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## [REVIEW]

# A History of the Cultured Pearl Industry

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During the 18th and 19th centuries, studies of how pearls are formed were conducted mainly in Europe. The subsequent pearl culturing experiments conducted worldwide in the early 20th century, however, failed to develop into a pearl industry. In Japan, however, Kokichi Mikimoto succeeded in culturing blister pearls in 1893 under the guidance of Kakichi Mitsukuri, a professor at Tokyo Imperial University (now the University of Tokyo) and the first director of the Misaki Marine Biological Station, Graduate School of Science, University of Tokyo. This success and subsequent developments laid the foundation for the pearl farming industry, developed new demand for cultured pearls in the European jewelry market, and initiated the full-scale industrialization of pearl culturing. In addition, research at the Misaki Marine Biological Station resulted in noteworthy advances in the scientific study of pearl formation. Today, pearls are cultured worldwide, utilizing a variety of pearl oysters. The pearl farming industry, with its unique origins in Japan, has grown into a global industry. Recently, the introduction of genome analysis has allowed cultured pearl research to make rapid progress worldwide in such areas as the dynamics of mother-of-pearl layer formation and biomineralization. This signals another new era in the study of pearls.

**Key words:** cultured pearl industry, culturing technique, history, pearl, pearl formation

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## Origins of the cultured pearl industry

Molluscs form a hard shell of biomineral to protect their bodies and defend against outside enemies. Sometimes, by chance or outside cause, a sphere of biomineral is formed by the biomineral-producing mechanism in the mollusc's body. This is a pearl. Cultured pearls are made through artificial stimulation of the natural pearl-producing function. Today, cultured pearls are known worldwide as representative gems and have become important items of jewelry culture.

A review of the history of cultured pearls begins several thousand years ago, when beautiful pearls were found, rarely and by accident, in oysters taken from the sea. These were highly esteemed as precious gems among a few members of the privileged classes. Pearls were also highly prized for use in elixirs, and as cosmetics, by virtue of their unique existence in the natural world. Pearls have been treasured around the world since ancient times, including by civilizations in Egypt, China, India, Persia, and Rome. (Nishikawa, 1904a, b, c; Kunz and Stevenson, 1908a; Fujita, 1923).

How were these rarely found pearls made? Many people throughout history have had interest in, and ideas for, explaining the mysteries of pearl formation. As the brilliant shine of the pearl gave an impression of tears or dew in sunlight, it was believed that pearls were formed by the entry of

the tears of God or an angel, by the dew of heaven, or by lightning that had passed into an oyster's body causing a pearl to grow inside. Notably, Gaius Plinius Secundus (Pliny the Elder, born in AD 23) stated in his *Naturalis Historia* that the pearl was formed from dew. From that time until the eleventh century or so, the theory of "pearl formation by the action of dew" was widely accepted. Thus, it was believed from ancient times that, in nature, pearls formed in the body of an oyster as the result of the accidental introduction of a 'seed' of the pearl. However, the cause of pearl formation was still a mystery.

When modern science began to develop in the middle of the 16th century, interest in pearls remained and inquisitive people sought to make pearls artificially, prompting scientific research to uncover the secret of pearl formation. From the 18th century to the beginning of the 19th there was intensive research on pearl formation, centered in Europe. Along with academic studies, there were attempts to establish a cultured-pearl industry in many places throughout the world. In China, however, techniques to culture hemispherical blisters and blisters with the Buddha's image, using freshwater mussels, had already been developed between the 11th and 13th centuries, although the results were far removed from the pearls we consider gems today. Chinese techniques were introduced to Europe, and many attempts were made to produce hemispherical blisters by similar methods. However, outside Japan there were no successes in producing pearls suitable for the jewelry industry. At present, cultured pearls are produced in Australia, the

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Philippines, Indonesia, Myanmar, and French Polynesia, in addition to China, by using various species of pearl oyster, and it is expected that pearl culture will continue to develop as a worldwide industry. However, all of the culturing techniques used in these countries are based on those developed in Japan.

Japan is fortunate to be surrounded by a sea inhabited by Akoya oysters (*Pinctada fucata martensii*), with their beautiful nacre. Research on pearl culturing in this country proceeded in secret at the end of the 19th century, and by the beginning of the 20th century, ahead of the developments in Europe, the first techniques for producing spherical pearls (i.e., free pearls) were already established.

In Japan, by the end of the 19th century the mother-of-pearl Akoya oyster was on the verge of extinction because of overfishing for natural pearls, which were traded overseas at very high prices. The history of Japan's pearl culturing industry started with Kokichi Mikimoto, who dreamed of producing gem-quality pearls using the Akoya oyster. He met Professor Kakichi Mitsukuri of Tokyo Imperial University and became convinced that making cultured pearls was possible. Dr. Mitsukuri was also the first director of the Misaki Marine Biological Station of The University of Tokyo, located in Kanagawa Prefecture, and had a thorough knowledge of pearl research. The encounter between Mikimoto and Mitsukuri, and their subsequent joint research, resulted in great successes in the development of cultured pearls. After receiving instructions from Dr. Mitsukuri, Mikimoto began experimenting with pearl culture and succeeded in culturing hemispherical *Han-en* blisters in 1893. With this success he set up a full-scale program towards developing a pearl culturing business in Japan. In 1899 he started selling ornaments using *Han-en* blisters for the first time and carved out a new market in which cultured pearls were handled as jewelry.

In addition to building the foundation of the cultured pearl industry, Mikimoto established a business for producing cultured spherical pearls, causing the cultured pearl industry to develop into a major jewelry industry. Meanwhile, at Misaki Marine Biological Station, Tokichi Nishikawa began an active program of academic research into pearl culturing techniques. In 1907, Nishikawa established a prototype "piece method" of pearl culture, a method of stimulating the formation of spherical pearls by inserting a small piece of mantle as a nucleus into the oyster body (gonad or mantle). He contributed greatly to the development of pearl culturing techniques. At present, the main oysters used for spherical pearl culturing are the Akoya (*Pinctada fucata*), silver lipped (*Pinctada maxima*), and black lipped (*Pinctada margaritifera*), along with freshwater mussels (*Hyriopsis cumingii*). The basic pearl-forming technique used to produce spherical (free) pearls from these pearl oysters is the application of the piece method.

By 1918, the commercial production of spherical cultured pearls was in sight. In 1919, Mikimoto began to sell spherical cultured pearls in Europe, the central market for natural pearls, starting in London. However, the entry of cultured pearls into the European market had a shocking impact on jewelers of the time and the pearls became a target for attack. Questions arose as to whether the cultured pearl was real or fake. In Paris, the attack on cultured pearls

as fraudulent was so vehement that various actions were suggested, including an embargo. The affair developed into a lawsuit later known as "the Paris trial," with the French Association of Commerce and Industry trying to prove that cultured pearls were fakes. However, highly reputable scholars such as Professor H. Lyster Jameson of Oxford University and Professor Louis Boutan of Bordeaux University testified in support of the scientific view that "there is no fundamental difference between natural and cultured pearls in terms of their formation and structure." Consequently, in 1924 a French court of justice judged that "Cultured pearls do not differ from natural pearls at all." Through this process, cultured pearls were finally acknowledged as gems in world jewelry markets. Today, the term "pearls" generally refers to cultured pearls, and they are widely known and acknowledged as gems in the world's jewelry markets, within which the cultured pearl market pioneered and formed in Japan is a large part. It is worth noting that the cultured pearl industry was thus established in Japan and contributes to the world pearl industry.

