

NATURAL HISTORY OF THE PEARLS

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Resumen*

Se da la siguiente definición del término "perla": Una perla es una concreción de material esquelético; para que tenga el valor de piedra preciosa tal concreción debe ser más o menos esférica, de brillo nacarino y con iridaciones. Resulta evidente que solo los moluscos provistos de la capa madreperla en su concha pueden producir perlas preciosas. Dada la identidad de estructura entre las perlas y las conchas donde se originan, queda explicada la fina constitución de tales conchas productoras de perlas, así como del manto, es decir del órgano blando del animal que tiene a su cargo la elaboración de la concha y de las perlas. Teóricamente las perlas se pueden originar en toda la extensión del manto, pero se señalan seis regiones en las cuales el proceso se efectúa casi exclusivamente. La forma y la estructura de las perlas depende de la región del manto en que se originan. Se dan medidas del crecimiento anual de las conchas y perlas en algunas especies de moluscos productores.

Después de una corta discusión de las teorías propuestas para explicar la formación de las perlas, se detalla la más moderna, actualmente aceptada. Esta teoría es resultado de minuciosas investigaciones de fisiología celular, especialmente las relativas al comportamiento de tejidos animales separados del cuerpo del animal y alimentados artificialmente en cultivos colocados en cápsulas de Petri. De los hechos observados en estos experimentos y de los estudios microscópicos hechos con las perlas en estado de formación, tomadas de moluscos vivos, se llegó a la evidencia de los siguientes hechos: Células aisladas de la superficie del manto secretora de la concha, separadas de su propia lugar en un trozo del epitelio pueden ser transportadas al interior del manto por un accidente cualquiera, por ejemplo

por la penetración de un parásito: allí estas células se multiplican en uno de los espacios lacunosos del manto, disponiéndose en forma de saco o cisto, y empiezan a segregar material de concha, el cual, al concretarse, tendrá que adoptar forma globular, y será una perla.

Variaciones en el ritmo de la secreción en estos cistos son la causa de que las perlas no tengan generalmente una constitución uniforme, ya que pueden presentarse en ellas unidos dos o tres elementos componentes de la concha. Ello influye mucho en el valor de la perla, de tal modo, que solamente aquellas que están enteramente formadas de nácar o que por lo menos éste cubre la superficie, son las que constituyen una verdadera joya.

Desde tiempo inmemorial se ha ensayado incitar a los moluscos a la producción de perlas, pero hasta hace poco sin resultados positivos. Ahora que se conoce el papel que las células epiteliales secretoras del manto desempeñan en este proceso, se han llevado a cabo experimentos prometedores. Biólogos europeos han resuelto el problema inyectando células epiteliales dentro del tejido del manto, estimulando así la formación de un cisto perlígeno, capaz de producir perlas, y estas fueron obtenidas. No obstante, las especies utilizadas en estos experimentos son de crecimiento muy lento y están sujetas a influencias ambientales que pueden destruir poblaciones enteras de estos moluscos de agua dulce. Los japoneses han aplicado estas técnicas a una especie perlígena marina de más rápido crecimiento con muy buen éxito. Estos moluscos japoneses pueden criarse en bahías abrigadas de poca profundidad y sujetas a escasas variaciones térmicas del agua.

Actualmente ya existen métodos para aprender a distinguir las perlas espontáneas de las producidas por instigación del hombre. Pero para el biólogo no existe tal diferencia, a él no le importa si el estímulo que ha originado la perla es espontáneo o antropógeno.

*) La versión española de este resumen la debo a mi querido amigo y colega, el Dr. JOSE CUATRECASAS.

Some years ago, a Philippine gentleman brought to the U.S.A. an enormous pearl, which he claimed to be the largest in the world, and which he publicly exhibited for a while at New York. He subsequently tried to sell it. The exciting history of the finding of this so-called "Pearl of Allah" and of its later fate was published in 1939¹. Unsuccessful in finding a buyer in New York, the owner of this "largest pearl of the world" offered it to scientific institutions and museums in other cities in the United States, and thus also to the Chicago Natural History Museum. Its purchase was not considered since this monster pearl was by no means the priceless gem its owner believed it to be, but only a large roundish concretion of shell substance, devoid of any gem value. Nevertheless, it was a "pearl", a very, very big pearl, measuring 9.5 x 5.5 in., and thus according to a general belief, it should have been very, very valuable. What was wrong with it, that it had no market value? The use of the word "pearl" in two entirely different meanings is responsible of the disappointment of the owner of the "Pearl of Allah". Thinking of a pearl as a very highly esteemed gem whose value rises in proportion with the square of the number of carats (1 carat = 50 milligrams) and applying the gem dealers' and gem lovers' conception of a pearl to his specimen, he must have dreamed of a fantastic sale value; but while his pearl was really a pearl in one sense, it was not one in the sense of a "precious pearl", it possessed neither regular shape nor nacreous lustre without which such a shelly concretion has no gem value.

Gem pearls, with the adventurous story of the pearl fishery, their market, and their use in jewelry, have a vast and interesting literature. To the scientist, however, they have no more significance than pearls without the gem qualities, which, in fact, represent only a special case. Both types of pearls are built up in exactly the same way, and since the stimulus of pearl formation in general lies within the field of biology, the life history of valuable pearls may be elucidated by the description of pearl formation in general.

First of all we have to learn what is understood by the word "pearl" in natural history. To the scientist, a pearl is simply a more or less roundish concretion of skeletal material; such concretions can develop in most animals provided with some kind of skeleton, and it does not matter whether the material by which these skeletons are built up, is organic or inorganic; it is self-evident, however, that a pearl

formed in a certain kind of animal can consist only of the material that constitutes the skeleton of that animal. Considering this broad interpretation of the word "pearl", it is not surprising to learn that chitin pearls have been found in insects, horn pearls at the base of the horns of cattle or antelopes, and bone pearls at the base of the antlers of deer. Vegetable pearls have been claimed to exist in coco-nuts, but this is not true.

Pearls from non-molluscan animals are comparatively rare, while those formed in snail, oyster, or nautilus shells, etc., in short in mollusks in general, are very frequent. We shall restrict our description to them entirely and remark only casually that the mode of pearl formation in other animals is basically identical with that in mollusks.

