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31.—A Historical Consideration of the Siphonophores. By Mary P. Winsor. (With 2 plates)

In his report of the *Challenger* siphonophores Ernst Haeckel sketches a picture of biological debate and solution calculated to excite historians and philosophers of biology. Here is a distinct zoological issue, Haeckel suggests, to which Darwin's theory of evalution both gives new meaning and offers a solution. Only an evolutionist, Haeckel implies, could see the flaws in previous ideas and wield the powerful tool of embryology to uncover the truth. It sounds as if the siphonophores can provide what has long been wanted, a nice case-study of the impact of Darwinism upon classical zoology, that is, upon comparative anatomy, morphology and classification.

Siphonophores are a small group of jellyfish, including the Portuguese man-o'-war and others more delicate. Unlike other jellyfish (medusae and ctenophores), siphonophores are not radially symmetrical but present a confusing array of tentacles, stalked mouths, swimming bells, and reproductive capsules (see pl. 1). Today few people have even heard of this group, but in the mid-nineteenth century siphonophores basked in the attention of the most influential zoologists. Popular audiences in London, Boston and Berlin were told that these creatures, besides having a fascinating jewel-like beauty, held important lessons about the organisation of all life (Agassiz 1849; Huxley 1852; Haeckel 1869). No wonder the famous and busy Haeckel accepted the chore of describing the *Challenger* collection.

The story turns out to be far less straightforward than Haeckel, the propagandist for Darwin, would have us believe. The fact is that by 1859 zoologists had already reached a consensus about the nature of siphonophores and their place in the animal kingdom. They were thought to be colonial and nearly related to the hydroids. In 1851 Rudolf Leuckart had elaborated this interpretation into his brilliant theory of polymorphism, a theory which very easily could be translated, and soon was, into evolutionary terms, for it not only identified the ancestors of siphonophores, the hydroids, but even detailed the cause of evolutionary change, the physiological advantage of the division of labour. Haeckel himself for years supported Leuckart's theory, and it is essentially the one which prevails today. The alternative theory of Mechnikov, from which Haeckel's 1888 'solution' differs only trivially, purports to be based upon the biogenetic law, but ironically these two avid Darwinians made little real use of evolutionary reasoning.

Haeckel said that the issue was whether siphonophores evolved from polyps or medusae (Haeckel 1888, p. 1) but it must be realised that the definitions of those divisions underwent a change about mid-century. The change is exemplified by the difference between Louis Agassiz's classifications of Radiata in 1848 and 1860. In both we find the same three classes, Echinodermata, Acalephae and Polypi. In the earlier arrangement, the Acalephae are what would commonly be called jellyfish, that is, ctenophores, medusae and siphonophores; polypi too are just what would be expected, namely *Hydra*-like forms like corals, sea anemones and hydroids. In 1860 we find the hydroids classed as Acalephae, and the siphonophores reduced to a subgroup within the hydroids. What had caused these changes?

Hydroids are *Hydra*-like animals which begin from a single egg but proliferate by budding into a colony or community of connected individuals. Besides additional polyps, some species can produce, by budding, small medusae, which separate from the colony, swim free and become sexually mature. Many of these medusae had been named before their origin was known. The discovery of this metamorphosis was what necessitated the reclassification of hydroids from the Polypi to the Acalephae.

The life cycle of hydroids was placed in a bright spotlight when Steenstrup included them in his much-discussed theory of the alternation of generations in 1842. Steenstrup regarded the polypoid individuals as the first generation, which by asexual reproduction gives birth to a second generation, the medusae. The sexually produced offspring of the medusae do not resemble their parents, as in normal reproduction, but their grandparents, the polyps. In this sense the generations alternate. But various hydroids refused to co-operate with Steenstrup's system. They produced a medusoid which would release eggs or sperm without ever breaking loose from the colony. In some species this medusoid lacked mouth or tentacles, or both, while other hydroids bore a sexual capsule only slightly reminiscent of a medusa. The transition from free medusae through medusoid sexual organs to simple capsules was so gradual that their homology could not be denied for long, yet this homology created a dilemma. If it seemed absurd to call a simple egg capsule an entire second generation in Steenstrup's sense, the choice seemd to be to call a perfect and independent medusa nothing but an elaborate reproductive organ. Both extremes had their advocates (Huxley 1877, p. 135; Allman 1865), but it was generally recognised that the words 'organ' and 'individual' were inadequate in their usual sense, and that a new terminology was needed.

