Introduction

HOW THE ANIMAL NATURE OF MARINE CNIDARIANS WAS RECOGNIZED AND THE NEMATOCYST DISCOVERED

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SUMMARY

Such aquatic organisms as bryozoans, and corals and hydrozoans of the Cnidaria, were once termed "zoophytes." The designation connoted organisms which had properties of both plants and animals. Through the early eighteenth century, views that the so-called zoophytes were animals were not taken seriously, and beliefs that zoophytes were of plant origin prevailed. In 1727, the French physician and naturalist, Jean-André Peysonnel, presented strong reasons for refuting the dominant belief that the polyps of corals were plants. He was not believed, however, until René-Antoine Ferchault de Réaumur, a leading figure in science of the time, became influenced by the work of Abraham Trembley on hydra and on the bryozoan *Lophopus*. At Réaumur's request, his colleague, Bernard de Jussieu, extended Peysonnel's observations, affirming that a wide variety of organisms said to be zoophytes were animals. Nonetheless, objections to recognizing zoophytes as animals persisted even in the 1750s when John Ellis published his thorough works in which he examined large numbers of cnidarians and bryozoans. We describe this saga of the "zoophytes" in which authority and belief long prevailed over evidence from observation and experiment.

Although nematocysts are considered the diagnostic feature of cnidarians, they were not discovered until nearly 100 years after cnidarians were finally recognized as animals. Functional and morphological clues as to the existence of nematocysts were observed in the mid-eighteenth century by Trembley, Martin Folkes, and Henry Baker. Not until the techniques of histology were developed in the mid-nineteenth century, however, were nematocysts actually detected. By the 1860s, the structure, role, and overall function of nematocysts were relatively well worked out.

I. ANIMAL NATURE OF MARINE CNIDARIANS

> *I felt keenly that nature was too vast and too little known for us to decide without temerity that such and such a property was not to be found in such and such a class of organisms.* (A. Trembley, 1744)

In the mid-eighteenth century, Abraham Trembley (1744), using hydras or "freshwater polyps" as he called them, startled the scientific world with his revolutionary discoveries of regeneration, asexual reproduction by budding, grafting of animal tissues, and phototaxis in eyeless animals. It also took Trembley's breakthrough experimentalism and refusal to accept unquestioned theories of long standing to set the stage for widespread recognition of large groups of marine cnidarians as animals. Trembley's careful studies of his freshwater polyps convinced him early on that, despite certain plant-like characteristics, they were definitely animals, not sensitive plants and not "zoophytes." At the time that Trembley published his first revolutionary findings in the early 1740s the term "zoophytes" was applied to such aquatic organisms as corals (Fig. 1) and hydrozoans of the Cnidaria, and bryozoans; the designation connoted organisms which had properties of both plants and animals.

Fig. 1. "Coral Flowers" as depicted in the early eighteenth century (from Hughes, 1744).

To some, the presumed zoophytes represented the connecting link between the plant and animal kingdoms. They were thus an important construct in the venerable and broadly accepted concept of a Great Chain or Ladder of Being, or Scale of Nature, that included all living things, and sometimes in addition, angelic creatures at the top and mineral matter at the bottom (see Lovejoy, 1936).

The animal nature of the so-called zoophytes, especially corals, was first postulated by Ferrante Imperato in his 1599 volume, *Historia Naturale*. His views, however, were not taken seriously, and the beliefs that zoophytes were of plant origin continued to prevail for almost 150 years longer. This belief was further promulgated by the Count de Marsigli. In 1711 he published his *Histoire Physique de la Mer* in which he referred to the polyps of corals as "flowers and blossoms." His definition was accepted even by the reknowned French scientist and model for Trembley, René-Antoine Ferchault de Réaumur, who stated, "this discovery of the 'flowers' of the coral made a great noise in the world of naturalists" (see Pennington, 1885, p. 3).

