STARFISH, JELLYFISH, AND THE ORDER OF LIFE

Issues in Nineteenth-Century Science

Mary P. Winsor

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4. Thomas Henry Huxley's Ideas about the Relationships between Polyps and Acalephs

Although the exploring expedition of the frigate *Rattlesnake* was supposed to "form one grand collection of specimens and deposit it in the British Museum or some other public place,"[1] the eager twenty-one-year-old assistant surgeon who had been chosen for the voyage because of his interest in science later admitted, ". . . I am afraid there is very little of the genuine naturalist in me. I never collected anything, and species work was always a burden to me. . ."[2] Rather than preserve and label a large number of species, he occupied his time with microscopic observation and dissection of a small number of common marine invertebrates. Thomas Henry Huxley knew what kind of science he wanted to do. He described himself as interested in the functional and mechanical side of biology, but this meant comparative morphology in the tradition of Savigny, not experimental physiology. "What I cared for was the architectural and engineering part of the business, the working out the wonderful unity of plan in the thousands and thousands of diverse living constructions, and the modifications of similar apparatuses to serve diverse ends."[3]

Huxley's first entry in his diary aboard the *Rattlesnake* expresses his dislike of "naturalising for systematic purposes," by which he evidently meant the collection and identification or naming of species after species. At the same time he recognized that the voyage offered him special opportunities, and that his "future prospects" depended upon his taking advantage of them. His background and situation "clearly point to the study of the habits and structure of the more perishable or rare marine productions as that most likely to be profitable."[4] Among the specific projects he then listed were:

5. Careful dissections of the large Radiata, especially of the Trepang holothuria;

1. Leonard Huxley, *Life and Letters of Thomas Henry Huxley*, 2 vols. (New York, 1901), 1 : 27.
2. Ibid., p. 7.
3. Ibid., pp. 7–8.
4. Julian Huxley, *T.H. Huxley's Diary of the Voyage of H.M.S. Rattlesnake* (London, 1935), p. 8.

6. Zoology-Anatomy-Histology of the Acalephae with especial care and for the purpose of being fully acquainted with this subject study carefully the works of Lesson and Will;

7. Careful studies of all matters relating to coral and corallines, especially relating to the animals of the latter. [The expedition was ordered to explore the Great Barrier Reef.] [5]

Already he had decided to give special attention to the radiates and specifically to the acalephs. The day on which he caught his first *Physalia* (Portuguese man-of-war) he decided that the books he had with him described it very badly and that his own examination "puts in a much clearer light the true analogies of these animals."[6]

In a letter written during the last days of the voyage, Huxley described his approach to the study of jellyfish:

> But I paid comparatively little attention to the collection of new species, caring rather to come to some clear and definite idea as to the structure of those which had been indeed long known, but very little understood. Unfortunately for science, but fortunately for me, this method appears to have been somewhat novel with observers of these animals, and consequently everywhere new and remarkable facts were to be had for the picking up.
>
> It is not to be supposed that one could occupy one's self with the animals for so long without coming to some conclusions as to their systematic place, however subsidiary to observation such considerations must always be regarded, and it seems to me (although on such matters I can of course only speak with the greatest hesitation) that just as the more minute and careful observations made upon the old "Vermes" of Linnaeus necessitated the breaking up of that class into several very distinct classes, so more careful investigation requires the breaking up of Cuvier's "Radiata" (which succeeded the "Vermes" as a sort of zoological lumber-room) into several very distinct and well-defined new classes, of which the Acalephae, Hydrostatic Acalephae [siphonophores], actinoid and hydroid polypes, will form one.[7]

5. Ibid., p. 9.
6. Ibid., p. 26.
7. Ibid., p. 63.

This gives the impression that Huxley considered systematics of secondary importance, and that he formed opinions on this subject only *after* long observation, but his diary leaves a different impression.

Finding the systematic place of a group was subsidiary to observation in the sense that it must be based upon careful and objective anatomy, but it was not subsidiary in importance; he wrote to his sister that "the reduction of two or three apparently widely separated and incongruous groups into modifications of the single type" (which is exactly the process of forming a new distinct class out of the radiate "lumber-room") is "one of the great ends of Zoology and Anatomy."[8]

Huxley's conclusions as to the systematic arrangement of jellyfish began to take shape during the third month of the cruise, not at the end of his researches. After further studies on the structure of *Physalia*, Huxley noted in his diary on February 25, 1847, ". . . I think I can already perceive that it will form a great link in the chain of Acalephae at once explaining and explicable by many as yet isolated structures in the Diphydes, the Physophoridae, and even the Medusae."[9]

There is nothing remarkable in this, for a zoologist, like any scientist, cannot make his observations first and frame his theories afterwards. Systematics played the role of theoretical framework within which Huxley's observations were made.

Huxley titled his paper on *Physalia*, "On the anatomy and physiology of *Physalia*, and on its place in the system of animals," and in his own outline of the paper, he planned Section III thus: "Comparison of structure thus set forth with that of other animals. Hence determination of zoological place and of the homologies of the organs."[10] But in the paper itself the portion answering to this intent consisted of only his two final sentences:

> Finally if the account above given of the structure of the Physalia be correct, its true Zoological place will be that long ago assigned to it by Eschscholtz, viz. among the Physophorae and near Discolabe or Angela—in fact, the Physalia

8. Ibid., p. 36.
9. Ibid., p. 22.
10. The Huxley Papers at the Imperial College of Science and Technology in London include Huxley's notes on *Physalia* (34 : 16), which I have seen in microfilm at the American Philosophical Society in Philadelphia.

> is in all its essential elements nothing but a Physophora whose terminal aeriferous dilation has increased at the expense of the rest of the stem, and hence carries all its organs at the base of the dilation.[11]

His next project was an examination of the other siphonophores whose relation to *Physalia* he had postulated. He wrote to his sister that he was working on *Diphyes* in order to show their affinity to *Physalia*. He hoped that his work on both *Physalia* and *Diphyes*, combined with new material not studied yet, would contribute to another, larger paper. "If my present anticipations turn out correct, this paper will achieve one of the great ends of Zoology and Anatomy, viz. the reduction of two or three apparently widely separated and incongruous groups into modifications of the single type, every step of the reasoning being based upon anatomical facts."[12] This project, already envisioned by August 1, 1847, Huxley also announced at the end of his paper on *Diphyes*. The "widely separated and incongruous groups" were the hydroid polyps and the siphonophores. "But in the absence of any original observations on the structures of Polypi I must leave this question without further consideration."[13]

The implication of linking hydroid polyps to siphonophoran acalephs was a linking of the entire two classes of Polypi and Acalephae; at this early stage, when his actual observations had been limited to siphonophores, Huxley saw that larger connection. He wrote to Edward Forbes in September or November of 1847, that his observations

> have given rise in my mind to some ideas of much wider scope which if they be well founded must necessitate a complete rearrangement of several extensive groups.
>
> . . .
>
> We at once perceive strong indications of a connexion among several hitherto widely separated families—I mean the Acalephae proper, the hydrostatic acalephae [siphonophores] & the Polypes.[14]

11. Huxley Papers, 34 : 1; Huxley's article on *Physalia* was not published, but an abstract of it appeared in 1851 (*Scientific Memoirs*, 1 : 361–62).
12. Huxley, *Life and Letters*, 1 : 36.
13. "Observations on the anatomy of the *Diphydae* and the unity of organization of the *Diphydae* and *Physophoridae*," Huxley Papers, 34 : 64. A brief abstract of this article was published in 1855 (*Scientific Memoirs*, 1 : 363–64).
14. Huxley Papers, 16 : 154.

