Revision of the Holothurioidea.

I. Cucumaria frondosa (Gunner) 1767.

By

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With Plate 13—14.

In retaining the class name Holothurioidea for this series of papers, I have followed current usage. Before accepting so far reaching and disturbing a change to Bohadschiidae, as suggested by Gill, 1907, and adopted by Fisher, 1907, or Bohadschioidea, by Poche, 1907, I agree with Clark, 1907, and Bather, 1907, that we should have the question decided by the International Commission on Nomenclature. In such a decision I trust with Bell, 1891, that common sense, rather than a rigid adherence to the law of priority which may be found to apply, will make it plain that we should retain *Holothuria* and *Actinia* for groups to which they have been applied for more than a century.

In this Revision of the Holothurioidea it is proposed to present the results of a thorough study of the anatomical characters of each species considered. Jäger, 1833, Selenka, 1867, Semper, 1868, Hérouard, 1889, Ludwig, 1889—1892, 1898, 1898a, Östergren 1896, 1898, Mitsukuri, 1897, and Edwards, 1905, 1908, 1909a, have demonstrated that there are differences which make it possible to separate the young from the adult. Among the characters which differ in the two age groups are the size of the body and its parts, the number of pedicels and papillae, and sometimes the form of the spicules. In certain cases the number of Polian vesicles, and of stone-canals, is greater in the adult. In these revised descriptions all available stages in the life-history are utilized, so that as often as possible the establishment, development, and growth, as well as the adult condition, of the various important parts, may be included.

When possible biometry is employed as a method for the analysis of the more important data. An objection may be raised to seriating together individuals from widely scattered regions. In reality the various localities of the habitat of a species are ordinarily more or less continuous, and the material considered proves to be measurably homogeneous. Sometimes it may be claimed that the number of specimens is not large enough for biometric purposes. There is no generally applicable ideal number of variates, and even if there were, it is necessary to deal in the best manner with the material one has in hand and not with a possible ideal number one may desire, but does not possess. In the establishment of a locus race a large number of individuals is called for. Independently of local races it is necessary to discuss the phases of the variabitity of a species taken as a whole. For this pourpose I believe that biometry should be employed whenever available as a method most searching in analysis and exact in statement (cf. Edwards, 1908).

Beginning with the original description, the literature has been critically examined and classified. Under each character it has been my endeavor to give credit to the author, or authors, who have made original contributions, or important suggestions. The synonymy given includes only the first use of either the different generic, or specific names, or combinations of the same.

For the opportunity of investigating the large collections of the United States National Museum, I desire to thank Dr. Richard Rathbun, Assistant Secretary of the Smithsonian Institution. For similar courtesies I would express my indebtedness to Professors Théel, of Stockholm, Wirén, of Upsala, and Jungersen, of Copenhagen.

Cucumaria frondosa (Gunner) 1767.

1767. *Holothuria frondosa* Gunner.
1776. *Holothuria pentactes* O. F. Müller.
1830. *Cuvieria frondosa* Blainville.

1833. *Pentacta frondosa* Jäger.
1839. *Holothuria grandis* Forbes et Goodsir.
1839. *Holothuria fucicola* Forbes et Goodsir.
1841. *Holothuria* (*Cladodactyla*) *pentactes* Gould.
1841. *Cucumaria frondosa* Forbes.
1841. *Cucumaria fucicola* Forbes.
1851. *Botryodactyla grandis* Ayres.
1851. *Botryodactyla affinis* Ayres.

Historical and general. — v. Marenzeller, 1874, has shown that *Cucumaria*, first proposed by Blainville, 1830, is the valid name for this genus and that *Pentacta* should replace *Colochirus*, and not be used for the stichopodous species of *Cucumaria* as proposed by Verrill, 1867—1871. (Cf. Bell, 1891a.)

The quaint original description of *Cucumaria frondosa* by Gunner notes a black color, egg-like form, thick skin, muscles, ten tentacles, and intestine. He thinks the animal gets food „by sucking itself fast with other objects that can give nourishment" and that it cannot swim. He mentions „some protruding, round, partly depressed and flat warts", but does not realize them to be the sucking feet.

Fabricius, 1780, gives a better, but still very incomplete description and notes that this species besides dwelling in the depths of the sea, among the rock-weed, may be seen swimming in the open sea near the shores, expanding and contracting its tentacles. Fabricius considers the form viviparous for in the month of March he has seen its young, of a reddish color, swimming freely within it, near the anus. Since the time of Fabricius no one seems to have verified this interesting observation. Ganong, 1888, says that „it passes through a metamorphosis in which the fullygrown larva (Auricularia) is of a red color, cylindrical, with a few constrictions or annulations and four or five bands of cilia by means of which it can swim freely about."

Ludwig, 1889—1892, shows that Danielssen & Koren, 1856, are in error in their identification of *Holothuria tremula*, and that they really describe the embryology of one of the Dendrochirotae. Prof. Théel tells me that he believes this species is *Cucumaria frondosa*.

In the description of this species given by Packard, 1897, with a drawing by J. S. Kingsley, there are several remarkable errors. Only one respiratory tree is given instead of the two normally present. The „ring-canal (*vr*)" of the water-vascular system and the „nervous ring (*nr*)" are given as if anterior of the insertion of the introvert retractors, and thus one-fifth of the length of the drawing in front of where they actually exist! Just how the stone-canal and Polian vesicles, which are properly located in the drawing, enter the misplaced ring-canal, is a mystery.

