

[from Ludwig, Hubert. 1889-1892. Zweiter Band. Dritte Abtheilung. Echinodermen (Stachelhäuter), I. Buch. Die Seewalzen, VI+2+460 pages, XVII plates, In H. G. Bronn (editor), Klassen und Ordnungen des Thier-Reichs. Leipzig: C. F. Winter; pages 1-23; translated by Alexander M. Kerr.]

A. Introduction.

I. Name.

Among the older authors (Belon, Aldrovandi, Jonstonus) the sea cucumbers were called: *genitale marinum*, *mentula marina*, *priapus marinus*, *pudendum*, what the Italians called *cazzo di mare* and the Greeks *psolo*, whose meanings are the same and in the sense described by Bohadsch:

aquam ejicit, corpusque instar ligni indurescit, quae indurescentia, aquae ejaculatio una cum cylindrica corporis forma ansam dedisse videtur, quod hoc genus veteres mentulam appellarent.

Aristotle's name *ὄλοθούριον* has a similar meaning, a name taken up by Rondelet and which has come into general use since Linnaeus. The root *θούριος* equals *θούραϊος*, which has among its meanings "vulgar."

The comparison to a cucumber is based on Pliny: *cucumis marinus*, and according to Grube's information, *cucumero di mare* is still used today in the Adriatic.*

Of the Scandinavian researchers, Gunner calls it a sea sack (Swedish *sjö punge*) and Luetken, sea sausage (Danish *sø pølser*).

As a German appellation, Oken tried to introduce the name "Trule," which he gave up later, however, and replaced with Spritzwürmer [squirting worm]. Burmeister called it Lederhäuter [leather skin], also and Sternwürmer [star worm]. Bronn used the

*for *Cucumaria Planci*, while *Holothuria tubulosa* is differentiated there as *cazzo di mare*. Furthermore, and according to Krohn, *Stichopus regalis* is called *pagnotella di mare* by Neapolitans "because of its similarity to a biscuit."

names Walzenstrahler [cylinder/roller bar] and Lederstrahler [leather bar]. Others preferred the designations Seewalzen [sea roller] and Seegurken [sea cucumber]. From all of these designations the German name Seewalzen became the standard term for the whole class.

In the scientific terminology, one most frequently meets designations which are derived from the name of the class, hence Holothuridea with Blainville, Holothurina with Brandt, Holothurida with Gray, Holothurioidae with L. Agassiz and finally with v. Siebold Holothurioidea. Siebold's term was applied by Bronn in the first volume of this work. Of the other scientific names that have been coined, neither Fleming's Fistulidae, the Cirrhi-Vermigrada suggested by Forbes, Bronn's Scytactinota nor Austen's Ascidiastella came into widespread use. Burmeister's Scytodermata, however, still frequently used.

II. Literature.

(Entries in this relatively complete bibliography are referenced by enparentetical Arabic numerals behind the name of the relevant author mentioned in the text.)

[287 citations excluded – A.M.K.]

III. History.

As a common animal on the coasts of the Mediterranean Sea, the holothurian has long been known by local residents. It is however doubtful whether the animal which Aristotle mentions by the name *ὀλοθούριον* and describes as comparable to sponges, unfeeling, plant-like in nature (unattached and motionless) is in fact a holothurian. Joh. Müller and Grube believe rather that Aristotle mentions a sea cucumber elsewhere when he refers to a black, round, uniformly thick and bar-shaped animal. Pliny mentions under the name *cucumis marinus* a sea animal of eponymous shape, which we call today *Cucumaria Planci*. After the time of Pliny there is no mention of holothurians until the end

of the Middle Ages. Only by the mid-16th century are they again mentioned as scientific inquiry develops.

Belon (26) was the first to provide an undoubted description of a holothurian under the name *genitale marinum* and, even then, he correctly detected the similarity of their movement and organs with those of the sea urchin and sea stars. Belon's description is the oldest, here literally:

genitale marinum vulgus italicum cazo marino, graecum psoli nuncupat. Exanguie maris purgamentum. Suas promuscides quando vut exserit. Acetabulis quae in promuscidibus habet, lapidibus haeret, in quibus plus quam quattuor millia nonnunquam annumeres. Ex anteriore autem capitis parte rursus crinitas emittit veluti arbusculas acetabulis plenas, quibus quidquid palpat ad os adducit. Os in gyrum ossiculis dentatum habet, praeterea nullis ossibus alibi praeditum.