We see as he goes on that he means anthozoan as well as hydroid polyps.

He presented this hypothesis formally in the longer paper he had promised himself, "On the anatomy and the affinities of the family of the *Medusae*." He (or rather the captain of the *Rattlesnake*) sent this paper to the Royal Society in April 1848, and it was published in the *Philosophical Transactions* of 1849. He had supplemented his work on siphonophores with considerable study of various medusae, and with a brief study of two unidentified species of the hydroid *Plumularia*, which he did not describe systematically but used for comparison. He proposed that the medusae have important connections to hydroid polyps and to siphonophores. The wider connections he had revealed privately to Edward Forbes, Huxley still could not substantiate:

> I have purposely avoided all mention of the Beroidae [ctenophores] in the course of the present paper, although they have many remarkable resemblances to the animals of which it treats: still such observations as I have been enabled to make upon them have led me to the belief, that they do not so much form a part of the present group as a link between it and the Anthozoic Polypes. But I hope to return to this point upon some future occasion.[15]

Although the Great Barrier Reef should have offered Huxley a marvelous opportunity to test his belief by studying the anthozoan polyps, he did comparatively little further work in this area; he apparently suffered an incapacitating depression.[16] Nevertheless, when he described his work on *Diphyes* and *Physalia* to the British Association for the Advancement of Science in 1851, he proposed the extensive union of polyps and acalephs which he had envisioned in 1847, naming the new group Nematophora for the presence of the stinging cell, the nematocyst.[17]

Huxley's correspondent Edward Forbes had felt that the life histories discovered by Sars and others showed the polyps and acalephs to be "intimately allied."[18] If we grant the facts described by Steenstrup, wrote Forbes, we must reclassify the radi-

15. Huxley, *Scientific Memoirs*, 1 : 28.
16. Julian Huxley discusses this in Huxley's *Diary*, pp. 110–24.
17. Huxley, *Scientific Memoirs*, 1 : 100.
18. Edward Forbes, *A Monograph of the British Naked-eyed Medusae* (Ray Soc., London, 1848), p. 1.

ates; the classes Polypi and Acalephae must be united. "That the *Anthozoa* are intimately related to the Medusae is evident to any unprejudiced naturalist who has studied the structure of *Lucernaria*, or of the *Actineadae*, especially of any floating form of the last tribe."[19] It seems very probable that Forbes decided that such a union was necessary on those grounds before he heard of Frey and Leuckart, but by June of 1848 when he completed his monograph on medusae, Forbes reported that "The close affinity of these tribes has been excellently treated of in an Essay by Drs. Frey and Leuckart,"[20] and that the larger grouping had been named Coelenterata. Huxley should have noticed this when in 1849 he studied Forbes' monograph. The fact that his grand new group had already been proposed and christened was perhaps too keen a disappointment for Huxley to handle. He took no notice of Forbes's discussion nor of the name "coelenterate." He could not ignore that fact upon his return to England, for Forbes lent him a copy of Frey and Leuckart's *Beiträge*.[21] In his British Association lecture of 1851, Huxley did mention that the groups he wanted to unite had already been united:

> and it is curious enough that this has been done—for other reasons—by Messrs Frey & Leuckart in their valuable "Beiträge-" However my own *conclusions* may agree with those of these naturalists—I cannot think the physiological reasoning on which they base their proposed name for the class—Coelenterata—is correct—nor do I think that they have properly estimated the essential differences among its members.[22]

A brief abstract of this lecture was published that did not include this reference, only Huxley's own proposal that the group be named "Nematophora." It is perhaps an indication of the strain this situation put upon a man of Huxley's ambition that five years later, he had forgotten a fact so unpleasant to him: "Nine years ago [1847] MM. Frey and Leuckart clearly proved the necessity of uniting together the other 'Polypi,' the acalephae, and the beroidae, under the title of 'Coelenterata,' a circumstance of which I

19. Ibid., p. 88.
20. Loc. cit.
21. Huxley, *Scientific Memoirs*, 1 : 85.
22. Huxley Papers, 37 : 35.

was ignorant, when, in 1851, I ventured to propose the term 'Nematophora,' for a group with identical limits."[23]

Huxley was correct, however, when he said that he had based his Nematophora on entirely different reasoning than that employed by Frey and Leuckart. He did not start, as they did, by analyzing the anatomy of a standard acaleph and standard polyp, showing how the typical form of one class was essentially homologous to that of the other. By the accident of having *Physalia* and *Diphyes* available for study, when he knew that they were among the least well-known jellyfish, Huxley had approached the class Acalephae with an analysis of asymmetrical animals that looked nothing like most medusae. He found a similarity between some of the most aberrant, atypical acalephs, the siphonophores, and the most atypical polyps, the hydroids. He followed lines of affinity leading from one family to the next to the next, from *Physalia* to *Diphyes* to hydroids. The similarities between these forms Huxley listed in his own notes thus:

1. Body composed of two membranes out of which all the organs are modelled
2. Thread cells universally (?) present
3. Gemmiparous generation
4. Sexual generation—spermatozoa and ova being formed in vase like external sacs[24]

He had analysed *Physalia* as composed of two "membranes" or "foundation layers"; he recognized these same two layers in every coelenterate he studied, making especially constructive use of this idea in establishing the homologies of the medusae (fig. 8).[25]

The "thread cells" were nematocysts, a very distinctive kind of cell when seen under a good microscope. In the 1847 letter to Forbes quoted above, Huxley attached importance to the presence of the "urticating [stinging] cell," in both acalephs and polyps. "It may probably be taken for a rule in Zoology that when a well

23. Huxley, "Lectures on general natural history," *Med. Times and Gazette*, n.s. 12 (May 17, 1856) : 483.
24. Huxley Papers, 34 : 64.
25. Huxley, *Scientific Memoirs*, 1 : 10–28, and plates 2–4. His comparison of the two foundation layers to the germ layers of an embryo makes him a precursor of Haeckel's gastraea theory.