Even today, over a century since the establishment of pearl culturing techniques, research continues, using various pearl oysters, on the water environment, health care for pearl oysters, culturing and affiliated techniques for nucleus insertion operations, larval production, and oyster breeding. Parallel studies in the field of life science using genetic research have recently made rapid progress. In pearl research, genome analysis is also making rapid progress (Shen and Morse, 1997; Kono et al., 2000; Zhang and Zhang, 2003; Wang et al., 2008, 2009), and there have been many significant studies in the field of biomineralization, such as the elucidation of the nacre-forming mechanism (Suzuki et al., 2009; Jackson et al., 2010; Joubert et al., 2010; Kinoshita et al., 2011; Fang et al., 2011; Gardner et al., 2011; Montagnani et al., 2011; Isowa et al., 2012; Marie et al., 2012; Wang et al., 2012). An important milestone was reached in 2012 when, in a world first, a group including the Okinawa Institute of Science and Technology Graduate University and others performed draft genome sequencing of the Japanese Akoya oyster (Takeuchi et al., 2012). Research on pearls is again entering a new era, and these types of basic research should contribute to the management of bioresources and the improvement of pearl culturing techniques, leading toward stable production of high quality pearls. Furthermore, this research will lead to developments in many fields beyond pearl culture, such as medical treatments, medicine, and industries closely related to the daily lives of people. Both the quality of human life and the quality of pearls as gems will be enriched.

### Studies of the causes of pearl formation

Scientific inquiries into the mysterious cause of pearl formation began in the mid 16th century when modern science started to emerge. Guillaume Rondeletius believed that pearls were morbid accumulations and in 1554 published the "disease causation theory" to explain their formation (Nishikawa, 1914). At about the same time, in his book entitled *Voyage to the South Sea in 1593*, Sir Richard Hawkins rejected the widely believed "dew causation theory" as absurd. Also, in *Historia del Mondo Nuovo* published in 1578, Urbain Chauveton described Girolamo Benzoni's

denial of the dew causation theory and proposed the “egg origin theory” to explain pearl formation, stating that “the most noble part of the eggs of the oyster” became the pearl (Kunz and Stevenson, 1908a).

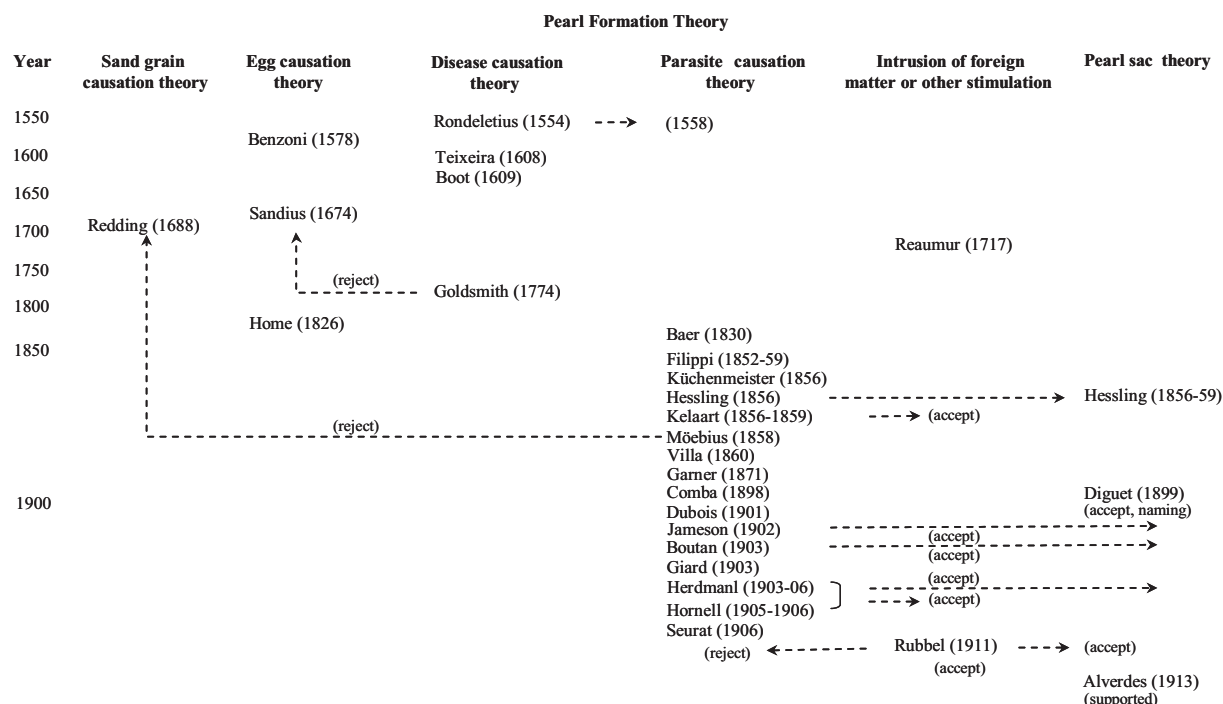
In *The Travels of Teixeira*, published at the beginning of the 17th century (1608), Pedro Teixeira described the pearl as consisting of the same substance as the mother oyster shell, and a product of disease. Around 1609, Anselmus de Boot pointed out in *Gemmarum et lapidum historia* the similarity of pearl and the inside of the shell, and he suggested that the pearl was formed by disease (Matsui, 1965a). In contrast, in his study of Norwegian freshwater mussels in 1674, Christopher Sandius stated that when egg-laden mussels release eggs, the egg residue in the body of the mussel becomes a pearl. In 1674, he also applied the “egg causation theory” to saltwater pearl oysters. Sir R. Redding stated that the cause of pearl formation was a sand granule intruding in the oyster body (Redding, 1688). In the 18th century, Rene Antoine Ferchault de Réaumur of France made an important contribution to the understanding of pearl formation (Réaumur, 1717). He suggested that a pearl is a lump of excreta of a pearly substance secreted in the oyster’s body, that it is homogeneous with the shell, and that the pearl is formed by excessive secretion of the pearly substance through the destruction of the organ that produces the shell, caused by the intrusion of foreign matter or some other stimulation. He also stated that a pearl is an abnormal product of the shell-forming substance and that it is made by a process whereby the covering substance (nacre) inside the shell accrues in concentric spherical layers (Kunz and Stevenson, 1908a; Matsui, 1965a, 1975; Fujita, 1923). Later, in 1774, Oliver Goldsmith rejected the egg causation

theory proposed by Sandius and others, and stated that pearls were a disease or an accident in the animal, because pearls occur more frequently in old and diseased shells (Kunz and Stevenson, 1908a).

Thus, between the 16th century and the beginning of the 18th, research into pearl and pearl-yielding oysters progressed and prior speculative ideas were rejected. Because many pearls were found in diseased oysters, and because pearls came from the mantle or gonad of oysters, and because pearl nuclei were observed, theories such as the disease causation theory, egg causation theory, and sand grain causation theory were proposed. These later became the subjects of study. Furthermore, the homogeneity of pearl and shell led to the idea that pearls were an abnormal product composed of the shell-forming substance.

From the 19th to the beginning of the 20th century, centered in Europe, various experiments were performed from a histological perspective to elucidate how pearls were made, including examinations of the nuclei that formed the center of the pearl, and the pearl oyster itself. As a result, there was considerable progress in the study of pearl formation, and the latter part of the 19th century saw many sequential important discoveries. Theories to explain pearl formation were proposed and variously accepted or rejected (Fig. 1). The primary animals used for research were the saltwater bivalves black lipped oyster, Akoya oyster, and common blue mussel (*Mytilus edulis*), and the freshwater mussels freshwater pearl mussel (*Margaritifera margaritifera*) and cockscomb mussel (*Cristaria plicata*).

In the middle of the 19th century, Theodor von Hessling of Germany decided that the pearl was a globular shell. Karl Möbius also stated that the nacreous structure of the pearl



**Fig. 1.** Outline of changes in theories of pearl formation and their acceptance or rejection. Authors’ names appear under the theories that they first supported. Arrows pointing to the left of an author’s name signify rejection of an earlier theory; arrows to the right indicate acceptance of a different theory.

was concentrically spherical. Moreover, he reported that its constituent substance matched the shell substance, merely having a different order of accumulation from that of the shell, and that the nacreous structure appeared with various combinations of three layers: conchin (conchiolin), a prismatic layer, and a nacreous layer (von Hessling, 1858; Möbius, 1858). Thus, by the middle of the 19th century, it was clear that the pearl had the same characteristics as the shell, that the nacreous layers formed in concentric spheres, and that, as in the shell, there were organic and prismatic layers together with nacreous layers.