Following soon after this first description, came the first figure of a holothurian, by Rondelet (216). He added to his figure a short description, from which it can be inferred that the animal was a type of aspidochirote. Rondelet was also the first to apply the Aristotelian name *Holothurium* to an animal in the sense that the term is used today. He included, however, with the holothurian the heteropods, by illustrating and describing a type of Pterotrachean as a second species of holothurian. Also a *cucumis marinus* is included by Rondelet, which can hardly be interpreted from the figure as a true holothurian. Later, Columna (41) under the name *puendum regale* refers to a specimen nearly identical in form to that of *Stichopus regalis*. After almost a hundred years, Aldrovandi (4) repeated Rondelet's description without modification. Another century passes again until Bianchi (Janus Plancus) (205) who illustrated and described a species obviously of the cucumarian type (probably today's *Cucumaria Planci* v. Marenz. [in errata given correctly as "Br."]) and noted correctly its relationship with the sea urchins via the description "*novum genus echinorum marinorum coiaceum seu cartilagineum.*"

Bohadsch (30) made the first exacting investigation of a holothurian, a Mediterranean species (probably *Holothuria tubulosa*). He differentiated them from the *Hydra*, calling them "Zitterblase" [trembling bladder], a translation of his Latin term by Leske. Bohadsch mentioned the back of the animal having atop

small bumps "feeling threads," which he compares with the appropriate organs of the sea stars and sea urchins. He also observed the movement of the twenty tentacles taking in food and the cloacal opening squirting out water, as well as the occasional discharging of entrails. He knows the transverse musculature of the body already, though not the longitudinal musculature, and interprets the appearance of intestines with blind ends near the "esophagus" quite correctly as the gonads, even if he errs in the fact that he lets the eggs exit by the mouth. The "twenty worm-like bands," which he found attached to the calcareous ring, are certainly the tentacle ampullae. Also the first description of the intestinal tract is due to Bohadsch.

Gärtner (68), publishing at nearly the same time as Bohadsch, described a dendrochirote holothurian from the south coast of Cornwall under the name *Hydra corolliflora** (his other species of *Hydra* are Actinians), and compared its locomotory organs with the suckers of sea stars and gave a figure of a specimen, which with some confidence, is recognisable as today's *Cucumaria elongata* Düb. and Kor.

Many more later authors treated holothurians in detail. Strussenfelt (252) did so with the northern European form *Psolus phantapus* under the name "Seegespenst" [sea ghost] ("Hexenfuss [witches' foot], *Phantapus*"). He was the first to examine the internal anatomy of a dendrochirote holothurian, and today that work still provides a useful account. He detected not only the five longitudinal muscles of the body wall, the muscles retracting the throat, the calcareous ring (though already mentioned by Belon), the tentacle ampullae and the intestine, but also the mesenteries, as well as the attachment strands of the cloaca. He also mentions the Polian vesicle (naturally, not yet under this name) and what he calls two bundles of intestine-like threads at the dorsal mesentery, undoubtedly the reproductive organs.

Also at that time, S. Pallas supplied the first anatomical investigation of a southern European holothurian (195). Under the name *Actinia doliolum*, he described a species called *Colochirus australis* recently reported from the Cape of Good Hope and strove to investigate its organisation. Pallas gave a detailed description that was good for its day and now pardonable because of its age.

* not *corallifera*, according to Semper (238) and, more recently, Théel (267).

For example, he regards the sex organs as "glands producing a digestive juice," and that which he interprets as ovary is obviously the respiratory organs, while he lets the respiratory organs insert at the throat. Longitudinal muscles he calls tendons. And finally he records, as did Strussenfelt before him, that the calcareous ring, which he compares with the lantern of sea urchins, is composed of only five pieces.