At the same time as the evidence for the medusoid affinities of hydroids was appearing, a number of naturalists began to see similarities between siphonophore structure and that of hydroids (Milne-Edwards 1840; Sars 1846; Leuckart 1847; Vogt 1848; Agassiz 1849; Huxley 1849). Siphonophores consist essentially of numerous simple sacs, which may take the shape of stalked mouths like polyps bare of tentacles, of isolated tentacles or of other organs, all connected together by a common cavity which serves for digestion and distribution of nourishment. Their reproductive organs clinched the argument, for they ran the gamut from a capsule like that found in some hydroids all the way to free-swimming medusae. From about 1848 the idea that siphonophores were really a kind of floating hydroid was rapidly accepted, and Germans began to call the group *Schwimmpolypen*.

Still, siphonophores are by no means as simple as hydroids. They have a number of organs all their own, such as air sacs, feelers, suckers, tentacles, protective shields and locomotory cups, whose form is so peculiar that zoologists had to invent a special siphonophore vocabulary. Comparative anatomists expected to be able to trace homologies from one group to another, so the unique organs of siphonophores were a puzzle and a challenge.

In 1851 Rudolf Leuckart offered a solution not only to the puzzle of siphonophore morphology but to the dilemma of the alternation of generations in hydroids as well. Zoologists already are in agreement, Leuckart argued, that each polyp in a hydroid colony is an individual, and likewise they must acknowledge that each organ of a siphonophore is a morphological individual. The common stock which unites the colony, and in some species is enlarged into an air sac, is comparable to the common stock or roots connecting hydroid polyps. The sex capsule, medusoid or not, is of course homologous to that part in hydroids. But what about the other elaborate organs seemingly unique to siphonophores? Leuckart proposed that these elements were individual animals, highly modified polyps or medusae, united into a community. If his colleagues balked at being told that a single tentacle was equivalent to an entire animal, Leuckart reminded them that he was referring to morphological, not physiological, equivalence. Within a morphologically comparable organ, such as the limb of a vertebrate, zoologists were accustomed to accept an immense range of differences, and they understood that those differences depend on whether the limb functions for swimming, running, flying or grasping. They traced the homologies of the appendages of insects or crustacea through parts modified for biting, sucking or piercing, and legs that could swim, walk or carry eggs. Just as an organ may be drastically modified according to its function in an organism, so too, said Leuckart, entire individuals may be modified according to their role in the community to which they belong. And how are they modified? In obedience to the principle of the division of labour, answered Leuckart. As early as 1827 it had been suggested that physiological economy, like the economy of a nation, required a specialisation of function by the division of labour (Milne-Edwards 1827, 1851). Now Leuckart suggested that siphonophores were communities in which the jobs of capturing prey, swallowing food, sensing the environment, and so on were divided up among individuals specialised for these functions. The phenomenon of polymorphism which results from the principle of the division of labour is not limited to the peculiar case of siphonophores, in Leuckart's view. Steenstrup's alternation of generations he called nothing more than a special case of polymorphism, where some individuals are specialised for taking nourishment and others for sexual reproduction. The difference between the polyps and medusae of a hydroid were no longer fundamental, the medusae being simply individuals specialised for the distribution of eggs.

Leuckart's notion of polymorphism sounds very nice to modern ears, but in 1851 there were many men striving to rid zoology of just such teleological reasoning. What meaning could modification, purpose or specialisation have in a purely material world? Indeed, Leuckart's teleology was so blatant it even had political implications. After describing the siphonophore as a community connected by a channel in which nourishment circulates, he observed,

> What the individual acquires, becomes the property of society and goes to the good of every member. In the same way will damage to a single member be sustained by all. As in a communist state, there are here no poor by the side of the rich, no hunger beside surfeit, but also no lazy next to the industrious. Each one contributes his part to the existence and welfare of the whole, each according to his powers (Leuckart 1851*b*, p. 10).