From the explanation above, it is evident that the structure of the shells of those mollusks that regularly or occasionally produce pearls throws light on the structure of the pearl. In spite of its frequently striking resemblance to porcelain or earthenware, the molluscan shell differs basically from pottery of any kind by not consisting of a single layer. At least two mostly three layers are found to constitute the calcareous shells of snails or mussels. In no case is the outer, organic layer, the conchin or conchyolin — often, but inaccurately called periostracum — missing. This is a thin film of horn-like appearance, though chemically very different from horn. This conchin layer is the base on which the hard building material of the shell, the calcareous layers, is deposited; these are thin and fragile in the beginning, growing thicker and heavier in the course of time. Since this deposition of the calcareous part of the shell, which consists of calcium bicarbonate, begins at the edges of the shell, these are always much thinner than the shell zones away from the edge, which are subsequently re-enforced by additional layers secreted by the mantle-cells. In many marine mollusks, whether snails or bivalves, the outer layer, the conchin, disappears after the formation of the hard shell; in most snail shells and in many mussel shells, only a single layer of calcareous material is involved in the shell formation; but in some kinds of snails, such as the abalones (*Haliotis*) and the turban shells (*Turbo*), in the pearly nautilus, or, finally, in the marine pearl-oysters and in the pearly freshwater mussels, two calcareous layers of different structure are developed in addition to the always present conchin film and it is this type of mollusk shell that produces the fine pearls of gem value. Since both the calcareous constituents involved may

build up pearls, each alone or both in combination, we must examine these layers more in detail.

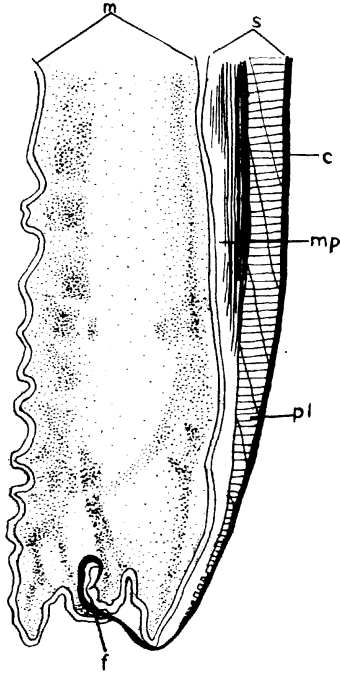


Fig. 1. Cross section through the marginal portion of the shell of a freshwater, pearly mussel. f = fold, c = conchitic layer, pl. = prismatic layer, mp = mother-of-pearl, s = shell, m = mantle. After F. HAAS.

Figure 1 shows how the various parts of a shell composed of three shell layers are situated in relation to each other and to the mantle, which is part of the mollusk's soft body, and which produces the shell. Within a fold of the mantle (f), the outer, organic shell layer, the conchin, is constantly produced. This serves as the base on which the next following layer, the calcareous prismatic layer, is deposited; starting as a very thin film (pl), the prisms grow longer away from the edge of the mantle, and, after having reached a certain length, the third shell layer, the likewise calcareous mother-of-pearl, is laid down upon them; since this layer also starts as a very thin film, increasing in thickness away from the edge of the mantle, its cross-section, together with that of the previously mentioned prismatic layer look somewhat wedge-shaped. Whereas

the conchin layer increases uniformly in thickness, the prismatic layer gradually thickens with increasing distance from the margin of the shell, and the prisms stop growing inward only when the mother-of-pearl starts to be deposited upon their inner surface. The mother-of-pearl, or nacre, remains in contact with the mantle-cells and increases in thickness as long as the mollusk grows, and possibly even longer.

From the above explanation, it appears that the cells on the inner mantle surface produce conchin on their outer edge, prisms in the following rather narrow belt, and nacre on the remaining surface, which constitutes by far its greatest portion. The division of labor of the shell-secreting mantle cells plays an important role in pearl formation. The two calcareous shell components, the prismatic and the nacreous layers, require a little further description.



Fig. 2. Isolated prism of an *Anodonta* shell. Enlarged. After W.J. SCHMIDT.

The prismatic layer receives its name from the shape of its individual component prisms, of which one is shown in fig. 2. These prisms stand vertically on the conchin layer and thus a view from the inside of the shell does not show their length, but their pentagonal or hexagonal bases, resembling together a pavement

of flagstones (fig. 3). In contrast with the prismatic layer, the nacreous layer is formed by many tiny and very thin calcareous platelets, which are deposited on the prism pavement, and at right angles to the prisms. These nacre-platelets have a diameter of about $10\ \mu$ ($= 0.01$ mm), and their outline may be either round or angular; their thickness varies from about $0.5\ \mu$ ($= 0.0005$ mm), in the pearl oyster, to about $1.5\ \mu$ ($= 0.0015$ mm) in the pearly freshwater mussels. These platelets join in a single layer to form lamellae, the so-called "elementary lamellae", the thickness of which, of course, is always that of the constituent platelets. The borders of the platelets do not coincide in the successive elementary lamellae, so that cross sections through a piece of nacre offer a view resembling brick work. The thickness of the nacreous layer depends, directly on the number of elementary lamellae involved (fig. 4). The formation of nacre does not take place by the construction of successive elementary lamella over the entire surface. In fact, the building of the mother-of-pearl goes on rather independently in various parts of the nacreous area, more rapidly on some parts than on others, so that the surface is not entirely even, but is provided with various levels of different heights. When viewed with a strong magnifying glass, the nacreous surface of a shell is not like that of a polished gem, but resembles a relief map or a hilly landscape seen from an airplane; fig. 5 gives an idea of this surface structure, which is called the "growth-vein" of the mother-of-pearl.

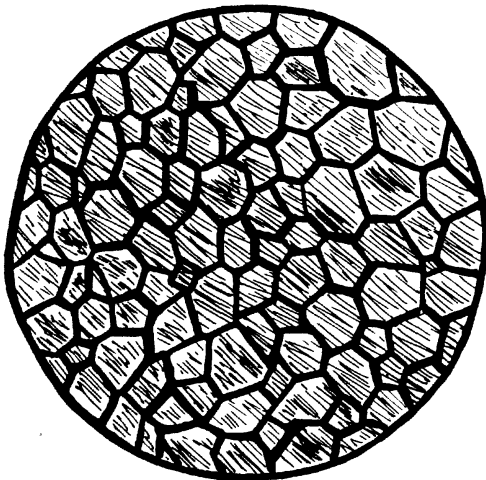


Fig. 3. View upon inner end of prismatic layer of a *Pinna* shell. Enlarged. After W. J. SCHMIDT.

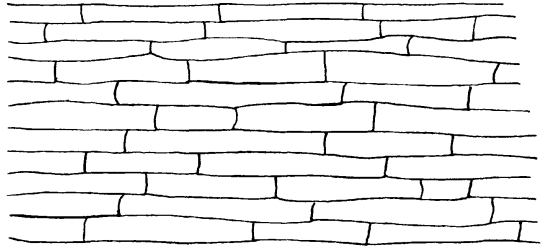


Fig. 4. Cross section of the nacreous layer of a Pearl Oyster, *Pinctada margaritifera*, showing brick work structure. Enlarged. After W. J. SCHMIDT.