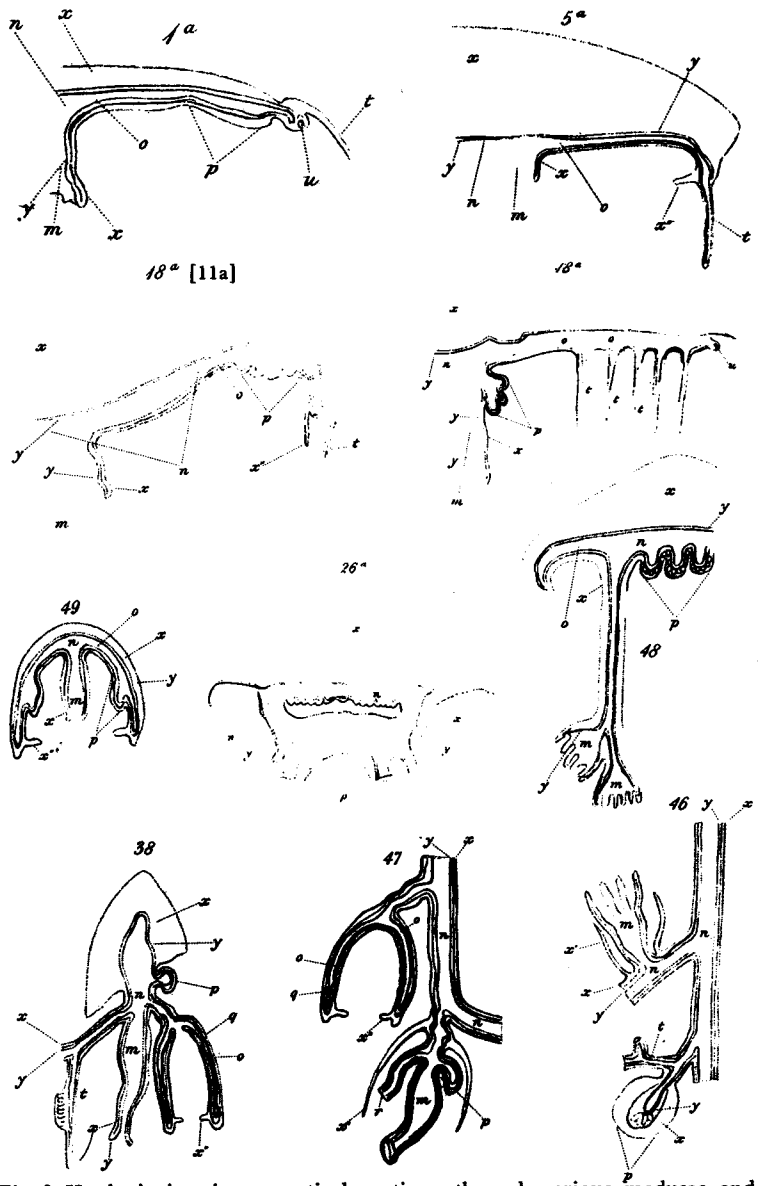


Fig. 8. Huxley's imaginary vertical sections through various medusae and hydroids. *1a, 5a, [11a], 18a, 49:* Various medusae. *26a, 48:* Rhizostome medusae. *38, 47:* Two kinds of *Diphyes*. *46:* A hydroid. (*Phil. Trans.*, pl. 37–39).

marked and peculiar structure adapted to a particular purpose is found to exist in a number of animals—that these however different in appearance they may be, are in reality affined."[26] The clue that mammae give to the class Mammalia, nematocysts give to a new class combining polyps and acalephs.

Huxley described *Diphyes* as a chain of "polypoids" each with a digestive cavity, tentacle, and generative organ, and what he meant by the gemmiparous generation of *Diphyes* was evidently the addition of new polypoids to the chain by budding, just as a hydroid colony buds new polyps as it grows. The similarity of the cup-shaped generative organs of *Diphyes*, *Physalia* (where indeed he guessed their function from this similarity) and hydroid polyps was certainly one of the peculiarities that strongly suggested to him the connection of these groups.

When extending his comparison to the Medusae in his *Philosophical Transactions* paper, Huxley noted the presence of the two foundation membranes, the presence of the nematocysts, and the fact that egg and sperm develop between the two foundation layers.

Aboard the *Rattlesnake* on its way from England to Australia, the implications of a connection between siphonophores and hydroids formed "the subject of many a quarter deck watch's musing"[27] for Huxley; he had in mind the necessity and importance of a rearrangement of Cuvier's Radiata and only wondered just what form that rearrangement would take. When he arrived in Sydney, Huxley became acquainted with William Sharp MacLeay, whose library and conversation was of great importance to him. After his return to England, Huxley wrote to MacLeay, "Believe me, I have not forgotten, nor ever shall forget, your kindness to me at a time when a little appreciation and encouragement were more grateful to me and of more service than they will perhaps ever be again."[28] And a number of Huxley's early papers include expressions of gratitude to MacLeay.[29] Huxley had heard nothing of the reception of his papers in England, so that "save for the always kind and hearty encouragement of the celebrated William MacLeay, whenever our return to Sydney took me within reach of his hos-

26. Huxley Papers, 16 : 154.
27. Huxley Papers, 37 : 38.
28. Huxley, *Life and Letters*, 1 : 102–3.
29. Huxley, *Scientific Memoirs*, 1 : 28–29, 34, 82, 100.

pitality, I know not whether I should have had the courage to continue labours which might, so far as I knew, be valueless."[30] As Huxley was not friendly with the *Rattlesnake*'s naturalist, John MacGillivray,[31] and his closeness to Edward Forbes developed only after his return to England,[32] MacLeay was the only scientific mind with whom Huxley exercised his thoughts during his four years away from England.

William Sharp MacLeay, like his father Alexander, was a civil servant, amateur entomologist, and member of the Linnean Society. William left England in 1826, living first in Cuba and later in Australia. When Huxley met him, MacLeay was still remembered in England as the author of a peculiar system of classification known as "Quinarianism" or the "circular system." He had in 1819 published a small volume, *Horae Entomologicae*, about certain beetles, in which he concluded that the species of the genus *Scarabaeus* are linked to one another by a chain of affinity which "may be represented by two circles meeting at one point, and having altogether an analogous structure at their corresponding points."[33] MacLeay expanded this idea in 1821, describing how all the other chains of affinity within the animal kingdom run back to themselves, forming circles. A discussion group called the Zoological Club was formed within the Linnean Society; throughout its existence from November 1823 to November 1829 it served as a forum for papers and debate about MacLeay's method of classification. After MacLeay's departure for Cuba in 1826, N.A. Vigors and others continued to advocate his system.[34]

30. Huxley, *Oceanic Hydrozoa* (London, Ray Soc., 1859), p. viii.

31. Huxley's *Diary* records definite ill-feeling toward MacGillivray (pp. 279–86). Julian Huxley describes their difference of scientific interest (MacGillivray was a collector) but the only evidence that Huxley and MacGillivray "got on well" during the voyage, as Julian Huxley assumes, shows merely that Huxley respected his knowledge and zeal as a collector (pp. 53–54, fn.).