Many researchers admitted that the constituents and structures of pearl and shell were the same. The most important discovery for the cause of pearl formation was the finding of the pearl sac, and of pearl formation within the sac. In 1856, von Hessling found through detailed histological observation that outside stimulation caused the epithelium of the mantle to intrude into the oyster body to form a cyst, and that within this cyst a pearl was formed (Matsui, 1950). Furthermore, in his study from 1858 to 1859, he suggested that pearl formation was caused by the presence of a foreign object intruding from outside the shell, or by excess conchin (conchiolin) left in the mantle; these granular substances would serve as nuclei, covered by secretions to form pearls (von Hessling, 1858, 1859).

The cyst that von Hessling found was later named "sac de la perle" by Leon Digue of France in 1899 (Matsui, 1958). It was also concluded that the same type of epithelial cells in the mantle that pearl oysters use to form the shell also coat the substance comprising the nucleus, and that the pearly substance secreted by these cells is the same as that produced to form the shell. In other words, the pearl was made in a sac comprised of the same types of cells as those of the mantle, cells that form the shell. Researchers subsequently realized that the pearl sac was deeply linked to pearl formation. However, the discussion focused on whether the epithelial cells comprising the pearl sac were derived from the mantle, or resulted from a change to the connective tissue.

Sir Everard Home of England often found small pearls in the gonads of oysters that had at their center a particle nearly the same size as an oyster egg, and in 1826 he concluded in his egg origin theory that pearls were formed around the nuclei of sterile, dead egg cells (Home, 1826). However, as many parasites were found in oysters from which pearls were harvested, scientists of the time thought that there was some cause of pearl formation by parasites. In 1830, D. E. von Baer discussed the relationship between pearls and parasites, and the disease causation theory attracted attention as the "parasite causation theory." Various parasites, such as Trematoda and Cercaria, were observed in both saltwater and freshwater bivalves, leading to the idea that parasites and their larvae and eggs played an important role as nuclei in pearl formation (Sasaki, 1896; Nishikawa, 1907). In the latter half of the 19th century, in particular, there was intense interest in research targeting the relationship between parasites and pearl formation.

Filippo de Filippi of Italy vigorously researched the freshwater mussel *Anodonta cygnea* from 1852 to 1859, finding a relationship between the trematode parasite *Distomum duplicatum* and pearls, concluding that parasites caused

pearl formation, and proposing a parasite origin theory (de Filippi, 1852, 1859). Later, he also pointed out the participation of parasites such as the water mite *Atax ypsilophorus*. The relationship between pearl and parasite was also suggested by Friedrich Küchenmeister, T. von Hessling, Karl Möbius, Edward Frederik Kelaart, and A. Villa (Küchenmeister, 1856; von Hessling, 1856; Möbius, 1858; Villa, 1860; Herdman, 1903; Shiplev and Hornell, 1904). Robert Garner later added his support to the parasite origin theory (Garner, 1872), and in 1898 Der Cavaliere Comba also held forth parasites as possible contributors to pearl formation in oysters. Furthermore, Raphael Dubois (Dubois, 1901), H. Lyster Jameson (Jameson, 1902), Louis Boutan (Boutan, 1903), and M. Alfred Giard (Giard, 1903) supported the idea of parasites as the cause of pearl formation. Moreover, on the basis of their research between 1901 and 1906, M. L. G. Seurat, W. A. Herdman, and J. Hornell stated that pearl formation was caused by parasites (Nishikawa, 1907; Dakin, 1913; Fujita, 1923; Ogushi, 1938; Matsui, 1958, 1965a).

Many researchers from the 19th to the 20th century likewise supported the parasite origin theory as explaining the cause of pearl formation. Thus, many academics concluded that the larva, egg, or remains of parasites such as trematodes and tapeworms prompted pearl formation. This was a firmly established theory.

However, there were some observations that were not explained by the parasite theory. In 1859, E. F. Kelaart found many parasites in pearl oysters from Sri Lanka (then Ceylon), and accepted a role for parasites in pearl formation. However, he also suggested that there were multiple causes of pearl formation, finding an egg inside a pearl taken from the gonad, and discovering that a minute silicic diatom test stimulated the mantle and became a pearl nucleus. At the same time, the egg origin theory and sand grain theory attracted much criticism (Kunz and Stevenson, 1908a). These studies, however, were obscured by the large volume of parasite origin studies, and did not draw attention.

In contrast, the pearl sac that T. von Hessling found in the middle of 19th century and that L. Digue identified as important in pearl formation received much attention at the beginning of the 20th century. In 1902, H. Lyster Jameson of England stated that a parasite could stimulate the formation of the pearl sac, that the pearl sac was derived from epithelial cells of the mantle, and that the epithelial cells in the pearl sac were in a distinct disease state (Jameson, 1902). In 1903, L. Boutan of France also lent his support to the parasite origin theory, stating that parasites were the cause of pearl formation (Boutan, 1903). However, in 1904, he concluded from experiments with *M. edulis* that when a parasite entered the space between mantle and shell, and subsequently moved into the recess in the cell layer of the mantle, it pulled in connective tissue of the mantle along with part of the mantle and died (Boutan, 1904). Ultimately, this material separated from the surface of the mantle and became free-floating, finally becoming enclosed by pearl-sac cells and forming a pearl. He described in detail the process of pearl-sac formation. Similarly, William A. Herdman and James Hornell conducted research in Sri Lanka from 1902 to 1906 and concluded that pearls were made by parasitic intrusion

into the connective tissue of the mantle; however they also reported occasions when foreign substances such as sand granules became the stimulus to nucleus formation (Herdman and Hornell, 1906). They also reported that tapeworm eggs often caused the formation of large, high-quality pearls that were important from a commercial viewpoint, although the proportion of eggs resulting in pearl formation was far lower than initially forecast. They also indicated that multiple substances could form nuclei, and they demonstrated two causes of pearl formation, one in which the pearl had a parasite nucleus, and another in which the pearl was produced not around a parasite but by stimulation of the epithelial cells of the mantle by a foreign substance. Herdman and Hornell indicated that the latter pearl was produced when the mantle enveloped a minute calcium particle onto which it deposited nacre. This pearl was always formed close to the outer layer of the mantle. Through these studies, it gradually became clear that not only parasites but also a variety of other substances caused pearl formation (Nishikawa, 1907; Kunz and Stevenson, 1908a; Dakin, 1913; Fujita, 1923; Ogushi, 1938; Isowa, 1956; Matsui, 1965a).

In the middle of this period, in 1911, A. Rubbel of Germany found many parasites in a shell, but judged them not to have caused pearl formation. He stated that a small piece of yellow-brown substance, similar to the outer layer of the shell, was the cause of pearl formation, and rejected the existing parasite theory. He described the pearl as being formed by a process whereby the shell fragment stimulated the epithelial cells of the mantle, after which some of the cells separated, and finally, as they surrounded the intruding substance, it moved little by little into the connective tissue of the mantle (Rubbel, 1911). In 1912, as the result of his research on pearls from the orient, H. L. Jameson also came to roughly the same conclusion as A. Rubbel (Jameson, 1912a, b). Thus, the leading research at the beginning of the 20th century suggested that it was not the nature of the substance that served as the nucleus that was important in causing pearl formation. Rather, it was that the epithelial cells of the mantle were stimulated by some outside object and that this became surrounded by the connective tissue of the mantle to form a pearl sac, in which the pearl formed.

In 1912 and 1913, Friedrich Alverdes of Germany succeeded in forming pearls experimentally by using *M. margaritifera*, and thus the theory gained support. He announced his results in the journal *Zoologischer Anzeiger*; specifically, that, for pearl formation, the important component is a pearl sac consisting of epithelial cells of the mantle; the intrusion of a foreign nucleus is not always needed (Alverdes, 1913a, b). A foreign nucleus occasionally aided pearl-sac formation. When a foreign substance such as a parasite egg invaded connective tissue and epithelial cells, it became a suitable substance around which epithelial cells could adhere and form a round pearl sac, by which nacre is secreted and a pearl formed. Suspecting that the pearl sac was formed by the invasion of outside foreign substances, he selected mantle epithelial cells derived from ectoderm tissue, inserted them into the hypodermal connective tissue, and succeeded in experimentally producing pearls and clarifying the cause of pearl formation (Isowa, 1956; Matsui, 1965a; Strack, 2006). Three hundred years after the suggestion by R. A. de Reaumur in 1717 that pearl formation was derived from a

change in the secretory condition of shell material from the mantle and a morbid change in some part of the mantle, the cause of pearl formation was finally clarified by multiple researchers, including T. von Hessling, L. Diguët, W. A. Herdman, A. Rubbel and F. Alverdes. It became clear that pearls were not caused by parasites or other foreign substances, but by a process whereby epithelial tissue of the mantle separated owing to some natural cause and intruded into the connective tissue of the mantle, forming a sac in which a pearl would form. Thus, in the beginning of the 20th century, studies in Europe into the causes of pearl formation elucidated this process. These studies included not only academic pursuits, but also many attempts toward industrialization.