The same analogy of siphonophore to socialism was developed by Carl Vogt in his 1851 *Untersuchungen über Thierstaaten.*

Not long after the publication of Leuckart's theory, Professor Albert Kölliker spent some months with students in Messina, and in 1853 he published an elegant monograph on siphonophores. Considering with care all previous opinions about these animals and adding many new observations, Kölliker concluded that siphonophores were indeed more like hydroids than like simple medusae. To him the decisive observation was their manner of development, which was neither direct growth nor metamorphosis but resembled the production of new polyps in a hydroid by budding. Nevertheless he saw no need whatsoever to follow Leuckart in homologising every organ of a siphonophore with an individual polyp. Only the feeding polyps were in a certain sense individuals, the remaining structures were for Kölliker simply the organs they seemed to be.

Accompanying Kölliker to the sea coast, Carl Gegenbaur had devoted much attention to the same question. Torn between the judgments of his professor and the daring theory of his contemporary, Gegenbaur tried to create a vocabulary which could reconcile the two. A medusiform organ is surely just an organ in a physiological sense, yet it is analogous to the second generation of those species which do produce perfect medusae. We must remember, Gegenbaur cautioned, that the transition we see here between organs and individuals takes place only in our imagination.

Just back from Messina and struggling with these issues, in 1853 Gegenbaur met the 19-year-old Ernst Haeckel. Their friendship blossomed into

> such an intimate and continual interchange, in daily communication and conversation so reciprocally penetrating and clarifying, that it would indeed be impossible for either of us to determine the special contribution of each to our mutual intellectual property (Haeckel 1866, **1**, p. x).

One of the fruits of those discussions was Haeckel's *Generelle Morphologie*, a book attempting to base morphology upon laws of mechanism and Darwinian evolution. Although the siphonophores themselves received no special mention in this work, Haeckel did put great emphasis on the problem of individuality, discussing the role of 'persons' on a common stock. Likewise he gave central importance to the idea of polymorphism, which he called one of the fundamental processes of development. Both embryonic differentiation and the divergence of character in evolution spring from the same law of the division of labour. Although the other elements of development (generation, growth and degeneration) can be directly explained by physical and chemical laws, said Haeckel, polymorphism is a product of the struggle for existence (Haeckel 1866, **2**, p. 250).

Gegenbaur's special contribution to the study of siphonophores had been to follow their embryonic growth by means of artificial fertilisation, and in December 1866 Haeckel took up this line of investigation. Gegenbaur had only succeeded with one species, but on the Canary Islands Haeckel followed the development of three more species of siphonophores. He sent his description of these studies to the Utrecht Society of Arts and Science and was awarded their gold medal in 1868. Although his paper was submitted for the prize anonymously, as the rules required, Haeckel made no secret of his admiration for the author of the *Generelle Morophologie*. Referring to his own ideas in the third person, he expressed his faith in the biogenetic law, and said that the motto of his approach to siphonophores had been Haeckel's statement,

> All phenomena which attend the individual development of organisms, are to be explained purely by the paleontological development of their ancestors (Haeckel 1869*a*, p. 103).

In animals which leave no fossil remains, embryology becomes all the more valuable for determining ancestry, he added.

Haeckel's discussion of siphonophore development shows how slippery his biogenetic law could be. While admitting surprise at the differences between the early forms of the four siphonophores whose embryology was known, Haeckel confidently proceeded to label one of these the primitive type. Without the help, or restraint, of a geological record, he identified primitiveness on the basis of what seemed to him the simplest, most direct course of development (equal division of the egg rather than its specialisation into formative and nourishing parts). He skimmed calmly over some logical thin ice:

> . . . the simpler case of *Physophora* must represent the original condition, and the differentiation of nutrient and structural yolk must generally moreover represent a later event, postulated on the law of shortened inheritance.
>
> If this interpretation is correct, then the general ancestor of our siphonophore genera in an earlier time would have followed a simpler individual course of development as follows: the larval body coming from cleavage . . . changes completely into the primitive polypite (Haeckel 1869*a*, p. 97).