Fig. 5. Growth-veins of the nacre of a River Pearl Mussel, *Margaritifera margaritifera*, highly magnified. After J. W. SCHMIDT.

Both the prismatic and the nacreous layers require some material to cement together their tiny constituents, the prisms and the nacre-platelets. A very thin film of conchin, which sheathes every prism and platelet serves this purpose, and a somewhat thicker film of the identical material glues the nacre to the prisms. This fact shows that even those mantle cells that are charged with the secretion of prisms and of nacre may continue to secrete conchin; furthermore, there are occasional layers of conchin and of prisma within the nacre, showing that the nacre-producing cells may also secrete the two other shell layers. This must be borne in mind when we attempt the description of the structure of the pearl.

Pearls in the broad sense are only shelly concretions. Let us begin their examination with some types of pearls which, though without a constant market value, have, nevertheless, some importance as "fancy pearls".

First of all come "oyster pearls", about which much false information is spread among the public. The almost legendary report that eaters of oysters occasionally find gem pearls in the common edible oyster, comes from two different sources. First of all, the common oyster, the prize of the gourmet, is confounded through its name with the pearl-oyster, which is the true and principal producer of gem pearls. "Oyster" is used in loose general sense, just as is the word "fish" or "starfish", "shell fish", etc. The pearl-oyster is no more closely related to an edible oyster, than a starfish is to a fish. Unfortunately, the habit of abbreviation leads to the reduction of "pearl-oyster" simply to "oyster", thus confusing them hopelessly with the common oyster, whose quite different merits are not within the field of our present topic. The myth of the occurrence of gem pearls in the edible oyster is based further on the fact that these shells are capable of building up pearly, but not nacreous concretions. The material of the oyster shell consists of a dull whitish mass, devoid of mother-of-pearl qualities, and their pearls exhibit these identical features and are accordingly without any gem value. The oyster pearl myth is, however, further supported by the fact that in very, very rare cases even these otherwise lusterless, porcelain-like concretions may possess a fine, satiny polish and may thus have some gem value. The rarity of these satiny pearls in the edible oyster makes the expectation of the finding of a gem pearl by an oyster consumer very low, the probability being almost zero.

Another type of "fancy pearls" without a constant market, but with some curiosity value, is produced by the "giant clam" or *Tridacna* of the Indopacific Ocean; (of which an average sized pair of shells is on exhibition in Museum Hall M) according to the considerable size attained by these tridacnas, almost 3 feet of length and over 1 foot of width, their pearls can grow to much larger dimensions than those found in smaller kinds of shells. The "Pearl of Allah" mentioned in the beginning of this article is such a *Tridacna* pearl and apparently the biggest one ever known. The shell of the giant clam consists of a very deciduous and, therefore, usually absent conchin layer, and of a single calcareous layer of a minutely fibrous structure, called, on account of its appearance, the porcelain layer. This shell ma-

terial, which is still little known as to its finer structure, is not restricted to the tridacnas, but is in fact the principal material of most clams and related forms with non-nacreous shell, as well as of most snail shells. The porcelain-pearls of *Tridacna*, though mere curios and not gems, nevertheless play a certain role on the market, and this on account of a strange and only very recently disentangled misunderstanding. The Malays of the Dutch East Indies regard them as charms and call them "coconut pearls", since their satiny white color gives them a resemblance to the flesh of this palm fruit. Apparently the first European travellers to these countries believed that these pearls had really originated in coconuts. Thus the myth grew that the cocopalms could produce pearls, and these "vegetable" pearls were much sought for and highly prized as curios. Only two white persons ever claimed to have witnessed such a pearl find in a coconut and all the remaining so-called coconut pearls known had been acquired as such from natives and from curio dealers. In 1939, a Dutch zoologist, A. REYNE², published a report upon his investigations on coconut pearls. He had been able to see 70 of them in public and private collections, and all of them were plainly *Tridacna* pearls. REYNE, in addition, tried to locate those two coconut pearls which allegedly had been taken from coconuts in the presence of Europeans. One of these, found a long time ago, could not be traced. The second, obtained in 1922 on the Tenimber Islands, was examined; it proved to be an unmistakable *Tridacna* pearl, and its owner had apparently been tricked by the native who opened the coconut and claimed to find a pearl in it. Thus, the coco palm has to be cancelled from the list of pearl-producing beings and its alleged pearls from now on must be known as *Tridacna* pearls. Pearls of porcelain substance can be found in most clams whose shell is made of that material, and they even occur in some snail shells formed of the same substance. Pearls found in the East Indian "Chank" shells and in the West Indian stromb shells occasionally show a rosy color, corresponding to the coloration of the porcelain substance of their mother shells, and they are locally esteemed and often highly valued, though their pink color quickly fades.

The "fancy pearls" thus far dealt with are all composed of concentric though not always very discernible layers. There is another type of fancy pearls exhibiting a different structure, characterized by elements radiating from their center, each of these elements growing individually by apposition of calcareous material to

the free end of the radial constituents. Since this growth in length goes on simultaneously in all of the individual elements, the pearls produced become rather symmetrical. The pearls we are speaking of are produced by the ham-shaped, thin-shelled bivalves of the family Pinnidae, and the radial elements constituting them are prisms derived from the prismatic layer. In the Pinnidae, the prismatic layer is almost the only shell material, and it is covered, in the parts of the shell remote from the margin, by a very thin, polished layer of a procelain-like substance. According to the general color of the pinnid shells the pearls produced by them are of a reddish blackish color and they show, when fresh, a very high luster, which, unfortunately, does not last indefinitely. The prisms radiating from the center of the pearl are glued together by comparatively thick films of conchin, and under the influence of the air, these conchin sheaths dry and shrink, loosening the connection between the individual prisms and causing thus the gradual deterioration of the pearl (fig. 6). Occasional conchin layers around the entire pinnid pearl may produce the delusion of a concentric structure, which, in fact, was until recently thought to be the nature of these pearls.

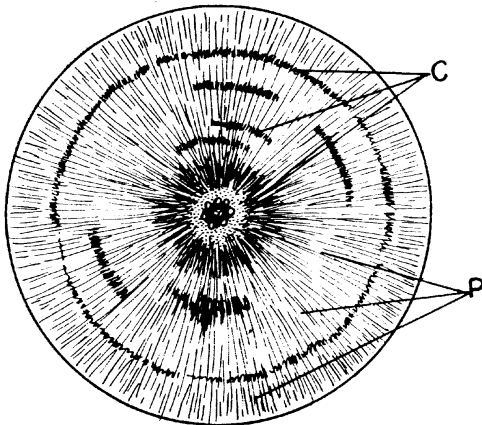


Fig. 6. Cross section of a pearl of *Pinna*, exhibiting the radial prismatic structure and concentric conchinc layers. p = prisms, c = conchinc layer. About enlarged
After. R. DUBOIS.