32. He had met him once before his departure (*Life and Letters*, 1 : 102), and sent Forbes reports on his progress, but became exasperated on receiving no replies (*Life and Letters*, 1 :42).

33. William Sharp MacLeay, *Horae Entomologicae* (London, 1819–21), pt. 2, p. 162.

34. The Zoological Club is not to be confused with the Zoological Society, responsible for the maintenance of a zoo. The Club was limited to members of the Linnean Society and met in its quarters. Its meetings were reported upon in the pages of the *Zoological Journal*, whose lifetime coincided with its own: 1 (1825) : 132–33, 279–80, 418–21, 585–87; 2 (1826) : 133–36, 279–83, 548–54; 3 (1828) : 298–303, 691–707; 4 (1829) : 131–34, 503–8; 5 (1835) : 131–33. The Club was evidently dominated, as was the *Zoological Journal*, by Vigors, who classified birds by MacLeay's method. On

A fire at the bookseller's destroyed most copies of the second part of MacLeay's book,[35] the volume specifically devoted to the principles of MacLeay's system and its application to the entire animal kingdom. Probably the details of his ideas would have been known only to the few members of the Zoological Club had not one of their number, William Swainson, turned to writing popular science as a source of income. One of the volumes of Lardner's Cabinet Cyclopedia is Swainson's *Treatise on the Geography and Classification of Animals*, published in 1835; about half the book is an exposition of MacLeay's system with Swainson's own elaborations. MacLeay's ideas gained further publicity, or notoriety, by being praised in 1844 in the pages of the *Vestiges of the Natural History of Creation*, that anonymous argument for evolution.

There are three ideas essential to MacLeay's system of classification. The first is that natural affinities, relations of closest similarity, lead from one form to the next in linear fashion. The second is that such series of affinity may run parallel to one another, the parallelism being established by connections, like rungs of a ladder, linking each member of one series across to the corresponding member of the other series. The third idea is that in any natural group, the series of affinities may be represented by a circle, for we find, when following the affinity of A to B to C to D to E, that the next link is the affinity of E to A. It is a corollary of the idea that series are parallel, corresponding member for member, that each series must have the same number of members;

May 25, 1824, James Ebenezer Bicheno read a paper to the Club "'On the quinary arrangement of nature,' and the subject subsequently underwent a lengthened discussion" (1 : 419). On April 25, 1826, "A discussion took place on the principles of arrangement in natural lists" (3 : 298). The heat of such discussions may be imagined from the rhetoric and sarcasm of some of the articles on classification in this period, for example MacLeay's "A letter to J.E. Bicheno, Esq., F.R.S., in examination of his Paper 'On systems and methods,' in the Linnean Transactions," *Zool. J.*, 4 (1829) : 409–15. The history of this complex and sometimes bitter debate, involving a particular group of English naturalists, would explain many otherwise puzzling comments within taxonomic papers of this period. For example, Professor Frank Egerton called to my attention the fact that Loren Eiseley (*Firmament of Time*, p. 34) suggests Lyell as the author of an anonymous review of Bicheno's "On systems and methods in natural history," which appeared in *The Quarterly Review*, 41 (1829) : 302–7. But Lyell was not involved in the well-defined debate of which that article was part; a reply by MacLeay shows he knew the author to be the Rev. John Fleming (see MacLeay's *Dying Struggle*, cited below).

35. William S. MacLeay, *A Letter on the Dying Struggle of the Dichotomous System, addressed to N.A. Vigors* (London, 1820), p. 3.

this number turned out to be five. MacLeay himself put less emphasis on his "discovery" that there were five members in a natural group, or even that they were connected in a circle, than on his "discovery" of the meaning of the difference between affinity and analogy. An affinity is the close tie linking members of one circular series; analogy is the relationship between corresponding members of parallel series.[36]

MacLeay's own favorite example was from the animals he knew best, the insects. MacLeay did not create these orders, nor their grouping into two divisions; what he created was the pattern of their relationship.

Mandibulata (insects with biting mouthparts)	(Both orders have)	*Haustellata* (insects with sucking mouthparts)
HYMENOPTERA	metamorphosis incomplete, or coarctate; larvae apod or vermiform	DIPTERA
COLEOPTERA	metamorphosis incomplete; larvae various or unknown	APTERA
ORTHOPTERA	metamorphosis semicomplete; larvae resembling adult	HEMIPTERA
NEUROPTERA	metamorphosis subsemicomplete; larvae hexapod	HOMOPTERA
TRICHOPTERA	metamorphosis obtect; larvae eruciform	LEPIDOPTERA[37]

36. Much of the debate over MacLeay's system concerned the nature of affinity and analogy, and a number of respectable scientists (William Kirby, James Dwight Dana, Henri Milne-Edwards) praised him for helping to clarify those concepts. Undoubtedly the distinction between homology and analogy (first explicitly defined by Richard Owen in 1843) has important roots in this debate, as Jean-Claude Cadieux pointed out in a paper read to the Chicago meeting of the History of Science Society in December 1970. Yet MacLeay himself complained that the people who praised him for it had in fact quite misunderstood his meaning. The misunderstanding, or rather, difference of opinion, was the same as occurred between Huxley and MacLeay.

37. These two groups of insects are listed, with the analogy between the metamorphosis of the typical members of the orders, in MacLeay's *Horae Entomologicae*, pt. 2, p. 367; he drew the same two lists (but commencing with the two last orders, which he had noted return to the first) in 1822, adding more correspondences of the larval forms and changing "subsemicomplete" to "various" ("Remarks on the identity of certain general laws," *Linn. Soc. Trans.*, 14 (1825) : 66-7).

The relationship connecting each order to the one above and below it, and the last back to the first, is their affinity, the relationship which justified associating species into a genus or genera into families or orders into classes in any "natural" classification. The relationship between corresponding orders of insects, seen in their type of larvae and metamorphosis, is their analogy.

MacLeay argued that such a complex and regular pattern of relations could not have arisen by chance, but really existed in nature, as part of the original plan of creation.

> Suppose the existence of two parallel series of animals, the corresponding points of which agree in some one or two remarkable particulars of structure. Suppose also, that the general conformation of the animals in each series passes so gradually from one species to the other, as to render any interruption of this transition almost imperceptible. We shall thus have two very different relations, which must have required an infinite degree of design before they could have been made exactly to harmonize with each other. When, therefore, two such parallel series can be shown in nature to have each their general change of form gradual, or, in other words, their relations of affinity uninterrupted by any thing known; when moreover the corresponding points in these two series agree in some one or two remarkable circumstances, there is every probability of our arrangement being correct. It is quite inconceivable that the utmost human ingenuity could make these two kinds of relation to tally with each other, had they not been so designed at the creation. A relation of analogy consists in a correspondence between certain parts of the organization of two animals which differ in their general structure.[38]

It provided a powerful new key for revealing the true natural classification, for if the proper course of affinities were difficult to trace in a particular case, analogies to a more certain series (circle) of affinities could suggest the proper order. For indeed, the fact that his arrangements were orderly and symmetrical was an integral part of MacLeay's reason for believing them to be natural: it was inconceivable that animals would appear to fit a pattern so

38. MacLeay, *Dying Struggle*, p. 21. This identical passage also occurs in *Horae Entomologicae*, pt. 2, pp. 362-63.

well if it were not correct, and it was consistent with God's creative intellect as seen elsewhere, for example in the mathematical laws of mineralogy.