At an early stage this larva consisted of yolk, air sac, protective umbrella, and a polyp with one tentacle. Its umbrella is not radially symmetrical and lacks the canals characteristic of medusae, and the tentacle springs from its centre, not its rim, but Haeckel saw the larva as homologus with a medusa. A modern expert has expressed outright shock at this homology (Totton 1965, pp. 9–10). The apex of the umbrella was pierced, Haeckel claimed, by a canal representing the canal which links a hydroid medusa with its parent colony (pl. 2a). As is to be expected in a useless vestigial organ, he added, this canal varies from one individual to the next and is often absent. Enthusiastically he described it as a 'very valuable ancient certificate of aristocracy' (Haeckel 1869*a*, p. 100), relic of the time when ancestors of the siphonophores had budded off hydroids. Rudimentary structures were beloved by Darwinians; Fritz Müller congratulated him (Müller 1921, p. 168).

Haeckel could the more easily see this larva as a medusa because he had in mind certain unusual medusae. He cited a species, recently pictured by Louis Agassiz, which had only one tentacle (pl. 2b). It also had the ability to produce other medusae by budding, an ability ordinarily limited to polyps. Haeckel himself had published a series of articles about the budding of medusae upon other medusae, a curious case because the offspring looked like a distinct species (in fact he had been deceived by medusae which are parasitic on other species; see Brooks 1885). There was therefore no obstacle to his making a medusa the first individual in a budding colony.

In general, his results were added proof, said Haeckel, that siphonophores are homologous with hydroid colonies, but as for the homologies of the various parts, he could offer no certainty. Probably the stock, the feeding polypites and the feelers were polypoid persons, while the swimming bell, protective shields and sex organs were medusoid persons; other parts might be merely organs. Here as in all nature, he said, there are no sharp lines, for extremes are joined by transitional forms.

Haeckel scarcely referred to the theory of polymorphism, except to say that the medusoid larva was not what Leuckart had predicted. However, as his *Generelle Morphologie* had already made clear, he gave polymorphism a much wider application and a much greater importance than Leuckart had. Indeed, the siphonophores were now just a simple example of a very fundamental biological law. Haeckel put the siphonophores to use in his campaign to popularise materialism and Darwinism. Lecturing to working men in 1868, he chose as an appropriate theme the division of labour. After a brief mention of man and much about the social organisation of bees and other insects (in which he denied the current notion of instinct), Haeckel set forth the siphonophore story. His descriptions are beautifully clear for his lay audience, and they confirm that he had embraced the essence of Leuckart's theory. He showed in detail how the various parts of the animal are either polypoid or medusoid individuals, but went beyond Leuckart in sketching the evolutionary history of the group. The ancestor of all hydroids, medusae and siphonophores had been a simple polyp, later the medusoid form had appeared, and later still a hydromedusa stock became a swimming siphonophore. In keeping with the biogenetic law, embryology recapitulates this history, and the egg of a siphonophore first develops, he said, into nothing but a simple polyp. This becomes the stock of the colony and buds off polypoid and medusoid persons.

Siphonophores provided an important link in the chain of Haeckel's general argument. What are separate individuals in the community of bees are here physically and physiologically joined together, just like the organs and cells of an animal or plant. Life itself is not the mysterious product of a vital force 'but the mechanical total result of the activities of various organs separated through the division of labour' (Haeckel 1869*b*, p. 35). Man himself is simply an animal, whose soul is nothing more than the combined activity of millions of cells, the tiny citizens ('*Staatsbürger*') of which he is composed. If jellyfish were modest, they would have blushed at their philosophical implications.

Twenty years after this lecture, the *Challenger Report* on siphonophores appeared. In it Haeckel asserts that the group needs reinterpretation, that a siphonophore is not a community of polypoid and medusoid individuals after all. Haeckel's new theory, presented in such elaborate dress as to be almost incomprehensible, is that a siphonophore is a 'medusome', that is, a community made up of medusoid individuals plus isolated medusoid organs. For some reason Leuckart's theory, which had served Haeckel so well in his campaign for Darwinism, was no longer adequate. What had induced Haeckel to abandon it and invent a new one?

I suspect the answer is that his scientific manhood had been challenged. Ernst Haeckel, of all people, had been accused of being unfaithful to his own biogenetic law. In 1874 Il'ya Mechnikov, agreeing with Haeckel's conclusion that larval siphonophores are in the form of a medusa, asserted that the polymorphism theory was thereby quite disproven. The Russian's opinion carried some weight, for his embryology of other marine animals had already provided evolutionary links between the vertebrates and invertebrates, and between echinoderms and annelids; his comments on siphonophores accompanied a detailed report of the embryology of six species. Mechnikov claimed that Leuckart's theory had assumed the young siphonophore to be a simple gastric sac (representing a polypoid individual) from which further individuals will bud. Haeckel's recognition of the homology between a young siphonophore and a simple medusa should have been sufficient to overthrow that theory, according to Mechnikov.