According to Forbes, 1841, the Shetland fishermen class this sea-cucumber as Pushen (poison) and throw it away as unlucky and dangerous but Stimpson, 1851—1854, regards it „when boiled, quite as palatable as lobsters". The latter author, 1853, reports this species at Grand Manan just below the ordinary low-water mark on rocky shores and exposed at spring tides. Sometimes areas of several square rods are entirely occupied by them, and he also says, 1851—1854, „They usually adhere to the bare surface of the rocks by the suckers of one side of the body (which is always of a lighter hue than the other side), but they are pleased to find a chink, or some pebbles, in which to bury themselves, when nothing can be seen of them but their tentacula; ten beautiful purple tufts radiating from a center and occupying a circle of six inches in diameter".

In addition to the above authors, more or less complete descriptions have been given by Forbes & Goodsir, 1839; Düben & Koren, 1846, 1846a; Dalyell, 1851; Ayres, 1851; Lütken, 1857; Selenka, 1867; Semper, 1868; Duncan & Sladen, 1881; Lampert, 1885; Levinsen, 1886; Théel, 1886; Koehler, 1895; Michailovskij, 1902, 1904; Clark, 1904; and Edwards, 1907, 1909.

The following authors have added to the habitat very short descriptions with nothing new, or of especial importance; — Müller, 1776, 1788, 1806; Linné, 1788—1793; Lamarck, 1816; Blainville, 1822, 1830, 1834; Jäger, 1833; Sars, 1850; Ayres, 1855; Forbes & Goodwin-Austen, 1859; Verrill, 1866; Norman, 1868; Pourtalès, 1869; M'Intosh, 1875; Duncan & Sladen, 1877; Kükenthal & Weissenborn, 1886; Knīpovīch, 1901; Rankin, 1901 and Clark, 1901a.

The habitat only is given by the following authors, and when any author is not certain of the identification, a ? precedes his name; — Encyl. méth. Hist. Nat. des Vers. 1827; Thompson, ? 1840, 1844; ? Gould, 1841; Sars, 1850, 1858, 1861; Forbes, 1852; McAndrew & Barrett, 1857; Stimpson, 1857, 1863; F. Dujardin & H. Hupé, 1862; Packard, 1867; Verrill, 1867, 1871, 1879, 1885; Heuglin, 1874; Norman, 1876, 1901, 1903; Ljungman, 1879; Danielssen & Koren, 1882; Ludwig, 1882, 1883, 1898, 1900a; Ganong, 1884; Jarzynsky, 1885; ? Murdock, 1885; Fischer, 1886;

Nordgaard, 1893; Grieg, 1889, 1896, 1907, 1907a; Pfeffer, 1890, 1894; Sluiter, 1895; Kingsley, 1901; Whiteaves, 1901; Høring, 1902; Östergren, 1903; Schmidt, 1904; and Clark, 1905.

The present paper gives a revised description of all the characters of *Cucumaria frondosa* including particularly a more adequate account of the spicules in the body-wall, pedicels and tentacles. In addition I have described as new the vestigeal anal teeth and the sexual differentiation in the form of the genital papilla (cf. Edwards, 1909), and the detailed order of appearance of the pedicels from one, or the other, or both sides, of the different radial canals.

Form. — The dorsal surface of the subcylindrical body is more flattened than the ventral. The posterior end is rounded, and from the expanded oral disc the dendritic tentacles are broadly extended in life although contracted in alcoholic specimens (Pl. 13, Fig. 1).

When irritated, the powerful retractors pull in the introvert, and the holothurid becomes more or less ovoid, with deeply wrinkled skin.

Size in centimeters. — Of 120 specimens in the collection, 59 individuals are of less than 3 cm in length and are classed as young. The following determinations are made from the 61 adult specimens.

Length of body, introvert retracted. Mean 8,755 $\pm$ 0,319. Standard deviation 3,714 $\pm$ 0,225. Coefficient of variability 42,421 $\pm$ 2,59. Range 3—16. Bell, 1892, says that it „may be as much as a foot long, and four or five inches wide, capable of extension to twice this length or more“. In 30 of these alcoholic specimens the introvert is extended and averages 1,573 cm long, or when added to the above body length, is about $^1/_7$ of the total length.

Dorso-ventral diameter. Mean 4,066 $\pm$ 0,178. Standard deviation 2,063 $\pm$ 0,125. Coefficient of variability 50,737 $\pm$ 3,098. Range 1—8,8.

Color. — Specimens in alcohol are liverbrown to vinaceous-cinnamon, darker dorsally, and often nearly white ventrally. In some cases the tint is very dark. The young are lighter and more uniform in color.

As is generally true when specimens are kept in alcohol certain colors greatly fade (cf. Edwabds, 1908).

For living individuals Fabricius, 1780, notes the color as greenish brown. Dalyell, 1851, describes them as varying from chocolate and wood-brown to mulberry or purple, with pedicels sometimes almost white.

Stimpson, 1853, records them as black, or dark purple above and pale brown or yellowish below, some specimens being of a uniform bright yellow.

Pourtalès, 1869, describes an individual as „milk-white with yellow spots".