MacLeay felt fairly confident of the truth of the first arrangement he had discovered, that of various beetles, and he was sure that similar principles would be found for other groups. His basis for this expectation, in addition to his success in arranging the orders of insects, was the realization that Lamarck, whose search for chains of affinity MacLeay admired, had proposed a broken, branching series of affinities for the entire animal kingdom which, with only minor alterations, could be transformed into a circular set of connections.

MacLeay's *Horae Entomologicae* (Part 2) of 1821 is his most complete exposition of his system, but he there made no claim to have discovered the proper arrangement for all groups. He did suggest that there were five major groups of the animal kingdom, adding to Cuvier's four branches by making the simplest radiates, the polyps and worms, into a fifth and lowest branch, Acrita. And he proposed that these groups were linked by a chain of affinity running from Acrita, to Mollusca, to Vertebrata, to Annulosa [articulates], to Radiata, with the last of course leading back to the first. He likewise proposed five classes for each branch and showed how they too might be arranged in a circle. He often simply listed five groups vertically and stated that the last must be understood to have affinities with the first, but he did also show some printed in a circle. Two parallel circles he represented by two equal circles touching or "inosculating," at one point.

Clearly, if every group, from genus to order to class, is circular, and has parallel relations with some other group, the entire system of affinities and analogies of all species is geometrically complex; do the circles come in pairs, or are all five circles of a group parallel to one another? MacLeay did not venture into this jungle, which he may not have even seen, but William Swainson, in attempting to elaborate on this approach to classification, became involved in much intricacy and absurdity in his versions of the circular system.[39]

39. Swainson, *Fauna Boreali-Americana; or the zoology of the northern parts of British America* (with John Richardson and William Kirby) (London, 1829–37); and Swainson, *A Treatise on the Geography and Classification of Animals* (Lardner's Cabinet Cyclopedia, London, 1835).

Huxley found in MacLeay not only a generous and sympathetic elder zoologist, but a philosophic mind who shared his interest in finding a meaningful and natural classification. Huxley wrote to Edward Forbes, in October 1849,

> I have a great advantage in the society and kind advice (to say nothing of the library) of Mr. MacLeay in Sydney. Knowing little of his ideas, save by Swainson's perversions, I was astonished to find how closely some of my own conclusions had approached his, obtained many years ago in a perfectly different way. I believe there is a great law hidden in the "Circular system" if one could but get at it, perhaps in Quinarianism too; but I, a mere chorister in the temple, had better cease discussing matters obscure to the high priests of science themselves.[40]

I do not know when Huxley's friendship with MacLeay began, but in the light of his testimony that he had independently reached conclusions similar to MacLeay's, it seems likely that the ideas on classification expressed in a letter to Forbes in September, 1847, were largely or entirely Huxley's own.[41] After noting the similarities of medusae, siphonophores, and hydroids, Huxley declared that he had found

> the beautiful unity of organization running through the whole of these extensive groups—but perhaps unity of organization is hardly a proper term for I think I shall be able to shew that—the various forms are in reality corresponding modifications of *two* primary types—one series starting from the Anthozoid form of polype the other from that of the Hydra—and both running through a parallel and strictly equivalent set of modifications.

In his draft Huxley had crossed out a fuller statement of the same idea:

> Each of these [hydrozoan and anthozoan polyps] forms the basis of a series—running up to the Acalephae proper; each series being precisely parallel to the other—Each series again has its peculiar characteristics and the characteristics of the one are equivalent to the characteristics of the other.

40. Huxley, *Scientific Memoirs*, 1 : 34.
41. Huxley Papers, 16 : 154.

Huxley described the anthozoan series thus:

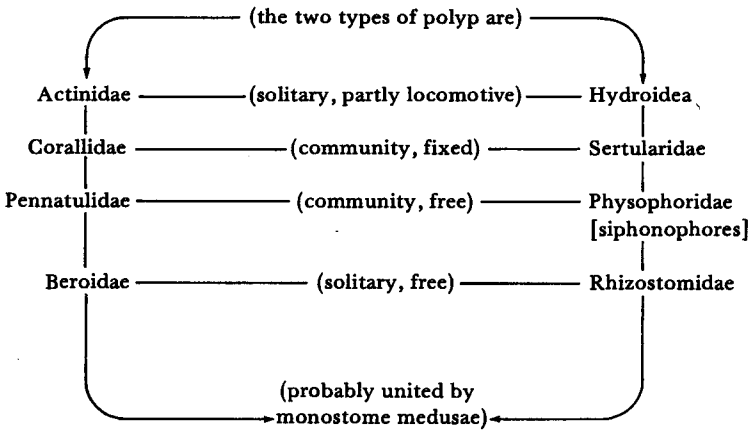
Actinidae	solitary	partly locomotive
Corallidae	a community of individuals	fixed
Pennatulidae	" " "	free
Beroidae	solitary	free

and the hydroid series:

Hydroidea	partly locomotive	solitary
Sertularidae	fixed	community
Physophoridae	free	"
Rhizostome medusae	free	solitary

[This is roughly how he listed them in his notes.]

Ordinary medusae, he suggested, "may probably be considered as uniting the Beroidae & Rhizostomiae . . ." The pattern he was describing may be drawn thus:



Most of the affinities involved were commonly accepted, being represented by ordinary classifications. The Actinidae, Corallidae and Pennatulidae were always arranged together in the class Polypi, and the Hydroidea and Sertularia were always closely associated. Likewise, the Beroidae, monostome medusae, rhizostome medusae, and siphonophores were recognized to be related, and therefore formed the class Acalephae. The importance of the distinction between hydroid and anthozoan polyps had of course

already been pointed out. The direct affinity between Sertularidae and siphonophores was Huxley's basic innovation and insight, though not based on first-hand knowledge of the hydroids. The transition from siphonophores to rhizostome medusae he suspected would be supplied by *Porpita* and *Velella* (siphonophores that approach radial symmetry). The detailed study of the monostome and rhizostome medusae which Huxley undertook was the logical step in his pursuit of this pattern. But the other series, beginning with the Actinidae, was based on the most general considerations. The step from Pennatulidae to Beroidae is particularly questionable, the animals are so totally unlike. His characterization of the Pennatulidae as free is also a stretch of the imagination.[42]

The similarity of this plan to the ideas of MacLeay is evident: affinities connect group to group in a linear fashion, and there are correspondences between members of one series and the members of a parallel series. Finally, although Huxley did not present it to Forbes as a circle, it would form one if the Hydroidea and Actinidae are considered to be affined, as his calling them both polyps implies, and if he did believe that the Beroidae and Rhizostomidae were linked, as he said "may probably" be the case. Within that large circle, however, the pattern of correspondences does not agree with MacLeay's. The pattern would be like MacLeay's if the two series were instead two circles, so that the analogies would be from a member of one circle across to the corresponding member of its neighbor circle.

