Barnacle Larvae in the Nineteenth Century

A Case Study in Taxonomic Theory

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JOHN VAUGHAN THOMPSON was an army surgeon by profession but a field naturalist by inclination, and he made use of every locality to which the army brought him for his amateur investigations. He had traveled to Gibraltar, Madagascar, and the West Indies with the military and had made natural history notes of those places with sufficient competence to admit him to membership in the Linnean Society. He settled in Cork as an inspector of hospitals and made Cork Harbor his laboratory.[1]

One spring evening in 1823, returning homeward after a day of field studies, Thompson was taking the ferry across the harbor when he discovered a new and strange crustacean (see Fig. 1). He had cast overboard a muslin towing net to collect plankton, a technique he had first learned when searching for the cause of nocturnal luminescence in the Indian Ocean. By the spring of 1823 he was entertaining the suspicion that many of the animals of the plankton were nothing more than the young of more familiar species. He therefore did not publish a description of this new crustacean, but made drawings of it and awaited the day when he would be able to announce its true nature.[2]

A few weeks later Thompson collected another planktonic crustacean, this time one he already knew as the genus *Zoea* (see Fig. 2). Thompson was aware that a Dutch microscopist, Martinus Slabber, had in 1768 observed a similar animal, and had claimed that his specimen, which he had kept alive in sea water some days, underwent a change in form.[3] Thomp-

1. F. W. G[amble], 'John Vaughan Thompson,' *Dictionary of National Biography*, XIX, 698–700.

2. John Vaughan Thompson, *Zoological researches, and illustrations; or, natural history of nondescript or imperfectly known animals, in a series of memoirs* (Cork, 1828–30). This scarce work has just been republished by the Society for the Bibliography of Natural History (Sherborn Fund Facsimile no. 2, 1968). See especially pp. 3, 47, and 75–77.

3. Martinus Slabber, *Natuurkundige verlustigingen, behelzende microscopise waarneemingen van in- en uitlandse water- en land-dieren* (Haarlem, 1778), pp. 35–40. Thompson suggested that Slabber had not

son daily supplied his *Zoea* with fresh sea water, in hopes of seeing this transformation, but when at the end of a month the animal finally started to molt, it died. It had at least managed to free five of its new legs, which was sufficient to show that the *Zoea* would have become morphologically very different (compare Figs. 3 and 4). Because of the structure of the emerging limbs, Thompson felt sure that the genus *Zoea* was simply a larval crab, what is now called the zoea stage.

Still, he wanted more conclusive proof. He probably anticipated that his announcement of this discovery would take biologists by surprise. While some of the lower crustacea were known to undergo considerable changes of form, virtually nothing was known of the life history of the higher crustacea, and very young crabs do look like miniature adults. Indeed, taxonomists sometimes used the absence of metamorphosis as one character separating the higher crustacea from the insects. Marine biology was then a fairly untouched field, so it was not realized that a great many of the oddly shaped animals of the plankton are larvae.

In 1826 Thompson again captured some bivalved crustacea with stalked eyes, like those he had caught from the ferry. He tended them as he had the zoeae, thinking that they too might change their form. Reported Thompson:

> . . . they were taken May 1st, and on the night of the 8th, the author had the satisfaction to find that two of them had thrown off their exuvia, and wonderful to say, were firmly adhering to the bottom of the vessel and changed into young Barnacles! . . . On the 10th another individual was seen *in the act of throwing off its shell*, and attaching itself as the others, to the bottom of the glass.[4]

Here was an unexpected metamorphosis, which the scientific world would find all the more remarkable because barnacles had not been thought to belong to the class Crustacea at all.

Linnaeus had grouped barnacles among the mollusks.[5] Barnacles' calcareous shell and apparent lack of segmentation had kept them associated

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seen the metamorphosis after all but had inadvertently introduced the new form while adding fresh sea water, because the emerging form which Thompson saw was not like Slabber's. Later carcinologists agree that Slabber erred. See Henry Charles Williamson, 'Crustacea Decapoda. Larven,' *Nordisches Plankton*, Karl A. H. Brandt, ed. (Kiel & Leipzig, 1915), [VI], p. 319. The name *Zoea* dates not from Slabber but from Bosc, 1801.

4. Thompson (n. 2), p. 78.

5. Carl Linnaeus, *Systema naturae* (Stockholm, 1758), 10th edition, 2 vols., I, 667–669. The Linnaean genus *Lepas* was under the Vermes Testacea, as were most mollusks; the Vermes Mollusca contained the shell-less mollusks like slugs and octopuses and a wide variety of other animals. Linnaeus did therefore group barnacles with most mollusks, though not in his group 'Mollusca.'

with the mollusks even while some of their anatomical differences began to be appreciated. In 1809 Lamarck decided they required a class to themselves, the Cirripedia, which he saw as forming a transition from the class of annelids to the class of mollusks.[6] But Cuvier in 1812 denied the possibility of any intermediate between his articulate and mollusk *embranchements* and kept the cirripedes in the latter.[7]

As Thompson saw it, his discovery of larval barnacles established beyond question that the cirripedes were not a class of mollusks, nor a transitional class, but were members of the class Crustacea. But he had not yet published his discovery that some higher crustacea, not just a few lower ones, undergo metamorphosis, so he hesitated to claim that their metamorphosis proved that cirripedes were crustacea. In fact, long before he saw their larvae, Thompson's own conviction about the proper classification of the cirripedes had been formed on the basis of their molted skin or exuviae, which becomes a feathery flotsam periodically common in coastal water.