But in order to become reconciled with [Leuckart's theory], Haeckel comes to the conclusion that only the first-formed gut of the siphonophore is homologous with the gut of a medusa, . . . but that all subsequent guts . . . represent entire individuals, exactly as the dominant polymorphism theory requires! It is truly wonderful to encounter such an inconsistency in Haeckel, who certainly does not fear to remain consistent in other matters, all the way up to extremes. . . . I follow Haeckel absolutely, when he considers the *Physophora* larva to be an animal corresponding to a medusa; but instead of being unfaithful to this notion, like the scientist just mentioned, I take this as my basis, and founding myself upon that I declare that all of the guts, and likewise the feelers, tentacles, protective pieces and swimming bells, are not individuals, but merely organs, corresponding to parts of a medusa (Mechnikov 1874, p. 38).

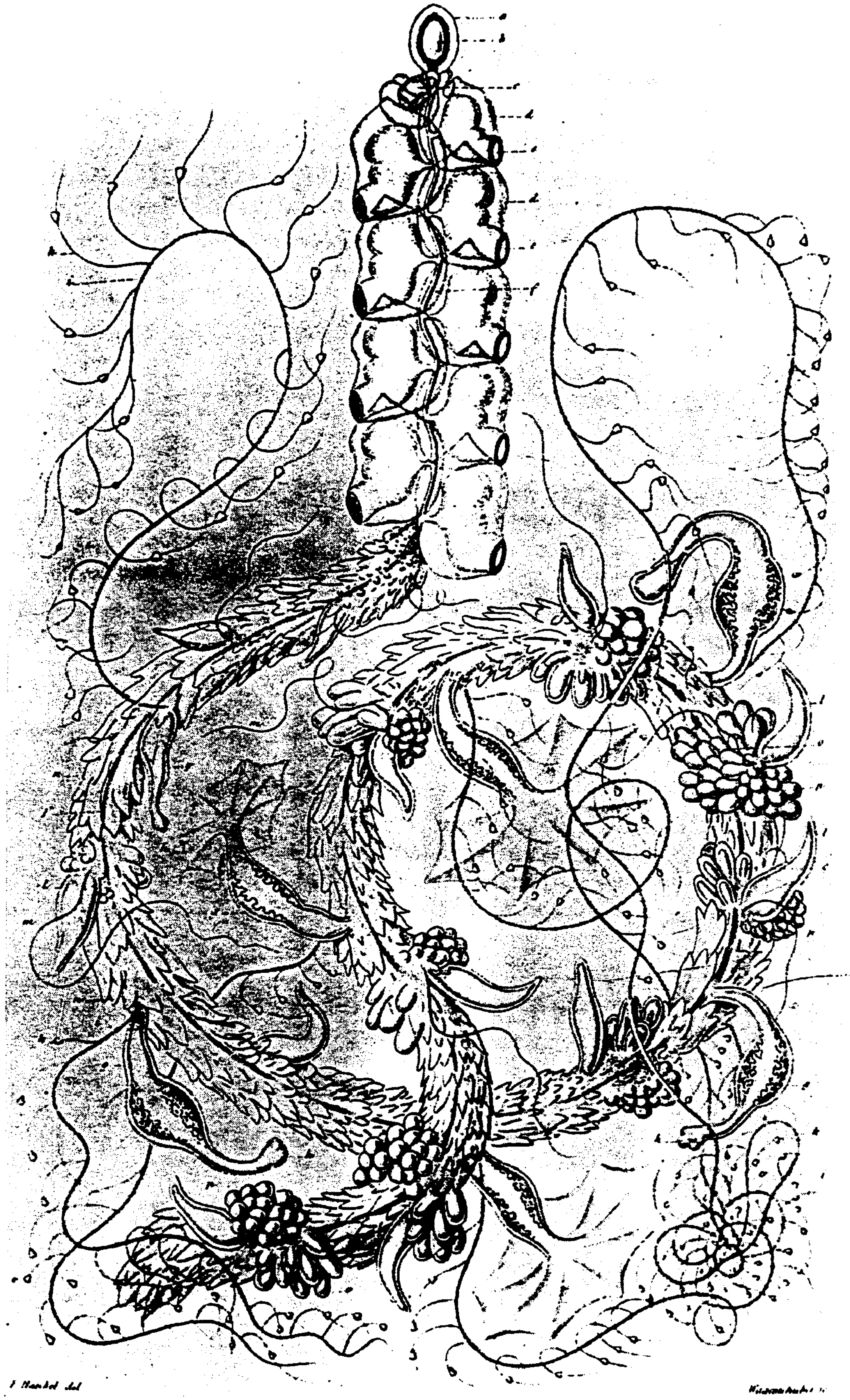
T. H. Huxley is always grouped with Mechnikov as a proponent of this 'poly-organ' theory, but the connection is a superficial one. Huxley's ideas had taken shape before he had heard of Leuckart's idea of polymorphism (Winsor 1971, chap. 4), and he could never bring himself to call a piece of an animal an individual. Recognising the homology of siphonophore sex organs to free hydroid medusae, he had to call the latter organs too. So while it is true he would not call a siphonophore a community, he believed it to be fundamentally like a hydroid, whose polyps he also called organs. As to the implications of all this for evolution, he steadfastly refused to speculate (Huxley 1877, p. 42); in fact his ideas about all these animals remained untouched by the *Origin of Species*.