It seems likely that it was this pattern, or one close to it, that Huxley referred to when he wrote that he had reached conclusions similar to MacLeay's. The coincidence of his independent discovery is really not too surprising. Huxley had known of Swainson's "perversions," and furthermore, some English naturalists who scorned those who would force nature into highly patterned systems nevertheless thought in terms of chains of affinity, and noted parallels and analogies where they seemed evident. Edward Forbes, whose classifications of living and extinct echinoderms were respectably technical, revealed in his popular *History of British Starfishes* of 1841 that he subscribed to the basic notion of analogies existing between parallel series. He asserted that

42. The "sea-pens" are more free than corals, in that they are capable of changing their anchorage, but are not free-swimming as are the other groups he calls "free."

echinoderms and acalephs were parallel groups, and that *therefore* their divisions must be based on the same character, in this case their means of locomotion. He believed that echinoderms that deviated from their normal five-part symmetry may do so in "representation" of the four-part symmetry of other radiates. He tried to explain how the order of crinoids have *affinity* to starfish but *analogy* to polyps.[43]

During his friendship with MacLeay, Huxley's own ideas about the meaning of affinity and analogy developed. At one point he noted to himself that analogies may be sought for between natural groups, but until the existence of analogies has become an established law of zoology, a supposed analogy must not be taken as evidence contributing to the formation of groups.[44] The warning should not have been directed only against others, for on another occasion, when sketching the analogies he was finding within radiates, he noted, "This uniformity is surely in favour of the arrangement and tends to strengthen the conviction that it is really natural and well founded."[45] He was convinced of the accuracy of MacLeay's basic ideas, but felt MacLeay had not gone far enough.

43. Edward Forbes, *A History of British Starfishes* (London, 1841), pp. xi-xvi, 104. His statements are brief, but he felt sure enough of these ideas to express them as laws; he wrote, "I hold it as a law that the divisions of parallel groups should be based on a common principle" (p. xiv), and that it is "a law in which I put firm trust, that *when parallel groups vary numerically by representation they vary by interchange of their respective numbers*" (p. xvi). But I am confused as to exactly how he would arrange his three classes of radiates; it may be that I have overlooked some source in which Forbes explained his system in more detail. On the other hand, though he expressed belief in these laws, at the same time he said, "The humility which the knowledge of the abundance of undiscovered things teaches the practical naturalist, prevents him retorting on such would-be philosophers; and knowing how little we yet know, he scarcely ventures to pronounce any law general. He knows too well that the conclusion he drew in the morning is often over-turned by the discovery he makes in the evening, to pronounce himself the lawgiver of nature; yet also knowing, from the perfection of all he sees around him, that the machinery of nature is perfect, and hoping the laws of that machinery discoverable, he points out the indications of those laws wherever he perceives a glimpse of their influence, and works as trustfully towards the developement of the truth" (*British Starfishes*, p. 58). Huxley later said of Forbes, "he has more claims to the title of Philosophic Naturalist than any man I know of in England" (*Life and Letters*, 1 : 102).

44. Huxley Papers, 40 : 149. I am sorry I cannot date these manuscripts, though they clearly belong to the *Rattlesnake* period.

45. Huxley Papers, 37 : 45; see figure 9.

> The Circular System appears to me to stand in the same relation to the true theory of animal form as Keplers Laws to the fundamental doctrine of astronomy—The generalizations of the Circular system are for the most part, true, but they are empirical, not ultimate laws—
>
> That animal forms may be naturally arranged in circles is true—& that the planets move in ellipses is true—but the laws of centripetal & centrifugal forces give that explanation of the latter law which is wanting for the former. The laws of the similarity & variation of development of Animal form are yet required to explain the circular theory—they are the true centripetal & centrifugal forces in Zoology.[46]

Huxley felt that the explanation for the existence of affinities and analogies that form distinctive patterns would be found in the forces that operated during the early growth of an organism; he had not found the answer, biology's law of gravity, but he was searching in that direction. He knew that a homology could be established, not just by the traditional comparisons of comparative anatomy, but also by the alternative method of comparative embryology. Embryology had taken on an important role in classification as well as in physiology, both because of the German discussions culminating in the assertion of Baer that there was a distinct mode of development in each of the four embranchements, and because of the clarification given such anomalous groups as cirripedes, parasitic copepods, and *Comatula* by the discovery of their larval forms. If the clue to MacLeay's system was indeed in the laws of development, then the essential difference between analogy and affinity should lie there. Most naturalists would define affinity as a strong similarity in important characters, and analogy as a peculiar similarity between species not related by affinity. Huxley suggested that affinity (or homology) should be defined in terms of two forms sharing the same course of development, while forms which were similar, even to the point of identity, were merely analogous if they had come about through different processes of growth. He mentioned as an example the similarity between the free-swimming capsules of hydroids described by Dujardin and true medusae, which, he be-

46. Huxley Papers, 40 : 149.

lieved, is only an analogous relation because medusae have a different origin.[47] For support of this approach, Huxley referred to the science of philology, which describes words as being related by analogy or affinity, dependent not on their own similarity but on whether they may be traced back to the same or distinct points of origin.[48]

MacLeay quickly replied that Huxley's approach was impossible in the light of the system of affinities and analogies which MacLeay had so long before shown to exist: the *analogy* between the parallel orders of insects was based on their mode of development, their larvae and metamorphosis![49] MacLeay explained that the difference between the two kinds of resemblance lay simply in the pattern of their arrangement; affinity was that relation which existed between members of the same series, and analogy was that relation which existed between members of parallel series. They were not different in essence, for where two parallel circles touch, analogy and affinity become indistinguishable. The two words "have always been used by me as words expressing the mode in which relations of resemblance take place rather than as two kinds of resemblance different in themselves." To Huxley it must have sounded as if Kepler were explaining ellipses by repeating their mathematics, instead of understanding the need for a law of gravity.