When the exuviae are examined, the characters of cirripedes which come to one's attention are that they do molt, that the limbs are jointed, and that the jaws are similar to those of many crustacea. The characters of cirripedes which were influencing taxonomists, such as the calcareous shell, hermaphroditism, and the visceral anatomy, are all left behind when the barnacle's skin floats into a collector's net. Years later James Dwight Dana, ignorant of Thompson's publications, similarly based his decision about the nature of the cirripedes partly on the exuviae.[8] But, in general, zoologists prided themselves on being followers of Cuvier in that they took into consideration the entire animal rather than a few convenient characters.

Thompson still hoped to show more conclusively that zoeae were the young of crabs. However, it is fairly difficult to keep these planktonic animals alive long enough for them to complete their development. The alternative method of establishing the nature of zoea was to follow crab development from the egg. Year after year he had been collecting female crabs

6. J. B. Lamarck, *Philosophie zoologique, ou exposition des considérations relatives à l'histoire naturelle des animaux; à la diversité de leur organisation et des facultés qu'ils en obtiennent; aux causes physiques qui maintiennent en eux la vie et donnent lieu aux mouvemens qu'ils executent; enfin, à celles qui produisent, les unes le sentiment, et les autres l'intelligence de ceux qui en sont doués* (Paris, 1809), 2 vols., I, 314–315.

7. Georges Cuvier, 'Sur un nouveau rapprochement à établir entre les classes qui composent le règne animal,' *Annales du Museum d'Hist. nat.*, 1812, *19*, 73–84.

8. James Dwight Dana, *Crustacea*, U. S. Exploring Expedition . . . under the Command of Charles Wilkes, U.S.N. (Philadelphia, 1852–53), 2 vols., I, 3.

with eggs on their abdomens, but no eggs had hatched. Finally, in June 1827, he was successful: 'the young burst from their envelopes and swam about in myriads,'[9] and they were not miniature crabs, but zoeae. Now at last his argument was complete. He published his results as a series of memoirs, his *Zoological Researches*, with figures he engraved himself. The title of his first memoir, published in September 1828, reveals his excitement: 'On the Metamorphoses of the Crustacea, and on Zoea, exposing their singular structure, and demonstrating that they are not, as has been supposed, a peculiar Genus, but the Larva of Crustacea! !'

Perhaps because he was sure that many other planktonic crustacea would be found to be larvae, and because the life histories of other decapods (higher crustacea) had not been studied, Thompson asserted that the metamorphosis he described in the common crab was the general rule among higher crustacea. (He did not contend that there were no exceptions, for he himself described *Mysis* as an exception in his second memoir.) Thompson was right about this, but by an unfortunate coincidence one of the other exceptions to his rule, the common crayfish, had been chosen as a convenient subject for study by Heinrich Rathke. Rathke was to become a prominent embryologist, now remembered especially for his discovery of gill slits in a pig embryo.[10] His detailed memoir on the development of the crayfish appeared in 1829, and showed the development to be gradual and direct.[11]

The metamorphosis of decapods was not accepted, partly because it was known not to occur in the crayfish, and partly because it was not expected to occur in any other decapods. J. O. Westwood, a leading British entomologist, reasoned that since the crustacea were more closely allied to the vertebrates than were the insects, and since extreme metamorphosis was characteristic of the insects, then the higher crustacea should approach the vertebrates rather than the insects in this respect.[12]

Likewise Henri Milne-Edwards did not expect metamorphosis to occur among the higher crustacea, though his reasoning was not based upon such

9. Thompson (n. 2), p. 64.

10. E. S. Russell, *Form and function: a contribution to the history of animal morphology* (London, 1916), p. 134.

11. Heinrich Rathke, *Untersuchungen über die Bildung und Entwickelung der Fluss-Krebses* (Leipzig, 1829). Rathke's results are related in detail, and his drawings reproduced, in Henri Milne-Edwards' *Histoire naturelle des Crustacés* (Paris, 1834), 3 vols., I, 175–195.

12. J. O. Westwood, 'On the supposed existence of metamorphosis in the Crustacea,' *Phil. Trans.*, 1835, [*125*], 312.

distant comparisons as Westwood's. The 'beautiful researches' of Rathke, and his own observations on decapods, gave no indication of a zoea stage, so it would be contrary to analogy for Thompson to be right.[13] And analogy was for Milne-Edwards an important consideration. Efforts of all taxonomists were bent on arranging animals not for convenience but according to their 'natural affinities,' a difficult task which was made worthwhile 'by the immense advantage of making known to us, solely by the place which the animal occupies, all the most important points of its history, considered with respect to anatomy, physiology, and zoology.'[14]

Thompson's research was within the next few years repeated by others and his accuracy acknowledged; Rathke himself apologized for his doubts.[15] Thompson had by then gone to Australia and never returned to Europe.