Sixteen years later, Jean-André Peysonnel, a physician from Marseilles, came up with strong reasons for refuting the dominant belief that the polyps of corals were plants and the mineralized (calcareous) coral productions were the result of plant or inanimate activity. Peysonnel entrusted his notes to Réaumur, asking him to present them to the Academy at Paris. Réaumur, still influenced by the prestigious savant, Marsigli, did not want to embarass his young friend. Although he transmitted Peysonnel's findings to the Academy of Sciences in Paris, he did not reveal their authorship, including them instead in "Observations upon the formation of Coral and other productions called Stony Plants," (Réaumur, 1729) In this paper, Réaumur does not support Peysonnel's views.

Almost another fifteen years passed and the views of the recognized "authorities" regarding the "coral flowers" still held sway. At that point, however, the work of Réaumur's young follower, Trembley, on hydra (the "polyp with arms shaped like horns") and on the bryozoan (polyzoon) *Lophopus* (the "plumed polyp,") began to raise doubts in Réaumur's mind as to the plant-like nature of "marine flowers."

At Réaumur's request, his colleagues, Bernard de Jussieu and Jean-Étienne Guettard, went to the French coasts and to the rivers around Paris to investigate some of the organisms in question. Their research led them to conclude that Peysonnel was correct in his conclusions regarding the animal nature of the so-called "zoophytes" (see Réaumur, 1742). De Jussieu extended Peysonnel's observations, affirming that a wide variety of organisms said to be zoophytes were animals.

In the preface to his sixth volume on the *Insectes* (1742) in which he first describes Trembley's discoveries on hydra, Réaumur makes amends for his mishandling of Peysonnel's work and admits that Peysonnel's original interpretation was the correct one. As he wrote, "The care taken by Monsieur Peysonnel in making his observations should have convinced me sooner that the flowers [of] ... Count de Marsigli ... were really animals" (translated by Baker, 1952).

Réaumur also salutes Trembley's findings for leading the way to "these new knowledges" which had escaped so many astute observers. In a letter to Trembley (see M. Trembley, 1943) he wrote, "The vast and curious country of the polyps has devolved upon you ... ," and he urged Trembley to investigate marine polyps. Trembley, however, continued to devote those years to the study of freshwater organisms; somewhat later he did study the hydroid *Sertularia* that he obtained on the English coast (see Baker, 1952, p.127).

After the revelations of de Jussieu, Guettard, and Réaumur, Peysonnel returned to the attack. In 1751 he wrote a 400 page manuscript and transmitted it to the Royal Society of London rather than to the Academy in Paris. In it he restated the results of his researches of the previous 30 years. [According to Johnston (1847), the manuscript was never published as such and is in the library of the Paris Museum.]

Johnston pointed out that at first Peysonnel's treatise "excited considerable attention among members of the Royal Society." Eventually, however, he met opposition in England, chiefly from Dr. James Parsons and Henry Baker. Baker, the microscopist, who was intrigued with the crystallization of salts, stated his belief based on reason and analogy , but no evidence, that stony corals were nothing more than mineral productions. In Baker's (1753) words:

> Great Disputes have arisen among *Naturalists* concerning the formation of *Corals* and *Corallines*... .Such as believe these corals to be the *Work* of *Insects*, ground their Opinions ... on the sole Supposition that each of their *starry Cells* or *Hollows* is inhabited by *an Insect*, who therefore was the Maker of it. ...I say, to conclude thus, is somewhat over-hasty and unphilosophical. ...[Regarding] the *stony Corals* ... they are certainly formed by an *Apposition* of Particles some how or other brought together ... [to] ... be produced with all their beautiful Regularity and Variety ... [as] concreted by Frost. ... I have seen, in Winter Time, formed this Way, upon Windows ... very elegant Representations in Miniature of Landscapes, with Groves of Trees, and a seeming Variety of Shrubs and Herbs ... .

As for the horny and more pliant coverings of some forms, Baker thought them to be of a vegetable nature:

> Though, living far from the Sea, I have never been able to examine *Corallines* just taken from thence...[Their] Cases are of a membraneous Texture ... entirely different from the *stony Corals* ... . I believe that the most accurate Examiner, *void of any Hypothesis*, would declare it to be vegetable. (Baker, 1753)

Parsons, a physician and naturalist, also based his objections on belief. Without performing any experiments or making any observations, he said that he could not believe "that so fine an arrangement of parts, such regular ramifications, and such well-contrived organs to serve for vegetation, should be the operations of little, poor, jelly-like animals." Instead, Parsons believed that the inanimate "productions" of zoophytes were made by plants (see Pennington, 1885, p. 7). A popular view at that time held that once these non-animal productions had been made, then small polyp-like animals would inhabit them.

