecten maximus, Donax vittatus, Pholas candida, Mactra stultorum, Mya truncata, Petricola pholadiformis, Cardium edule, Mactra subtruncata, Donax trunculus, Mytilus edulis,* and a number of gastropods. Among his conclusions are that the burrowing species, which suffer little from changes of environment, have always the same quantitative composition, in contrast to *Mytilus edulis,* for example, which is influenced by different *milieux.* Food is an important factor. Moreover (p. 88), the mechanism of the formation of shells is imperfectly known. The composition of the shells also varies with the species, but this variation does not affect the solidity of the tests.

A paper by Schmidt (1922) deals with the structure of the shell of *Nucula, sensu stricto.* He concluded, freely translated (p. 181) :

« But in any case the research just presented has shown that the shell of *Nucula* — whether of all nuculids is still uncertain — has a layer of conspicuous thickness and very characteristic structure between the periostracum and mother-of-pearl. This layer scarcely permits one to consider the structure of the nuculid shell as entirely primitive. Naturally, one should not, because of this, raise an objection against the primitive character of the nuculids in general; but it does not necessarily follow that we see in the shell of *Nucula,* which reminds one of the Prodissoconcha, the shell of the original clam. »

His remarks on the shell structure are stated on page 172 and the following; some of his notes are freely translated here:

« According to my investigations, the shell of *Nucula nucleus* consists of three layers: the outer one, periostracum; the middle ribbed layer *(Rippenlage)* (4), as I may call it — it is the same

(4) This is probably the *ostracum,* recently well described by Prashad (1928). However, see pages 10 and 14.

as Carpenter's « tubular structure » and Stempell's « longitudinal-oval districts » (*längsovale Bezirke*) ; and the inner nacreous layer (5)...

« ...The periostracum, which comes off readily as a thin membrane from its lower layer (the ribbed layer), appears yellowish brown in transmitted light and is wavy, corresponding to the concentric growth lines of the shell. The nacreous mass exhibits the typical condition, a structure of large nacreous lamellae (tabular after the aragonite crystals forming them) which are arranged in horizontal layers. In certain places, the boundaries of the adjacent nacreous lamellae more or less coincide as superimposed lamellae and, at the same time, a vertical lamination comes to lie next to a horizontal one in the nacreous mass, especially in the vicinity of the ribbed layer. The nacreous lamellae bend towards the ribbed layer so that they form, with its lower wall, an acute angle whose summit is turned toward the periphery of the shell. In those tangential sections which are parallel to the growth lines of the shell, the upper nacreous lamellae assume a wavy course on account of the sectioned form of the ribs; also upon them is visible the so-called vertical layer. Just as Rubbel wrote for *Margaritana,* the nacreous layer in *Nucula* is differentiated by a very thin zone — a lighter layer — into outer and inner layers. This light layer marks the path of the mantle line during growth; in the mass, as the mantle muscles give up their temporary points of attachment, the light layer is overgrown by the inner nacreous layer... »

Schmidt found that after removal of the periostracum, by careful scraping with a scalpel, the « ribbed layer » is exposed as a dull matte-white layer.

Some notes on and illustrations of the shell of *Mytilus edulis* were published by Field (1922). The shell layers recognized were the periostracum, prismatic, and nacreous layers. He observed (p. 134) that the nacreous layer is the only one that continues to grow in thickness throughout the life of this mollusk.

Weymouth (1923) proved that in the case of *Tivela stultorum* Mawe there is a definite relation betweeen the shell structure and growth lines, the age significance of which was established.