While anatomical knowledge of holothurians begins with Bohadsch, Strussenfelt and Pallas, knowledge of their diversity expands further as well. Gunner (89) described two northern European species: *Cucumaria frondosa* under the name of *Holothuria frondosa*, as well as a species still known today as *Holothuria tremula*. Forskål (65) described four species* from the Roth Sea, which he arranged in the genus *Fistularia* (while placing *Velella* and *Porpita* [siphonophore hydrozoans] under the name *Holothuria*). O.F. Müller (187 and 188) knew of a number of northern European species, which he combined under the generic name *Holothuria*,** and Pennant (199) described under the name *Holothuria pentactes* today's *Cucumaria frondosa*, while Strussenfelt correctly placed the "Seegespenst" [sea ghost] (*Psolus phantapus*) specified as *Ascidia rustica* in the holothurians. Among the three previously mentioned researchers, it is however only O.F. Müller, who included anatomical considerations in his investigations, without coming much further in this regard, however, than many of his predecessors. His only novel finding is a "fat vessel," as he understood the function of the respiratory organs to be, but whose true interpretation still remained hidden.

Later, Diequemare (51) with Havre observed a *cucumarie* which is probably identical with Gärtner's *Hydra corolliflora*, describing it under the name *le fleurilarde*. O. Fabricius' (61) *Fauna grönlandica* also appeared in which he discussed four species (excluding his two forms belonging to the Gephyrea) of holothurians not only from external features, but also from their internal anatomy. Fabricius certainly mentions the bends of the intestine first, by speaking of an *intestinum triplicatum*. However, he perpetuates the misleading view that the gonadal tubules are

* among them also two synaptids, the first of this group to occur in the literature.

** After Linnaeus (145) in the 12th Edition of his *Systema naturae* had modified the linguistically more correct *Holothurium* (Aristotle, Rondelet) to *Holothuria* and had applied the latter term to some genuine sea cucumbers.

appendices of the intestine. On the other hand, he shows the calcareous ring of his *Holothuria* (now *Chiridota*) *laevis* to be assembled, quite correctly, from twelve pieces. He makes other observations as well, which follow those from Belon, Gärtner, Forskål, Bohadsch and O.F. Müller.

In anatomical relationships, the next advance was due to Cuvier (76 ["46" in errata]), who correctly interpreted the function of the respiratory organs and described for the first time the intestinal vessels. Cuvier is also aware of the cloaca and the double bend in the intestine and is the first to note the nervous system. Cuvier has the calcareous ring formed from ten pieces, but errs in calling the tentacle ampullae saliva organs and in designating as male gonads the organs that he discovers which are later named Cuvierian organs. In connection with the aforementioned mistake, he regards the actual gonads as exclusively ovaries and therefore considers all holothurians as hermaphrodites. Cuvier is also credited with discerning the systematic relationship between holothurians and the sea urchins and sea stars, which up to then had only been noted by Belon and Plancus, and for placing these animals in the echinoderms.

Later, Motagu (175) described two English species and Oken (193) attempted to systematically organise taxa well-known up to then (and whereby he revised the species of *Thyone* and *Psolus*). Tiedemann (273) produced a landmark work on the anatomy of the tubular holothurian (*Holothuria tubulosa*) of Triest. In this work the first investigation is made into the finer structure of the individual organs, e.g. the intestine and the skin, as well as subjecting the digestive organs to an exacting description. He included a description of the haemal and water-vascular systems. The divisions of the latter (Tiedemann does not know the term "water vascular system" yet) are recognized here for the first time as related components of a single system. Only the true nature of the stone canal remains hidden to Tiedemann, as he supposes them to be the testicles. He is also the discoverer of the exterior genital aperture.

After Tiedemann, advances in the knowledge of the internal anatomy experience a short hiatus and the next years bring mostly systematic works and descriptions of new taxa by Cuvier, Goldfuss, Chamisso, Lesueur, Delle Chiaje, Risso, Fleming, Rüppell and F.S. Leuckart, Eschscholtz, Blainville, Lesson and Quoy and Gaimard.

Also, Jäger (110) added only a few new insights to Tiedemann's anatomical discoveries. He did correct the not quite applicable description that Tiedemann had given to the position of the intestinal loops and respiratory organs. The main service of Jäger's paper, however, is in his attempt to make a high-level systematic arrangement of all the forms well-known to then.