Ellis's book on the corallines (1755) and his subsequent volume with Solander (1786) would seem sufficient to have resolved the issue once and for all. Using a strong single-lens microscope (Ellis, 1755, Plate XXXVIII), Ellis examined a great many live and preserved organisms; he also carried out a few crude chemical tests. His evidence regarding the animal nature of the many organisms he studied, complete with accurate drawings, was most convincing in confirming Peysonnel's original contention.

Dr. John Baker, the author of the biography of Trembley (1952), wrote (1945) that: "Ellis, more than any other single man, caused scientists to accept into the animal kingdom the great and diverse groups of hydroids, sea-fans and their allies, and Polyzoa. No other man has ever made so great an enlargement of the subject matter of zoology."

Nonetheless, even after Ellis' convincing work, there were still those who clung to their beliefs and maintained that zoophytes were either partly or wholly "vegetable in nature." Linnaeus, in a letter to Ellis, wrote "Zoophyta ... are therefore vegetables, with flowers like small animals, which you have most beautifully delineated." He suggested that zoophytes were somewhere between animal and plant, with the plant portion building the hardened stem. In a letter to Linnaeus, Ellis responded to a conjecture that zoophytes became more plant-like as the stem material increased, by wryly asserting that "Artful people may puzzle at the vulgar, and tell us that the more hairy a man is, and the longer his nails grow, he is more of a vegetable than a man who shaves his hair or cuts his nails... ." In another letter to Linnaeus, Ellis wrote "I can not reconcile myself to vegetating animals ... . We have not sufficient proof to determine it; and I am averse to hypothesis." (See Johnston, 1847, pp. 424-429.) Clearly, Ellis was not intimidated by the views of Linnaeus, this giant figure among biologists, and his followers. In strong and certain terms, Ellis (1768) wrote that "zoophytes are true animals, and in no way part vegetable..."

To summarize, in the eighteenth century, it was Peysonnel who first proposed that the "sea-flowers" of corals were animals, but his findings were ignored; it was Trembley's research on hydra and on the bryozoan *Lophopus* that stimulated students of natural history to reopen the question regarding the possible animal nature of the so-called zoophytes; and it was the work of Ellis that finally provided conclusive evidence to put to rest the question of the animal or vegetable nature of the "zoophytes," in particular the marine cnidarians.

These, we now know, were the animals which in the 19th century were to become the objects of research for an incredible number of distinguished biologists, among them Dujardin, Morgan, Loeb, Wilson, Metchnikoff, Nussbaum, Agassiz, Haeckel, Allman, Hertwig, and Huxley.

It seems fitting to close the subject of how the animal nature of large groups of cnidarians was recognized with a cautionary comment by Abraham Trembley (1744):

> [Until we] know precisely all the attributes of plants and animals ... it is much more natural to consider the polyps and various other animals which have been given the name of zoophytes as animals which show more noteworthy similarities to plants than do other animals. ...It is too dangerous in the subject of natural history to abandon experience and allow the imagination to lead us. In following such a path, one risks arriving at uncertain hypotheses which can become detrimental to the progress of this science should one have the misfortune to become prejudiced in their favor. Instead of clarifying phenomena through new experiments, we have recourse to a hyphothesis, or rather a prejudgment, which not only spares us the trouble of observing, but which also serves to compound our errors.

II. STUDIES LEADING TO THE DISCOVERY OF NEMATOCYSTS

> *Thus we cannot do better to explain the facts we know than by trying to discover new ones. Nature must be explained by nature and not by our own views.* (A. Trembley, 1744)

It was Antony van Leeuwenhoek in 1703, in his one paper mentioning hydra, who first described "knot-like lumps" on the "horns" of the hydra that he observed (see Dobell, 1960, pp. 282-283). From his drawings it is obvious that he is referring to the batteries on the tentacles. Leeuwenhoek even goes one step further to state "These lumps look to me as though they were made up of seven round globules; to wit, one in the middle, which sticks up a bit above the others, and the rest lying round it in a rosette." The "round globules" probably refer to the nematocysts in the battery, and the "one in the middle," to a stenotele.