### A history of pearl culturing attempts

From ancient times there has been a desire to make pearls by human action. In China, part of the dew theory widely believed in Europe was not accepted, and in the 5th century knowledge of pearl formation already existed (Joyce and Addison, 1993). It is clear that China has the oldest description of attempts at pearl culturing. In 1168, Wenchangzalu published a book that describes a method of producing hemispherical cultured pearls (cultured blisters) by using the cockscomb pearl mussel (*Cristaria plicata*); the method was first described in a 1082 publication. According to this publication, Yu-Shun Yang secretly produced shell-attached hemispherical cultured pearls by using freshwater cockscomb mussels that inhabited Lianghu Lake in Zhejiang Province. Later, in 1127, Hou-Tchen Fou studied the developments of Yang and succeeded in culturing original shell-attached Buddha pearls by inserting images of Buddha made from thin lead plates (Matsui, 1975). These pearls were sold as ornaments and charms, or as souvenirs with the shell attached. In 1735, an overview of Chinese cultured pearls was introduced throughout Europe in a fishery book published in France and England, and the culturing technique attracted worldwide attention. However this type of pearl production did not develop into a modern jewelry industry. In present-day China, both freshwater and saltwater pearls are cultured by using Akoya and similar oysters, but the production technique is based on techniques established in Japan.

Outside China, there were attempts to create pearls by hand throughout the world. In 1748, Swedish scientist Carl von Linnæus told Swiss scientist A. von Hallers that he could make a pearl by boring a hole through the shell of a freshwater mussel, inserting a small limestone bead into the space between shell and mantle by using a thin silver wire, and waiting five or six years. By 1761 there was evidence that he had performed experiments to produce pearls artificially by using this technique (Kunz and Stevenson, 1908b). From the 19th to the beginning of the 20th century, out of scientific curiosity or with the aim of industrialization, there were many attempts to make pearls in many parts of the world. A variety of techniques were tried as pearl-forming methods, such as the method of Linnæus for the formation of mainly hemispherical pearls, or pearl formation via parasite. In 1825, J. E. Gray announced that pearls could be made artificially by inserting a piece of nacre into the space between the shell and mantle. In 1838, J. Watzl tried to make

pearls in accordance with Gray's method by culturing *M. margaritifera*, boring a hole in the shell, and inserting an irregularly shaped pearl as a nucleus. This, however, did not succeed (Haas, 1931, 1933). In 1859, E. F. Kelaat of the Netherlands tried pearl culturing on the Sri Lanka side of the Gulf of Mannar (Kume, 1963), but the outcome of this venture is unknown. In 1884, Bouchon-Brandely conducted an experiment in the culture of hemispherical pearls in Tahiti (French Polynesia) by using black lipped oysters (Bouchon-Brandely, 1885). The experiment consisted of boring a hole about 0.5 inches in diameter in the shell, inserting a small nucleus such as a glass bead, closing the hole and keeping the oyster in the sea. He confirmed that nacre surrounded the small bead nucleus. In 1896–1898 in Iowa, USA, Vane Simmonds reportedly conducted an experiment with freshwater mussels, inserting a small bead made of wax, or some other small particle covered with nacre, into the gap between mantle and shell, and got an acceptable result to operate the shell with appropriate anesthetic chemicals (Kunz and Stevenson, 1908b). L. Boutan of France reported in 1898 at the meeting of the Science Academy in Paris that a pearl could be made by boring a hole in an abalone shell, inserting a small bead between the shell and the mantle, and closing the hole (Boutan, 1898). Furthermore, in 1904, he succeeded in culturing hemispherical pearls with this method using abalone inhabiting Dover Strait. In 1908–1909, Chmielewski tried to produce hemispherical pearls with shell using freshwater mussels. Later he reportedly made free pearls, but the method was never clarified (Haas, 1931, 1933). In 1913, C. L. Edward of the USA also succeeded in producing hemispherical pearls experimentally by using green abalone (*Halotis fulgens*) and disc abalone (*Halotis discus*) and the same method as L. Boutan (Kume, 1963).

There were also attempts to make free pearls via parasites. L. Dubois, who from 1903 subscribed to the parasite origin theory, tried to produce pearls by transplanting parasites from mussels inhabiting the English Channel into pearl oysters (Akoya) in Sri Lanka. D. C. Comba also appears to have conducted the same experiment, but there was no subsequent report; neither seems to have succeeded (Nishikawa, 1907). As for entrepreneurial activity, F. Nicholson and J. Hornell set up a commercial venture in Sri Lanka in 1906. They tried to culture pearls using Akoya oysters at Krusadai Island, in the Gulf of Mannar. However, the attempt failed and the business dissolved. Saville-Kent conducted an experiment to culture pearls in the Torres Strait between Australia and New Guinea and elsewhere in Australia. From 1890 to 1893, he succeeded in making hemispherical pearls. Although he set up the Natural Pearl Shell Cultivation Co., Ltd., in 1906 with a plan to culture pearls, he died in 1908 and the enterprise ended. Saville-Kent's method of forming pearls is unclear due to the paucity of material describing his plans. During the same period (1909), James Clark established the Pilot Cultivation Co. in Australia to culture silver lipped and black lipped oysters for purposes of breeding, but his work ended in failure (Dakin, 1913). Gaston J. Vives set up a company, Compañía Criadora de Concha y Perla, near La Paz in Baja California, Mexico, and by 1909 he had invested heavily for trials in breeding and pearl culturing of Panamic black lipped oysters

(*Pinctada mazatlanica*) and abalone (Kunz and Stevenson, 1908b). This business, however, did not succeed. Around 1905, Alvin Seale tried to culture pearl oysters and pearls by using silver lipped oysters inhabiting the Sulu Archipelago (Jolo Island, Philippines). In 1906, Thomas Haynes established Monte Bello Pearls Co. in Monte Bello Island, Western Australia, and tried to culture pearl oysters using Shark Bay pearl oysters (*Pinctada albina*); this venture also ended in failure. Around 1909, John I. Solomon of the USA set up the India Pearl Co. to culture hemispherical pearls using silver lipped oysters inhabiting the Mergui Islands (Myanmar/Burma) (Dakin, 1913). For the years 1911 and 1912 he had success, and sold silver lipped hemispherical cultured pearls in London and New York. However, this business was discontinued after 1912. In Sri Lanka, too, businesses culturing pearls by means of parasites were started, but there are no subsequent reports (Kume, 1963).

Attempts at pearl culturing from the end of the 19th to the beginning of the 20th century were conducted not only on the level of scientific experiments, but also as business enterprises around the world. Although these attempts reported experimental or short-term successes, none developed into an industry for culturing pearls for jewelry. On the other hand, research in Japan proceeded in secret beginning at the end of the 19th century, and full-scale experiments toward commercialized cultured pearl production had already started.