The nacreous pearls, the only true gem pearls, may originate in many different kinds of mollusk shells, bivalves, snails and cuttlefish, all of which have one feature in common, namely the possession of a layer of mother-of-

pearl on the inner surface of their shells. Pearls of this type, which are not the products of either pearl-oysters or pearly fresh water mussels are more or less accidental products of their respective mollusks and they are rarely perfect as to shape or luster, so that they are treated as merely a secondary type of pearl in the pearl market.

Among the cuttlefish, the pearly nautilus furnishes such accidental pearls, and among the snails, the heavy *Turbo*-shells and the abalones or *Haliotis* may be named in this connection; according to the relative flatness of the abalone shells their pearl products are mostly elongated or irregularly shaped, so-called "baroque pearls" more used for ornaments than as individual gems.

Even in the pearl-oysters and the pearly freshwater mussels, which are the producers of really fine pearls, not every pearl formed is a gem. According to the three layered structure of these pearl-yielding shells, the pearls produced may be built up by only one of the three constituents, by two of them in any combination, or by all three; and even repeated sequences of the layers that share the structure of an individual pearl may occur. It is self-evident that pearls consisting only of the horn-like conchin layer are destitute of any value. Those composed of prisms only often show a high luster; this type of pearl is frequently found in pearly freshwater mussels. Our fig. 7 gives an idea of the structure of such a prismatic pearl; we see the prisms radiating from a central dark mass, the nucleus, which may consist of various objects, as we shall learn later. Other pearls, most of the marine ones and about half of the river pearls, are built up by concentrically deposited layers of nacre or mother-of-pearl, around a nucleus of some kind; our fig. 8 illustrates in a schematic way how this type of pearl is constructed; for obvious reasons, the thickness of the individual nacre platelets has to be considerably exaggerated in the figure.

In a general way, such simple pearls, exhibiting only one kind of shell layer aside from the nucleus, are rare, for most pearls are compound in one way or another. So, concentric zones of conchin layer may be found in many pearls otherwise consisting only of prisms or of nacre; others may show an original nacreous center around which prisms are deposited (a rare case) or the original prismatic center becomes later enveloped by nacreous layers. In most cases of such sequences of different calcareous pearl constituents, a more or less conspicuous cap of conchin is found between the two kinds of pearl layers, and such a change of structure may be repeated several times.

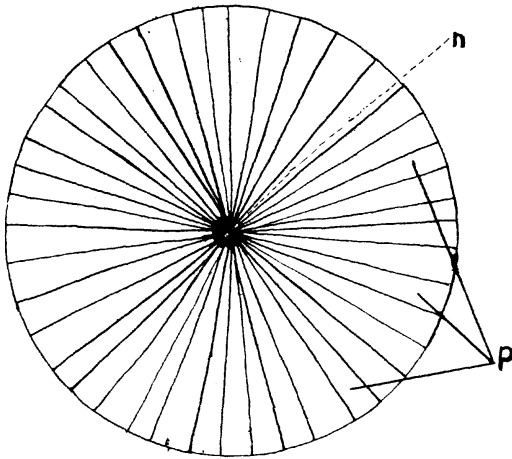


Fig. 7. Schematic cross section of a prismatic pearl. n = nucleus, p = prisms. After J. W. SCHMIDT.

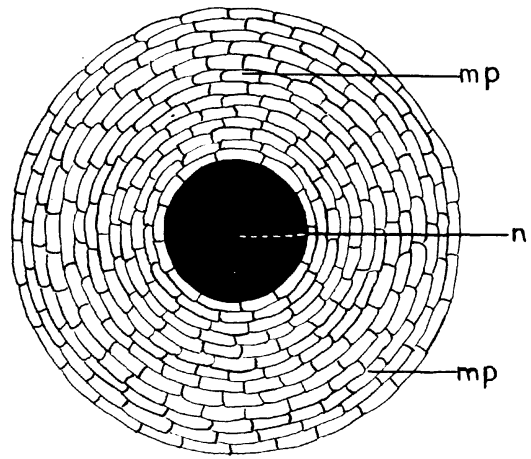


Fig. 8. Schematic cross section of a nacreous pearl. n = nucleus, mp = mother-of-pearl. After W.J. SCHMIDT.

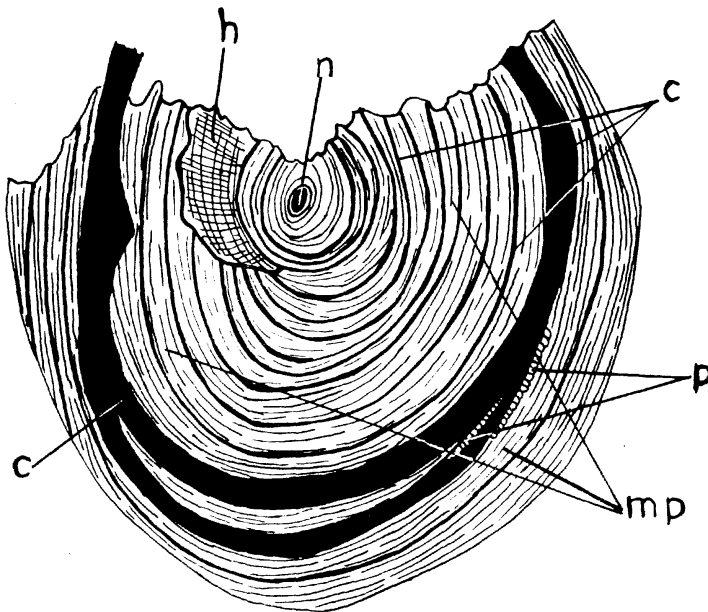


Fig. 9. Cross section of a river pearl, showing asymmetric growth. n = nucleus, c = conchin, p = prisms, mp = mother-of-pearl = nacre, h = hypostracum.

It would, however, be entirely incorrect to assume that the formation of pearls, simple or compound, goes on symmetrically. In fact, nacre may be deposited on one pole of a pearl under construction, while on the other the for-

mation of prisms is still continued, or a cap of conchin may cover one side of a pearl while on the opposite one the mother-of-pearl is still growing. A section through such a compound pearl is shown in fig. 9. The presence of con-

chin layers within a pearl does not affect its gem value provided that these dull layers are so deeply hidden beneath the shiny mother-of-pearl that they do not show through.

Pearl with a nacreous surface show the same picture of growth veins as does the nacre of the shell (see fig. 5). It has been maintained, but never adequately proven, that Oriental pearls, i.e., marine pearls, can be identified, by supposedly characteristic features of this vein-system, as to their point of origin, whether they come from the Red Sea, from India, from Australia or from Mexico, etc.