It was not until Trembley's investigations of hydra (1744) stimulated thorough studies by others, however, that we began to gain our first notions of the function of nematocysts. Despite his careful observation, ingenious experimentation, and amazing findings, Trembley was not destined to become the discoverer of the structure and function of these complex cellular secretions. He does start the process of investigating these organelles by publishing certain "facts he knows." For example, in his *Mémoires* (see Lenhoff and Lenhoff, 1986, p. 34) Trembley describes "beads" on the "arms" of hydra:

> Imagine an arm as it extends. Little by little one sees these surface granules, which touched or nearly touched each other when the arm was strongly contracted, become spaced wider apart ... . When the arm reaches a certain degree of elongation, its surface appears merely sprinkled with beads ... . Drawing further away from each other as the arm continues to elongate, the beads finally turn out to be strung in a single row and separated by a transparent thread ... . These beads are formed by a clustering of a number of granules.

We now know that the "beads" described by Trembley were the nematocyst batteries and the "granules" the nematocysts. But because Trembley also saw "granules" in the endoderm (i.e. food granules), he mistakenly thought that they were the same and functioned in some manner to aid the nutrition of the hydra.

Trembley also described hairlike structures (Fig. 2) along the arms of the polyps (see Lenhoff and Lenhoff, 1986, p. 35):

> The hairlike structures ... become noticeable in the elongated arm of a polyp when it is examined under the strong lens of a microscope. They appear to be transparent.

Fig. 2. Portion of a tentacle of a hydra showing "clustering[s] . . . of granules" and "hairlike structures" (from Trembley, 1744, Plate 5).

Some modern authors have thought the hairs depicted in Plate 5 of the *Mémoires* to be cnidocils. Weill (1934) was not sure whether they were cnidocils or discharged threads of nematocysts. From their relatively long size as drawn by Lyonet, we presume the hairlike structures described by Trembley to be the tubules of discharged stenotele nematocysts.

Fig. 3. Drawing of tentacle, emerging from head of a hydra, showing the "little Papillae*" (from Folkes, 1744).*

While observing the capture of prey, Trembley deduced that the arms of the polyps were able to hold the prey fast by some unexplained means (see Lenhoff and Lenhoff, 1986, pp. 54-55):

> [The millepede] need but touch the arm for it to be seized. As soon as the millepede feels itself captured, it struggles vigorously, making great efforts to free itself... Rarely do they free themselves from the polyp at all..

The first mention of the possibility of "hooks" being present on the arms of the polyps was made by a non-biologist, Martin Folkes (1744), President of the Royal Society of London, who took an avid interest in Trembley's experiments.

> [It] appears to me, that the little *Papillae* [Fig. 3] described on the Surface of the Arms assist them like so many Hooks or Tenters to hold their Worms barely by touching them; for I have more than once seen a *Polypus* draw a Worm to him, and nimbly turn it about with a single Arm, only laid over it, without folding or clasping it; which last method, however, he makes use of also, when the Worm comes to struggle and strive hard to be disengaged.

Actually, the microscopist Henry Baker, whose erroneous views about the marine cnidarians we have noted, was first to show the tubules of discharged nematocysts along the tentacles of hydra. Baker (1744) thought that if he could fix and then dry a polyp, he might be able to see some features not otherwise visible in the live animal. After applying a variety of fixatives - vinegar, dissolved salts, and spirits of wine - he comments:

> By observing the Arms thus dried, we obtain a clear Idea of the Means whereby this Creature catches fast hold of its Prey, the Moment of its touching it, and before it can bring its Arms to clasp about it: For we plainly see here, that the Arms are thick beset with Hairs

[Fig. 4], or rather sharp Hooks, which possibly are moveable, and can strike easily into the Body of a tender Worm. But these Hooks or Hairs perhaps, some-how or other generally drawn in, or laid flat and close along the Sides of the Arms, as I have seen them in some sorts of Star-fish.

