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Japanese sea cucumber

V. S. Levin

Chapter I. SYSTEMATICS

7*

Understanding the scope of the species

In 1867 E. Selenka described two new species of holothurians: Stichopus japonicus and Holothuria armata (Selenka, 1867). In the first species, on the basis of a study of a specimen with a length of 110 mm, he noted two types of ossicles in the body wall: regular tables with a tapered or apically widened spire

* The numbers in the right-hand margin indicate the corresponding pages in the original text. (Tr.).

and the "Hemmungsbildungen", small oval platelets with openings. In H. armata he found only perforated platelets with openings, similar to the ossicles of H. floridana Pourtalés.

E. Marenzeller (1881) studied several individuals of S. japonicus, of which the largest had a length of 70 mm. He described only one type of ossicle - the tables, some of which had a reduced spire; this author did not find platelets with openings.

In a study of one specimen of S. japonicus (dimensions not indicated) H. Théel (1886) found, in addition to regular tables with a round disk, a large number of round and oval perforated platelets, some of which resembled buckles or clasps. In two individuals, 220 mm in length, he described tables with a low or deformed spire and a disk which had an uneven or serrated margin. On the basis of the form of the tables and the absence of small perforated platelets, Théel distinguished the new variety S. japonicus var. typicus.

In his classical study Mitsukuri (1897) showed that the discrepancies which had arisen in the descriptions of S. japonicus may be explained by the extremely strong variability with age of the ossicles in this species. He reduced H. armata Selenka and S. japonicus var. typicus Theel to synonyms of S. japonicus Selenka, and demonstrated that the specimens studied by Selenka, Marenzeller and Théel represented different age stages of a single species. The species S. roseus which was described by E. Augustin (1908) has also been recognized as a sexually immature individual of S. japonicus (Ohshima, 1918, cited according to Choe and Ohshima, 1961; Clark, 1922; Chang and Chao, 1951).

The authors of several studies in Russian, which treated the scientific names of the animals very freely, have introduced a certain confusion into the question of the taxonomic affinity of the holothurians known as "trepang" which live off the shores of our country.

Thus, in the very thorough study by S. Maslennikov (1894) the Far-Eastern trepang, which was an object of the commercial fishery in the waters of the Ussuriisk Gulf and was undoubtedly S. japonicus, was called Holothuria edulis. In P. Yu. Shmidt's (1905) review this same species from Sakhalin was called Holothuria sp. Several erroneous taxonomic statements are contained in M. Aleksin's book (1912). Fortunately, these taxonomic follies had no significant negative effect, since the Far Eastern trepang or Japanese sea cucumber is the only representative of the aspidochirotan holothurians in the shallow water parts of our seas.

Thus, the taxonomic status of the species under consideration appeared to be fully established by the beginning of the century. However, some data obtained in the sixties by Japanese investigators (Choe and Ohshima, 1961; Choe, 1963) and very recently by the present author suggest that S. japonicus is a polytypic species or even a composite one.

It is evident that considerable effort and time are required to settle this question once and for all. In the present study I adhere to the generally accepted understanding of the scope of this species.

Systematic position

The Japanese sea cucumber Stichopus japonicus Selenka belongs to the phylum Echinodermata, class Holothurioidea, order Aspidochirota, family Stichopodidae and genus Stichopus.

ORDER ASPIDOCHIROTA

D i a g n o s i s . Tentacles shield-shaped, numerous (from 15 to 30, usually 20). Respiratory trees present. Mesentery of the posterior descending loop of the intestine attached to the body wall in the right ventral interradius. Retractor muscles absent. Longitudinal muscles of body in the form of double bands. (After Pawson, 1963).

Family Stichopodidae

D i a g n o s i s . Gonads in two clusters, one on each side of the dorsal mesentery. Stone canal connected with the body wall, but not opening to the outside. Ossicles - tables or, more rarely, buckle-like forms. (After Pawson, 1963).

Genus Stichopus

D i a g n o s i s . Aspidochirotan holothurians with a flattened ventral side, which is markedly demarcated from the dorsal side. The tube feet more or less completely cover the ventral side. Dorsal side, at least laterally, with tube feet or papillae. Usually 20 tentacles. Gonads in two clusters, situated to the sides of the dorsal mesentery. Cuvierian organs absent. No anal teeth or pronounced papillae around the cloacal opening. Ossicles in body wall - numerous tables. Polian vesicles few in number. One stone canal. (After Clark, 1922).

Stichopus japonicus Selenka

Stichopus japonicus Selenka, 1867: 318, Plate XVIII, Fig. 33-36; Semper, 1868: 74; Marenzeller, 1881: p. 18-19 (136-137), Plate V, Fig. 11; Lampert, 1885: 104; Théel, 1886: 160, 194-195, Pl. VII, Fig. 3; Ludwig, 1887: 26 (1242); Mitsukuri, 1896: 408; - 1897: 31-42, 3 text fig.; Sluiter, 1901; Clark, 1902: 563-564; Britten, 1906: 9-11 (131-133); Mitsukuri, 1912: 163-171, Pl. IV, Fig. 32-44, text Fig. 29; Ohshima, 1915: 247-248; Clark, 1922: 61; Chang, 1934: 4-7, Fig. 1; Savel'eva, 1933: 38; - 1941: 74; Panning, 1944: 33-35, Fig. 5-6; Ushakov, 1953: 298; Savel'eva, 1955: 216-217, Pl. XIV, Fig. 4.

Holothuria armata Selenka, 1867: 330, Pl. XVIII, Fig. 66; Lampert, 1885: 91. 9

Stichopus armatus Semper, 1868: 75; Marenzeller, 1881: 121; Théel, 1886: 196; Mitsukuri, 1896: 408; Augustin, 1908: 10-11.

Stichopus japonicus var. typicus Théel, 1886: 161-162, Pl. VIII, Fig. 2.

Stichopus japonicus var. armatus D'yakonov, 1949: 68; Baranova, 1957: 237; D'yakonov et al., 1958: 366; Baranova, 1971: 247-249; - 1976: 115, col. phot. 46.

Name . The scientific name is formed from the Greek nouns "stichos" - row and "pous" - foot, and the Latin adjective which indicates the geographical affinity.

Various names are used in different languages for designating the holothurians belonging to the species S. japonicus; the most important of these are presented below.

In Russian this species of holothurian was previously called "trepang" and this name is also often used at the present time. However, the adoption of such a term, which is used in many countries, as the name for a specific species of holothurian must be acknowledged as being extremely unfortunate. In recent years the more accurate term "Far Eastern trepang" has come into use, and we recommend that this be adhered to.

In Japanese the most widely used name is "namako". In different regions of Japan the following names are used: "akako", "kuroko", "torako", "tawaraga", "uta" and others.

In Ancient China S. japonicus was called "hsiasong" or "shiaking", while in later times the name "haishen" (sea root) came into use. In English it is called "Sea cucumber", "Common sea cucumber" and "Japanese sea cucumber"¹.

In French it is called "Bêche-de-mer japonaise" (from the Portuguese "Bicho-do-mar" - Japanese sea worm).

In Spanish it is called "Cohombro de mar japonés"¹ (Japanese sea cucumber).

Diagnosis. Body length up to 43 cm. 20 tentacles. On the dorsal side the papillae are on large conical outgrowths, arranged in four rows; in individuals from the southern part of the distribution range the outgrowths may be small or almost absent. The ventral ambulacral tube feet are arranged in three more or less distinct bands or they evenly cover the whole of the ventral side. Normally one polian vesicle, which is large and has a rounded or drawn-out end. Ossicles in body wall of

¹ Name used in the official publication "Yearbook of fishery statistics. Rome, FAO, 1977-1979.

young individuals - only regular tables; as the holothurian grows the tables become deformed and reduced, and small perforated platelets are encountered as well; in fully grown individuals tables are absent and only platelets are found. C-shaped ossicles absent.

Description. Large holothurian with a body length of up to 43 cm and a width of up to 9 cm. Body elongate, almost trapezoidal in cross section; ventral side flattened into a distinct creeping sole. Integument fairly dense. 20 tentacles. Tube feet with a sucking disk, numerous, arranged in three more or less distinct bands along the ventral radii; in large individuals they often completely cover the ventral surface. On the dorsal side there are four rows of large conical outgrowths which bear papillae, two double rows along the dorsal radii and two along the lateral ventral radii. Between the large outgrowths the papillae are situated on small elevations or directly on the body. The dimensions, number and arrangement of the dorsal outgrowths are very variable and depend on the geographical latitude of the habitats and the size of the animals. The mouth is more or less subventral. The anus is terminal.