Tentacles. — Ten, large and equal. The normal number prevails in all but two of the 73 specimens examined. Each of the two variates has 9. In one of these, the left tentacle from the mid ventral radial canal is missing; in the other specimen the ventral from the left dorsal radial canal. Since, in each case, the tentacular canal is well developed, it may be assumed that the holothurid originally had 10 tentacles and that the apparent variation is due to the loss of the tentacle by accident.

Genital papilla. — Sexual differentiation is shown in the form of the genital papilla which arises between the two dorsal tentacles just posterior to the outer line of their bases. In my preliminary report (1909), it is noted that in the female (Pl. 13, Fig. 2), the genital papilla is a simple conical structure from 2,5 to 3,0 mm. in height and 2 mm. in diameter at the base. In the summer of 1909 I examined 12 specimens in the museum of the Academy of Science of Stockholm, 10 specimens in the University of Upsala, and 13 in the University of Copenhagen. Among these I find 4 cases in which the female papilla varies from the above simple condition. In two specimens the genital papilla is bifid, in the third, trifid (Pl. 13, Fig. 3), and in the fourth has the form of a flattened disc without subdivisions, but with 5 openings leading into the somewhat expanded cavity of the papilla. In one case an apparently bifid papilla proved to be simple, with merely a little solid elevation of skin simulating a second branch. It is evident that these variations are quite different from the condition in the male as described below and hence that sex differentiation in the form of the genital papilla is established in *Cucumaria frondosa*, and as I have shown in another paper, in some of its close allies.

In the male (Pl. 13, Fig. 4), the genital papilla is subdivided into from 4 to 30, or more, parts with a general average of 10. In side view, the papilla often resembles a cock's comb, and sometimes it has right and left halves. In one case the main papilla is made up of 21 branches, while a final single branch is quite separated from the principal part. A genital pore terminates each distal branch, while the proximal portions of the branches fuse to form larger subdivisions, lobes, which may be more or less distinct, or else all united as the common base of the papilla. The whole papilla may be extended posteriorly to a length of 6 mm or 7 mm.

A reconstruction from serial sections of the male papilla (Pl. 13, Fig. 5), demonstrates that the vas deferens (*vd*), gives off a tubule below the base of each subdivision of the papilla. Soon the tubule bifurcates to supply each of the distal branches (*a, b, c, d, e, f, g*). The gonaduct is ciliated.

Previous to my paper (1909), a subdivided genital papilla, or multiple papillae, have been known only in a few of the Elasipoda, while there is no record of differentiation in the form of male and female genital papilla. A genital papilla has been reported in the male only of *Thyone aurantiaca*, *Cucumaria elongata*, and *Cucumaria laevigata* (cf. Ludwig, 1889—1892).

Distribution of the pedicels. — Table I gives the distribution of the pedicels from the 5 radial canals in 10 of the smallest, and 2 of the larger individuals, of the collection.

The youngest stage I sectioned and reconstructed. In most of the other small specimens, the muscle sheet was stripped from the body-wall in order to count the pedicels more exactly and to determine from which side of a given radial canal the pedicel arises. All of the specimens have the 10 tentacles, enteric canal, stone-canal, Polian vesicle and gonad of the adult. Specimen 1 has in all 40 pedicels some being only rudimentary buds and all are radial. From the mid-ventral radial canal 4 arise to the right and 7 to the left. From the right and left ventral radial canals, 9 and 7, respectively, are given off ventrally and none dorsally (Pl. 13, Fig. 6).

From each of the right and left dorsal radial canals, 5 pedicels arise ventrally and 1 is terminal posteriorly, while there are none dorsally (Pl. 13, Fig. 7). In connection with the older pedicels of this stage ampullae have developed.

In following Table I, it is to be noted that in specimen 2, with 51 pedicels, the appendages have begun to appear dorsally from the lateral ventral radial canals, but not as yet similarly from the dorsal canals. Specimen 3, with 78 pedicels, has 4 pedicels dorsally from each lateral dorsal radial canal. Specimens 4 and 5, with 142 and

Table I.

Distribution of the pedicels.

Specimen			Radial canals															Interradii			
Number	Size in cm		Right ventral			Mid ventral			Left ventral			Left dorsal			Right dorsal			Right dorsal	Mid dorsal	Left dorsal	
	Length	Dorso-ventral Diameter	V	D	Total	R	L	Total	V	D	Total	V	D	Total	V	D	Total				Total
1.	0,9	0,3	9	0	9	5	7	12	7	0	7	5 1)	0	5	5 1)	0	5	0	0	0	40
2.	0,5	0,3	9	3	12	6	5	11	9	3	12	8	0	8	8	0	8	0	0	0	51
3.	0,7	0,45	13	5	18	10	10	20	13	4	17	7	4	11	8	4	12	0	0	0	78
4.	1,5	0,6	22	20	42	20	16	36	12	9	21	12	7	19	16	8	24	0	0	0	142
5.	1,5	0,3	19	16	35	19	19	38	19	16	35	11	8	19	10	8	18	0	0	0	145
6.	1,0	0,7	24	18	42	26	26	52	23	18	41	12	10	22	12	9	21	0	2	0	180
7.	2,3	1,1	25	22	47	26	26	52	25	20	45	14	16	30	14	15	29	6	17	6	232
8.	2,7	1,1	28	25	53	30	30	60	25	20	45	14	15	29	15	14	29	6	11	7	240
9.	1,9	1,2	33	26	59	34	35	70	33	23	56	20	16	36	18	15	33	12	25	11	302
10.	1,7	0,9	35	31	66	38	38	76	35	31	66	17	19	36	14	16	30	17	26	17	334
11.	8,8	4,1	116	73	189	115	113	228	108	71	179	54	44	98	50	42	92	45	70	52	953
12.	12,3	4,9	106 3)	80	186	105	105	210	105 2)	76	181	53	43	96	52	46	98	78	103	76	1028

V ventrad. D dorsad. R to right. L to left.