#### Development of the pearl-culturing industry in Japan

Throughout history in Japan, natural pearls were gathered from Akoya oysters and abalone and were prized as things of value. At the beginning of the Meiji era, natural pearls were especially valued and were traded for high prices among marine products exported overseas. As a result, overfishing for pearls led to a decrease in the number of Akoya oysters, and consequently the quantity of natural pearls also decreased. Ago Bay, with its famously beautiful Rias coast, located in the Ise-Shima area of Mie Prefecture, also suffered from dangerously sharp decreases in the abundance of Akoya oysters because of reckless overfishing, and the catch of natural pearls declined drastically. Kokichi Mikimoto, who dealt in natural pearls, started his experiments to culture Akoya oysters on 11 September 1888 in the vicinity of Shinmeiura Benten Island, Ago Bay, aiming to increase oyster populations. In 1890, he was introduced to Professor Kakichi Mitsukuri of Tokyo Imperial University by Narayoshi Yanagi, Secretary General of the Japan Fisheries Association. Later, Mikimoto visited the Misaki Marine Biological Station of The University of Tokyo and in one week received comprehensive instruction from Professor Mitsukuri as to the theory of pearl formation, including the state of research on pearl formation in Europe, examples of pearl culturing, and the results of research. Professor Mitsukuri particularly impressed upon Mikimoto the theory of T. von Hessling regarding the importance of the pearl sac to pearl formation (Ototake, 1976). With advice from Dr. Kenkichi Kishinoue, the joint research by Mikimoto and Mitsukuri opened a path forward to a pearl culturing industry by both the development of techniques for the establishment of industrial culturing, and academic research. Mikimoto became convinced of the possibility of making pearls by

hand following the instructions from Dr. Mitsukuri, and immediately in 1890, the year following their meeting, he began experimental pearl culture in innermost Ago Bay.

From the beginning, Mikimoto attempted to culture spherical pearls. He tried to insert foreign material into the oyster body to stimulate pearl-sac formation. He conducted continuous trial-and-error experiments to determine the best kind of foreign substance and point of insertion. In July 1892, Dr. Chujiro Sasaki of Tokyo Imperial University visited the pearl farm and offered many suggestions. Unfortunately, in November 1892 all of the experimental Akoya oysters in Ago Bay died in a red tide. However, hemispherical pearls were found serendipitously at another experimental site on Ojima in Toba Bay (Japan). Mikimoto therefore established a technique and acquired a patent (Japan Patent Office, No. 2670: "Method of pearl formation"). For the formation of hemispherical pearls with shell, the insertion location was between mantle and shell. Seizing upon this result he aimed for full-scale industrialization. He opened pearl culturing farms on Tatoku Island in Ago Bay on 26 October 1893 to advance the techniques for producing pearls, and succeeded at the industrialization of hemispherical pearl culturing. With the hemispherical pearl culturing enterprise heading in the right direction, and with improvements in culturing techniques, the consequent mass culturing of Akoya oysters became possible. However, he continued his research to achieve his original dream of producing spherical pearls.

Meanwhile, at the Misaki Marine Biological Station in Kanagawa Prefecture, Tokichi Nishikawa, a disciple of Dr. Mitsukuri, began vigorous research on pearl culturing techniques from an academic perspective. When red tides occurred at the Mikimoto pearl farm, he often visited Tatoku Island in Mie Prefecture to investigate. In 1903, he married the second daughter of Kokichi Mikimoto. With his interest in pearl culturing, Nishikawa conducted his research at Misaki Marine Biological Station and Mikimoto Pearl Research Laboratory, under the guidance of Dr. Kakichi Mitsukuri and Dr. Isao Iijima. Beginning in April 1906, Nishikawa conducted his own research and developed a pearl forming method to make pearl sacs by cutting away a part of the mantle that secretes the nacreous substance and inserting that tissue alone or with a nucleus. In October 1907, he applied a series of his research results to obtain patents, which were granted in 1916 and 1917 (Nos. 29630 and 30771: "Method of pearl formation"). He continued research at the pearl farm that he himself had opened at Awaji Island, Hyogo Prefecture, and at Misaki Marine Biological Station.

During this period (1902), Mikimoto invited former dentist Otokichi Kuwabara to join him, and they undertook the development of a technique for culturing spherical pearls. Kuwabara modified dental tools for use in the nucleus insertion operation. For example, the shell opening tool that was modified from the dental instrument known as "clamp forceps" is still used today for nucleus insertion operations. In 1903 (Meiji Year 36), the pearl culturing industry became so widespread as to occupy 1,130,000 *tsubo* (about 373 km<sup>2</sup>) of sea area. The number of breeding oysters reached over 1 million in 1905. However, in 1905 a red tide occurred at Ago Bay from 10 January into March, and 850,000 oysters for culturing pearls (four-fifths of the total

number of oysters) died. Nevertheless, spherical (free) pearls were unexpectedly found among the surviving oysters that had been operated on that same year, and using them as proof of their success, the patent for the "Meiji method" (Method 38) was applied for in 1907 and granted in 1908 (No. 13673: "Method of pearl formation"). Unfortunately, the yield from this method was too low for industrialization.

Additional technical research on spherical pearl formation at the laboratory of Mikimoto pearl farm was conducted, with Kuwabara as the lead investigator. From a patent granted in 1914 for the "Taisho method" (No. 29409: "Method of pearl formation"), a patent for the "wrapping method" was applied for in 1918 and granted in 1919 (No. 33640: "Grafting of coated nucleus under epidermis"). This method involved inserting a round shell bead, completely wrapped in mantle tissue and of a fixed shape, into the gap between the retractor muscle and digestive diverticula of a living oyster. In 1918 many good quality pearls produced by this method were harvested. They were first sold in 1919, on the London market. At first, the wrapping method was considered suspect due to technical difficulties. However, a survey report in 1926 by the Imperial Association for the Encouragement of Inventions mentions an ingenious micro-technique used in a study by Professors Chujiro Sasaki, Kamakichi Kishinouye, and Seitaro Goto of Tokyo Imperial University (Sakatani, 1926). During this period, many instruments, such as the bead nucleus insertion tool, were designed.

Mr. Kokichi Mikimoto signed an agreement with Professor Nishikawa to perform experiments at the Tatoku Research Laboratory of Mikimoto to confirm the Nishikawa's hypothesis that was a pearl forming method to form pearl sac in the oyster body by a small piece of mantle. Experiments were conducted for about three months beginning in September 1907, and about 27,000 oysters were operated on. In order to keep this research secret, the Pearl Research Laboratory was moved in February 1907 from Tatoku Island to Osaki (the present location of the Mikimoto Pearl Research Laboratory), on the opposite side of Western Tatoku Island. Unfortunately, Nishikawa died in 1909 at age 35 without achieving his ambition, although he conducted a great many experiments. In August 1913, at the first interim survey to monitor the progress of cultured pearl production, sample pearls were harvested in the presence of Dr. Isao Iijima, Sukeyo Fujita, Masayo Fujita, Shinjuro Nishikawa, and Otokichi Kuwabara. The pearls harvested at the research farm were true spherical pearls created by hand, and a fair number were collected. However, the results in terms of pearl size, yield, and quality were not satisfactory. Subsequently, the principles of culturing techniques were improved and spread by Dr. Masayo Fujita, a disciple of Nishikawa; they are widely used in present-day pearl culturing in a technique known as the "piece method". Nishikawa's technique spread to foreign countries, and patents were granted to his son Shinkichi Nishikawa in Australia and other places (No. 13959 [1914]: "Artificial method of enforcing the formation of free pearls of regular form by pearl producing mollusca").

Separately from Nishikawa and his coworkers, Tatsuhei Mise advanced his research on pearl formation technique as well. In 1907, the same year as Nishikawa's patent application, Mise, from Matoya Village in Mie Prefecture, also



applied for his patent for spherical pearl formation, whereby cells of mantle tissue were placed into connective tissue of the mantle (No. 12598: "Needle to insert a nucleus into mantle tissue of an oyster"). His technique was to inject a tiny silver nucleus into the mantle of an Akoya oyster by using an injection needle. With this and subsequent developments, Mise applied for a patent on his "inducing method" in 1917; it was granted in 1920 (No. 37746: "Formation of free pearls").

The pearl formation technique of both Nishikawa and Mise is to create a pearl sac in the oyster body by inserting a small piece or fragment of mantle. However, in 1978, C. Denis George insisted in his review paper "Debunking a Widely Held Japan Myth – Historical aspects on the early discovery of the pearl cultivating technique", published in *The International Pearling Journal*, that William Saville-Kent in Australia had already established the technique developed by Nishikawa and Mise, and that they got their idea from his technique (George, 1978; Harrison, 2005; Taylor and Strack, 2008).