The coloration of the dorsal side is yellowish, dark-green, brownish-red or black; the dorsal outgrowths may be differentiated in colour from the basic background. The ventral side is green (often with a longitudinal darker band), red or black. Tube feet and tentacles dark-green, red or black. Papillae white or brownish.

The stone canal is curved and is attached to the dorsal mesentery. The madreporite is pear-shaped, situated in the mid-dorsal interradius. Normally one polian vesicle (rarely two or three), situated along the mid-ventral radius, very large. The closed end of the vesicle is rounded or drawn-out. Gonads in two clusters, situated along the sides of the dorsal mesentery.

The pharyngeal ring is sturdy and is composed of ten platelets of approximately equal width; the dorsal platelets are markedly taller than the ventral platelets. The dermal ossicles are tables and round or oval platelets with three to six openings (Selenka's platelets). In the youngest individuals the tables are regular and very numerous, while Selenka's platelets are very few in number. Disk of table with a variable number of openings (up to 150), up to 125 μ in diameter; margin smooth, even or arcuate, more rarely irregularly serrated. Spire of table up to 125 μ in height, formed by four rods which converge apically and are connected by one to four crosspieces the tip of the spire and the outer margins of the rods bear varying numbers of spines. In the dorsal papillae there are numerous elongate buckle-shaped platelets with two complete or incomplete rows of openings, curved supporting rods and small terminal platelets. In the tube feet there are round terminal platelets, buckle-shaped forms, supporting sieve-like platelets with large openings, tables and/or (depending on the age of the holothurian) Selenka's platelets. In the walls of the cloaca and the respiratory trees there are numerous sieve-like branched platelets with openings of irregular form. In the gonads and wall of the digestive tract there are straight, curved or branched rods with an uneven surface.

Conditions of life. This species lives in bays and in open sections off the coast on substrates of various types, with the exception of moving sandy and liquid oozes. Accumulations are usually found on mixed substrates, along the boundary of a stony slope with a sandy substrate, on stony detritus, close to overgrowths of eel grass and massive colonies of attached bivalve mollusks. Adult individuals live at depths of 0.5 - 150 m, generally from 1 to 25 m, while young animals are found from the littoral to 20 m. They are found at a water temperatures ranging from negative in the winter to 26 - 28°C in the summer, and with a salinity not lower than 25 ‰.

Distribution. A Pacific, Asiatic, sub-tropical to low-boreal species. Distributed off the coast of Primorye, extending northward to Vladimir Bay, off Moneron Island, along the western and eastern coasts of Southern Sakhalin, in Aniva Bay, off Kunashir Island, along the western and eastern coasts of Japan southwards to Kagoshima Bay, off the coast of Korea, in the Yellow Sea along the Asiatic coast southwards to approximately 35° lat. N.

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Intraspecific systematics

At the end of the last century K. Mitsukuri (1897) distinguished two varieties of *S. japonicus*: var. armatus and var. australis. To the first variety, characterized by high dorsal outgrowths, he assigned the sea cucumbers from the island of Hokkaido and the northern parts of Honshu Island, while to the second variety he assigned those holothurians, almost devoid of outgrowths, which were found in the southern regions of Japan.

In the same work Mitsukuri noted that he associated the mentioned morphological characteristics also with the habitat conditions of the animals, primarily with the character of the substrate.

In his last work, published posthumously, Mitsukuri made use of the more neutral term "form" in place of the term "variety" (in connection with which the spelling was also changed: armata in place of armatus). He was quite specific about the reason for this change:

"These are not varieties in the sense that they differ from the typical form of the species, but rather two extremities of a large group of forms connected by intermediate forms" (Mitsukuri, 1912, p. 169).

Considering the character of the geographic distribution of the "varieties" of the Japanese sea cucumber and taking into account Mitsukuri's above-cited statement, one can scarcely doubt that the forms armata and australis are geographical clines in size and number of dorsal outgrowths (the Japanese investigator could not use the term 'cline', since it only appeared a quarter of a century later). The fact that Mitsukuri did not ascribe a taxonomic status to these forms is also corroborated by his omission of them from the synonymy which he presented in his 1912 publication.

It remains unclear whether the clinal changes affect the population of the Japanese sea cucumber in the whole of its distribution range or are restricted only to Japan. Mitsukuri noted that, while only the form armata was distributed in the north of Japan, both forms were encountered in the south. Britten (1906) reported a specimen of S. japonicus

from the western coast of the Korean peninsula which could be considered, in his opinion, as being intermediate between aust-ralis and armata. This provides evidence for the existence of clinal variability in the Japanese sea cucumber living along the continental coast. At the same time, the description of this species made on the basis of material collected in China (Chang, 1934) gave no indication of the presence of individuals with low outgrowths in this region.

Taking into consideration the clinal character of the variability of such morphological features of the Japanese sea cucumber as the size and number of the dorsal outgrowths, and guided by article 45 of the "International Code of Zoological Nomenclature", one should renounce the use of the designation "var. armatus", which is widespread in the Russian literature, in connection with the species name S. japonicus.

In recent years increasing taxonomic significance has been ascribed to the data associated with the existence, off the coast of Japan, of groupings of the Japanese sea cucumber differing in the coloration of the individuals. K. Mitsukuri (1912) was the first to report the existence of two colour-forms (green and red) of the Japanese sea cucumber. Considerably later Choe and Ohshima (1961) distinguished a third colour form, a black or "commercial" form, as it was called. The work of the Japanese investigators (Choe and Ohshima, 1961; Choe, 1963) showed that these "commercial" forms were differentiated not only by their coloration but also by other significant morphological features.

The question of the taxonomic status of the principal "commercial" forms remains open at the present time. In his most recent study S. Choe (1963, p. 221) wrote: "... the morphological and ecological differences between the green and red forms allow us to conjecture that these are more than simply variations, and provide sufficient grounds for establishing a new species". Unfortunately, his premature death prevented Choe from successfully completing the studies which he initiated on the biology and systematics of the Japanese sea cucumber living off the coast of Japan.

The data that I obtained show that the Japanese sea cucumber which lives off the coast of Primorye possesses several morphological features which differentiate it from the holothurians which are found off the coast of Japan. These differences, as well as the differences between the "commercial" forms, are very significant and allow us to raise the question as to whether S. japonicus combines at least two different subspecies or possibly, as S. Choe considered, even different species. For a definitive resolution of this question it is necessary to make a thorough revision of the material from different parts of the distribution range, enlisting the newest methods of investigation, including genetic methods.

Chapter 2. MORPHOLOGY

General structural plan and symmetry

The body of the Japanese sea cucumber, as of other echi-
noderms, may be divided into ten parts (sectors). The sectors
in which are situated the radial canals of the ambulacral system
and where ~~the~~ bulk of the ambulacral appendages are concentrated
are called ambulacra or radii; in the spaces between the latter
are situated the interambulacra or interradii.² As in all of
the holothurians, the radii and interradii in the Japanese sea
cucumber are not set apart but blend together with the overall
body of the animal.

An analysis of the structural plan and evolution of the
holothurians shows that these animals in fact creep on their
sides. In this case radius A, which lies in the plane of the
madreporite, is turned towards the substrate. Together with
the two neighbouring radii B and E it forms the physiologically
ventral side, while radii C and D correspond to the physiologi-
cally dorsal side. The three ventral ambulacra with the two
interambulacra enclosed between them are called the trivium,
while the two dorsal ambulacra with their three interambulacra
are called the bivium (Figure 1).

The body structure of holothurians is basically subordi-
nated to a pentactinal symmetry. This is manifested in the ar-
rangement of the more important structures: the elements of
the ambulacral, blood-vascular and nervous systems, the platelets

² The term radius (interradius) is usually utilized when we
are concerned principally with the topographical characteristics
of the structure, while ambulacrum (interambulacrum) is used when
referring to the morphological characteristics.