For completeness, it must be added that even the common mussel of the Atlantic, *Mytilus edulis*, whose shell is composed of conchin, prisms and nacre, is an occasional pearl producer, but since the *Mytilus*-pearls whether prismatic or nacreous or compound, never attain the size of valuable pearls, they do not play an important role on the pearl market. The study of pearl formation in *Mytilus* in more recent years has materially contributed to a better understanding of the process.

Besides the many types of pearls discussed, which are all free pearls or mantle-pearls, another kind of calcareous concretion is pearl-like in many respects, but differs from them in being attached to the inner surface of the producing shell. These shell-pearls, mostly termed blister-pearls or half-pearls, may assume various shapes, from half- or even three-quarter-globes to low pads, and they may be regularly round or irregular. Those that combine a good luster with a roundish shape are often used in jewelry in ornaments that are to be viewed only from one side; the imperfect part of the blisters, which was in connection with the shell, is covered by the framework of the setting.

These shell-pearls show how pearl formation begins and continues. In the case of the shell-pearls themselves, the stimulus which causes their formation is obvious. Some foreign body, such as a small stone, a grain of sand, a bit of clay, a piece of coral, or shell, or even a living being like a fish or a crab, forces its way between the inner surface of the shell and the outer surface of the mantle. Once in this position the intrusion is gradually covered by the shell layers, secreted by the cells of the outer mantle surface. These layers, had such an intrusion not taken place, would have thickened the shell, but under these circumstances they gradually envelop the foreign body. The shape of the intruder shows through the shell layers deposited upon it, and in fact, cases are known in which the blisters reveal with-

out any doubt that they cover a little fish or a crab. Roundish or globular foreign bodies develop into similarly shaped, half-pearl like blisters.

These facts have been known for thousands of years, but only lately has the primitive idea been refuted that the incrustation by shelly material represents an act of defence on the part of the mollusk, aiming to kill and to hermetically close up a living intruder or to reduce the pain suffered from a dead foreign body provided with sharp point or edges. We now know definitely that no such reaction of defence is involved in the process of blister formation, but that the normal process of shell secretion is simply continued by the mantle cells, even after they have been separated from their natural base, the inner mantle surface.

The primary causes of shell-pearl formation were so obvious that anyone could see how a foreign intruder would induce this process; it is therefore understandable that the insight gained from shell-pearl formation was generally applied also to the formation of free pearls. Foreign bodies entering into the deeper layers of the mantle were not thought to be responsible for the origin of the pearl, for up to the middle of the 19th century the general idea, at least of pearl fishers, dealers, and the interested public, was that the free pearls started as flat, pad-like shell-pearls, which, under favorable circumstances, grew to a more globular shape, pressed themselves into the tissues of the mantle and, when almost perfectly ball- or drop-shaped, detached themselves from the shell and remained in the interior of the mantle, which closed upon them at the point of their entry. Such a primitive concept could not stand the weight of scientific research, though it was by no means the most fantastic of the many ideas held in prescientific times about the origin of pearls. All of these other theories are more poetical than matter-of-fact and we may omit them from our report. In connection with the theory that attached shell-pearls grow and, when globular, detach themselves like ripe fruits, it may be stated that occasionally the opposite occurs, i.e. that free mantle-pearls situated close to the shell may be captured by enveloping shell layers and may thus become shell-pearls; our fig. 10 shows in a diagrammatic way how this is effected.

The scientific attitude, which has prevailed over the former scholastic and traditional way of thinking since about the middle of the 18th century, was that free pearls start as such; but no reasonable information about the factors inducing the formation of a mantle-pearl

or free pearl was available, though it was beyond doubt that the stimuli for the origin of both free and of shell-pearls must be alike. In the middle of the 19th century, European biologists found water-mites at the center of river-pearls, and the old theory in connection with shell-pearls seemed corroborated. Later on, larvae of tape-worms, and larvae of some kind of fluke were found to be the nuclei of pearls of the common mussel, *Mytilus edulis*. During the latter half of the nineteenth century scientists drew the generalization that pearl formation in the inner tissues of the mantle starts as the consequence of an animal, whether parasitic or not, forcing its way into this tissue. Indirectly, this statement implied that the process of pearl formation is an act of defense against an invader, the formation of an unbreakable cage in which the intruder is unable to do any harm. Sand grains or other inorganic materials, in one case even a grain of river gold may constitute the nucleus and are enveloped, according to this theory, by shelly layers in order to render their sharp edges or points inoffensive. Under these circumstances it is understandable that a noted French authority on pearls made the following general statement: "After all, the most gorgeous pearl is nothing but the splendid coffin of a miserable minute worm."

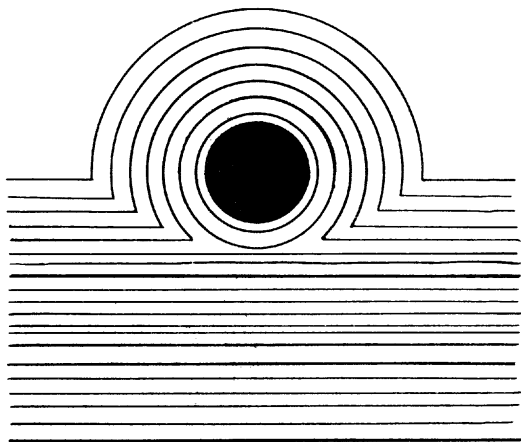


Fig. 10. Incorporation of a free pearl into a shell-pearl. Schematic, after W.J. SCHMIDT.

The man who had originated the "stimulus theory" of pearl formation was satisfied with the statement that the inner tissues of the mantle are the place where the building of free pearls must begin, and that the process of pearl

formation generally is started after some foreign body has entered these regions. Even the encystation of the intruder by a layer of cells differing from those of the surrounding mantle tissues had been correctly watched, and so had been the formation of a sac in which the pearl formation was to start and which, therefore, was later to contain the growing and mature pearl.

The observations made by these scientists were correct, but their interpretation was premature. Better information about the division of labor in animal tissues, about the specificity of cell and gland activities, and about the behaviour of tissues in transplantations, was required for the explanation of the real nature of pearl formation. Thus our knowledge of the natural history of the pearl is still by no means complete.