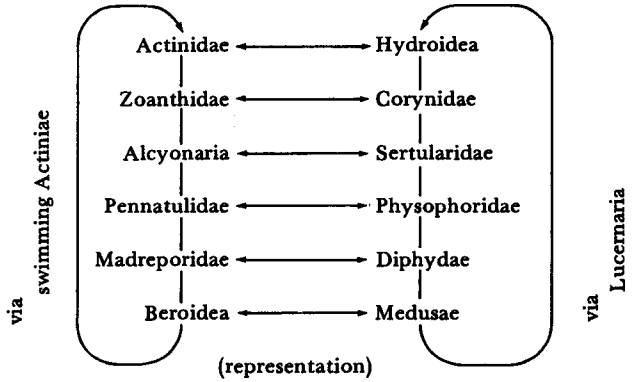
After Huxley's return to England, he still continued to think that there was an important truth hidden in MacLeay's method of

47. Huxley Papers, "Some considerations upon the meaning of the terms Analogy & Affinity," 37 : 1.

48. Loc. cit. When he explained the difference between analogy and homology or direct affinity by development, and especially with reference to the historical development of words, Huxley sounds to us as if he were very close to an evolutionary explanation, but I have found no indication that he speculated beyond the embryological history of the individual to the historical development of the entire species. It is interesting that the science of philology, looking for support for its methods in the early part of the century, had taken comparative anatomy as its model; now the role was reversed. Friedrich von Schlegel wrote in 1808, "Comparative grammar will give us entirely new information on the genealogy of languages, in exactly the same way in which comparative anatomy has thrown light on natural history" (quoted from *Ueber die Sprache und Weisheit der Indier* in Holger Pedersen, *The Discovery of Language: linguistic science in the nineteenth century*, John Webster Spargo, trans., Bloomington, Ind., 1962, p. 19).

49. Huxley Papers, 22 : 135. This is a letter by MacLeay dated March 13, 1849, and beginning, "As you have asked me to give you my opinion on what you have written on *Affinity* and *Analogy* . . .", indicating that the manuscript cited in fn. 47 was the draft of an essay submitted to MacLeay.

classification, and that the clue to the mystery lay in the laws of embryological development. In November 1851 he wrote back to MacLeay, "I am every day becoming more and more certain that you were on the right track thirty years ago in your views of the order and symmetry to be traced in the true natural system."[50] This was not mere flattery, for Huxley had a few months earlier declared to the British Association for the Advancement of Science his belief in an ordered arrangment of polyps and acalephs, much like the one he had confided to Forbes four years earlier, even though he had very little new evidence.[51] But where his earlier arrangement was not explicitly circular, yet did tend to form one large circle, this arrangement was closer to MacLeay's in explicitly forming two circles. "Furthermore, each group returns into itself; the free floating Actiniae nearly approximate Beröe, and *Lucernaria* [sometimes classified as a hydroid] is but a fixed *Medusa*."[52] He had increased the number of members in each series by subdividing the families, but this was not an important change. He still believed that "As might be expected a mutual representation runs through these great groups,"[53] the hydroids being "represented" by the actiniae and so on. His system of 1851 may be diagrammed thus:



At this 1851 lecture Huxley not only explained his ideas about the coelenterates, which he called "Nematophora," he also ex-

50. Huxley, *Life and Letters*, 1 : 100.

51. Huxley, *Scientific Memoirs*, 1 : 98–101.

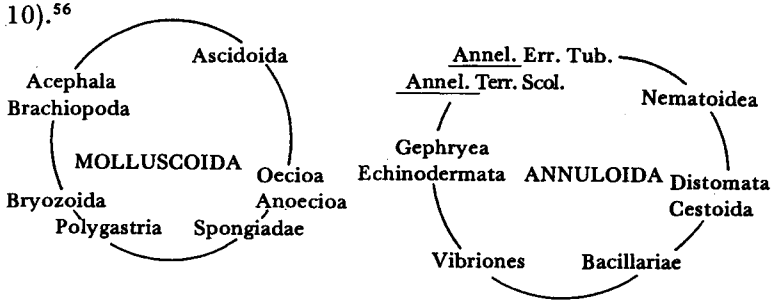
52. Ibid., p. 101.

53. Loc. cit.

pressed his thoughts on the distribution of all the other groups that had belonged to Cuvier's Radiata. In the course of developing his ideas on this larger problem, Huxley had followed the same model of regular analogies and affinities that he had used for the coelenterates. Among his notes are some sketchy charts, evidently attempts to find an orderly arrangement for the various worms, protozoa, coelenterates, echinoderms, and other denizens of this "lumber-room." In one, reproduced as figure 9, Huxley seemed to be setting up parallel columns, with analogies represented by dotted lines, and stronger relations represented by solid lines.[54] I transcribe that sketch thus:

Brachiopoda		Acephala	Cirrhigerous Annelida		Lumbricoides
Bryozoida	Molluscoida	Ascidioida	Gephyrea	Annuloida	Hirudinida
		Nematophora	Echinodermata		
~~Anoecioa~~		~~Oecioa~~	?Nematoidea		
			~~Echinodermata~~		Distomata
			?Filariae		?Nematoida
			~~Nematoidea~~		
			Vibriones		
Polygastria		Spongiada ?	~~Bacillariae~~		Cestoida

The sketch labeled "Arrang[emen]t of Radiata" which accompanies the draft of his 1851 British Association lecture is clearly derived from the above attempt.[55] Just as in his vision of the anthozoan and hydrozoan series forming the circle of nematophores, now the pairs of columns have become circles of affinities (fig. 10).[56]



54. Huxley Papers, 37 : facing p. [53].

55. Huxley Papers, 37 : 43.

56. For help in deciphering these names I turned to Huxley's "Lectures on General Natural History," published in the *Medical Times and Gazette* in 1856. For example, he there refers (July 12, p. 27) to the errant and tubicular Annelids of Cuvier and the Terricola and Scoleidae of Milne-Edwards.

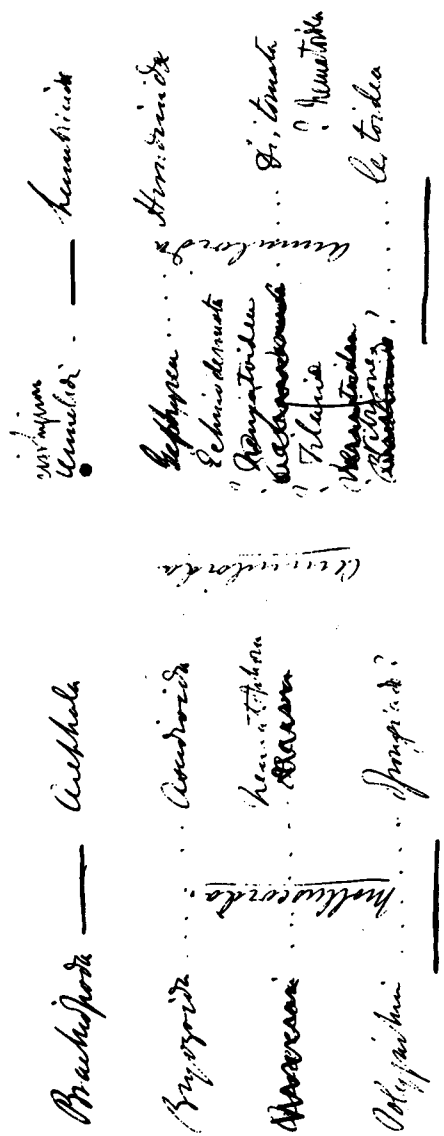


Fig. 9. Huxley's manuscript notes on classification (Huxley Papers 37:45). My reading of the chart is given on the facing page. I am grateful to the Imperial College of Science and Technology for permission to photograph and publish this manuscript and the one on page 96.