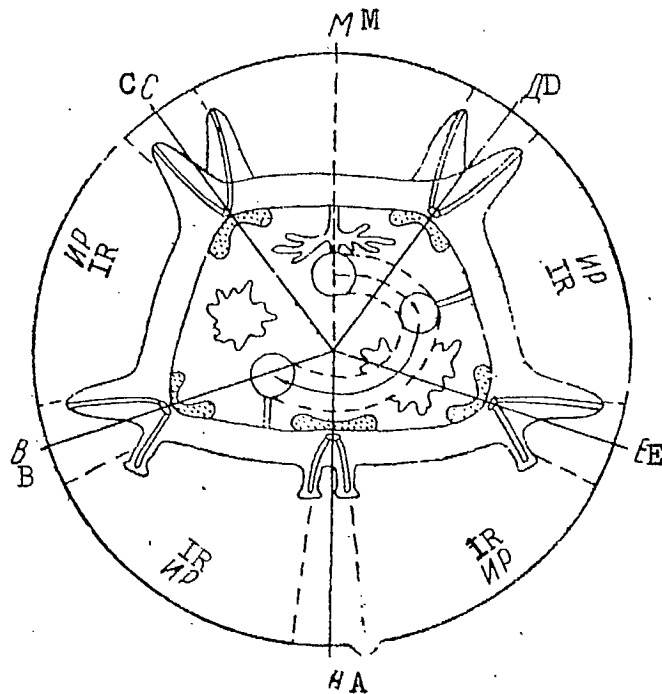


Рис. 1. Симметрия тела дальневосточного трепанга. Вид спереди. А, В, С, Д, Е — радиусы; ИР — интеррадиусы; АМ — madreporная плоскость

Figure 1. Body symmetry of the Japanese sea cucumber. Anterior view.
A, B, C, D, E - radii; IR - interradial;
AM - plane of madreporite.

of the skeletal pharyngeal ring, the tentacles and other structures. In addition to the pentactinal symmetry there is clearly displayed a secondary bilateral symmetry which is manifested in the position of the genital opening, the madreporite and the mouth, and in the arrangement of the tube feet and the papillae. The two indicated types of symmetry are combined with the dissymmetry of the intestine and its associated structures.

Form of body

The body of the Japanese sea cucumber is elongated, cylindrical, with a well developed creeping sole. At the anterior end of the body is situated the mouth, displaced onto the ventral side; at the posterior end the anal opening is located terminally. Large conical outgrowths (called spines by fishermen) bearing the papillae are present on the dorsal side (Figure 2, see insert). The outgrowths normally form four rows: two double rows along the dorsal radii and two lateral rows along the ventral radii. In the dorsal rows the outgrowths are arranged in a zig-zag fashion, while in the lateral rows they are usually drawn out in a single line. The interradial areas between the rows of large outgrowths bear papillae on small elevations or directly on the surface of the body. In cross section the body of such individuals has a characteristically trapezoidal form.

However, alongside the animals which have the described body form, sea cucumbers are found with a different arrangement of the dorsal outgrowths. In such individuals the spaces between the doubled radial rows are enlarged, additional outgrowths appear in the interradia, and in the most strongly deviant individuals it may be difficult to establish any systematic pattern in the arrangement of the outgrowths. The cross section of the body of the sea cucumber in such cases approximates to a semicircle.

The dimensions and form of the outgrowths also vary considerably. An inverse relationship is found between their relative size and their numbers: some individuals bear a small number of very large "spines", while in others numerous small

outgrowths cover the whole of the dorsal side. The number of outgrowths in one row, with a body length of the sea cucumber of about 15 cm, may vary from 10 to 30, with their height ranging from 5 to 20 mm. In small (young) individuals the relative height of the outgrowths is larger, while their total number is considerably smaller, than in large individuals. The ventral tube feet in young animals are arranged in three clearly demarcated bands along the radii. In the lateral radii the tube feet are arranged in two rows, while in the medial radius they are arranged in four (two double) rows. As the holothurian grows the number of tube feet in the width of a band increases, though the medial band remains twice as wide as the marginal bands. In individual cases such an arrangement of the tube feet is retained in large individuals, but more frequently the tube feet then cover the whole of the ventral side evenly, without pronounced gaps. The impression of an arrangement of the tube feet in rows is, to a considerable degree, created (or intensified) by the widespread characteristic coloration of the ventral side with a dark band along the medial radius (Figure 3, see insert). The number of tube feet in large individuals may be as high as 800-1000, although in some individual cases in animals of that size there are only 100-200 tube feet.

There is a definite relationship between the arrangement of the ambulacral appendages on the ventral and dorsal sides of the body of the Japanese sea cucumber. In individuals with a few large dorsal outgrowths arranged in orderly fashion the ventral locomotory tube feet are also relatively few in number and show a tendency to be arranged along the radii; in the animals

which bear numerous small outgrowths the ventral tube feet are numerous and densely distributed.

The mouth opening of the Japanese sea cucumber, as has already been mentioned, is displaced onto the ventral side. It is surrounded by an extensible circumoral (buccal) membrane, along the periphery of which are situated the tentacles (Figure 4, see insert). Normally there are 20 tentacles, sometimes 19 or 18 are found, rarely fewer.

The circumoral tentacles represent evaginations of the body wall, into which extend branches of the radial canals of the ambulacral system. The tentacles of holothurians are usually considered as modified ambulacral podia (sometimes they are even called buccal podia), but in the opinion of O. M. Ivanova-Kazas (1978) this view needs to be amended (see Chapter 9).

The tentacles of the Japanese sea cucumber have the form that is characteristic of all of the representatives of the order Aspidochirota. They are composed of a cylindrical stem and an oval shield, formed by the branching outgrowths which extend in one plane from the tip of the stem. The size of the tentacles depends on the degree to which they are filled by the ambulacral fluid. In the fully extended state the length of the stem may be 25-30 mm, with a diameter of 5 mm.³

The shield of the tentacle is asymmetrical: the branches which are directed forwards along the stem, i.e. to the outside, are the longest, while those directed to the side and especially backwards, to the mouth, are short. According to the graphic

³ Here and subsequently, if the body size of the sea cucumber is not mentioned, the data refer to animals 15-20 cm in length.

description of L. Hyman (1955) the overall form of the shield resembles the leaf of a nasturtium. The size of the shield in the fully extended state may be as much as 15 mm along its larger axis.

The mouth and tentacles are located within the circumoral funnel. Its margin and outer wall are formed by a corolla of numerous outgrowths of the body wall, which are densely accreted with one another and which bear large papillae. The inner wall of the funnel forms a wide, extremely extensible circumtentacular membrane, which is clearly evident when the tentacles are partially or completely extended. Different individuals of the sea cucumber are strongly differentiated from one another by the degree of development of the corolla of the circumoral funnel. The corolla is more strongly developed in young animals than in the adults.

The conical outgrowths on the posterior part of the body, with which the dorsal rows terminate, are always well developed. They are usually set close together and are directed backwards, but they do not form a corolla around the anal opening. The anus is covered by a thin circumanal membrane.

Coloration

The coloration of the Japanese sea cucumber is very variable. In the sea cucumbers living off the coast of Primorye the dorsal side may be coloured from a light greenish-yellow to almost black, in various combinations (Table 1). Variants of an uneven coloration may be encountered separately or be present in combination in one individual.

Table 1. Coloration of the dorsal side of the Japanese sea cucumber from the coast of the Primorye Territory

Type of coloration	Basic background	Outgrowths
Even	Reddish-brown Light-brown Greenish-yellow	
Uneven		
outgrowths more lightly coloured than background	Brown Reddish-brown Black	Light-brown Greenish-yellow Dark-brown
lower part of side of body more lightly coloured than upper part	Light-brown Reddish-brown	Greenish-yellow Light-brown Reddish-brown
dark zones around the dorsal outgrowths in the inner rows		Greenish-yellow Light-brown

This table reflects only the most common types of coloration, while the actual colouring of specific individuals is considerably more complex. The coloration of the papillae plays a very considerable role in this. White papillae with a black rim are the most common but, in contrast, dark papillae with a more lightly coloured rim are also found (in the latter case the body of the sea cucumber has a characteristic "marbled" coloration). In some individuals the papillae that are situated directly on the body have the form of long white cones, while on the outgrowths they are very small and barely evident. The character of the transition between the colours on the body and outgrowths also varies, from a very gradual to an abruptly demarcated transition.

The combinations of the various types of coloration of the body, outgrowths and papillae provide a great diversity of colours. For this reason, even with the same colour of the basic background, the individuals of the Japanese sea cucumber may appear to be quite different.

The ventral side is most frequently coloured in light yellowish-greenish hues. Along the medial radius there is often situated a darker greenish-brown or almost black patch. This may be only slightly darker than the background and not very prominent; it may have the form of a distinct dark band or may embrace almost the whole width of the ventral side. At the same time, irrespective of the intensity of the coloration and the width of the patch, it does not, as a rule, affect the regions near the mouth and near the anus.

The ventral tube feet are of a greenish colour or they may have a wide reddish-brown rim around the sucking disk. In many individuals tube feet with both types of coloration are present. The oral tentacles are usually of a greyish-green colour. It should be noted that in live sea cucumbers the colour of the tentacles is determined to a considerable degree by the coloration of the circumoral cone, and therefore the tentacles appear darker in darkly coloured animals.