Thompson's larval barnacles fared better than his larval crabs. He described that discovery in January 1830 under the title, 'On the Cirripedes or Barnacles; demonstrating their deceptive character; the extraordinary Metamorphosis they undergo, and the Class of Animals to which they indisputably belong.' After showing what confusion the Cirripedia had caused taxonomists, Thompson described his observation of the bivalved, stalk-eyed crustacean which became transformed into a sessile (not stalked) barnacle. He concluded his memoir with the prediction that the stalked barnacles would be found to have similar larvae.

Most stalked barnacles live attached to objects floating in the open sea rather than on rocks at the seashore, so that they were not readily available in Cork, but in July of that year (1830), two ships came into the harbor with stalked barnacles covering their bottoms. Thompson had been alert to such an opportunity. '. . . having persons employed expressly for the purpose, numbers of these were brought alive in sea water, amongst which were many with the ova in various stages of their progress, and some ready to hatch, which they eventually did in prodigious numbers.

13. Henri Milne-Edwards, 'Zoé,' *Dictionnaire classique d'histoire naturelle* (Paris, 1830), XVI, 783. Milne-Edwards did think it likely that *Zoea* was a larval form, but deduced from its morphology that it might metamorphose into the genus *Megalopa*. This prediction was borne out by Thompson's discovery that the second stage in the life history of the crab, after the zoea stage, is what had been named *Megalopa*.

14. '. . . l'avantage immense de nous faire connaître, par la seule place que l'animal occupe, tous les points les plus importans des son histoire, considérée sous le rapport de l'anatomie, de la physiologie et de la zoologie,' Henri Milne-Edwards, *Histoire naturelle des Crustacés, comprenant l'anatomie, la physiologie, et la classification de ces animaux* (Paris, 1834–40), 3 vols., I, 206.

15. Heinrich Rathke, 'Zur Entwickelungsgeschichte der Dekapoden,' *Arch. Naturgesch.* (Wiegmann's), 1840, *6*, 248; trans. in *Ann. & Mag. Nat. Hist.*, 1841, *6*, 263–268.

. . .'[16] The larvae surprised him, however, by being quite unlike the one he had described for the sessile barnacle (compare Figs. 1 and 5).[17]

Barnacles hatch out in a form now known as a nauplius, which later changes into a second very different stage called the cypris larva. Thompson was not yet aware of this, so he attributed the difference between the larvae he had seen develop into sessile barnacles and the larvae which were produced by the stalked barnacles to some fundamental difference between the two kinds of cirripede. He concluded that sessile and stalked barnacles 'were not so closely related as generally supposed.' This was a reversal of opinion from his earlier memoir, and shows the great taxonomic weight which Thompson gave to the larval forms.

Although Thompson did not know that the first stage of sessile as well as stalked barnacles was naupliar, he did recognize the form of the young stalked barnacle as one seasonally common in the plankton of Cork Harbor (see Fig. 6). The parent of those larvae he thought he already knew, having seen them hatch from a large parasite of crabs.[18] This parasite, *Sacculina*, is a shapeless mass, consisting of absorptive tissue sunk within the crab and gonads outside. This formless animal could not be classified. 'That . . . [*Sacculina*] agrees with no tribe of the Crustacea is apparent, not even with the Cirripedes; nevertheless, its concealed affinity to these latter becomes evident, on a comparison of the respective larvae [compare Figs. 6 and 7]; and yet how different and masked is the perfect animal. . . .'[19]

Henri Milne-Edwards apparently felt unsure of Thompson's reliability. He was well prepared to accept evidence from larval forms as revealing taxonomic affinity, for he had been impressed by the life history of the parasitic copepods. These had been classed with various worms until the discovery of their larvae showed them to be crustacea. Nevertheless, Milne-Edwards' great work on the Crustacea contains only this comment on barnacles: 'In the future it may perhaps be necessary to also combine with the Crustacea barnacles and the other unusual animals which com-

16. John Vaughan Thompson, 'Discovery of the metamorphosis in the second type of the *Cirripedes*, viz. the Lepades, completing the natural history of these singular animals, and confirming their affinity with the *Crustacea*,' *Phil. Trans.*, 1835, [*125*], 355.

17. It is curious that Thompson was apparently unaware that Martinus Slabber had already made the same observation, since Thomspon did know Slabber's work (see n. 3). Slabber reported that he had provided stalked barnacles with sea water, and that clouds of tiny animals issued forth. Slabber gave a clear figure and description of one (pl. 6, Fig. 1), named it *Monoculus marinus*, but did not suggest it was larval (n. 3, pp. 63–66).

18. The nauplii in plankton, which Thompson identified with those he obtained from the parasite, were almost certainly not *Sacculina* but the first stage of local sessile barnacles.

19. John Vaughan Thompson, 'Natural history and metamorphosis of an anamalous crustaceous parasite of Carcinus Moenas, the Sacculina Carcini,' *Ent. Mag.*, 1836, *3*, 455.

pose the class Cirripedia; but, in the present state of science, we do not possess the necessary data to make a decision on this matter.'[20] Milne-Edwards almost certainly knew of Thompson's memoir on the sessile barnacles at this time but was awaiting confirmation of its accuracy.