Meanwhile, H. Mertens (viz. Ludwig 152) during his journey around the earth to several islands in the Pacific Ocean had been employed in anatomical investigations of holothurians. It is unfortunate that the death of the talented researcher prevented him from publishing his observations which are still today available only in manuscript form. From the systematic aspects of Mertens' records, J.F. Brandt (33) constructed an artificial system for holothurians which included a considerable number of new genera and larger divisions without consideration of the far more natural arrangement and delimitations by Jäger, thus demonstrating the need to avoid untenably small divisions in the future (e.g., the dismantling of the footed holothurians into *Homoiopodes* and *Heteropodes*, then the groups of the *Detopneumones* and the *Homoiopodes apneumones*, furthermore the genera *Oncinolabes*, *Liosoma*, *Aspidochir*, *Diploperideris*, *Dactylota*).

Burmeister (35) introduced the name *Scytodermata* for holothurians, but in which he also counted gephyreans, just like most former researchers. The new order was included in *Echinodermata* (i.e. the *Crinoidea*, *Asteroidea* and *Echinoidea*) and divided into four families, *Pentactidae*, *Holothuridae*, *Psolidae* and *Synaptidae*. Also Lamarck (133) and Dujardin produced a systematic arrangement, which remained however in its worth far below the work of Jäger, Brandt and Burmeister.

Substantial progress in the knowledge of European forms resulted from Grube's (81) investigations in the Mediterranean and Forbes' (64) description of the species living on the coasts of England. The current use of tentacle morphology in the delimitation and diagnosis of the aspidochirotes, dendrochirotes and chirodotes* (= synaptids) is also due to Grube.

Anatomical knowledge was also moving forward through the work of Delle Chiaje (39), as well as by Krohn's discovery

*The taxon *Chirodota* was designated only later; viz. footnote p. 27. [Footnote from page 27: However, *Chirodota* is not the correct spelling. Eschscholtz, to which the name is due, derives it from *Χειριδωτός* and always writes it, just like the next authors after him, *Chiridota*.]

(123) of the up to then only presumed nervous system. Krohn (122) is also first to correctly interpret the stone canal as the homolog of the eponymous structure in sea stars. Also at this time, Wagner (285) along with Valentin finally disproved using *Holothuria tubulosa* (Gmel.) that holothurians are hermaphrodites, a view firmly held by Cuvier, Tiedemann and Jäger.

Then, Quatrefages (210) published the first detailed investigation of a *Synapta*, in which he also endeavored to examine finer histological details. He gave the first detailed description of the anchors and anchor plates in the skin, discussed the structure of the skin, the musculature and the intestine, found "suction cups" at the tentacles which are now known as sensory organs and he discovered the secondary condition of the gonads of the synaptids. On the other hand, he could find neither the blood vessels nor the nervous system and described the nesselorgane [nettle organ] of the skin and pores of the body cavity, **welche von allen späteren Forschern in Abrede gestellt wurden.**

The anatomical knowledge of the dendrochirotes was pioneered by Koren (119) with his splendid description of the internal morphology of *Thyone fusus* (O.F. Müll.) and *Psolus squamatus* (Düb. and Kor.). Together with Düben (53 and 54), there was for the first time a detailed investigation of the diversity of calcareous ossicles and a demonstration of their importance in systematics, as well as a pioneering systematic treatment of Scandinavian species. Then, descriptions of numerous new species and genera follow by Troschel (274), Ayres (7), Stimpson (245, 246, 247), Pourtalés (207), Steenstrup (244), biological observations of Peach (198) and Dalyell (48) and attempts to arrange everything known up to then by anatomical and systematic relationships, namely, v. Siebold (240), Gray (76), van der Hoeven (104).