The described types of coloration may be considered as being the most typical for populations of the Japanese sea cucumber distributed off the coast of Primorye. In other parts of its distribution range the coloration may be markedly different. Unfortunately, a comparative study of the types of coloration is made extremely difficult because of the

Table 2. Coloration of the principal "commercial" forms of the Japanese sea cucumber from the coast of Japan

Form	Dorsal side	Ventral side	Tube feet	Tentacles	Body wall in section
Green	Dark-green	Dark-green	Dark-green	Dark-green	Light-blue
Red	Brown-red	Red	Red	Red	Light-brown
Intermediate between green and red					
type I	Dark-green	"	"	"	Light-blue
type II	Dark-brown-	Dark-green	Dark-green	Brown-red	Light-brown
Black	Black	Black	Black	Black	Light-blue

complete impossibility of preserving this feature in fixed material, and therefore it is necessary to make use of descriptions which are almost always inaccurate and insufficiently detailed.

The commonest types of coloration found in the commercial forms of sea cucumber living off the coast of Japan are green, red and black (Table 2). Data on the distribution of the first two forms off the coast of Honshu Island were presented by S. Choe and H. Ohshima (1961). The information on the colour variations encountered in other parts of the distribution range of this species is extremely fragmentary. Thus, N. A. Pal'chevskii (1897) wrote that the black specimens of the sea cucumber from Hokkaido Island were considered as the prime variety by the Chinese; it may be assumed that the numbers of

black individuals in this region were fairly considerable. Bright-red individuals of the Japanese sea cucumber have been found in Sagami Bay on Honshu Island (Augustin, 1908; described as S. roseus) and in the Yellow Sea (Chang and Chao, 1951). Apparently the numbers of sea cucumbers with this type of coloration are very small.

Such a deviation from the normal coloration as albinism has also been encountered in the Japanese sea cucumber. Albino individuals have been encountered off the coast of Japan (Mitsukuri, 1912; Ohshima, 1932), in the Yellow Sea (Chang and Chao, 1951; Chang Feng-ying and Wu Pou-lin, 1954) and off the coast of Primorye (Levin, 1979). Unpigmented individuals of the Japanese sea cucumber have sometimes been taken as other species and have required special studies to corroborate their taxonomic affinity (Chang and Chao, 1951). The identification of albino individuals is important among other things because almost everywhere they are encountered, professional fishermen ascribe a special gastronomic and pharmacological value to them.

The studied albino Japanese sea cucumbers were of various sizes, some individuals being fairly large. The depigmentation of the body may be partial or complete. In the former case the coloration is usually retained in the form of spots and rings on the dorsal outgrowths (Figure 5, see insert). In the full albinos the whole body, including the tentacles and tube feet, is pure white. The unpigmented integument acquires a certain transparency and the body of the albinos

sometimes has a bluish tinge (it is apparently this which served as the basis for the legend of the "blue sea cucumbers" which exists among professional fishermen).

Structure of the body

Body wall. The body wall of the Japanese sea cucumber is very thick and elastic, and it forms a well developed musculo-cutaneous sac. It is composed of an outer epidermis, a thick layer of connective tissue, a layer of circular muscles and an inner coelomic epithelium.

The structure of the body wall of the sea cucumber has been studied in detail by S. Kawaguti (1966). The outer epidermis consists of a single layer of cells. The nuclei are concentrated in the proximal part of these cells and therefore the surface layer of the epidermis has the form of a light-coloured fringe on examination with the light microscope. The cells of the epidermis (Figure 6) are very strongly elongated and become narrower towards their proximal end, forming a "neck", while on the surface of the epidermis their marginal part forms thin protoplasmic expansions which are contiguous with the expansions of neighbouring cells. The expansions of the epidermal cells have a thickness of less than 0.2μ and a diameter of $1-2 \mu$.

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The cells of the epidermis are separated by the thick layer of connective tissue and they do not have any other contacts with the neighbouring cells apart from the above-mentioned expansions. Most of the epidermal cells contain one or two large (up to 1μ in diameter) mucous vesicles and may be called mucous cells. Some of the epidermal cells are sensory.

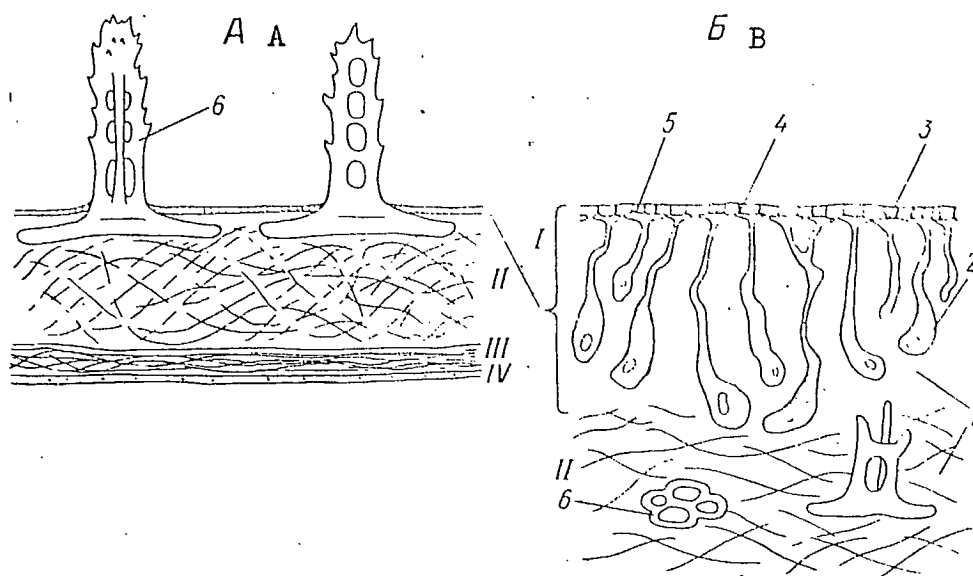


Рис. 6. Схематический разрез через стенку тела молодого (А) и взрослого (Б) дальневосточного трепанга.
 I — эпидермис; II — соединительнотканый слой; III — кольцевые мышцы; IV — целомический эпителий. 1 — соединительная ткань; 2 — эпидермальные клетки; 3 — расширение шейки эпидермальной клетки; 4 — микроворсинки; 5 — слизистое вещество; 6 — спикулы

Figure 6. Schematic section through the body wall of a young (A) and fully grown (B) Japanese sea cucumber.

I - epidermis; II - connective tissue layer;
 III - circular muscles; IV - coelomic epithelium.
 1 - connective tissue; 2 - epidermal cells; 3 -
 expanded necks of epidermal cells; 4 - microvilli;
 5 - mucous substance; 6 - ossicles

The outer surface of the protoplasmic expansions is furnished with long (about 1μ) outgrowths (microvilli). Between these outgrowths is contained the diffuse mucous substance secreted by the mucous cells of the epidermis. The inner surface of the expansions is associated with the fine collagen fibrils which are included in the composition of the connective tissue. Because of this association the expansions of the epidermal cells, in spite of their very slight thickness, may fulfill the role, in conjunction with the underlying connective

tissue, of an integument of the body of the Japanese sea cucumber. At the same time during certain procedures, in particular in the course of histological fixation, this association may be disrupted, and the epidermal cells themselves may be broken down in the region of the "neck". As a consequence of this during histological treatment the thin surface layer of the epidermis separates away from the underlying tissue. In the opinion of Kawaguti, it is this phenomenon which led to the widespread but erroneous idea of the existence of an outer cuticular layer in the integument of holothurians (see Hyman, 1955).

As has already been mentioned, the epidermal cells are embedded in the connective tissue layer, composed of a diffuse substance and fine collagen fibrils with a diameter of about 0.1μ . In the deeper layers of the connective tissue very numerous thick collagen fibres may be seen under the light microscope. Electron microscope studies show that these are actually groups of fibres, joined together into bundles; according to the data of Kawaguti, the diameter of each fibre is about 0.05μ , rarely up to 0.2μ . The collagen fibres are arranged in a random fashion within the connective tissue layer, forming a dense network. Elastin fibres have not been found in the connective tissue (Slutskaya, 1971).

An electron microscope study of the connective tissue of the Japanese sea cucumber, disaggregated by chemical treatment (Matsumura et al., 1973; Matsumura, 1974), has shown the presence of collagen fibrils with a distinct cross striation, created by alternating dark and light-coloured zones. The distance between neighbouring zones, accepted as the unit of the

striation, is about 0.064μ ; the diameter of the fibril is 0.092μ , and the average length is about 150μ . Differential centrifugation of suspensions of the disaggregated tissue has revealed a considerable heterogeneity of the collagen fibrils from different fractions.