Thompson's description of larval stalked barnacles appeared in 1835, but, unknown to him, both of the larval stages of these barnacles had been described the year before by Hermann Burmeister.[21] Milne-Edwards had after this the highest praise for Thompson's discovery of metamorphosis in barnacles. Since 1829 Milne-Edwards had been developing a theory of the dominant importance of embryology for revealing taxonomic affinities.[22] According to his theory, the characteristics of the higher group to which an animal belongs appear before those of the lower group, so that in the course of its development, its phylum, class, order, and so on would be identifiable in sequence.[23] This theory must have influenced the taxonomic rank which Milne-Edwards gave to the Cirripedia when he finally revised his classification of the Crustacea in 1852.[24] He not only accepted the cirripedes as crustacea, he considered them to belong to the copepod type.

Thompson felt sure that the nature of the barnacle larva should put an end to the status of the Cirripedia as a distinct class, but in 1835 Martin-Saint-Ange attempted to establish the proper place of this class and depended very little on Thompson's evidence. His careful anatomical study showed that previous authors were mistaken in thinking barnacles to be unsegmented; with this and other considerations he eliminated the affinities which had been seen between cirripedes and mollusks. He believed lack of locomotion to be a significant character, and it was in this respect only that he referred, in a footnote, to Thompson's 'valuable researches' on the free-swimming larvae. His anatomical evidence showed that barnacles have more points of affinity to the Crustacea than to any other class, but to say that they should be a sub-class, or lower, within the class Crustacea seemed not to have occurred to him. The principal point of affinity with the anne-

20. 'Par la suite il faudra peut-être réunir aussi aux Crustacés les Anatifs et les autres animaux singuliers dont se compose la classe des Cirripèdes; mais, dans l'état actuel de la science, on ne possède pas les données nécessaires pour se prononcer à cet égard.' Milne-Edwards (n. 14), 1, 230.

21. Hermann Burmeister, *Beiträge zur Naturgeschichte der Rankenfüsser* (*Cirripedia*) (Berlin, 1834).

22. Henri Milne-Edwards, 'Considérations sur quelques principes relatifs à la classification naturelle des animaux, et plus particulièrement sur la distribution méthodique des mammifères,' *Ann. Sci. Nat.*, 1844, *ser. 3, 1*, 66.

23. He points out the similarity of his views to those of Karl Ernst von Baer, but says that they were arrived at independently. Russell (n. 10) discusses the connection of this idea to the biogenetic law of Haeckel.

24. Henri Milne-Edwards, 'Observations sur les affinités zoologiques et la classification naturelle des crustacès,' *Ann. Sci. Nat.*, 1852, *ser. 3, 18*, 109–166.

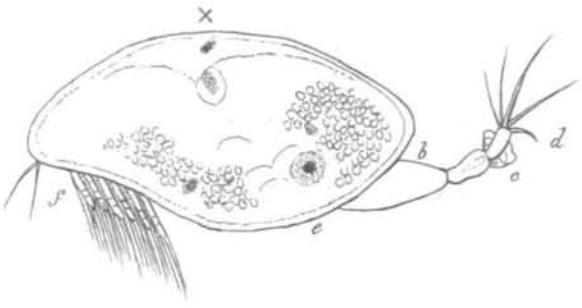

FIG. 1. Cypris-larva of *Balanus porcatus* da Costa (from Thompson [n. 2], Memoir IV, pl. IX, fig. 3).

FIG. 2. Zoea of crab found by J. V. Thompson in May 1823 (from his *Zoological researches* [n. 2], Memoir I, pl. II, fig. 2).

FIG. 3. Maxillipeds of zoea (from Thompson [n. 2], Memoir I, pl. II, figs. 6 and 7).

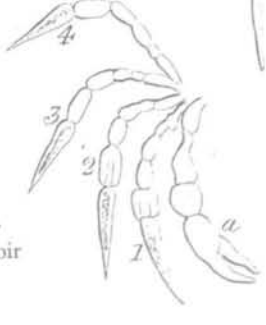

FIG. 4. Thoracic limbs of megalope-larva (from Thompson [n. 2], Memoir I, pl. II, fig. 11).

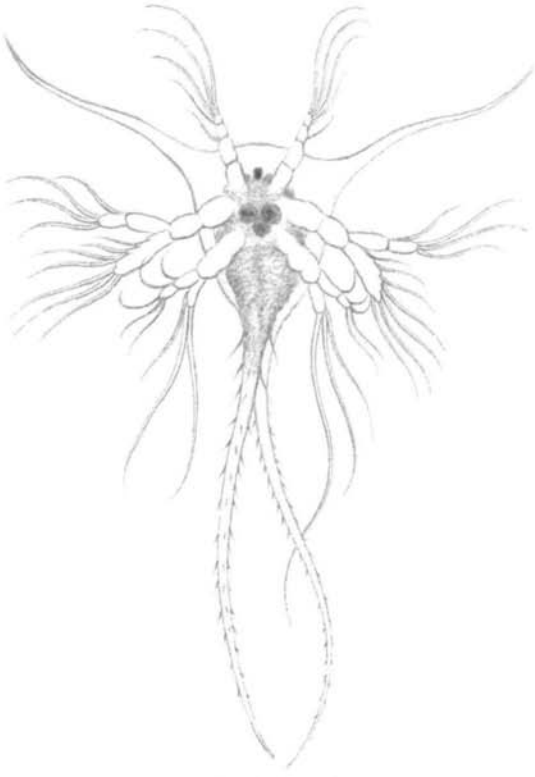

FIG. 5. Nauplius larva of *Lepas anserifera* Linn. (from Thompson [n. 16], pl. v [incorrectly labelled vi], fig. 5, opp. p. 358).