We now know that the secretion of shell material in the mollusk's body is confined to the outer epithelium of the mantle, whose cells are unicellular glands, and that, since the shell and the pearls are constituted by identical materials, both of them must be secreted by these outer mantle cells. A division of labor has taken place in this cell layer, since three zones of shell material production can be distinguished: the marginal conchin belt, the submarginal prismatic belt, and the central mother-of-pearl belt. In laboratory experiments on the behaviour of tissues detached from their natural place and transferred into glass-dishes, where they are artificially nourished, these tissues not only continue functioning in their natural way, but even grow by cell multiplication. Other experiments, which dealt with pond-mussels, gave evidence to the fact that wounds in mantle-tissues that were prevented from closing were promptly lined by the cells of the outer mantle surface invading the wound channel. When injurious objects remained within the mantle, the invading outer mantle cells surrounded them, thus forming a cyst. In most cases the exit of the wound channels, whether the injuring object was still in them or had been removed, closed up after some days, separating the epithelium cells that had immigrated into them from the outer mantle surface, and confining them to a hollow within the deeper layers of the mantle.

Comparing the results of the experiments just described with the established facts of pearl formation, it is easy to see that the foreign body introduced experimentally into the deeper layers of the mantle is replaced, in nature, by the invading water-mite or the worm larva; in both cases the opening leading into the inner mantle tissues serves as a gateway

for the invasion by the cells of the outer mantle surface, which, step by step, penetrate deeper into the channel, until they reach the place where the foreign body comes to rest. This foreign body they will surround forming thus a pearl-cyst or sac. When the penetrating animal is sub-microscopic, as is the case with the larvae of the flukes known as pearl inducers, the act of penetration into the deeper mantle tissues does not constitute a real injury, with a gaping wound, but the minute invaders merely force their way between the epithelial cells of the outer mantle surface. Even in this case, some individual epithelial cells may be detached from their connection, stick to the penetrating larva, and are carried by it into the depth of the mantle, where the invader may come to rest in one of the many hollows of the spongy connective tissue. Here the accompanying epithelial cells may multiply and arrange themselves, in the course of time, into an epithelial layer lining the available space, namely the tiny hollow in which the invader stays and dies and is gradually covered by these cells, which thus form a pearl-cyst. Once the formation of a cyst in one way or another is completed, the cells constituting it will start again their normal function of shell secretion, which in this case will, of course, create a shell of spherical shape; in other words, a pearl. Thus, experiments and natural processes combine perfectly to furnish a more adequate explanation of how a pearl is started. This explanation is further supported by the existence of pearls without any foreign body nucleus. Such pearls have at their center either a tiny ball of conchin or an empty space, filled originally, perhaps, by a bubble of gas or a drop of the body fluid. Thus it becomes impossible to adhere further to the belief that pearl formation is an act of defense against an unwelcome intruder.

But how does the formation of a pearl-cyst go on, when there is no center around which the emigrated cells of the outer mantle epithelium can establish themselves, and when there is no carrier that brought these cells into the deeper mantle layers, and which made an opening for invasion of the secretory cells? Experimental studies on the behaviour of detached parts of tissues again give us the clue to the answer. Detached epithelial cells, even if isolated from their epithelial connection, and in an irregular mass, rearrange themselves into a pavement-like flat epithelium if placed upon an even background, and when fed by adequate nourishing solutions they even multiply and thus expand over a wider area. These same

cells, if transferred to a nourishing solution, but denied a suitable, solid stratum to settle upon, will arrange themselves, step by step, into a hollow ball which gradually increases in diameter with the multiplication of these cells. Since the thickness of the epithelial layer does not increase, the growth in diameter of the tiny cyst enlarges the hollow space in its center. In an experiment made with European river mussels, a mass of scraped-off cells of the outer mantle surface was shot with a syringe into the deeper mantle tissues; after some weeks an examination showed that these injected cells, torn from their epithelial connection, had rearranged themselves into a continuous epithelium that had lined the hollow in the connective tissue where it had come to rest; this newly arranged epithelium had already started shell secretion, that is to say the formation of a pearl. These observations explain the existence of pearls without a nucleus, and though the circumstances are not yet fully known under which the transportation of such epithelial masses into the deeper mantle layers occur under natural conditions, there cannot be any doubt about the fact that such passive transfers of surface cells into the interior can take place. We know of cases in which pearls without a nucleus have been found within the mantle tissues, while an unenclosed foreign body was present close by; this seems to indicate that such a foreign object could be the carrier of isolated, detached surface cells, and that these cells could become detached before the invader came to rest, and could start the formation of an empty or fluid-filled cyst, leaving uncovered the object that had introduced them into the mantle. From these results of laboratory work on tissue transplantation and from the histological study of the pearl-producing tissues under natural conditions, we are now able to understand the mechanism of the pearl-starting stimulus and of the process of pearl-formation, at least in a general way. But we are still compelled to confess that many minor features of the process are as yet imperfectly or not at all known and that it will take more time and more research, before the pearl - the biological gem - has revealed to us all secrets.

Since the mantle covers the entire soft part of the mussel, and since the mantle on its entire outer surface is lined by the shell-secreting epithelium, the formation of pearls in any part of the mantle is theoretically possible. Actually, however, search for pearls for many centuries has shown that there are six parts of the body in which pearl-formation mainly occurs; these are (fig. 11):

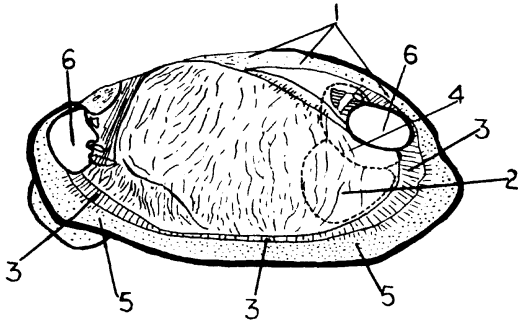


Fig. 11. Pearl-building zones of a river pearl mussel. Reduced.

1. the back of the mantle, where the ligament of the shell is secreted.
2. the anterior portion of the mantle.
3. the mantle-line, i.e., the impression of the muscle which attaches the mantle to the shell and which runs parallel to and in a short distance of the shell margin.
4. the part of the mantle which surrounds the anterior adductor muscle.
5. the margin of the mantle, i.e., the part that lies outside of the mantle-line.
6. the muscles, mainly the large ones, the anterior adductor and still more the posterior.