Some of the epidermal mucous and sensory cells are connected with nerve fibres which penetrate into the connective tissue layer. These fibres form a superficial nerve plexus which is very weakly represented in the Japanese sea cucumber. In contrast, the nerve plexus which lies on the inner side of the body wall, under the layer of the coelomic epithelium, is well developed, it is quite thick and is composed of a large number of fibres (Kawaguti, 1966). In the epidermis of the body wall are located the calcareous skeletal elements, the ossicles. Depending on the type, they lie at different depths and are either scattered in a random manner or are oriented in a particular fashion. Thus, the tables are positioned with their spire towards the outer surface (Figure 6, B). In the very young individuals the disks of the tables are almost contiguous, while the spires penetrate the integument and protrude to the outside (Figure 6, A). These spires are visible to the naked eye and give to the young Japanese sea cucumbers a characteristic "bristly" appearance. As the sea cucumber grows the spires of the tables become embedded within the epidermis.

The connective tissue layer of the body wall is underlain by the layer of circular muscles, separated by a foundation of longitudinal muscle bands into five elongated interradial areas. The fibres of the circular muscles are collected together

in metameric groups, which may be distinguished on the inner surface of the wall in the form of gently sloping ridges.

In the anterior part of the body the circular muscles pass into the buccal membrane, forming the oral sphincter, and into the circumtentacular membrane. In the posterior part the muscles of the body join together with the circular muscles of the cloaca and form the powerful anal sphincter. Circular muscles are also located in the circumanal membrane.

The most powerful body muscles of the Japanese sea cucumber are the longitudinal muscles. The five muscle bands are arranged along the radii, jutting out into the body cavity (Figure 7). Each band is divided into two strips by a connective tissue partition, by means of which the longitudinal muscle bands are bound to the layer of the circular muscles. Furthermore, the epithelium which covers the muscle bands is connected with the coelomic epithelium of the body by regularly spaced transverse "bridges".

The longitudinal muscle bands of the Japanese sea cucumber are of a whitish colour. They are semi-transparent and through them can be seen the openings of the canals leading to the tube feet. The width of the muscle bands in the middle part of the body is about 20 mm (in the relaxed state), with a thickness of 3 mm. In the anterior part of the body the bands taper abruptly and are attached to the radial platelets of the skeletal ring. At the site of attachment to the ring the thickness of the bands is considerably enlarged and exceeds their width. Moving towards the posterior end of the body, the muscle bands become gradually narrower and in the region of the anal sphincter on the circumanal membrane they are replaced by small radial

dilator muscles which participate in the process of the opening of the anus. Similar dilator muscles are also located within the buccal and circumtentacular membranes.

On the contracted fibres of the longitudinal muscle bands of the Japanese sea cucumber, as in other species of holothurians, there can often be seen a weak cross striation. This may be explained by the fact that several fibres are in close contact with one another, forming groups and creating the impression of a syncytium. The free surfaces of the fibres facing the connective tissue contain numerous long outgrowths that are directed into the tissue. In addition, on strong contraction of the muscles the crimped myofilaments arranged along the longitudinal axis of the fibres create the impression of a cross striation. However, in the relaxed state of the muscles it is evident that the fibres have the typical structure of smooth muscles (Kawaguti, 1964).

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In the relaxed state the muscle fibres are drawn out along the body axis; many of them are collected together into bundles of two or more fibres. The average diameter of a fibre is 2.5μ . On contraction of the muscles most of the fibres acquire a crimped or zig-zag form, and their diameter increases to 5μ . According to the data of S. Kawaguti and N. Ikemoto (1965) a zig-zag form of the fibres is also found with fixation of the muscles in the relaxed state.

The myofilaments are divided (Shida, 1971) into two types: thick (diameter $0.015 - 0.035 \mu$) and thin (0.005μ). The thick filaments are furnished with numerous protuberances. The thin filaments are even, with a smooth surface, and they

are drawn out along the thick filaments, forming an irregular network.

The thick filaments are made up of several subfilaments, twisted into gentle spirals. Both the thick and the thin filaments are embedded in an electron-dense substance, in which may be distinguished fusiform structures $0.1 - 0.4 \times 0.01 - 0.1 \mu$ in size, resembling the dark bodies in the smooth muscles of vertebrates. The most pronounced changes during the contraction of the muscles consist of a decrease in the diameter of the thick myofilaments from $0.035 - 0.05$ to $0.015 - 0.035 \mu$ and the disappearance of the spiral structures.

Protruding above the surface of the body of the Japanese sea cucumber are the ambulacral appendages: the podia and the oral tentacles, representing tubular outgrowths of the body wall. In the places where the tube feet are situated the canals of the ambulacral system pass through the whole thickness of the body wall; some of the canals penetrate the conical dorsal outgrowths and are directed into the papillae located on the tips of the outgrowths.

The ambulacral podia are divided into two groups: the locomotory tube feet and the papillae, which have lost the locomotory function and retain only a sensory function. The structure of the wall of the ambulacral podia is similar to that of the body wall. On the outside the podia are covered with epidermis, which is a continuation of the epidermis of the body; then follows a layer of connective tissue and a longitudinal muscle layer. The cavity of the podia is lined with coelomic epithelium, connected with the epithelium of the ampullae and the lateral canals of the ambulacral system. There is no layer

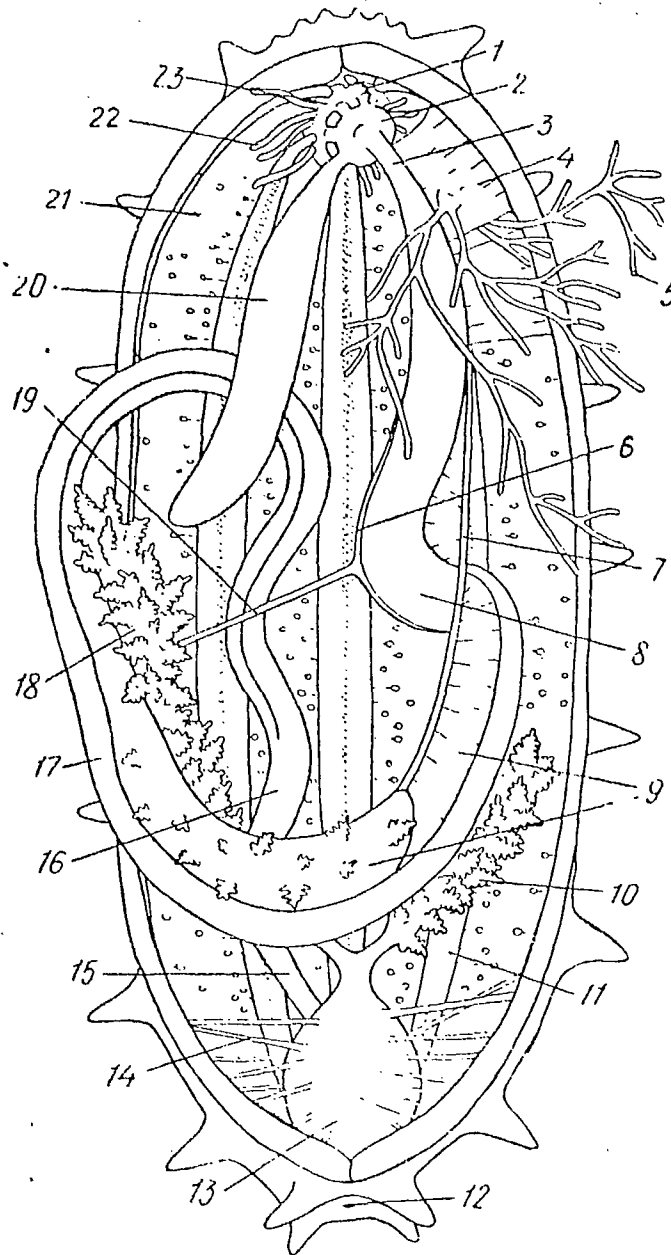
of circular muscles in the wall of the podium, since the motor function is filled by the fluid which moves under pressure into its cavity. Between the cells of the outer epithelial layer there lie the fibres of the subepithelial nerve plexus, which is especially developed on the sucking disk. On one side of the podium (namely on the side of the lateral canal) these fibres pass into the longitudinal nerve trunk, connected with the radial trunk of the nervous system. The podial nerve is accompanied by an epineural sinus over a considerable distance.

The epithelium of the sucking disk of the locomotory tube feet contains a large number of mucous cells. Under the layer of the connective tissue in the disk there lie some ossicles: a very large perforated terminal platelet, and also platelets of varying form with large openings. Numerous ossicles are also situated in the outer layer of the connective tissue in the stem of the podium. These are predominantly tables and Selenka's platelets, in a stage of development corresponding to the stage of development of the ossicles in the body wall. The disposition of the ossicles in the wall of the podia is the same as in the body wall.

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The papillae or papilla-like podia are differentiated from the locomotory podia by the absence of the terminal disk and by the more robust development of the epithelium at their apex. The papillae which are situated directly on the body of the Japanese sea cucumber are usually considerably longer than those situated on the conical outgrowths of the body wall.