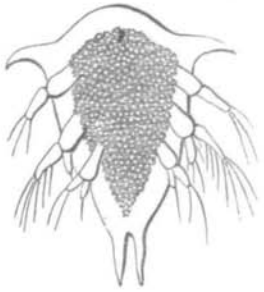

FIG. 6. Newly hatched nauplius of *Sacculina carcini* Vaughan Thompson (from Thompson [n. 19], p. 453).

FIG. 7. Newly hatched nauplius of *Conchoderma virgatum* (Spengler) (from Thompson [n. 16], pl. v [incorrectly labelled vi], fig. 7, opp. p. 358).

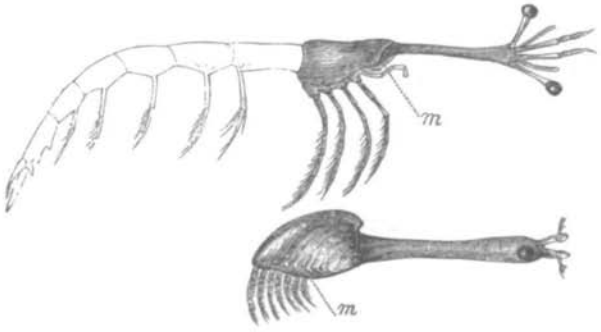

FIG. 8. General view of crustacean homologies of barnacles. Darwin supposed, for sake of comparison, the barnacle's larval antennae and eyes to have been retained (from Darwin [n. 38], vol. 1, p. 28).

lids displayed by the cirripedes was that they were hermaphroditic. Martin-Saint-Ange concluded: 'It is therefore between these two classes [Crustacea and Annelida] that they find themselves naturally placed, ending the crustacean series and forming the passage from that class to that of the annelids, which we regard as the last of the articulates.'[25]

One result of this arrangement, Martin-Saint-Ange pointed out, was that it much improved the pattern of the zoological system of Ampère, who had arranged the animal kingdom into two parallel series, each of which ran from the simple to the complex, and which was symmetrical, that is, each group in some way corresponded to the group at the same level on the other series. I assume this was the physicist, André Marie Ampère, who published a classification of all knowledge, but I do not know if the scheme to which Martin-Saint-Ange referred was published. A pattern of parallel lines with correspondences was used by others, especially Isidore Geoffroy Saint-Hilaire. According to Martin-Saint-Ange, the tradition of linking the cirripedes to the mollusks had interrupted the regularity of this system, but the cirripedes could now stand opposite the cephalopods, to which they corresponded in having a soft body within a shell-secreting mantle.

Ampère's attempt to find a logical, regular pattern in taxonomic systems was a far from uncommon kind of interest at that time. The one which came to be most widely known was that of William S. MacLeay, which was expounded by William Swainson as a wonderful revelation of fundamental truth. A considerable number of zoologists, if they did not embrace MacLeay's system, did sympathize with his attempt. His system had this in common with Ampère's: it traced separate lines of affinity and then established correspondences between groups not on the same line. In MacLeay's system, as for Martin-Saint-Ange, the cirripedes were a valuable connecting link.[26]

Because the structure of such systems depended upon similarities which would now be called analogies as well as upon homologies, they often sounded fantastic. Swainson, for example, asserted a correspondence be-

25. 'C'est donc entre ces deux classes qu'ils se trouvent naturellement placés, en terminant la série des Crustacés et en formant le passage de cette classe à celle des Annelides, que nous regardons comme la dernière des Articulés,' G. J. Martin-Saint-Ange, 'Memoire sur l'organisation des Cirripèdes et sur leurs rapports naturels avec les animaux articulés,' *Memoires présenté par divers savans à l'Academie des Sciences de l'Institut de France, ou collection des mémoires des savans étrangers*, 1835, *16*, 545.

26. MacLeay mentioned the shape of sessile barnacles as a link to the radial symmetry of echinoderms. W. S. MacLeay, *Horae entomologicae: or essays on the annulose animals* (London, 1819–21), vol. 1, pt. 2 [pts. published separately, vol. 2 never published], 304–315. This work is scarce; I know of no copy of pt. 2 in the United States.

tween tigers and zebras, both being wild and striped.[27] If the pattern being discovered was to be regular, every collection of groups had to be based on the same number. The controversy over the correct number probably helped end the popularity of these systems.

Milne-Edwards, too, was trying to see some over-all order in the animal kingdom and gave MacLeay and Swainson credit for calling attention to a real tendency in nature, that the kinds of modifications on any type are often very similar, so that parasites and carnivores, herbivores and scavengers, land and water animals are to be found within many separate groups.[28] Biologists must be aware of this type of similarity and not confuse it with the similarities which determine taxonomic position, he said. For example, the heavy shells of barnacles had masked 'the fundamental resemblances of *natural affinities* which the derivatives of the same zoological type have among themselves,' until the studies of Thompson, Burmeister, and others had shown that 'cirripedes are, in reality, true crustacea.'[29]

The numerical complexities of the circular systems of MacLeay, Swainson, and others, Milne-Edwards called bizarre.[30] James Dwight Dana called them 'a splendid failure.' In his report on the crustacea collected on the Wilkes Expedition, which appeared in 1852, Dana passed judgment on the circular systems:

> It was a brilliant scheme when first brought forward, embracing much respecting the relations or affinities of species that then seemed almost like a new revelation; but as the first glare has now passed, we can perceive that while it attempted to rid science of the straight and rigid bars of artificial systems, it only modified the mode of coercion by bending the bars into circles. There are neither straight lines nor circles in nature, but main branching lines, with subordinate branches, and almost endless reticulations or anastomoses, by curves of all kinds and of all grades of divergence and convergence.[31]

This by no means meant that Dana was disinclined to find some way to make taxonomic groups intelligible as representing more than an artificial

27. William Swainson, *A treatise on the geography and classification of animals, Lardner's Cabinet Cyclopedia* (London, 1835), p. 240.