Presumably in response to Mechnikov's criticism, Haeckel tacked on to his lecture on the division of labour, when it was republished in 1878, a statement to the effect that all the 'persons' of a siphonophore are medusoid (Haeckel 1878, p. 141). His more elaborate medusome theory of 1888 allowed him to retain the idea of a polymorphic colony while admitting as mere duplicated or displaced organs those parts which seemed indeed to be so, just as Gegenbaur's earlier compromise had done. But furthermore, by excluding the polypoid form, Haeckel was giving new weight to his biogenetic law. Since the larva was a medusa, so must have been the ancestor.

Haeckel presents his medusome theory as if it were the solution to an important zoological problem, but the ideas he calls the 'poly-organ' and 'poly-person' theories are extremes which were not in fact held by anyone. The intricacies of the medusome theory and its actual rivals are not important here, because the search for a likely ancestor of siphonophores had been narrowed, well before 1888, to a limited taxonomic area, the Hydrozoa. In speculation as to the origin of siphonophores, all the 'polyps' and 'medusae' cited were hydroid, and never anthozoan polyps nor scyphozoan medusae.

Discussion which seemed concerned with what kind of animal siphonophores evolved from, was in fact concerned with the question, How did its transformation take place? Had a hydroid colony learned to swim, by somehow acquiring a siphonophoran air bladder, or by using its attached pulsating medusae? Had a medusa, being freed from its hydroid stock, budded more medusae to form a colony, or had it grown complex by the reduplication of its organs? Could such a medusa have been one of the sort which lacks a polypoid stage? To appreciate this game, one should not watch the scoreboard but the players' style.

A quick glance at Haeckel's contemporaries is enough to reveal some differences in



Haeckel's drawing of the siphonophore *Anthemodes canariensis*, which formed the frontispiece of his 1869 lecture on the division of labour.

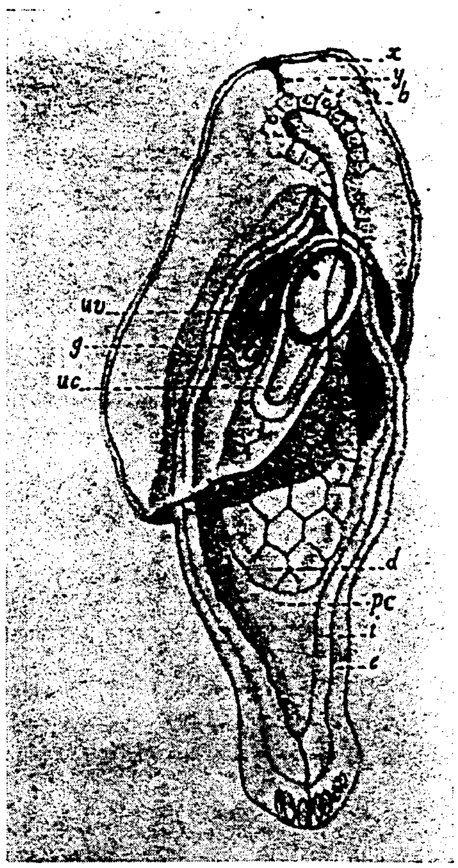


PLATE 2*a*.—Haeckel's drawing of a twelve-day-old larva of *Physophora* including at the top the canal he called rudimentary. (Haeckel 1896a, Pl. 1, fig. 15.)