There is, however, no detailed technical record of spherical pearl culturing, so it is difficult to say that Saville-Kent clearly reported the establishment of spherical pearl production. Previously established facts from research in Europe provided hints that were available to all investigators. At one time, it was rumored in Europe that the technique of Alverdes, who demonstrated a method for the formation of free (spherical) pearls, led to success in production of spherical pearls at the Mikimoto Pearl Farm. However, this rumor has been shown to be untrue (Strack, 2006). As mentioned earlier, by this time in Europe, research had already shown how the pearl sac is formed, following its discovery by von Hessling. In 1899, L. Diguët described the pearl sac as being formed from epithelial cells of the mantle. In Europe, debate as to the cause of pearl formation focused on parasites until the beginning of the 20th Century. By the time of Rubbel's announcement of a pearl formation theory in 1911, and the experimental proof by Alverdes in 1913, the main focus of industrialization of man-made pearl production was hemispherical pearls or spherical pearls via parasite infection. In Japan, however, it was difficult to find a relationship between parasites, such as trematodes and tapeworms, and pearl formation in the Akoya oyster, except with shell-boring parasites such as *Polydora* spp. However, at Tokyo Imperial University, building upon the results of von Hessling's research (namely, by emphasizing research on sac formation), the importance of knowing how to stimulate the formation of a pearl sac in an oyster body was already understood. Then, together with the work of Mikimoto, and ahead of the rest of the world, research advanced beyond that of the extant pearl culturing industry.

In addition to sophisticated technical skill in experiments by the Japanese, directed not only toward the pearl forming principle but also with the aim of improving technique so as to elevate pearl quality to that of gems, the Akoya oyster also had many advantages for pearl culture. Compared with the molluscs used in European research, such as the salt-water *Mytilus* and the freshwater *M. margaritifera*, the Akoya oyster played a large role in the establishment of the pearl industry thanks to its suitability as an experimental subject and its exceptional pearl production.

Leading the rest of the world, Mikimoto and others raised culture techniques to a higher level, succeeded in the industrialization of spherical cultured pearls, exploited a new jewelry market, and achieved great success in industrialization. According to the first official statistics in 1926, there were 33 cultivators and 669,000 pearl oysters. Ten years later in 1936, the number of cultivators had increased to 258 and the number of pearl oysters to 7,071,000. In the next year, 1937, the number of cultivators was still 258, whereas the number of pearl oysters reached 10,858,000. Thus, with oyster numbers exceeding 10 million, both the number of cultivators and of pearl oysters had increased explosively in just over 10 years. In addition to the establishment of a technical base for the nucleus insertion operation, there was also an accumulation of oyster management techniques, and an original pearl culturing industry was established in Japan.

#### Development of pearl culturing techniques in Japan

By applying the understanding of processes learned from the accidental formation of natural pearls, a powerful production technique for creating gem-quality pearls was developed in Japan (Cahn, 1949; Isowa, 1956). Spherical-pearl producing techniques were perfected, allowing the spread of cultured pearls. Furthermore, techniques to enhance pearl quality to gem level were energetically promoted by many people. Together with improvements in technique for the nucleus insertion operation, such as techniques for producing large pearls through the ova extraction method and the improvement of surgical tools, techniques for culture management such as shell cleaning and winterizing also progressed rapidly. Thus, the basic system of pearl culturing techniques was nearly complete by around 1930 (Matsui, 1965b). From then on there were various technical improvements, such as improvements to the nucleus insertion operation (Aoki, 1957, 1959a, b, 1961; Kawakami, 1953; Machii and Nakahara, 1957; Machii, 1959), improvements in pearl quality and yield by preparation of the oyster before and recuperation after the operation (Uemoto, 1961, 1962; Hasuo, 1966, 1967), and improvements in culture management such as shell cleaning (Miyamura and Makido, 1958; Wada, 1961, 1962, 1969a, 1972; Mizumoto, 1964). In addition to these advancements, other improvements were made, such as the development of oyster breeding techniques by natural spawning, as well as hatchery breeding to maintain a stable oyster supply (Kuwatani, 1965). The quality of the pearl oyster was also improved via hatchery breeding, for example to control the pigment of mantle donor cells, such as the yellow pigments specific to the pearl oyster (Wada, 1969b; Wada K. T., 1984, 1985, 1986). Genetic and hereditary approaches are expected to make large contributions in the future development of technologies for improvements in pearl quality and yield.

It is important to maintain a perspective that accounts for the natural environment and for oyster resources. In particular, rapid increases in demand for oysters and deterioration of the natural environment result in oyster death and reductions in pearl yield, with consequent lower productivity. Decreases in specific oyster resources and oyster death through red tide or disease (Matsuyama et al., 1995;

Sorimachi, 2000; Nagai, 2008) are related problems in world industry, based on the natural environment and bioresources. An understanding of living things from a genetic viewpoint becomes more and more important. In the past, for example in the 19th century, the pursuit of scarce natural pearls led to overfishing of natural pearl oysters, which yield very few pearls, and to a collapse of oyster resources worldwide. The establishment of the pearl culturing industry has resulted in both expansion of oyster resources and rapid progress in improving the pearl yield ratio, greatly contributing to the protection of oyster resources. However, natural oyster resources are again decreasing in coastal areas due to environmental pollution. Furthermore, the various problems associated with the transplantation of foreign oysters, and decreases in genetic diversity because of hatchery breeding, will make genetic management increasingly important in the future.