A review of some of the literature on the subject of shell structure, with citations to publications not consulted by me, has been prepared by Prashad (1928) and although the mono-

(5) The inner nacreous layer is perhaps the *hypostracum,* also described by Prashad.

graph is concerned with gastropods, it deserves mention here because of its fundamental character. He proved that the « secretion of the shell is entirely due to the mantle » (p. 289). Thiele, he pointed out on page 278, distinguished in the shells of all mollusks three layers : the outer cuticular *periostracum,* the outer calcareous layer (*ostracum*), and the inner calcareous layer (*hypostracum*). Robert, in 1900, distinguished in *Trochus* the periostracum, the ostracum (consisting of an outer pigmented porcellanous zone and an inner lamellar mother-of-pearl zone), and the hypostracum, but Frank, in 1914, « found that the hypostracum is not always present, and that it is possible to distinguish three separate strata in the ostracum ». Prashad himself considers (p. 283) that the « shell of the Viviparidae, as indeed of all gastropods », is divisible into two constituent parts : an outer membranous organic periostracum and the thick inner calcareous layers, divisible into two « zones » by the arrangement of the calcareous plates composing them, and these two « *zones* » are designated the *ostracum* (probably the « ribbed layer » described by Schmidt), and the *hypostracum,* both being admirably illustrated by photomicrographs. The plates of both the ostracum and hypostracum are « formed of large numbers of bundles of fibrils ». The layers and structure are specially well illustrated by figure 3 on page 24 of his paper. The calcareous plates of the ostracum « appear alternately light and dark, and run more or less parallel to each other » (p. 284) and those of the hypostracum « are almost uniform in thickness, do not branch to any extent, and are arranged with great regularity. They run parallel to one another, and at right angles to those of the ostracal plates, and show the same light and dark arrangement ». The following summary is quoted from page 289 :

« The ostracum and hypostracum in the calcareous part of the shell are identical in structure, and the different appearance of the elements in the sections is due to different planes along which they are cut during sectioning. Each of the zones is formed of a large number of strata or layers which are arranged parallel to one another in each zone, but the layers of the ostracum lie at right angles to those of the hypostracum. Each layer in its turn is formed of numerous plates, arranged parallel to one another. The plates consist of large numbers of bundles of fibrils, which in adjacent plates run at right angles to one another. The fibrils are the final elements, which can be distinguished by means of the microscope. »

The following is a quotation (p. 297) of interest :

« The deposition of the calcareous layers of the shell in the form of fibrillae appears to be due to the interaction of an organic albuminous substance on the calcareous material, both of which are found in the secretion of the cells, but, with our present knowledge, it is not possible to determine the influences which are at work... The ostracal layers of the shell are secreted by the gland cells of the supramarginal ridge, while the hypostracal part is secreted by the general epithelium which covers the outer surface of the mantle. »

The illustrations and descriptions of the shell structure of these gastropods are of interest not only to students of the mollusks but also to those of the Foraminifera. The fibrils resemble the « pillars » seen in many of the orbitoidal foraminifers, and the structure of the ostracum, as shown by some of the figures, is much like the keriotheca of the Fusulinidae as so well redescribed recently by Dunbar and Condra (Nebraska Geol. Surv. Bull. II, 2nd ser., 1927).

Attention is directed, in passing, to the results of X-ray examinations of shells by Jinzo Tsutsumi (1929) who found that the axes of the fibrous arrangement are in a direction nearly perpendicular to the surface of the shell, coinciding with the principal axis of calcite or with the orthorhombic *c* axis of aragonite.

Epoch 1930-1934.

Bergenhayn's (1930) contribution is primarily concerned with chitons of the order *Loricata* Schumacher, a taxonomic division to include the families Chitonidae, Ischnochitonidae, Lepidopleuridae, and others. He homologized the *periostracum* of these Mollusca with that of the pelecypods, and the « *tegumentum* » of the loricates with the *ostracum* of the bivalves. The pigment is located in the outer part of the « *tegumentum* » and, furthermore, this part of the shell is always traversed by canals. The « hypostracum » is under the « tegumentum » when the « articulamentum » is absent, but when present the « hypostracum » is in contact with the « articulamentum ». The author differentiated a « tegumentum » and a « suprategumentum » on a chemical basis. In thin sections, one notes a differentiation between a weakly and a strongly pigmented part, the former of a fine fibrillar structure.