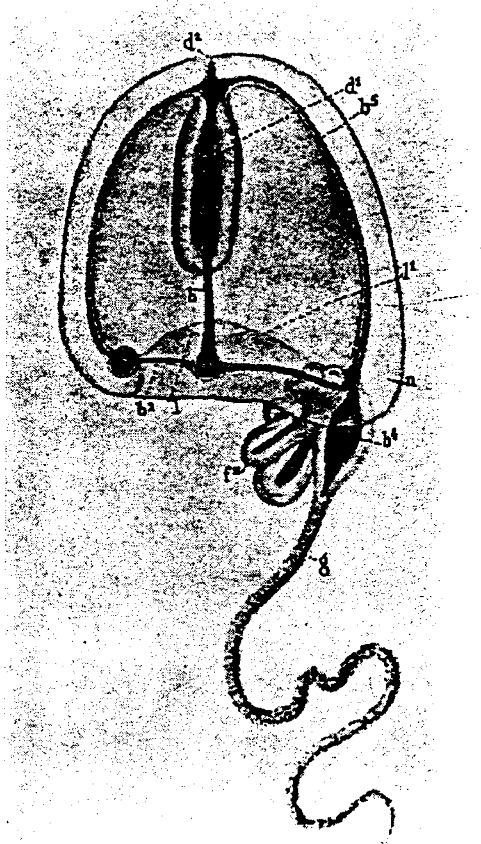


PLATE 2*b*.—A newly-released medusa of the hydroid polyp Hybocodon prolifer, showing the apical canal which connected it to its parent. Next to the base of the sole tentacle may be seen the buds of secondary medusae. (L. Agassiz 1860. 4. Pl. 25. fig. 14.)

style. The limitations of classical morphology with respect to such simple and plastic animals was recognised more clearly by Edmond Perrier and Carl Claus than by either Haeckel or Mechnikov. As to the origin of the siphonophores, Perrier speculated rather boldly. He argued that most hydroids live in shallow water, so that larvae drifting into the open ocean would perish. Only those individuals able to accumulate gas in their tissue would survive.

> The floating larvae thus maintain themselves, transmitting to some of their descendants the precious faculty to which they owed their salvation. This faculty consequently becomes widespread, and by the most simple of mechanisms, the quite remarkable class of siphonophores comes into existence (Perrier 1881, p. 269).

Claus admitted that it was hard to imagine an attached hydroid colony becoming free-swimming, but saw even greater difficulties in Mechnikov's suggestion that medusoid organs had been duplicated and dislocated.

> . . . what advantage could such a change of position [of its organs] bring to the organism? Wouldn't a medusa thus [changed], have to arise as a monstrosity, which in free nature would have been again immediately suppressed, and certainly would not have been intensified and become established through natural reproduction (Claus 1884, p. 9).

Haeckel's medusome theory lacks this Darwinian flavour. In essence he does rely on the appearance of monstrosities; indeed, his first research on siphonophore larvae had included experiments designed to induce abnormal development. Furthermore, his evaluation of embryonic morphology fails to consider the larval activities which must play a role in natural selection. Finally, he virtually abandons the idea that classification should represent phylogeny. Although he decides that siphonophores, and the medusae too, contain animals with different origins, he retains these groups. Even more surprising, he keeps in separate groups animals which he knew to be related, not merely historically, but as different stages of one life cycle.

Haeckel's own description would lead us to expect that his *Challenger Report* on siphonophores was both a significant contribution to knowledge and a fine example of an evolutionist at work. Upon examination the picture is totally altered. The excitement of great ideas was well over by 1888, and the famous defender of Darwin seems lacking in imaginative power. Instead of a case study of the clear impact of the *Origin of Species* upon a zoological problem, the siphonophores provide an example of the surprising success in interpreting animal relationships achieved by pre-Darwinian biologists.

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