28. Milne-Edwards (n. 22), p. 79.

29. 'Ces ressemblances secondaires, que l'on désigne sous le nom d'*analogies*, sont quelquefois si frappantes, qu'elles masquent, pour ainsi dire, les différences essentielles, et font perdre de vue les ressemblances fondamentales ou *affinités naturelles* qu'ont entre eux les derivés d'un même type zoologique. . . . les Cirripèdes sont, au fond, de véritables Crustacés . . .' Henri Milne-Edwards, *Introduction à la zoologie générale ou considérations sur les tendences de la nature dans la constitution du règne animal* (Paris, 1851), p. 125.

30. Milne-Edwards (n. 22), p. 79.

31. Dana (n. 8), p. 54.

arrangement. Although Dana built up no explicit argument, and adopted for the most part Milne-Edwards' judgments, there was throughout his discussion a concern with the question of grade or level, whether an animal was superior or represented a degradation. In this his ideas were much influenced by Louis Agassiz.

The general principle which Dana saw operating in zoology was that superior grades are characterized by a greater centralization or cephalization, that is, a triumph of animal forces over vegetable. This is an argument with a long history. The grade of the immobile cirripedes seemed to Dana to be made clear by this sort of consideration. 'This then, is an example beyond dispute, of a system overgrown through the vegetative process, so as to be too much for the motive energies within.'[32] Dana said that Thompson had removed all question as to whether cirripedes were to be included in the class Crustacea.

Dana's copy of Richard Owen's textbook on invertebrates is now in the Yale College Library. Next to the heading 'Cirripedia' Dana penciled in, 'should be arranged with the *Crustacea*.'[33] But Owen had left the cirripedes out of the crustacea intentionally. In 1843, when his *Lectures on the Comparative Anatomy and Physiology of the Invertebrate Animals* was first published, Owen showed himself familiar with the most recent works, and he related in great detail the discoveries of John Vaughan Thompson, including a clear and fair description of the controversy over zoeae. He reprinted Thompson's figures of the young of sessile and stalked barnacles, still unaware however that these represented two different stages rather than two different types. He placed high importance upon these larval forms.

> The naturalist has often been baffled or led astray in his attempt to discover the real nature and affinities of an animal by investigations limited to the structure and habits of such animal in its mature state. There are some species which undergo such extraordinary metamorphoses before attaining that state as to mask their true relations, not only to the class, but to the primary division of animals to which they belong.[34]

Still Owen did not allow the cirripedes to be true crustacea, and he removed the parasitic copepods (which Milne-Edwards included) as well. Viewing the increase of powers of locomotion as a progress in animal function, he

32. *Ibid.*, p. 1408.

33. The handwriting is the same as that which fills the margin of Dana's copy of Milne-Edwards' *Histoire naturelle* (n. 14) with taxonomic notes unmistakably Dana's.

34. Richard Owen, *Lectures on the comparative anatomy and physiology of the invertebrate animals* (London, 1843), pp. 147–148.

pointed out that in the latter, 'the advance was but transitory, and both organs and faculty of spontaneous motion were quickly lost. In the Cirripedes, jointed appendages to the body are retained, but their rapid actions are subservient to the acquisition of food, not to locomotion.'[35] The place Owen gave to the cirripedes was the same as that given by Martin-Saint-Ange, and his reasons were essentially the same.

William Bell dedicated his *History of the British Stalk-Eyed Crustacea* to Owen, 'the faithful and unchanged friend of many years,' so it is not surprising that he too excluded the cirripedes from the Crustacea. By then the first volume of Darwin's monograph on the group had appeared, in which of course Darwin considered them to be crustacea, and a monographer's judgment is usually taken to be authoritative. Bell did, however, imply that his separation was made in order to simplify his definition of the Crustacea.[36]

The second volume of Darwin's monograph on the Cirripedia appeared in 1854. The next year Richard Owen published a second edition of his *Lectures*, in which he made such extensive use of Darwin's work that his cirripede section more than doubled in size. He described the homologies which Darwin had traced between the parts of cirripedes and crustacea, reproducing Darwin's figures showing this, and described the orders into which Darwin had divided the Cirripedia. Nevertheless, Owen persisted in his view that neither barnacles nor the parasitic copepods were to be admitted within the class Crustacea. Repeating the reasons he had previously given for his arrangement, Owen added:

> . . . were we cognisant of the Lernaeans [parasitic copepods] and Cirripedes in no other than their locomotive state, we might be led, with those naturalists who judge of an animal from one of its vital stages only, to classify them with the Crustacea. . . .
>
> We make the easiest and most natural transition from the lower forms of Articulata [the annelids] to the Crustaceous class, by passing to it from the larval state,—which I have argued to be the typical one [that is, revealing the type]—of the . . . *Cirripedia*; in which view we may regard the *Crustacea* as representing those larvae on a gigantic scale, and so retaining the typical character with the faculty of motion.[37]

He saw the larvae of cirripedes as being fully crustacean, indeed practically

35. *Ibid.*, p. 163.
36. Thomas Bell, *A history of the British stalk-eyed Crustacea* (London, 1853), p. x.
37. Owen (n. 34), 2nd ed. (London, 1855), pp. 296–297.

the archetype of the Crustacea, but when the adults lost their motility, they lost their membership in the class.