1) One terminal posteriorly. 2) Two interradial. 3) Three interradial.

145 pedicels respectively have a more nearly even distribution from both sides of the radial canals of the trivium. Not until specimen 6, with 180 pedicels, are found the first two pedicels budding into the mid-dorsal interradius. In the remaining 4 young holothurids there is a steady increase in the total number of pedicels and a general tendency to bilateral symmetry and an even distribution from the two sides of each radial canal. The pedicels are clearly arranged in two rows in each radius and are zigzag from side to side. It is only in the earliest stages that one can really speak of „single" rows, and then on the ventral sides of the lateral ventral and dorsal radii.

In the older specimens the pedicels are very retractile. In certain cases, near the middle of the body, some pedicels grow beyond the two typical primary rows, thus constituting irregular partial secondary rows, one to each side of the radial rows.

In the 10 very young specimens of Table I, the average ratio of pedicels in the dorsal to those in the ventral radii is as 3 : 5. This agrees with Levinsen, 1886. In the older specimens, 11 and 12, of Table I, the ratio is 3 : 6. Hence, with age, the radial series of the trivium increase in numbers proportionately more than those of the bivium.

If, including the dorsal interradial pedicels, the total number is taken, the ratio of dorsal to ventral increases from 3 : 5,4 in specimen 1, to 3 : 9 in specimen 6 which has only 2 dorsal interradial pedicels. As the number of dorsal interradial pedicels is augmented (specimens 7—12), the average ratio of dorsal to ventral pedicels again becomes 3 : 5.

Previous to this paper we have, in addition to Levinsen's observations quoted above, the following brief notes upon the distribution of the pedicels in the young. Lütken, 1857, relates that in many small examples the feet are almost solely in single radial rows. Duncan & Sladen, 1881, say of a specimen 9 mm. long, that the 2 dorsal radii have fewer pedicels and these are „in an almost straight line, except at the extremities, where the zigzag alternating character of the series is clearly manifest". In an individual of 20 mm. the more numerous feet are „in double rows of alternating suckers". Théel, 1886, notes that in small individuals the pedicels are radial, with only a very few on the dorsal interradius, while in very small specimens the pedicels are only radial. Michailovskij, 1904, records for his smallest specimen, 17 mm. long, numerous pedicels in the 3 ventral radii, but not yet in complete double rows, while fewer pedicels are irregularly distributed over the whole bivium.

With the formula $v = \frac{\pi l r^2}{2}$ (cf. EDWARDS, 1908) the mean volume of the 7 young over 1 cm long is 0,483 ccm, and their mean number of pedicels is 225. Specimen 11, of about the mean adult size, with a volume of 55,292 ccm, has 953 pedicels. Thus while the number of pedicels has increased 324%, there has been a gain in volume of 11348%, or in other words the ratio or increase in number of pedicels to volume is as 1 : 35.

Body-wall. — Tough and leathery. In the adult the thickness varies from 0,5 to 5 mm, or sometimes more, according to the degree of contraction.

Spicules of the body-wall. — While several of the authors cited on page 336 have described the spicules, still it is necessary to add certain facts and that can be done best in a redescription. The majority of the spicules lie within the most superficial layer of the body-wall. The typical well developed perforated plate is irregularly square, rounded, or more or less elongated, and about 22 μ thick.

Two sizes, small and large, may be distinguished in the long series of variates from both young and adult holothurids. We may define the large plates as those having more than 25 holes, and the small plates, with from 4 to 25 holes, bearing in mind that the whole series is more or less continuous and that probably the two sizes, in most cases, represent stages in growth. In the young a large majority are of the small size having the mean number of holes, 10, with a range from 5 to 19, the mean length 153,9 μ, with a range from 90 to 220,5 μ, and the mean diameter, 110,7 μ with a range from 49,5 to 162 μ.

In the large size the perforated plates generally have from 25 to 30 holes, but include variates with up to 62, or more, holes. These large plates average 243 μ in length, with a range from 171 μ to 315 μ, and 176 μ in diameter, with a range from 90 μ to 230 μ. The perforated plates may be smooth, or with pointed, or truncated, spines irregularly distributed over both surfaces and along the edge. Often, particularly in the plates of the large size, an irregular perforated ridge arises near the center of the plate, as in those of the tentacle (cf. Fig. 19) and the margin is extended into processes.

In some of the young holothurids, most of the spicules belong to the developmental series (Pl. 13, Fig. 8—11), beginning with a simple rod from which bars grow out to form first one larger central hole (Fig. 8), and then a second (Fig. 10), and at the same time one smaller terminal hole at each end (Fig. 9, 10). The average size of these plates is 85 $\mu \times 72$ μ.

Thus in this series a well marked button with 4 holes is formed (Fig. 10). These plates average 99 μ in length, with a range from 68 μ to 176 μ, and 63 μ in diameter, with a range from 33 μ to 86 μ. In some young individuals most of the plates are small and with few holes. In the further development of these plates, bars may grow across the larger central holes (Fig. 11), or other terminal and lateral holes may be formed, to enlarge the plate into the typical form.