Leydig (142) added to the anatomy of the *Synapta* given by Quatrefages by providing new histological data for a number of organs. But before and during this time, Joh. Müller (178-185) had also been studying synaptids. The outstanding results of his ground-breaking research on the development of holothurians, generalisable to the remaining classes of echinoderms, extended and deepened the anatomical and systematic knowledge of this group, and above all cleared the darkness which was up to then upon the history of the development of these animals. At this juncture, the relevant points of Joh. Müller's investigations can be

made only briefly. In systematic matters, he promoted knowledge of the tropical synaptids, provided the first description of a genuine molpadid whose relationships with the remaining holothurian families he argued. Concerning anatomy, it is to be emphasised that he found the intestinal blood vessels overlooked by Quatrefages in the synaptids, as well as described in greater detail the peculiar ciliated cups of the body cavity already seen by Mertens. He also described the structure of the stone canals and Cuvierian organs in great detail for the first time, as well as giving those organs their name. Finally, he introduced and justified the still useful distinction of back and ventral sides as bivium and trivium, respectively, along with the terms ambulacrum and interambulacrum. The history of development owes to him the discovery of metamorphosis in holothurians via its larval form called an *Auricularia*, whose body and whose transformation **in die sog.** His investigations of the larva were pioneering. Also, his pupil Krohn (124 and 125) gave a small evolutionary contribution and Danielssen and a Koren (220) included the Nordic holothurians in evolutionary studies by proving that in addition to the involved metamorphosis investigated by Müller, there is also an abbreviated manner of development.

After Joh. Müller's work, the remainder of the decade brought the discovery of the remarkable genus *Rhopalodina* by J.E. Gray (75) and some histological publications of Leydig (143 and 144) and Kölliker (118), a number of smaller and larger contributions to systematics and anatomy by Lütken (162), M. Sars (221 and 222), M'Andrew and Barrett (163), Stimpson (248 and 249), Held (95), Philippi (204), Woodward and Barrett (286), Kererstein (115), Grube (84 and 85) and Anderson (5). Of the work by the researchers just mentioned, that from Lütken and M. Sars are most outstanding. Lütken gave a detailed critical description of the Greenland holothurians and discussed also their geographic and bathymetric [Ludwig says here "horizontal and vertical"] distributions. M. Sars on the other hand turned himself first to all of the Mediterranean forms, whose knowledge he increased in a substantial way, and, only a few years later, published his important, anatomically detailed account of the species occurring on the Norwegian coast.

Just before this, Bronn (34), in the first edition of this work, delivered a comprehensive account of the entire class, characterised by a prudent and, for the time, rather exhaustive

treatment, while a similar attempt from Dujardin and Hupé (55) remained in all ways far behind Bronn's performance.

Highlights from the intense research achieved in the years 1861-1876, are on the one hand, the evolutionary investigations of Baur (10), Kowalevsky (121), Meschnikoff (169) and Selenka (231), and on the other hand, the global systematic and anatomical work of Selenka's (229 and 230) and, quite notably, Semper's (238 and 239).

Baur surmised that Joh. Müller's "*Auricularia* with calcareous wheels" is the larva of *Synapta digitata* (Mont.), and he followed its development from the larval stage to its formation into a young *Synapta* in order to more deeply investigate the development of the individual organs. In this regard, the investigations of Metschnikoffs were more successful still, succeeding quite well in making clear the significance of the enterocoel. The first developmental studies of organs were of the gonads and carried out by Kowalevsky on their furrowing and structure, then Selenka investigated their development in a more detailed fashion. One also owes to L. Agassiz (1) from this time a small communication on the development of *Psolus fabricii* (Düb. and Kor.).

The systematic handling that Selenka had done of the whole class, his list of numerous new genera and species, a compilation of all forms known up to then, plus a quantity of excellent observations on anatomy was nevertheless very soon outdated by the even broader work of Semper. Semper had used his stay of several years on the Philippines for a detailed study of the tropical holothurians and was thereby in a position to supply an extensive monograph, which not only promoted knowledge of the forms, but also the rougher and finer structure, as well as the way of life and the geographical distributions to quite an extraordinary degree and, at the same time, sufficiently energized other researchers to perform investigations in this area.

From the fewer significant works coming out of the next and longer time period, it is worth mentioning here a number of substantial systematic contributions. Verrill (276-278) and Pourtalés (208 and 209) investigated the American species, M. Sars (224) and the late G.O. Sars (219) those of northern Europe, Heller (96) and v. Marenzeller (164) the Mediterranean fauna, also through Hutton (108), who steered attention to the species of New Zealand and myself (147), who described a number of new forms

from different areas. In addition, smaller reports appeared by Herapath (97), Herklots (99), Lankaster (136), Norman (191), Grube (86-88), Brady and Robertson (32), Hodge (103), Graber (72), M'Intosh (172), Möbius and Bütschli (173) and Stossich (251). Finally, from these years also comes the first news of an undoubted occurrence of a fossil holothurian by Schwager (228), who discovered skin spicules in Jurassic deposits.