Owen seems to have held a minority opinion, for Darwin had said in 1851 that the cirripedes were placed within the class Crustacea 'by almost universal consent.'[38] It was not the question of the proper rank of the whole group Cirripedia which had challenged Charles Darwin but rather the need for an arrangement of species within the group and interesting problems of cirripede biology. It has been questioned whether the time Darwin spent on his monograph represented valuable zoological training or merely an unnecessary delay in the publication of his theory of evolution. Be that as it may, the result was a definitive monograph of great detail and soundness.

Darwin felt no need to explain at length his conviction that the cirripedes were indeed crustacea, but did briefly show that some of the non-crustacean characters attributed to them were based on mistaken interpretations or incomplete knowledge of the group. Hermaphroditism, for example, he showed to be not universal among barnacles. In Darwin's opinion, facts of the adult morphology of barnacles discussed by Martin-Saint-Ange should have been sufficient to transform the class Cirripedia into a sub-class of the Crustacea. The larvae were important to him primarily as a means of determining the homologies of the parts of cirripedes with other crustacea (see Fig. 8).

Milne-Edwards, to whom Darwin dedicated his monograph, developed the idea that crustacea consist of a series of homologous segments and that any species may be referred to an archetypal crustacean. Depending heavily upon the studies of his colleague, V. Audouin, Milne-Edwards had proposed the principle that the normal number of segments in a crustacean is twenty-one. Here the word 'normal' means not average but standard; it is the number of segments in a conceptual archetype to which actual species may be compared. The comparative anatomy of the crustacea is conducted today upon the ideas outlined by Milne-Edwards.

Within the Cirripedia, where the very existence of segmentation had long been undetected, Darwin declared the existence of seventeen segments (six cephalic, eight thoracic, and three abdominal), a number respectably close to twenty-one.

In the larva in the first stage, an eye and two pairs of antennae are in process of

38. Charles Darwin, *A monograph on the sub-class Cirripedia, with figures of all the species* (London, Ray Society, 1851), 2 vols., I, 1.

formation or are developed; here, then, according to the analogy of all Crustaceans, we have evidence of the existence of the first three cephalic segments. The mouth always consists of three pairs of gnathites, and hence again, from analogy, this part may be inferred to be formed of, and supported on, three other segments; making thus far six segments.

In the order Thoracica, the abdomen is quite rudimentary, though often still bearing the caudal appendages; in the pupa, however, of this order, as in the mature animal of the two other orders, it is formed of three segments.[39]

(The order Thoracica contained all but two species of barnacles, those two each having an order to itself.) Six rather than eight thoracic segments were present in the Thoracica, the other orders being depended upon for the archetypal number. Again, Darwin employed evidence from the larval form, this time to determine from which end of the thorax the segments were missing.

Now between the mouth of the pupa and the first pair of natatory legs, there is a space of membrane, equalling, when stretched out, the three succeeding thoracic segments in length and breadth: this interspace, I conceive, must have some homological signification; here then we have at least an appearance of the abortion of appendages; whereas, at the posterior end of the cephalo-thorax, no such appearance is presented.[40]

Such use of larval morphology to construct the archetypal cirripede would now be rationalized by means of the idea that the larval form is more likely to have retained ancestral characteristics. Of course it was Darwin's theory of evolution which first introduced this explanation, but the theory of the relationship of embryological development to the construction of typical forms was already well established, especially for the vertebrates.[41]

At one point Darwin did relate the concept of archetype to the history of a species. '. . . the highly remarkable position of the mouth in the larva . . . forcibly brings to mind the anomalous structure of the mouth being situated in the middle of the under side of the thorax, in Limulus,—that most ancient of crustaceans, and therefore one likely to exhibit a structure now embryonic in other orders.'[42] This probably reflected the association he had privately made between the concepts of archetype and ancestor, but it is consistent also with Louis Agassiz's theory of parallelism between the fossil record and the individual development of a species.

The question of whether cirripedes are of high or low grade, which was

39. *Ibid.*, 1854, II, 10–11.
40. *Ibid.*, II, 111–112.
41. Russell (n. 10), Ch. 10.
42. Darwin (n. 38), I, 12.

of interest to Dana and Owen, Darwin attempted to answer, although he warned that 'in all cases this, as it seems to me, is a very obscure enquiry.'[43] The problem, of course, is to decide what criteria are to be used. Darwin judged the cirripedes by the various criteria which different authors had used, the contradictory results showing in themselves the pointlessness of the question.