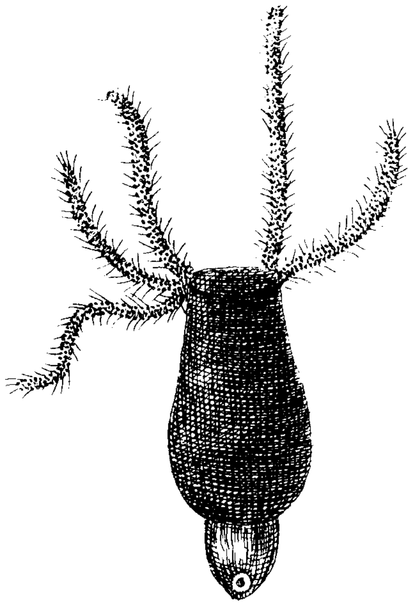

Fig. 4. Drawing of dried hydra showing tentacles "beset with Hairs" after the animal was exposed to vinegar, salts, and wine (from Baker, 1744).

Baker got carried away by his observations, and again was too quick to draw conclusions. For example in his book on the polyp (1743, p.64) he wrote:

> [The Polyp's] Arm's ... sense of Feeling is so delicate, that if a Worm touches even the utmost Extremity of these slender Arms, they immediately lay hold of it ... [The Arms] invelop and fetter it in so many Places, and to such a Degree, that notwithstanding it be much larger and seemingly stronger than they, it is soon rendered uncapable of struggling to any Purpose. In this Condition the *Polype* lengthens out his Snout, and bites the Worm violently on one Side, which not only gives it a great deal of Pain, as its wriggling motion testifies, but likewise makes the Blood run out: and it continues sucking at the Wound till the internal Juices are so far extracted, that the Body of the Worm is reduced to a size not over-large for the *Polype*'s Mouth ... .

Despite his erroneous speculations, Baker was a keen observer. For example, he suggested that the same structures present in the arms that capture prey, might also be present along the body of the hydra (Baker,1743, p. 30), a fact we now know to be true.

> Although I do not pretend to have yet been able perfectly to distinguish such, I have Reason to believe there may be certain minute Scales, or Protuberances, or some Sort of little *Spiculae* or Hooks all over the *Polype*'s Body, which can lengthen and protrude ... [If] a Worm happens to touch any Part of the Body, one shall plainly see it catch'd and held fast, one knows not how ... .[The] worm too instantly begins to struggle, and shews great Sense of Pain, but can very seldom get away; which almost proves it must be held by some invisible Hooks or Claspers [along the body] running into it, and which are probably of the same Sort as those along the Arms.

Baker also was the first to suggest that a poisonous substance might be transmitted from the polyp to the prey leading to a "sudden death." But he goes a little too far when he suggests that the poison may come from the "bite" of the "*Polype*'s snout." (Baker, 1743, pp. 32-33):

> We shall never, perhaps, be able to discover, certainly, by ocular Demonstration, whether the Mouth of this Creature is really armed with Teeth; but we may conjecture it so to be, from the Ease wherewith it bites or breaks the Skin of a Worm, in order to suck the Blood and Juices .... There is, likewise, a farther Probability of its having such offensive Weapons, from the violent and painful Agonies a Worm expresses the Moment it is taken hold on by the *Polype*'s Snout, and from the sudden Death that follows ... [One] would almost incline ... to imagine there must be something poisonous in the Bite; and that the *Polype*, as well as the Viper, does not only bite, but even inject a Venom into the Wound it gives, for the more speedy Destruction of its Prey.

Thus Trembley, and much more so Baker, approached the concept of the nematocyst, but did not describe it because histology was not developed as an art or science during their time. It took nearly 100 years more before nematocysts were clearly identified both as to their structure and function.

Ehrenberg (1836) carried out the first systematic investigation of nematocysts, studying primarily the stenotele of hydra, which he called "anglers." He made one serious error based upon one observation in which the tip of a discharged stenotele was found imbedded in the operculum of an undischarged stenotele. Ehrenberg concluded that the discharged tube was contractile, that the nematocyst could invaginate after it was discharged, and that at the end of the discharged tube was a capsule (Fig. 5).