From this list it is obvious that the various types of pearls named above (p.114) have some connection with the individual pearl-producing areas of the mantle. Indeed, these six zones account for the differences among the various pearl types in structure and shape. Thus, the pearls produced in the outer mantle edge, very close to the margin of the shell, in a region where the epithelium secretes the conchin layer, will be brown or blackish, built up by conchin exclusively or by alternating layers of low prisms and conchin. A little more toward the center of the shell, but still in the marginal zone, in the prismatic belt, pearls will consist mostly of prisms, perhaps with an occasional layer of conchin. Pearls which originated in muscles or in adjoining parts of the mantle are entirely or partly built up by a special modification of the mother-of-pearl, the so-called hypostracum, or bright layer, which replaces the ordinary nacre in places where muscles attach themselves to the shell. This hypostracum has a minute structure somewhat different from that of the mother-of-pearl and is even recognizable

to the unaided eye by its rather bright, silvery appearance. Combinations of ordinary nacre and the bright layer in one and the same pearl are by no means rare. Such pearls, produced in a cyst touching a muscle, may show a cap of nacre on one side and a cap of hypostracum on the other. Pearls from the mantle zones not yet mentioned consist mostly of nacre. Compound pearls, i.e. those containing all the three shell components, are produced, apparently, only in those parts of the mantle that secrete nacre. It has been noted above that the cells that produce mother-of-pearl may change their function and secrete conchin or prisms, or both alternately, and may then revert to their main function.

It may easily be understood that perfect, globular pearls can develop only in places where the pearl-cyst does not find any resistance during its growth, enabling it thus to preserve a spherical shape, i.e. only in parts of the mollusk's body that are sufficiently wide. Thus most of the valuable, perfectly shaped pearls are found in the zones 1 and 4 of the mantle (see fig. 11). In zone 2, the growing and widening pearl-cyst just cannot expand in excess of the narrow space available, and hence assumes an elongated shape, which governs the shape of the pearl produced within it. The greatest resistance to the expansion of the pearl-cyst is found within the two large muscles (6 in fig. 11), where it is surrounded by the tough muscle fibers, which are, furthermore, mostly in the state of partial contraction, and the pearls secreted within these muscles assume elongated and irregular shapes; they are called "baroque" pearls and may be of considerable value, if the irregularity of their shape is limited to its deviation from the spherical but otherwise shows a certain symmetry.

While valuable pearls are rare even in the kinds of shells that are the main pearl producers, pearl-cysts and imperfect pearls are present in a rather large percentage of these bivalves. As a reasonable guess, only every hundredth mussel is likely to contain a pearl, and only one in a thousand of these is valuable. The ratio between pearls and pearl-producers varies from locality to locality, from year to year and, most of all, from species to species.

Considering the absolute rareness of truly valuable pearls in relation to the labor involved gathering them, it is not surprising that early in history and in many countries, man has tried to stimulate the growth of pearls in pearl-oysters to bring about a greater harvest. Conditions in early times, before the invention of diving devices, compelled man to confine his experiments to the freshwater mussel, which is much easier

to obtain and to work with. Basing the procedure on the old belief that free pearls had started as flat, pad-like shell-pearls growing in thickness, attaining almost globular shape and detaching themselves finally from the shell to wander into the deeper layers of the mantle, the Chinese introduced semi-globular foreign bodies of metal or baked clay between shell and mantle of a large oriental pond-shell, and, by this device obtained shell-pearls, which were cut out, and which found a wide market in the East.

In Europe, the only bivalve available for attempts to initiate an intended pearl-production is the pearly freshwater mussel (*Margaritifera*), though its relatives in streams, creeks, and ponds are also capable of yielding the desired gem. Thus, in the Old World, almost all the research work was restricted to a species that lives under rather unfavorable conditions, since sudden floods, deep winter temperatures, or pollution by sewage often decimate or even destroy its entire populations in certain waters. Nevertheless, attempts to compel these bivalves to yield pearls have been made since the 17th century, though little is known of the methods employed. The first attempt of this kind of which we are better informed, is that made by the father of modern zoology, the great Linnaeus who, in the latter half of the 18th century, developed a "secret art of inducing pearl-formation in mussels", which he kept so secret that his method only became known a century later, from old documents and letters. He regarded free pearls as derived from shell-pearls; accordingly he drilled a hole into the shell without injuring the mantle, then introduced into the hole, a wire that carried a little ball of limestone on its end, the ball thus pushing the mantle a little inwards, and kept the wire in position by sealing the hole with some waterproof cement. After several years, the introduced stone ball had been covered by thin layers of shell substance, representing thus a stalked pearl. Pearls of this origin are still preserved, together with Linnaeus' shell collection, in the museum of the Linnaean Society in London, and everybody who has seen them, agrees that they are very inferior pearls. They have a historical importance, as representing the first step toward procedures that have recently lead to the intentional production of pearls of gem value.

In the United States, where there is an abundance of freshwater mussels capable of pearl-formation, the first attempt to start the cultivation of pearls apparently was made, or at least planned, by this century's first natura-

list at large, C. S. RAFINESQUE. In 1820³ RAFINESQUE published the following note in the Kentucky Reporter: "How 'Real Pearls' can be formed in the 'muscle' shells found in the Ohio River....." RAFINESQUE did not explain the procedure he had in mind.

The first use of marine pearl-oysters to produce pearl-like concretions appears in Japan, where a MR. MIKIMOTO operated a pearl-oyster farm in a protected bay, in which shell-pearls, or half-pearls, were obtained by the old process of introducing semiglobular objects between shell and mantle. We shall return to this pearl-oyster farm again in another connection.

The ideas about the origin of pearls developed during the second half of the 19th century, led to curious attempts to stimulate pearl-production. Instead of attempting to cultivate pearls, it was attempted to increase the incidence of what was believed to be the stimulus of pearl-formation. The conviction that the organic nucleus of a pearl, a little animal such as a watermite or the larva of a fluke or tapeworm, was the agent stimulating the infected mussel to cover the foreign body with pearly substance and thus to make a pearl, led to the suggestion that the number of "pearl inducing parasites" could be artificially and purposely increased. Fortunately for the fishes and birds that might have been affected by a highly increased number of parasites, no solution of this problem was found. For only a minute proportion of them would have entered pearl-producing mussels to become converted into pearls. This episode of the history of pearl cultivation represents the only attempt known to induce pearl-formation by an indirect method, i.e., without touching the pearl-producer with human hands.

An early forerunner among pearl experimenters, in 1838, WALTZ, thought that the deeper mantle-tissues were the seat where free pearls are formed, and had experimentally attempted to induce pearl-formation. His experiments failed, partly on account of the very primitive techniques available and, partly because his river pearl mussels were killed by disease or by floods and ice before the pearls initiated could attain any considerable size. But WALTZ had been on the right track, and in 1913 his experiments, repeated with the more refined technique of hypodermic syringes, showed definite success.