Böggild (1930) believes it settled that the shells of mollusks consist of calcite and/or aragonite, and he summarizes some of the methods of distinguishing the two minerals (pp. 237-39). Of all the shell-bearing invertebrates, only the Mollusca have calcite and aragonite in the same shell. « Between the salinity of the water and the composition of the shells there seems... to be a pronounced connection » (p. 242) for he found only one example of calcite-bearing shells among all the mollusks living in fresh water. « It is a general rule, from which there is no exception, that all aragonitic shells are non-magnesian, but the calcite ones behave in a more complicated manner » (p. 243). He also discussed the alteration of aragonite into calcite, and states that (p. 245) « in rocks containing very little carbonate of lime, such as siliceous or ferrugineous rocks, the calcareous shells are mostly altered rather quickly and the calcite ones are not preserved very much longer than the aragonitic ones ».

The second part of the monograph, pages 245-257, deals with shell structures. The following table (page 13) is an attempt to summarize the broader features of the author's classification.

Since third part of Böggild's monograph, a systematic treatment of the shells of the mollusks, follows the arrangement in the 1915 edition of Zittel's « Grundzüge der Paläontologie », it is no wonder that the different families display a great variation in shell structure. Modern classifications probably would exhibit a closer relation between the families and shell structure. Thus, in the Nuculidae, according to the arrangement followed by the author, one finds in addition to *Nucula* some genera now customarily grouped in the family Nuculanidae. The latter lacks the nacreous layer that is so characteristic in the Nuculidae proper, although the Eocene « *Nucula* » *trigona*, Böggild reports, has no nacreous layer. In Copenhagen, however, I examined the specimens of this species and it is not *Nucula*, but a representative of another family. His tabulated summary (pp. 294-295) of the shell structure of the different families of pelecypods is suggestive: broadly considered, structure and composition of the shell may prove to be a useful adjunct in defining families. For example, aragonite is entirely absent in the Ostreidae and only in the Anatinidae is there a prismatic layer under the nacreous one.

The illustrations are of the shells given under the following names: *Acmaea, Ampullaria, Aporrhais, Aptychus, Argonauta, Astarte, Aturia, Avicula, Belemnitella, Belemnites, Bellerophon, Biradiolites, Buccinum, Cadoceras, Cardium, Cassidaria, Cassis, Chama, Chiton, Cladiscites, Cyrena, Cytherea, Dentalium, Donax, Durga, Ervillia, Exogyra, Gryphaea, Haliotis, Harpa, Har-*

Structure	Mineralogical composition	Appearance in ordinary light	Appearance under crossed nicols	Structure displayed in such genera as
Homogeneous . .	« Typically developed among calcitic shells». Sometimes aragonite.	No visible structure.	Extinction in one direction; main axes parallel; usualy normal to surface of shell.	*Yoldia*. « *Tapes* ». *Lima*.
Prismatic	Aragonite (rare) and calcite (common).	Prismatic, with prisms generally normal to surface of the shell.	Normally, each prism is a single crystallographic individual.	*Avicula*. *Donax*. *Pinna*.
Foliated	Always calcite.	Layer built up of more or less parallel leaves.	May resemble crossbedding in sandstone.	*Bellerophon*. *Patella*.
Nacreous	Always aragonite.	Consists of thin leaves (less than 0.001 mm) of equal thickness separated by equally thin leaves of some organic substance.	Optic axes always normal to the leaves.	*Avicula*. *Haliotis*. *Nautilus*. *Nucula*.
Grained	Calcite and aragonite.	Irregulary formed grains.	Optic orientation irregular.	*Janthina*. *Argonauta*.
Crossed lamellar .	Generally aragonite.	Layer built up of larger « lamels », each rectangular; short axis generally vertical. Length of the single « lamel » of the first order may be several mm. This structure an aggregate, as in serpentine.	Although each large « lamel » is built up of smaller « lamels », each one is a single crystal individual. Acute bisectrix forms an angle of 75° with edge of « lamel ».	*Astarte*. *Avicula*. *Cardium*. *Dentalium*. *Neritina*. *Tellina*. (Never in the Cephalopoda).
Complex	Always aragonite.	Layer consists of sub-layers of two kinds: one finely prismatic and the other complex crossed lamellar.	Prismatic layers very thin; irregular extinctions.	*Cyrena*. *Lucina*. *Isocardia*.