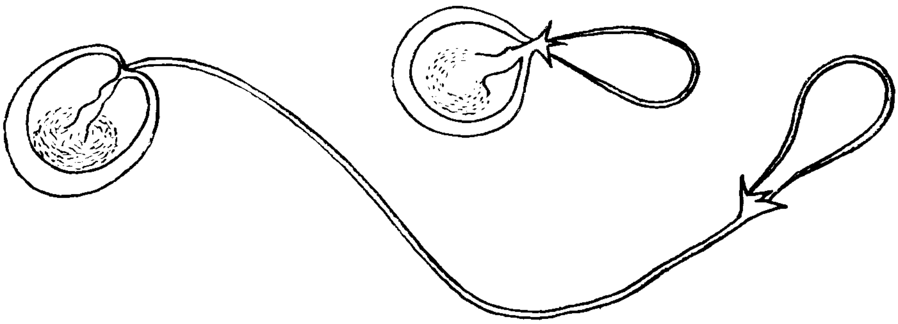

Fig. 5. Drawings of first nematocysts (stenoteles) seen; these show the tip of a discharged one imbedded in the operculum of an undischarged one (from Weill's, 1934, redrawing of Ehrenberg, 1836).

Wagner (1835) made an even more serious error while observing nematocysts in acontia. He concluded that the acontia were testicles, and the tadpole shaped discharged nematocysts were sperm, with the capsule being the head of the sperm and the thread the tail; however, he did draw the barbed armature at the base of the tube. In 1841 he corrected his errors. From his studies of *Pelagia noctiluca* he postulated that a stinging filament innoculated the prey with a venomous liquid which was contained in a capsule.

Corda in 1837 described a structure resembling a stenotele, but said that it contained muscle and that the barb was able to go in and out of the capsule. He also postulated that the structure was capable of innoculating prey with a venom. Finally it was Erdle (1841) who correctly described the stenoteles of hydra as well as nematocysts of some actinians.

Doyère (1842) accurately described hydra nematocysts. He correctly pointed out that the tube is invaginated and coiled at the bottom of the undischarged stenotele, and that it everts on discharge. He also was the first to point out the three points on the calyx, the glutinant nematocysts, and cnidocils. Dujardin (1845) made some exact drawings of the nematocysts that he observed, and suggested that nematocysts might be used for taxonomic purposes.

By the middle of the nineteenth century, however, the facts began to be sorted out. Haime (1854) said that he "would call them nematocysts." Gosse (1858, 1860), known to coin numerous new terms, was the first to use the term "cnidae." Huxley's drawings of nematocysts (1859) are quite accurate and sophisticated.

Weill (1934) credits the first major large work on nematocysts as that of Moebius (1866). Moebius described the fine structure, function, and development of nematocysts (see Fig. 1 in Tardent, this volume). He said that there was general agreement that the nematocyst is an intracellularly-produced body, formed from a capsule open at one end, with a tube that is long and complicated which invaginates into its capsule, and which could be made to evaginate under certain conditions.

III. CONCLUSION

> *It seemed to me from the start of my observations that knowledge of the remarkable properties of the polyps could bring pleasure to the inquisitive and contribute something to the progress of natural history.* (Trembley, 1744)

From Trembley to the nineteenth century researchers studying the nematocyst stretched a hundred years of trial and error and of "authoritative" theories dethroned only with great difficulty. Gradually advances were made in the understanding of the marine cnidarians and their enigmatic nematocysts, organoids that still fascinate and intrigue us today. Trembley's pioneering studies stimulated much of the ensuing work on the "polyps," both freshwater and marine.

As Réaumur had predicted in 1742, later naturalists have indeed sought out additional species of marine polyps and studied differences in their morphology, feeding, growth, and reproduction. As we now begin a symposium to stimulate the unraveling of the mysteries still locked up in this complex cellular secretion, we continue to fulfill Réaumur's cherished hope that: "At last, a part of natural history that is so interesting and new and that has been sketched only roughly, will be studied thoroughly as it deserves."

REFERENCES

Baker, Henry. 1743. *An Attempt towards a Natural History of the Polype*. R. Dodsley, London.

Baker, Henry. 1744. Some Observations on a *Polype* dried. Phil. Trans. 42:616-619.