In the very young, the spicules may be large, well developed, and so crowded that they overlap, or else are imperfectly developed and scattered. In either case the distribution is about the same in trivium and bivium hence my specimens do not agree with the observation of Théel, 1886, that the plates are more common in the dorsal perisome while rare, or totally absent, in the ventral.

Often one end of the perforated plate, spinose like that of the pedicel, projects from the outer surface of the body-wall. When these plates occur in large numbers the skin feels rough to the touch. In some cases longitudinal sections through the body-wall of the cloacal region reveal several heaps of larger perforated plates which are not so compact, so extensive, or composed of such large plates as the similarly placed heaps of *Cucumaria japonica.* Since these heaps are not limited to the radial regions they are not to be confused with the vestigeal anal teeth described later.

Spicules of pedicels. — a) Supporting rods and plates. The most frequent form is a somewhat elongated supporting perforated plate (Pl. 13, Fig. 12), with one end rounded, or with several larger prongs, while the other is dentate with small spines. The holes are larger toward the center and smaller and more crowded at the ends, particularly at the spinose end which projects from the surface of the pedicel wall (Pl. 13, Fig. 13).

In some spicules both ends are equally spinose. Frequently the base is curved with the wall of the pedicel. In the adult the mean number of holes is 44 with a range from 23 to 86. The mean length is 211,5 μ, with a range from 162 to 351 μ, and the mean diameter 166,5 μ, with a range from 121,5 to 301,5 μ. In the young, the mean number of holes is 7 and the size 144 $\mu \times 54$ μ, thus demonstrating a growth in these spicules correlated with the general growth of the animal. Among the supporting plates are found smaller, slender, curved supporting rods (Pl. 13, Fig. 14), with a few perforations and an outwardly projecting crest at the middle.

b) End-plates. Contrary to Selenka, 1867, and Clark, 1904, but in agreement with Ayres, 1851, Lütken, 1857, and Michailovskij 1902, 1904, I find end-plates present. The pedicel end-plate may be in the form of a single large, rounded, perforated plate with jagged edge, about 260 μ in diameter (Pl. 13, Fig. 15). The single end-plate is characteristic of the young, albeit some pedicels of holothurids of this age have a few multiple rods and rosettes.

In the adult the end-plate is always multiple, being made up of several to many rods, smaller rosettes and simple plates. In one case 65 of these elements were counted as parts of the end-plate.

The youngest specimen, and the regenerating pedicel of the adult, have the beginnings of the single, or multiple end-plates in the form of one, or several, simple, or branched rods. These appear before the other spicules develop. Sometimes, particularly in older specimens, only vestigeal end-plates are present, or they may be completely absorbed. In most cases, except in the very young holothurids, the end-plates are difficult to distinguish because of the retraction of the pedicel.

Spicules of the tentacles. — The supporting rods, plates, and rosettes are usually crowded in the contracted tentacles. These spicules are generally elongated, have knobbed spines and vary in size from that of the ordinary body-wall perforated plates in the base and main branches of the tentacles to one-half, or one-third the size, in the distal twigs of the tentacles.

The rods may be straight but very often are curved (Pl. 13, Fig. 16) in conformity to the tentacle wall. They may be without holes but usually have a few perforations. The wider perforated plates (Pl. 13, Fig. 17) are more frequent proximally, while distally the spicules are simple rods or more or less rosette-like (Pl. 13, Fig. 18).

Very often the perforated plates have toward the center a number of interconnected vertical rods and thin plates forming a crest (Pl. 13, Fig. 19). Such sharp-pointed structures, together with the spinose ends of many of the other spicules projecting from the surface of the tentacles would assist the holothurid in catching and retaining the minute organisms upon which it feeds. MICHAILOVSKIJ, 1902, briefly describes tentacular spicules.

Formless deposits. — Within the inner half of the body-wall are often found the formless deposits which DÜBEN & KOREN, 1846, 1846a, describe and figure as „irregular conglomerated calcareous lumps". DÜBEN & KOREN declare these as the only spicules of the body-wall in this species. In accord with MICHAILOVSKIJ, 1902, 1904, I find these formless deposits in the deepest layers of the body-wall of some individuals.

Anal teeth. — One anal tooth is found at the posterior termination of each mid-radial line just beyond the bases of the last pair of pedicels (Pl. 13, Fig. 20).

The anal tooth is small, 0,9 mm long and 0,6 mm wide at its base, and probably for that reason has hitherto been overlooked. The free point of the tooth projects posteriorly, slightly above the perianal surface just outside of the thickened rim of the anus (Fig. 20). Under a magnification of 420 diameters the anal tooth is seen to be constructed in the same manner as the perforated plate and seems as if made up of layers of such material interwoven to form the well defined tooth. Of the 60 holothurids examined for this character, 58% have the 5 anal teeth clearly marked while in most of the others, owing to contraction of the body-wall, their presence is not determinable. In two cases the teeth are lacking. Even in the very young, where the anal teeth are well marked they are comparatively small, not functional, and hence, in this species, must be regarded as vestigeal structures.