In the wall of a tentacle the same layers may be distinguished histologically as are found in the body wall: an epidermis, a layer of connective tissue, a layer of muscles



Р и с. 7. Внутреннее строение дальневосточного трепанга.

1 — каменный канал; 2 — кольцевой канал абулакальной системы; 3 — пищевод; 4 — мезентерий; 5 — половая железа; 6 — антимезентеральный кровеносный сосуд; 7 — мезентериальный кровеносный сосуд; 8 — переднее нисходящее колено кишки; 9 — «чудесная сеть»; 10 — правое водное легкое; 11 — продольные мышечные ленты; 12 — анальное отверстие; 13 — клоака; 14 — подвесочные тяжи клоаки; 15 — задняя кишка; 16 — заднее нисходящее колено кишки; 17 — среднее восходящее колено кишки; 18 — левое водное легкое; 19 — соединительный кровеносный сосуд; 20 — поллиан пузырь; 21 — ампулы амбулакальных ножек; 22 — ампулы щупалец; 23 — окологлоточное скелетное кольцо

Figure 7. Internal structure of the Japanese sea cucumber.

1 - stone canal; 2 - ring canal of ambulacral system; 3 - oesophagus; 4 - mesentery; 5 - gonad; 6 - antimesenterial haemal vessel; 7 - mesenterial haemal vessel; 8 - anterior descending loop of intestine; 9 - "rete mirabile"; 10 - right respiratory tree; 11 - longitudinal muscle bands; 12 - anus; 13 - cloaca; 14 - cloacal suspensors; 15 - hind gut; 16 - posterior descending loop of intestine; 17 - middle ascending loop of intestine; 18 - left respiratory tree; 19 - connective haemal vessel; 20 - polian vesicle; 21 - ampullae of tube feet; 22 - ampullae of tentacles; 23 - circumpharyngeal skeletal ring.

(longitudinal, in contrast to the body wall) and the coelomic epithelium which lines the cavity of the tentacle. The development of these layers is not uniform in different portions of the tentacle: as one moves from the stem towards the tips of the branches of the shield the thickness of the connective tissue layer decreases, while the epidermis increases in thickness. On the side of the branches that is turned towards the substrate the epidermis forms discrete protuberances, the nodes or nodules, which are demarcated from one another (Roberts, 1979). The nodular structure of the epidermis of the tentacles is of decisive significance in ensuring the capture of food particles by the tentacles. Mucus-secreting cells have not been found in the epidermis of the tentacles of the Japanese sea cucumber, nor in other species of the aspidochirotan holothurians.

Within the connective tissue of the tentacles there lie numerous supporting calcareous ossicles: straight or slightly curved rods with simple or branched spinules on their surface. The mass of the supporting rods comprises about $33 \pm 3\%$ of the total dry mass of the tentacles.

Between the muscle and the connective tissue layers on the inner (facing the mouth) side of the stem of the tentacle there runs a wide band of nerve, connected with the circumpharyngeal nerve ring. At the tip of the stem the nerve produces branches into the branches of the shield of the tentacle, which terminate in the neural plexuses in the bases of the nodules. Along the course of the nerve small fibres separate off from it and pass through the connective tissue layer to the receptor cells in the epidermis.

Skeleton. The skeleton of the Japanese sea cucumber is made up of microscopic calcareous bodies, the ossicles, which are distributed within the skin and walls of some of the internal organs, and of the massive circumpharyngeal ring.

In spite of the extremely important role which the ossicles play in the systematics of the holothurians, no unified terminology for designating the types of these elements has been elaborated. In the English language alone four terms are used for the concept "spikula"*: spicules, sclerites, ossicles and deposits. Also ambiguous is the sense of the terms for designating the different types of ossicles, which considerably complicates their classification. Another difficulty in the study of the ossicles of the Japanese sea cucumber is due to the strongly expressed age-determined variability of these structures.

Most numerous and characteristic in their form are the ossicles in the skin of the body, which is why they are widely used for systematic purposes, age determination etc.

The main type of ossicle in the body wall of the Japanese sea cucumber is the "bashenka"** (English - table; German - Turm; French - tourelle). Such ossicles are normally composed of a perforated disk (flat or concave) and a spire, which extends from the central part of the disk and consists of straight or curved rods that are joined together at several levels by crosspieces. In the upper part of the spire the rods

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* The Russian word "spikula" (literally - spicule), occurring throughout this text, has been consistently translated here by "ossicle". (Tr.).

** Similarly "bashenka" (literally - turret) has been consistently translated by "table". (Tr.).

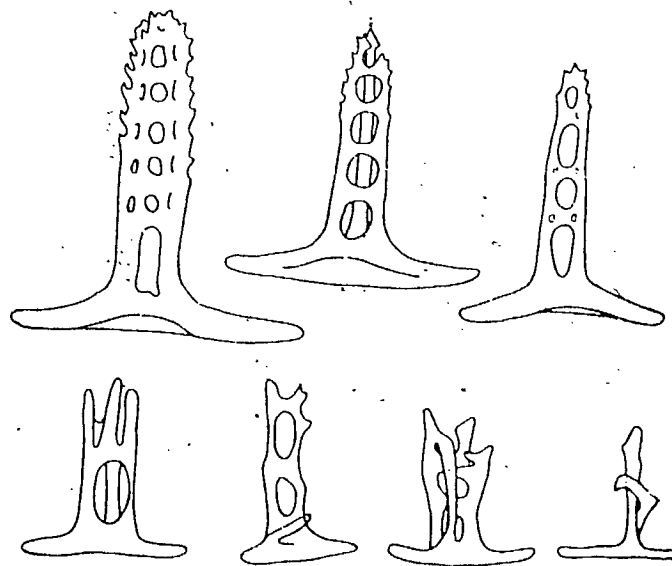


Рис. 8. Башенки из кожи тела дальневосточного гребанга. Вид сбоку

Figure 8. Tables from the body wall of the Japanese sea cucumber. Side view.

may converge, forming a tip of varying configuration, or they may remain separate.

During the process of growth the tables in the body wall of the Japanese sea cucumber are subject to considerable deformation and become reduced, so that the characteristic features of their structure are manifested most completely in the young individuals. The general configuration of such tables is regular, with a flat disk and a conical spire, the height of which is equal to or greater than the diameter of the disk (Figure 8). The maximal size of the ossicles is about 125 μ .

The spire is formed by four rods which are perpendicular to the disk in their lower part; higher up they incline towards one another and become fused together at the tip. Along the outer margin of the rods and on the tip of the spire there are some (comparatively few) large, sharp, upwardly directed spines.

The thickness of the rods and of the crosspieces in different ossicles varies considerably and therefore the spaces which separate these elements may be either fairly considerable or be reduced to small oval windows.

In its general appearance the disk of the table is an almost round platelet with openings. The openings are arranged in a particular order. The center of the disk is occupied by a cruciform structure, the derivative of the original cross from which the development of the ossicle commenced. Around the primary cross are situated the primary openings (order I openings), outside which are the openings of orders II, III etc. Using the method for recording the arrangement of the openings in the ossicles that was accepted by H. Ludwig (1889 - 1892), the structural scheme of the disk of a table may be represented in the following manner: order I - 4; II - 4; III - 8; IV - 12; in the following rows the system of the arrangement of the openings is usually severely distorted. The total number of openings varies from 4 to 150 and more. The size of the disk ranges from 40 to 125 μ .

The comparative sizes of the openings, the number of rows of the latter, and the width and configuration of the margin of the disk vary considerably (Figure 9). In itself the size of the disk is not a characteristic feature, since a positive correlation is by no means always found between this index and the number of openings in the disk, and so it is necessary to count the number of rows (orders) of openings, which is fairly easy to do up to orders III - IV.