poceras, Helix, Hippurites, Isocardia, Janthina, Litorina, Lucina, Murex, Nassa, Natica, Nautilus, Neritina, Nucula, Ostrea, Paludina, Patella, Pecten, Phorus, Phasianilla, Pileopsis, Pinna, Pupa, Purpura, Radiolites, Scalaria, Sepia, Solenomya, Sphaerulites, Spirula, Spondylus, Subemarginula, Tapes, Tellina, Tentaculites, Turbo, Voluta and *Zirphaea.*

The survey of the subject of the shell structure of bivalves prepared by Haas (1931) is drawn especially from the papers by W. J. Schmidt. The calcareous shell layers fall into the following four groupes :

a) Nacreous, as in the case of the Nuculidae, Trigoniidae, etc., where the inner layer is nacreous.

b) Calcite Ostracum (« *Kalzitostrakum* »), as Schmidt calls the inner shell layer in the case of the Ostreidae, Anomiidae, Spondylidae, and Pectinidae.

c) The porcellanous layer, which forms the inner layer of most of the marine clams.

d) The prismatic layer, situated between the outer layer (« *Konchinschicht* ») and the innermost layer. The prisms are forms of calcite (Aviculidae, Mytilidae, etc.) or aragonite (Unionidae).

The nacreous « mass », following Schmidt's definition, consists of microscopically small, tabular aragonite crystals arranged in layers parallel to the surface of the shell and cemented by conchyolin. The « light layer « (*helle Schicht*) is said to be the hypostracum (*Hypostrakum*) of Thiele. The prismatic layer is, as in the case of the others, described in detail, and is said to correspond to the « *Rippenlage* » of the nuculids. The interested reader will consult the original, so I shall not attempt to make further extracts from this work.

Schmidt (1932) has also contributed to the study of pearls, a subject that cannot be treated here. Mention is made of his paper, however, because it contains useful remarks on his technique, and because he gives his observations on the constitution of the shell of *Pinna:* prismatic, nacreous and « light » layers lie under the periostracum. Each prism in *Pinna* consists of an individual crystal of čalcite. (Karney (1913) and many others have also recognized this.) The nacreous layer is an aggregate of microscopically small aragonite crystals, and he remarked (pp. 240-241) :

« Dabei ist charakteristisch für *Pinna,* dass häufig in einer Elementarlamelle noch Lücken zwischen den Kristallen bestehen, wenn bereits auf dieser eine neue Lamelle sich zu bilden beginnt. Diese Lücken schliessen sich nach und nach durch Vergrösserung der angrenzenden Aragonitkristalle, jedoch oft nicht vollkommen, so dass in der Perlmuttermasse feine, in der trockenen Schale lufterfüllte Hohlräumchen übrig bleiben können. »

The « helle Schicht » is composed of aragonite crystals, and although related to the prismatic layer the two are readily distinguished.

Some of Schmidt's conclusions (pp. 265-266) are at variance with those arrived at by Böggild (1930), namely, the Danish scholar did not take into account sufficiently the history of individual prisms and that his observations on some interference figures were not precise.