Presence or Absence of Spicules. — LÜTKEN, 1857, and SEMPER, 1868, describe the perforated plates as only near the pedicels. THÉEL, 1886, remarks that the plates are rare in old specimens and usually he finds them only in the pedicels, or in their neighborhood; while in very small forms, when present in all parts of the holothurid, the spicules are more crowded in the ambulacral appendages. Sometimes the spicules are entirely lacking in both young and adult specimens. SELENKA, 1867, finds no plates and „only very minute arragonite needles" which must have been of foreign origin as shown by SEMPER, 1868.

In order to determine the presence, or absence, of spicules, and their distribution when present, I have carefully examined 46 specimens, 36 being adult. Of these 15 adults, and 9 young, have the typical spicules in the body-wall, pedicels and tentacles, ranging in number from a very few and scattered to many and densely crowded. Of the remaining adults 7 have spicules only in the walls of the pedicels and tentacles, and 6 others have only the multiple end-plates in the pedicels but with abundant typical tentacle spicules. 9 specimens (20 %), 8 adult and 1 young, do not seem to have spicules in the body-wall and pedicels, but 3 of these have a few, and 1, many spicules in the tentacles. Where the spicules are not present, in many cases, especially in the walls of the pedicels, the spaces from which these calcareous structures have been dissolved are clearly seen. It might be thought that the spicules had been dissolved by acid alcohol. However in all but 4 of the 46 specimens here considered this cannot be the case because of the presence of spicules, at least in the tentacles. Of the 3 remaining specimens, 1 was preserved in the same jar with individuals having numerous spicules, hence we may safely conclude the dissolution of spicules to have been during the life of the holothurids.

Usually the spicules are relatively much more abundant in the young of *Cucumaria frondosa* and are often densely crowded. With advancing age, and possibly under changes in the physiological condition of the individual at present unknown, the spicules are dissolved first in the body-wall, then in the walls of the pedicels, until only their end-plates persist, and finally in the tentacles. There is not, in this species, a series of degenerative changes analogous to those described for *Stichopus japonica* by Mitsukuri, 1897. In *Cucumaria frondosa* it is simply a question of the presence, or absence, of the spicules in certain parts, or the whole, of the specimen. Östergren, 1896, showed that the young of *Mesothuria intestinalis* (Ascan.) have many tables like those of *Mesothuria multipes* Ludwig while in the adult such tables occur but rarely. The same author, 1898, demonstrates that *Holothuria aphanes* Lampert is the young stage of *Holothuria impatiens* (Forsk.). The smaller, and slightly different, spicules of the former are dissolved and after a period with none of these calcareous particles present, the larger tables and buckles of *Holothuria impatiens* appear. Hérouard, 1889, says that in *Thyone subvillosa* the spicules are more complicated in the young than the large majority of them are in the adult, and that in some species they disappear entirely.

Polian vesicle. — Of the 79 specimens examined all have the mode of one Polian vesicle in the left dorsal inter-radius. Five of these specimens have two vesicles; three with one additional vesicle in the right dorsal inter-radius; one with one additional in the right ventral inter-radius; and one with one additional in the left ventral inter-radius.

Thus there is an adherence of 93,7% to the above described modal condition in the number and location of the Polian vesicle. The length in centimeters is: mean 7,882 ± 0,435; standard deviation 4,964 ± 0,307; coefficient of variability 62,978 ± 3,909; range 0,6—16.

Stone-canal. — Single, more or less folded and running along, or just back of, the free anterior edge of the mid-dorsal mesentary (Pl. 13, Fig. 21). Length in millimeters; mean 4,734 ± 0,196; standard deviation 2,250 ± 0,138; coefficient of variability 47,528 ± 2,926, range 1—10,2.

The madreporite projects freely (Fig. 21), and is greatly convoluted. Of the 60 madreporites examined, 55 (91,6%) are spherical in form (Fig. 21), 2 (3,3%) elongated (Pl. 13, Fig. 22), 1 (1,7%) pear-shaped, 1 (1,7%) conical, 1 (1,7%) irregular, and 1 (1,7%) not determinable. The spherical madreporite has the following diameter in millimeters; mean 1,273 ± 0,068; standard deviation 0,750 ± 0,048; coefficient of variability 58,915 ± 3,789, range 0,7—4.

In the very young (Pl. 13, Fig. 23), the stone-canal is almost straight and the folding of the primitive terminal disc into the three first lobes is shown.

Selenka, 1867, describes the folded madreporite as „composed of 12—20 small leaflets"; Clark, 1904, figures a variate with the madreporite divided into 6 parts distributed along the stone-canal.

Calcareous ring. — Not always perfectly preserved, particularly in the older specimens. All of the 5 radialia and the 5 interradialia have anterior prolongations and have the posterior margins notched. The radiale is somewhat larger and more deeply notched than the interradiale and these differences are accentuated with age. In the young (Pl. 13, Fig. 24), the pieces of the calcareous ring have a more definite outline.

Selenka, 1867, erroneously describes a second, or „upper, calcareous ring" from which posterior projections extend to the interradialia of the „chief ring". Selenka's „upper calcareous ring" consists of calcareous fibres which bind together the anterior ends of all of the pieces of the calcareous ring (Lampert, 1885), and the posterior projections of Selenka's „upper ring" are merely the anterior processes of the interradialia (Semper, 1868). Théel, 1886, describes the calcareous ring as „slender, pliable, spongy, and in a comparatively low stage of development without posterior prolongations".

Gonads. — In two tufts, one either side of the mid-dorsal mesentery. In a very young specimen (number 3, Table I), about 5 genital tubes have sprouted from each half of the gonad anlage (Pl. 13, Fig. 25), but at this time the cells are primordial.