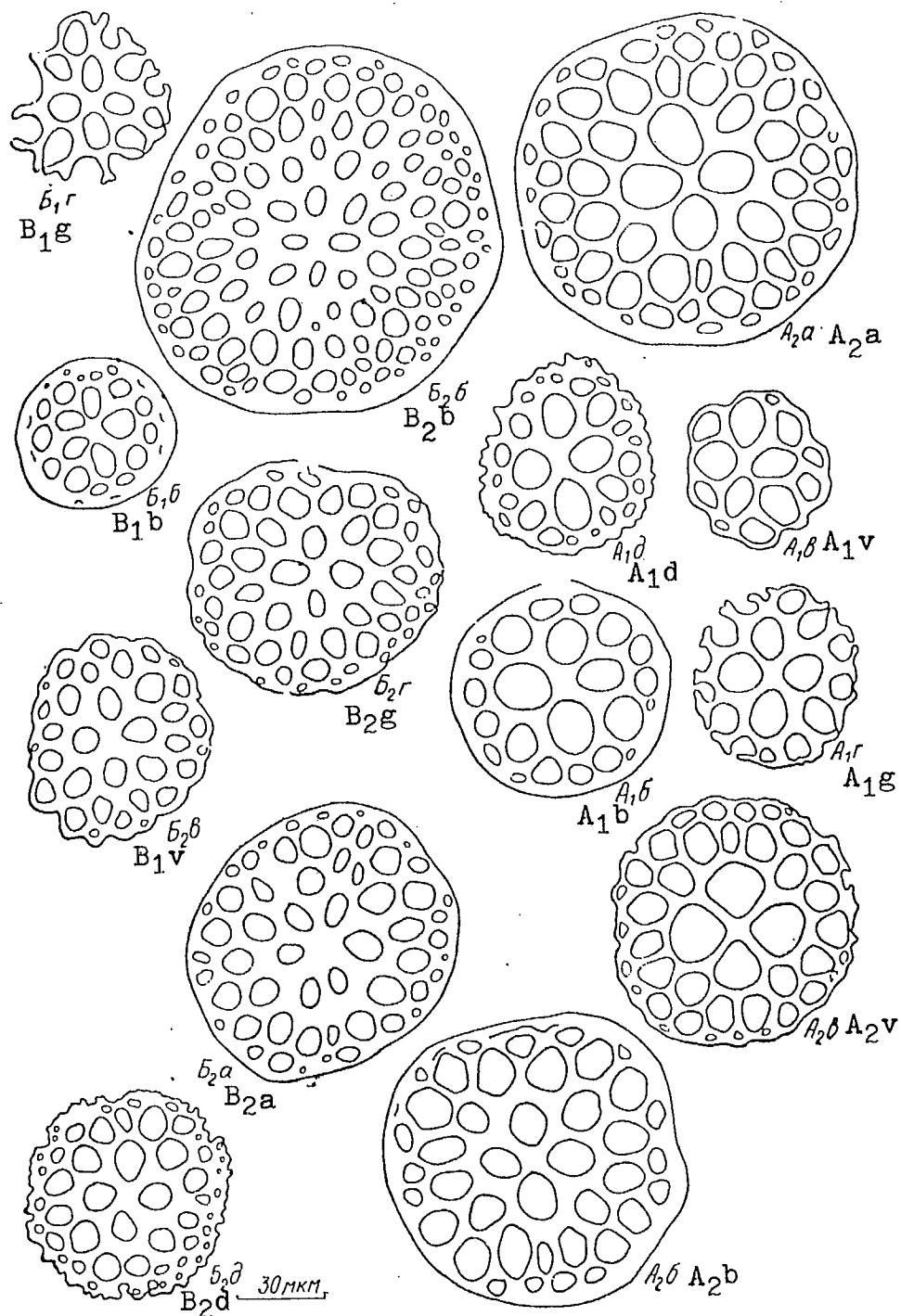


Рис. 9. Основные формы диска башенок из кожи дальневосточного трепанга. Обозначения индексов формы диска соответствуют табл. 3

Figure 9. Principal forms of the disk of tables from the skin of the Japanese sea cucumber. The designations of the form indices of the disk correspond to Table 3.

Table 3. Types of disk of tables from the body wall of juvenile individuals of the Japanese sea cucumber.

Openings			Margin of disk				
size	number of rows		even		arcuate		dentate
			narrow	wide	closed	open	
			a	b	v	g	
Large	1 - 3	A ₁	-	++	++++	+	+
	More than 3	A ₂	++	+	+	-	-
Small	1 - 3	B ₁	-	+	-	+	-
	More than 3	B ₂	+	+++	+	+++	+

Note. The number of "+" signs corresponds to the relative frequency of occurrence of the given type of ossicle.

On the basis of the relative size of the openings (or the relative width of the connecting pieces between the openings) all of the tables may be divided into two groups, which in most cases are easily distinguishable visually; there are very few disks with openings of a size that might be considered as being intermediate. In the group of disks with large openings the ratio of an order I opening to the width of the connecting piece comprises 3-8, while with the small openings this ratio may be as low as 1 or even 0.8. Related to the relative size of the openings is their form, which is almost round or five-sided with the large openings and elongately ellipsoidal with the small openings. Also differentiated is the character of the change in size of the openings in the different rows. In disks with large primary openings the higher order openings are

smaller. When the primary openings are small the order II-IV openings are of similar dimensions or are markedly larger.

Also subject to considerable individual variation are such features as the width and configuration of the margin of the disk. Five principal forms of the margin may be distinguished (Table 3). The frequencies of occurrence of the different types of form of the disk are not the same. Types A_1v , B_2b and B_2g occur most frequently; six of the combination types were not found by us. The two form groups of the disk, with large and small openings (A and B), are clearly differentiated by the frequency of occurrence of the same combinations of features.

A larger number of rows is more characteristic of the disks with small openings, while in the disks with large openings higher than order III rows are rarely found (for example, the A_1v combination is the most frequently found, while the "homologous" B_1v combination was not encountered). The mentioned differences corroborate that the relative size of the openings in the disk is an important index characterizing significant morphological features of the ossicles.

Besides the tables, a very important type of ossicle is that which Selenka (1867), in the original description of the species, very unfortunately designated the "Hemmungsbildungen". Because of the difficulty of interpreting this term, subsequent authors (for example, Mitsukuri, 1897) employed the German word, without translation. To facilitate the use of this type of ossicle we propose naming them "Selenka's platelets", after the author of the species.

Selenka's platelets are ossicles of a round, oval or irregular form, with three to six openings (Figure 10). Although

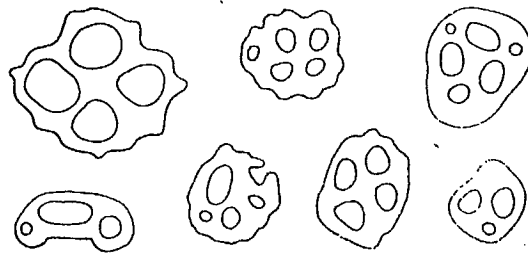


Рис. 10. Пластинки Селенки

Figure 10. Selenka's platelets

a platelet with six openings was illustrated in the original description of the species (Selenka, 1867, Fig. 36), the most common number of openings in this type of ossicle is four. On the basis of the arrangement and form of the openings, Selenka's platelets correspond to the central part of the disk of the tables, with which, apparently, they are genetically related.

Besides the regular tables and Selenka's platelets, which represent, as it were, extreme forms in the developmental series of the tables, in individuals of the Japanese sea cucumber of different ages there are also found tables that are reduced or deformed to varying degrees (Figure 8). The variants of the disk of the tables are generally expressed by a decrease in the number of openings and the development of a strongly serrated or festooned margin. The spire of the tables is lower, with a smaller number of crosspieces. The rods of the spire do not join together at the tip, but run parallel or are inclined outwards in the upper part. The number of rods may be decreased to two or, more rarely, increased to five. Some tables are found with rods of different heights, which are strongly deformed.

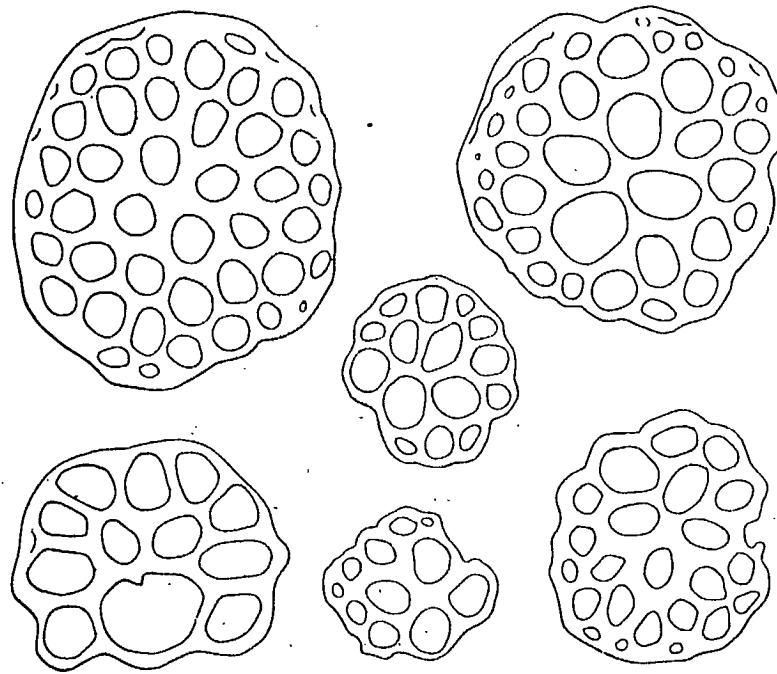


Рис. 11. Диски башенок с нарушенным строением

Figure 11. Disks of tables with a disrupted structure.