Kühnelt (1933) figured schematically (p. 379) cross sections of the shell of *Naranio* and *Lithodomus,* showing the periosstracum, nacreous layer *(Perlmutterschicht),* prismatic layer *(Prismenschicht),* and crystalline and noncrystalline incrustations. The paper offers notes on numerous boring bivalves, including remarks on the mineralogical constitution (chiefly aragonite) of many of the shells, such as *Gastrochaena, Brechites, Claudiconcha,* and *Petricola.*

Compernolle (1933) reported upon the phosphorus content of *Mactra, Cardium, Petricola, Tapes, Mya, Solen,* and *Donax.*

Chemical analyses of the shells of *Pecten, Solenomya,* and *Anadonta* are among those made recently by Turek (1933).

Conclusions.

The results of many investigations on the structure and chemical composition of the shells of pelecypods establish certain facts. That most of the shells are composed chiefly of calcite and/or aragonite (except for the periostracum) is one basic generalization. Second, it is clear that there is a certain differentiation of material so as to produce characteristic structures. Third, the shell is a secretion product of the cells of the mantle of the animal. Fourth, the shells carry traces of the growth stages of the animal. Fifth, fresh-water mollusks rarely have calcitic shells.

Lack of uniformity in the descriptive terminology is brought out by an analysis of the literature. The divergent use of terms is confusing. For example, the outer layer of shells like « *Unio* » and *Inoceramus* has been called the fibrous layer, prismatic, prismatic cellular, orthoprismatic, etc.; and the inner layer of certain ones has been described according to its material (nacreous or porcellanous) and after its structure (e. g., lamellar). Exactly how to correlate the « structures » (foliated, homogeneous, crossed lamellar, etc.) with the « zones » (ostracum and hypostracum) also needs clarification.

I have found no objective data to show just what is the influence of external factors upon the character of the shell. Would a change of salinity, for example, affect the appearance and composition of the shell layers ?

Little effort has been made to homologize the shell structures of different phyla. It is possible, for example, that the ostracum in the pelecypods corresponds to some part of the shell of the foraminifers? One must know whether the structures in one phyla differ from those in another before fragments can be employed by the stratigraphic paleontologist. The apparent likeness between the shell of a rudistid pelecypod and that of certain other invertebrates has confused more than one scientist and has even lead to the belief that typical Mesozoic pelecypods (the rudistids) were still living during the Tertiary in South America.

We do not know the exact relation between shell structure and the decomposition or efflorescence of shells. For example, in examining the Linnean collection in London, I found that the following gastropods show signs of decomposition : *Cypraea caurica, C. erosa, C. lynx, C. lurida, C. carneola, C. zebra, C. spurca, Bulla ampulla,* and « *Buccinum* » *areola* (a cassid). None of the pelecypods exhibit traces of efflorescence. There is doubtless a chemical reaction taking place, but why only on certain forms? Perhaps a detailed study of the structure of the shells will answer this query and aid in the important problem of conserving type specimens.

Finally, the contributors whose works are so sketchily reviewed in the preceding pages have discovered much that should be of profound interest to the taxonomist. We are sure that certain families include genera having shells with nacreous interiors, and other families are of genera with porcellanous interiors. Nacreous and porcellanous forms in the same family would make one suspicious either of the identifications or of the classification. We do not know, however, exactly how close is the correlation between shell structure and such « phylogenetic » classifications as have been proposed.

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My interest in this subject was first aroused at the University of California in 1923 and since that date I have examined numerous thin sections and have discussed the problems with many, among whom I should like to name especially Professor A. F. Rogers and Dr. James L. Hoard, Stanford University, California; Mr. John F. Mahoney, formerly of the University of California; Dr. W. Adam, of the Musée royal d'Histoire naturelle de Belgique; Dr. J. R. M. Bergenhayn, of the Riksmuseum in Stockholm; Professor O. B. Böggild, Universetets Mineralogiske og Geologiske Museum in Copenhagen; and Mr. L. R. Cox, British Museum (Natural History) in London.

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