ALVERDES, as a result of extensive histological study of the formation of both shell and pearls, had recognized that in order to produce pearl-formation in the inner mantle tis-

sues, it was only necessary to insert cells of the shell-secreting epithelium of the outer mantle surface. A minute ball of such cells detached by scraping, was shot into the connective tissue of the mantle, where these cells gradually arranged themselves into the shape of a hollow ball and, then, began shell-secretion that filled the empty space inside the ball with a pearl. This success was, unfortunately, condemned to remain a theoretical one, since ALVERDES could experiment only with the best of the European pearl-yielders, the river pearl mussel, which, besides being exposed to environmental danger has the additional disadvantage of growing very slowly and of producing thick dark layers of conchin between its successive nacreous deposits. Subsequent experiments with the same species of mussel in certain creeks in Austria, where life conditions, by means of dams, had been somewhat stabilized, and by employing a more developed technique of injecting (adding an artificial nucleus to the mantle cells), had some success, but were far from becoming commercially successful. It was attempted to eliminate the hampering effect of the slow pearl-growth of the European river pearl mussel by the introduction of more rapidly growing North American river clams. Two years after the introduction of several hundred of such North-American river pearl mussels, all of them had died, for reasons unknown. No mentioning of intentional pearl-production in freshwater clams in this country has come to my attention.

For many years Mr. MIKIMOTO, whom we have already reported as the producer of cultivated shell-pearls, in Japan had attempted the formation of free pearls. He had always failed, though he enjoyed the advice and active help of the most prominent Japanese biologists. After the results obtained by ALVERDES in inducing pearl-production in freshwater shells had been published and had been made available to him by translation into the Japanese, MIKIMOTO's efforts were crowned by success. Imitating the method indicated by the German biologist and perfecting it step by step, he was able to start real pearl-cultivation on a large scale. MIKIMOTO's next improvement of the original method of shooting cells of the outer mantle epithelium into the mantle and letting them form a pearl cyst there, consisted in injecting an already prepared pearl-cyst into the inner mantle tissues. This cyst was made by taking a piece of the outer epithelium of the mantle from its base without separating the cell constituents and wrapping this layer over a little ball turned from nacre. When this artificial pearl-cyst is brought into the con-

nective tissue of the mantle, it produces a free pearl in due time. It is not so much the improved method, as the stable life conditions under an almost constant temperature, that led to MIKIMOTO's success, while his competitors in Europe had failed. The low wages of labor in Japan add to the prosperity of an industry that sells in a world market.

The problem of pearl-cultivation was only successfully solved after the study of the shell and of the shell-secreting mechanism had been sufficiently advanced. One interesting item in the process of shell-formation, that had never been exactly observed, was elucidated by the study of cultivated pearls, which thus repay their debt to science. It had never been possible to learn the exact amount of annual increase in thickness of shells.

It had been shown, by studying artificially induced pearls, that the thickness of the nacreous layer deposited in the European river pearl mussel during a year averages 0.05 mm. In other words, the diameter of such a river pearl increases about 0.1 mm within this length of time, if only the nacre is taken into consideration. Almost all river clams and their pearls show a rhythm of secretion, involving alternating cycles of conchinc, prismatic, and nacreous layers. The conchinc mass deposited at one time is a very thin film and may be omitted in this calculation, but the prismatic layer averages 0.157 mm in the year, adding, thus, approximately 0.3 mm to the yearly increase of the diameter of the pearl. The real growth of diameter equals, therefore, about 0.4 mm, and consequently a pearl 8 mm in diameter would be about 20 years old. This is the averaged result of many individual cases, which vary a good deal among each other. Thus, the yearly increase of the prismatic layer may vary from 0.095 to 0.230 mm and that of the mother-of-pearl layer from 0.047 to 0.064 mm.

In the Japanese pearl-oyster, on the other hand, the increase in size of the pearls consists almost entirely of nacreous layers, with occasional alternating prismatic layers or none. The yearly increase of diameter averages 0.09 mm, almost twice that of the European river pearl (0.05 mm). Since the life span of the Japanese pearl oyster is only about 13 years, their pearls could not possibly grow beyond the size of $13 \times 0.09 = 1.17$ mm; but since the artificial nucleus inoculated into the mantle together with the pearl cyst has a diameter of about 3.5 mm, the resulting pearl will measure 4.6 to 5 mm in diameter.

Pearl-secretion and shell-secretion being equal, these two statements provide us with rather exact data concerning the rates of secretion and of the increase in thickness of the shells of the two kinds of shells in question.

We may end this report on the natural history of the pearls with a brief discussion, from a biologist's standpoint, of the difference between natural and cultivated pearls. Both being secreted, in an identical way, by the identical epithelium cells arranged in an identical, sac-like shape, the only difference between them is constituted by the nucleus, which is accidental and mostly small and organic in natural pearls, where as it is intentionally introduced, larger, and inorganic in the cultivated ones. But in a general way, since the vast majority of all pearls have a nucleus - every pearl is a "pearled" foreign body. Exactly as we speak of heavy or light plating of objects with gold or silver, we might term the natural pearls, with their thicker nacreous layer over a minute nucleus, "heavily pearled", and value them, accordingly more highly than the "lightly pearled" Japanese cultivated pearls, in which a nucleus of about 3.5 mm in diameter is covered by a layer of mother-of-pearl not thicker than 0.6 mm. It has been maintained that the thinness of the pearling in these Japanese cultivated pearls does not allow the nacre to develop its full luster, since the optically different nucleus may show through. This may be true in some cases, but certainly not in general, for otherwise gem-dealers and jewellers would not have developed such varied machinery for distinguishing the two types of pearls. If a pearl can not be recognized as cultivated by external inspection even by a pearl expert, some device has to be used to decide whether it possesses an artificial nucleus or not. Undrilled pearls

are inspected by translucent or fluorescent light, or by X-rays, but conchinc layers in the deeper parts of the pearl may give the illusion of an artificial nucleus, so that this method is of only restricted value.

Even the behaviour of pearls in a magnetic field has been used for the differentiation of natural and artificially grown pearls. Natural pearls made up entirely of concentric layers are indifferent to the magnetic lines of force, whereas the nuclear balls of artificial pearls, turned from nacreous shells and hence consisting of flat, parallel layers, will arrange themselves so that these layers run parallel to the magnetic lines.

Direct inspection of the inner parts of a pearl by complete drilling or drilling to the center, of course discloses any artificial nucleus. A specially constructed glass-needle is introduced into the drill hole and a beam of light sent through the needle illuminates the central portion of the pearl and allows it to be thoroughly scrutinized under a microscope.

The last, but still vague information we have received of the Japanese technique of pearl cultivation, is that a method is being developed by which a solid artificial nucleus is unnecessary and either an air-bubble or a drop of some liquid takes its place in the center of the prepared pearl-cyst. It is not yet known if this method has been successful and how the pearls produced by it are constructed, i.e., if their center is a hollow space or if it is entirely filled by concentric nacreous layers. In any case, the cultivated "pearl without a nucleus" is certain to come in the future, and will make a differentiation between natural and cultivated pearls much more difficult, much more meaningless, and almost artificial; the biologist will not recognize it at all.

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