In the following years, anatomical research of holothurians was again taken up by Greeff (77 And 78), Teu (261) and Kingsley (177) and with greater emphasis on histology, Jourdan (114), Hamann (91, 92, 93) and Semon (233-236), followed by Vogt and Yung (284) and Hérouard (101 and 102). Knowledge of developmental history was furthered by Selenka (232), who continues detailed analysis of the gonads and records important observations on the emergence of the nervous system and the musculature, as well as by Semon (237), who made the metamorphosis and organ development of *Synapta digitata* (Mont.) the subject of a profound investigation. Goette (70) and Metschnikoff (170) published smaller articles on ontogeny, while A. Agassiz (2) provided a review up to the year 1883 on the generally agreed upon aspects of holothurian development.

Zoological research of the deep sea has provided the most important results since 1877 to date. Théel is to be considered here before all others by informing us first of the up to then quite unknown organisation of *Elpidia glacialis* (263), and using it to set up the order of the elasipods, or deepsea holothurians. Soon this order populated itself with a quantity of these most interesting animal forms, some by Danielssen and Koren (49 and 50) from the yield of the Norwegian North Sea expedition, but most of which were described by Théel (264, 266 and 268) from the collections brought home from the travels of the English ship "Challenger" and the North American "Blake." Recently, also the French sea expeditions contributed to the knowledge of the elasipods, though only provisional messages have appeared, in particular from Perrier (200) and Petit (201-203).

In addition, since 1876, the older orders of holothurians have experienced a substantial increase in new genera and species, in consequence of the larger research travels, by the results of smaller expeditions (like the "Gazelle," already mentioned, the "Vettor Pisani" and "Prince Albert," among others), and in part by more exacting research on the European and non-European coastal

fauna. Particularly noteworthy are the quantity of the contributions referring to the Arctic holothurians, firstly those of Danielssen (120), Danielssen and Koren (49 and 50) and Théel (262), then of v. Marenzeller (166), Ljungman (146), Duncan and Sladen (56), Hoffmann (105), Stuxberg (256 and 257), Levinsen (141), Fischer (62) and me in this regard (158). The Antarctic forms, which are characterised partially by mechanisms for a more or less inward breeding system, were reported by Studer (253-255), Verrill (279), Thomson (271 and 272), Smith (243), Bell (11), Lampert (135) and myself (157, 160 and 161a). Brazilian holothurians are referred to by Rathbun (212) and me (153 and 155), west African forms by Greeff (79) and me (148, 161a and c). Concerning the fauna of the Roth Sea, as well as the Indian and Pacific Oceans, contributions are supplied by Sluiter (241 and 242), Haacke (in Möbius 174), v. Marenzeller (167), Bell (13, 17, 19-22) and myself (152, 154, 156, 157, 160, 161a and b), while Hutton (109) and Parker (197) contributed some species from New Zealand. Verrill (281 to 283) continued in his earlier efforts to know the North American species. And finally, for the European forms, in particular those of the Mediterranean, I (149) produced a synonymy, Carus (36) a diagnostic outline of Mediterranean holothurians, while v. Marenzeller (165), myself (151) and Semon (235) described new or poorly known species and Bell (15 and 16), Herdman (98), Barrois (9) and Hérouard (100) merit mention for increasing knowledge of the species living on the English and French coasts.

For biological contributions we owe Gräffe (73), Schmidlein (226) and Noll (190a), in particular the physiological-chemical work by Krukenberg (126-131) and, recently, also to Howell (106 and 107).

Also on the palaeontological side, knowledge increased by the observations of Etheridge (60) and Počta (206).

Finally, and almost at the same time, Lampert (134) and Théel (267) gave global overviews, describing and placing all the up to then well-known species in systematic order, as well as their geographic and bathymetric distributions in tabular outlines. Of these two larger works, with which we want to conclude this historical introduction, Théel places himself into the foreground by

the broader base of his observations, by better descriptions and sharper criticism.