### REFERENCES

- Alverdes F (1913a) Über Perlen und Perlbildung. Zeitschrift für Wissenschaftliche Zoologie 105: 598–633
- Alverdes F (1913b) Versuche über die künstliche Erzeugung von Mantelperlen bei Süßwassermuscheln. Zoologischer Anzeiger 42: 441–459
- Aoki S (1957) Some experiments on the nuclear insertion in the pearl culture of the pearl oyster (*Pinctada martensii*). 1. Formation of the pearl-sac and pearl when the inserted nucleus was placed in contact with the retractor muscle of the gonad. Bulletin of the National Pearl Research Laboratory 2: 113–118 (in Japanese with English summary)
- Aoki S (1959a) Some experiments on the nuclear insertion in the pearl-culture of the pearl oyster (*Pinctada martensii*). 3. Formation of the pearl-sac and the pearl when the pieces from three different parts of the mantle were inserted. Bulletin of the National Pearl Research Laboratory 5: 503–515 (in Japanese with English summary)
- Aoki S (1959b) Some experiments on the nuclear insertion in the pearl culture of the pearl oyster (*Pinctada martensii*). 4. On the quality and shape of the cultured pearl in relation to the site of the pearl formation. Bulletin of the National Pearl Research Laboratory 5: 516–540 (in Japanese with English summary)
- Aoki S (1961) Some experiments on the nuclear insertion in the pearl-culture of the pearl oyster (*Pinctada martensii*). 5. Pearl-sac formation in the material with a space between the inserted nucleous and adjacent tissues. Bulletin of the National Pearl Research Laboratory 6: 647–656 (in Japanese with English summary)
- Bouchon-Brandely G (1885) Sur La Pêche et la Culture des Huîtres Perlières à Tahiti; Pêcheries de l'Archipel Tuamotu. Imprimerie du Journal Officiel, Paris, 31, 4–73
- Boutan L (1898) Production artificielle des perles chez les Haliotis. Comptes Rendus de l'Académie des Sciences, Paris, 77
- Boutan L (1903) L'Origine réelle des perles fines. Comptes Rendus de l'Académie des Sciences, Paris, 137, 1073–1075
- Boutan L (1904) Les perles fines. Leur origine réelle. Arch Zool Exper 4 2: 47–90
- Cahn AR (1949) Pearl Culture in Japan. General Headquarters Super Commander for the Allied Powers, Natural Resources Section, Report Number 122, 10–19
- Dakin WJ (1913) The Origin of Pearls, Pearls. Cambridge at the University Press., London, pp 91–116
- de Filippi F (1852) Sull' origine delle perle. Il Cimento rivista di Scienza, Lettere, ed Arti, (Torino, 1852), 1, 429–439
- de Filippi F (1859) Troisième mémoire pour servir à l'histoire génétique des Trématodes. Memorie della Reale Accademia delle Scienze di Torino, Torino, 18, 201–232
- Dubois R (1901) Sur le mécanisme de la formation des perles fines dans le *Mytilus edulis*. Comptes Rendus de l'Académie des Sciences, Paris, 133, 603–605
- Fang D, Xu G, Hu Y, Pan C, Xie L, Zhang R (2011) Identification of Genes Directly Involved in Shell Formation and Their Functions in Pearl Oyster, *Pinctada fucata*. PLoS ONE 6: 1–13
- Fujita M (1923) Study of The Pearl Culture Industry. Rakusuikai, Tokyo, pp 1–34 (in Japanese)
- Gardner LD, Mills D, Wiegand A, Leavesley D, Elizur A (2011) Spatial analysis of biomineralization associated gene expression from the mantle organ of the pearl oyster *Pinctada maxima*. BMC Genomics 12: 455–469
- Garner R (1872) Notes on Anatomy and Pearls of *Alasmodon margaritifera*. P Zool Soc Lond 9: 426–428
- George Denis C (1978) Debunking a Widely Held Japan Myth –Historical aspects on the early discovery of the pearl cultivating technique. The International Pearling Journal
- Giard MA (1903) L'épithélium sécrétoire des perles. Comptes Rendus de la Société de Biologie, séance du 29 decembre, Paris, 55, 1222–1225
- Haas F (1931,1933) Die Perlen. Akademische Verlagsgesellschaft m.b.H., Leipzig, (Translation; Hayashi K, Jinnou Press, Shiga, 1972), pp 87–97
- Harrison J (2005) Saville-Kent, William (1845–1908), Australian Dictionary of Biography, Supplementary Volume, Melbourne University Press, pp 352–353
- Hasuo M (1966) On the relation between change of physiological condition and appearance of the gonad in so called "Shitate" (control of physiological condition of the pearl oyster *Pinctada martensii* for the operation). Bulletin of the National Pearl Research Laboratory 11: 1334–1347 (in Japanese)
- Hasuo M (1967) The influence on the qualities of cultured pearls caused by difference of the activity control period in so called "Shitate" (control of physiological condition of the pearl oyster for the operation). Bulletin of the National Pearl Research Laboratory 12: 1432–1444 (in Japanese)
- Herdman WA (1903) Report on the Pearl Oyster Fisheries of the Gulf of Manaar. Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar by W. A. Herdman, Colonial Government by The Royal Society, London, pp 1–16
- Herdman WA, Hornell J (1906) Pearl Production. Ceylon Pearl Oyster Fisheries and Marine Biology Report on the Pearl Oyster Fisheries of the Gulf of Manaar, 5, 1–42
- Home E (1826) On the Production and Formation of Pearls. Philos Trans R Soc London 156: 338–341
- Isowa K (1956) Historical view of the pearl formation studies. Bulletin of the National Pearl Research Laboratory 1: 47–56 (in Japanese)
- Isowa Y, Sarashina I, Setiamarga DHE, Endo K (2012) A Comparative Study of the Shell Matrix Protein Aspein in Pteroid Bivalves. J Mol Evol 75: 11–18
- Jackson DJ, McDougall C, Woodcroft B, Moase P, Rose RA, Kube M (2010) Parallel Evolution of Nacre Building Gene Sets in Mollusc. Mol Biol Evol 27: 591–608
- Jameson HL (1902) On the Origin of Pearls. Proceedings of the Zoological Society of London for 1902, London, 1, 140–166
- Jameson HL (1912a) Studies on Pearl-Oysters and Pearls. The Structure of the Shell and Pearls of the Ceylon Pearl Oyster *Margaritifera vulgaris* Schumacher): with an Examination of the Cestode Theory of Pearl-Production. Proceedings of the Zoological Society of London, London, 260–358
- Jameson HL (1912b) An Examination of the Causes, which have led to the Failure of the Biological work recently undertaken on the Ceylon Pearl Fisheries. Journal of Economic Biology, London, 7, 10–22
- Joyce K, Addison S (1993) Pearls: Ornament and Obsession.