The tables of the Japanese sea cucumber are rarely completely regular structures; in most cases their typical structure is more or less strongly distorted. The deformation of these ossicles, which increases progressively with the age of the animals, is already found in the youngest individuals. Irregularity of the spire is expressed in the differing number of spines on the rods, the inclination of the crosspieces and the overall asymmetry. Defects in the disk are manifested in the deviations of its form from a circle, disruptions in the order of laying down of the openings (the probability of such disruption increases towards the periphery of the disk), the fusing together of openings and unevenness in the width of the margin of the disk. These disruptions may already be traced

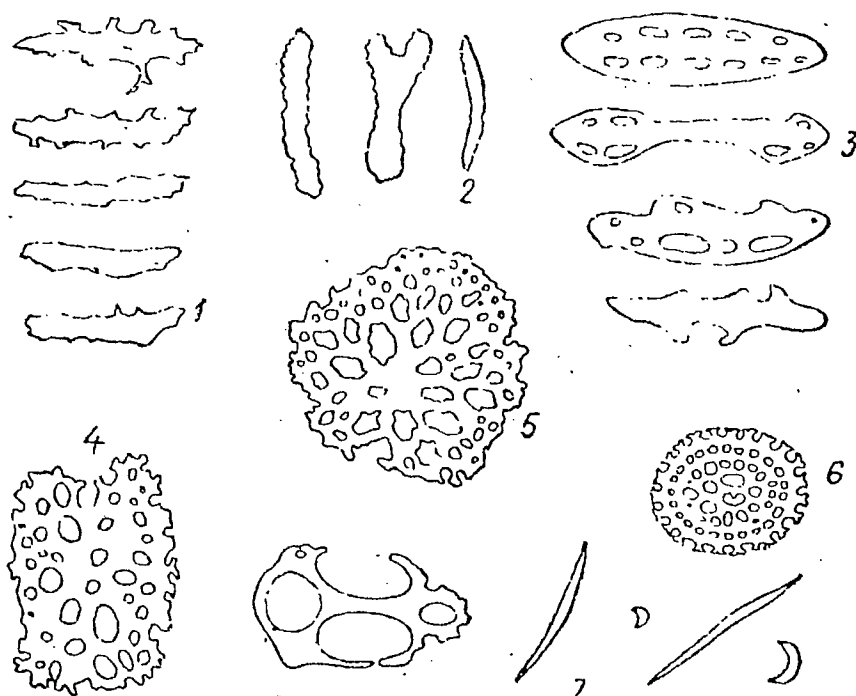


Рис. 12. Спикюлы из тканей разных частей тела дальневосточного трепанга. 1—палочки из щупалец; 2—палочки из стенки гонады; 3—пряжки из папилл; 4—фрагмент опорной пластинки амбулакральной ножки; 5—пластинка из стенки клоаки; 6—пластинка из стенки водного лёгкого; 7—иголки и крючки из разных тканей

Figure 12. Ossicles from tissue of different parts of the body of the Japanese sea cucumber.

1 - rods from tentacles; 2 - rods from wall of gonad; 3 - buckles from papillae; 4 - fragment of supporting platelet of tube foot; 5 - platelet from wall of cloaca; 6 - platelet from wall of respiratory tree; 7 - needles and hooks from different tissues.

in the typical forms of ossicles, although in some specimens they are especially strongly expressed (Figure 11).

Besides the tables other types of ossicles are also found in different parts of the body of the Japanese sea cucumber (Figure 12). In the skin of the body curved pointed rods are occasionally found. In the ventral tube feet and dorsal papillae there are scattered numerous supporting buckle-shaped

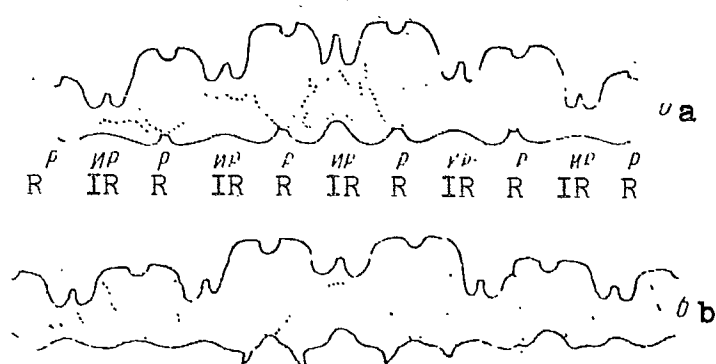


Рис. 13. Окологлоточное скелетное кольцо дальневосточного трепанга. Р — радиальные пластинки, ИР — интеррадиальные. Разрез выполнен вдоль срединной брюшной радиальной пластинки

Figure 13. Circumpharyngeal skeletal ring of the Japanese sea cucumber. R - radial platelets, IR - inter-radial platelets. The cut was made along the middle ventral radial platelet.

platelets with parallel rows of openings, which are often incomplete. In the disk of the ventral podia are situated a very large terminal platelet and numerous platelets with large openings; small terminal platelets are sometimes noted also in the tip of the dorsal papillae. In the oral tentacles there lie numerous slightly curved supporting rods with numerous simple or branching spines. Straight, slightly curved or branched rods with rounded ends and very small spinules are scattered in the walls of the gonad and the intestine. Numerous large platelets of complex configuration are encountered in the walls of the cloaca and the base of the respiratory trees. In addition to the mentioned types of ossicle, in individual cases there have been noted needles, hooks and bodies of indeterminate form.

The most strongly developed skeletal formation of the Japanese sea cucumber is the circumpharyngeal ring. This is composed of ten calcareous platelets, five radial and five interradial, tied together by connective tissue (Figure 13).

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The radial platelets are about twice as high as the interradial platelets. Their anterior margin is slightly convex and bears a deep notch in its middle part, through which run the canals of the ambulacral and haemal systems and the nerve trunks; the posterior margin is concave. The anterior margin of the interradial platelets is almost straight and bears a high triangular process medially, forming fossae for the ampullae of the tentacles; the posterior margin is roundly concave. Along the posterior margin of the ring at the site of contact of the radial and interradial platelets is situated a round protrusion (Figure 13, a), sometimes furnished with a backwardly directed triangular process (Figure 13, b), which in some cases may be developed only on the platelets on the dorsal side of the circumpharyngeal ring. The platelets bear a characteristic sculpturing.

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The platelets of the ring are not of the same height. The two radial platelets belonging to the dorsal radii are the highest; somewhat smaller are the platelets of the lateral ventral radii, and the smallest radial platelet belongs to the medial ventral radius. The height of the interradial platelets also varies in a similar fashion. At the same time the width of both the radial and the interradial platelets remains almost constant. The varying height of the platelets of the circumpharyngeal ring is apparently related to the subventral position

of the mouth and ensures the necessary inclination of the posterior plane of the ring and, consequently, of the pharynx and the oesophagus.

The circumpharyngeal ring of the Japanese sea cucumber is very flexible, thanks to both the movable articulation of the platelets with respect to one another and their own intrinsic elasticity. Because of this, the form of the platelets of the ring and especially their height to width ratio may differ fairly considerably, depending on the state of the animal prior to preparation. Apparently it was this that led E. Selenka (1867) to conclude that the ring platelets in this species varied in their width. The error of this conclusion has already been noted (Marenzeller, 1881; Mitsu-kuri, 1912).

Coelom and coelomocytes. Characteristic of the Japanese sea cucumber, as of other echinoderms, is the differentiation of the coelom into an extensive body cavity and several complex systems of canals, i.e. the ambulacral and blood-vascular (haemal) systems, and the system of canals that are associated with the hyponeural trunks of the nervous system. The latter are most frequently named perihæmal or pseudohæmal canals.⁴ The structure of the ambulacral and hæmal systems will be considered in special chapters.

The body cavity is also subdivided into several sections. The largest is the body cavity proper, or perivisceral cavity, within which are located the principal internal organs: the

⁴ I subscribe to the opinion of L. Hyman (1955) that the use of these terms leads to confusion and that they should be avoided. See also the note on page 46.

intestine and the structures associated with the latter, the respiratory trees, the gonads and others. The perivisceral cavity is demarcated by the epithelium of the walls of the body and of the internal organs. The mesentery onto which the intestine is attached divides the cavity into several sections which, however, communicate extensively with one another.

In the anterior part of the body of the Japanese sea cucumber a second section of the coelom is situated around the pharynx; this is the peripharyngeal sinus (Figure 14). This sinus is the space which is demarcated on its inner side by the wall of the pharynx and on its outer side by the walls of the radial and ring canals of the ambulacral system.