Baker, Henry. 1753. *Employment for the Microscope*. R. Dodsley, London.

Baker, John R. 1945. *Science and Planned State*. MacMillan. New York.

Baker, John R. 1952. *Abraham Trembley of Geneva: Scientist and Philosopher 1710 - 1784*. Edward Arnold. London.

Corda, A. J. 1837. Anatome *Hydrae fuscae*. Ann. sc. nat. Zool. 8:363-366.

Dobell, C. 1960. *Antony van Leeuwenhoek and his "Little Animals."* Dover, New York.

Doyère. 1832. Note sur quelques points de l'anatomie des Hydres d'eau douce. C. R. Ac. Sc. 15:429-432.

Dujardin, F. 1845. Mémoires sur le developpement des Polypes hydraires et Meduses. Ann. sc. nat. Zool. 4:257-281.

Ehrenberg, C. G. 1836. Beobachtungen uber die organisation der Armpolypen. Mitt. Naturf. Ges. Berlin. 2^0 Quartal:27-29.

Ellis, John 1755. *An Essay Towards a Natural History of the Corallines, and other Marine Productions of the like Kind*. Millar, Rivington, and Dodsley, London.

Ellis, John 1768. An Account of the Actinia Sociata, or Clustered Animal-flower, lately found on the Sea-Coasts of the new-ceded Islands. Phil. Trans. 57:428-437.

Ellis, J. and D. Solander. 1786. *The Natural History of Many Curious and Uncommon Zoophytes, Collected from Various Parts of the Globe*. B. White & Son, London.

Erdle, P. 1841. Über Organisation der Fangarme der Polypen. Arch. Anat. Physiol. 423-434.

Folkes, Martin. 1744. Some Account of the Insect called the Fresh-water *Polypus*, before-mentioned in these *Transactions*. Phil. Trans. 42:422-436.

Gosse, P. H. 1858. Researches on the poison apparatus in the Actiniidae. Proc. Roy. Soc. 9:125-128.

Gosse, P. H. 1860. *A History of the British Sea-Anemones and Corals*. Van Vorst, London.

Haime, J. 1854. Memoire sur le Cerianthe. Ann. Sc. nat. Zool. 1:341-389.

Hughes, G. 1744. Concerning a *Zoophyton*, somewhat resembling the Flower of the *Marigold*. Phil. Trans. 42:590-593.

Huxley, T. H. 1859. *Oceanic Hydrozoa; Calycophoridae and Physophoridae*. Ray Society, London.

Johnston, George. 1847. *British Zoophytes*, Vol. 1, John Van Voorst, London.

Lovejoy, A. O. 1936. *The Great Chain of Being*. Harvard, Cambridge, MA.

Moebius, K. 1866. Uber den Bau, den Mechanismus und die Abhdln. naturw. Ver Hamburg. 5:1-22.

Pennington, A. S. 1885. *British Zoophytes: An introduction to the Hydroida, Actinozoa, and Polyzoa found in Great Britain, Ireland, and the Channel Islands*. L. Reeve, London.

Réaumur, R. A. F. 1729. Observations sur la formation du corail , & des autres productions appelées plantes pierreuses. Hist. Acad. Roy. Sci. (Mém. Math. Phys.) pp. 226.

Réaumur, R. A. F. 1742. *Mémoires pour servir à l'histoire des insectes*. Vol 6. Imprimerie Royale, Paris.

Trembley, A. 1744. *Mémoires, pour servir à l'histoire d'un genre de polypes d'eau douce, à bras en forme de cornes*. Verbeek, Leiden.

Trembley, M. 1943. *Correspondance inédite de Réaumur et d'Abraham Trembley comprenant 113 lettres recueilles et annotées par Maurice Trembley*. Introduction by É. Guyénot. Georg, Geneva.

Tardent, P. 1988. History and current state of knowledge concerning discharge of cnidae (this volume).

Wagner, R. 1835. Entdeckung männlicher Geschlectsteile bei den Aktinien. Arch. Naturg. 2:215-219.

Weill, R. 1934. *Contribution a l'etude des cnidaires et de leurs nematocystes*. Vols. 1 and 2. University Press of France, Paris