Darwin wrote, in his most famous work, '. . . even the illustrious Cuvier did not perceive that a barnacle was, as it certainly is, a crustacean; but a glance at the larva shows this to be the case in an unmistakeable manner.'[44] The larval form provided the clue because members of one group are often more alike as young than as adults. That this well-known rule of embryonic resemblance should generally hold true, and yet have numerous exceptions, is comprehensible, said Darwin, if taxonomic affinity represents descent from a common ancestor.

This explanation made sense to Fritz Müller. Müller was particularly interested in the larvae of crustacea and had found, to his exasperation, that any attempt to apply the widely taught laws of embryology to taxonomic arrangement resulted in absurdity. In 1864 Müller published a short description of the way in which some of Darwin's ideas were borne out by facts about the crustacea, especially by the larval developments in various groups; this book he entitled *Für Darwin*. Müller had decided that 'if the higher and lower Crustacea were at all derivable from common progenitors, the former also must once have passed through Nauplius-like conditions. Soon afterwards I discovered Naupliiform larvae of Shrimps . . . and I must admit that this discovery gave me the first decided turn in Darwin's favour.'[45] Darwin's theory also suggested to Müller that a group having affinities to the decapods, the Edriopthalma, must have had ancestors which had zoea larvae. It therefore seemed to Müller a further confirmation of the theory of evolution when a few zoeal characters were found in one species of this group.

In the course of surveying the metamorphoses of crustacea, he described the great similarity of development in cirripedes to that in rhizocephalans such as *Sacculina*. Thompson had seen only the naupliar stage of *Sacculina* and had been unaware that the barnacle larvae to which he compared this parasite would metamorphose into a cypris before finally settling. Müller

43. *Ibid.*, II, 19.

44. Charles Darwin, *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life* (London, 1859), p. 440.

45. Fritz Müller, *Facts and arguments for Darwin*, W. S. Dallas, trans. (London, 1869), pp. 13–14.

showed that rhizocephalans went through a cypris stage very like that found in barnacles.[46]

Darwin had asserted in his monograph that a fundamental characteristic of cirripedes was their attachment by means of antennae containing cement-glands. The manner of attachment of rhizocephalans had not been observed, but Müller argued that the larval antennae of *Sacculina* seemed to contain such a cement-duct, so that the roots which the parasite sinks into a crab were, Müller said, homologous with the ramifying cement-ducts which fix a barnacle to its substrate. It would be very simple and probable, Müller continued, for evolution by natural selection to convert a barnacle which chose a living substrate into a parasite, since the enlargement of its cement-duct would fix it more securely, and further enlargement would give it extra nourishment from the body fluids of its host. This whole process he showed to be plausible by the existence of a cirripede, described in Darwin's monograph, which is parasitic on sharks; it has roots instead of cement-ducts, and its limbs are rudimentary.[47]

John Vaughan Thompson had felt the necessity for some explanation as to why an active crustacean larva should become transformed at maturity into a parasitic glob, but could suggest only that it 'may have its use in filling up some link in the scale of natural affinities.'[48] Müller could scoff, 'It would certainly never appear to any one to be a pastime worthy of the Deity, to amuse himself with the contrivance of these marvelous cripplings . . . ,'[49] because he had found a more satisfying answer in the theory of evolution.

Müller, while believing the rhizocephalans to have evolved from Cirripedes, advised that the two groups be placed close together but not merged. This was the same sort of problem which Darwin had faced when he decided to create a separate order to contain one aberrant species. 'I do not feel myself able,' Darwin explained, 'to draw a line of distinction between the being a very abnormal member of one group, and belonging to a distinct group.'[50] The basis for such a decision is largely convenience; if the definition of a group would have to be considerably modified to include an aberrant member, zoologists often prefer to create a separate group.

46. Fritz Müller, 'Die zweite Entwickelungsstufe der Wurzelkrebse (Rhizocephalen),' *Arch. Naturgesch.*, 1862, *29*, 24–33.
47. Müller (n. 45), pp. 135–140.
48. Thompson (n. 19), p. 456.
49. Müller (n. 45), pp. 3–4.
50. Darwin (n. 38), II, 565, fn.

It was very much this same situation which had been created by the crustacean larvae of the cirripedes. If cirripedes were to be included in the Crustacea, zoologists would have to alter their concept of crustacea as being locomotive bisexual animals. (One researcher therefore went to great lengths to show that barnacles are not hermaphroditic.)[51] Whether it was necessary or advisable to make this change was moot for some period of time. An individual zoologist's decision was often clearly related to his beliefs about what a taxonomic system should look like. For example, Martin-Saint-Ange and Richard Owen subscribed to the traditional view that animals could be arranged in linear series, and viewed the Cirripedia as a link between two larger classes. Milne-Edwards and Dana, although lacking the idea of a phylogenetic tree, saw in nature irregular groupings around conceptual types.

Though closer knowledge of the characteristics of adult cirripedes accumulated and tended to confirm the group's connection with the crustacea, interpretations of the importance of the larval form both depended upon and influenced general theories about the taxonomic significance of embryology. The variety of uses to which zoologists put Thompson's discovery of larval barnacles reflects the active role theoretical considerations play in the process of zoological classification.

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51. Henry D. S. Goodsir, 'On the sexes, organs of reproduction, and mode of development, of the cirripeds,' *Edin. new phil. J.*, 1843, *35*, 88–97.