It is only after the holothurid is much larger that sex is determinable.

Respiratory trees. — Two respiratory trees arise from the anterior end of the cloaca one to the right, and one to the left, of the termination of the intestine. The inner wall of each tree, at its opening, is continuous with the enteric wall and the trees and the branches are fastened to the body-wall by strands of connective tissue. Each tree consists of a major, primary stem, lying in a lateral dorsal interradius, and of a minor, secondary stem, in a lateral ventral interradius. These two stems diverge from a common basal trunk from 3 to 5 mm long. The secondary is about one-third the length of the primary stem. The right primary stem extends forward to near the anterior end of the coelom while the left one is not quite so long. In a holothurid 9,4 cm long and 4,8 cm in diameter, the right primary stem gives off 50 lateral branches, of which 10 are about as long as the secondary stem and considerably branched, while the rest are either simple or with few branches. The left primary stem has 40 lateral branches, of which 10 are much branched and as large as the secondary stem. This stem is crossed and bound down by the mesentery of the second enteric loop in its diagonal course anteriorly along the left dorsal interradius.

In a very young specimen (0,7 cm long, 0,45 cm diameter), the primary stem (Pl. 13, Fig. 26a), the secondary stem (b), and the buds of 10 branches have appeared. The fine strands of connective tissue (c) which anchor this organ to the body-wall are to be noted. Levinsen, 1886, says that in a specimen 2,3 cm long, one respiratory tree has 38, and the other, 42 branches.

Muscles. — The five radial, longitudinal muscle bands are simple. Each band is broad and thinner along the median line so that sections of a transversely contracted band show a deep furrow toward the body-wall, and it appears almost as if the band were divided and the halves connected by a thin bridge of the common muscle substance.

The similarly constructed introvert retractors split off from the longitudinal muscles, somewhat back of the middle of the body in a contracted specimen. Each retractor is inserted upon the anterior projection of the related radiale. In some cases the simple retractor muscle divides into a pair of bands.

The circular muscles and the cloaca extensors are well developed.

Enteric canal. — Östergren, 1907, shows how prone we are to take for granted as true the long accepted descriptions of anatomical structures. This author finds (1898), contrary to the established rule for holothurians in general, that in the Cucumariidae, except the Psolinae, the mesentery of the third enteric loop is attached to the left of the mid-ventral radial muscle and the third loop really belongs to the mid-ventral radius. I too find this attachment to the left of the radial muscle of the mid-ventral radius in *Cucumaria frondosa* and other species of the genus *Cucumaria*. In some specimens of *Cucumaria frondosa* the mesentery is found on the muscle band itself for the posterior third of its course.

In agreement with Östergren, 1898, I do not find Cuvierian organs as described by Joh. Müller.

Habitat. — Two-thirds circumpolar; south to Britain in the eastern Atlantic; to some 60 miles south and a little east of Nantucket Island, Mass. (lat. 40° 19′ 30″ N., long. 69° 29′ 10″ W.); also once reported by Pourtalès, 1869, of Florida in 118 fathoms, in the western Atlantic.

Ludwig, 1900, gives an admirable statement of the details of the geographical distribution up to that time. The occurence of *Cucumaria frondosa* in the Pacific Ocean was reported by Ayres, 1855, but was questioned by Verrill, 1867, Ludwig, 1900, and Clark, 1904. In my paper of 1907 this species was given from the Pacific but since then from my work on the large collections of the United States National Museum, I have concluded that there are at least four species in the Pacific similar to but distinct from *Cucumaria frondosa*. One of these is *Cucumaria japonica* Semper, 1868, while the specimens identified as of this type by Lampert, 1885, Clark, 1902, and Edwards, 1907, belong to a second form, *Cucumaria miniata* Brandt, 1835. The other 2 species are *Cucumaria californica* Semper, 1868, and *Cucumaria fallax* Ludwig, 1874.

Würzburg, Jan. 8, 1910.

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Explanation of plate.

All the figures were drawn with the aid of an Abbe camera lucida, from preparations of *Cucumaria frondosa* (Gunner).

Plate 13.

Fig. 1. Adult female. Dorsal view, introvert extended. The genital papilla appears in the mid-dorsal line, just back of the contracted tentacles. At the base of the introvert four or five pedicels in each of the two lateral dorsal, and the two lateral ventral, radii, are partly extended, but most of the pedicels are deeply retracted, leaving pits in the wrinkled skin. The anus marks the posterior end of the body. Natural size.

Fig. 2. Female genital papilla. 8 : 1.

Fig. 3. Female genital papilla with three subdivisions. 7 : 1.

Fig. 4. Male genital papilla, subdivided into seven lobes, each bifid, and with two terminal pores. 8 : 1.

Fig. 5. Reconstruction of the male genital papilla represented in Fig. 4. The end of the vas deferens, *vd*, with its bifurcated terminal tubules, *a—g*, is shown. 8 : 1.

Fig. 6. Ventral view of a young specimen with tentacles and pedicels partly extended. 9 : 1.

Fig. 7. Dorsal view of specimen shown in Fig. 6. Six pedicels appear in each lateral dorsal radius, and none in the mid-dorsal interradius. The anus lies dorsally, near the posterior end of the body. 9 : 1.

Fig. 8—11. Stages in the development of the perforated plates. 210 : 1.