- Simon & Schuster, p 54
- Joubert C, Piquemal D, Marie B, Manchon L, Pierrat F, Zanella-Cléon I, et al. (2010) Transcriptome and proteome analysis of *Pinctada margaritifera* calcifying mantle and shell: focus on biomineralization. *BMC Genomics* 11: 613–625
- Kawakami IK (1953) Studies on pearl-sac formation. The effect of water temperature and freshness of transplant on pearl-sac formation. *Annot Zool Japon* 26: 217–223
- Kinoshita S, Wang N, Inoue H, Maeyama K, Okamoto K, Nagai K, et al. (2011) Deep sequencing of ESTs from nacreous and prismatic layer producing tissues and a screen for novel shell formation-related genes in the pearl oyster. *PLoS ONE* 6: 1–19
- Kono M, Hayashi N, Samata T (2000) Molecular mechanism of the nacreous layer formation in *Pinctada maxima*. *Biochem Biophys Res Commun* 269: 213–218
- Küchenmeister F (1856) Über eine der häufigsten Ursachen der Elsterperlen und das Verfahren, Welches zur Künstlichen Vermehrung der Perlen dem Königl. -Sächsischen Ministerium der Finanzen vorgeschlagen wurde. *Müller's Archiv für Anatomie, Physiologie. und wissenschaftliche. Medicin, Berlin*, pp 269–281
- Kume T (1963) *Gemology*. Kazama Shobo, Tokyo, pp 625–644 (in Japanese)
- Kunz GF, Stevenson CH (1908a) *Origin of Pearl, The Book of The Pearl*. New York The Century Co., New York, pp 35–47
- Kunz GF, Stevenson CH (1908b) *Pearl-Culture and Pearl-Farming, The Book of The Pearl*. New York The Century Co., New York, pp 285–298
- Kuwatani Y (1965) Studies on the breeding of the Japanese pearl oyster, *Pinctada martensii* (Dunker), I. Change in the maturation of the eggs obtained from the excised gonads during the spawning season. *Bulletin of the National Pearl Research Laboratory* 10: 1228–1243 (in Japanese with English summary)
- Machii A (1959) Studies on the histology of the pearl-sac. 4. On the pearl-sac tissue of so-called “kokuhan” pearls (black spotted pearls). *Bulletin of the National Pearl Research Laboratory* 5: 407–410 (in Japanese with English summary)
- Machii A, Nakahara H (1957) Studies on the histology of the pearl-sac, 2. On the speed of the pearl-sac formation different by season. *Bulletin of the National Pearl Research Laboratory* 2: 107–112 (in Japanese with English summary)
- Marie B, Joubert C, Belliard C, Tayale A, Zanella-Cléon I, Marin F, et al. (2012) Characterization of MRNP34, a novel methionine-rich nacre protein from the pearl oysters. *Amino Acids* 42: 2009–2017
- Matsui Y (1950) On the formation of pearls in the pearl oyster. *Venus* 16: 1–4 (in Japanese)
- Matsui Y (1958) On the Formation Theories of Pearl. *B Jpn Soc Sci Fish* 24: 402–406 (in Japanese with English abstract)
- Matsui Y (1965a) Formation of Pearl. *Shinju no Jiten.*, Hokuryukan, Tokyo, pp 247–285 (in Japanese)
- Matsui Y (1965b) Technique of Pearl Culture – History of Pearl Culture. *Shinju no Jiten*, Hokuryukan, Tokyo, pp 437–455 (in Japanese)
- Matsui Y (1975) On the origin of pearl-culture and the history of it in Japan. *Memoirs of the Faculty of Agriculture of Kinki University* 8: 1–6
- Matsuyama Y, Nagai K, Mizuguchi T, Fujiwara M, Ishimura M, Yamaguchi M, et al. (1995) Ecological features and mass mortality of pearl oysters during red tides of *Heterocapsa* sp. in Ago Bay in 1992. *Nippon Suisan Gakkaishi* 61: 35–41 (in Japanese with English abstract)
- Miyamura M, Makido T (1958) Quality of the pearl examined in association with the graft tissues taken from various parts of mantle. *B Jpn Soc Sci Fish* 24: 441–444
- Mizumoto S (1964) Studies on disease of the shells of the pearl oyster (*Pinctada martensii*). On the species of parasitic polychates in shells, the condition of the damages and the extirpation technique. *Bulletin of the National Pearl Research Laboratory* 9: 1143–1155 (in Japanese)
- Möbius K (1858) Die echten Perlen. Ein Beitrag zur Luxus-, Handels- und Naturgeschichte. *Abhandl. Naturw. Verein, Hamburg* 4: 1–83
- Montagnani C, Marie B, Marin F, Belliard C, Riquet F, Tayalé A, et al. (2011) Pmarg-pearlin is a matrix protein involved in nacre framework formation in the pearl oyster *Pinctada margaritifera*. *ChemBioChem* 12: 2033–2043
- Nagai K (2008) Akoyasinju no genten wo motomete. Research on means of alleviating damage by *Heterocapsa circularisquama* red tides and Reddening adductor disease, causes of the mass mortality of Japanese pearl oysters (*Pinctada fucata martensii*). *Sinju sinbunsha, Tokyo* (in Japanese with English summary and Conclusions)
- Nishikawa T (1904a) *Shinju*. *Doubutugaku zassi* 15: 51–67 (in Japanese)
- Nishikawa T (1904b) *Shinju* (Zengou no tuduki). *Doubutugaku zassi* 15: 129–140 (in Japanese)
- Nishikawa T (1904c) *Shinju* (Zenkaï no tuzuki). *Doubutugaku zassi* 15: 203–214 (in Japanese)
- Nishikawa T (1907) Ikko no kaiyori shouzuru shinju no kazu. *Doubutugaku zassi* 19: 42–57 (in Japanese)
- Nishikawa T (1914) *Shinju*. ed. Nishikawa S., Tokyo, p 77 (in Japanese)
- Ogushi J (1938) *Shinju no Kenkyu*. Itoubunshindo, Tokyo, pp 123–134 (in Japanese)
- Otake H (1976) Historical Development of Cultured Pearl Industry in Japan. 2, *Houseki gakkaiishi* 3: 114–116 (in Japanese)
- Réaumur RAFd (1717) Observations sur le coquillage appelé Pinne marine ou Nacre de perle, à l'occasion duquel on explique la formation des perles. *Mémoires de l'Académie des Sciences, Paris*, pp 177–194
- Redding Rs (1688) Structure, Color, etc., of Irish pearls. *Philos Trans R Soc Lond* 18: 659
- Rubel A (1911) Über Perlen und Perlbildung bei *Margaritana margaritifera* nebst Beiträgen zur Kenntnis ihrer Schalenstruktur. *Zoologische Jahrbücher, Abteilung für Anatomie, Marburg* 32: 287–366
- Sakatani Y (1926) Report on the Study of the Mikimoto Cultured Pearl. Imperial Association for the Encouragement of Inventions, pp 1–8 (in Japanese)
- Sasaki C (1896) *Sinju chousahoukoku* 1. *Sinjugaisinju*. Suisan-chousahoukoku, The ministry of Agriculture and Commerce fisheries Station. Shuueisha, Tokyo, 4, 1–9 (in Japanese)
- Shen X, Morse DE (1997) Molecular Cloning and Characterization of Lustrin A, a Matrix Protein from Shell and Pearl Nacre of *Haliothis rufescens*. *J Biol Chem* 272: 32472–32481
- Shiplew AE, Hornell J (1904) The Parasites of the Pearl Oyster. Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar. Note on Pearl formation in the Ceylon pearl Oyster. by W. A. Herdman 2 Colonial Government by The Royal Society, London, pp 77–106
- Sorimachi M (2000) Mass mortalities of Japanese pearl oyster *Pinctada fucata martensii*. *Aquabiology* 22: 39–44 (in Japanese with English abstract)
- Strack E (2006) Pearls. Early Beginnings, Rühle-Diebener-Verlag, Stuttgart (Original Edition 2001 “Perlen”), pp 311–313
- Suzuki M, Saruwatari K, Kogure T, Yamamoto Y, Nishimura T, Kato T, Nagasawa H (2009) An Acidic Matrix Protein, Pif, is a Key Macromolecule for Nacre Formation. *Science Express* (online) 325(5946): 1388–1390
- Takeuchi T, Kawashima T, Koyanagi R, Gyoja F, Tanaka M, Ikuta T, et al. (2012) Draft Genome of the Pearl Oyster *Pinctada fucata*. A Platform for Understanding Bivalve Biology. *DNA Res* 19: 117–130

- Taylor J, Strack E (2008) Pearl Production, The Pearl Oyster, eds. Southgate PC and Lucas J, pp 273–301
- Uemoto H (1961) Physiological studies on the nuclear insertion operation of pearl oyster 1–3. Bulletin of the National Pearl Research Laboratory 6: 619–635 (in Japanese with English summary)
- Uemoto H (1962) Physiological studies on the nuclear insertion operation of pearl oyster 4. On the control of physiological condition after the operation. Bulletin of the National Pearl Research Laboratory 8: 896–903 (in Japanese with English summary)
- Villa A (1860) Sull'origine delle perle et sulla possibilità di Produrle artificialmente. Politecnico Fascicle 48: 19
- von Hessling T (1856) Über die Erzeugung künstlicher Perlen, Münchener gelehrte Anzeigen, 2, 105–172
- von Hessling T (1858) Ueber die Ursachen der Perlbildung bei Unio margaritifera. Siebold und Kölliker, Zeitschrift für Wissenschaftliche Zoologie, Leipzig, 9, 543–546
- von Hessling T (1859) Die perlmuscheln und ihre perlen. verlag von wilhelm engelmann, Leipzig
- Wada K (1961) The influence of the life-activity upon pearl formation in the pearl culture of *Pinctada martensii* (Dunker). 2. The seasonal changes of crystal growth and luster of the pearl. Bulletin of the National Pearl Research Laboratory 6: 586–606 (in Japanese with English summary)
- Wada K (1962) Biomineralogical studies on the mechanism of pearl formation. Bulletin of the National Pearl Research Laboratory 8: 948–1059 (in Japanese with English abstract)
- Wada K (1969a) Relation between growth of pearls and water temperature. Bulletin of the Japanese Society of Fisheries Oceanography (Prof. Uda's Commemorative Papers), 299–301
- Wada K (1969b) Experimental biological studies on the occurrence of yellow color in pearls. Bulletin of the National Pearl Research Laboratory 14: 1765–1820 (in Japanese with English summary)
- Wada K (1972) Relation between calcium metabolism of pearl sac and pearl quality. Bulletin of the National Pearl Research Laboratory 16: 1949–2027 (in Japanese with English summary)
- Wada KT (1984) Breeding study of the pearl oyster, *Pinctada fucata*. Bulletin of National Research Institute of Aquaculture 6: 79–157 (in Japanese with English abstract)
- Wada KT (1985) The pearls produced from the groups of pearl oysters selected for color of nacre in shell for two generations. Bulletin of National Research Institute of Aquaculture 7: 1–7 (in Japanese with English abstract)
- Wada KT (1986) Color and weight of shells in the selected populations of the Japanese pearl oyster *Pinctada fucata martensii*. Bulletin of National Research Institute of Aquaculture 9: 1–6 (in Japanese with English abstract)
- Wang N, Lee Y, Lee J (2008) Recombinant perlucin nucleates the growth of calcium carbonate crystals: molecular cloning and characterization of perlucin from disk abalone, *Haliotis discus discus*. Comp Biochem Phys B 149: 354–361
- Wang N, Kinoshita S, Riho C, Maeyama K, Nagai K, Watabe S (2009) Quantitative expression analysis of nacreous shell matrix protein genes in the process of pearl biogenesis. Comp Biochem Phys B 154: 346–350
- Wang N, Kinoshita S, Nomura N, Riho C, Maeyama K, Nagai K, Watabe S (2012) The Mining of Pearl Formation Genes in Pearl Oyster *Pinctada fucata* by cDNA Suppression Subtractive Hybridization. Mar Biotechnol 14: 177–188
- Zhang Y, Zhang R (2003) A novel matrix protein participating in the nacre framework formation of pearl oyster, *Pinctada fucata*. Comp Biochem Phys B 135: 565–573

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