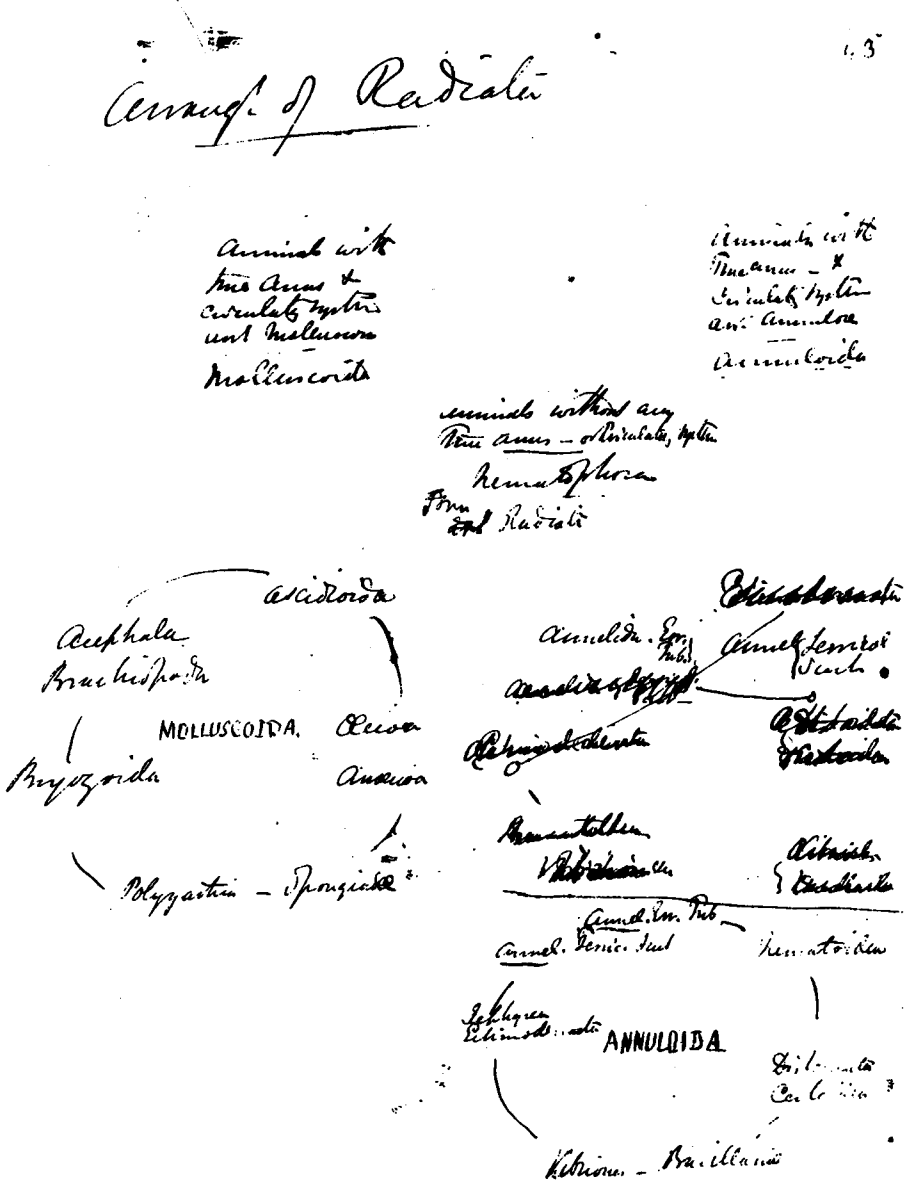
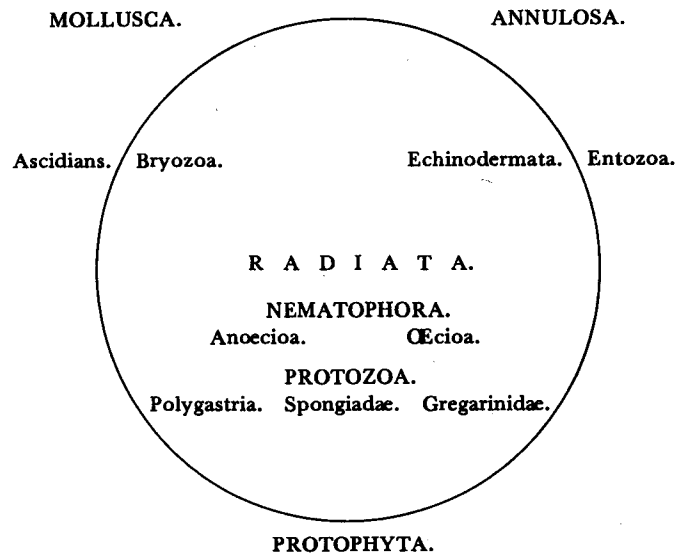


Fig. 10. Huxley's manuscript "Arrang[emen]t of Radiata" (Huxley Papers 37:43). My interpretation of his circles is given on p. 94. The text above the circles reads: "Animals with true Anus & Circulat^y System arr[angemen]t Molluscous Molluscoida"; "Animals without any true Anus —or Circulat^y System Nematophora Form Radiate"; "Animals with true Anus —& Circulat^y System Arr[angemen]t Annulose Annuloida."

In his lecture Huxley did not speak of circles of affinity, but he did propose a new arrangement of the Radiata. His new "Annuloida" and "Molluscoida" were not identical to those sketched earlier, for he suggested two other groups as well, the Nematophora (Anoecioa and Oecioa) and the Protozoa (Polygastria and Sponges). Still, chains of affinity remained part of his argument; he stated that echinoderms lead towards dioecious annelids and that nematodes and intestinal worms lead towards monoecious annelids. Likewise within the Molluscoida, ascidian polyps lead to bivalve mollusks (Acephala) while bryozoan polyps lead to brachiopods, according to Huxley. His lecture notes include the assertion, "these groups mutually represent one another."

We can only speculate on how his audience, including men like Forbes whose approval was precious to him, would have reacted to these echoes of William Sharp MacLeay. Perhaps Huxley's own further research served to undermine the idea that a natural arrangement would be uniform in its pattern of analogies and affinities. Something turned him aside, for the published abstract of his lecture contained only this untidy diagram:



His later writings give no hint of his youthful flirtation with circular classification.