Fig. 12 and 13. Supporting perforated plates of the pedicel. 210 : 1.

Fig. 14. Supporting rod of the pedicel. 210 : 1.

Fig. 15. End-plate of the pedicel from a young holothurid. 210 : 1.

Fig. 16—18. Knobbed and spinose supporting rods, plates and rosettes of the tentacles. 210 : 1.

Fig. 19. Profile view of a tentacle perforated plate with a central crest. 140 : 1.

Fig. 20. View of the posterior end of a very young specimen. Just outside of the thickened rim of the central anus are the five anal teeth, each posterior to, and between, the last two pedicels of the radius. *Bv* bivium, *Tv* trivium. 7 : 1.

Fig. 21. Stone-canal, along the mid-dorsal mesentery, from the edge of which the distal, much folded, spherical madreporite projects. $4^1/_2$: 1.

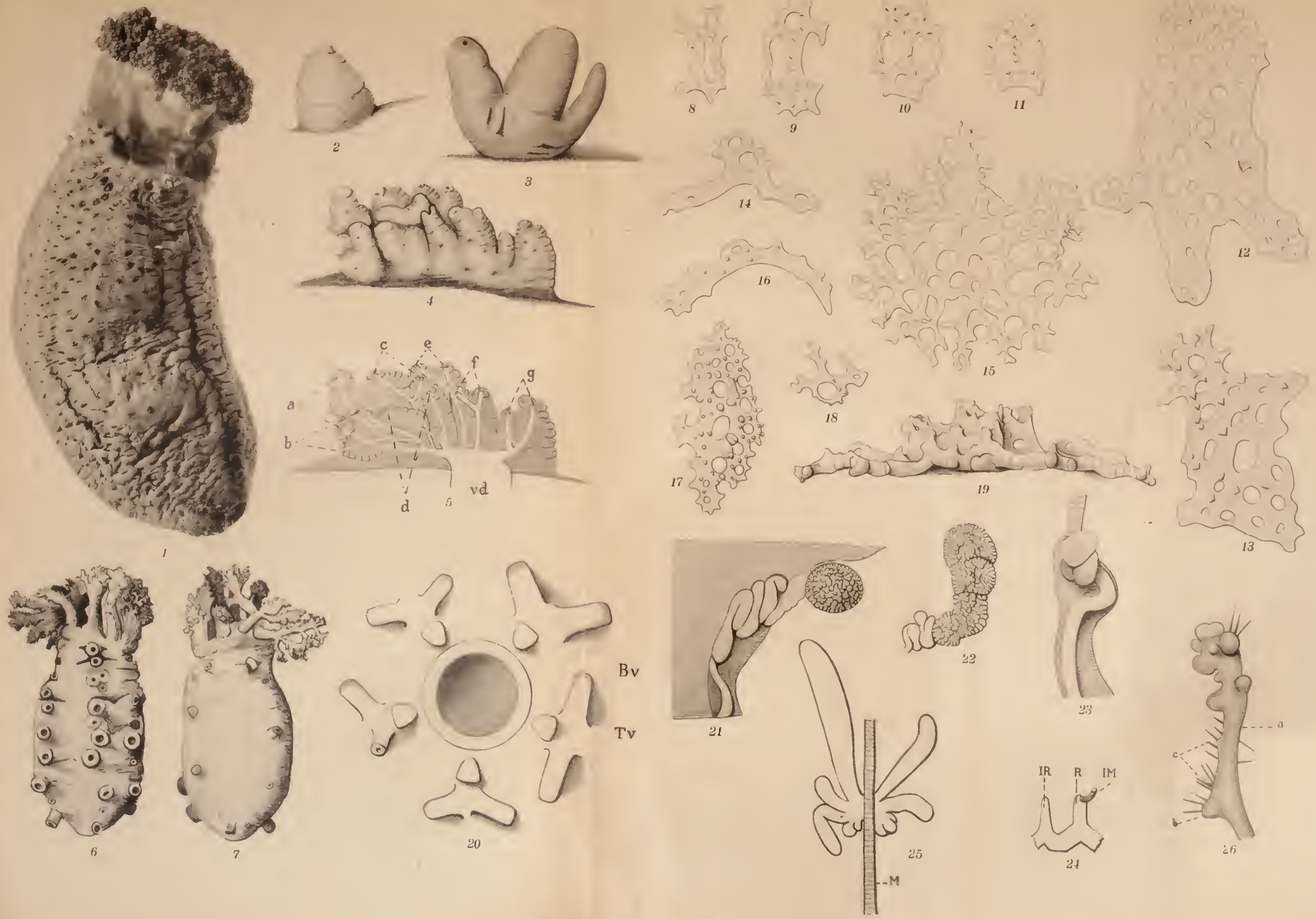
Fig. 22. Elongated form of madreporite. $4^1/_2$: 1.

Fig. 23. Developmental stage of the stone-canal and the madreporite, from a very young specimen. Madreporite in three folds. 54 : 1.

Fig. 24. Radiale, *R*, and interradiale, *IR*, of the calcareous ring from a young specimen. Introvert retractor muscle, *rm*. 9 : 1.

Fig. 25. Gonad of a very young individual. *M* mesentery. 108 : 1.

Fig. 26. Right respiratory tree of a very young specimen. *a* primary stem, *b* secondary stem, *c* connective tissue strands. 18 : 1.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